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Effects of *Pueraria montana* and *Melastoma dodecandrum* Intercropping on Soil and Tea Plant Growth in Terraced Tea Gardens: A Sustainable Agricultural Practice

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Abstract. **Tea, a predominant economic crop in China, often thrives on terraced fields, but the long-term monoculture practiced in these terraced tea gardens has led to soil degradation, adversely affecting tea tree growth. Intercropping offers a sustainable solution, but its specific effects on soil and tea trees remain unclear. This study investigated the complex interactions between soil microorganisms, soil, and tea trees in two intercropping systems: tea/*Pueraria montana* var. *culaishanensis* (HWT) and tea/*Melastoma dodecandrum* Lour. (YP). The results showed that both intercropping modes significantly improved bud density, hundred-bud weight, and yield, thereby promoting tea tree growth. HWT significantly increased soil porosity, organic matter, available N, and available P in tea garden soils, while YP significantly increased soil porosity, organic matter, available P, and available K, all of which improved soil conditions. Both intercropping modes also affected the diversity and richness of bacterial communities and the community structure at the phylum level. Microbial co-occurrence network and topological characteristics analysis further indicated that the soil microbial community structure under intercropping was more intricate and tightly connected. Linear discriminant analysis effect size analysis demonstrated that beneficial microbial groups were significantly higher under both intercropping modes compared with monoculture tea plantations. Moreover, both intercropping modes promoted the C and N cycles in the soil, significantly enhancing microbial functions related to cellulolysis. In conclusion, both intercropping modes can promote tea tree growth, improve soil physical and chemical properties in tea gardens, increase beneficial microbial groups, and positively affect soil microbial community structure and function. However, HWT has a greater impact on functional microorganisms related to C and N cycles, especially N cycling. Therefore, intercropping with suitable slope-protection crops provides a potential solution for the sustainable development of terraced tea gardens, offering strong support for the construction of green and environmentally friendly tea gardens.**

Tea stands as an important economic crop in Southeast Asia, with its cultivation predominantly flourishing in sun-kissed, terraced tea gardens of Southern China's hilly and mountainous regions (Pan et al. 2022). These undulating landscapes offer optimal conditions, with generous sunlight exposure and well-drained soil, that are conducive to the thriving growth of tea trees (Janakiram and Rakesh et al. 2016). Nevertheless, the long-standing practice of monoculture within these terraced tea estates has precipitated a cascade of environmental challenges: a marked decline in biodiversity, soil compaction, and the increasing acidification of the soil (Arafat et al. 2019). Furthermore, the persistent cultivation of a single tea tree species has disrupted the equilibrium of soil microbial ecosystems, thereby impairing the soil's inherent fertility and constraining the productivity potential of these monoculture tea plantations (Arafat et al. 2017, 2019; Yasir et al. 2017). In light of these pressing issues stemming from prolonged monocultural practices, there is an urgent imperative to investigate and implement effective remediation strategies to safeguard the sustainability of the tea industry.

Ecological niche separation is the primary ecological mechanism driving intercropping benefits, enabling optimal utilization of diverse spatial and soil strata on a given plot to foster symbiotic plant coexistence and maximize resource efficiency (Tamburini et al. 2020; Yang et al. 2021). Strategic intercropping has been shown to enhance tea bud length and hundred-bud weight, thereby boosting overall tea production (Alcázar et al. 2007; Lee et al. 2013). For example, intercropping tea trees with edible mushrooms such as *Morchella*, *Auricularia auricula*, and *Ganoderma lucidum* can positively affect tea yield (Zhen et al. 2013). Intercropping landscape tree species such as *Magnolia denudata*, *Sapindus mukorossi*, and *Prunus serrulata* has varying degrees of positive impacts on tea tree yield. Notably, intercropping *Sapindus mukorossi* can significantly enhance both the yield and quality of tea gardens, resulting in a 51.81% increase in tea green yield compared with controls (Yang et al. 2024). The fertility status of tea garden soil is a crucial factor for the growth of tea trees (Li et al. 2015). A well-designed intercropping system, like combining *Castanea mollissima* and tea trees, can substantially elevate soil organic matter, N, P, and K levels, alleviate soil acidification, and improve soil structure compared with monoculture of tea trees (Ma et al. 2017). Intercropping with *Glycine max* effectively boosted soil organic matter and total N content (Huang et al. 2022). Lu et al. (2019) indicated that intercropping *Arachis hypogaea* with oil tea can enhance soil porosity to some extent. These findings suggested that intercropping patterns significantly improve soil ecological conditions (Li et al. 2020). Furthermore, soil microorganisms are vital for soil fertility and overall ecological health (Duan et al. 2022).

Soil microorganisms, comprising small entities such as bacteria, actinomycetes, fungi, protozoa, and algae, are integral to stable ecosystems and serve as sensitive indicator for soil quality changes (Neemisha 2020). Their diversity is crucial for ecosystem evaluation and ecological balance maintenance (Jiao et al. 2021). Appropriate intercropping strategies can modify the structure and function of subterranean microbial communities, enriching microbial diversity and fostering beneficial associations (Senghor et al. 2023; Wu et al. 2022). In studies comparing tea–*Juglans regia* intercropping systems with monoculture setups, increased abundances of microbial phyla like Proteobacteria, Bacteroidetes, Firmicutes, Chlamydiae, Rozellomycota, and Zoopagomycota were observed in the mixed plantings (Bai et al. 2022). Similarly, intercropping tea with *Lycoris radiata* led to heightened relative abundance of genera including *Acidothermus*, *HSB-OF53-F07*, and *FCPS473*, alongside enhanced microbial functions related to the C cycle such as methane nutrition, methyl nutrition, and cellulose hydrolysis (Shi et al. 2024). The combination of tea trees with rhododendrons further amplified the Chao1 and Shannon diversity indices of soil bacterial assemblages, stimulating microbial processes involved in cellulolysis, aromatic hydrocarbon degradation, and other key ecological functions (Xiong et al. 2024).

