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Characteristics of Bacterial Communities under Different Tree Species and Their Response to Soil Physicochemical Properties

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Abstract: This study investigates the structure of soil bacterial communities in the brown mountain soils beneath the deciduous broadleaf forests of Dongling Mountain and their response to soil physicochemical properties. Aiming to provide a scientific basis for soil conservation and sustainable forest development under deciduous broadleaf forests, this research utilized high-throughput sequencing technology to examine the diversity and community structure of bacteria in soil under different tree species, alongside assessing soil physicochemical properties. The results revealed significant differences in nutrient content between the 0–20 cm and 20–40 cm soil layers. Additionally, the N:P in the brown mountain soils of Dongling Mountain was found to be below the national average, indicating potential nitrogen limitation. Dominant bacterial phylum included *Actinobacteria*, *Proteobacteria*, and *Acidobacteria*. The study also found that soil bacterial community structure was similar under different tree species at the same depth but varied significantly with soil depth. Furthermore, redundancy analysis (RDA) showed that the available potassium (AK), total nitrogen (TN), and ammonium nitrogen (NH_4^+-N) significantly influenced the structural changes in the soil bacterial community. This research highlights the characteristics of soil bacterial community structure beneath deciduous broadleaf forests and its relationship with soil physicochemical properties, offering valuable insights for regional soil ecosystem conservation and forest management.

Keywords: forest soil; soil nutrient; soil microorganism; community structure

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1. Introduction

Soil microorganisms are the most important decomposers on Earth. They are widely involved in soil substance transformation and cycling processes, serving as the link between aboveground and underground interactions within land-based ecosystems; they are also important drivers of preserving the variety and productivity of plants, playing crucial roles in many key ecological processes [1–3]. For example, they facilitate compound exchange between forest vegetation and forest soil through decomposition and mineralization processes mediated by bacteria and fungi [4], executing critical ecosystem functions. Soil bacteria constitute the largest group of microorganisms in soil, typically accounting for 70%~90% of soil microorganisms, with the richest genetic diversity [5]. They effectively promote organic material decomposition [6] and the liberation of soil mineral nutrients [7]. In addition, soil bacteria take part in in the cycling processes of carbon, nitrogen, phosphorus, potassium, and other substances, playing important roles in maintaining ecosystem energy-flow and material circulation [8,9]. For instance, phosphorus-solubilizing bacteria may enhance soil phosphorus availability by releasing phosphatases to form available phosphates with insoluble iron and aluminum phosphate complexes [10]. Studying the diversity and composition of bacterial communities in forest soil is critically important for safeguarding the stability of forest ecosystems.

Mountain forest systems, as a type of forest ecosystem, have relatively high ecological service values, including water retention, soil preservation, carbon capture, oxygen production, and biodiversity protection [11]. Deciduous broad-leaved forest ecosystems are an important component of northern mountain forest systems and are also the zonal vegetation in North China. However, due to frequent human disturbances, large areas of pristine deciduous broad-leaved forests are rare, making protecting existing natural secondary forests particularly important. Deciduous broad-leaved forests have a wide distribution range, and there have been relatively more studies on them, ranging from subtropical regions in the south, such as Guilin and Guangxi [12], to northeastern areas such as Xiaoxing'anling and Changbai Mountains [13]. Research on deciduous broad-leaved forests mainly focuses on biodiversity, community structure, spatial patterns, etc. [14–17]. Forest soil serves as the substrate, providing essential substances for plant development and reproduction and highlighting the undeniable significance of soil bacteria [18]. Studying bacterial communities under deciduous broad-leaved forests holds significant importance for gaining a more comprehensive understanding of the distribution characteristics of mountain soil bacteria and soil physicochemical properties' conditions.

Dongling Mountain deciduous broad-leaved forest is one of the relatively well-preserved natural secondary forests in China's warm temperate forest zone, representing typical vegetation in China's warm temperate forests [19,20]. In this deciduous broad-leaved forest, various tree species coexist, forming a rich and diverse vegetation community, with a wide distribution of brown mountain soil.

This study focuses on the brown mountain soil under the deciduous broad-leaved forest of Dongling Mountain, using high-throughput sequencing technology to analyze the abundance, diversity, and composition of soil bacterial communities associated with various tree species and across different soil depths, while also measuring soil physicochemical properties. The study aims to explore (1) the traits of bacterial community composition associated with various tree species and soil depths; (2) the impact of soil physical and chemical characteristics on the composition of soil bacterial communities. The results of this study will not only help understand the status of soil physical and chemical properties and the impact of soil physicochemical properties on soil bacterial communities in the brown mountain soil under deciduous broadleaf forests but will also provide insights into the distribution characteristics of soil bacteria in deciduous broad-leaved forest soils and a theoretical basis for forecasting how soil bacterial communities will react to alterations in the environment.

2. Materials and Methods

2.1. Study Area Description

Dongling Mountain (40°00′~40°02′ N, 115°26′~115°30′ E) is situated in the northern subsection of the warm-temperate deciduous broadleaf forest zone in China. This area experiences a warm-temperate continental monsoon climate, marked by clear seasonal changes, concurrent rainfall and warmth, an average yearly temperature of 5.4 °C, about 195 frost-free days annually, around 2600 h of sunshine per year, and an annual rainfall ranging 500~650 mm [20]. The vegetation consists of typical deciduous broad-leaved secondary forests, predominantly composed of species such as Liaodong oak (*Quercus wutaishanica*), white birch (*Betula platyphylla*), Manchurian walnut (*Juglans mandshurica*), David's poplar (*Populus davidiana*), and maple (*Acer mono*).

2.2. Plot Setup and Sample Collection

Four plots with different compositions of deciduous tree species were selected in the brown soil distribution area of Dongling Mountain. These plots were named L1 (Liaodong oak, David's poplar), L2 (David's poplar), L3 (Liaodong oak, white birch), and L4 (Liaodong oak, white birch, and Mongolian birch). Three 20 × 20 m plots were set up at each sampling site. Within each plot, three soil profiles were excavated, and intact soil samples were collected using an auger at depths of 0–20 cm (B) and 20–40 cm (D). Analytical samples

were collected using a five-point sampling method. Plant roots and stones were removed, and then the samples were thoroughly mixed. Subsequently, fresh soil was obtained using a quartering method. Some fresh soil was transferred into bags and stored in a −80 °C freezer in the laboratory for subsequent bacterial sequencing analysis. The rest of the samples were dried in the air, sieved through sieves of 2 mm and 0.2 mm mesh sizes, and then kept in sealed bags so that the soil physical and chemical properties could be assessed.

