

Article

Vegetation-Driven Differentiation of Soil Bacterial and Fungal Diversity: Distinct Edaphic Determinants in *Atractylodes japonica* Cultivation Systems

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Abstract

As key drivers of soil biogeochemical cycles, soil microbial communities play essential roles in maintaining soil fertility, nutrient cycling, and plant growth. In this study, high-throughput sequencing of 16S rRNA and ITS genes was used to investigate the diversity, the composition, and the driving factors of bacterial and fungal communities in bulk soils across four soil groups collected from different vegetation covers (forest soil (FS), soybean field (PGS), and two *Atractylodes japonica* cultivation soils (ALO and ALR)) under identical climatic conditions. The results showed that the bacterial α -diversity remained stable across all the vegetation types, whereas the fungal α -diversity and richness were more sensitive to the vegetation type, with the PGS generally exhibiting lower Shannon and Chao1 indices. The β -diversity analysis revealed significant differences in the microbial community structure among the vegetation types, with a stronger effect on fungi ($R^2 = 0.737$, $p = 0.001$) than on bacteria ($R^2 = 0.493$, $p = 0.001$). At the phylum and genus levels, the fungal communities displayed more pronounced shifts than the bacterial communities, which remained relatively stable. A redundancy analysis indicated that the soil chemical properties significantly shaped the microbial community structure ($p = 0.002$). The microbial communities in the *A. japonica* soils (ALO and ALR) were primarily driven by pH, available phosphorus, and available potassium, while the FS and PGS communities were more strongly influenced by soil organic carbon, total nitrogen, and nitrogen forms (NH_4^+ -N and NO_3^- -N). The Spearman correlation and functional prediction analyses further confirmed that the key soil factors differentially regulated the abundance and ecological functions of the dominant microbial taxa. These findings demonstrate the vegetation-specific assembly of soil microbial communities and highlight the distinct edaphic drivers associated with *A. japonica* cultivation, providing a scientific basis for soil health management and the sustainable cultivation of this medicinal plant.



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Keywords: *Atractylodes japonica*; soil; fungal community; bacterial community; high-throughput sequencing

1. Introduction

Soil microorganisms drive the biogeochemical cycling of the key elements examined in this study. They regulate the transformation and the availability of soil organic carbon

(SOC), nitrogen forms (TN, NH_4^+ -N, NO_3^- -N), phosphorus (TP and AP) and potassium (TK and AK) through extracellular enzyme production, mineralization, solubilization and weathering processes. The soil pH simultaneously acts as a master controller of microbial community composition and is itself modified by microbial metabolism [1–6].

Vegetation type is a major driver of these microbial and edaphic patterns. Different plant species alter litter quality, root exudates and rhizodeposition, selectively recruiting microbial consortia. Fungal communities typically respond more strongly to vegetation change than bacterial communities, while soil pH remains one of the strongest predictors of bacterial assembly [7,8].

A. japonica is an important medicinal herb whose large-scale cultivation in Northeast China has been accompanied by continuous-cropping obstacles (soil-borne diseases, yield decline and quality deterioration). Studies on closely related species have shown that the continuous monoculture of *A. lancea* and *A. macrocephala* consistently alters rhizosphere bacterial and fungal diversity, enriches potential pathogens, reduces beneficial taxa, and is linked to changes in soil pH and available nutrients [9–12]. Autotoxic allelochemicals further exacerbate the microbial imbalance. Regional comparisons also indicate that the rhizosphere microbiome composition can correlate with the medicinal active-ingredient accumulation [13,14].

However, most of the existing work has focused on the rhizosphere soils of related *Atractylodes* species under continuous cropping or different planting years. Comprehensive comparisons of bulk-soil bacterial and fungal communities, together with their linkages to soil chemical properties, across *A. japonica* cultivation systems and contrasting vegetation types (natural forest and conventional cropland) under identical climatic conditions remain limited. It is still unclear (i) how strongly the vegetation type structures the bulk-soil communities relative to the rhizosphere effect within *A. japonica* and (ii) which edaphic factors (pH, available P and K versus organic C and nitrogen forms) dominate in *A. japonica* soils compared with the reference vegetation.

In this study, we therefore characterized the bacterial and fungal communities in the bulk and rhizosphere soils of *A. japonica* and two reference vegetation types (forest and soybean) in the Yichun region of Northeast China. Our specific aims were (1) to quantify the vegetation-driven differences in the α - and β -diversity and community composition under identical climatic conditions; and (2) to identify the primary edaphic factors associated with these patterns, with particular attention to the distinct drivers operating in *A. japonica* cultivation soils. The results provide a baseline for understanding plant–soil–microbe interactions in this medicinal-herb system and for future efforts to mitigate continuous-cropping obstacles.

2. Materials and Methods

2.1. Site Description and Soil Sampling

This study was conducted in Tieli, Yichun, Heilongjiang Province, Northeast China (E 128°15'50.30", N 47°09'19.38") under identical climatic conditions. The design addressed two complementary comparisons: (i) vegetation-type effects on bulk (non-rhizosphere) soil microbial communities (forest soil, FS; soybean field, PGS; and *Atractylodes japonica* bulk soil, ALO), and (ii) the rhizosphere-versus-bulk effect within *A. japonica* (ALO vs. ALR). Rhizosphere soil (ALR) was collected to examine root-associated microbial assembly and was not treated as an independent vegetation type.

Three independent sampling plots (biological replicates, $n = 3$) were established within a single representative field of each soil group. Consequently, vegetation-type differences cannot be fully separated from potential field-specific effects; results are interpreted with this limitation in mind.

In each plot, five soil cores (0–20 cm depth) were collected and mixed to form one composite sample. Bulk soil was taken from root-free areas; ALR was obtained by brushing soil tightly adhering to *A. japonica* roots (≈ 1 mm). After removal of roots, stones and debris, samples were sieved (2 mm) and divided into two portions stored at 4 °C (chemical analyses) and –80 °C (DNA extraction).

Detailed information on soil type, texture, stand composition, fertilization (including manure type and composition), crop rotation and exact sampling dates is provided in Supplementary Materials.

2.2. Soil Physicochemical Parameters Analysis

The soil–water suspension (soil:distilled water = 1:2.5, *w/v*) was homogenized on an orbital shaker for 30 min, followed by 30 min of sedimentation. Subsequently, the supernatant was collected and soil pH was determined with a calibrated pH meter [15]. Soil organic carbon and total nitrogen (TN) contents were determined by elemental analyzer [16] (Elementar, Langenselbold, Germany). The concentrations of NO_3^- -N and NH_4^+ -N were determined by phenol–disulfuric acid colorimetry and indigo phenol blue colorimetry [17]. Soil total phosphorus (TP) was measured via a standard colorimetric method after alkaline digestion with NaOH. For available phosphorus (AP), samples were first extracted using a 0.5 M sodium bicarbonate solution and then analyzed through colorimetric detection [18]. The soil total potassium (TK) was extracted using the sodium hydroxide (NaOH) fusion method, while the available potassium (AK) was obtained by NH_4OAc extraction. Both TK and AK concentrations were determined through atomic absorption spectrophotometry. All soil chemical properties were measured with three independent replicates per sample.

2.3. DNA Extraction, PCR Amplification, and MiSeq Sequencing

DNA was extracted from both bulk and ALR samples (1 g per sample) using the MolPure® Soil DNA Kit (Yeasen Biotechnology (Shanghai) Co., Ltd., Shanghai, China) according to the manufacturer's instructions. Three biological replicates were prepared for each sample type to ensure reliability, and the extracted DNA was then used for microbial community profiling. DNA quality assessment included dual verification through UV spectrophotometry (NanoDrop 1000, Thermo Fisher Scientific, Wilmington, DE, USA) and electrophoretic evaluation in 1% (*w/v*) agarose gels. Bacterial 16S rRNA genes were amplified using primer pair 341F (5'-CCTAYGGGRBGCASCAG-3') and 806R (5'-GGACTACNNGGTATCTAAT-3'), whereas fungal ITS regions were targeted with primers ITS1F (5'-CTTGGTCATTAGAGTAA-3') and ITS2R (5'-GCTGCGTTCTTCATCGATGC-3'). Three independent PCR reactions (20 μL each) were prepared to ensure reproducibility. Each reaction included the following components: 10 ng of DNA template, 0.4 μL of FastPfu DNA polymerase, 0.8 μL of each primer (5 μM concentration), 2 μL of a 2.5 mM dNTP mixture, and 4 μL of 5 $\times$ FastPfu reaction buffer. The PCR protocol began with an initial step to separate DNA strands at 95 °C for 5 min. This was followed by 30 repeated cycles, each involving a 30 s heating phase at 95 °C to further unwind the DNA, 55 °C for 30 s (annealing), and 72 °C for 45 s (extension); followed by final elongation at 72 °C for 10 min. PCR amplicons were fluorometrically quantified using the QuantiFluor™-ST system (Promega, Madison, WI, USA) and purified with the AxyPrep DNA Gel Extraction Kit (Axygen Scientific, Union, CA, USA) according to manufacturer specifications. Paired-end sequencing (2 $\times$ 300 bp) was subsequently performed on the Illumina MiSeq platform through commercial services provided by Majorbio BioPharm Technology Co., Ltd. (Shanghai, China).