Wuyi Mountain, situated in subtropical monsoon humid climate zone, is a renowned tea-producing area in China. As of 2023, its total tea garden area stands at 9866.67 ha. The majority of Wuyi Mountain's tea gardens are hilly terraced tea gardens with many farmers planting tea trees on hillside walls. Moreover, most of the tea gardens have a single species. In recent years, the prosperity of Wuyi Mountain's tea industry economy has led to excessive development of tea gardens, soil fertility decline, water and soil erosion, and increasingly fragile ecology (Huo et al. 2021). Therefore, it is imperative to propose scientific and reasonable management measures to maintain a good tea garden ecological environment. The selection of appropriate slope protection plants for intercropping in terraced tea gardens, leading to the formation of ecological coverage, is a key developmental direction for sustainable and green ecosystems in tea gardens (Huang et al. 2022; Sanaei et al. 2018). Among the various slope protection plants, *Pueraria montana* var. *culaishanensis* and *Melastoma dodecandrum* Lour. are particularly noteworthy due to their unique attributes. *P. montana* var. *culaishanensis*, a leguminous plant with a long history of dual use as both medicine and food, boasts a relatively developed root system that enables it to fix N, retain soil moisture, prevent soil erosion, and improve soil quality, thus making it an excellent choice as slope-protection vegetation (Zang et al. 2016). *M. dodecandrum*, a member of the Melastomataceae family, offers value in food, medicine, and horticulture application and can serve as a green cover crop for slope protection (Huang et al. 2021; Zheng et al. 2021).

Therefore, both the *P. montana* var. *culaishanensis* and *M. dodecandrum* are theoretically suitable for intercropping with tea trees. However, it remains uncertain whether such intercropping practices can ameliorate soil conditions within tea gardens and simultaneously promote the growth of tea trees. Hence, this research sought to elucidate the impacts of intercropping on soil physicochemical attributes and microbial community structures in tea gardens. The objective is to ascertain the effects of *P. montana* var. *culaishanensis* and *M. dodecandrum* on soil fertility, microbial diversity, and functional aspects within tea garden ecosystems, thereby offering insights for the establishment of environmentally sustainable tea gardens that prevent water and soil loss without compromising tea production.

Materials and Methods

Overview of the study area. The experimental site is situated in the National Soil and Water Conservation Garden of Wuyi University, Wuyishan City, Fujian Province (118°00′35″E, 27°44′25″N). This tea garden is characterized by a typical southern subtropical monsoon climate, boasting an average annual temperature of 19 °C and an abundant average annual rainfall of over 2000 mm. The spring tea harvest season generally spans from mid-April to early May. In Oct 2021, a compound fertilizer with an N–P–K ratio of 21N–8P–16K was applied at a rate of 700 $\text{kg}\cdot\text{hm}^{-2}$. Three types of treatments were established: tea monoculture (CK), tea/*P. montana* var. *culaishanensis* intercropping (HWT), and tea/*M. dodecandrum* intercropping (YP). Each treatment consists of four randomly selected plots, each with a size of 10 m × 10 m. In Mar 2021, *P. montana* var. *culaishanensis* and *M. dodecandrum* were planted on the terraced slopes of the intercropping plot, with a minimum distance of 0.3 m from the tea leaves and a planting spacing of 0.18 m × 0.18 m, while consistent agronomic management practices were implemented.

Soil sample collection. Soil samples were collected on 29 Apr 2022 (spring, 20 to 25 °C, sunny) using the method described by Zhong et al. (2019). Five-point sampling was employed to randomly collect tea soil from different treatment areas at a depth of 10 to 20 cm. The samples were transported to the laboratory in an ice box. Each soil sample was divided into two parts: one part was air-dried, ground, and passed through a 100-mesh sieve for soil nutrient analysis, while the other part was temporarily stored at −80 °C in a refrigerator for DNA extraction. Subsequently, the samples were sent to Shanghai Personalbio Biotechnology Co., Ltd., for DNA extraction, amplification, and high-throughput sequencing to determine the diversity and community composition of soil bacteria.

Determination of tea tree growth indicators. On 29 Apr 2022, under spring conditions with temperatures ranging from 20 to 25 °C and sunny skies, the growth indices of tea plants were meticulously assessed. To determine shoot density (ST), three measuring frames, each encompassing an area of 0.1 m^2, were randomly positioned within the test site. The bud density enclosed within these frames was examined, using the count of harvestable buds and leaves within a 10-cm depth as the benchmark (Zhang et al. 2021). New shoot length (SL) evaluations were conducted by selectively identifying 20 standard shoots, each aydorned with three or four mature leaves, across the testing regions. A tape measure was then employed to quantify the distance between the base of the nascent shoot and the apex of the dormant bud (Zaman et al. 2023). The hundred-bud weight (HBW) was ascertained through the random extraction of 100 one-bud, three-leaf shoots, complete with bud termini and three unfolded leaves, from each plot. These samples underwent weighing, a procedure that was repeated thrice more to ensure reliability. The average weight derived from these iterations represented the replicate (Zaman et al. 2023). Tea yield (YD) measurements were executed by arbitrarily marking off three sections of 40 m^2 within the tea gardens. Harvesting in accordance with conventional tea-plucking norms was then performed. The yield was averaged and subsequently converted to represent the fresh leaf produce per hectare of the garden (Zhang et al. 2023).

Determination of soil physical and chemical properties. Soil pH was measured by the potentiometric method (Kicińska et al. 2022). Soil porosity (SP) was determined using the ring knife method (Toková et al. 2020). Soil organic matter (SOM) content was analyzed via the oxidation–reduction titration with potassium dichromate (Alguacil et al. 2014). The available nitrogen (AN) was assessed by the alkaline diffusion method (Chen et al. 2023). Available phosphorus (AP) was determined by the molybdenum–antimony colorimetric method (Jing et al. 2014), and available potassium (AK) was measured using the flame photometric method (Pramanik et al. 2019).

