

Article

The Changes in Soil Microbial Communities and Assembly Processes along Vegetation Succession in a Subtropical Forest

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Abstract: Soil microbes are the primary drivers of the material cycling of the forest ecosystem, and understanding how microbial structure and composition change across succession assists in clarifying the mechanisms behind succession dynamics. However, the response of soil microbial communities and assembly processes to succession is poorly understood in subtropical forests. Thus, through the “space instead of time” and high throughput sequencing method, the dynamics of the soil bacterial and fungal communities and assembly process along the succession were studied, where five succession stages, including Abandoned lands (AL), Deciduous broad-leaved forests (DB), Coniferous forests (CF), Coniferous broad-leaved mixed forests (CB), and Evergreen broad-leaved forests (EB), were selected in a subtropical forest on the western slope of Wuyi Mountain, southern China. The results demonstrated that succession significantly decreased soil bacterial α -diversity but had little effect on fungal α -diversity. The composition of soil bacterial and fungal communities shifted along with the succession stages. LEfSe analysis showed the transition from initial succession microbial communities dominated by *Firmicutes*, *Bacteroidota*, *Ascomycota*, and *Chytridiomycota* to terminal succession communities dominated by *Actinobacteriota* and *Basidiomycota*. Distance-based redundancy analysis (db-RDA) revealed that soil total organic carbon (TOC) was the main factor explaining variability in the structure of soil bacterial communities, and multiple soil environmental factors such as the TOC, soil total nitrogen (TN), C:N ratio, and pH co-regulated the structure of fungi. The null models illustrated that deterministic processes were dominant in the soil bacterial communities, while the stochastic processes contributed significantly to the soil fungal communities during succession. Collectively, our results suggest that different patterns are displayed by the soil bacterial and fungal communities during the succession. These findings enhance our comprehension of the processes that drive the formation and maintenance of soil microbial diversity throughout forest succession.

Keywords: soil microbes; microbial community; assembly process; high throughput sequencing; vegetation succession



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1. Introduction

Forest succession is a continuous change in the species composition, structure, and function of a forest through time following disturbance. In general, vegetation succession could alter the functioning of forest ecosystems, affecting both above-ground ecological

functions and below-ground material cycling processes [1–4]. Soil microorganisms are the main drivers of underground material cycling along the succession stages [5,6]. The diversity of soil microorganisms is an important foundation for driving material cycling, and it is mainly determined by multiple factors such as environmental factors, community structure, and community assembly [7,8]. Investigating how soil microbial community composition and assembly processes respond to forest succession helps to reveal the mechanisms driving below-ground material cycling.

Forest succession can affect soil microorganisms by changing vegetation and altering soil physicochemical properties [9,10]. In terms of soil physicochemical properties, substrates may be the most important factor regulating soil microbial communities [11,12]. The effects of substrates on soil microorganisms can change based on the species of trees present in a given forest succession [13]. Previous research has shown that soil pH tends to be more acidic with the progression of forest succession, and that soil pH also significantly affects microbial communities [14,15]. In the meanwhile, there are variations in soil background values in different regions, and whether succession series may cause soil acidity and alter the soil microbial communities is still up for debate. As the main distribution area of forests, the shift of soil microbial communities along with the forest succession through the impact on the soil's physical and chemical factors still needs further exploration in subtropical forests.

The establishment and maintenance of soil microbial communities are the core issues of microbial ecology [16]. Forest succession is typical environmental filtering, influencing the soil microbial communities through altering soil properties and vegetation [17,18]. However, there are currently two mainstream theories to explain microbial community structure, which are the niche theory and the neutral theory [19,20]. The niche theory emphasizes deterministic processes and holds that the succession of microbial communities is the consequence of selection and screening by biotic (e.g., competition, mutualism, and commensalism) and abiotic factors (e.g., pH and substrate) [21,22]. In contrast to the niche theory, the neutral theory emphasizes stochastic processes and asserts that community assembly is determined by stochastic processes (e.g., dispersal and drift) [22,23]. After a long debate, it is more widely acknowledged that microbial community assembly involves both stochastic and deterministic processes [23,24]. The majority of research on the influence of forest succession on soil microorganisms primarily examines the diversity and composition of the soil microbial communities [25,26]. Apart from the deterministic influence of forest succession, the neutral theory is also crucial for maintaining soil microbial diversity along the succession stages. However, the relative importance of the two processes during forest succession needs to be further studied, especially in subtropical forests.

Wuyi Mountain is one of the main distribution areas for subtropical forests in southern China [27]. It underwent deforestation during the early stages of its reform and opening up, and is currently in a period of forest vegetation recovery [28,29]. Therefore, this region will help us to understand microbial community succession patterns along forest succession. Previous studies have shown the direction of succession from conifer forests to evergreen broad-leaved forests in subtropical forests [30]. Evergreen broad-leaved forests are the most structurally derived, occurring at various elevations in subtropical forests [31]. According to the types of vegetation and leaves, we selected five succession stages: Abandoned lands (AL), Deciduous broad-leaved forests (DB), Coniferous forests (CF), Coniferous broad-leaved mixed forests (CB), and Evergreen broad-leaved forests (EB), to evaluate the impact of forest succession on soil microorganisms. The soil microbial communities can be impacted along forest succession by altering the input amount and types of substrates [17,32]. Increasing substrate input may increase microbial competition and select for specific microbial communities. Given this knowledge, we propose the following hypothesis: (i) the soil bacterial and fungal diversity and composition decreased along with the succession stages; (ii) the relative importance of deterministic and stochastic processes in soil bacterial and fungal assembly processes varies during the succession; and

(iii) the soil pH and total organic carbon (TOC) may be the key soil environmental factors regulating the structure of the soil bacterial and fungal communities.

