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Impact of Tea Tree Cultivation on Soil Microbiota, Soil Organic Matter, and Nitrogen Cycling in Mountainous Plantations

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Abstract: This study focused on examining the early stages of tea cultivation (1, 3, and 5 years) in mountainous tea plantations. It specifically aimed to investigate the changes in soil micro-ecology at different locations (inter-row, terrace surfaces, and terrace walls). It was revealed that as tea tree cultivation progressed over the years, bacterial diversity and co-occurrence networks annually decreased in different locations. The results of soil physicochemical index analysis showed that the soil's available nutrients and the activities of cellulase and protease increased. Furthermore, the amplitude of variation of these indexes in the inter-row soil was significantly higher than that on the terrace surfaces and the terrace walls ($p < 0.05$). Alterations occurred in the soil microbial community structure, with an enrichment of bacterial genera such as *Sinomonas*, *Granulicella*, and *Sphingomonas*, as well as fungal genera such as *Trichoderma*, *Penicillium*, and *Talaromyces*; an increase in the proportion of plant pathogenic fungi (*Cladosporium*, *Fusarium*, and *Curvularia*) was observed in the inter-row soil. The results of soil microbial function prediction showed that nitrification and nitrogen fixation decreased, but denitrification increased ($p < 0.05$). In conclusion, cultivating tea trees in mountainous terraced plantations significantly impacted the soil microbial community, accelerated the metabolism of soil organic matter, disrupted soil nitrogen cycling functions, and increased the presence of plant pathogenic fungal pathogens. Moreover, the changes in the structure and functions of the soil microbial community demonstrate a spatial distance effect across different terrace locations.

Keywords: mountainous tea plantations; soil microbiota; high-throughput sequencing; co-occurrence network; functional predictions

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1. Introduction

Mountainous tea plantations are one of the main types of tea garden in south China. In Fujian Province alone, there are more than 2000 km^2 of mountain tea plantations [1]. Terracing involves constructing strip-like terraced fields along the contour lines on hilly slopes, comprising both terrace surfaces and terrace walls [2]. The distribution of tea trees is limited by climatic conditions and the mountain area in south China has a monsoon subtropical climate, which is suitable for growing tea trees. Furthermore, this terracing technique enhances air circulation due to elevation variations between terrace surfaces and walls, creating favorable conditions for producing high-quality tea leaves [3]. Recent research indicated a strong connection between soil environments and soil microbiota [4]. Soil microorganisms, crucial components of soil ecosystems, have been shown to play a vital role in nutrient cycling, organic matter formation, and decomposition processes [5,6]. Human agricultural activities, particularly land cultivation, have significantly impacted soil environments, eliciting prompt responses from soil microbial communities [7]. Plants release substantial amounts of metabolites into the soil through both above-ground litter

and below-ground exudates during their growth and senescence. These metabolites have been shown to regulate the composition and functional diversity of soil microbial communities [8,9]. Furthermore, soil microbes exhibit a distinct adaptability in response to different ecosystems. For example, in swamp ecosystems, N application reduced the potential function of partial nitrogen (N) and sulfur (S) cycling in the bacterial community, while having little impact on the fungal community and function [10]. The metabolic functions of the soil microbial community in forest ecosystems were also significantly affected by nitrogen application [11], facilitating archaea-mediated ammonia oxidation processes [12]. However, there is a paucity of understanding regarding the remodeling process of soil ecosystems using tea tree cultivation.

Previous research has primarily focused on the effects of long-term (more than 10 years) tea cultivation on rhizosphere soil. Research shows that that soil microbial biomass carbon and enzyme activity significantly increased, while soil nutrients exhibited an initial increase followed by a subsequent decline with the duration of the tea plantation, ultimately affecting nutrient absorption by tea plants [13–15]. Guo et al. have suggested that long-term tea cultivation results in the accumulation of acidic compounds in the rhizosphere soil, leading to soil acidification, nutrient depletion, and a significant decrease in soil aggregate stability [16]. Additionally, the accumulation of secondary metabolites and above-ground litter in tea trees is able to cause autotoxicity, which inhibits tea tree growth [17,18]. In addition to rhizosphere soil, the microecological conditions of the surrounding soil also have a profound impact on the productivity of the plantations. Lange et al. showed that the stability and carbon uptake of the soil microbial community were determined by the differences between rhizosphere and non-rhizosphere soil [19]. Huang et al. showed that the microbial community structure of non-rhizosphere soil in an apple plantation was more complex and diverse than that of rhizosphere soil [20]. Mountainous tea plantations are mainly composed of terrace surfaces and terrace walls. However, research into the processes that reshape soil ecosystems, especially in relation to the structure and function of soil microbial communities during the initial planting stages of mountainous tea plantations, remains limited.

The Wuyi Mountain Range is a vital tea-producing region in China, embodying the topographical characteristics of terraced tea plantations in the southern mountainous areas. This location provides a valuable research environment for studying the impact of tea cultivation on soil in mountainous terraced fields. Focusing on a newly established mountainous tea plantation, a five-year consecutive site-specific experiment to dynamically analyze the changes in the microbial community structure and biochemical indicators in the soils of inter-row, terrace surface, and terrace wall locations within the tea plantations was conducted in this study. This approach enables a comprehensive assessment of the overall impact of tea cultivation on mountainous terraced soils. The findings from this study will contribute to our understanding of the soil ecology in mountainous tea plantations, which is crucial for maintaining soil productivity and ecological stability in these regions.

2. Materials and Methods

2.1. Experimental Site and Soil Sample Collection

The experimental tea plantation was situated in Wuyishan City, Fujian Province (Figure 1A). The region has a subtropical monsoon humid climate with an average annual rainfall of 1926.9 mm and an average annual temperature of 18.3 °C. Before the establishment of the experimental tea plantation, it was a wasteland, mainly covered with shrubs and weeds, and no plants were planted. The tea plantation has been set up in a terraced style, with a total area of 14 hectares. The terrace surfaces were 1.2 m wide and the terrace walls were 0.8 m high, representing a typical terraced tea plantation (Figure 1B). Three test sample areas (10 m × 10 m) were randomly set up in the tea plantation and the distance between each sample area was more than 30 m. The tea variety used for the experiment was *Camellia sinensis* L. Rougui, with a large row spacing of 1.6 m and a planting pattern of double rows with single plant rows. Rougui tea trees were planted in February 2017

and were subjected to manual weeding and routine management practices. Each year in late October, 700 kg/ha of compound fertilizer (N:P:K = 21:8:16) was applied to tea plantation. Soil samples were collected in mid-April in the years 2018, 2020, and 2022. The sampling method followed a five-point sampling approach [21], where soil samples were collected at a distance of 15 cm from the base of the tea tree trunk and a depth of 10 to 20 cm, representing inter-row soil (IR). Soil samples were also collected at a distance of 50 cm from the tea tree trunk (TS). Additionally, samples were collected from the central position on the slope of the terrace walls (TW). Simultaneously, native soil samples within the plantation without tea tree cultivation were collected as the control (CK). These samples were preserved in ice bags, transported to the laboratory, and passed through a 2 mm sieve to remove stones and visible impurities. These were then stored in −80 °C and 4 °C refrigerators, respectively.