2.3. Determination of Soil Physicochemical Properties

To assess soil physicochemical attributes, distinct methodologies were employed. The acidity or alkalinity, denoted by pH, was gauged following the dilution of soil with water at a ratio of 2.5 parts water to 1 part soil. The soil's electrical conductivity (EC), an indicator of its salinity, was quantified utilizing a higher dilution ratio of 5 parts water to 1 part soil. The bulk density (BD) of the soil, which reflects its compactness, was measured through the application of the ring knife technique. For nutrient analysis, the total nitrogen (TN) level was established via the Kjeldahl procedure, which chemically digests the soil to measure its nitrogen content. The concentration of nitrate nitrogen (NO_3^--N) was identified using ultraviolet spectrophotometry, a method that measures the absorbance of UV light by nitrate ions in the soil solution. The amount of ammonium nitrogen (NH_4^+-N) present was determined through indophenol blue colorimetry, which involves a color-change reaction to quantify ammonium concentrations. The total and available phosphorus (TP and AP, respectively) concentrations were ascertained through a molybdenum antimony colorimetric technique, which relies on the formation of a colored complex between phosphorus in the soil and molybdenum antimony reagent. The assessment of total potassium (TK) and its available form (AK) was conducted via flame photometry, a process that measures the intensity of light emitted by potassium ions when they are excited in a flame, indicating the potassium concentration. Lastly, the soil organic carbon (SOC) content, indicative of soil fertility and quality, was determined using the potassium dichromate volumetric method. For detailed methods, refer to the soil agrochemical analysis by Bao [21].

2.4. Analysis of Soil Bacterial Community Diversity and Composition

For DNA extraction from soil samples, 0.5 g of each was processed using the PowerSoil DNA isolation kit (provided by MoBio Laboratories, Carlsbad, CA, USA). We checked the integrity of extracted genomic DNA via 1% agarose gel electrophoresis. Amplification of the bacterial 16S rRNA gene's V4 region was carried out using PCR with the 515F-806R primer pair, under conditions of initial denaturation at 95 °C for 3 min, followed by 27 cycles of 95 °C for 30 s, 55 °C for 30 s, and 72 °C for 30 s, ending with a final elongation at 72 °C for 10 min (using the ABI GeneAmp® 9700 PCR system, Waltham, MA, USA). Triplicate PCR assays were performed for each soil sample, and the products were subsequently combined and verified via 2% agarose gel electrophoresis. The resulting PCR fragments were then purified using the AxyPrep DNA Gel Extraction Kit (AXYGEN, Union City, CA, USA), quantified using the QuantiFluor™ -ST system (Promega, Madison, WI, USA), and used for library construction as per protocols for the Illumina MiSeq platform. Sequencing was conducted on the MiSeq platform with the PE300 strategy. Following sequencing, overlapping PE reads were merged, and the sequences underwent quality checks and filtering. Operational taxonomic units (OTUs) were then identified and analyzed for taxonomy at a similarity threshold of 97%, employing bioinformatics processing by Shanghai Meiji Biomedical Technology Co., Ltd. (Shanghai, China).

2.5. Data Processing

Data organization was carried out with Microsoft Excel 2016, while SPSS 24.0 was employed for statistical analysis. We applied one-way analysis of variance (ANOVA) to determine if there were significant differences ($p < 0.05$) among the soil physicochemical attributes and the diversity of soil bacteria; this was complemented by Duncan's post hoc test for further insights. The relationships between soil physicochemical characteristics and

bacterial diversity were assessed using Pearson's correlation analysis, and the resulting data visualizations were created using Origin2023 software. Additionally, we explored the association between soil bacterial types and soil physicochemical features utilizing the R programming language, from which we generated a heatmap for clearer visualization. Furthermore, Redundancy Analysis (RDA) was conducted within the R environment using the 'vegan' package, aimed at exploring the interactions between the soil's microbial community composition and its physicochemical properties.

3. Results

3.1. Soil Physicochemical Properties Characteristics

In Figure 1, the analysis reveals that the pH, EC, and water content levels in the topsoil layer (0–20 cm) across the four different locations exhibited no notable variations. However, the BD in site L1 was found to be significantly greater compared to sites L2 and L3 ($p < 0.05$). In the subsoil layer (20–40 cm), no marked differences were noted in pH and EC among the sites; however, the moisture content at site L1 was significantly less than that at site L2 ($p < 0.05$), and the BD at site L4 exceeded that of the other three locations ($p < 0.05$). Between sites L1 and L3, no substantial variations were detected; yet both displayed significantly elevated values in certain measures when compared to site L2 ($p < 0.05$). In general, the topsoil exhibited higher moisture content and lower BD, while the pH and EC values were relatively consistent across different soil depths.

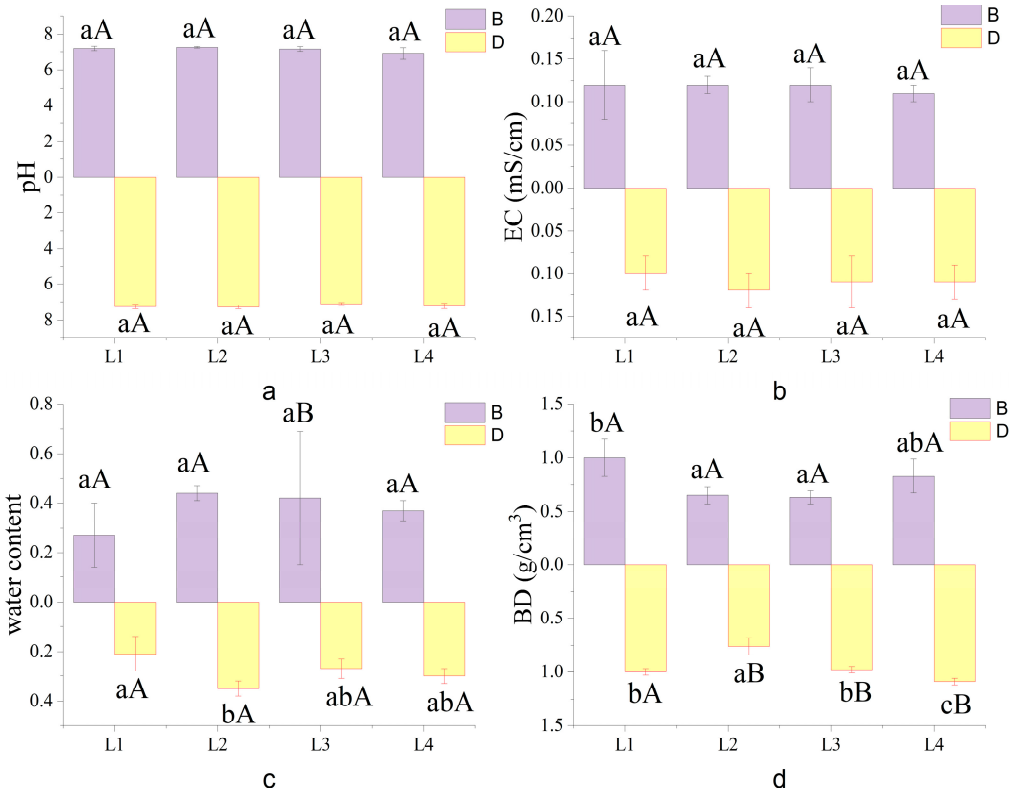


Figure 1. Physical and chemical properties of brown soil under different tree species. Note: (**a**): pH; (**b**): EC; (**c**): water content; (**d**): BD; B: 0–20 cm; D: 20–40 cm; L1: Liaodong oak, David's poplar; L2: David's poplar; L3: Liaodong oak, white birch; L4: Liaodong oak, white birch, and Mongolian birch; lowercase letters a, b, and c indicate significant differences between tree species at the same depth of soil, and uppercase letters A and B indicate significant differences between different depths of soil for the same tree species ($p < 0.05$); EC: electrical conductivity; BD: bulk density.