2. Materials and Methods

2.1. Study Area and Soil Sampling

This study was conducted in a subtropical forest in Jiangxi Province, southern China (27°40'50" N, 117°09'11" E), within the Matoushan National Nature Reserve on the western slope of the Wuyi Mountains. The climate in the study area is classified as a humid subtropical monsoon climate, and average annual temperature was ranging from 16 to 18 °C. The temperature may drop as low as −5 °C in January and reach as high as 27.2 °C in July. The average annual precipitation is 1930 mm, with around 47% of it falling in the months of April and June. The main biome of this study site is primarily dominated by Evergreen broad-leaved forests and Coniferous broad-leaved mixed forests. The soil composition comprises mountain red, yellow-red, and yellow soil, which is a consequence of the weathering of granite [27].

In October 2020, we selected each stage of forest succession in Matoushan National Nature Reserve. The Abandoned lands (AL) are covered with herbaceous plants dominated by species such as *Euphorbia latiris*, *Echinochloa crus galli*, *Cyperus rotundis*, and *Equisetum ramosissimum*. *Liquidambar formosana* and *Cunninghamia lanceolata* are dominant tree species in Deciduous broad-leaved forests (DB) and Coniferous forests (CF), respectively. The Coniferous broad-leaved mixed forests (CB) are dominated by *C. lanceolata*, *Alniphyllum fortunei*, *Sassafras tzumu*, *Syzygium buxifolium*, etc. The Evergreen broad-leaved forests (EB) are dominated by that of evergreen and deciduous trees such as *Castanopsis eyrei*, *Castanopsis nigrescens*, *Cyclobalanopsis glauca*, *Syzygium buxifolium*, etc. [33]. Specific information about the sampling sites can be found in Table 1. A total of 30 composite soil samples were collected from five stages of succession, with three replicates and two depths (5 succession stages × 2 depths × 3 replicates). For each succession stage, three 40 m × 40 m plots were established, from which five soil cores (5 cm in diameter) were collected from each plot, encompassing the 0–10 cm and 10–30 cm layers. The soil samples, totaling 30, were transported to the laboratory packed with dry ice, and were subsequently sieved to eliminate rocks and visible roots. Soil samples were then stored at 4 °C for chemical analysis, or at −80 °C for DNA extraction.

Table 1. Detailed successional information on dominant tree species, soil types, and altitude in the subtropical forests on the western slope of the Wuyi Mountains. Abandoned lands (AL), Deciduous broad-leaved forests (DB), Coniferous forests (CF), Coniferous broad-leaved mixed forests (CB), and Evergreen broad-leaved forests (EB).

Successional Stages	Dominant Tree Species	Soil Types	Altitude (m)
AL	<i>Euphorbia latiris</i> and <i>Echinochloa crus galli</i>	yellow-red soil	250–318
DB	<i>Liquidambar formosana</i>	yellow-red soil	273–488
CF	<i>Cunninghamia lanceolata</i> and <i>Pinus massoniana</i>	yellow-red soil	452–501
CB	<i>Cunninghamia lanceolata</i> , <i>Alniphyllum fortunei</i> , <i>Sassafras tzumu</i> , <i>Syzygium buxifolium</i>	yellow-red soil	297–453
EB	<i>Castanopsis eyrei</i> , <i>Castanopsis nigrescens</i> , <i>Cyclobalanopsis glauca</i> and <i>Syzygium buxifolium</i>	yellow-red soil	287–454

2.2. Determination of Soil Physicochemical Properties

Soil pH was analyzed in a 1:5 (soil/water, *w/v*) ratio with a bench-top electrode pH meter. The oven-drying method was used to measure soil water content. In order to determine soil nutrient contents, air-dried soil samples were milled and passed through a 0.15 mm sieve. The concentrations of soil total organic C (TOC) and total N concentrations (TN) were measured using an elemental analyzer (Flash 2000 HT, Thermo Fisher Scientific, Bremen, Germany).

2.3. DNA Extraction, Amplicon Library Preparation, and Sequencing

Total microbial genomic DNA was extracted from 0.5 g of soil samples using the E.Z.N.A.[®] soil DNA Kit (Omega Bio-tek, Norcross, GA, USA) according to manufacturer instructions. The hypervariable region V3–V4 region for the bacterial 16S rRNA and the broad-spectrum primers for fungi were amplified with the primer pairs 338F (5'-ACTCCTACGGGAGGCAGCA-3'), 806R (5'-GGACTACHVGGGTWTCTAAT-3') and ITS1 (5'-CTTGGTCATTTAGAGGAAGTAA-3'), ITS2 (5'-GCTGCGTTCTTCATCGATGC-3'), respectively [34]. All samples were amplified in triplicate. The amplified and purified amplicons were pooled in equimolar amounts and paired-end sequenced on an Illumina MiSeq PE300 platform (Illumina, San Diego, CA, USA) using the standard methods provided by Majorbio Bio-Pharm Technology Co., Ltd. (Shanghai, China).

2.4. Sequence Data Processing

Paired-end sequences were demultiplexed using QIIME 2 [35], followed by further processing of the raw sequences with DADA2. The default settings were used, with the exception of trimming the forward and reverse reads to 240 bases for the 16S rRNA gene. No length filtering was carried out for the ITS region. Following the removal of low-quality reads and the merging of paired reads, operational taxonomic units (OTUs) clustering was conducted based on a 97% similarity threshold using non-redundant sequences (excluding single sequences) based on the SILVA r138 database [36] and the UNITE v8.0 database [37] for prokaryotes and fungi, respectively, through naïve Bayes classifier [38]. Singletons and 16S rRNA sequences identified as belonging to the Eukaryota were discarded. In total, 1,831,407 high-quality sequences for prokaryotes and 2,569,298 high-quality sequences for fungi were obtained.

