

Article

Investigating the Effects of Elevation on Microbial Communities and Soil Properties at Fanjing Mountain, China

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Abstract: Elevation is one of the most influential factors affecting soil characteristics and microbial communities in forest ecosystems. Nevertheless, there is no consensus on how soil characteristics, soil microbials, and their relationships response to the elevation of the mountain ecosystem. We investigated the soil physicochemical characteristics, the activity of soil enzymes, and the microbial community at elevational sites from 600 to 2400 m above sea level (asl) in the western slopes of the Fanjing Mountain ecosystem, China. The soil microbial communities were determined by high throughput 16S rRNA and ITS amplicon sequencing. The results demonstrated that soil total nitrogen (TN) showed a slight decrease, whereas total phosphorus (TP) and total potassium (TK) gradually tended to increase with increasing elevation. The large macroaggregates (>2 mm) accounted for the largest proportion of the aggregate fraction (66.23%–76.13%) in the 0–10 cm soil layer with elevation. The average values of the soil electrical conductivity (EC), soil organic carbon (SOC), and cation exchange capacity (CEC) concentration in the 0–60 cm layer undulated with increasing elevation, and the highest values were observed at 1500–1800 m asl and 1800–2100 m asl, respectively. The activities of soil urease, sucrase, acid phosphatase, and catalase clearly differed ($p < 0.05$) with increasing elevation, and the minimum values were found at 2100–2400 m asl. Interesting, with increasing soil depth, the values of these factors tended to decrease, indicating surface aggregation. In addition, the soil microbial (bacterial and fungal) community diversity exhibited a single-peak pattern with elevation. Our results also revealed that the soil bacterial and fungal communities varied significantly at different elevation sites. The bacterial communities were dominated by the phyla Acidobacteria, Pseudomonadota, and Chloroflexi, and the phyla Basidiomycota and Ascomycota dominated the fungal communities. The Pearson and redundancy analyses revealed that the SOC, TP, four soil enzymes, and soil aggregates were significant factors influencing the soil microbial community. In conclusion, soil properties and enzyme activities jointly explained the elevational pattern of the soil microbial community in the Fanjing Mountain. The results of this study provide insights into the influence of elevation on soil characteristics, microbial communities, and their relationships in the Fanjing Mountain ecosystem.

Keywords: soil physiochemical properties; extracellular enzymes; high-throughput sequencing; soil microbial community; elevation



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1. Introduction

Soil microorganisms are fundamental biological units of soil ecosystems, and their community structure, diversity, and functioning can be utilized to evaluate their health [1,2].

As the link between soil and plants, soil microorganisms play important roles in the storage of various types of soil carbon, soil organic matter (SOM) decomposition, mineralization, plant community assembly, nutrient immobilization, and other biochemical processes [3,4]. In recent years, changes in soil characteristics and microbial community structures according to variety environmental factors have attracted considerable interest for novel perspectives on the influence of environments on biological communities [3,5,6], especially in various forest soils [7]. Elevation is a critical aspect of mountain topography and can lead to spatial heterogeneity of biological and abiotic elements by influencing ecological factors such as temperature, precipitation, and light [7,8]. For example, several studies have demonstrated that elevation is the main factor affecting the diversity and abundance of soil microbial communities in various forest soils because it can cause variations in precipitation and temperature, which in turn will influence different forest soil microbial community structures and species diversity [9–11]. Nevertheless, the response of the soil microbial community and diversity differ across the elevation of different forest ecosystems, in which the climate, forest type, and azonal soil properties covary even over small spatial distances [12–14]. Moreover, there is no decisive pattern response of soil microbial diversity along elevation; it is essential to study the distribution and abundance of the soil microbial community and its relationships with soil property factors at different elevation sites, which may provide insight into the effects of elevation on the soil properties and microbial community composition in montane ecosystems.

Elevation has been taken as a strong “natural laboratory” to explore the elevational patterns of soil microorganism communities and their properties because of the dramatic climate variation at small spatial scales [15–17]. Compared with the elevational patterns of plant and animal communities, microbial diversity displays a different trend at the same increasing elevation owing to the greater sensitivity of microorganisms to environmental variations [18,19]. Currently, although diverse modes of elevation-associated soil microbial community and diversity have been extensively studied, including monotonously linear increasing [8], monotonously linear decreasing [9], humpback [20], concave [21,22], or no regular change distribution patterns related to [23], a consensus remains complicated. The lack of accordance potentially suggests that the elevational pattern of microbial diversity and community composition is site-dependent, confirming the conclusions of a global synthesis study [9,24]. Additionally, numerous studies have demonstrated that greater diversity and richness of understory vegetation are beneficial to litter decomposition and matter cycling and that the litter decomposition rate is controlled by the types and activities of soil enzymes, and higher soil enzyme activity in turn accelerates plant growth and development [24,25]. Thus, soil enzyme activity can be a crucial indicator of soil health status and microbial activity because of its functional properties and susceptibility to environmental stress [26,27]. The relationships among elevation, soil physicochemical characteristics, enzyme activities, and microbial communities still need to be explored further, which is beneficial for enhancing our comprehension of the spatial changes in active soil substances in mountain ecosystems. In conclusion, the elevational patterns of soil microbial community structure and enzyme activity were closely correlated with geographical distributions, which verified the importance of exploring the elevational patterns of microbial diversity and enzyme activity in soils from more habitats.