2.4. Analysis of Sequencing Data

Raw sequencing data were subjected to quality control processing using Trimmomatic (V 0.33) to obtain clean paired-end reads. Subsequently, overlapping paired-end sequences were assembled into full-length fragments through FLASH (V 1.2.11) based on read overlap relationships, generating preliminary merged sequences. In this study, samples were differentiated by their unique barcode and primer sequences. The Mothur software (V 1.35.1) was then applied to analyze and classify the targeted DNA regions. DADA2 within QIIME2 (v2023.5) was used to remove chimeras [19] and form ASV tables. The RDP classification Bayesian algorithm was used to classify and analyze the ASV representative sequences with a confidence threshold of 0.7 [20] and compared with Sliva1 (version 38.1) bacterial database and Unite (version 8.2) fungal database. The sequences obtained from this study were deposited into the NCBI database under the project number PRJNA1235941 (Table S1).

2.5. Biological Information Analysis

Soil chemical properties and microbial α -diversity indices (Shannon and Chao1) were compared among the four soil groups (FS, PGS, ALO, ALR). Prior to analysis, data normality was assessed by Shapiro–Wilk test and homogeneity of variances by Levene’s test. When assumptions were met, one-way analysis of variance (ANOVA) followed by Tukey’s HSD post-hoc test was applied. When assumptions were violated, the non-parametric Kruskal–Wallis test followed by Dunn’s test with Benjamini–Hochberg false-discovery-rate correction was used.

Given the limited number of biological replicates ($n = 3$ per soil group), formal tests of normality (e.g., Shapiro–Wilk) have low statistical power. Therefore, both parametric (one-way ANOVA) and non-parametric (Kruskal–Wallis) approaches were applied for univariate comparisons of soil chemical properties and α -diversity indices [21]; results were considered consistent only when both methods yielded congruent conclusions. Pearson and Spearman correlation analyses between microbial indices/taxa and soil variables were performed for exploratory purposes only. With $n = 3$ –4, correlation coefficients are statistically unstable, and p -values should not be interpreted as robust evidence of association. These correlations are presented as descriptive patterns and are not used for strong inference. PERMANOVA (999 permutations) was used to test differences in community structure; while this method is more robust to small sample sizes than parametric multivariate tests, the resulting R^2 values are reported with appropriate caution regarding generalizability.

All statistical analyses were performed in R (v4.3.1) unless otherwise stated. All figures were generated with ggplot2 (v3.4.x) and “vegan” packages. Principal coordinate analysis (PCoA) based on Bray–Curtis was performed at a 97% similarity level to analyze the similarity between samples, reflecting their differences and spatial separation. Taxonomic groups with significant abundance differences were identified using the non-parametric Kruskal–Wallis test and rank tests, with species exhibiting an LDA value > 2.0 and a p -value < 0.05 defined as differentially abundant taxa [22]. One-way ANOVA of soil physical and chemical characteristics was performed using SPSS software (version 22.0). Differences between groups were considered significant when the probability value (p) was less than 0.05. Differences in soil microbial communities were analyzed using a statistical tool (LEfSe) that evaluates microbial groups across taxonomic levels from broad categories (phylum) to specific ones (genus). Key microbial groups showing notable variations were identified by applying a threshold value to focus on biologically meaningful results. Constrained ordination was used to examine relationships between soil physicochemical properties and microbial community structure. Bacterial communities were analyzed by redundancy analysis (RDA) and fungal communities by canonical correspondence analysis (CCA) on Hellinger-transformed relative abundance data using the vegan package in R.

The significance of the overall model and of individual constrained axes was tested with 999 permutations. The significance of individual environmental variables was assessed with envfit (999 permutations). Two statistical approaches were applied to assess the links between soil properties and microbial communities. First, the Mantel method evaluated overall associations between microbial composition and environmental factors. Second, Spearman analysis identified specific relationships between individual microbial groups and soil characteristics [23].

Bacterial functional potentials were predicted using FAPROTAX (Functional Annotation of Prokaryotic Taxa, version 1.2.4) based on the taxonomy assignments against the SILVA 138.1 database. Only functions with at least one contributing taxon were retained. Fungal functional guilds were predicted using FUNGuild (version 1.2) against the UNITE database (version 8.2). Assignments were filtered to retain only those with confidence rankings of “Highly Probable” or “Probable”; taxa assigned as “Possible” or unassigned were excluded from subsequent analyses. The relative abundances of predicted functional groups were then correlated with soil physicochemical properties using Spearman’s rank correlation.

3. Results

3.1. Soil Chemical Properties

A comparison of the soil properties between the ALO and the ALR revealed significant variations across most of the measured parameters (Figure 1). The soil pH ($p = 0.012$), SOC ($p = 0.008$), and AK ($p = 0.019$) were significantly higher in the ALO than in the ALR, whereas TN ($p = 0.023$) and NO_3^- -N ($p = 0.007$) were significantly higher in the ALR. Additionally, TP and NH_4^+ -N levels in ALR were notably higher than those in the ALO ($p < 0.05$), while no significant differences were observed for AP and TK between the two soils (Figure 1), as detailed in Table S2.

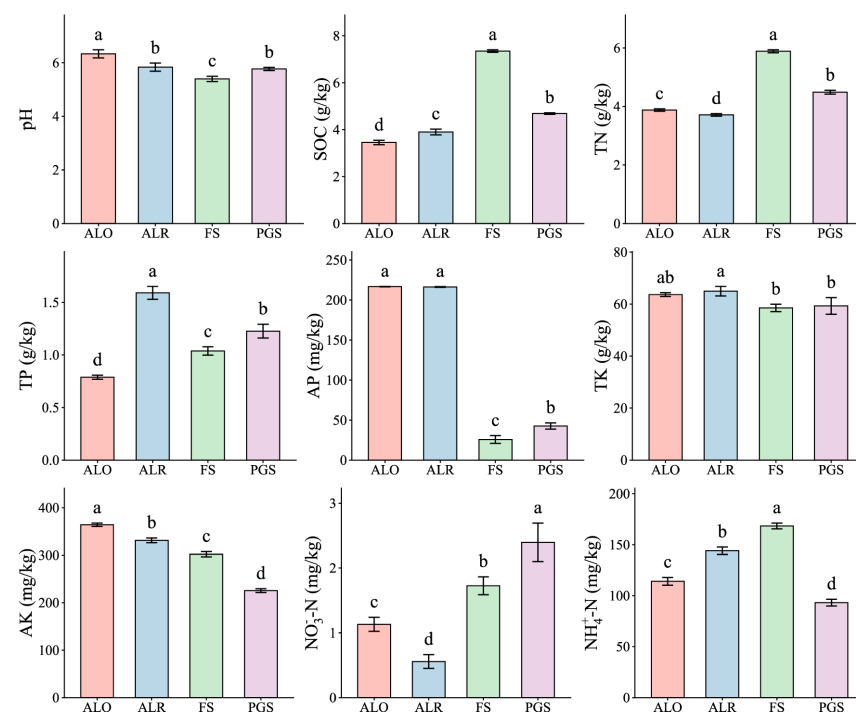


Figure 1. Chemical characteristics of different soils under identical environmental conditions. Bar charts illustrate the levels of soil pH, SOC, TN, TP, AP, TK, AK, NO_3^- -N, and NH_4^+ -N across the four soil groups (ALO, ALR, FS, and PGS). Different lowercase letters above the bars indicate statistically significant differences among the soil groups based on one-way ANOVA followed by a post-hoc test ($p < 0.05$).

3.2. Diversity Indices (α and β) Under Different Vegetation Cover Types

Under identical environmental conditions, the α -diversity analysis (Chao1 richness and Shannon diversity index) was compared across the four soil groups (FS, PGS, ALO, ALR). For the bacterial communities, no significant differences were observed in either Shannon diversity index or Chao1 richness among the four soil groups ($p > 0.05$; Figure 2A,B). This indicates that the bacterial α -diversity and richness remained stable across the different vegetation cover types. For the fungal communities, significant differences were detected in both the Shannon diversity and Chao1 richness indices ($p < 0.05$; Figure 2A,B). The PGS showed the lowest fungal diversity and richness, significantly lower than the FS ($p < 0.05$). The ALR showed a significantly higher Shannon diversity than the PGS ($p < 0.05$) and was statistically similar to the FS and the ALO. No significant differences were observed between the ALO and the ALR for either index. Overall, the fungal α -diversity was more sensitive to the different soil groups than the bacterial α -diversity, which remained stable across all four groups ($p > 0.05$). Overall, the differences among the four soil groups were more pronounced for the fungal α -diversity than for the bacterial α -diversity. The ALR and the ALO generally showed comparable or higher fungal diversity/richness relative to the PGS, with no significant differences between the ALR and the ALO across all the measured parameters.