2.5. Statistical Analysis

All statistical analyses were conducted using the vegan package in R (Version 4.0.2), unless specifically mentioned. The Chao1 and Shannon index for both bacterial and fungal communities was computed to assess the changes in soil microbial species richness and diversity. To evaluate the significance of differences along successional stages at the $p < 0.05$ level, such as soil properties and microbial diversity indices, one-way analysis of variance (ANOVA) or the Kruskal–Wallis rank-sum test were performed employing the Prgirmess packages. The linear discriminant analysis (LDA) effect size (LEfSe) was used to detect significant variations in the phyla of bacteria and fungi (LDA score > 2.0 , $p < 0.05$) [38]. The principal coordinate analysis (PCoA) based on Bray–Curtis dissimilarity was applied to examine the differences in community composition during the succession. The analysis of similarity (ANOSIM) and (Adonis) was performed based on the Bray–Curtis distance. Distance-based redundancy analysis (db-RDA) was performed to investigate the effect of soil physicochemical properties on soil bacterial and fungal community structure. The visualizations were finished using the ggplot2 package.

To understand the microbial community assembly, the Null model-based approach was applied to calculate the weighted β nearest taxon index (β NTI) and Bray–Curtis-based Raup–Crick (RC_{bray}) values [39,40]. Based on the β NTI and RC_{bray} indices, the relative importance of the deterministic and stochastic processes in soil microbial community assembly was determined [40]. The “iCAMP” package in R was used to calculate the β NTI by comparing the standard deviation of observed data with the null distribution of phylogenetic β -diversity metrics [20]. When the absolute value of β NTI is greater than 2, it means that the assembly of the community is dominated by deterministic processes. In a more specific categorization, the heterogeneous selection is represented by β NTI > 2 , whereas the homogeneous selection is represented by β NTI < -2 . In addition, the absolute value of β NTI is less than 2, indicating the dominance of stochastic processes. RC_{bray} was calculated by estimating the standard deviation between the empirical data and the null distribution of taxonomic β -diversity metrics [20]. Three types of random processes may be classified using β NTI and RC coupling. (1) $|\beta$ NTI| < 2 and $RC_{\text{bray}} > 0.95$: dispersal

limitation; (2) $|\beta\text{NTI}| < 2$ and $\text{RC}_{\text{bray}} < -0.95$: homogenizing dispersal; (3) $|\beta\text{NTI}| < 2$ and $\text{RC}_{\text{bray}} < -0.95$: drift [41].

3. Results

3.1. Soil Physicochemical Properties along the Succession Stages

Regarding soil characteristics, soil TOC ranged from 18.04 g kg⁻¹ in the Abandoned lands (AL), 57.80 g kg⁻¹ in the Coniferous forests (CF), and 79.14 g kg⁻¹ in the Evergreen broad-leaved forests (EB) at 0–10 cm soil depths (Table S1). Soil TOC ranged from 16.33 g kg⁻¹ in the Abandoned lands (AL) and 55.73 g kg⁻¹ in the Evergreen broad-leaved forests (EB) at 10–30 cm soil depths (Table S1). Soil TOC showed a notable increasing trend from the initial to the terminal phases of succession ($p < 0.05$). pH decreased significantly from 5.33 in the AL to 4.96 in the EB at 10–30 cm soil depths ($p < 0.05$), and there were no dramatic changes in pH at 0–10 cm soil depths among succession stages (Table S1). However, there were no significant differences in TN, C:N ratio, and moisture among succession stages (Table S1).

3.2. The Diversity and Composition of Soil Microbial Communities along the Succession Stages

During the succession stages, 1,402,689 and 2,001,323 high-quality effective sequences of bacteria and fungi, respectively, were obtained. The sequences were resampled to 33,560 and 49,363 OTUs for bacteria and fungi, respectively. The six main phyla of bacteria along the succession stages were *Proteobacteria* (10.41%~51.41%), *Acidobacteria* (7.18%~34.22%), *Actinobacteria* (5.69%~28.71%), *Chloroflexi* (2.90%~20.85%), *Planctomycetota* (0.59%~9.88%), and *Firmicutes* (0.92%~10.28%) (Figure 1A). For fungi, *Ascomycota* (22.74%~90.28%) and *Basidiomycota* (2.99%~61.08%) were the dominant fungal phyla, whereas *Mortierellomycota* (0.37%~44.72%) and *Rozellomycota* (0.07%~13.10%) were the main fungal phyla (Figure 1B). There was similarity in the relative abundances of bacteria and fungi phyla at 0–10 cm and 10–30 cm soil depths.