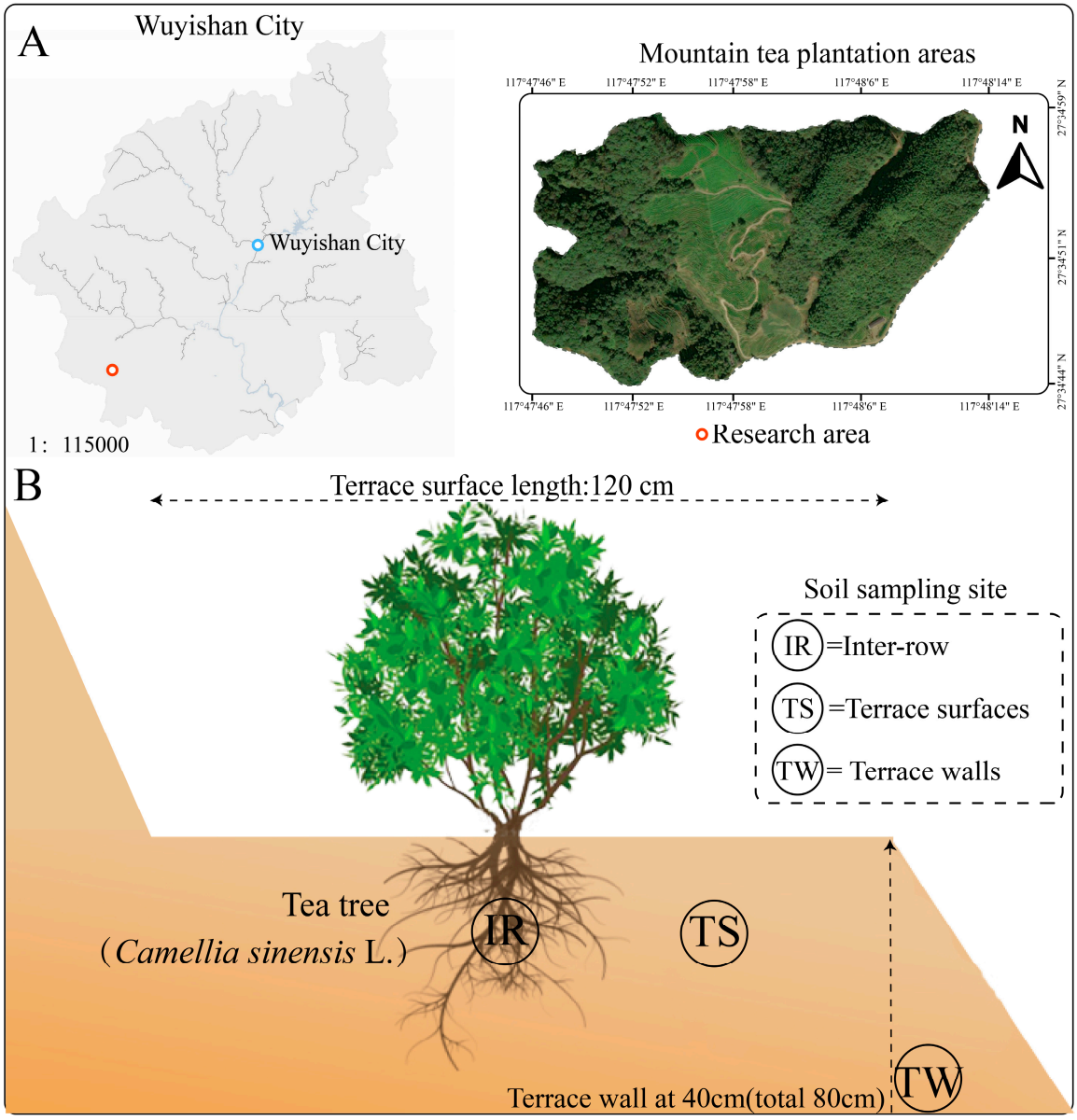

Figure 1. Geographical location of the study area (**A**) and soil sampling site (**B**).

2.2. Soil Physicochemical Properties and Enzyme Activity Analysis

The contents of total nitrogen (TN), total phosphorus (TP), total potassium (TK), available nitrogen (AN), available phosphorus (AP), available potassium (AK), soil organic

matter (SOM), urease (UE), polyphenol oxidase (PPO), peroxidase (POD), protease (PT), and cellulase (CE) were determined according to Liu et al. [22].

2.3. Soil Total DNA Extraction

Total DNA from the soil samples was extracted using the BioFast Soil Genomic DNA Extraction Kit (BioFlux, Hangzhou, China). Subsequently, the DNA concentration was determined using a NanoDrop 2000C Spectrophotometer (Thermo Scientific, Waltham, MA, USA). DNA samples that meet the quality criteria were utilized for 16S/18S rDNA high-throughput microbial community sequencing analysis.

2.4. High-Throughput Sequencing Analysis of 16S/18S rDNA

Amplifications were carried out for bacterial 16S rDNA and 18S rDNA. Detailed information on primers and thermal cycling programs can be found in Table S1. The PCR instrument used was the ABI Gene Amp® 9700 model; subsequently, soil microbial sequencing was performed using the Illumina HiSeq sequencing platform. The sequencing data were processed through the Qiime platform (http://qiime.org/scripts/assign_taxonomy.html, accessed on 12 May 2022) to remove low-quality sequences with an average quality score of less than 20 ($Q < 20$) and sequences shorter than 100 base pairs. This result in the final dataset of effective tags. Uparse was utilized to cluster all effective tags from each sample into Operational Taxonomic Units (OTUs), using a default 97% sequence similarity threshold. Further taxonomic annotation of the OTU sequences was conducted using the blast method in Qiime against the Unit (v7.2) database, providing microbial abundance at different taxonomic levels.

2.5. Data Analysis

The soil biochemical data were initially organized using Microsoft Office 2021. Significant analyses of the soil biochemical data were performed using IBM SPSS (Version 26.0. Armonk, NY, USA, IBM Corp) software, employing ANOVA and LSD tests ($p < 0.05$). For the soil microbial community data, α-diversity and β-diversity analyses were conducted based on Bray–Curtis. Diversity indices plots were generated using GraphPad Prism (Version 7, San Diego, CA, USA, GraphPad Software). The co-occurrence network was computed using the "igraph" package in R software (Version 4.3, Paris, France, Lucent Technologies), with a Spearman correlation threshold of $r > 0.7$ and $p < 0.01$. Subsequently, the co-occurrence network was visualized using Gephi (0.9.7) and Cytoscape (3.9.1). The neutral community model (NCM) was computed using the "minpack.lm" package. Functional predictions of the soil bacterial and fungal communities were performed using the FAPROTAX and FUNGuild databases. A structural equation model (SEM) was conducted on the data using IBM SPSS Amos (28) to construct the structural equation model.

3. Results

3.1. Impact of Tea Cultivation on Terraced Soil's Physicochemical Properties and Enzyme Activity

Analysis of soil's biochemical properties in soil samples revealed distinct trends (Figure 2 and Table S2). In comparison to control soil, soils under different treatments exhibited gradual increases in TP, TK, AP, and AK with increasing years of tea cultivation. Moreover, CE and PT significantly increased, indicating improved capabilities for organic macromolecule degradation and enhanced nutrient characteristics in the soil of the mountainous tea plantation. However, it is noteworthy that different soil locations showed varying degrees of decline in TN, AN, UE, pH, and SOM. Additionally, POD and PPO gradually increased in the inter-row (IR) soil. The magnitude of the changes in each soil biochemical and enzymatic parameter between different locations in the tea plantation followed the order: IR > TS > TW.