The Fanjing Mountains have the most biodiversity-rich terrestrial zones at the same latitude in the world and are typical representatives of global hotspots for biodiversity conservation [28,29]. The vertical zone spectrum of vegetation in Fanjing Mountains has the general structure of the vertical band spectrum of humid subtropical mountain vegetation in eastern China; for example, it is an evergreen broad-leaved forest belt below 1300 and 1400 m, a mixed evergreen and deciduous broad-leaved mixed forest belt between 1400 and 2000 m, and a subalpine coniferous and broad-leaved mixed forest and shrub meadow belt between 2200 and 2570 m [29,30]. Although many researchers have reported that the soil characteristics can be used to evaluate the elevation-dependent variations in the microbial community structure of mountain ecosystems [30,31], our understanding of the impact

of elevation on soil characteristics and the microbial community in Fanjing Mountain is limited. The aims of this work were to (1) investigate the response of soil physicochemical characteristics to elevation on the western slope of Fanjing Mountain; (2) explore the changes in soil microbial diversity and communities at different elevation sites; and (3) identify the possible environmental driver factors that could change soil microbial communities among the determined physicochemical factors of soil. We hypothesized that soil physicochemical characteristics, the activities of soil enzymes, soil microbial communities, and diversity respond differently to the elevation. Consequently, we examined the alterations in soil properties, enzyme activities, and the microbial community at six elevation sites on Fanjing Mountain (600–2400 m asl) and to identify the possible environmental drivers of elevational changes in the soil microbial community. This research provides important basic information and novel understandings of the formerly substituted soil properties and microbiomes of Fanjing Mountain and will help us better understand the effects of elevation variation on belowground microbial communities.

2. Materials and Methods

2.1. Study Area Description

The Fanjing Mountain is located in the northeastern part of Guizhou Province in China ($27^{\circ}49'50''$ – $28^{\circ}1'30''$ N, $108^{\circ}45'55''$ – $108^{\circ}48'30''$ E, Figure 1) [28,29]. Fanjing Mountain, with 96.5% forest coverage, has a subtropical humid monsoon climate. The forests in the study area are largely mountainous deciduous broad-leaved secondary forests and evergreen broadleaf forests. The highest peak elevation is 2570.0 m asl, and the relative height difference of the mountain body is more than 2000 m. The annual precipitation is 1100–2600 mm and is mainly concentrated in April–October. The average temperature in the hottest month (July) is 25.3°C , the coldest month (February) average temperature is 2°C , the annual frost-free period is 270–278 d, and the annual average relative humidity is 80% [28,29]. There is an evergreen broad-leaved forest belt below 1300–1400 m, an evergreen and deciduous broad-leaved mixed forest belt between 1400 and 2000 m, and a subalpine coniferous and broad-leaved mixed forest and shrub meadow belt between 2200 and 2570 m in Fanjing Mountains [29,30].

Additionally, the parent material of soil is mainly the residual and slope deposits of Proterozoic Banxi group metamorphic rock weathering, and the predominant soil types include yellow soil and yellow-brown soil, alongside pronounced soil thickness, clay content, total iron, and free iron-oxide content, all of which exhibited a reduction with increasing elevation in Fanjing Mountain [29,30]. Meanwhile, the annual average temperature decline rate is 0.5 – $0.56^{\circ}\text{C}/100\text{ m}$, and the rainfall increases with the increase of elevation in Fanjing Mountain, which has obvious vertical zonal mountain climate attributes [30,31].

2.2. Study Plots and Soil Sample

In Sept 2022, the experimental sites were established at various elevations, from west to east, following the Niuwei River on the western slopes of Fanjing Mountain (Figure 1). The elevation sites were set at intervals of 300 m and split into an elevation range from the bottom to the top of 600–2400 m asl (Figure 1). At each elevation site, three replicate soil sampling plots ($20\text{ m} \times 20\text{ m}$) more than 100 m apart were established at the same elevation along an “S” path drawn at each site. Soil samples were obtained from the 0–10 cm, 10–20 cm, 20–40 cm, and 40–60 cm layers at each elevation. A total of 72 (3 replicate samples $\times$ 6 elevations $\times$ 4 soil layers) soil samples were obtained from all elevation locations. All the soil samples were brought back to the laboratory and separated into two parts: one part was air-dried, sieved through 2.0 and 0.25 mm meshes, and stored at room temperature for the determination of soil physicochemical characteristics, and the other part was sieved through 2.0 mm mesh immediately stored at -80°C for the determination of soil microorganisms. The soil profiles of different elevations are shown in Figure S1.