Soil total DNA extraction. Genomic DNA was extracted from 0.5-g samples using a soil DNA isolation kit (Omega Bio-tek, Norcross, GA, USA) according to the manufacturer's instructions. Before polymerase chain reaction (PCR) analysis, three independent DNA extractions from each sample were pooled. The extracted DNA was then assessed for both quality and quantity. Fluorescence spectrophotometry with a QuantiFluor-ST fluorometer (catalog number E6090; Promega, Madison, WI, USA) and the Quant-iT PicoGreen double-stranded DNA assay kit (catalog number P7589; Invitrogen, Waltham, MA, USA) was used to measure the absorbance of DNA at 260 and 280 nm, which determined the DNA concentration. The quality of the DNA was also evaluated using 1% agarose gel electrophoresis. The concentration of DNA solution was adjusted accordingly, and working solutions were stored at 4 °C, while storage aliquots were kept at −20 °C.

High-throughput sequencing analysis of 16 s/ITS rDNA. Firstly, the 16 S rRNA variable region was amplified. A PCR pre-experiment was performed to target the specific V region

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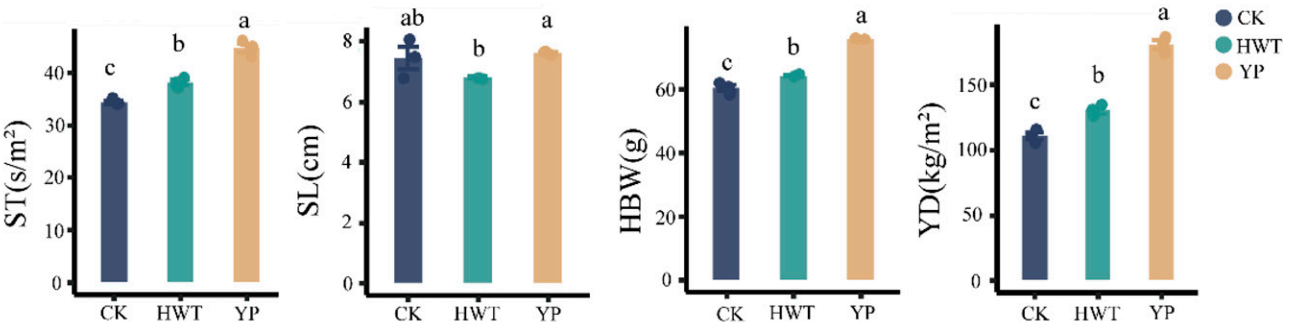


Fig. 1. Growth indicators of tea tree under different intercropping treatments. Whiskers represent standard error. Different letters indicate significant differences among the three planting systems. CK = Monoculture, HBW = hundred-shoot weight, HWT = tea/*P. montana* var. *culaishanensis* intercropping, SL = new shoot length, ST = shoot density, YD = yield, YP = tea/*M. dodecandrum* intercropping.

of the sample DNA. Next, a large-scale PCR amplification was carried out using Pyrobest DNA polymerase (catalog number DR500A) from TaKaRa (Kusatsu, Japan). Subsequently, gel extraction and purification were performed by targeting the desired bands to obtain purified samples employing the AxyPrep DNA gel extraction kit (catalog number AP-GX-500) from Axygen (Union City, CA, USA). Afterward, quantification of each sample was conducted using the BioTek enzyme marker. Finally, the required on-machine sequencing was performed by adopted the standard Illumina (San Diego, CA, USA) TruSeq DNA library preparation experimental process as outlined in the Illumina TruSeq DNA sample preparation guide.

Data analysis. Significant analysis was conducted using SPSS software (version 26; IBM, New York, NY, USA), employing analysis of variance with the least significant difference test ($P < 0.05$). Boxplots were computed using the "ggplot" package in R software (version 4.3.1; R Project, Fort Worth, TX, USA). After normalizing the soil microbial community data, α-diversity analysis and principal coordinates analysis (PCoA) were performed using the Bray–Curtis algorithm. Diversity index plots were generated using Prism (version 9.5; GraphPad, San Diego, CA, USA). The co-occurrence network was computed using the "igraph" package in R software (version 4.3.1) with Spearman correlation, requiring a correlation coefficient greater than 0.7 and a significant level of $P < 0.05$. Gephi (version 0.9.7; Paris, France) and Cytoscape (version 3.9.1; San Diego, CA, USA) were used to visualize the co-occurrence network. Linear discriminant analysis (LDA) effect size (LEfSe) analysis was used to estimate the relative abundance of species, with a logarithmic LDA score threshold of 3 (Li et al. 2023). LEfSe analysis was performed to identify significant differences from phylum to genus levels among the three treatment groups and to determine the characteristics most likely to explain the differences among the categories (Segata et al. 2011). The vegan software package (version 2.5.6) was used to rank microbial and soil properties by redundancy analysis (RDA) (He et al. 2023). Functional predictions for bacterial communities in the soil microbiota were performed based on the Functional Annotation of Prokaryotic Taxa (FAPROTAX) databases. The data were analyzed by using IBM SPSS Amos (version 28) software to construct a structural equation model (SEM) to examine the significance of the relationships between different variables under intercropping.

Results

Impact of intercropping on tea tree growth. As shown in Fig. 1, when contrasted with the control (CK), HWT and YP significantly increased ST by 10.68% and 30.10%, respectively. Similarly, both intercropping modes augmented HBW by 6.45% for HWT and 25.57% for YP and increased tea YD by 17.80% for HWT and an impressive 63.32% for YP, all with statistical significance ($P < 0.05$). In contrast, SL remained statistically unaltered across the various intercropping methods when compared with the CK. Overall, the adoption of either intercropping treatment promoted the growth and development of tea plants.

Impact of intercropping on soil physical and chemical properties. As shown in Fig. 2, a comparison with the control group (CK) revealed that HWT significantly increased soil properties such as SP, SOM, AN, and AP in the tea garden soil ($P < 0.05$). However, there was no significant difference observed in AK, whereas a notable decrease in pH was evident. On the other hand, YP intercropping significantly elevated SP, SOM, AP, and AK in the tea garden soil ($P < 0.05$), but it did not significantly affect soil pH or AN levels. Overall, both intercropping strategies positively influenced the physicochemical properties of tea garden soil.