The Pearson correlation analysis revealed distinct relationships between the soil microbial α -diversity and the key soil properties across the four soil groups (Table 1). For fungal communities, the species richness (Chao1 index) showed a significant positive correlation with ammonium nitrogen ($\text{NH}_4^+\text{-N}$) concentration ($r = 0.728$, $p < 0.05$). In contrast, the fungal Shannon diversity index exhibited a significant negative correlation with TP ($r = -0.756$, $p < 0.05$) and a significant positive correlation with AK ($r = 0.730$, $p < 0.05$). For bacterial communities, the Chao1 richness index was significantly and positively correlated with soil pH ($r = 0.766$, $p < 0.05$), AP ($r = 0.686$, $p < 0.05$), and TK ($r = 0.704$, $p < 0.05$). The bacterial Shannon diversity index was significantly positively correlated only with the soil pH ($r = 0.698$, $p < 0.05$). Additionally, in a comparison between the root-associated and non-root-associated soils of *A. japonica*, TK was the only soil property that showed a significant positive correlation with the fungal species richness (Chao1 index) ($p < 0.05$), suggesting specific measures of microbial composition show strong ties to nutrient levels and soil chemistry (Table 1). Additionally, in a comparison between the root-associated and non-root soils of *A. japonica*, TK was the only soil property that showed a significant positive correlation with the fungal species richness (Chao1 index) ($r = 0.862$, $p < 0.05$; Table 2).

A PCoA based on the Bray–Curtis distance was performed to evaluate the β -diversity patterns of the soil microbial communities across the four soil groups (FS, PGS, ALO, ALR). For the bacterial communities, the β -diversity analysis (PERMANOVA) revealed significant differences in the community composition among the four treatments ($R^2 = 0.493$, $p = 0.001$; Figure 3A). The bacterial communities in the ALO and the ALR soils clustered relatively closer to each other, while both showed clear separation from the FS and PGS groups. For the fungal communities, a stronger treatment effect was observed ($R^2 = 0.737$, $p = 0.001$; Figure 3B). The fungal communities in the ALO and ALR soils were more similar to each other but distinctly separated from those in the FS and PGS soils. The separation between the fungal communities of the different vegetation types was more pronounced than that of the bacterial communities. Overall, the vegetation cover type exerted a significant influence on the structure of both the bacterial and fungal communities in the bulk soils, with a stronger structuring effect on fungi than on bacteria.

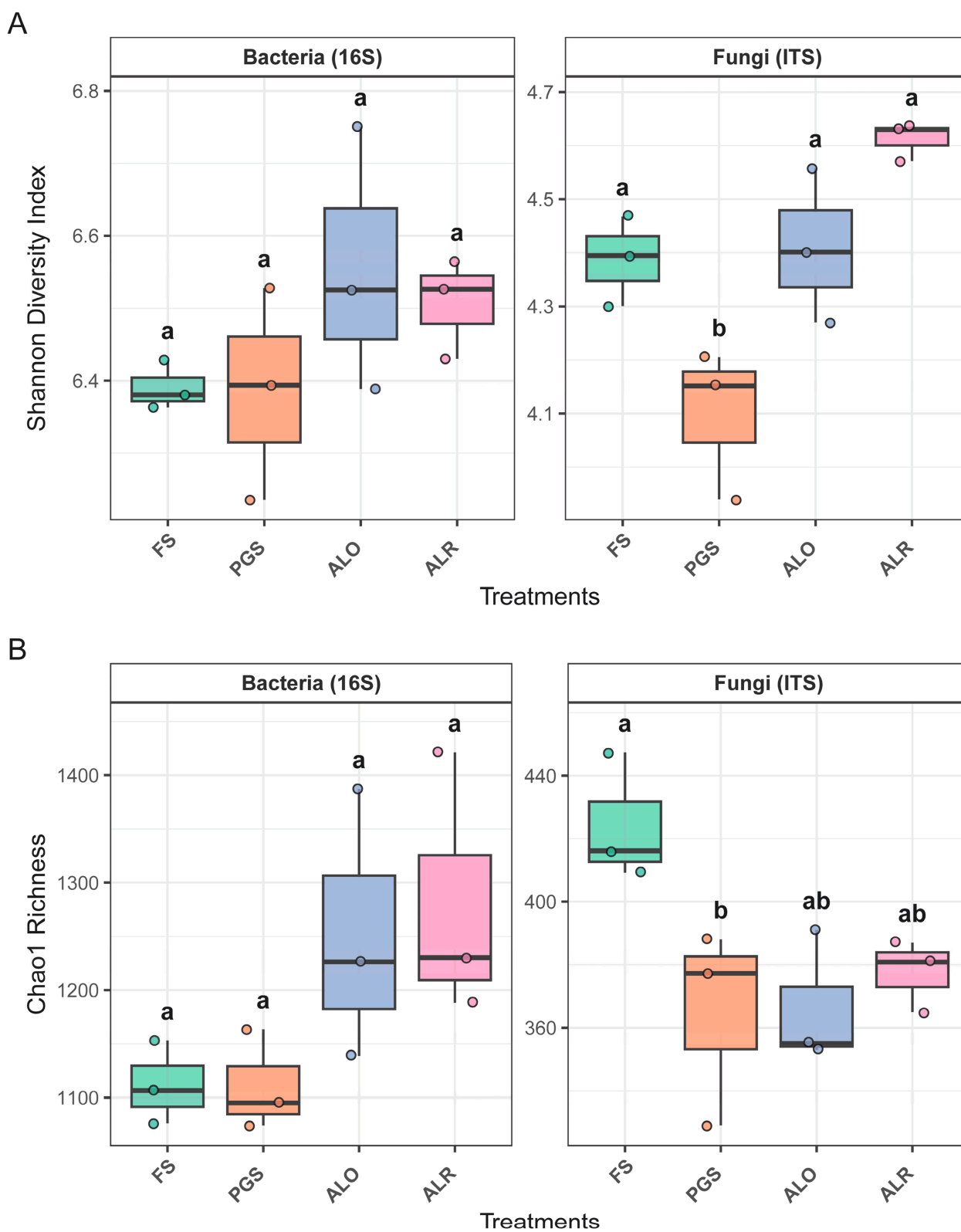


Figure 2. Comparative analysis of microbial α -diversity indices across the four soil groups: (A) Shannon index; (B) Chao1 richness. Left panels: bacteria; right panels: fungi. The lowercase letter indicated the one-way anova test at $p < 0.05$ level.

Table 1. Pearson's rank correlations between the soil bacterial and fungal diversity indices and soil physicochemical parameters.

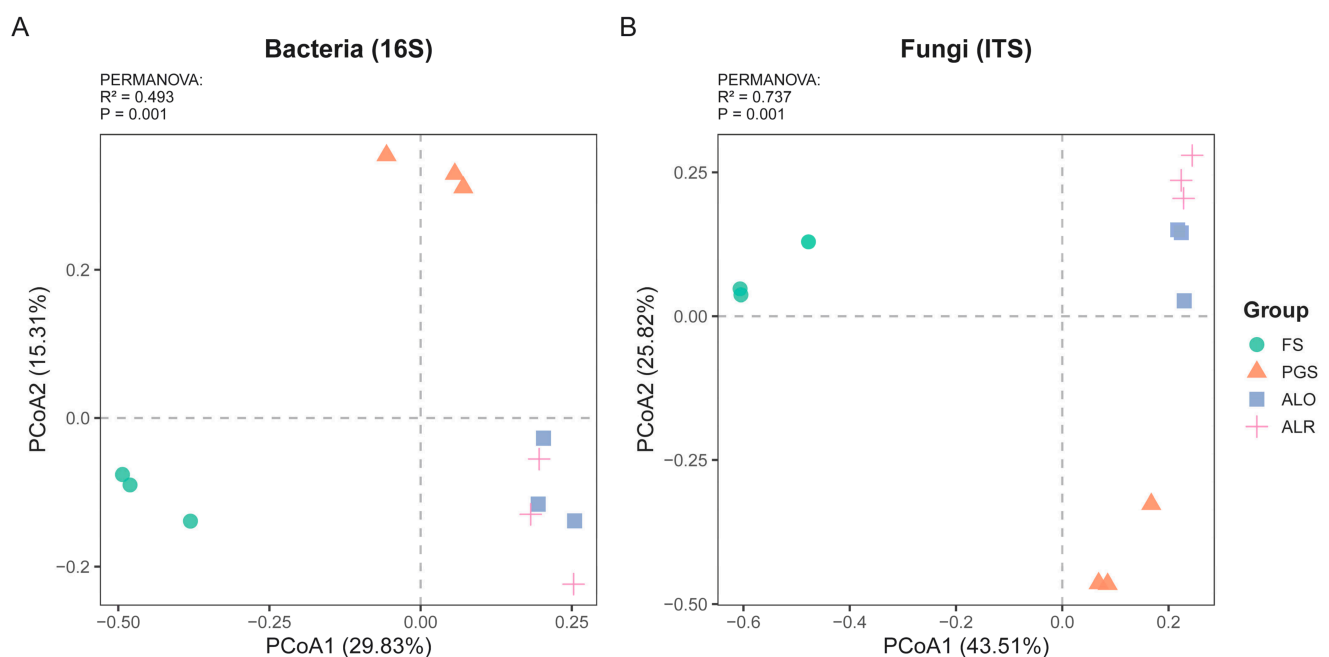
	pH	SOC	TP	AP	TN	NO ₃ ⁻ -N	NH ₄ ⁺ -N	TK	AK
Fungi Chao1	−0.174	0.625	−0.289	−0.160	0.627	0.032	0.728 *	0.071	0.369
Fungi Shannon	0.534	−0.110	−0.756 *	0.600	−0.112	−0.398	0.228	0.657	0.730 *
Bacteria Chao1	0.766 *	−0.517	−0.501	0.686 *	−0.503	−0.510	−0.362	0.704 *	0.403
Bacteria Shannon	0.698 *	−0.558	−0.361	0.598	−0.540	−0.560	−0.505	0.647	0.199

Notes: * 0.05 (one-tailed).