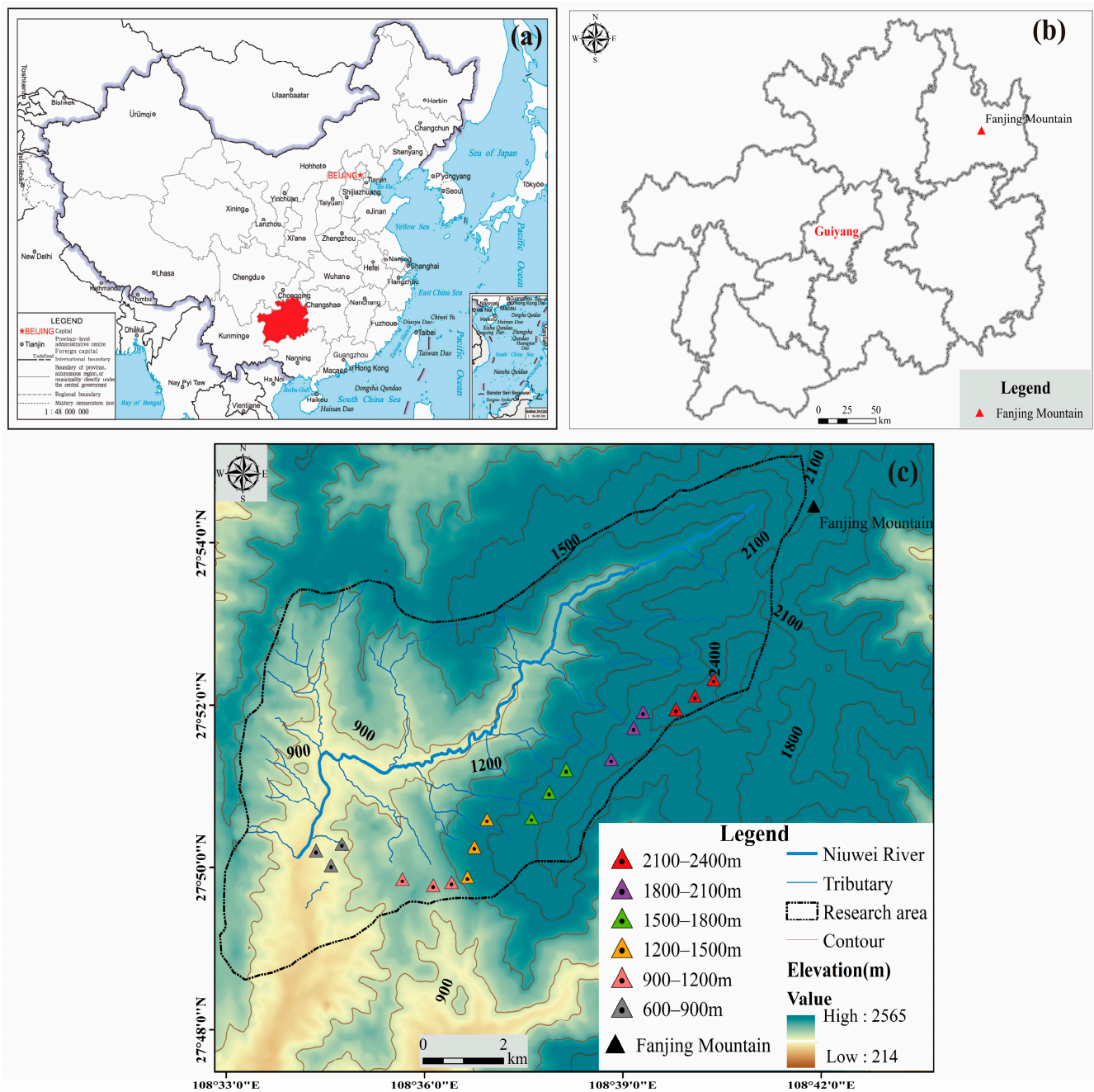


Figure 1. (a) Map of Guizhou in China. (b) Map of Fanjing Mountain in Guizhou, China. (c) Map of the study area in Fanjing Mountain, China.

2.3. Soil Physiochemical Property Determination

The soil pH was measured in a 1:2.5 (mass:volume) suspension of soil to water for 1–2 min via a pH meter (PHSJ-6L, Shanghai Yanfeng Electronic Technology Co., Ltd., Shanghai, China) [7]. The soil cation exchange capacity (CEC) was evaluated using the method of ammonium chloride [21]. The soil electric conductivity (EC) was determined via a conductivity meter (DDSJ-318 T, INESA, Shanghai, China) [32]. The soil aggregates were separated and analyzed using the dry-sieving method with different particle sizes of >5, 5–2, 2–1, 1–0.5, 0.5–0.25, and <0.25 mm [33]. Soil organic carbon (SOC) was quantified by the oil bath heating potassium dichromate-volumetric method, soil total nitrogen (TN) was determined by heating digestion-alkaline hydrolysis and the diffusion-semimicro Kelvin's method, soil total phosphorus (TP) was measured by the molybdenum antimony colorimetric method,

and soil total potassium (TK) was measured by the heating digestion-flame photometry method [21,32,33]. In addition, soil urease (SUE) activity was determined by the sodium phenol-sodium hypochlorite colorimetric method; soil sucrase (SS) activity was measured using the 3,5-dinitrosalicylic acid colorimetric method; the soil catalase (SCAT) activity was determined by titration with the KMnO₄ method; and the soil acid phosphatase (SACP) activity was assessed via p-nitrophenyl phosphate colorimetry [20,21,25]. The deionized water was used to analyze the above indicators.

2.4. Soil DNA Extraction and High-Throughput Sequencing

The microbial DNA was extracted from 0.5 g of fresh weight soil using soil DNA extraction kits (Omega, Norcross, GA, USA), following the manufacturer's instructions. The purity and quality of the extracted total DNA were examined via 1% agarose gel electrophoresis using a NanoDrop2000 spectrophotometer (Thermo Fischer Scientific, Waltham, MA, USA). For bacteria, the V3–V4 regions of the 16S rRNA gene were amplified using the universal primers 338F (5'-ACTCCTACGGGAGGCAGCA-3') and 806R (5'-GGACTACHVGGGTWTCTAAT-3'). For fungi, the universal primers ITS1 (5'-CTTGGTCA TTTAGAGGAAGTAA-3') and ITS2 (5'-TGCCTTCTTCATCG ATGC-3') were used to amplify the internal transcribed spacer (ITS) regions of fungal rRNA [34]. Polymerase chain reactions (PCRs) for bacteria and fungi were performed in detail [7]. The Illumina MiSeq platform (Illumina, San Diego, CA, USA) at Microeco Tech Co., Ltd. (Shenzhen, China) was used for high-throughput sequencing. The raw sequencing data were deposited into the NCBI Sequence Read Archive (SRA) database (BioProject ID: PRJNA1093166).

2.5. Sequencing Analysis

Reads were quality-filtered and demultiplexed to acquire available sequences via the QIIME (version 1.9.1) pipeline and based on the following criteria: (1) a minimum length of 150 bp, (2) Phred quality scores over 20, (3) no ambiguous bases, and (4) mononucleotide repeats <8 bp. The valid sequences were assigned to operational taxonomic units (OTUs) at 97% similarity using UPARSE software (version 7.0.1). The SILVA (release 128) and UNITE (version 7.2) databases were utilized for annotation of bacterial and fungal species information, respectively. The microbial taxonomic composition was drawn via R package version 3.2. The soil microbial alpha diversity was evaluated by the α -diversity (Chao 1 index, Shannon and Simpson index) indices via QIIME [11,34,35].