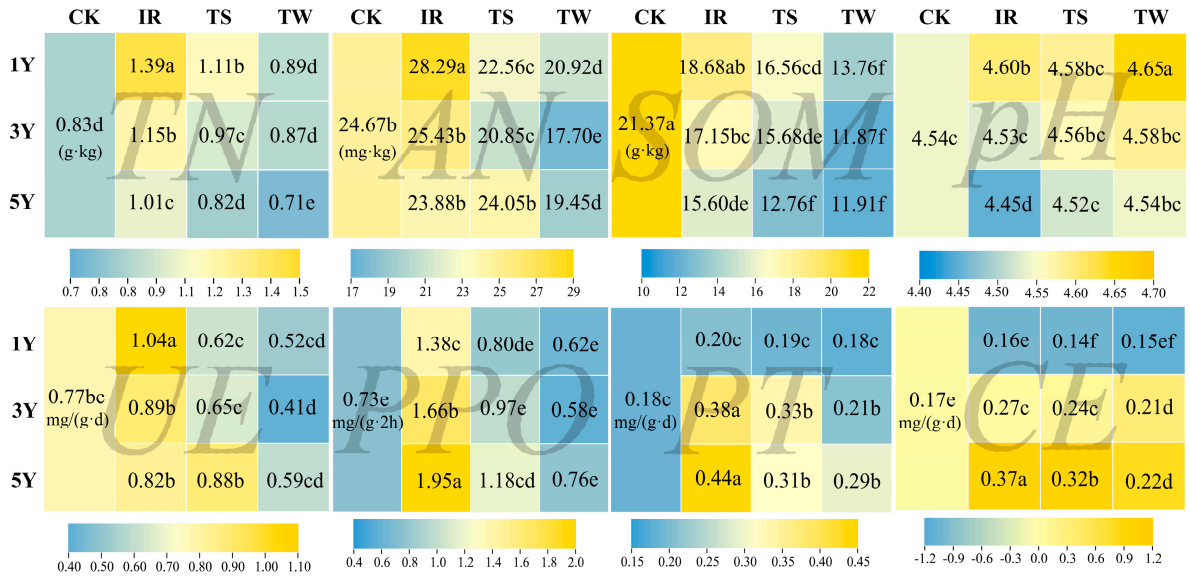

Figure 2. Soil biochemical properties in different locations of tea plantations under different cultivation durations. Different colors in the figure indicate different contents, while different letters denote significant differences (LSD, $p < 0.05$).

3.2. Impact of Tea Cultivation on Microbial Diversity in Mountainous Tea Plantations

In this study, we conducted a co-occurrence network analysis of soil bacterial communities at different planting durations (Figure 3A). The results indicated that with the progression of tea tree cultivation years, the number of modules, nodes, and edges within the bacterial co-occurrence networks gradually declined. Further analysis revealed that the complexity of the co-occurrence network in the IR soil decreased more sharply compared to the TS and TW soils (Figures 3B, S1 and Table S3). In year one, the number of nodes and edges of IR is significantly greater than TW (nodes = 193:137, edges = 1549:822). At five years, there is no significant difference between IR and TW (nodes = 137:143, edges = 643:657). Similar patterns were observed in the analysis of bacterial α-diversity indices (Figure 3C) for IR, TS, and TW soils. The number of nodes and edges in fungal co-occurrence networks at first decreased and then increased. Furthermore, the Chao1 and Shannon index for IR, TS, and TW soils in different years (Figure 3D) showed similar trends.

3.3. Impact of Tea Cultivation on Soil Microbial Community Construction and Dispersal in Mountainous Tea Plantations

The results of PCoA (Principal co-ordinates analysis) plots (Figure 4A,B) show that soil microbial communities had significant differences under different tea planting years. Moreover, analysis using the Neutral Community Model (NCM) demonstrated significant differences in the impact of tea cultivation on the assembly and dispersal of microbial communities in various locations within mountainous tea plantations (Figure 4C,D). As the distance between the soil and tea trees increased (IR < TS < TW), the R^2 values for bacterial communities consistently increased, while the R^2 values for fungal microbial communities continuously decreased. The migration rates (m value) of both bacterial and fungal communities decreased as the distance from tea plants increased, indicating that tea cultivation played a role in shaping the microbial community structure, with its impact diminishing as the distance from tea plants increased in IR, TS, and TW soils.