Table 2. Pearson's rank correlations between the relative abundances of dominant *A. japonica* rhizosphere and non-rhizosphere bacterial taxa and soil physicochemical parameters.

	pH	SOC	TP	AP	TN	NO ₃ ⁻ -N	NH ₄ ⁺ -N	TK	AK
Fungi Chao1	−0.469	0.672	0.544	−0.504	−0.527	−0.312	0.442	0.862 *	−0.510
Fungi Shannon	−0.361	0.653	0.633	−0.523	−0.491	−0.475	0.566	0.470	−0.683
Bacteria Chao1	0.222	−0.010	0.035	−0.612	0.044	0.176	−0.116	0.031	0.019
Bacteria Shannon	0.482	−0.184	−0.202	−0.251	0.316	0.347	−0.288	−0.132	0.142

Notes: * 0.05 (one-tailed).

**Figure 3.** PCoA integrating soil physicochemical parameters for (A) bacterial communities and (B) fungal communities.

3.3. Composition of Soil Microbial Communities at the Phylum Under Different Vegetation Types

The bacterial and fungal community composition at the phylum level varied across the four soil groups (FS, PGS, ALO, and ALR) (Figure 4). The bacterial communities (16S rRNA) were dominated by the following phyla (in decreasing order of average relative abundance): Acidobacteriota (18.3–35.9%), Proteobacteria (14.4–30.3%), Chloroflexi (8.6–23.9%), Actinobacteriota (8.3–20.6%), and Verrucomicrobiota (0.9–32.4%). Other phyla with lower abundances included Gemmatimonadota, Bacteroidota, Myxococcota, and Patescibacteria. Although the relative abundances of the dominant phyla showed some fluctuations among the treatments (e.g., higher Acidobacteriota in the FS and Proteobacteria in the ALR), no statistically significant differences were detected among the four soil groups ($p > 0.05$; Figure 4A).

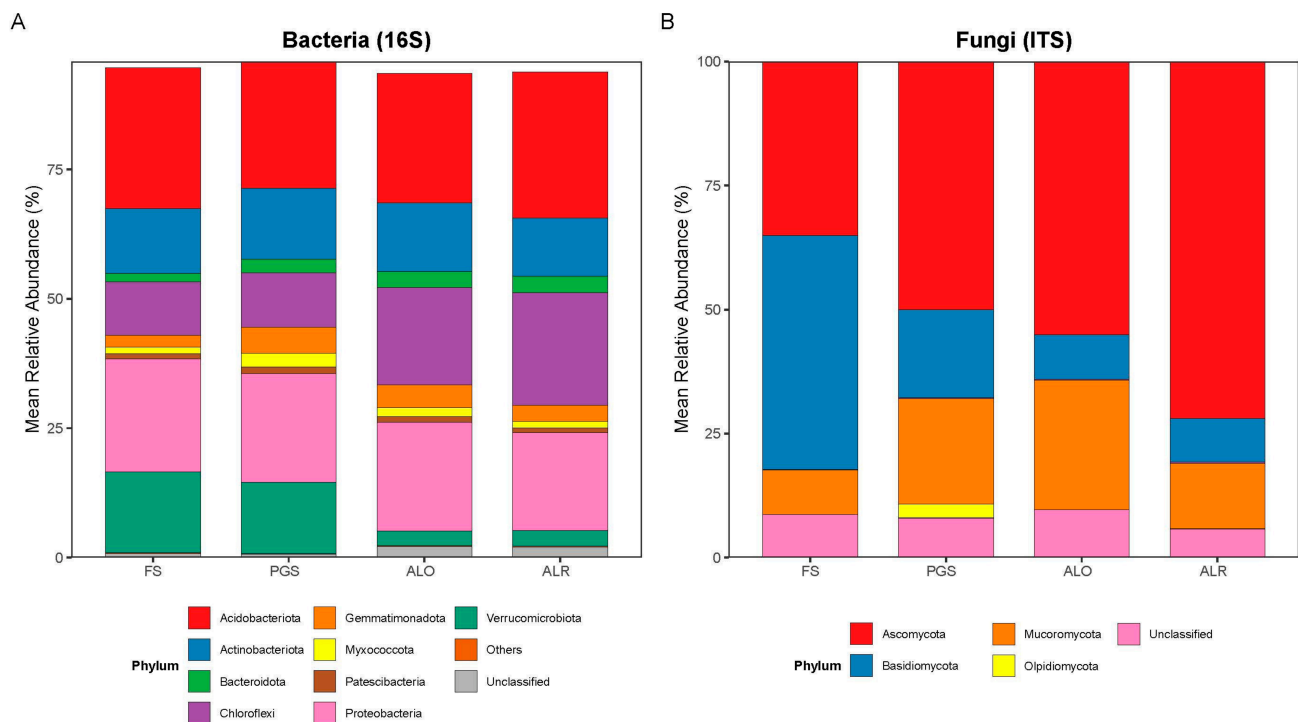


Figure 4. Bacterial (A) and fungal (B) phylum-level communities across the four soil groups.

The fungal communities (ITS) were primarily composed of Ascomycota, Basidiomycota, and Mucoromycota. Ascomycota was the most dominant phylum in all vegetations, particularly in the ALR. Basidiomycota showed higher relative abundance in the FS soil, while Mucoromycota was markedly enriched in the PGS soil and to a lesser extent in the ALO soil. Several low-abundance phyla (e.g., Chytridiomycota, Olpidiomyota) were also detected. Overall, the fungal community composition at the phylum level exhibited more pronounced shifts among the four soil groups compared to the bacterial communities (Figure 4B).

3.4. Indicator Species

A linear discriminant analysis effect size (LEfSe) was used to identify taxa that were significantly enriched in each soil group (LDA score > 2.0, FDR-adjusted $p < 0.05$; Figure 5). For the bacterial communities, the numbers of biomarkers were as follows: FS (6), ALO (13), PGS (16) and ALR (21). The highest number was observed in the ALR. The key high-effect-size biomarkers (LDA > 4.2) included *Pseudomonadaceae*, *Sphingomonadales*, and *Ktedonobacterales*. For the fungal communities, the differentiation was more pronounced: FS (36), PGS (36), ALO (21) and ALR (42). The ALR again showed the largest number of biomarkers. The prominent high-effect-size fungal biomarkers (LDA > 3.0) included *Diversisporales*, *Rhizophlyctidales*, *Agaricostilbomycetes*, and *Lecanoromycetes*. These results indicate that the different soil groups, particularly the ALR and the PGS, were associated with distinct sets of indicator taxa, with fungi showing stronger group-specific enrichment patterns than bacteria.

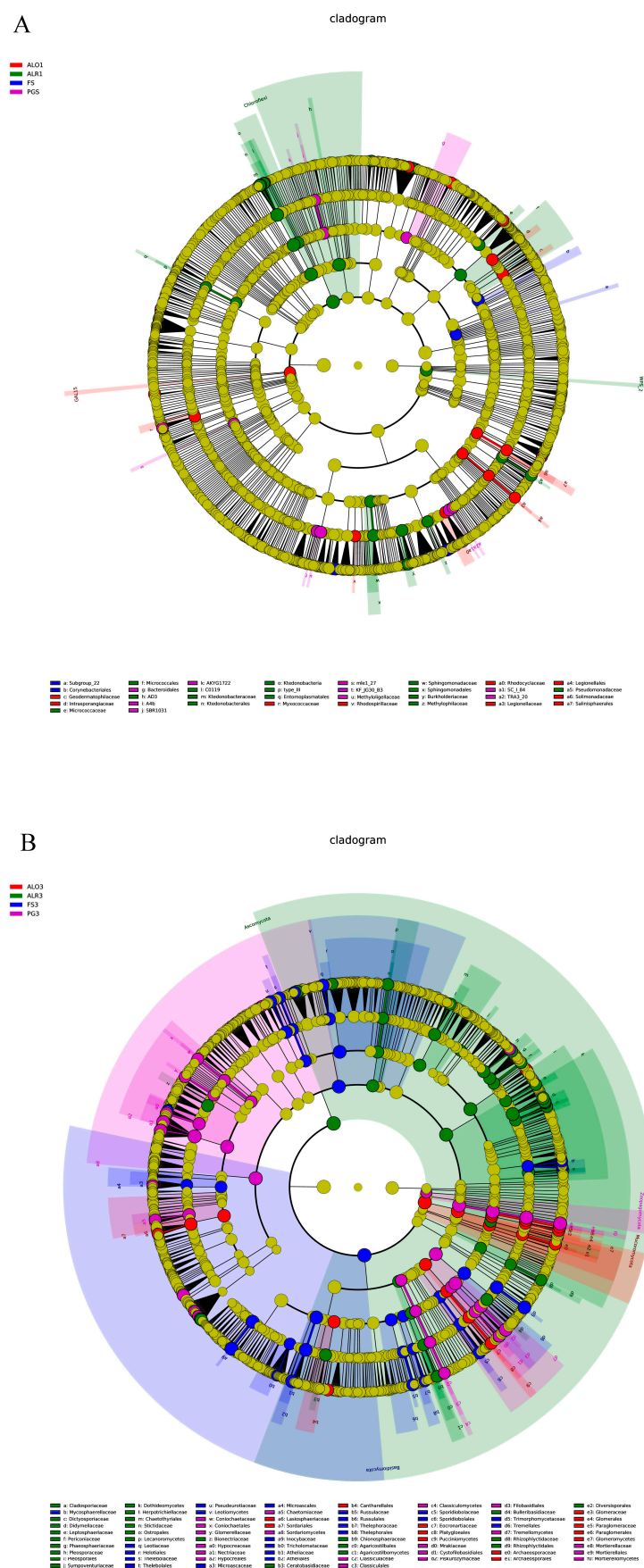


Figure 5. LefSe cladograms showing differentially abundant bacterial (A) and fungal (B) taxa among the four soil groups (LDA score > 2.0, FDR-adjusted $p < 0.05$). Circles represent phylogenetic levels from phylum to genus; the outermost labels indicate the most discriminative taxa.