2.6. Statistical Analysis

One-way analysis of variance (ANOVA) and Tukey's multiple comparisons test were employed to determine the obvious differences in soil physicochemical characteristics (such as soil pH, TN, TK, and soil enzyme activities, etc.), and the significance level at $p < 0.05$ was determined via SPSS 23.0 (IBM, Armonk, NY, USA). The data are presented as the means $\pm$ standard deviations of triplicate samples. Pearson correlation analysis was implemented to estimate the relationships between the soil physicochemical characteristics and the soil microbial composition. All the graphs were generated via Origin 2022 (Origin Lab, Northampton, MA, USA). Redundancy analysis (RDA) was performed to analyze the relationships between physicochemical characteristics and the dominant genera in the soil microbial communities via Canoco 5.0 software [9]. The network visualization was carried out using Wekemo Bioincloud (<https://www.bioincloud.tech/>), an online platform for data analysis.

3. Results

3.1. Elevation-Induced Influences on Soil Properties at Different Soil Depth

The measured soil TN, TP, and TK concentrations varied with elevation from 600 m to 2400 m asl (Figures 2a,b and S2a). The soil TN concentration slightly decreased, whereas the TP and TK concentrations gradually tended to increase with elevation (Figures 2a,b and S2a). At the same elevation, the concentrations of TN and TP decreased with increasing soil

depth, while the trend of the TK concentration was the opposite. The soil N concentration significantly differed among the different soil layers at the same elevation ($p < 0.05$). There were no significant differences between different elevation sites in the same soil layer at low and middle elevations (<1800 m asl), except at high elevations (>1800 m asl). The TP concentration did not vary significantly among the different soil layers at the same elevation when the elevation was less than 1500 m asl, whereas the opposite results were observed with increasing elevation (>1500 m asl). Similarly, there was a marked difference between high and low elevations within the same soil layer. In addition, the TK concentration of the same soil layer at high elevations (>1800 m asl) was remarkably greater than that at low and middle elevations (<1800 m asl). Interestingly, the TK concentration in the topsoil layer (0–10 cm) was lower than that in the deep soil layer (20–60 cm) at the same elevation. The above results revealed that the changes in the TN, TP, and TK concentrations in the surface soil and at high elevation in the Fanjing Mountain were more drastic than those at low elevations and in the deep soil layer.

We subsequently measured and analyzed the distribution of the changes in the soil aggregate size fraction with increasing elevation (Figure S2b). The main soil aggregates of Fanjing Mountain varied from microaggregates (<0.25 mm) to macroaggregates (>0.25 mm) in the same soil layer with increasing elevation, and the large macroaggregates (>2 mm) accounted for the largest proportion of the aggregate fraction (66.23%–76.13%) in the 0–10 cm soil layer. Moreover, the main soil aggregates changed significantly from macroaggregates (>0.25 mm) to microaggregates (<0.25 mm) with increasing soil depth at the same elevation. For example, the number of microaggregates (<0.25 mm) significantly increased from 10.79% to 32.64%, 4.87% to 7.89%, and 5.37% to 13.57% at 600–900 m asl, 1500–1800 m asl, and 2100–2400 m asl, respectively. Overall, with increasing elevation, the ratio of microaggregates in the same soil layer decreased and the proportion of macroaggregates increased, whereas the opposite trend occurred with increasing soil depth at the same elevation.

The soil pH was determined at different elevations 600–2400 m asl below 5.5, with the lowest soil pH being 4.09 in the topsoil layer (0–10 cm) at the 1800–2100 m asl (Figure S2c). Specifically, increased elevation did not significantly change the pH, but the soil pH was slightly acidic and generally increased with increasing soil depth. The average soil EC, SOC, and CEC concentrations in the 0–60 cm layer fluctuated with increasing elevation; the highest values were observed at 1500–1800 m asl or 1800–2100 m asl, and the maximum value was 1.64–3.36 times greater than the minimum value (Figures S2d and 2c,d). Moreover, the soil depth had a notable effect on the soil EC, SOC, and CEC, and their values in the topsoil layer (0–10 cm) were significantly greater than those in the subsurface layer ($p < 0.05$), indicating surface aggregation.

Our results revealed that the activities of soil urease (S-UE), sucrase (S-S), acid phosphatase (S-ACP), and catalase (S-CAT) clearly differed with variation at different elevation sites, and the enzyme activities were significantly greater in the topsoil layer (0–10 cm) than in the other soil layers ($p < 0.05$) (Figure 3a–d). Figure 3a shows the activity of soil urease detected at each elevation. The activity of soil urease was notably greater at sites 1200–1500 m asl and 1500–1800 m asl than at other elevations, and the lowest soil urease activity was found at 2100–2400 m asl, followed by 1800–2100 m asl. The urease activity of the surface soil layer was the highest at 1200–1500 m asl, which was 99.65% higher than that at 2100–2400 m asl. In contrast, the highest soil sucrase activity was observed at 600–900 m asl, and the lowest value was observed at 1800–2100 m asl, which linearly decreased with elevation (Figure 3b). Similar to the soil acid phosphatase and catalase activities, the lowest values were found at 2100–2400 m asl, and the variations in the two enzymatic activities were not significant at elevations less than 2100 m (Figure 3c,d). These results indicated that soil enzyme activity was significantly affected by elevation and soil layer.