Per Table 1, within the topsoil layer (0–20 cm), the levels of SOC and TN were markedly greater in site L4 compared to L1, denoting statistical significance ($p < 0.05$). Conversely, TK levels were significantly elevated in L1 in contrast to L4 ($p < 0.05$). Notably, NO_3^--N

concentrations in L2 significantly surpassed those in L1 and L3 ($p < 0.05$). L4 boasted the highest NH_4^+-N levels, while no significant variances were observed in AK, AP, and TP concentrations. However, AK levels were most pronounced in L2, exhibiting a 64.3% increase over the lowest, L3.

In the deeper soil stratum (20–40 cm), NH_4^+-N and AK showed uniform levels across different tree species. However, L2 stood out with the highest concentrations of SOC, NO_3^--N, AP, and TN; similarly, its AK levels topped the chart, being 65.8% greater than those of the lowest, L1. TP values did not significantly diverge between L1 and L3 but were appreciably less than those recorded for L4 and L2. L1's TK concentration significantly surpassed those of L3 and L4 ($p < 0.05$).

Comparatively, in the 0–20 cm layer, SOC, NH_4^+-N, AK, and TN levels exceeded those in the 20–40 cm layer, recording rises of 55.75%, 55.25%, 90.48%, and 62.37%, respectively. The changes in NO_3^--N, AP, TP, and TK were minimal.

As depicted in Figure 2, no notable disparities were found in the C:N, N:P, and C:P ratios across both depths under varying tree species. Yet, the subsoil's C:N ratio slightly outpaced that of the topsoil, whereas the N:P and C:P ratios in the topsoil were significantly greater than those in the subsoil ($p < 0.05$), with mean increases of 40% and 32.3%, respectively.

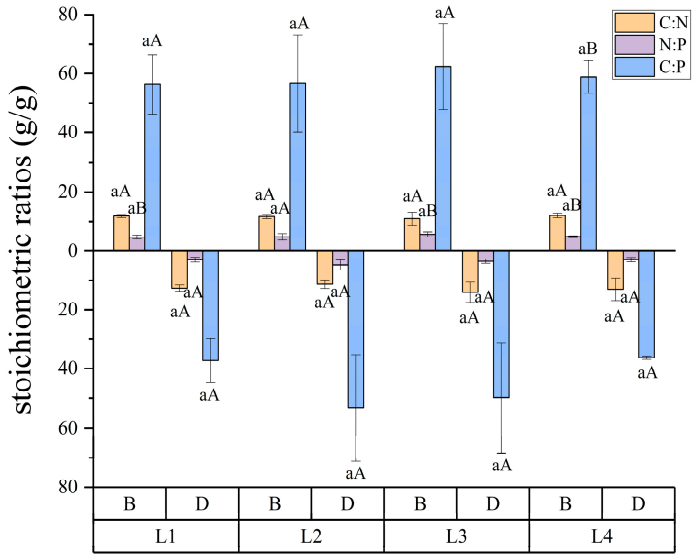


Figure 2. Nutrient chemical measurement ratio of brown soil under different tree species. Note: B: 0–20 cm; D: 20–40 cm; L1: Liaodong oak, David's poplar; L2: David's poplar; L3: Liaodong oak, white birch; L4: Liaodong oak, white birch, and Mongolian birch; lowercase letter a indicate significant differences between tree species at the same depth of soil, and uppercase letters A and B indicate significant differences between different depths of soil for the same tree species ($p < 0.05$).

Table 1. Nutrient content of brown soil under different tree species.

Treatment	SOC (g/kg)	NO_3^--N (mg/kg)	NH_4^+-N (mg/kg)	AK (mg/kg)	AP (mg/kg)	TN (g/kg)	TP (g/kg)	TK (g/kg)
L1-B	30.12 ± 4.6 aB	12.80 ± 3.6 aA	11.42 ± 2.55 aA	188.00 ± 51.88 aB	17.48 ± 1.14 aA	2.54 ± 0.4 aB	0.55 ± 0.13 aA	20.07 ± 1.1 bA
L2-B	37.17 ± 0.6 abA	18.96 ± 0.44 bB	11.89 ± 2.80 aA	221.33 ± 90.16 aA	17.57 ± 1.58 aA	3.18 ± 0.15 abA	0.69 ± 0.17 aA	19.93 ± 1.86 abA
L3-B	32.47 ± 7.91 abB	13.11 ± 2.33 aA	13.49 ± 3.06 aA	134.67 ± 36.50 aA	17.92 ± 4.09 aA	2.96 ± 0.58 abB	0.52 ± 0.03 aA	18.87 ± 0.12 abA
L4-B	41.03 ± 5.21 bB	16.96 ± 3.76 abA	24.67 ± 7.12 bB	162.67 ± 9.50 aA	15.82 ± 1.97 aA	3.39 ± 0.22 bB	0.70 ± 0.04 aA	17.87 ± 0.31 aA
L1-D	13.11 ± 7.84 aA	11.21 ± 3.77 aA	9.44 ± 6.37 aA	76.00 ± 28.48 aA	13.72 ± 0.30 aB	1.07 ± 0.72 aA	0.34 ± 0.15 aA	20.40 ± 1.22 bA
L2-D	34.90 ± 5.68 cA	29.93 ± 6.28 bA	10.71 ± 1.87 aA	126.00 ± 53.67 aA	16.43 ± 1.39 bA	3.16 ± 0.89 bA	0.69 ± 0.21 bA	19.87 ± 1.55 abA

Table 1. *Cont.*

Treatment	SOC (g/kg)	NO_3^--N (mg/kg)	NH_4^+-N (mg/kg)	AK (mg/kg)	AP (mg/kg)	TN (g/kg)	TP (g/kg)	TK (g/kg)
L3-D	17.10 ± 2.06 abA	10.71 ± 2.17 aA	9.68 ± 2.25 aA	81.00 ± 13.53 aA	14.25 ± 1.71 aA	1.27 ± 0.36 aA	0.37 ± 0.11 aA	18.07 ± 0.92 aA
L4-D	23.94 ± 0.87 bA	19.32 ± 4.47 aA	9.77 ± 4.49 aA	88.00 ± 35.79 aA	14.07 ± 0.26 aA	1.94 ± 0.53 abA	0.66 ± 0.03 bA	18.13 ± 0.12 aA

Note: B: 0–20 cm; D: 20–40 cm; L1: Liaodong oak, David's poplar; L2: David's poplar; L3: Liaodong oak, white birch; L4: Liaodong oak, white birch, and Mongolian birch; lowercase letters a, b, and c indicate significant differences between tree species at the same depth of soil, and uppercase letters A, B indicate significant differences between different depths of soil for the same tree species ($p < 0.05$).