3.5. Relationships Between Soil Physicochemical Properties and Microbial Community Structure

A redundancy analysis (RDA) for bacterial communities and a canonical correspondence analysis (CCA) for fungal communities were performed to explore the relationships between the soil physicochemical properties and the community structure (Figure 6). For the bacterial communities, the first two RDA axes together explained 27.49% of the total variation (RDA1: 14.57%, RDA2: 12.92%). The overall RDA model was significant (permutation test, $p = 0.002$), with RDA1 being highly significant ($p = 0.001$). The FS samples were primarily associated with TN, SOC and NO_3^- -N; the PGS samples with NH_4^+ -N and TP; the ALO and ALR samples with pH, AP, AK and TK. For the fungal communities, the first two CCA axes explained 46.48% of the total variation (CCA1: 28.1%, CCA2: 18.38%). The overall CCA model was significant ($p = 0.002$). The FS samples were closely related to SOC, TN and NH_4^+ -N; the PGS samples to NO_3^- -N and TP; the ALO and ALR samples to pH, AP, AK and TK. These results indicate that the different soil groups were associated with distinct sets of edaphic variables, with pH, AP and AK emerging as the main factors linked to the *A. japonica* soils (ALO and ALR).

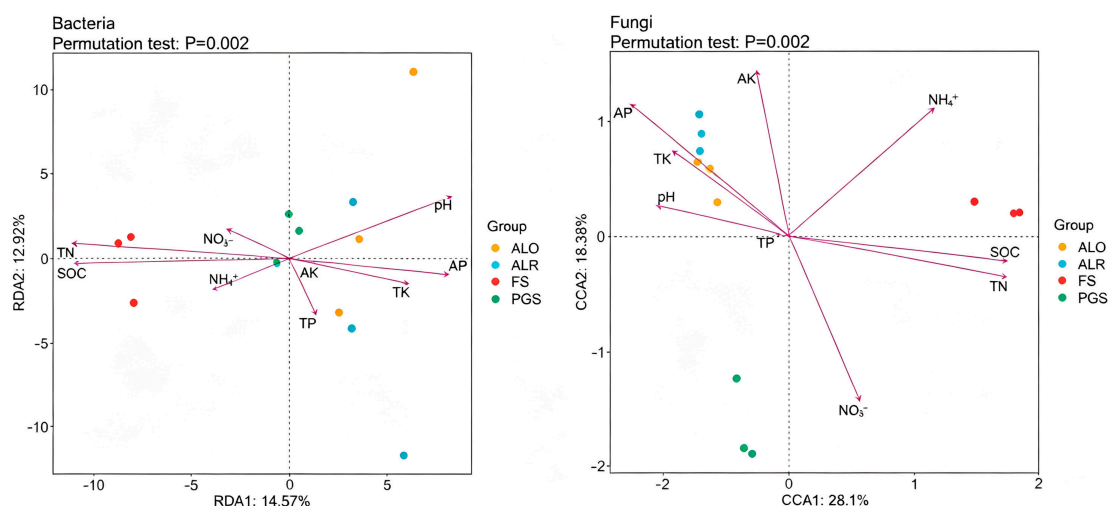


Figure 6. RDA of bacterial communities (left) and CCA of fungal communities (right) showing the relationships between soil physicochemical properties and microbial community structure under different vegetation cover types.

A Spearman correlation analysis was performed to evaluate the relationships between the soil physicochemical properties and the relative abundances of the dominant bacterial and fungal taxa at the phylum and genus levels (Figures 7 and 8). At the phylum level (Figure 7), Chloroflexi was significantly influenced by multiple soil factors, showing negative correlations with SOC, TN, and NO_3^- -N ($p < 0.05$ or $p < 0.01$), and positive correlations with TK (highly significant), AK, AP, and pH. Acidobacteriota and Proteobacteria also exhibited several significant correlations with soil nutrients and pH. Verrucomicrobiota and Bacteroidota displayed notable positive or negative associations with specific parameters such as TP and NH_4^+ -N. The three dominant phyla responded differently to the soil properties. Ascomycota showed significant negative correlations with TN and SOC and positive correlations with AP and TK. Basidiomycota was significantly positively correlated with SOC and TN but negatively correlated with AP and pH. Mucoromycota exhibited a significant positive correlation with pH and AP and negative correlations with SOC and NH_4^+ -N.

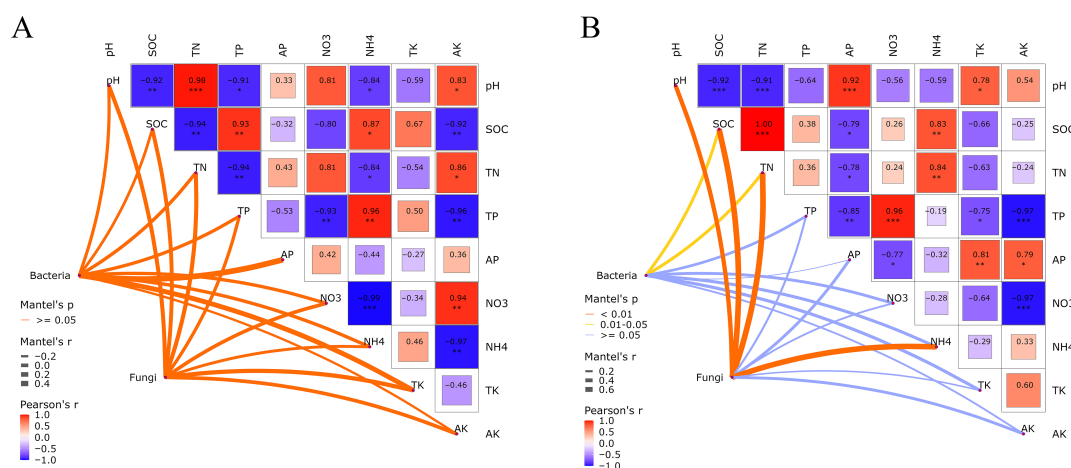


Figure 7. Mantel's test analyses (A) between *A. japonica* soil and different vegetation types of original soil and (B) between physicochemical properties and bacterial and fungal communities (genus level). *, ** and *** indicated significant correlation at 0.05, 0.01 and 0.001, respectively.