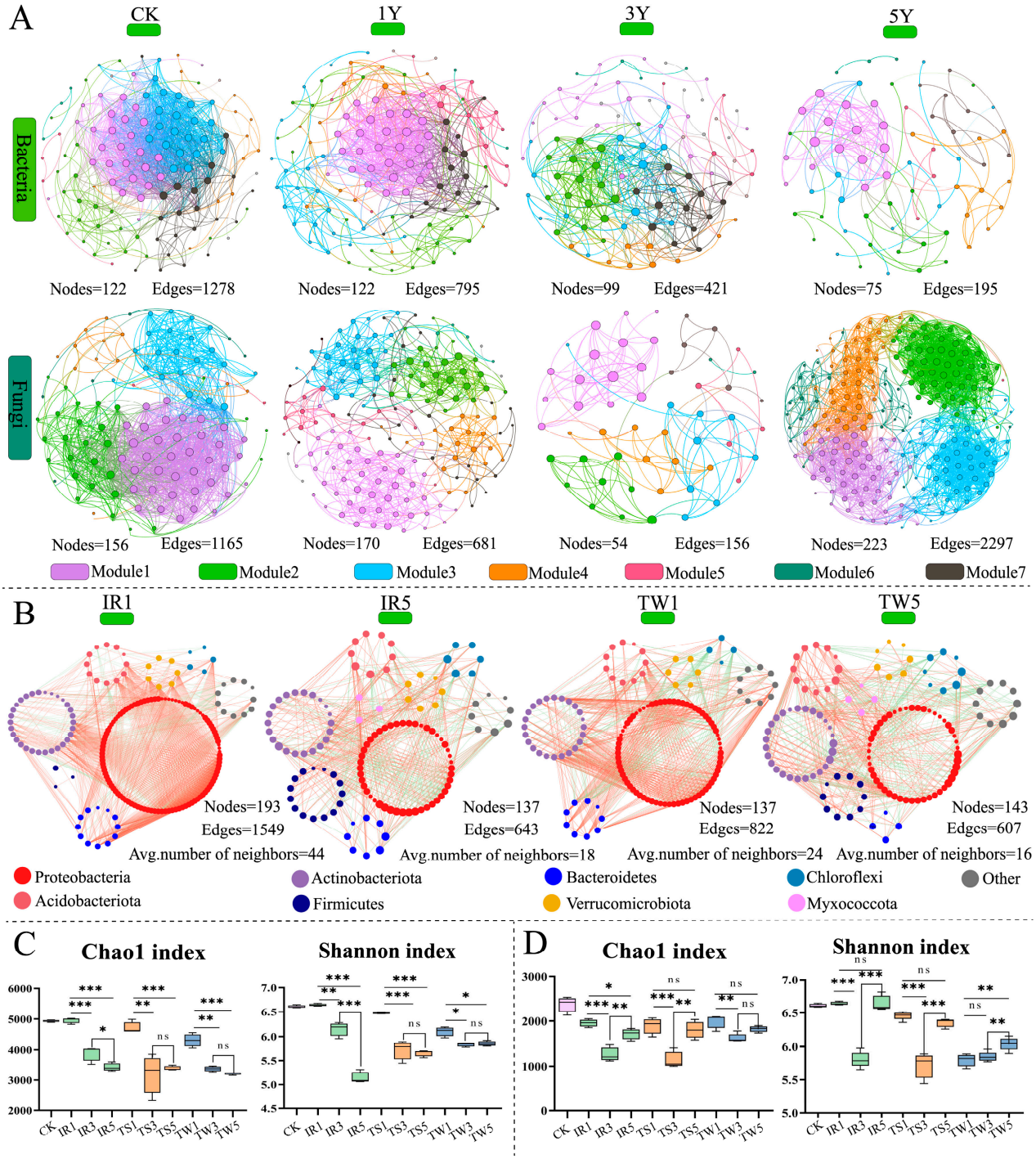

Figure 3. Comparison of co-occurrence networks and microbial diversity in terraced soil under different cultivation durations. (**A**) Co-occurrence networks of bacteria and fungi in different treatments (IR + TS + TW). The networks were constructed based on correlations among microbial OTUs. Node size represents the number of connections, and edges between nodes indicate significant correlation. (**B**) Co-occurrence networks of soil bacteria in IR and TW during the first and fifth years of cultivation. Different colors represent distinct bacterial phyla. (**C**) Soil bacterial diversity index (Chao 1 and Shannon). (**D**) Soil fungal diversity index (Chao 1 and Shannon). The number of asterisks (*) denotes the levels of significance. $p > 0.05$ = ns, $p < 0.05$ = *, $p < 0.01$ = **, $p < 0.001$ = ***.

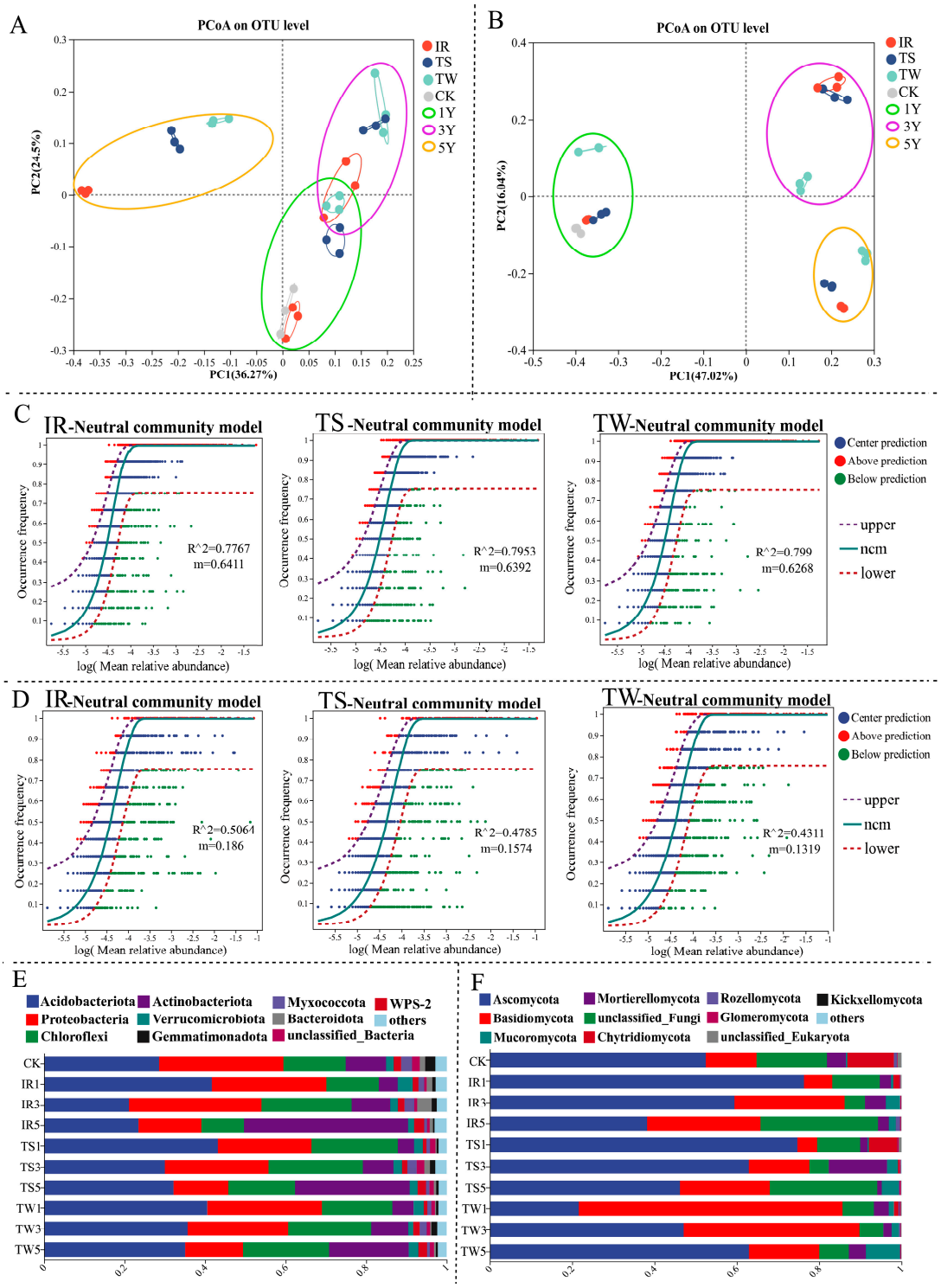

Figure 4. Differential analysis of microbial community structures was conducted using the NCM and PCoA. PCoA analyses are shown for bacterial (**A**) and fungi (**B**) communities in different soil samples, respectively. In panels (**C**,**D**), The R2 value represents the overall goodness of fit of the neutral community model, with higher R2 values indicating a greater influence of stochastic factors and a lesser influence of deterministic factors during microbial community assembly. The migration rate (m) quantifies the community-level dispersal, regardless of species. Higher m values indicate a greater ease of species dispersion within the entire community. Panels (**E**,**F**) display the relative abundance of species at the phylum level within different soil bacterial and fungi communities, respectively.

3.4. Effects of Tea Cultivation on Key Soil Bacterial Flora and Its Functions in Mountainous Tea Plantations

At the phylum level, there were notable changes in abundance as tea cultivation time increased. Specifically, the abundance of Proteobacteria in IR, TS, and TW soils significantly decreased over time. In contrast, there was a significant increase in the abundance of Actinobacteria. Furthermore, the proportion of Actinobacteria in IR soil was significantly higher than in TS and TW soils (Figure 4E). In terms of fungi, the abundance of Basidiomycota continuously decreased in both IR and TS soils, while it increased in TW soil. Conversely, the abundance of Ascomycota showed the opposite trend in these soils (Figure 4F).

Based on the LEfSe (Linear discriminant analysis Effect Size) analysis, heatmaps of the variation of soil signature microorganisms (genus level) abundance under different tea cultivation years were generated. The results indicate that with the increase in the duration of tea tree cultivation, the abundances of *Acidibacter*, *Pajaroellobacter*, *Acidothermus*, *Chujaibacter*, and *Gemmatimonas* gradually decreased in IR, TS, and TW soils. *Sinomonas*, *Granulicella*, and *Kitasatospora* showed an annual increase. On the other hand, in IR and TS soils, *Burkholderia*, *Xanthobacter*, *Sphingomonas*, *Vicinamibacterales*, and *Bradyrhizobium* decreased annually. Additionally, the abundance of *Bryobacter* continuously decreased in TS and TW soils.