Impact of intercropping on soil bacterial microbiota. Both HWT and YP intercropping significantly affect the diversity of soil microbial communities. This is evident from the boxplots, which are based on richness index

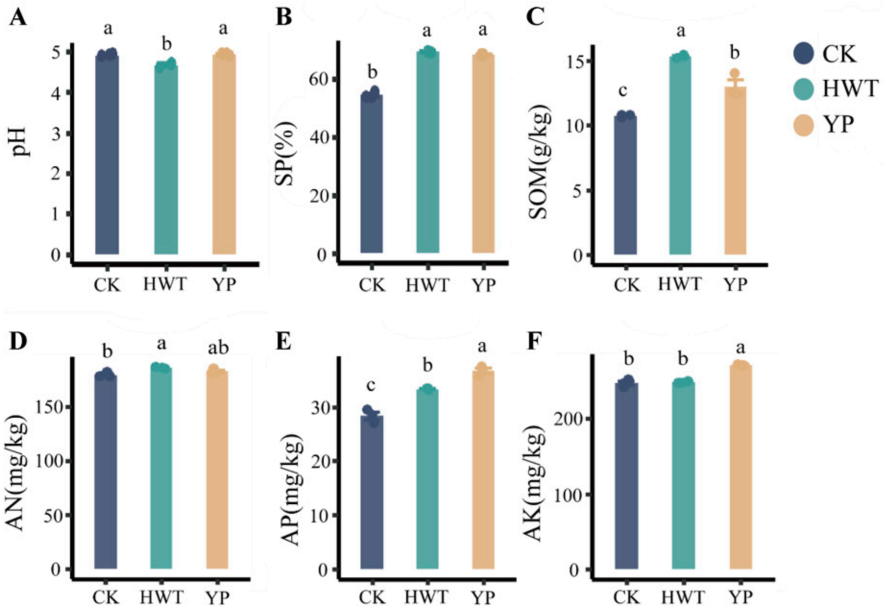


Fig. 2. Soil physicochemical properties under different intercropping treatments. (**A**) Soil acidity and alkalinity (pH). (**B**) Soil porosity (SP). (**C**) Available nitrogen (AN). (**D**) Available phosphorus (AP). (**E**) Available potassium (AK). (**F**) Soil organic matter (SOM). Whiskers represent standard error. Different letters indicate significant differences among the three planting systems. CK = Monoculture, HWT = tea/*P. montana* var. *culaishanensis* intercropping, YP = tea/*M. dodecandrum* intercropping.

(Chao1) and diversity index (Shannon), as presented in Fig. 3A and 3B. These plots clearly showed that both HWT and YP notably elevated the Chao1 of soil bacterial communities ($P < 0.05$). Additionally, HWT led to a significant enhancement in the Shannon index, whereas YP did not exhibit a significant change in this parameter. To further examine the variations in microbial community structure under different intercropping treatments, a PCoA was conducted at the operational taxonomic unit level. The results, as illustrated in Fig. 3C, revealed that the microbial communities corresponding to CK, HWT, and YP were distinctly separated. This separation underscored the significant impact that both intercropping modes have on the diversity and composition of soil microorganisms.

At the phylum level, the predominant phyla in all soil samples were Proteobacteria, Actinobacteria, Chloroflexi, Acidobacteria, Planctomycetes, Gemmatimonadetes, WPS-2, Verrucomicrobia, Bacteroidetes, and Firmicutes. Compared with the CK, both HWT and YP intercropping led to an increase in the relative abundance of Actinobacteria, Gemmatimonadetes, and WPS-2, with a significant uptick observed for WPS-2. Conversely, there was a decrease in relative abundance of Chloroflexi, Planctomycetes, and Firmicutes, with a significant reduction noted for Planctomycetes and Firmicutes. Notably, there were significant disparities in soil bacterial communities at the phylum level between the two intercropping modes for Proteobacteria, Chloroflexi, Acidobacteria, Planctomycetes, Gemmatimonadetes, and Verrucomicrobia. In conclusion, both HWT and YP intercropping exerted substantial effects on the community structure of soil bacterial phyla in the tea garden when contrasted with the CK.

In this study, we examined the symbiotic networks and calculated the topological properties of soil microbial communities in tea plantation soils to identify shifts in the co-occurrence relationships of microbial populations. Our findings revealed that the CK had 55 nodes and 236 edges, whereas HWT had 88 nodes and 652 edges; the YP treatment had 118 nodes and 1672 edges. Furthermore, the analysis of the topological properties of the co-occurrence networks demonstrated that betweenness centrality, closeness centrality, and node degree were all higher under the two intercropping treatments compared with the corresponding monoculture co-occurrence networks (Fig. 3E). This indicated that the microbial co-occurrence networks under the two intercropping treatments exhibited greater connectivity and stability. In conclusion, intercropping increased the aggregation of microbial communities (bacterial network edges/nodes = 4.29:7.41:14.17) and significantly enhanced the complexity and connectivity of the co-occurrence networks of soil microorganisms in tea gardens.

LEfSe analysis. LEfSe analysis was employed to discern differences in microbial community composition across various sample groups (Segata et al. 2011). Fig. 4 revealed that with an LDA score exceeding 3, the predominant bacteria differentially enriched in the CK soil are mainly HSB_OF53_F07 and KF_JG30_C25. In contrast, HWT soil was characterized by a significant presence of *Candidatus solibacter* from Acidobacteria; *Sphingomonas* from Bacteroidetes; *Phenylobacterium*, *Mycobacterium*, *Arthrobacter*, and *Noiherbaspirillum* from Actinobacteria; *Ellin6067* from Proteobacteria; and *Candidatus udaeobacter* from Verrucomicrobia. The YP soil primarily harbored MVP_88; *Actinomadura, Catenulispora*, and IMCC26256 from Actinobacteria; and *Rhodanobacter* from Proteobacteria.