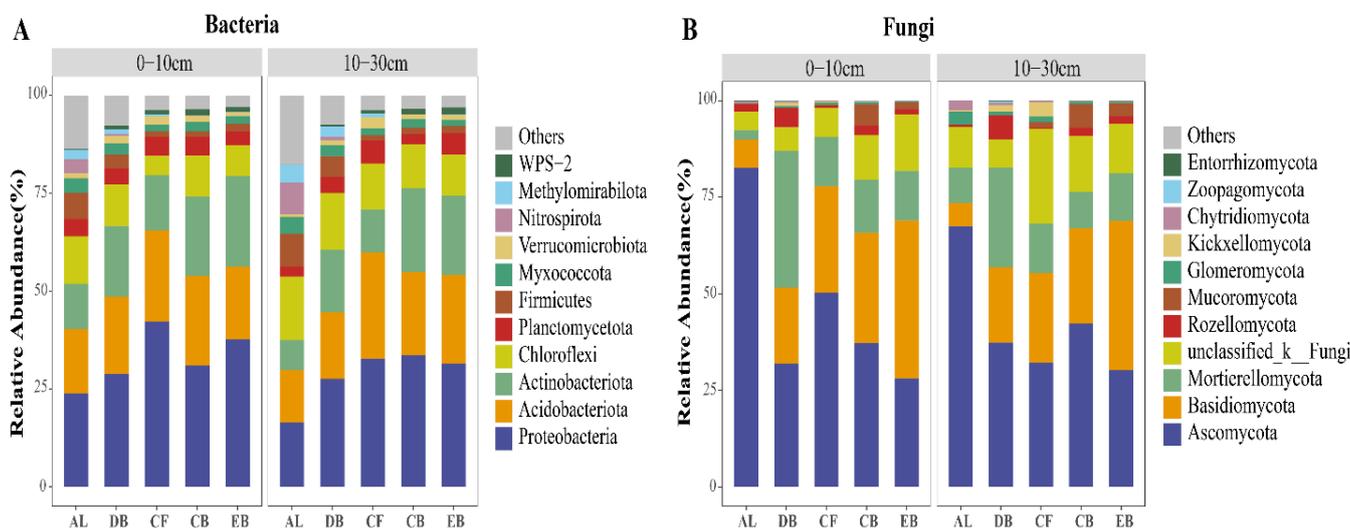


Figure 1. The relative abundances of the major soil bacterial (A) and fungal (B) phyla at different soil depths along the succession. The relative abundance of phyla less than 1% are merged into “Others”. Abandoned lands (AL), Deciduous broad-leaved forests (DB), Coniferous forests (CF), Coniferous broad-leaved mixed forests (CB), and Evergreen broad-leaved forests (EB).

The diversity (Shannon index) and richness (Chao1 index) of soil bacteria and fungi changed inconsistently along the succession stages (Figure 2). The bacterial Chao1 and Shannon index showed a notable decreasing trend from Abandoned lands (AL) to Coniferous forests (CF) to Evergreen broad-leaved forests (EB) at 0–10 cm and 10–30 cm soil depths ($p < 0.05$) (Figure 2A,B). The change of fungal Chao1 at 10–30 cm soil depth was opposite

that of bacteria, and it reached the maximum value in the EB forest (Figure 2C). The Chao1 index of fungi at 0–10 cm soil depth did not show an increasing trend (Figure 2C). The fungal Shannon indices showed no significant changes at 0–10 cm and 10–30 cm depths along the succession stages ($p > 0.05$; Figure 2D).

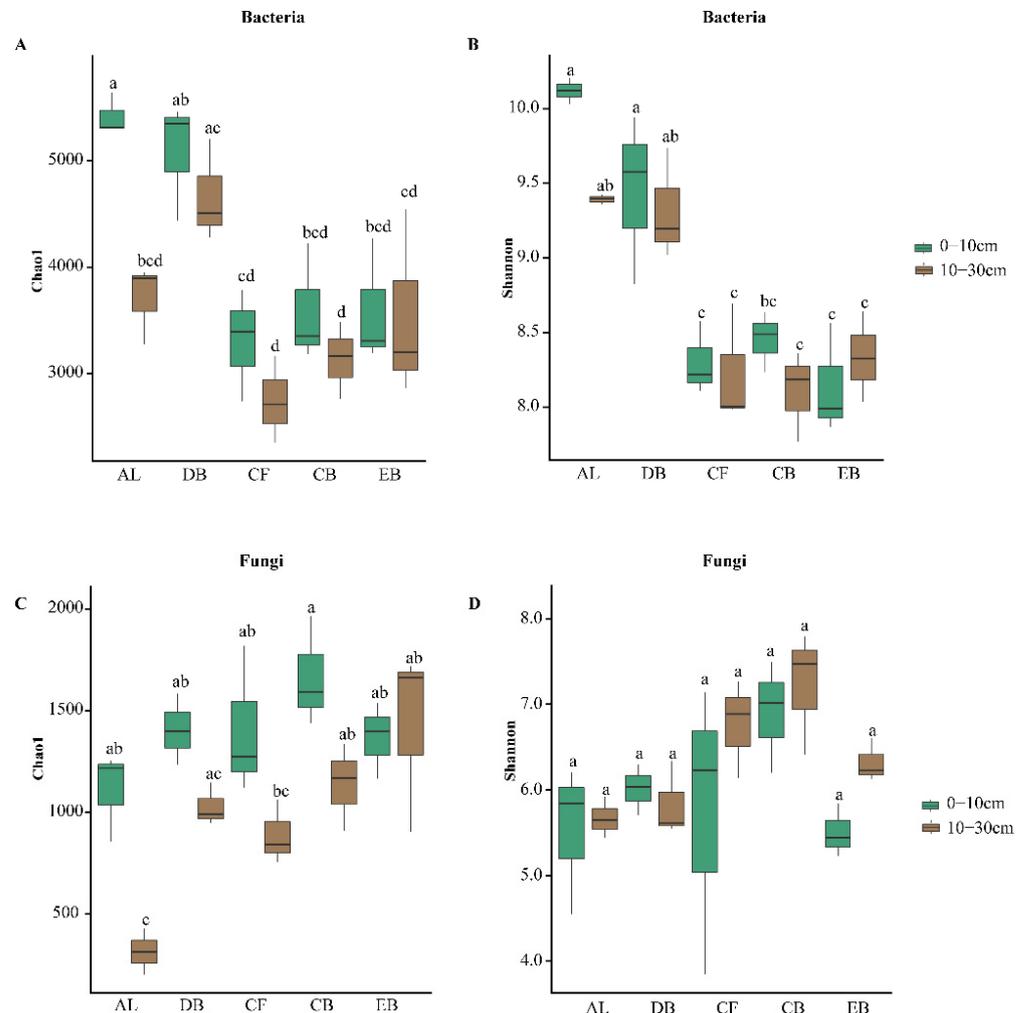


Figure 2. The changes in α -diversity index for both bacterial (A,B) and fungal communities (C,D) at different soil depths across the succession stages in subtropical forests. Significant changes are indicated by different letters ($p < 0.05$) among succession stages. Abandoned lands (AL), Deciduous broad-leaved forests (DB), Coniferous forests (CF), Coniferous broad-leaved mixed forests (CB), and Evergreen broad-leaved forests (EB).