This study conducted a functional annotation of soil bacteria using the FAPROTAX database. A total of 44 bacterial functions were identified and, among them, seven functions correlated to nitrogen cycling, showing significant changes under tea tree cultivation ($p < 0.05$) (Figure 5D). Specifically, there was a significant decrease in functions related to nitrification, ureolysis, and nitrogen fixation. On the other hand, functions associated with nitrite denitrification, denitrification, and nitrate respiration displayed a significant increase.

3.5. Effects of Tea Cultivation on Key Soil Fungal Flora and Its Functions in Mountainous Tea Plantations

Similarly, LEfSe analysis was conducted to examine the differing fungal flora between different soil samples (Figures 6A and S4). As tea tree cultivation duration increased, the relative abundance of *Penicillium*, *Talaromyces*, and *Trichoderma*, which are involved in organic matter metabolism, significantly increased in IR, TS, and TW soils. Additionally, it is noteworthy that in the IR soil, the abundance of plant pathogenic fungi such as *Cladosporium*, *Fusarium*, *Verticillium*, and *Sclerotium* significantly increased.

Based on the functional predictions made using the FUNGuild database for the fungal communities in soil samples (Figure 6D), the results highlight that there was a dominance of Saprotrophs and Pathogens in terms of fungal community functionality in IR and TS soil samples. In the case of TW, Symbiotrophs and Saprotrophs were the main functional groups in the first to the third years. However, in the fifth year, the abundance of Symbiotroph significantly decreased, while the abundance of Pathogen and Saprotroph increased and took over the dominant roles. Additionally, Figure 6E showed that under tea tree cultivation, soil fungal communities were primarily composed of Undefined Saprotrophs (24.24~58.70%), Animal Pathogens (9.52~36.92%), Fungal Parasites (2.94~26.46%), Plant Pathogens (1.26~22.46%), and Ectomycorrhizal fungi (1.34~34.78%). Other functional groups accounted for smaller percentages (<1%). It is noteworthy that in IR, the proportion of Plant Pathogens gradually increased over the first three years, while the abundance of Undefined Saprotrophs initially decreased but then increased. However, TS and TW show the opposite trend.

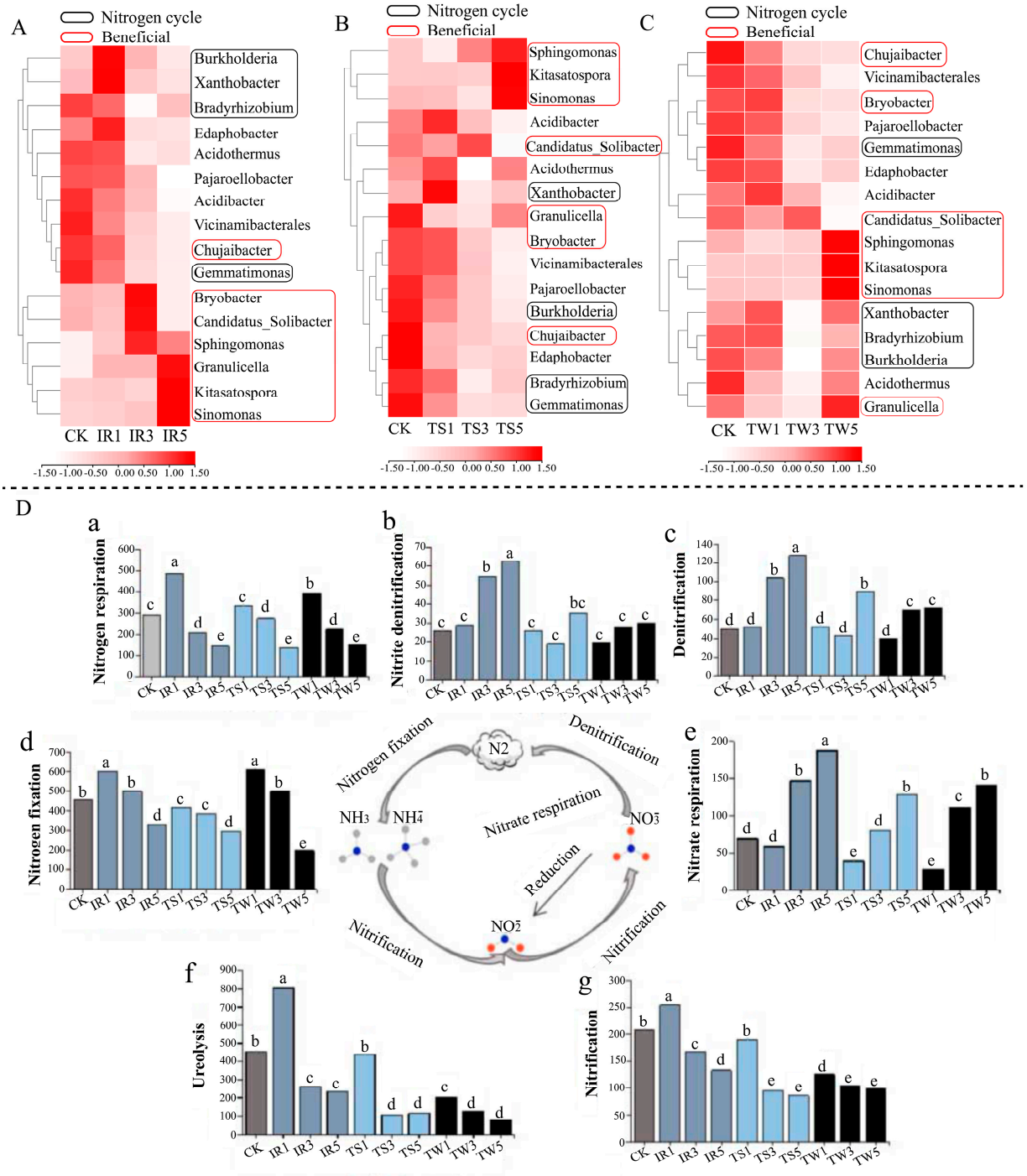

Figure 5. Key differentially abundant bacterial genera (LEfSe, LDA > 3.5) and functional analysis (FAPROTAX) of soil microbial communities among different cultivation years. (**A**) IR, (**B**) TS, and (**C**) TW soils: key differentially abundant bacterial genera. (**D**) Variations in the nitrogen cycling functions of microbial communities among different samples. Different letters indicate significant differences (LSD, $p < 0.05$). The references for the functions of the bacteria circled in the figure can be found in Table S11.