3.2. Bacterial Diversity

Figure 3 reveals that there were no notable variances in the diversity and abundance of soil bacteria between the surface (0–20 cm) and subsoil (20–40 cm) layers across various tree types. However, the Shannon diversity index was markedly higher in the subsoil layer, illustrating significant differences in bacterial diversity across depths ($p < 0.05$). Conversely, the Chao richness index for the surface soil was marginally higher, exhibiting an approximate 1% increase.

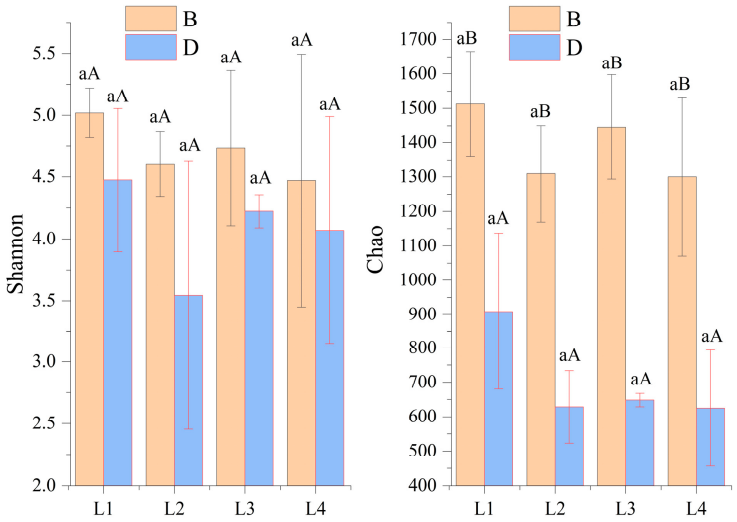


Figure 3. Alpha diversity index of soil bacteria. Note: B: 0–20 cm; D: 20–40 cm; lowercase letter a indicate significant differences between tree species at the same depth of soil, and uppercase letters A and B indicate significant differences between different depths of soil for the same tree species ($p < 0.05$).

In Figure 4, Principal Component Analysis (PCA) was applied to discern the variances in bacterial community configurations between the surface and subsoil strata among differing arboreal species. The analysis indicated that the first and second principal components accounted for 26.85% and 21.6% of the variation, respectively, amounting to a cumulative total of 48.45%. According to the PCA, the bacterial communities in the surface soil from varied tree species showed considerable overlap, suggesting a homogeneity in community structure at this depth across species. This similarity extended to the bacterial communities in the subsoil layer, indicating minimal impact from tree species variation on bacterial structure within this soil depth. However, a clear segregation was observed between the community structures of the surface and subsoil layers, highlighting significant disparities ($p < 0.05$) between the two depths. Therefore, while the influence of tree species on the soil bacterial communities was negligible, distinct differences were evident between the microbial communities at different soil depths.

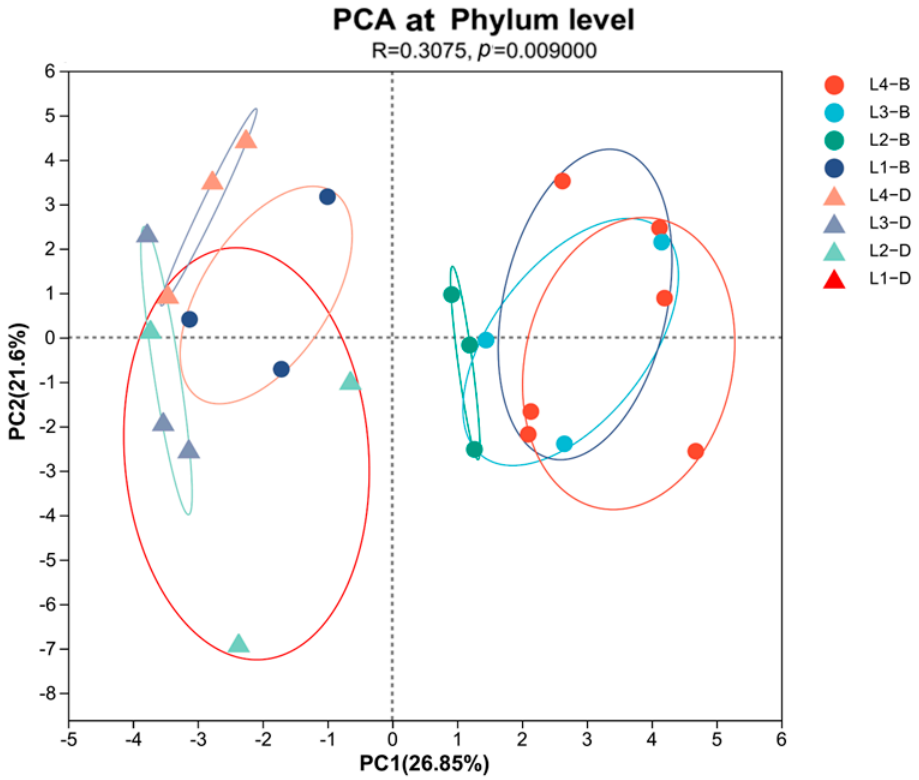


Figure 4. PCA analysis of the Beta diversity of soil bacterial communities. Note: B: 0–20 cm; D: 20–40 cm; L1: Liaodong oak, David's poplar; L2: David's poplar; L3: Liaodong oak, white birch; L4: Liaodong oak, white birch, and Mongolian birch; the colored ovals indicate three replicates of the same sample.