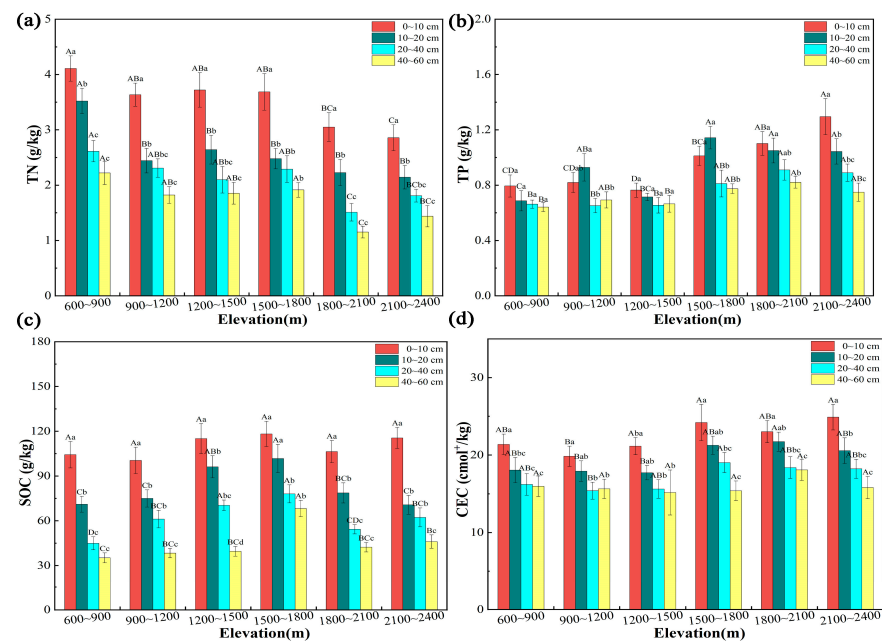


Figure 2. Soil properties, e.g., (a) TN, (b) TP, (c) SOC and (d) CEC under the different elevation sites. TN: total nitrogen; SOC: soil organic carbon; CEC: cation exchange capacity. Different capital letters indicate significant differences between different elevations in the same soil depth according to Tukey's HSD test. Different lowercase letters indicate significant differences between different soil depths at the same elevations. Bars indicate standard errors (mean $\pm$ SE, $n = 3$). The number in the upper right corner of the figure represents the soil depth.

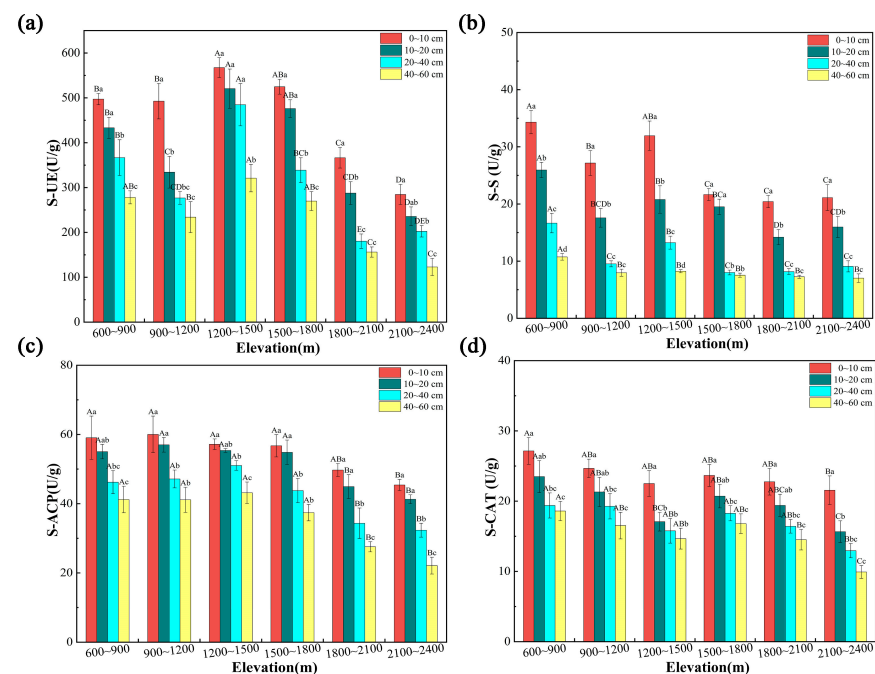


Figure 3. Soil enzyme activities, e.g., (a) soil urease, (b) soil sucrase, (c) soil acid phosphatase and (d) soil catalase along the elevation sites. S-UE: soil urease; S-S: soil sucrase; S-ACP: soil acid phosphatase; S-CAT: soil catalase. Different capital letters indicate significant differences between different elevations at the same soil depth according to Tukey's HSD test. Different lowercase letters indicate significant differences between different soil depths at the same elevation. Bars represent standard errors (mean $\pm$ SE, $n = 3$). The number in the upper right corner of the figure represents the soil depth.

3.2. Influence of Elevation on Microbial Composition

High-throughput pyrosequencing was used to characterize the influences of elevation on the alpha diversity of soil microbial communities at different depths in the soil. With respect to the topsoil layer bacterial richness (Chao1) and α -diversity (Shannon and Simpson indices), three indices generally first increased and then decreased with increasing elevation (Figure 4a–c). The highest bacterial Chao1, Shannon and Simpson index values were found at 1500–1800 m, at 1928.9, 9.60, and 0.9963, and the lowest values of the three indices were found at 2100–2400 m asl, at 1425.51, 9.03, and 0.9945, respectively. However, the Shannon and Simpson indices did not obviously differ at the different elevations. For fungi, the Chao1, Shannon and Simpson indices significantly decreased at 2100–2400 m asl compared with those 600–900 m asl and 900–1200 m asl and decreased with increasing elevation (Figure 4f,h). Additionally, the α -diversity of the fungal community was more strongly influenced by elevation than was that of the bacterial community.