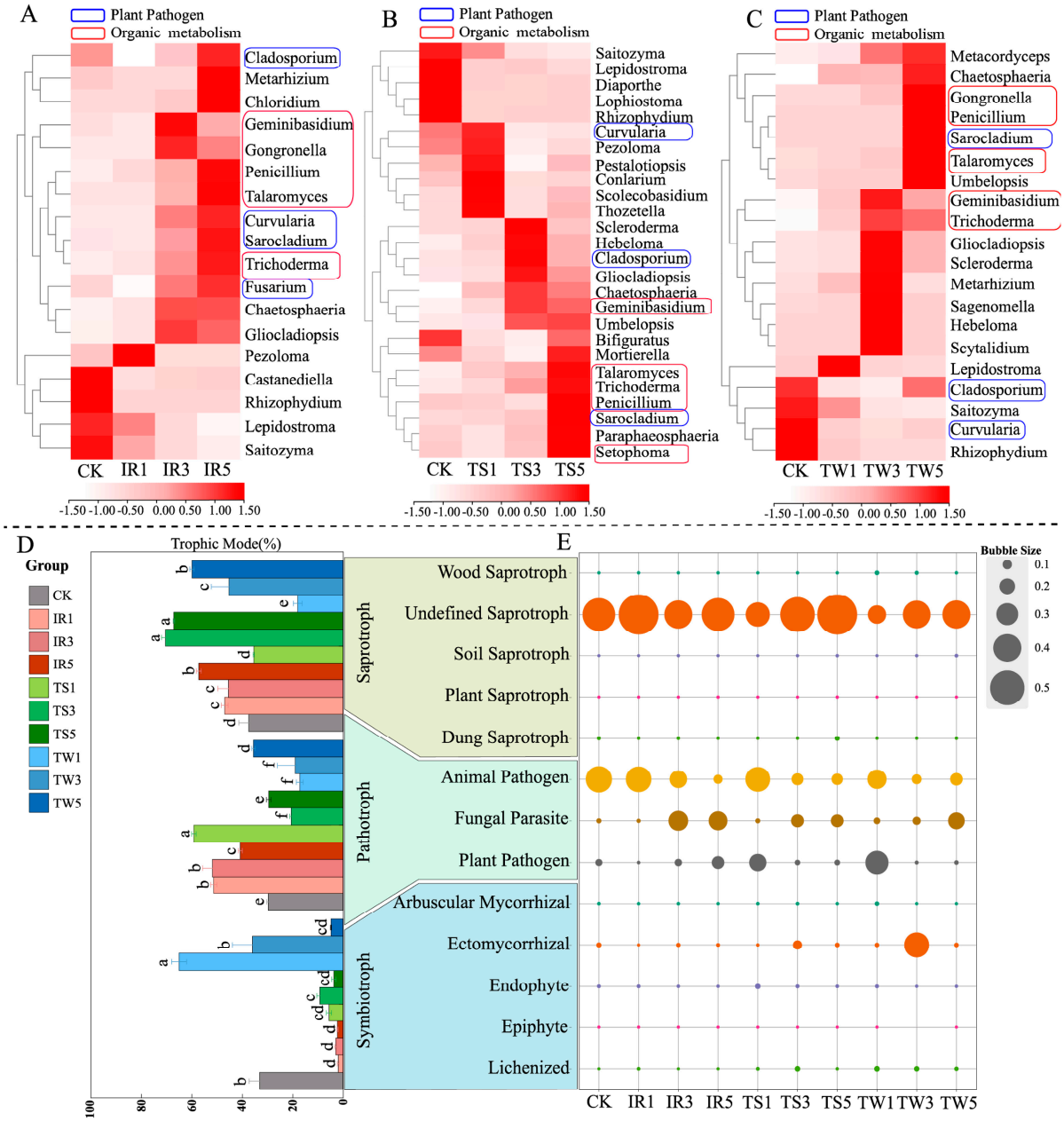

Figure 6. Key differentially abundant fungal genera in the fungal community (LEfSe, LDA > 3.5) and functional analysis (FUNGuild) of soil microbial communities among different cultivation years. The analysis was conducted on three different soil types: (**A**) IR, (**B**) TS, and (**C**) TW soils: key differentially abundant fungal genera. Panel (**D**) presents the analysis of primary trophic mode profiles of fungal communities in different soil samples using FUNGuild. Distinct letters indicate significant differences ($p < 0.05$). Panel (**E**) provides a further breakdown of fungal trophic mode. The references for the functions of the fungi circled in the figure can be found in Table S11.

3.6. Correlation between Soil Microbial Community Structure and Soil Biochemical Properties

In the analysis of soil microbial communities using redundancy analysis (RDA), the results showed that RDA1 and RDA2 explained a total of 84.58% of the variation in soil bacterial communities (Figure 7A) and 61.72% of the variation in soil fungal communities (Figure 7B). The soil community structure under tea tree cultivation was found to be significantly correlated with various environmental factors such as TN, TP, AP, PT, POD, UE, pH, and SOM ($p < 0.05$). An interesting observation from the distribution of soil samples was that as the distance between soil samples and the main trunk of the tea tree

increased, the correlation between environmental factors and the terraced soil microbial community gradually diminished, with the changing trend being IR (red circle) > TS (blue circle) > TW (green circle).