3.3. The Beta Diversity of Soil Microbial Communities along the Succession Stages

The results of the principal coordinate analysis (PCoA) revealed that the structure of the soil bacterial and fungal communities showed the same change along the succession stages (Figure 3A,B). The results of Adonis tests (Bray–Curtis distance) showed no significant disparity between CB and EB ($p > 0.05$; Table S2). However, a notable divergence was observed in the bacterial and fungal community structure between AL and natural forests, including DB, CF, CB, and EB (Adonis test, $p < 0.01$; Adonis test, $p < 0.01$; Figure 3A,B).

According to LEfSe analysis, the soil bacterial and fungal communities significantly changed along the succession stages. Among them, 21 bacterial phyla were abundant differently along the succession stages (Figure 4A). The most phyla (*Chloroflexi*, *Firmicutes*, *Nitrospirota*, *Methylomirabilota*, and *Bacteroidota*) were mainly enriched in the Abandoned lands (AL). *Proteobacteria*, *Acidobacteriota*, and *Actinobacteriota* were enriched in Coniferous forests (CF) and Evergreen broad-leaved forests (EB), respectively. For fungi, seven fungal

phyla were abundant differently along the succession stages (Figure 4B). *Ascomycota* and *Chytridiomycota* were mainly enriched in the Abandoned lands (AL), and *Basidiomycota* was enriched in the Evergreen broad-leaved forests (EB) (Figure 4B).

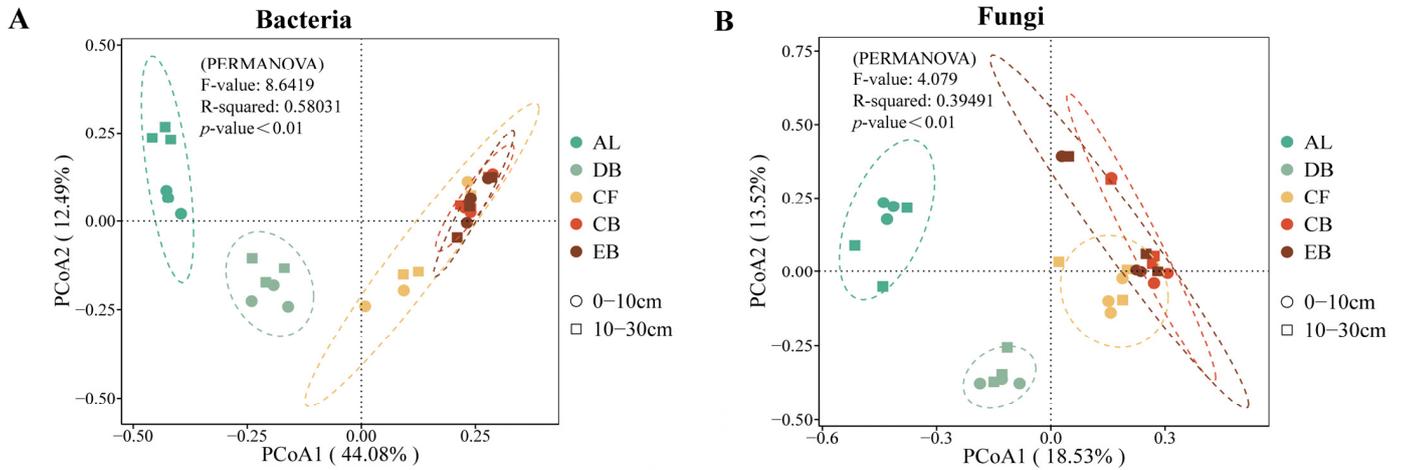


Figure 3. Principal co-ordinates analysis (PCoA) of soil bacterial (A) and fungal (B) communities at different depths along the succession stages. Abandoned lands (AL), Deciduous broad-leaved forests (DB), Coniferous forests (CF), Coniferous broad-leaved mixed forests (CB), and Evergreen broad-leaved forests (EB).