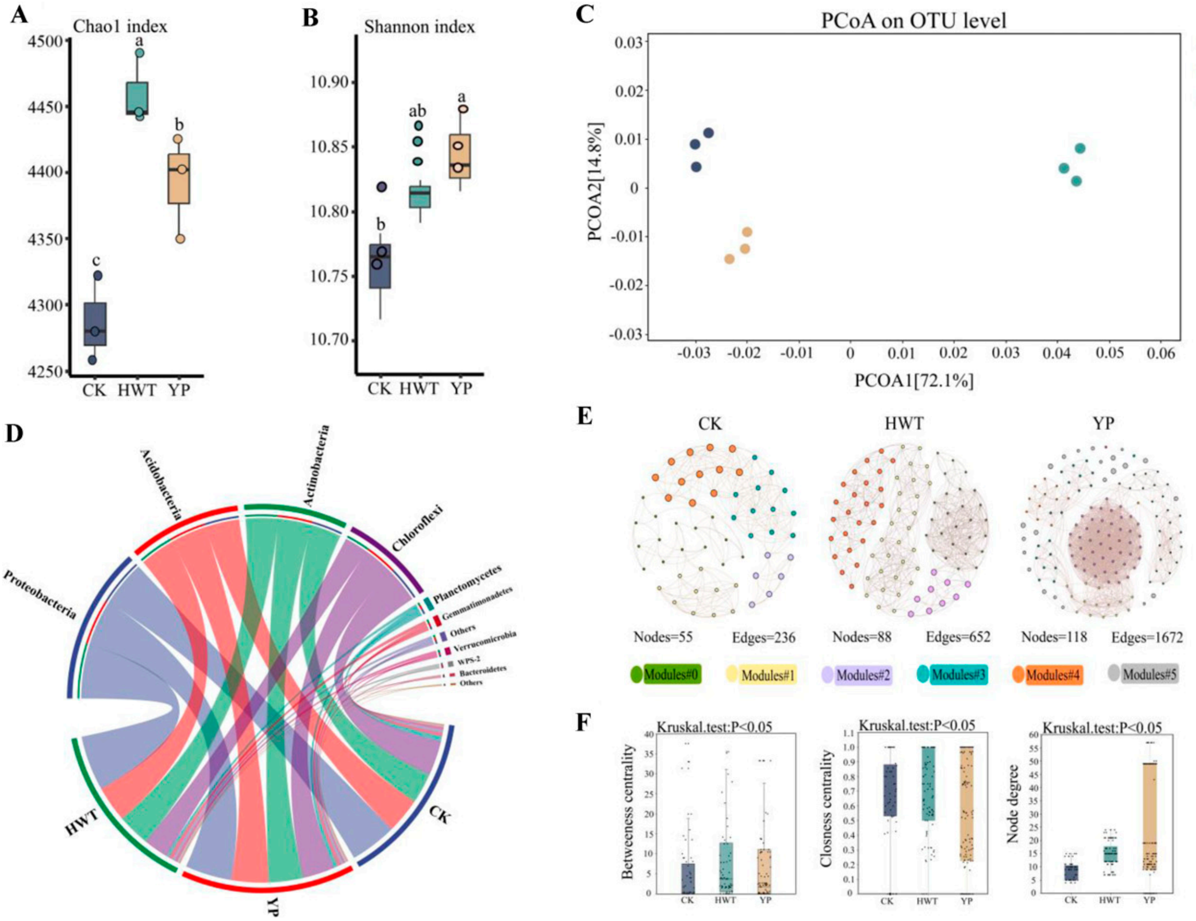


Fig. 3. Soil microbial α-diversity under different intercropping treatments. (**A**) Chao1 index for bacterial richness. (**B**) Shannon index for bacterial diversity. (**C**) Principal coordinate analysis (PCoA) for bacterial community structure. (**D**) Relative abundance of soil bacteria at the phylum level. (**E**) Symbiotic networks and their characteristics under different intercropping treatments, with comparisons between monoculture and intercropping systems. Symbiotic networks were constructed based on the correlation analysis of relative abundances of microbial genera. Node colors represent different microbiome modules. Connections between nodes indicate significant correlations (Spearman's rank correlation test; $P < 0.05$; $r > 0.70$). (**F**) Topological features of different bacterial networks, including betweenness centrality, closeness centrality, and node degree. CK = Monoculture, HWT = tea/*P. montana* var. *culaishanensis* intercropping, OUT = operational taxonomic unit, YP = tea/*M. dodecandrum* intercropping.