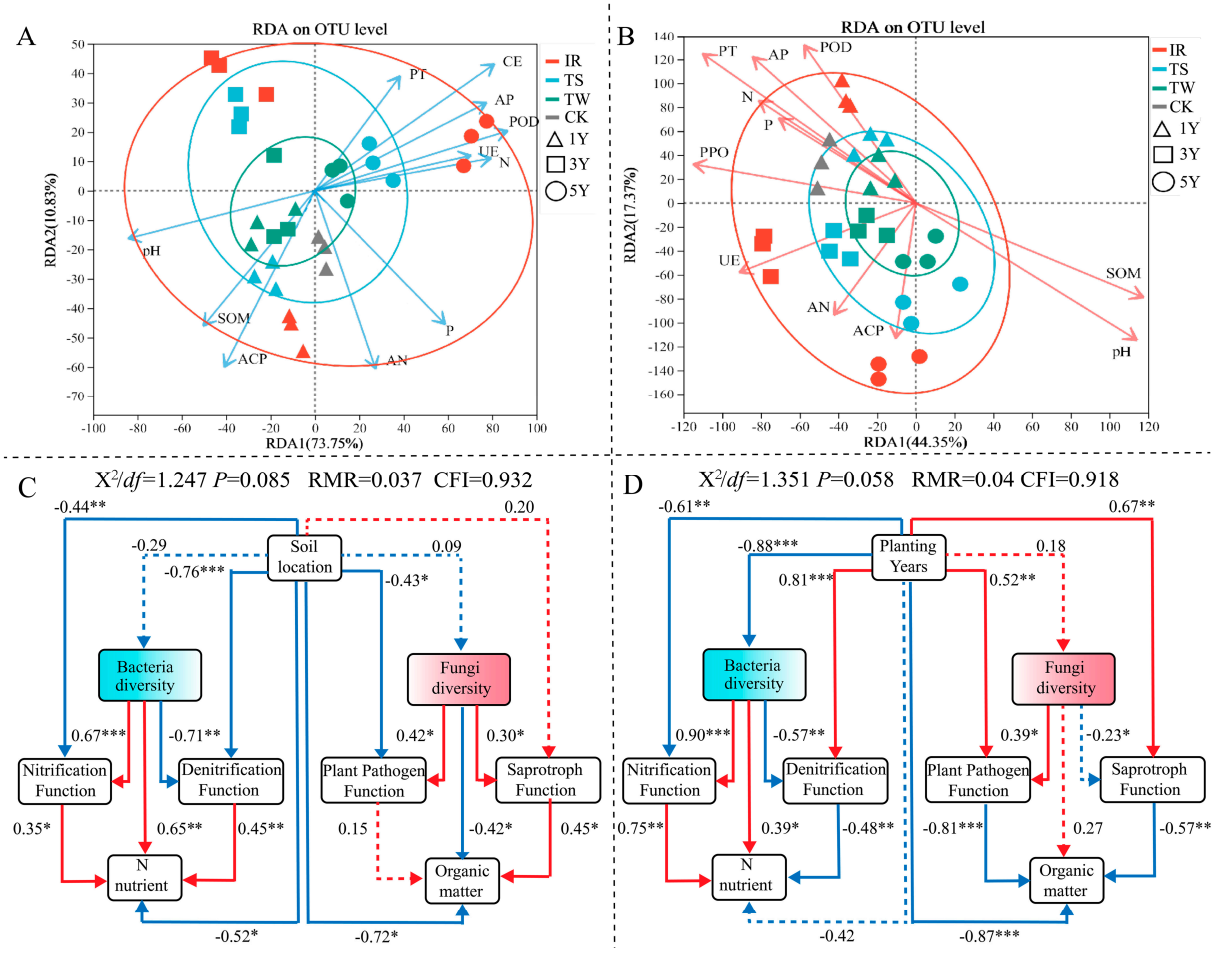

Figure 7. Interrelationship between soil physicochemical factors and microbial communities. RDA analyses were conducted to assess the correlations between soil bacteria (**A**) and fungi (**B**) communities and environmental factors. A structural equation model (SEM) was employed to evaluate the comprehensive impact of distances from tree (**C**) and tree planting years (**D**) on soil nitrogen nutrients and organic matter. The numbers next to the arrows represent path coefficients, indicating the strength of standardized path coefficients. Blue lines represent positive path coefficients, red lines represent negative path coefficients, and dashed lines represent non-significance. The significance levels are as follows: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

The analysis of soil position factors demonstrates that as the distance from tea trees increased (IR–TS–TW) (Figure 7C), both nitrification and denitrification functions declined. On the other hand, plant pathogenic microbes diminished, along with the content of soil organic matter. This indicates that soil closer to the tea trees has higher nutrient levels but, at the same time, it is also more prone to the enrichment of pathogens.

Furthermore, in an analysis when considering the factor of years of tea cultivation (Figure 7D), it was found that as tea cultivation years increased, the soil bacterial community diversity and nitrification function continuously declined, while the denitrification function rose, resulting in a decrease in soil nitrogen nutrients. Additionally, as the years of tea cultivation increased, the proportion of plant pathogenic and saprotrophic functions in the soil continuously rose, leading to a decrease in soil organic matter content.

4. Discussion

4.1. Tea Cultivation Induces Specific Microbial Communities to Accelerate Soil Organic Matter Metabolism

Terraced tea plantations in the mountainous regions of southern China, claimed from uncultivated land, have significant and far-reaching effects on soil microorganisms. Previous studies have observed an increase in soil nutrient content and enzyme activity during the early stages of crop cultivation on uncultivated land [23]. Over the 1–5 years of tea tree cultivation in our study, various physicochemical properties and enzyme activities in the soil, such as AP, AK, CE, and PPO, exhibited varying degrees of increase, accompanied by a continuous decline in soil organic matter content (Figure 2). The results are similar to those of previous studies [24].

To figure out why this is the case, soil microbes were shown to play a pivotal role in the transformation of soil organic matter, hydrolyzing insoluble organic compounds into their soluble forms. Cellulase, mainly produced by soil microorganisms and particularly fungi, aids in the degradation of cellulose and in the metabolism of organic matter, promoting the release of nutrients for plants in the soil [25,26]. During tea tree cultivation, the accelerated degradation and consumption of soil organic matter led to the activation of available nutrients due to the action of cellulase. This process also released polyphenolic polymers found in tea tree litter, providing the necessary materials for the enhanced activity of polyphenol oxidase.

Further analysis of the soil microbial community showed the abundance of Actinobacteria among soil bacteria as cultivation time increased (Figure 4C). Actinobacteria possess the capability to decompose and utilize various complex organic compounds, facilitating the cycling of organic matter [27]. Further examination of key differential bacterial genera in different locations within the tea plantation showed a gradual rise in Actinobacteria phylum genera (Figure 5), including *Sinomonas*, *Granulicella*, *Sphingomonas*, and *Kitasatospora*, with prolonged cultivation time. Previous research has demonstrated the involvement of these genera in promoting organic matter decomposition [28–33]. Additionally, *Kitasatospora* has been shown to enhance plant resistance and exhibit significant resistance to gray mold. *Granulicella* is known for its ability to degrade toxins produced by the plant pathogenic fungus Fusarium, such as Deoxynivalenol (DON) [34,35]. Therefore, the increase in the soil's available nutrients and the activities of cellulase and polyphenol oxidase during tea tree cultivation may be closely related to changes in the microbial community.

Regarding fungi, the abundance of members of the Basidiomycota phylum consistently increased with the length of cultivation in both IR and TS soils. The Basidiomycota phylum plays a crucial role in decomposing plant litter with a high lignin content in the soil [36]. Furthermore, as cultivation time increased, there was a significant increase in key differential fungal genera in different soil locations, including *Trichoderma*, *Penicillium*, and *Talaromyces*. *Talaromyces* have been shown to display resistance effects against plant diseases such as Fusarium head blight, while *Penicillium* and *Trichoderma* have been extensively studied for their functions in decomposing and utilizing organic matter [37–41]. Validation based on FUNGuild predictions confirmed a continuous increase in the proportion of saprotrophic fungi in TS and TW soils, with a trend of initially decreasing and then increasing in IR soil (Figure 6D). When combined with SEM (Figure 7D), it was found that the increasing saprotrophic function of fungi with a prolonged cultivation time had a significant negative impact on soil organic matter. In summary, under tea tree cultivation alone, specific fungal groups that promote the decomposition and utilization of organic matter become enriched, accelerating the depletion of soil organic matter.

4.2. Tea Tree Cultivation Regulates Soil Nitrogen Cycling Functional Bacteria and Reduces Soil Nitrogen Supply Capacity

Nitrogen is a significant nutritional component that influences the quality of substances in tea leaves and is crucial for the growth of tea trees [42]. In our study, we observed varying degrees of decreases in TN, AN, UE, and pH after cultivating tea plants in mountainous

terraced fields (Figure 2). The decline in soil pH is a common occurrence in monoculture tea plantations and has been shown to be closely associated with the release of organic acids from tea plant roots, loss of alkaline ions in the soil, and the preference of the tea plant for absorbing ammonium nitrogen absorption through proton exchange [43]. Furthermore, urease activity reflects the soil's capacity to decompose urea and its decrease further affects nitrogen transformation in the soil [44]. These declines in nitrogen-related biochemical indicators are most pronounced in IR soil, followed by TS and TW soils. Previous research on terrestrial ecosystems has indicated that microbial communities are highly sensitive to changes in artificial nitrogen inputs, thereby regulating soil nitrogen cycling [45,46]. However, the precise mechanisms by which the microbial flora in mountainous ecosystems influences nitrogen transformation during tea plantation renovation has remained unclear.

The results showed that the cultivation of tea trees significantly decreased the diversity of bacterial communities and the abundance of the Proteobacteria in various locations within the terraced fields (Figure 3). Previous studies have demonstrated that nitrogen, due to its osmotic potential and ion toxicity, directly impacts soil microbial communities. It was shown to promote the growth of bacteria that rely on inorganic nitrogen as a nutrient source (such as nitrifying and denitrifying bacteria), but it was also able to inhibit less nitrogen-tolerant genera. These changes directly affect the diversity of soil microbial communities. Bacterial diversity is more sensitive to nitrogen changes compared to fungal diversity and the addition of nitrogen has been shown to reduce bacterial community diversity, while having less of an impact on the fungal community diversity and richness [47,48].