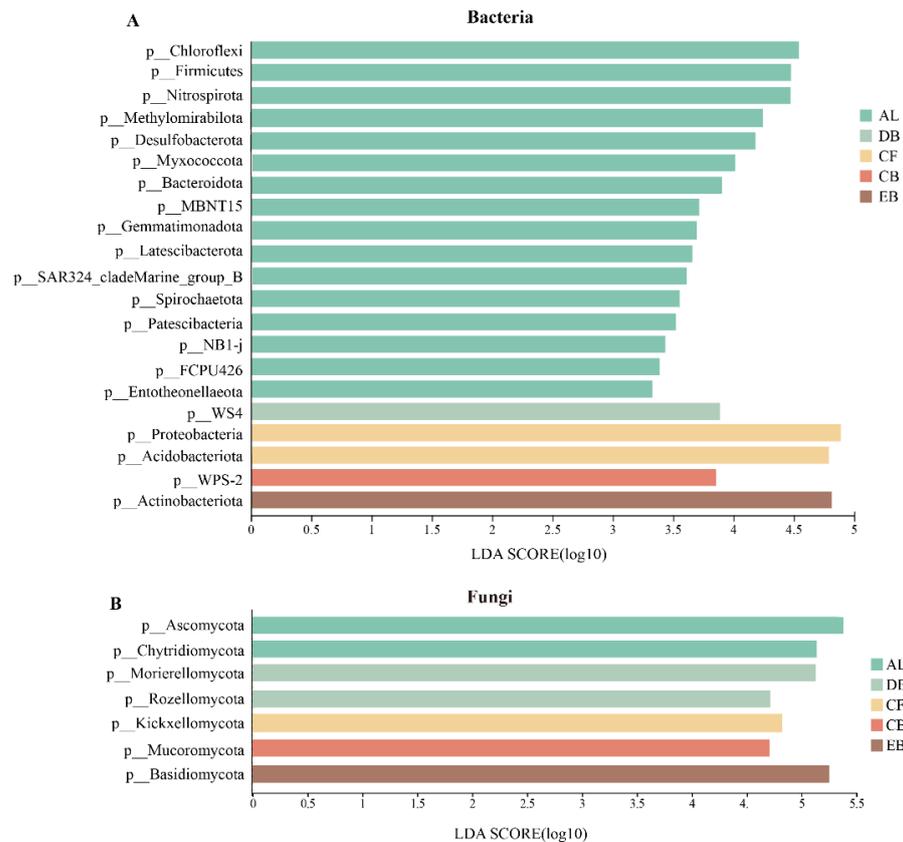


Figure 4. The linear discriminant analysis (LDA) effect size (LEfSe) illustrates the significant differences in bacterial (A) and fungal (B) phyla along the succession stages. The threshold value for distinguishing features based on the log LDA score was set at 2.0. Abandoned lands (AL), Deciduous broad-leaved forests (DB), Coniferous forests (CF), Coniferous broad-leaved mixed forests (CB), and Evergreen broad-leaved forests (EB).

3.4. The Changes in Microbial Assembly Processes along the Succession Stages

The β -NTI values and RCbray values were used to assess the ecological processes of soil microorganisms along the succession stages. The median β NTI values for the AL, DB, CB, and EB were greater than those of the CF ($p < 0.05$; Figure 5A). Meanwhile, the median β NTI values for the AL, DB, CB, and EB were more than two, whereas the median β NTI value for the CL was less than two (Figure 5A). This indicated that bacterial community assembly shifted from deterministic processes to stochastic processes to deterministic processes during the whole succession stages. For fungi, the community assembly processes were different from those of bacteria. The median β NTI values of the AL, DB, CB, and EB were higher than those of the CF ($p < 0.05$; Figure 5B). However, all values of the median β NTIs were less than two, indicating that stochastic processes mainly influenced fungal community assembly. Furthermore, the fungal community assembly remained unchanged across the whole succession stage (Figure 5B).

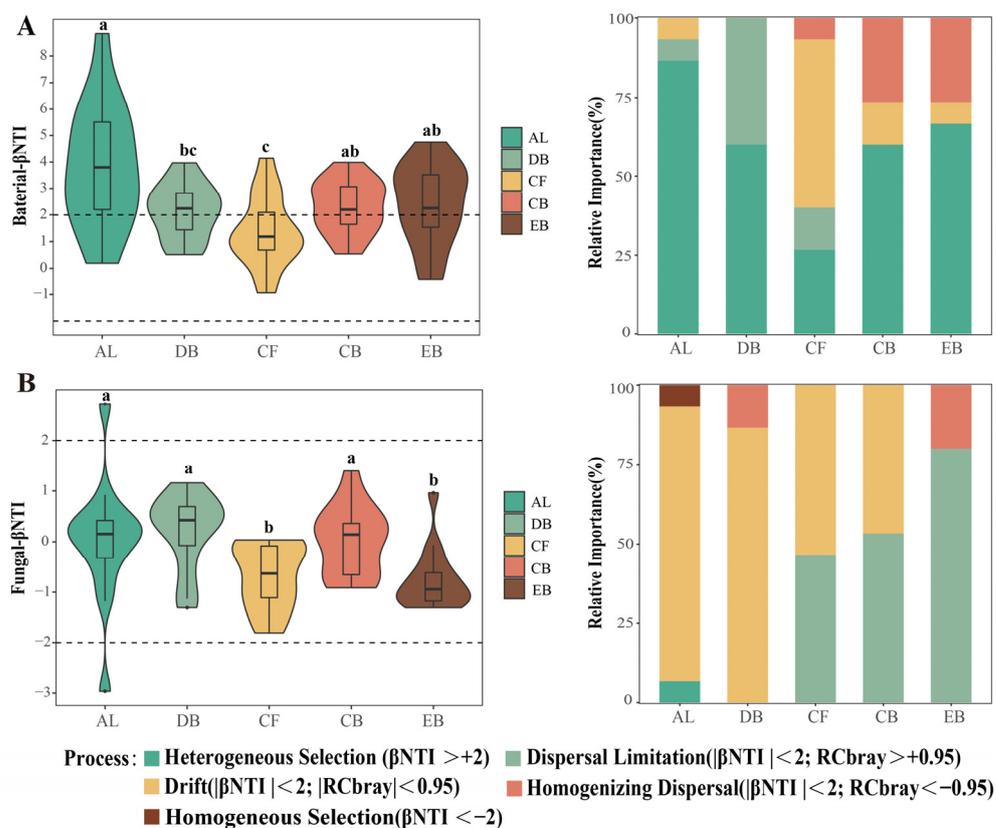


Figure 5. The β NTI values for pairwise community comparisons throughout the succession are distributed. Two dashed lines were added to distinguish between stochastic and deterministic processes according to β NTI values. Solid lines within violins represent the upper quartiles, median, and lower quartiles, respectively. The relative importance of assembly processes in bacterial (A) and fungal (B) communities during the succession. Significant changes are indicated by different letters ($p < 0.05$) among succession stages. Abandoned lands (AL), Deciduous broad-leaved forests (DB), Coniferous forests (CF), Coniferous broad-leaved mixed forests (CB), and Evergreen broad-leaved forests (EB).