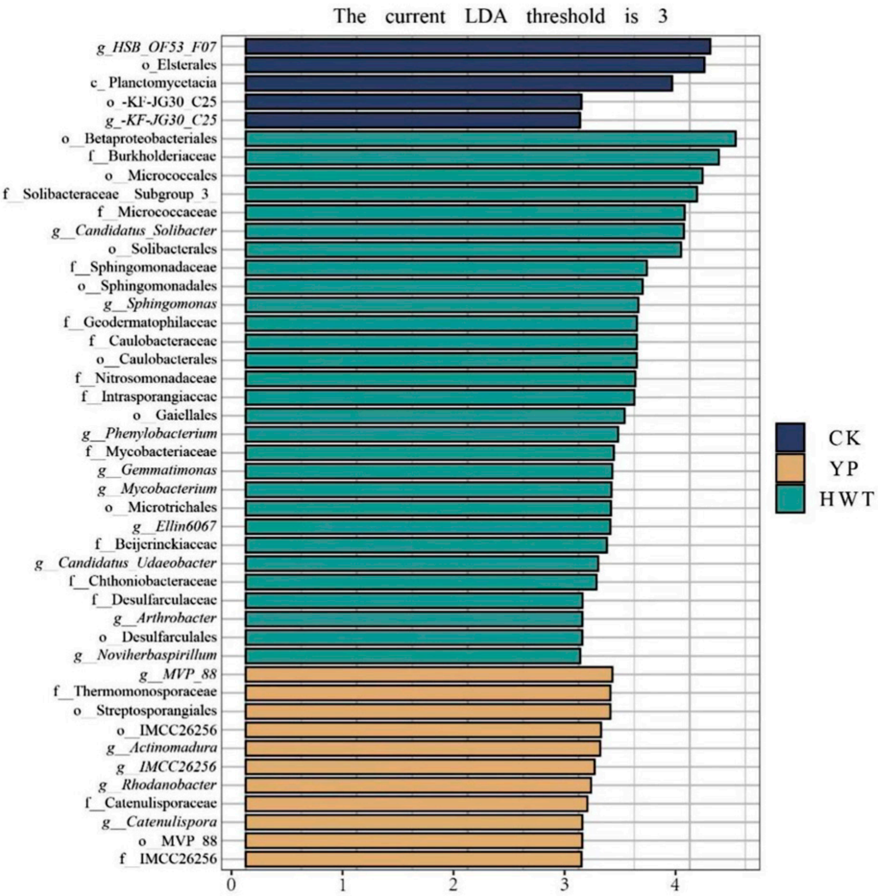


Fig. 4. Key differential bacteria genera in the microbial communities with a linear discriminant analysis (LDA) score greater than 3. CK = Monoculture, HWT = tea/*P. montana* var. *culaishanensis* intercropping, YP = tea/*M. dodecandrum* intercropping.

Notably, both intercropping modes demonstrated a substantive increase in beneficial microbial populations compared with the sole cultivation of tea plant, underscoring the impact of intercropping on soil microbiota.

Impact of intercropping on soil bacterial function. To delve deeper into the impacts of various intercropping treatments on the functional capabilities of soil bacterial communities, a FAPROTAX analysis was conducted, resulting in functional annotations for soil bacteria across different treatments. Notably, the principal functions were associated with C and N cycle processes. When compared with the control group, HWT exhibited significant disparities ($P < 0.05$) in one C cycle–related microbial function, specifically cellulolysis, and nine N cycle–associated microbial functions including nitrification, nitrate denitrification, nitrite denitrification, nitrous oxide denitrification, denitrification, N fixation, nitrite respiration, nitrate reduction, and ureolysis. In contrast, YP manifested significant differences ($P < 0.05$) in one C cycle function related to methane nutrition compared with the control group, yet it displayed no significant variance in N cycle–related microbial functions. These findings suggested that intercropping exerted a substantial influence on multiple C and N cycle functions. Nevertheless, YP intercropping appeared to wield a more pronounced impact on soil C and N cycle functionalities, with a particular emphasis on the N cycle. Concurrently, it was also observed that both intercropping methodologies significantly promote microbial functions linked to the C cycle, such as cellulolysis (Fig. 5).

Impact of intercropping on correlation between soil environmental variables and microorganisms. The impact of soil environmental variables on bacterial communities was demonstrated using RDA (Fig. 6A). The RDA1 and RDA2 axes collectively accounted for 39.56% of the overall variance in bacterial community structure. Each of the six soil environmental variables significantly shaped the soil microbial community, with factors such as pH, AP, SP, AN, SOM, and AK showing significant positive correlations with one another. Notably, YP treatment had the most profound impact on the soil bacterial community.

Additional exploration through tests delved into the association between environmental variables and bacterial communities. The findings revealed a significant positive correlation between SOM and both SP and AN. Meanwhile, tea YD exhibited a notable positive correlation with SP, AP, AK, ST, and HBW. Based on FAPROTAX analysis, we identified key differentially abundant bacterial genera within each treatment group, categorizing them into C and N cycle bacteria genera. In this context, the C cycle bacterial community displayed a significant positive correlation with AP and an extremely significant positive correlation with AK, ST, HBW, and YD. Conversely, the N cycle bacterial community showed a significant positive correlation with AP, HBW, and YD.

The impact of microbial diversity and key functional groups on environmental factors and tea tree growth under two intercropping modes was dissected using SEM. As shown in Fig. 6C, HWT significantly influenced C cycle elements (λ = 0.715). Bacterial diversity exerted a direct negative effect on soil physicochemical properties (λ = −0.438), whereas N cycle elements (λ = 0.692) and C cycle elements (λ = 0.509) indirectly positively affected tea tree growth to varying degrees. Soil physicochemical properties directly enhanced tea tree growth (λ = 0.521). Fig. 6D illustrated that YP treatment had a significant positive effect on soil physicochemical properties (λ = 0.961) and C cycle elements (λ = 0.963) in tea garden soils. Carbon cycle elements directly improved soil physicochemical properties (λ = 0.405) and indirectly fostered tea tree growth (λ = 0.414). Soil physicochemical