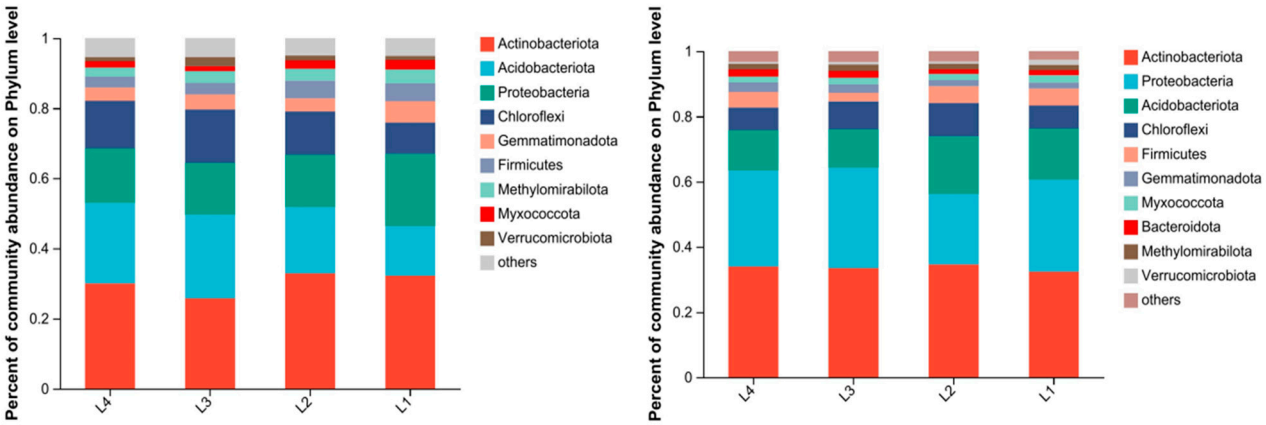
3.3. Bacterial Community Composition

The relative abundance accounting for more than 1% at the phylum level was depicted in Figure 5. In the brown mountain soil under deciduous broad-leaved forests, the dominant bacterial phylum include *Actinobacteria*, *Acidobacteria*, *Proteobacteria*, *Chloroflexi*, *Firmicutes*, *Gemmatimonadetes*, *Myxococcota*, *Bacteroidota*, *Verrucomicrobiota*, *Methylomirabilota*, and the other phylum, *Actinobacteria*, *Acidobacteria*, and *Proteobacteria* are the predominant phylum, collectively accounting for over 75% in the 0–20 cm soil and over 66% in the 20–40 cm soil. The relative abundance of soil bacteria under different tree species is shown in the attached (Table S1).

Across the varying depths of 0–20 cm and 20–40 cm beneath different tree species, the bacterial community composition remained largely uniform, with *Actinobacteria* emerging as the predominant group, forming more than 30% of the total bacterial population on average. Within the upper soil layer (0–20 cm), the presence of *Proteobacteria* from the L3 group was noticeably higher compared to that of the L2 group, exhibiting a 48.23% increase ($p < 0.05$). Conversely, in the deeper layer (20–40 cm), the L4 group's *Proteobacteria* saw a substantial increase, surpassing those of the L2 and L3 groups by 39.8% and 38.2%, respectively ($p < 0.05$). Additionally, in this deeper soil layer, *Chloroflexi* from the L4 group showed a remarkable increase of 70.85% compared to the L2 group ($p < 0.05$).

The distribution of *Bacteroidota* within the shallower soil ranged between 1.42% and 2.19%, which was significantly greater than their presence in the deeper soil ($p < 0.05$). With increasing soil depth, the relative abundances of *Acidobacteria*, *Chloroflexi*, and *Methylomirabilota* were found to escalate, with respective increases of 38.72%, 52.67% ($p = 0.03$), and 91.40% ($p = 0.002$) observed in the 20–40 cm layer compared to the 0–20 cm stratum. The hierarchy of bacterial phyla abundance in the surface soil typically followed the sequence of *Proteobacteria* > *Acidobacteria*, *Firmicutes* > *Gemmatimonadetes*. This sequence was inverted

in the deeper soil, except for L1, where *Proteobacteria* still surpassed *Acidobacteria*, and L2, where *Firmicutes* exceeded *Gemmatimonadetes*.



(**a**) (**b**)

Figure 5. The relative abundance of soil bacteria from 0–20 cm and 20–40 cm at the phylum level under different tree species. Note: (**a**): 0–20 cm; (**b**): 20–40 cm; L1: Liaodong oak, David's poplar; L2: David's poplar; L3: Liaodong oak, white birch; L4: Liaodong oak, white birch, and Mongolian birch.

The average prevalence of *Proteobacteria* and *Firmicutes* in the surface soil was higher by 66.05% ($p = 0.04$) and 7.65%, respectively, compared to their abundance in the deeper soil. In contrast, the average proportion of *Gemmatimonadetes* in the deeper soil was substantially higher: 94.23% greater than in the surface layer ($p = 0.01$).

3.4. Relationship between Soil Physicochemical Properties and Bacterial Alpha Diversity

In the upper soil layer (0–20 cm), as delineated in Figure 6a, the Pearson Correlation Analysis revealed that the Shannon diversity index had moderate associations with various environmental variables but exhibited a significant negative correlation with EC alone ($p < 0.05$). Within this soil stratum's environmental conditions, TN was found to be significantly positively associated with SOC and NO_3^--N ($p < 0.05$). TP correlated significantly and positively with NO_3^--N, AK, and TN ($p < 0.05$). TK demonstrated a significant positive relationship with AK ($p < 0.01$) but held a negative association with NH_4^+-N ($p < 0.05$). The N:P ratio was significantly positively correlated with the C:P ratio ($p < 0.001$) and negatively with TP ($p < 0.05$). Moreover, the C:P ratio was significantly positively linked to the C:N ratio ($p < 0.05$).

For the deeper soil layer (20–40 cm), as depicted in Figure 6b, the Pearson Correlation Analysis between soil parameters and bacterial diversity indices indicated a significant positive correlation of the Shannon index with factors including SOC, NO_3^--N, NH_4^+-N, AK, and TN ($p < 0.05$). Among the environmental metrics, SOC had strong positive relationships with NO_3^--N, TN, and TP ($p < 0.01$) and showed significant correlations with AK, water content, and the N:P ratio ($p < 0.05$). NO_3^--N was positively and significantly related to TN, TP, and water content ($p < 0.01$), as well as AK and N:P ($p < 0.05$). AK exhibited a highly significant positive correlation with both TN and N:P ($p < 0.01$). TN was strongly positively correlated with TP ($p < 0.01$) yet showed a strong negative correlation with BD ($p < 0.01$). Finally, the N:P ratio was significantly positively associated with both AK and C:P ($p < 0.05$).