The dominant classified bacterial and fungal phyla and genera were chosen to explore variations in the soil microbial communities at different elevations. Figure 4d shows that the main bacterial phyla were Acidobacteria, Pseudomonadota, Chloroflexi, Actinobacteria, and Verrucomicrobia, accounting for 42.51%–50.30%, 29.78%–40.74%, 1.5%–10.89%, 2.52%–5.24%, and 2.18%–4.55%, respectively, of the relative abundance of bacterial phyla at each spot, indicating that the relative abundance of the main bacterial phyla fluctuated pattern with increasing elevation. At the genus level, the primary bacterial species were *Candidatus Solibacter*, *Rhodoplanes*, and *Candidatus Koribacter*, which accounted for more than 22% of the bacterial sequences (Figure 4e). The relative abundances of *Rhodoplanes* and *Burkholderia* first increased but then decreased with increasing elevation. In addition, the soil fungal communities at all elevations were dominated by *Basidiomycota* (ranging from 31.63% to 69.96%), *Ascomycota* (ranging from 9.78% to 40.35%), unclassified (ranging from 5.66% to 32.09%), and *Mortierellomycota* (ranging from 3.51% to 11.20%) at the phylum level (Figure 4i). Specifically, the relative abundances of *Basidiomycota* and *Mortierellomycota* first increased but then decreased with increasing elevation. At the genus level, the dominant fungi were *Mortierella* among *Mortierellomycota* and *Russula*, *Sebacina*, and *Inocybe* among *Basidiomycota* (Figure 4j).

3.3. Relationships Among the Microbial Community, Enzymatic Activity, and Characteristics of the Soil

The partial Mantel test was conducted to evaluate the main variables driving the changes in the soil microorganism structure, soil enzyme activity, and soil physicochemical properties (Figure 5a). We found that the TK, SC, SACP, and SCAT were the determining factors of the soil bacterial communities at the different elevation sites (Figure 5a). Although these soil physicochemical characteristics had no remarkable influence on the soil fungal communities, pH, EC, SA₅, and SOC had a marginal influence on the fungal community structure. Furthermore, Pearson correlation analysis was performed on the soil properties, revealing that pH, SUE, SC, SACP, SCAT, and SA_{0.25} were positively correlated with TN; TK, EC, CEC, and SA₂₁ were positively correlated with TP; and SOC was positively correlated with CEC (Figure 5a). Interestingly, there were positive correlations between SUE, SC, SACP, and SCAT. Moreover, TN was strongly negatively correlated with TP, TK, EC, and SA₂₁; EC was notably negatively correlated with pH, SUE, SC, and SA_{0.5}; and CEC was strongly negatively correlated with the activities of the four soil enzymes. In addition, pH, SUE, SC, SACP, and SA_{0.25} were significantly negatively correlated with TP.

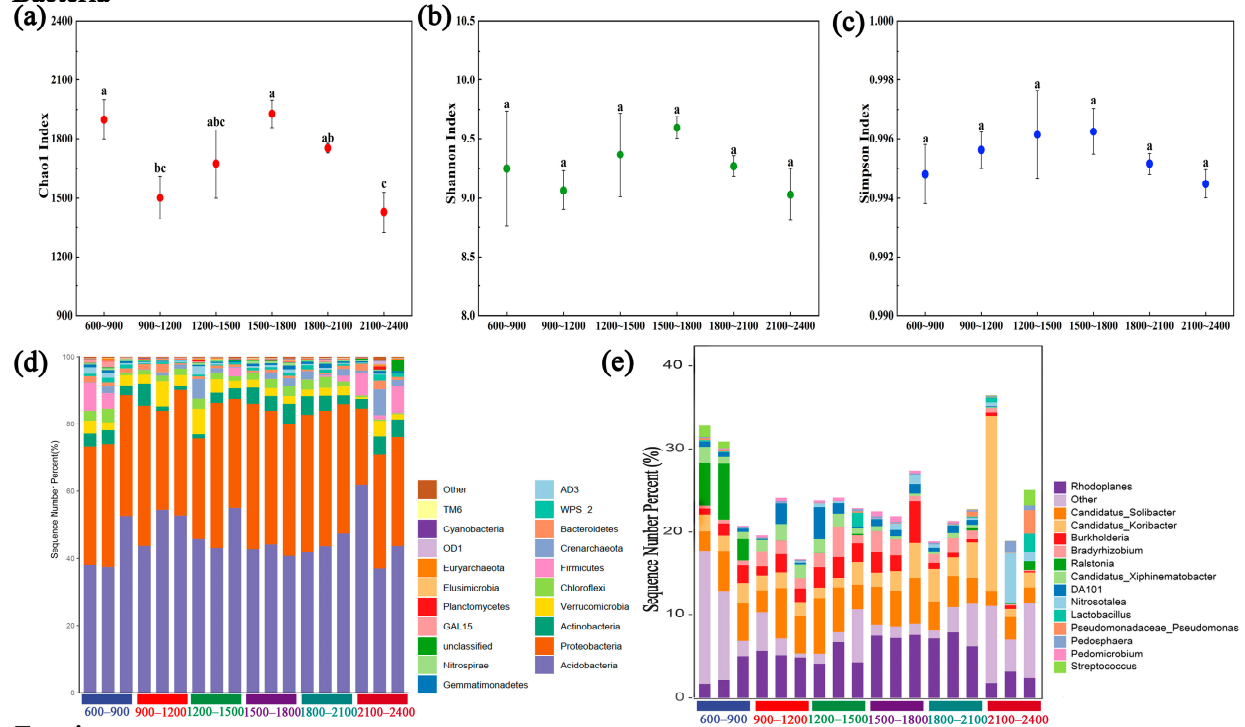
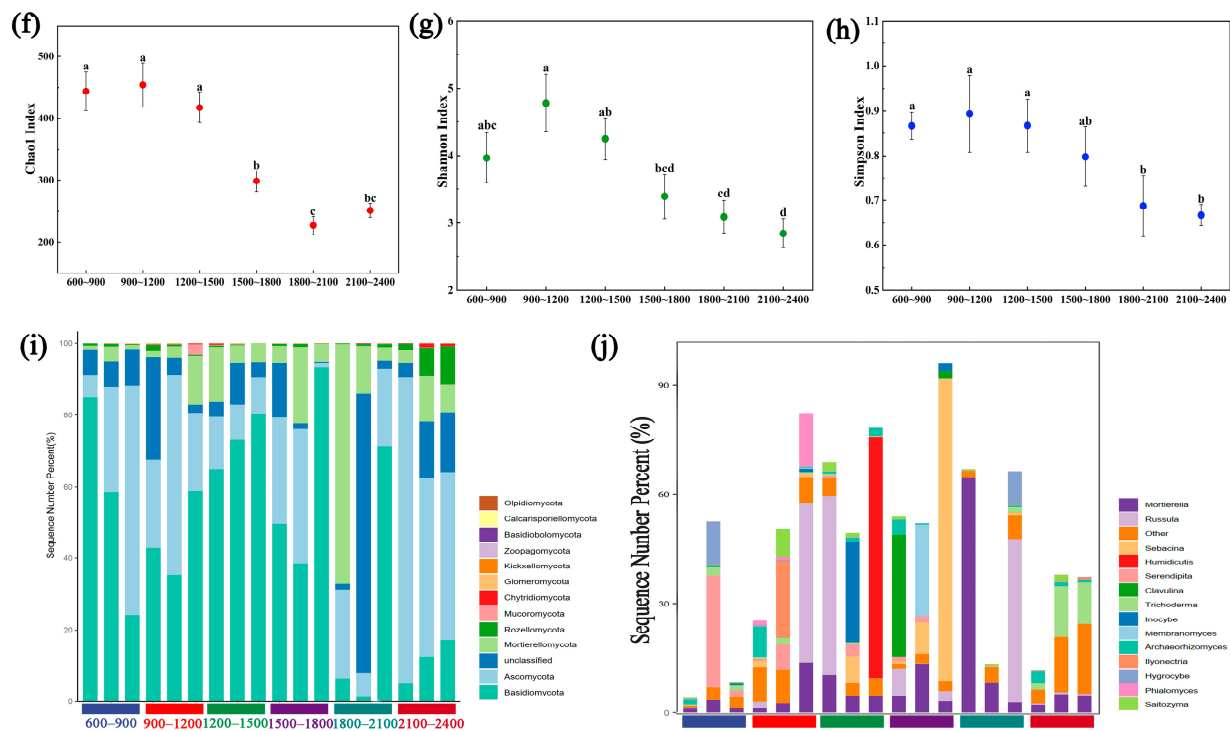
Bacteria**Fungi**