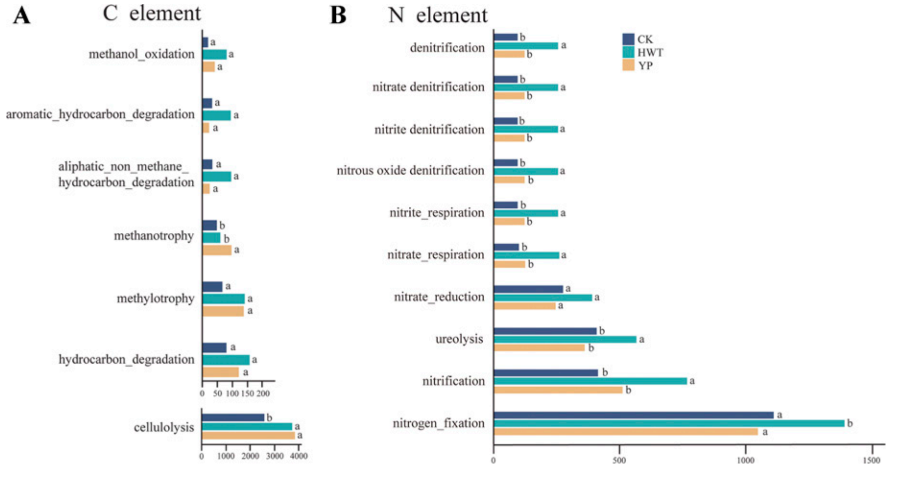
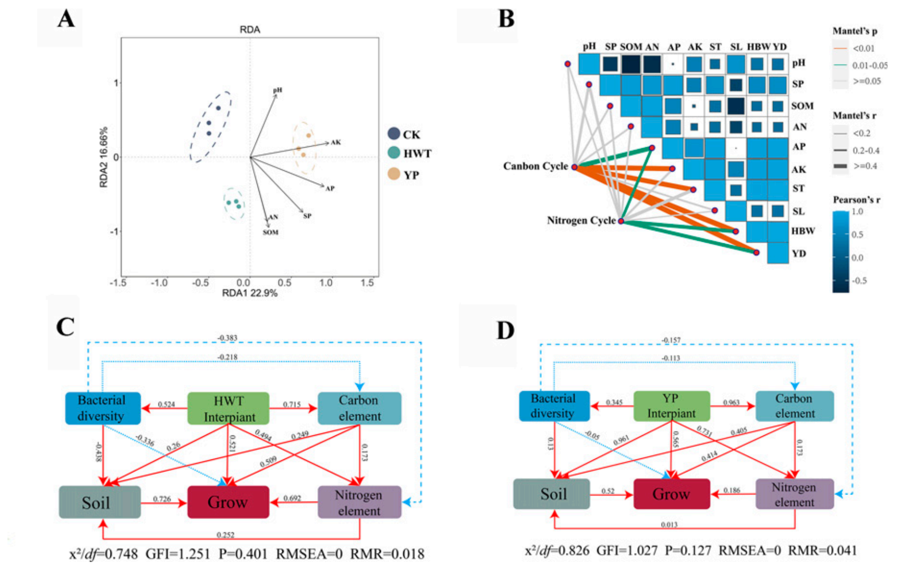


Fig. 5. FAPROTAX analysis of soil bacterial communities under different intercropping treatments. (**A**) Carbon element. (**B**) Nitrogen element. CK = Monoculture, HWT = tea/*P. montana* var. *culaishanensis* intercropping, YP = tea/*M. dodecandrum* intercropping.



x^2/df=0.748 GFI=1.251 P=0.401 RMSEA=0 RMR=0.018

x^2/df=0.826 GFI=1.027 P=0.127 RMSEA=0 RMR=0.041

Fig. 6. Analysis of the interaction between soil microbial bacterial communities and soil environmental factors. (**A**) Redundancy analysis (RDA). (**B**) Correlation analysis between environmental factors, growth factors, and C and N cycling communities. (**C**) Structural equation modeling analysis of tea/*P. montana* var. *culaishanensis* intercropping (HWT). (**D**) Structural equation modeling analysis of tea/*M. dodecandrum* intercropping (YP). AK = available potassium, AN = available nitrogen, AP = available phosphorus, CK = monoculture, HBW = hundred-shoot weight, pH = soil acidity and alkalinity, SL = new shoot length, SOM = soil organic matter, SP = soil porosity, ST = shoot density, YD = yield.

properties directly benefited tea tree growth (λ = 0.52). It is noteworthy that the intercropping mode governs all these influencing factors.

Discussion

Intercropping altered the microbial community structure in tea tree soil. In intercropping systems, the interaction between different plant species often enhances soil microbial community diversity through competition and promotion effects, which in turn regulates soil fertility (Stefan et al. 2021; Wagg et al. 2021). Understanding changes in microbial community structure and function is of great significance for optimizing tea garden management practices. In this study, both YP and HWT significantly increased the diversity of soil bacterial communities. This stability in microbial richness may result from self-regulation of existing microorganisms in response to changes in the soil microenvironment, allowing previously less dominant bacteria to thrive. This enhances community diversity without significantly altering species composition (Saleem et al. 2019). Both intercropping approaches positively affected the ecological health of tea gardens, indicating complex dynamics between soil bacterial communities and fertility that warrant further investigation to reveal their intricate regulatory mechanisms. Additionally, our findings reveal a significant enhancement in the betweenness centrality, closeness centrality, and node degree within symbiotic networks under both intercropping modes (Fig. 3E), implying improved overall functionality and stability of the microbial ecosystem. These results align with prior research (Senghor et al. 2023; Wu et al. 2022), reinforcing the importance of considering such network-based metrics when assessing the impact of agricultural practices on soil microbial ecology.

In this study, the dominant phyla in tea plantations under three different planting arrangements were Proteobacteria, Actinobacteria, Chloroflexi, and Acidobacteria. These findings are consistent with previous findings that have identified these as common in tea plantations (Li et al. 2016; Yang et al. 2022; Zhang et al. 2012). Furthermore, the phyla Proteobacteria and Actinobacteria showed significant variation under different planting systems, with a notable increase in the relative abundance of Proteobacteria in the HWT system compared with the control. Proteobacteria are known to include many copiotrophic genera commonly found in nutrient-rich soils (Delmont et al. 2018). In contrast, Actinobacteria are involved in the decomposition of various complex organic substances and play a vital role in cellulose degradation and humus formation (Ventura et al. 2007). Similarly, Sapp et al. (2015) observed significant enrichment of Proteobacteria in Triticum *aestivum* soils under intercropping conditions. Thus, intercropping may lead to the accumulation of organic matter around the tea tree base, altering the soil's C/N ratio (Liu et al. 2020). This change in the soil microbial community structure significantly enriches Proteobacteria and Actinobacteria. Consequently, the increased soil nutrients observed in the HWT system may be closely related to the enrichment of Proteobacteria.