3.5. The Correlations between Soil Microbial Communities and Soil Properties

Distance-based redundancy analysis (db-RDA) revealed the key soil environmental factors shaping the soil bacterial variation at the OTU level. (Figure 6A). The soil environmental factors accounted for a total of 58.89% of the variance in bacterial communities. Specifically, RDA1 and RDA2 explained 35.11% and 23.78% of the total variation, respectively (Figure 6A). The structure of the bacterial communities was mostly

determined by TOC ($p < 0.01$; Figure 6A). The soil environmental factors accounted for 11.7% (CCA1 = 6.7%, CCA2 = 5.0%) of the variation in the fungal community structure (Figure 6B). The TOC, pH, C:N ratio, and TN significantly influenced the variability in soil fungal communities ($p < 0.01$; Figure 6B).

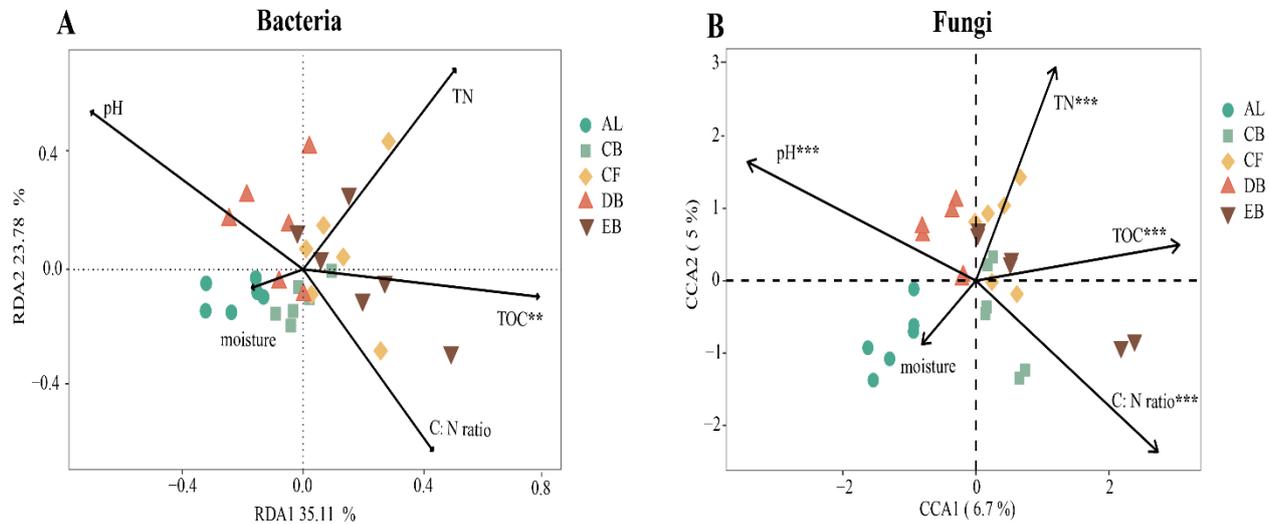


Figure 6. Distance-based redundancy analysis (db-RDA) of soil bacterial (A) and fungal (B) communities at different soil depths during the succession stages as related to soil environmental variables. TOC: total organic carbon; TN: total nitrogen; C: N ratio: the ratio of TOC and TN; pH: pondus Hydrogenii; Moisture: soil water content. **: $p < 0.01$; ***: $p < 0.001$. Abandoned lands (AL), Deciduous broad-leaved forests (DB), Coniferous forests (CF), Coniferous broad-leaved mixed forests (CB), and Evergreen broad-leaved forests (EB).

4. Discussion

4.1. The Structure and Diversity of Soil Microbial Communities during the Succession Stages

Soil bacteria and fungi are the main drivers of material cycling and play important roles along the forest succession [42]. The α -diversity of soil bacterial communities exhibited a notable decline from the initial to the terminal phases of succession, aligning with findings from previous research [15,26,43]. However, soil fungal α -diversity did not vary during the succession stages, which was supported by the previous studies [15,32]. This does not completely align with our first hypothesis. The reason for the different responses of bacterial and fungal α -diversity to forest succession is that they have different survival strategies. Compared with the EB, more weeds like *Euphorbia latiris*, *Echinochloa crus galli*, and *Cyperus rotundis* were prevalent in the AL. Seasonal variation in the plant community in the AL may create more dynamic and unpredictable conditions [44]. To adapt to this relatively unfavorable environment, soil bacteria adopt an r-strategy survival mode, resulting in higher diversity. Beginning in the succession stage of CF, the environment becomes relatively stable, and bacteria are subject to selection pressure from soil organic carbon [10]. As a result, the abundance of rare bacterial communities decreased, whereas bacteria that can utilize the substrate were enriched [45]. As a K-strategy survival mode, the diversity of fungi was less sensitive to the succession of forests [46], and the null models also indicated that the response of fungi to succession is primarily driven by stochastic processes.