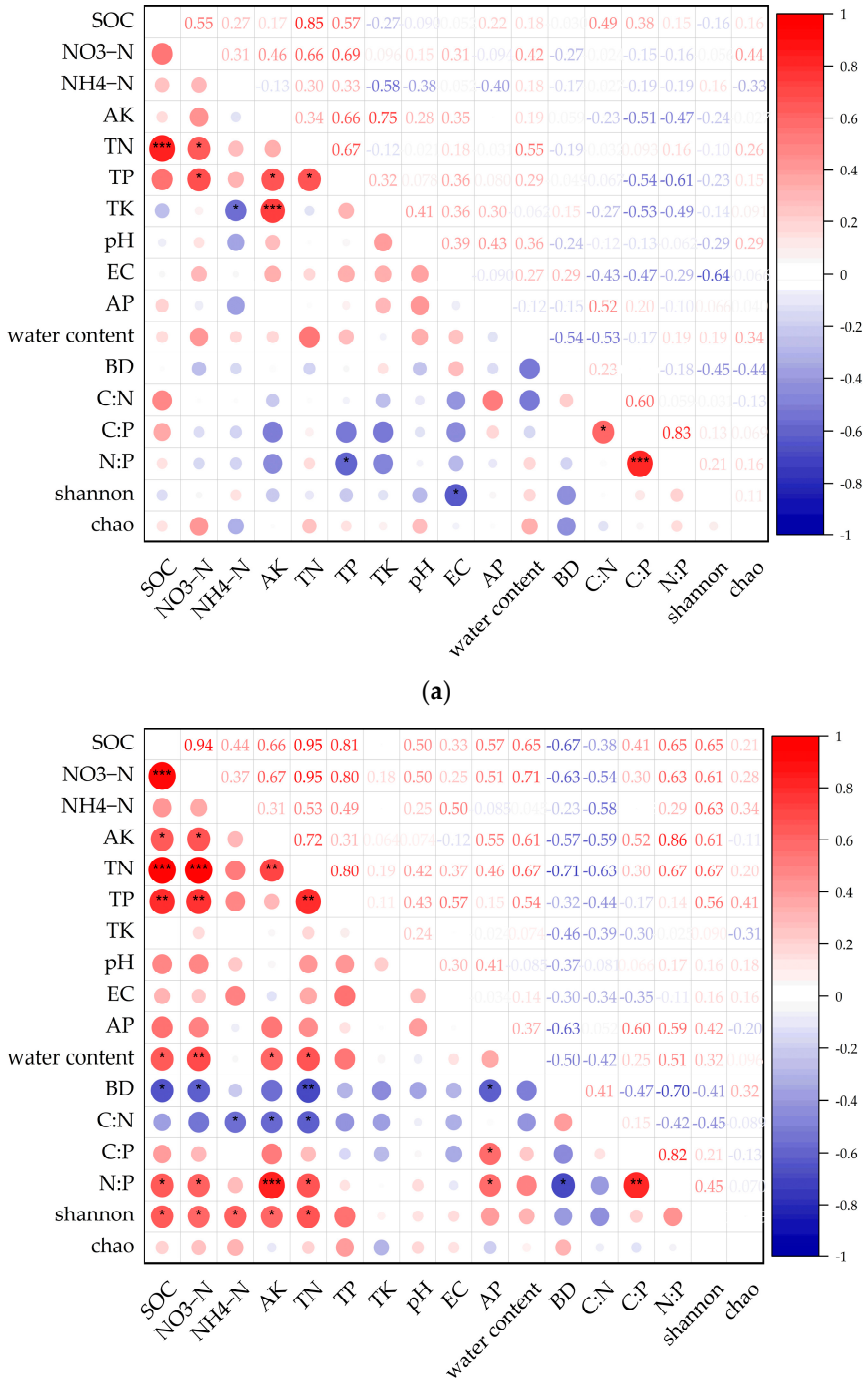


Figure 6. The relationships between 0–20 cm and 20–40 cm soil fertility factors and bacterial alpha diversity. Note: (**a**): 0–20 cm; (**b**): 20–40 cm; BD: soil bulk density; TN: total nitrogen; TP: total phosphorus; AK: available potassium; SOC: soil organic carbon; TK: total potassium AP: available phosphorus; NO_3^--N: nitrate nitrogen; NH_4^+-N: ammonium nitrogen (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

3.5. Soil Physicochemical Properties and Individual Bacterial Community Correlation Analysis

The correlation analysis depicted in Figure 7 between soil physicochemical characteristics and the dominant bacterial phyla showed that the interaction between soil parameters and bacterial communities was significant for 15 different factors. *Actinobacteria* were positively associated with AK, SOC, and TN, all showing significant correlations at $p < 0.01$.

In contrast, negative significant associations were identified between NH_4^+-N, AK, TN, and N:P with *Acidobacteria*, marked at $p < 0.05$.

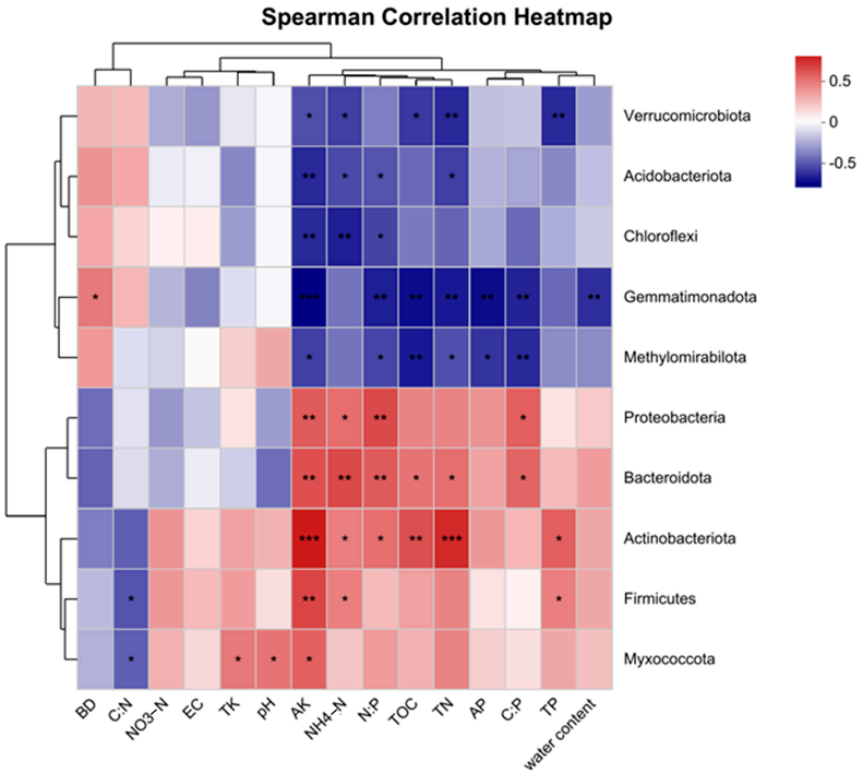


Figure 7. Correlation of soil fertility factors with soil bacteria at the level of phylum. Note: Same as Figure 6 (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

Furthermore, significant relationships were noted between NH_4^+-N, AK, C:P, and N:P with *Proteobacteria*, and similar significant correlations were also found with NH_4^+-N, AK, and N:P with *Chloroflexi* ($p < 0.05$). The *Firmicutes* displayed a positive significant correlation with NH_4^+-N, AK, and TP ($p < 0.05$). Conversely, *Gemmatimonadetes* were negatively correlated with AK, N:P, SOC, TN, AP, C:P, and water content ($p < 0.05$). Notably, AK was significantly correlated with additional bacterial groups such as *Myxococcota*, *Bacteroidota*, *Verrucomicrobiota*, and *Methylomirabilota* ($p < 0.05$). These results underscore the intricate interplay between soil physicochemical properties and the composition of the soil bacterial community.