Figure 4. Soil microbial community structure at different elevations. Comparison of bacterial alpha diversity at different elevation sites based on the Chao 1 (a), Shannon (b), and Simpson (c) diversity indices. Relative abundances of bacteria at the phylum level (e) and genus level (d). Comparison of fungal alpha diversity among different elevation sites based on the Chao 1 (f), Shannon (g), and Simpson (h) diversity indices. Relative abundances of fungi at the phylum level (i) and genus level (j). Significant differences were measured by Tukey's HSD test, and different lowercase letters above the point graph denote significant differences at $p < 0.05$ under different elevation sites.

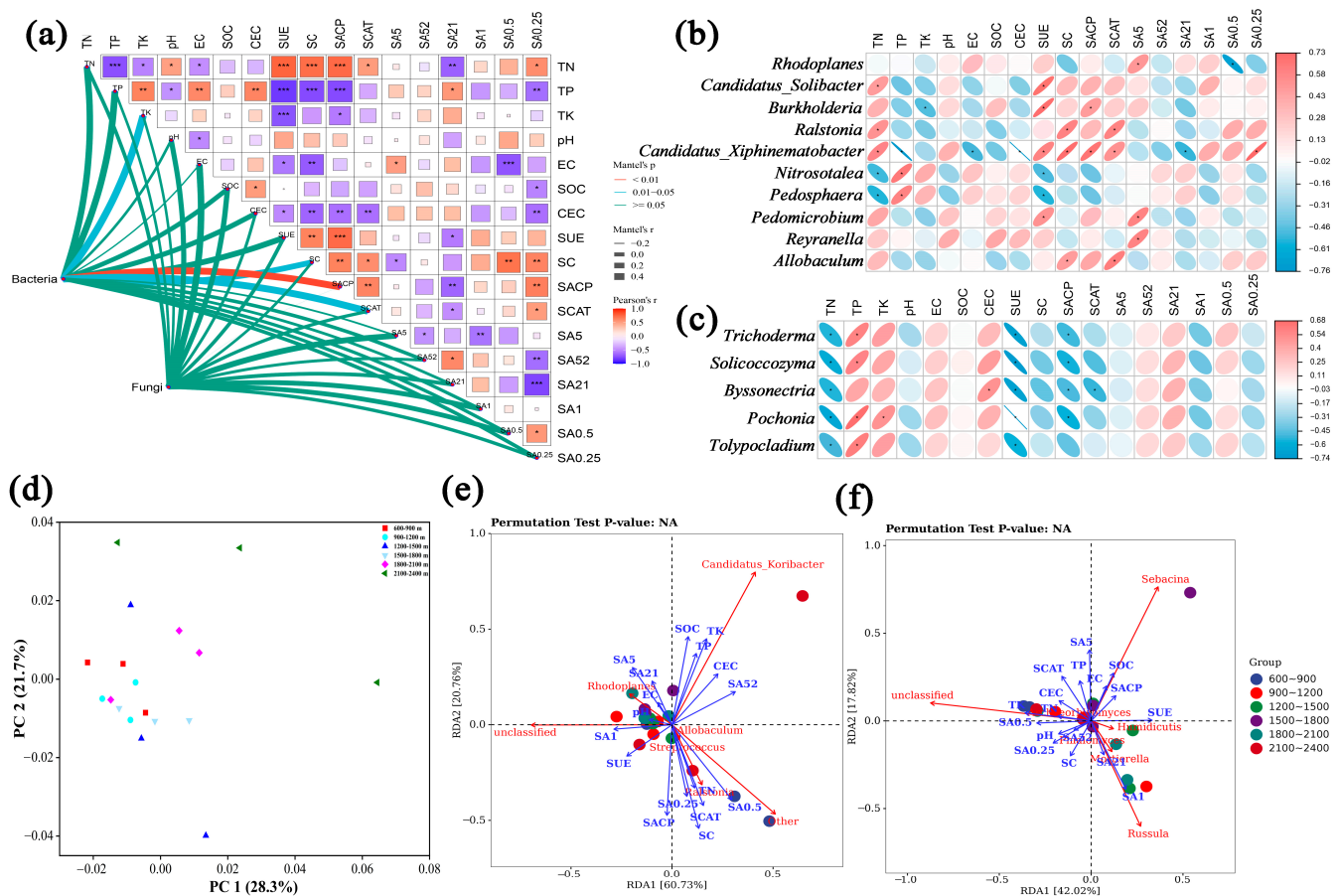


Figure 5. Mantel test of soil bacteria and fungi with respect to soil physicochemical characteristics at different elevations. (a). Pearson correlations between predominant bacterial (b) and fungal (c) genus and soil physicochemical characteristics at different elevations. PCA analysis of soil bacteria community in different elevations (d). RDA between elevation and soil properties (blue arrows) and the predominant (relative abundance) bacterial (e) and fungal (f) genus (red arrows) in Fanjing Mountain. Note: SA₅, soil aggregate (>5 mm); SA₅₂, soil aggregate (5–2 mm); SA₂₁, soil aggregate (2–1 mm); SA₁, soil aggregate (1–0.5 mm); SA_{0.5}, soil aggregate (0.5–0.25 mm); SA_{0.25}, soil aggregate (<0.25 mm); SUE, soil urease; SC, soil sucrase; SACP, soil acid phosphatase; SCAT, soil catalase. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

The Pearson correlations between the soil microbial communities at the genus level and the soil property indices are shown in Figure 5b,c. For the bacterial communities (Figure 5b), we observed that TN was significantly positively correlated with the relative abundances of 3 bacterial genera, *Candidatus Solibacter*, *Ralstonia*, and *Candidatus Xiphinematobacter*; TK was positively correlated with *Nitrosotalea* and *Pedospaera*; and TN was negatively correlated with these genera. *Ralstonia*, *Candidatus Xiphinematobacter*, and *Allobaculum* were positively related to SC and SCAT. Similarly, the SUE was positively correlated with *Candidatus Solibacter*, *Burkholderia*, *Candidatus Xiphinematobacter*, and *Pedomicrobium* but negatively correlated with *Nitrosotalea* and *Pedospaera*. However, *Candidatus Xiphinematobacter* was negatively correlated with TP, EC, CEC, and SA₂₁. TK was negatively correlated with the relative abundance of *Burkholderia*. In addition, for the fungal communities (Figure 5c), TN, SUE, and SACP were negatively correlated with *Trichoderma*, *Solicoccozyma*, *Byssonectria*, and *Pochonia*, whereas TP was significantly positively related. *Pochonia* was positively correlated with TK, and CEC was positively correlated with *Byssonectria*. In general, some soil physicochemical factors, such as TN, pH, SA₁, etc., were positively correlated with soil enzyme activity, whereas other factors, such as TP, EC, SOC, etc., were negatively correlated, and they were both positively and negatively correlated with soil microorganisms.