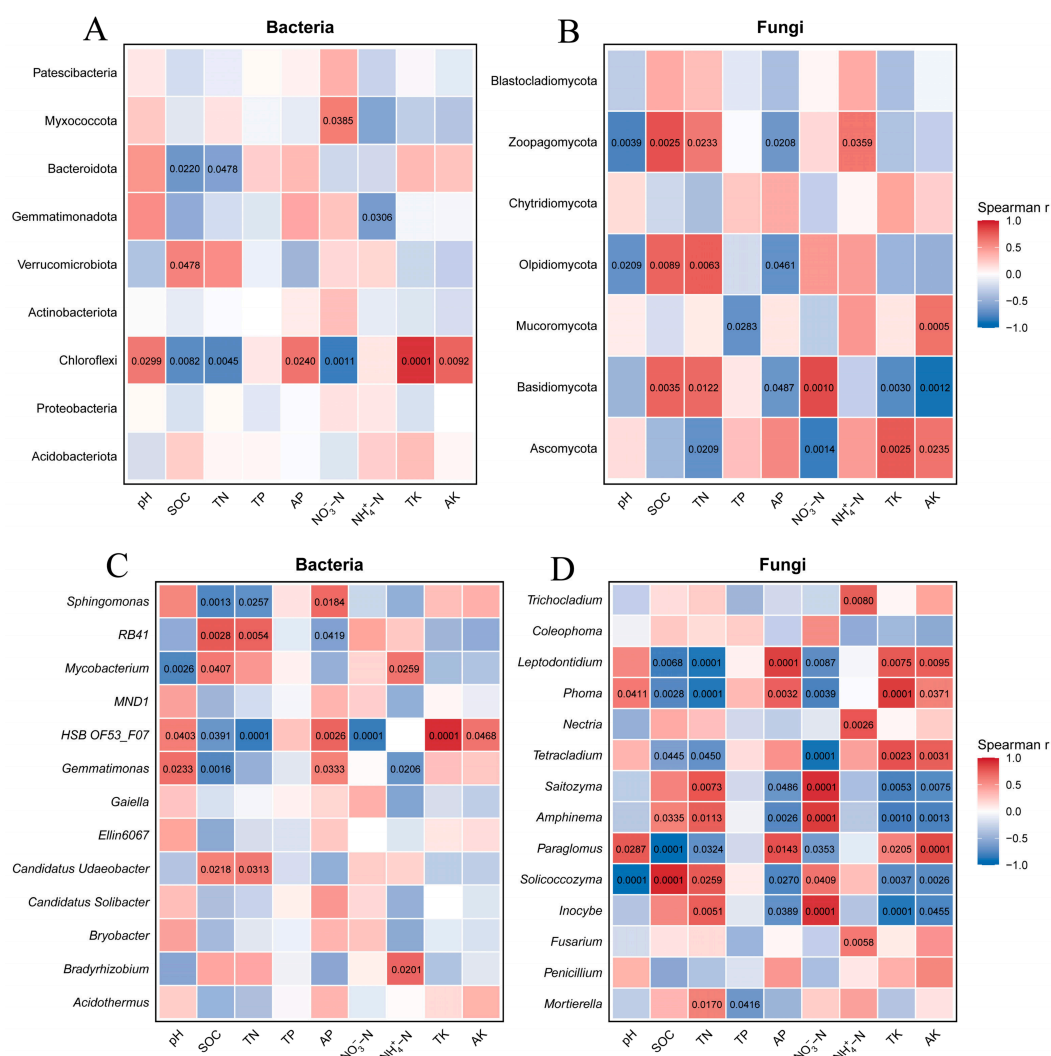


Figure 8. Correlation heatmap between soil chemical properties and bacterial (A,C) and fungal (B,D) communities at phylum (A,B) and genus (C,D) levels in *A. japonica* bulk and rhizosphere soils. Numbers in the heatmap indicate Spearman correlation coefficients, with exact p-values shown for significant correlations ($p < 0.05$).

At the genus level (Figure 8), more specific and stronger correlations were observed. Bacterial genera such as HSB_OF53_F07, Gemmatimonas, and RB41 showed highly significant positive correlations with TK and AK, while Candidatus Udaeobacter and Acidothermus were more associated with certain nutrient conditions in the FS soil. Fungal genera including Solicoccozyma, Inocybe, Saitozyma, and Phoma displayed strong and significant correlations with multiple soil factors (particularly pH, SOC, TN, and available nutrients), highlighting genus-specific responses to vegetation-driven soil chemistry changes.

These results indicate that the soil physicochemical properties, especially pH, nitrogen forms, SOC, and potassium availability, are the key drivers shaping the abundance of specific microbial taxa, with fungal taxa generally showing more diverse and stronger correlations than bacterial taxa.

3.6. Correlations Between Soil Physicochemical Properties and Predicted Microbial Functions

To explore the relationships between the soil properties and the microbial ecological functions, a Spearman correlation analysis was conducted between the soil physicochemical parameters and the relative abundances of the predicted functional groups in the bacterial and fungal communities (Figure 9).

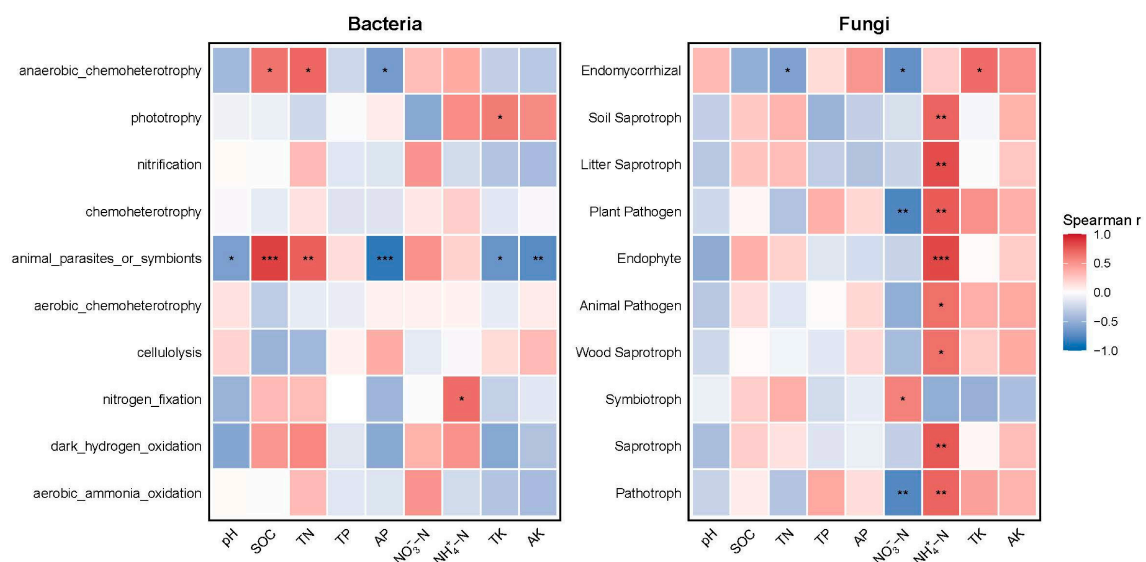


Figure 9. Spearman correlation heatmap between soil physicochemical properties and the relative abundances of predicted functional groups in bacterial (left) and fungal (right) communities. *, ** and *** indicated significant correlation at 0.05, 0.01 and 0.001, respectively.

The bacterial functional groups showed multiple significant correlations with the soil factors (Figure 9). Aerobic chemoheterotrophy and animal parasites or symbionts were significantly negatively correlated with pH, SOC, TN, and NH₄⁺-N but positively correlated with TK and AK. Nitrification and aerobic ammonia oxidation exhibited positive correlations with several nutrient parameters (e.g., AP, TK). Nitrogen fixation was positively correlated with NH₄⁺-N. Phototrophy and cellulolysis also displayed significant associations with specific soil properties such as TK and AK.

The fungal functional groups exhibited distinct correlation patterns (Figure 9). Endophyte was strongly positively correlated with NO₃⁻-N and NH₄⁺-N and showed significant correlations with multiple other factors. Plant pathogen and pathotroph were significantly positively correlated with NO₃⁻-N and NH₄⁺-N. Litter saprotroph and soil saprotroph showed strong positive correlations with TK and AK. Symbiotroph and endomycorrhizal displayed notable correlations with the pH and available nutrients.

These results indicate that soil pH, nitrogen availability (especially NO_3^- -N and NH_4^+ -N), SOC, and potassium (TK and AK) are the key drivers influencing the functional potential of both the bacterial and fungal communities. The fungal functions appeared more closely associated with nitrogen forms, whereas the bacterial functions showed stronger links to potassium availability and pH.

4. Discussion

4.1. Soil Microbial Diversity in Different Soils

Soil microorganisms, as core biological components maintaining ecosystem functions, exert an irreplaceable influence on soil health by driving critical processes such as organic matter decomposition and nutrient cycling. Meanwhile, different vegetation covers can indirectly reshape microbial community structures by regulating physicochemical properties such as soil pH and nutrient availability [24]. Simultaneously, allelochemicals secreted by plant roots can specifically enrich growth-promoting functional microorganisms while suppressing non-functional groups, forming a “rhizosphere screening effect” [25,26]. However, systematic research remains lacking regarding the structural characteristics of the rhizosphere microbiome in the medicinal plant *A. japonica* and its interaction mechanisms with soil factors.

Among all the soils, the ALR of *A. japonica* exhibited the highest bacterial richness. The PCoA ordination revealed no significant differences between the rhizosphere and bulk soils of *A. japonica*. The differences in the fungal Chao1 index between the ALR and the ALO might be associated with distinct microenvironments in the rhizosphere, such as localized variations in the soil pH or the root exudation patterns, which potentially enhance fungal proliferation and competitive advantages within the soil ecosystem [27]. A comparative analysis of the microbial α -diversity indices demonstrated significantly higher Shannon indices in the bacterial communities than in their fungal counterparts. A further comparison of the phylum- and genus-level microbial composition between the rhizosphere and bulk soils revealed distinct proportional distributions of bacteria and fungi [28], consistent with global soil microbial composition trends [29]. While the four soils showed similar microbial compositions at the phylum level, variations in the relative abundances at the genus level were observed (Figure 4). Previous studies corroborate that plants can modulate the relative abundances of specific taxa while maintaining overall microbial population stability [5].

Under the same climatic conditions, the distribution of different vegetation types reflects their distinct soil requirements [30]. Various vegetation types can indirectly alter microbial communities by modifying soil nutrients [31]. A comparison of soils from several different plants reveals that *A. japonica* uniquely harbors the microbial genus *Tetracladium*. In studies of *Panax notoginseng* rhizosphere microbial communities, *Tetracladium* showed a negative correlation with pathogenic *Fusarium* and significantly inhibited *Fusarium* spores [32]. The distribution of this fungal genus is significantly influenced by soil chemical properties, with its relative abundance positively correlated with the soil pH [33]. It can also decompose lignin and cellulose in fallen wood by secreting extracellular enzymes, promoting humus formation [34]. The enrichment of *Tetracladium* in *A. japonica* soils is noteworthy, as this genus has been reported to correlate negatively with pathogenic *Fusarium* in other medicinal plants and to participate in lignocellulose decomposition. Whether it contributes to disease suppression in *A. japonica* remains to be experimentally tested.