The PCoA and Adonis analyses revealed significant changes in the bacterial and fungal community structures at both depths throughout the succession. Many previous studies have obtained similar results [18]. LefSe analysis indicated that there was a general shift from *Chloroflexi*, *Firmicutes*, *Nitrospirota*, and *Bacteroidota* in AL to *Proteobacteria* and *Acidobacteria* in the CF to *Actinobacteria* in the EB. There were two possible reasons for our results. Firstly, it is widely accepted that copiotrophic microorganisms are associated with the r-strategy, while oligotrophic microbes are regarded as being intimately linked to the

K-strategy [31,47]. The relative abundance of *Actinobacteria* and *Acidobacteria*, which are indicative of k-strategy bacteria, has notably risen in comparison to the AL, whereas the relative abundance of *Bacteroides* belonging to the r-strategy bacteria showed an opposite trend. This suggests that the bacterial communities shifted from an r-strategy to a k-strategy in conjunction with the different phases of vegetal succession. Secondly, soil bacterial communities that were capable of sporulation and strong stress resistance were enriched in the AL. In hostile conditions, *Firmicutes* were able to produce resistant endospores [48]. For fungi, there was a general shift from *Ascomycota* enriched in the AL to *Basidiomycota* in the EB along the succession. This aligns with the findings of fungal community succession in the middle- and high-latitude regions [49,50]. Generally, members of the *Ascomycota* phylum demonstrate high resistance to disturbed environments. Meanwhile, *Basidiomycota* is crucial in breaking down stubborn organic matter because it contains several *ectomycorrhizal* and *saprophytic* fungi, which are vital for decomposing complex chemicals [51,52].

4.2. The Changes in Soil Microbial Community Assembly Processes during the Succession Stages

The establishment and maintenance of a vast variety of soil microorganisms has been a central issue in microbial ecology [16]. Our findings indicate that the median β NTI values decreased first and then increased along with the succession stages. The deterministic process was dominant in the four succession stages except for that in the CF. Although deterministic processes dominated both the initial and terminal succession stages, the factors of selection differed. At the initial stage of succession, soil bacteria are under multiple selective pressures due to the combination of harsh environments and substrates, whereas soil substrate was the main factor in selection at the terminal stage of succession [17]. The db-RDA findings indicated that TOC had a pivotal role in altering the bacterial community structures. Compared with the DB and EB, *Cunninghamia lanceolata* in the CF has lower nutrient content, higher lignin, and secondary metabolites, making it less susceptible to microbial utilization. Li et al. (2023) found that the decomposition rate of conifer litter was lower compared to that of broad-leaved species. Increased nutrient inputs may amplify the significance of stochastic processes in the relative abundance of taxonomic units [53].

For fungi, the median β NTI values significantly changed along with the succession stages. This is consistent with our second hypothesis. However, all of the median β NTI values were between 2 and -2 , indicating that the stochastic process was dominant in the soil fungal community. These findings were consistent with the results of previous research [54,55]. This result was the consequence of multiple factors. As mentioned earlier, fungi are considered K-selected species and exhibit relatively low sensitivity to environmental changes [46]. The CCA findings revealed that soil fungal community structure was impacted by soil physicochemical properties beyond only TOC, suggesting that other soil environmental factors (pH and C:N ratio) play a role in regulating fungal community composition. Almost all tree species are *ectomycorrhizal* (ECM) tree species throughout the complete succession stage. Free-living soil fungi, especially *saprotrophic* fungi, compete with ECM fungi for resources [56].

4.3. Soil Physicochemical Properties Drive Soil Microbial Community Changes

Many studies have demonstrated that forest succession modifies soil characteristics, which in turn impacts the composition and diversity of the soil microbial communities [31,32,57]. According to our findings, TOC showed an increasing trend along with the succession stages (Table S1). It is worth pointing out that only TOC was the main factor in the shift of the soil bacterial communities. This partly supports our third hypothesis. Numerous earlier investigations revealed strong positive relationships between TOC and the soil microbial communities [10,58]. Elevated TOC along with the succession indicated that more substrate and nutrients became available for soil microbes. Furthermore, extensive research has unequivocally shown that the alterations in tree species resulting

from secondary succession induce forest soil acidification. [15,59]. The soil pH exhibited a declining pattern in our investigation, while no notable disparity was observed (Table S1).

Unlike the findings for bacteria, the results of CCA analysis illustrated that soil pH, TN, and C:N ratio had an impact on the structure of the soil fungal community, in addition to TOC. The other related studies have also found that multiple environmental factors regulate the community structure of soil fungi [60,61]. Our research demonstrates that soil pH exerts a more significant influence on fungal communities in comparison to bacterial communities. Since fungi often have a greater pH tolerance range than bacteria, this is likely due to the intense interplay between pH and other variables [62]. Although multiple soil factors can affect the structure of fungal communities, the explanatory power of soil factors on fungi is lower than that of bacteria, which may be due to differences in the responses of bacterial and fungal community succession to forest succession.

5. Conclusions

From the Abandoned lands to the Evergreen broad-leaved forests, the diversity of soil bacteria decreased, while fungal diversity did not vary along with the succession stage, indicating that bacteria and fungi had distinct patterns along the forest succession. Moreover, soil bacterial and fungal communities shifted with the succession. More importantly, from Abandoned fields to Coniferous forests to Evergreen broad-leaved forests, the community assembly of soil bacteria shifts from a deterministic process to a stochastic process to a deterministic process. Throughout the whole succession, stochastic processes predominantly governed the community assembly of soil fungal communities. TOC was the influential soil environmental factor responsible for the change in the structure of the bacterial communities. More soil environmental factors such as, TOC, TN, C:N ratio, and pH co-regulate the changes in fungal community structure. Compared with soil fungi, the structure and composition of soil bacterial communities are more sensitive to substrates. In conclusion, our findings contribute to a better understanding of how the composition and assembly processes of the soil microbial community respond to plant succession in subtropical forests. For future work, co-occurrence networks, as well as abundant and rare taxa of soil microbial communities, will be further explored in subtropical forests.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/f15020242/s1>, Table S1: Soil physical and chemical characteristics along the succession; Table S2: Effects of forest succession on the composition of fungal and bacterial communities.

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