Impact of soil microorganisms on the soil C and N cycles. Microorganisms play a crucial role in regulating soil ecosystem functions such as nutrient cycling, organic matter decomposition, N fixation, and soil structure maintenance. They serve as the primary drivers of the earth's biogeochemical cycles, notably the C and N cycles (Gärdenäs et al. 2011). In this study, the HWT treatment led to a significant increase in the abundance of nine signature bacteria, including *C. solibacter*, *Sphingomonas*, *Phenylobacterium*, *Mycobacterium*, *Arthrobacter*, *Noviherbaspirillum*, *Ellin6067*, *Gemmatimonas*, and *C. udaeobacter*. Previous research indicated that *C. solibacter* was a beneficial bacterium that promoted the soil organic matter recycling and anaerobic degradation of aromatic compounds (Zhang et al. 2018). *Sphingomonas* could degrade various organic compounds like polycyclic aromatic hydrocarbons, pesticides, and dyes (Fagervold et al. 2021; Yang et al. 2020; Zhou et al. 2022). *Phenylobacterium* was capable of degrading diverse organic compounds and can be used for the biodegradation of aromatic compounds (Eberspächer 2015). *Gemmatimonas* played a key role in cellulose degradation, facilitating the release of organic matter (Banerjee et al. 2016; Guo et al. 2016). *C. udaeobacter* exhibited unique roles in the degradation of organic pollutants and carbohydrate metabolism (Aleluia and Ferrão 2016). *Ellin6067* was involved in the process of ammonia oxidation to nitrate or nitrite during N transformation (Sun and Zhu 2022). *Mycobacterium* participated in denitrification and dissimilatory nitrate reduction, contributing to the N cycle (Salazar et al. 2023). *Arthrobacter* was significant in the soil N cycle, engaging in processes such as ammonification, nitrification, and denitrification (He et al. 2017, 2020). *Noviherbaspirillum* regulated denitrification and N fixation processes (Li et al. 2023). Conversely, the tea/*M. dodecandrum* intercropping increased the abundance of five signature bacteria, namely *Actinomadura*, *Rhodanobacter*, *Catenulispora*, *IMCC26256*, and *MVP_88*. Actinomadur secretes xylanase to degrade hemicellulose, significantly promoting the C cycle (Taibi et al. 2012). *Rhodanobacter* possessed denitrification and bioremediation capabilities (Peng et al. 2022; Prakash et al. 2021). The beneficial microbial groups in both intercropping modes significantly outnumber those in the monoculture of tea trees. This suggested that both intercropping methods can enhance soil C and N cycles, improve soil nutrients in the tea garden, and consequently foster the growth and development of tea trees.

The functional predictions of the soil bacterial microbiota further substantiate the positive effect of intercropping on the soil C and N cycles. The HWT treatment resulted in significant improvements in cellulolysis, a process associated with C cycling, as well as in various N cycling functions such as nitrification, nitrate denitrification, nitrite denitrification, nitrous oxide denitrification, denitrification, N fixation, nitrite respiration, nitrate reduction, and ureolysis (Fig. 5B). In contrast, the YP treatment exhibited significant improvement only in cellulolysis compared with the control group, indicating that it has a more pronounced effect on C cycling (Fig. 5A). This suggested that intercropping affected multiple C and N cycling functions. Comparing the effects of HWT and YP, it is evident that HWT has a greater influence on both C and N cycling functions, particularly N cycling.

Advantages of intercropping P. montana var. culaishanensis/i with tea trees. In intercropping systems, the primary interactions between species include mutual facilitation and competition. When facilitation outweighs competition, it is referred to as an intercropping advantage; otherwise, it is considered an intercropping disadvantage (Stomph et al. 2020; Yin et al. 2020). Intercropping between Fabaceae plants and non-Fabaceae plants often demonstrates mutual facilitation. For example, intercropping tea trees with soybeans effectively promoted tea tree growth and increased yields for both tea and soybeans (Li et al. 2008). However, previous studies have not explored intercropping between Melastomataceae plants and non-Melastomataceae plants. In this experiment, soil porosity, organic matter content, AN content, AP content, AK content, and tea tree yield were all higher in the treatment of intercropping Fabaceae plant *P. montana* var. *culaishanensis* with tea trees compared with the control. This result aligned with the findings of Duan et al. (2022). Intercropping *P. montana* var. *culaishanensis* in tea gardens has been found to significantly decrease soil pH, although the levels remain within the optimal range for tea tree growth, consistent with the findings of Wang et al. (2023). This effect is likely attributed to *Pueraria lobata*'s ability to fix N and release H^+ ions into the soil during its growth cycle, thereby increasing soil N availability for tea trees while lowering soil pH. In another experiment, intercropping with *M. dodecandrum* resulted in higher soil nutrient content and tea tree yields compared with monoculture tea planting, also mitigating further soil acidification to a certain extent. These observations align with the research of Duan et al. (2019), highlighting the potential benefits of incorporating certain plant species into tea gardens to improve soil health and productivity. RDA analysis showed that environmental factors such as AK, AN, and SOM were important factors influencing the distribution of bacterial microbial communities. The test indicated that C and N cycling genera strongly correlate with various physiochemical factors and tea tree growth metrics. Integrating SEMs provides a more precise understanding of these interactions. Alterations in soil physicochemical properties due to both intercropping methods significantly affect tea tree growth rates (Fig. 6C and 6D). Moreover, shifts in soil bacterial microbial communities triggered by these intercropping techniques are intimately associated with these soil property changes, collectively affecting tea tree development. In summary, the intercropping system of HWT and YP has been shown to improve soil conditions and tea yield in tea plantations to a certain extent, making it a viable and beneficial strategy for ecological conservation and the sustainable development of tea plantations.

Conclusions

Both intercropping modes have altered the soil bacterial community associated with tea plants. These changes have enhanced N and C cycling, improved the soil environment, and promoted tea plant growth. This study highlights the ecological mechanisms behind yield advantage in HWT and YP intercropping from a soil microbial perspective. However, further studies are needed to assess the changes in tea leaf quality and fungal community structure and to conduct metagenomics analysis of soil microbiota functions in tea/Fabaceae and tea/Melastomataceae intercropping systems.

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