Further analysis revealed that among the key differing bacterial genera, the abundances of *Burkholderia* and *Bradyrhizobium* within the Proteobacteria phylum showed a continuous decline in all three soil types (Figure 4). Similarly, *Gemmatimonas*, belonging to the phylum Gemmatimonadota, exhibited a similar trend. *Burkholderia* has commonly been found in soil, often carrying the *nifH* gene, which is critical for plant nitrogen fixation [49]. *Xanthobacter* belongs to the Proteobacteria phylum and, similarly, possesses nitrogen-fixing capabilities [50]. *Bradyrhizobium*, and *Gemmatimonas* are known to promote nitrogen transformation and nitrogen fixation [51–54]. This indicated that tea plantation has diminished the nitrogen-fixing capabilities of soil microbes. Additionally, an increase in the duration of tea plant cultivation resulted in a reduction in soil bacterial community diversity, indirectly decreasing soil nitrogen supply levels (Figure 7B).

Changes in soil microbial communities inevitably impact their ecological functions [55,56]. Therefore, our study further conducted predictive analyses of soil nitrogen cycling functions (Figure 5D). The proportions of nitrification and nitrogen fixation functions in soils from different locations significantly decreased with an increase in years of tea tree cultivation, while nitrite denitrification, denitrification, and nitrate respiration functions experienced a significant increase. This stimulates ammonia oxidase activity, leading to the conversion of a significant amount of urea into nitrate [57]. Both nitrite denitrification and nitrate respiration are part of the denitrification process that reduces nitrate and nitrite to nitrogen gas, thereby contributing to nitrogen loss in soil [58]. SEM analysis provided additional clarity on these changes (Figure 7B), highlighting a negative impact on nitrification and a positive impact on denitrification. Consequently, the decline in bacterial community diversity, the reduction in nitrification and nitrogen fixation functions, and the increase in denitrification functions observed in soils from various locations all indicate a decrease in soil nitrogen levels in tea plantations under cultivation.

4.3. Tea Cultivation Reshaped the Soil Microbial Community Diversity and Structure in Terraced Tea Plantations

Environmental filtration, as a form of non-biological ecological selection, typically follows geographical patterns and restricts the distribution of organisms. It is considered a key driving factor in the spatial variation of soil microbial composition and diversity [59–63]. Soil microbial communities associated with locust trees were shown to exhibit varying sensitivities and assembly mechanisms in response to changes in distance from the tree [64].

Biological factors also significantly impacted the composition of soil microbial communities, with plant root exudates promoting the growth of specific genera in the surrounding soil [65]. Therefore, apart from changes in soil's physicochemical properties during the transformation of terraced tea plantations, the secretion products from tea tree roots and litter selectively shaped the structure of the rhizosphere microbial community [66–68]. RDA analysis explored the correlations between soil environmental factors and microorganisms, indicating that as the distance from the tea trees increases (from IR to TS and then from TS to TW), the correlation of soil environmental factors on microbial communities gradually weakens (Figure 7A,B). NCM (Figure 4) also revealed that the assembly of microbial communities in soils at different locations is closely correlated to the distance from tea trees, with the impact of tea tree cultivation weakening as the distance increases. Furthermore, overall changes in the biochemical properties and enzyme activities of the three soils exhibited a trend of IR > TS > TW (Figure 4C,D).

In summary, a new ecosystem primarily driven by the growth of the tea tree is gradually forming after they were planted in previously forested wasteland. This transformation has had an impact on the biochemical properties and microbial communities of soils in various locations within mountainous tea plantations (IR, TS, and TW), indicating a spatial distance effect. However, the interactions between plant exudates and soil microorganisms were found to be complex and specific correlations necessitate further exploration.

4.4. Tea Tree Cultivation Increases the Abundance of Pathogenic Fungal Communities in Soil and Raises Plant Disease Risk

The enrichment of soil pathogenic microorganisms after the long-term cultivation of tea plants (more than 10 years) has been identified as one of the obstacles of tea in successive monoculture [69,70]. This study reveals a significant increase in the abundance of key fungal genera, including *Sarocurium*, *Curvularia*, *Cladosporium*, and *Fusarium*, in the fungal flora of the inter-row (IR) soil after tea tree cultivation (Figure 6). Previous research has confirmed that *Curvularia* and *Sarocladium* can commonly be found in soil, parasitizing grass plants and causing root rot, while *Cladosporium* and *Fusarium* have been shown to infect various plants, leading to diseases such as root rot, flower decay, and leaf withering [71–77]. Functional predictions using FUNGuild also support these findings (Figure 6E), indicating that the proportion of plant pathogens in IR soil gradually increases with the duration of tea tree cultivation. Furthermore, the SEM analysis demonstrated that the duration of tea tree cultivation had a significant positive impact on plant pathogens within the soil microbial community, with a higher level of enrichment observed in IR compared to the TS, TW, and CK soils. Therefore, the results suggest that in mountainous terraced fields, tea cultivation leads to a significant increase in the abundance of plant pathogenic fungi in the IR soil.

Changes in soil plant pathogen functionality are regulated by various factors. The accumulation of secondary metabolites such as polyphenols, flavonoids, and alkaloids in soil is one of the causes of the continuous cropping obstacles of tea plants [78,79]. The accumulation of these secondary metabolites exerts direct auto-toxic effects on tea plants and is also able to disrupt the balance of the microflora, indirectly leading to an increase in the abundance of pathogenic microbes in the soil [80]. This study indicates that the adverse factors associated with the increase in the abundance of fungal pathogens due to tea tree cultivation are already evident in the early cultivation period in the IR soil.

5. Conclusions

This study focused on the effects of tea planting on soil micro-ecology in mountainous tea plantations. The results indicate significant changes in the community structure of soil microorganisms after tea tree cultivation. The microbial diversity and community co-occurrence networks in the soil, which were dominated by tea tree growth, were rebalanced, and dominant microflora underwent restructuring. Moreover, the cultivation of the tea tree enriched microflora indicated they were involved in organic matter metabolism,

such as *Sinomonas*, *Kitasatospora*, *Granulicella* (bacteria), *Penicillium*, *Talaromyces*, and *Trichoderma* (fungi). This enrichment resulted in enhanced activities of cellulase and polyphenol oxidase, accelerating the decomposition of organic matter and the release of available P and K in the soil. However, the study observed a decrease in the abundance of nitrifying and nitrogen-fixing bacteria and an increase in denitrifying bacteria, disrupting the soil's nitrogen cycling functions and leading to a decrease in soil nitrogen nutrition levels. The increase in pathogenic microbial abundance in inter-row soil during the early stage of tea tree cultivation was evident. Furthermore, the impact of tea plant cultivation on soil microbial communities and physicochemical properties varied between different locations within the terraced tea plantation, with diminishing effects as the distance from the tea plants increased, demonstrating a spatial distance effect. These findings highlight the importance of considering factors associated with monoculture in tea tree habitats, when transforming uncultivated land into tea plantations in mountainous regions. Strategies such as implementing multi-layer planting of other plants in tea plantations and developing specialized microbial agents for tea trees should be considered to maintain soil health.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/agronomy14030638/s1.

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