4.2. Soil Physicochemical Factor Effects on Microbial Community Composition

The soil organic matter, nitrogen, and phosphorus levels appeared to be linked to the soil fertility, serving as essential nutrients for plant growth and significantly influencing

microbial activity [35]. According to the results of this study, except for pH and TK, SOC, AP, TN, $\text{NH}_4^+\text{-N}$, and AK were higher in the rhizosphere of the *A. japonica* plants compared to the bulk soils, indicating an enhanced nutrient availability in the rhizosphere. This phenomenon may result from root exudates produced by *A. japonica* that promote nutrient decomposition and utilization [36], coupled with microbial-mediated nutrient cycling. The synergistic effects of these factors likely contribute to improved rhizosphere nutrient conditions that support *A. japonica* growth and development [37]. A comparative analysis of the original soils of the three plant species revealed that the *A. japonica* soil exhibited significantly higher TP but lower AP levels than the other plants. The AP, the directly plant-available form of phosphorus, is closely associated with the fungal community diversity and is regulated by multiple factors, including root activity, microbial functions, and soil chemical properties [38].

Numerous studies demonstrate that soil chemical properties are associated with the community structures of soil bacteria and fungi. Similarly, it is noteworthy that distinct plant species harbor unique microbial communities, a pattern explained by plant-specific alterations in soil nutrients, moisture [39], and pH [40]. Plants, microorganisms, and soil interact interdependently, collectively shaping the soil ecosystem.

A further important limitation is the small number of biological replicates ($n = 3$ per group). Under such conditions, assumptions of normality cannot be reliably verified, and correlation coefficients derived from only 3–4 paired observations are statistically fragile. Consequently, the reported correlations between the microbial indices and the soil variables are treated as exploratory patterns rather than robust evidence of an association. Future studies with larger numbers of independent replicates (and preferably multiple fields per vegetation type) are required to confirm the stability of these relationships.

4.3. Implications for *A. japonica* Cultivation and Continuous-Cropping Obstacles

The continuous cropping of *A. japonica* is known to be associated with soil-borne diseases and yield decline. Under the single-field design of the present study, the *A. japonica* soils (ALO and ALR) exhibited distinct microbial assemblages and were primarily associated with pH, AP and AK, whereas the forest and soybean soils were more closely linked to organic carbon and nitrogen forms. These observational patterns suggest that long-term monoculture may select for specific microbial consortia and alter key nutrient pools. However, the limited replication ($n = 3$ per group) and lack of multi-year or multi-site data preclude strong conclusions about the progressive development of continuous-cropping obstacles. Maintaining a balanced soil pH and the available P and K levels through appropriate organic amendments may help support beneficial microbial groups, but this hypothesis requires experimental validation. Similarly, the potential utility of the taxa enriched in the *A. japonica* soils (e.g., *Tetracladium*, *Penicillium*) as microbial inoculants remains speculative and warrants targeted isolation and greenhouse trials. Future work integrating multi-year rhizosphere and bulk-soil sampling, metagenomic/metatranscriptomic approaches, and controlled manipulation experiments will be essential to move from correlative patterns to mechanistic understanding and practical management strategies. Collectively, the results indicate that soils under different vegetation covers, sampled under identical climatic conditions, harbor distinct bacterial and fungal communities that are associated with different sets of edaphic factors.

5. Conclusions

In this study, bacterial and fungal communities were compared across four soil groups (forest bulk soil, soybean bulk soil, *A. japonica* bulk soil and *A. japonica* rhizosphere soil) collected under identical climatic conditions in Yichun, Northeast China. The bacterial

α -diversity remained relatively stable, whereas the fungal α -diversity and community structure showed clearer differences among the groups. The *A. japonica* soils were characterized by distinct microbial assemblages and were primarily associated with soil pH, AP and AK, while the forest and soybean soils were more closely linked to soil organic carbon, total nitrogen and inorganic nitrogen forms. These patterns highlight the plant–soil–microbe associations under the studied field conditions. The identified edaphic associations and characteristic taxa provide a useful baseline for future multi-site and multi-year investigations aimed at understanding and potentially mitigating the continuous-cropping challenges in *A. japonica* cultivation.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/d18080498/s1>, Table S1: Accession and SRA number of original sequencing data. Table S2: Soil physicochemical characteristics of bulk and rhizosphere soils of *Atractylodes japonica* Koidz.ex Kitam in different habitats.

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Abbreviations

The following abbreviations are used in this manuscript:

FS	Forest soil
PGS	Soybean field
ALR	Rhizosphere soil
TN	Total nitrogen
AP	Available phosphorus
AK	Available potassium
PCoA	Principal coordinate analysis
ALO	Bulk soil
TP	Total phosphorus
TK	Total potassium
RDA	Redundancy analysis
CCA	Canonical correspondence analysis

References

1. Fierer, N. Embracing the unknown: Disentangling the complexities of the soil microbiome. *Nat. Rev. Microbiol.* **2017**, *15*, 579–590. [[CrossRef](#)] [[PubMed](#)]
2. Sokol, N.W.; Slessarev, E.; Marschmann, G.L.; Nicolas, A.; Blazewicz, S.J.; Brodie, E.L.; Firestone, M.K.; Foley, M.M.; Hestrin, R.; Hungate, B.A.; et al. Life and death in the soil microbiome: How ecological processes influence biogeochemistry. *Nat. Rev. Microbiol.* **2022**, *20*, 415–430. [[CrossRef](#)] [[PubMed](#)]
3. Philippot, L.; Spor, A.; Hénault, C.; Bru, D.; Bizouard, F.; Jones, C.M.; Sarr, A.; Maron, P.-A. Loss in microbial diversity affects nitrogen cycling in soil. *ISME J.* **2013**, *7*, 1609–1619. [[CrossRef](#)] [[PubMed](#)]