3.6. The Influence of Soil Physicochemical Properties on the Bacterial Community Structure

The Redundancy Analysis (RDA) graph provides insights into how different soil factors affect the bacterial community composition. In this analytical representation (Figure 8), the length of the radii linked to specific factors is indicative of their impact on the bacterial community structure—longer radii suggest a more significant influence. Moreover, the proximity between the segments related to the bacterial communities and the axis illustrates the strength of their relationship, where closer distances reflect stronger correlations. Within this RDA framework, the first and second axes (RDA1 and RDA2) account for 60.99% and 10.46% of the total variance observed in bacterial community structures due to soil conditions, respectively, cumulatively explaining 71.45% of the variation. This significant cumulative percentage underscores the strong influence soil conditions have on microbial assemblages.

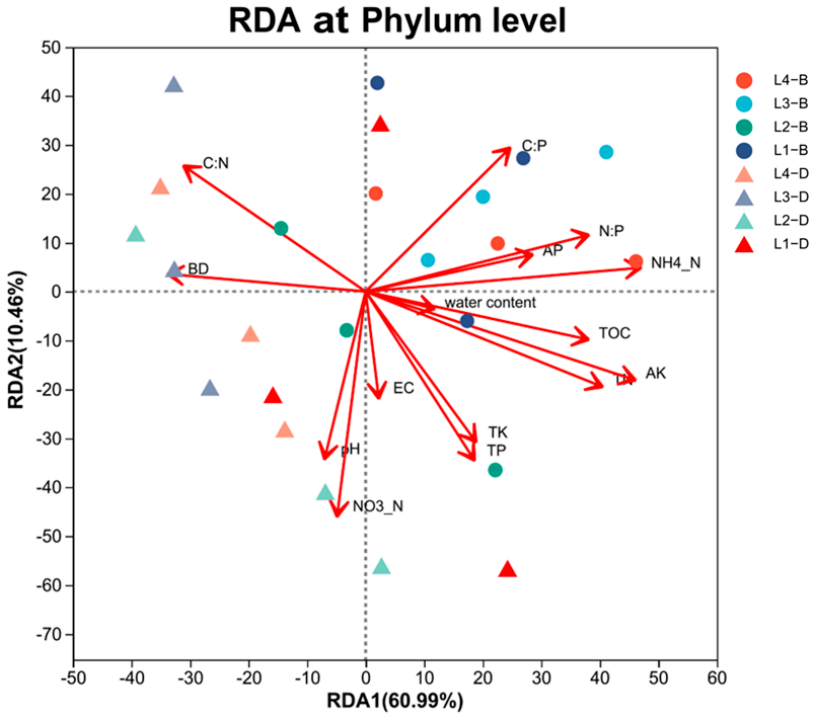


Figure 8. Redundancy analysis of soil fertility and soil bacterial community structure at the level of phylum. Note: B: 0–20 cm; D: 20–40 cm; L1: Liaodong oak, David's poplar; L2: David's poplar; L3: Liaodong oak, white birch; L4: Liaodong oak, white birch, and Mongolian birch; Same as Figure 6.

Specific soil physicochemical properties—namely AK, TN, and NH_4^+-N—were identified as having a substantial impact on the diversity and structure of soil bacterial communities, evidenced by significant *p*-values (AK at $p = 0.02$, TN at $p = 0.04$, and NH_4^+-N at $p = 0.01$). These findings highlight the integral roles these soil nutrients play in shaping the bacterial landscape within these environments.

4. Discussion

In our research, significant variations in soil physical and chemical properties were observed among different tree species. The L2 soil had overall higher nutrient content, which may be correlated with its lower BD density. Lower BD indicates relatively loose soil with stronger porosity, facilitating the downward leaching and absorption of nutrients released during litter decomposition, thus promoting nutrient retention in the soil. K content was abundant under various tree species, especially in the 0–20 cm soil layer, meeting the second-grade standard according to the National Soil Survey Office [22]. This might be attributed to potassium returning to the soil not only from plant litter but also from K-rich minerals such as orthoclase and biotite in the parent rocks of brown soil, which gradually release K during weathering processes [23,24]. SOC, AP, TN, and TK in the 0–20 cm soil layer reached third-grade standards or higher, whereas in the 20–40 cm soil layer, the nutrient content was within the third-grade standard or lower. This difference might be due to better air, light, temperature, and moisture conditions in the 0–20 cm soil layer, leading to more active microbial communities and faster decomposition of litter and release of nutrients from soil minerals [25,26].

No significant differences were found in soil C, N, and P stoichiometry among different tree species, but we found a potential issue in the soil of the study area. Soil C, N, P stoichiometry was an important indicator reflecting the internal C, N, and P cycles, indicating the coordination of element utilization and nutrient supply in the soil [27]. An imbalance in this ratio can restrict the supply of N or P, significantly affecting microbial composition and diversity [28,29]. In this study, soil C:N and C:P (mean 12.22, 51.34) were lower than the global averages (mean 13.5, 162.2) [30], with C:N lower than the average

for surface soils in China (mean 14.4) [31]. A lower C:N indicates faster nitrogen release into the soil for utilization, leading to higher levels of available N in the soil surface layer. C:P was also lower than the Chinese average (mean 136) [31], suggesting a tendency for P release during soil organic matter decomposition, leading to higher P availability in the soil, which is consistent with the study results. The N:P ratio serves as a gauge for N saturation, indicating the balance between N and P elements crucial for plant growth in soil, and can help establish thresholds that define nutrient limitations [32]. N:P (mean 4.28) was lower than global (mean 11.7) [30] and Chinese (mean 9.3) [31] averages, indicating relatively low N supply levels in the region and suggesting potential N limitations in the soil.

Our study showed that tree species do not significantly influence soil bacterial communities, suggesting uniform diversity and composition despite tree variation. Soil depth, however, plays a crucial role in shaping these communities, more so than tree species. While the bacterial species remained consistent across tree species, Proteobacteria showed significant relative abundance variations, and minor differences appeared in other phyla. Despite tree species exerting limited influence, significant differences in bacterial community structures were evident between soil depths of 0–20 cm and 20–40 cm, primarily due to variations in soil nutrient content. Mundra et al. [33] discovered that alterations in soil properties, specifically SOC and N content, driven by tree-mediated processes, were the primary factors influencing shifts in bacterial communities. Litter from different tree species has different chemical compositions and structural characteristics, and the decomposition process of litter also produces various metabolites, which significantly affect soil microbial communities and related processes [34]. In this study, minimal disparities were observed in soil physicochemical properties among different tree species. Additionally, alterations in tree species did not lead to significant modifications in soil properties, particularly pH, which is recognized as a key determinant shaping bacterial community structure [35]. Instead, substantial discrepancies in soil physicochemical properties were evident across different depths, with soil depth exerting a pronounced influence on nutrient content. Therefore, compared to differences between tree species, soil depth emerges as the primary determinant shaping soil physicochemical properties.