4. Richardson, A.E.; Simpson, R.J. Soil microorganisms mediating phosphorus availability update on microbial phosphorus. *Plant Physiol.* **2011**, *156*, 989–996. [[CrossRef](#)] [[PubMed](#)]
5. Fierer, N.; Jackson, R.B. The diversity and biogeography of soil bacterial communities. *Proc. Natl. Acad. Sci. USA* **2006**, *103*, 626–631. [[CrossRef](#)] [[PubMed](#)]
6. Lauber, C.L.; Hamady, M.; Knight, R.; Fierer, N. Pyrosequencing-based assessment of soil pH as a predictor of soil bacterial community structure at the continental scale. *Appl. Environ. Microbiol.* **2009**, *75*, 5111–5120. [[CrossRef](#)] [[PubMed](#)]
7. Fierer, N.; Leff, J.W.; Adams, B.J.; Nielsen, U.N.; Bates, S.T.; Lauber, C.L.; Owens, S.; Gilbert, J.A.; Wall, D.H.; Caporaso, J.G. Cross-biome metagenomic analyses of soil microbial communities and their functional attributes. *Proc. Natl. Acad. Sci. USA* **2012**, *109*, 21390–21395. [[CrossRef](#)] [[PubMed](#)]
8. Min, K.; Zheng, T.; Zhu, X.; Bao, X.; Lynch, L.; Liang, C. Bacterial community structure and assembly dynamics hinge on plant litter quality. *FEMS Microbiol. Ecol.* **2023**, *99*, fiad118. [[CrossRef](#)] [[PubMed](#)]
9. Chen, L.J.; Wu, X.Q.; Xu, Y.; Wang, B.L.; Liu, S.; Niu, J.F.; Wang, Z. Microbial diversity and community structure changes in the rhizosphere soils of *Atractylodes lancea* from different planting years. *Plant Signal. Behav.* **2021**, *16*, 1854507. [[CrossRef](#)] [[PubMed](#)]
10. Wang, M.; Deng, J.; Duan, G.; Chen, L.; Huang, X.; Wang, W.; Gong, L.; Zhang, Y.; Yu, K.; Guo, L. Insights into the impacts of autotoxic allelochemicals from rhizosphere of *Atractylodes lancea* on soil microenvironments. *Front. Plant Sci.* **2023**, *14*, 1136833. [[CrossRef](#)] [[PubMed](#)]
11. Yuan, X.F.; Song, T.J.; Yang, J.S.; Huang, X.; Shi, J. Changes of microbial community in the rhizosphere soil of *Atractylodes macrocephala* when encountering replant disease. *S. Afr. J. Bot.* **2019**, *127*, 129–135. [[CrossRef](#)]
12. Zhu, B.; Wu, J.; Ji, Q.; Wu, W.; Dong, S.; Yu, J.; Zhang, Q.; Qin, L. Diversity of rhizosphere and endophytic fungi in *Atractylodes macrocephala* during continuous cropping. *PeerJ* **2020**, *8*, e8905. [[CrossRef](#)] [[PubMed](#)]
13. Tang, J.; Han, Y.; Pei, L.; Gu, W.; Qiu, R.; Wang, S.; Ma, Q.; Gan, Y.; Tang, M. Comparative analysis of the rhizosphere microbiome and medicinally active ingredients of *Atractylodes lancea* from different geographical origins. *Open Life Sci.* **2023**, *18*, 1. [[CrossRef](#)] [[PubMed](#)]
14. Bai, J.; Lu, Y.; Dong, P.; Cao, Y.; Liu, J.-W.; Zhao, C.-Y. The impact of rhizosphere soil microorganisms on the medicinal active ingredients of *Atractylodes chinensis* from different regions. *Plant Signal. Behav.* **2025**, *20*, 1. [[CrossRef](#)] [[PubMed](#)]
15. Malik, A.A.; Puissant, J.; Buckeridge, K.M.; Goodall, T.; Jehmlich, N.; Chowdhury, S.; Gweon, H.S.; Peyton, J.M.; Mason, K.E.; van Agtmaal, M.; et al. Land use driven change in soil pH affects microbial carbon cycling processes. *Nat. Commun.* **2018**, *9*, 3591. [[CrossRef](#)] [[PubMed](#)]
16. Bahram, M.; Espenberg, M.; Pärn, J.; Lehtovirta-Morley, L.; Anslan, S.; Kasak, K.; Kõljalg, U.; Liira, J.; Maddison, M.; Moora, M.; et al. Structure and function of the soil microbiome underlying N₂O emissions from global wetlands. *Nat. Commun.* **2022**, *13*, 1430. [[CrossRef](#)] [[PubMed](#)]
17. Konnerup, D.; Brix, H. Nitrogen nutrition of *Canna indica*: Effects of ammonium versus nitrate on growth, biomass allocation, photosynthesis, nitrate reductase activity and N uptake rates. *Aquat. Bot.* **2010**, *92*, 142–148. [[CrossRef](#)]
18. Yan, M.; Zhu, C.; Li, B.; Su, S.; Li, H. Manure application facilitated electrokinetic remediation of antibiotic-arsenic co-contaminated paddy soil. *J. Hazard. Mater.* **2023**, *441*, 129897. [[CrossRef](#)] [[PubMed](#)]
19. Callahan, B.J.; McMurdie, P.J.; Rosen, M.J.; Han, A.W.; Johnson, A.J.; Holmes, S.P. DADA2: High-resolution sample inference from Illumina amplicon data. *Nat. Methods* **2016**, *13*, 581–583. [[CrossRef](#)] [[PubMed](#)]
20. Wang, Q.; Garrity, G.M.; Tiedje, J.M.; Cole, J.R. Naive Bayesian classifier for rapid assignment of rRNA sequences into the new bacterial taxonomy. *Appl. Environ. Microbiol.* **2007**, *73*, 5261–5267. [[CrossRef](#)] [[PubMed](#)]
21. Yuan, Z.S.; Liu, F.; Liu, Z.Y.; Huang, Q.L.; Zhang, G.F.; Pan, H. Structural variability and differentiation of niches in the rhizosphere and endosphere bacterial microbiome of moso bamboo (*Phyllostachys edulis*). *Sci. Rep.* **2021**, *11*, 1574. [[CrossRef](#)] [[PubMed](#)]
22. MacFarland, T.W.; Yates, J.M. Kruskal–Wallis H-test for oneway analysis of variance (ANOVA) by ranks. In *Introduction to Nonparametric Statistics for the Biological Sciences Using R*; Springer: Berlin/Heidelberg, Germany, 2016; pp. 177–211.
23. Gao, Y.; Zhang, G.; Jiang, S.; Liu, Y.X. Wekemo Bioincloud: A user-friendly platform for meta-omics data analyses. *iMeta* **2024**, *3*, e175. [[CrossRef](#)] [[PubMed](#)]
24. Costa, D.P.D.; Araujo, A.S.F.; Pereira, A.P.A.; Mendes, L.W.; França, R.F.D.; Silva, T.D.G.E.D.; Oliveira, J.B.; Araujo, J.S.; Duda, G.P.; Menezes, R.S.C.; et al. Forest-to-pasture conversion modifies the soil bacterial community in Brazilian dry forest Caatinga. *Sci. Total Environ.* **2022**, *810*, 151943. [[CrossRef](#)] [[PubMed](#)]
25. Sasse, J.; Martinoia, E.; Northen, T. Feed your friends: Do plant exudates shape the root microbiome? *Trends Plant Sci.* **2018**, *23*, 25–41. [[CrossRef](#)] [[PubMed](#)]
26. Xu, H.R.; Liu, W.D.; He, Y.H.; Zou, D.; Zhou, J.H.; Zhang, J.Y.; Bai, Y. Plant-root microbiota interactions in nutrient utilization. *Front. Agric. Sci. Eng.* **2025**, *12*, 16–26. [[CrossRef](#)]
27. Wang, C.; Kuzyakov, Y. Mechanisms and implications of bacterial-fungal competition for soil resources. *ISME J.* **2024**, *18*, wrac073. [[CrossRef](#)] [[PubMed](#)]

28. Li, Z.; Zu, C.; Wang, C.; Yang, J.; Yu, H.; Wu, H. Different responses of rhizosphere and non-rhizosphere soil microbial communities to consecutive *Piper nigrum* L. monoculture. *Sci. Rep.* **2016**, *6*, 35825. [[CrossRef](#)] [[PubMed](#)]
29. Li, Y.; He, X.; Yuan, H.; Lv, G. Differed growth stage dynamics of root-associated bacterial and fungal community structure associated with halophytic plant *Lycium ruthenicum*. *Microorganisms* **2022**, *10*, 1644. [[CrossRef](#)] [[PubMed](#)]
30. Gao, X.; Li, F.Y. The inverse texture effect of soil on vegetation in temperate grasslands of China: Benchmarking soil texture effect. *Geoderma* **2023**, *438*, 116641. [[CrossRef](#)]
31. Xu, M.P.; Wang, J.Y.; Zhu, Y.F.; Han, X.H.; Ren, C.J.; Yang, G.H. Plant biomass and soil nutrients mainly explain the variation of soil microbial communities during secondary succession on the Loess Plateau. *Microb. Ecol.* **2022**, *83*, 114–126. [[CrossRef](#)] [[PubMed](#)]
32. Yang, Y.L.; Wang, C.; Qu, Y.H.; Ru, R.H.; Sun, H.W.; Li, X.P.; Yang, Q.S.; Tao, Y.H. Study on fungal community diversity in rhizosphere of *Panax notoginseng* in different regions of Wenshan. *Chin. Agric. Sci. Bull.* **2024**, *40*, 94–101. [[CrossRef](#)]
33. Lazar, A.; Griffiths, R.I.; Goodall, T.; Norton, L.R.; Mushinski, R.M.; Bending, G.D. Regional scale diversity and distribution of soil inhabiting Tetracladium. *Environ. Microbiome* **2024**, *19*, 111. [[CrossRef](#)] [[PubMed](#)]
34. Lazar, A.; Mushinski, R.M.; Bending, G.D. Landscape scale ecology of *Tetracladium* spp. fungal root endophytes. *Environ. Microbiome* **2022**, *17*, 40. [[CrossRef](#)] [[PubMed](#)]
35. Ma, S.; Wang, L.J.; Wang, H.Y.; Zhao, Y.G.; Jiang, J. Impacts of land use/land cover and soil property changes on soil erosion in the black soil region, China. *J. Environ. Manag.* **2023**, *328*, 117024. [[CrossRef](#)] [[PubMed](#)]
36. Jones, J.W.; Hoogenboom, G.; Porter, C.H.; Boote, K.J.; Batchelor, W.D.; Hunt, L.A.; Wilkens, P.W.; Singh, U.; Gijsman, A.J.; Ritchie, J.T. The DSSAT cropping system model. *Eur. J. Agron.* **2003**, *18*, 235–265. [[CrossRef](#)]
37. Yadav, A.N.; Kour, D.; Kaur, T.; Devi, R.; Yadav, A.; Dikilitas, M.; Abdel-Azeem, A.M.; Ahluwalia, A.S.; Saxena, A.K. Biodiversity, and biotechnological contribution of beneficial soil microbiomes for nutrient cycling, plant growth improvement and nutrient uptake. *Biocatal. Agric. Biotechnol.* **2021**, *33*, 102009. [[CrossRef](#)]
38. Sun, H.; Wang, Q.X.; Zhang, L.L.; Liu, N.; Liu, Z.B.; Lv, L.; Shao, C.; Guan, Y.M.; Ma, L.; Li, M.J.; et al. Distinct leaf litter drive the fungal communities in *Panax ginseng*-growing soil. *Ecol. Indic.* **2019**, *104*, 184–194. [[CrossRef](#)]
39. Huang, F.Y.; Liu, Z.H.; Mou, H.Y.; Zhang, P.; Jia, Z.K. Effects of different long-term farmland mulching practices on the loessial soil fungal community in a semiarid region of China. *Appl. Soil Ecol.* **2019**, *137*, 111–119. [[CrossRef](#)]
40. Wang, J.T.; Zheng, Y.M.; Hu, H.W.; Zhang, L.M.; Li, J.; He, J.Z. Soil pH determines the alpha diversity but not beta diversity of soil fungal community along altitude in a typical Tibetan forest ecosystem. *J. Soils Sediments* **2015**, *15*, 1224–1232. [[CrossRef](#)]

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