Acidobacteria, *Actinobacteria*, and *Proteobacteria* were identified as the predominant soil bacterial phylum in deciduous broadleaf forests in the study. Fu et al. [36] confirmed that the major bacterial phylum in temperate forests at different latitudes are *Acidobacteria* and *Actinobacteria*, with *Proteobacteria* also present in forests at lower latitudes. Similarly, Landesman et al. [37] found that forest soils in temperate deciduous forests are predominantly composed of *Acidobacteria*, *Actinobacteria*, and *Proteobacteria*. Yang et al. [38] also obtained similar results in warm-temperate broadleaf forests. These studies collectively suggest that *Acidobacteria*, *Actinobacteria*, and *Proteobacteria* may constitute the core bacterial communities in temperate forest soils.

In this study, we analyzed microbial communities in brown mountain soils beneath deciduous broad-leaved forests of Dongling Mountain, focusing on depths of 0–20 cm and 20–40 cm. We discovered that *Bacteroidota* phylum was significantly more prevalent in shallower soil, with notable ecological correlations to soil nutrients. Statistically, *Bacteroidota* differed markedly between soil depths, showing strong associations with NH4+-N, AK, and N:P ratio, indicating a preference for specific soil conditions. *Bacteroidota* tend to thrive in nutrient-rich soils, especially those rich in C [39]. The higher relative abundance of *Bacteroidota* in soils with elevated soil nutrient levels, such as SOC, which was particularly notable in the 0–20 cm soil layer, suggests a favorable environment for their proliferation and growth.

Actinobacteria serve a vital ecological function in soil, such as decomposing organic matter and mineralizing nutrients [40,41]. In this study, *Actinobacteria* showed a significant positive correlation with key soil nutrients like AK, SOC, and TN ($p < 0.01$), highlighting their vital role in nutrient cycling and assimilation. Liu et al. [42] also found that the relative abundance of *Actinobacteria* decreased with the decrease in SOC, TN, and NH_4^+-N. *Proteobacteria* can utilize the active components of SOC for growth and metabolic processes

and exhibit faster growth rates in nutrient-rich soil environments [43]. In this investigation, we found that the prevalence of *Proteobacteria* was linked with the nutrient levels. Moreover, the proportion of *Proteobacteria* was noticeably greater in the topsoil layer that was rich in nutrients, specifically between 0–20 cm. This supports the notion that these bacteria thrive under carbon-rich conditions, facilitating robust metabolic activities and rapid proliferation. Ling et al. [44] emphasized a similar result: that *Proteobacteria* and *Actinobacteria* are usually adapted to conditions rich in carbon to achieve high metabolic activity, rapid growth, and reproduction.

The relative abundance of *Chloroflexi* increased with the depth of the soil layer and was negatively correlated with the soil nutrient content. This may be related to the nutritional mode of *Chloroflexi*, which has a diverse metabolism and anaerobic phototrophy, and has a higher competitive advantage in deep soil with low nutrient content [45]. *Acidobacteria* are typical oligotrophic bacteria, and thus are more adapted to nutrient-poor soil environments [46]. In our study, a significant negative correlation was observed between the relative abundance of *Acidobacteria* and soil nutrient content. *Acidobacteria* grow slowly, and when the soil nutrients or structure change, faster-growing bacteria will replace the oligotrophic growth of *Acidobacteria*. This correlation led to a decrease in the relative abundance of *Acidobacteria* [47]. Thus, the relative abundance of *Acidobacteria* in the 0–20 cm soil was lower. Similarly, Uroz et al. [48] also documented a layering of bacterial populations in soil, observing a significant prevalence of *Bacteroidota* and *Proteobacteria* in the nutrient-dense organic layers of soil, whereas *Acidobacteria* and *Chloroflexi* were notably abundant in the less nutrient-rich mineral layers.

The differing requirements of soil bacteria for soil nutrients were important factors driving changes in their community structure. The results of redundancy analysis further support this point, showing that soil physicochemical properties contribute cumulatively to 71.45% of the variation in soil bacterial community composition, among which AK ($p = 0.02$), TN ($p = 0.04$), and NH_4^+-N ($p = 0.01$) significantly influence the variation in soil bacterial community composition. This suggests that soil nutrients play a significant role in influencing the changes observed in the structure of soil bacterial communities, with N having a particularly significant impact. This finding is consistent with the analysis of soil physicochemical properties in the preceding text, which suggests the possibility of N limitation in the soil. It is well known that N is an essential element for the survival of soil bacteria. Under N-limited conditions, soil bacteria may need to adapt to the scarcity of nitrogen resources through different strategies, which may result in alterations to the community structure. Previous studies have consistently demonstrated the pivotal role of soil nutrients in shaping bacterial community structures, highlighting the essential nature of C, N, P, and K in bacterial survival and metabolic activities. These nutrients are integral to the assembly and functioning of bacterial communities, dictating not only community composition but also influencing critical metabolic processes within the bacterial ecosystems [49]. In support of this, research by Fallah et al. [50] highlighted the significant impact of soil nutrients, including NH_4^+-N, NO_3^--N, TN, and AP, on the composition of soil bacterial communities. This underscores the fact that variations in these nutrient levels can lead to discernible shifts in the microbial community dynamics. Therefore, in the context of brown mountain soils under deciduous broad-leaved forests, such as those found in the Dongling Mountain area, the nutrient profile plays an indispensable role. It not only determines the overall health and fertility of the soil but also fundamentally influences the structural dynamics of the resident bacterial communities. This underscores the necessity of maintaining balanced soil nutrients for the sustainability of soil health and the stability of microbial ecosystems in forested environments.

5. Conclusions

This research investigates the structural dynamics of bacterial communities within the brown mountain soils beneath the deciduous broad-leaved forests of Dongling Mountain, with particular focus on how these communities are influenced by variations in soil nutrient

levels. The findings from this study underscore the importance of soil nutrients in dictating the composition and structure of soil bacterial communities. Specifically, we observed that different bacterial phyla adapt and vary in distribution and abundance based on the soil's nutrient environment. The investigation into soil C, N, and P stoichiometric ratios further highlights a potential nitrogen limitation within the study area, prompting avenues for additional research. This revelation is crucial as it points towards the necessity of addressing nutrient imbalances for the maintenance and sustainability of forest ecosystems. Overall, the study offers valuable insights into the complex interactions between soil nutrients and bacterial ecosystems under the deciduous broad-leaved forests. The outcomes not only enhance our comprehension of microbial life in forest soils but also inform strategies for the conservation and sustainable management of these vital soil resources. Consequently, this research plays a pivotal role in guiding the stewardship of below-ground biodiversity and nutrient cycles within such forested areas.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/f15050740/s1, Table S1: Relative abundance of soil bacteria under different tree species.

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