Further insight into the difference of soil microbial community at different elevations was gained through principal component analysis (PCA); two principal components of soil bacteria and fungus were extracted, and the total interpretation was 50.0% and 50.9%, respectively (Figures 5d and S3). PCA analysis results showed that soil microbial community structure was more dispersed at high elevation than at low elevation. In addition, to further evaluate the remarkable environmental factors affecting the dominant genera in the microbial communities, a redundancy analysis (RDA) was conducted (Figure 5d,e). According to the RDA, the first axis was closely related to pH, SA₁, SUE, EC, and SA₅₂, which explained 60.73% of the total variation in the soil bacterial community structure. However, the second axis was related primarily to SACP, SOC, SA_{0.25}, and SC and explained 20.76% of the variation. SC, SOC, TK, SA_{0.5}, and SACP were significant factors influencing the bacterial community (Figure 5e). Meanwhile, axis 1 and axis 2 represented 42.02% and 17.82% of the total variation in the soil fungal community composition, respectively, and SA₁, SA₅, SUE, TK, SOC, and SCAT had substantial influences on the fungal communities (Figure 5f).

4. Discussions

The Fanjing Mountain is in a representative karst rocky desertification region in Southwest China [28,31] and is a considerable part of terrestrial ecosystems. In the present study, we investigated how elevation influences soil physiochemical characteristics, soil enzyme activities, and corresponding changes in soil bacterial and fungal community composition on the western slopes of Fanjing Mountain at elevations ranging from 600–2400 m. These changes obviously differed with the alteration in spatial scale.

4.1. Soil Characteristics and Enzymatic Activities with Elevation

Soil characteristics are shaped primarily by climate, organisms, parent material, and elevation, probably by regulating soil biogeochemical cycles, which influence plant growth and development, and plant-associated microbiota [1,23,25,36–38]. This study revealed a significant decrease in the soil TN concentration with increasing elevation on Fanjing Mountain, which may be related to elevation changes in soil temperature and precipitation, affecting nitrogen mineralization and inorganic nitrogen production [5,19]. The soil TP and EC concentrations had generally tended to increase with increasing elevation. Moreover, the soil TK and CEC concentrations did not markedly change with elevation. This difference might be associated with changes in the natural environment of Fanjing Mountain, which could influence litter decomposition, the degree of soil weathering, and other inputs into the soil to some degree [21,39]. In addition, we found that the soil pH and SOC usually exhibited a single-peaked model with increasing elevation. The changes in the characteristics of pH and SOC could be ascribed to one reason: the study area is situated in a mountainous area, where the plants are flourishing and the vegetation coverage rate is high, and a thick litter, as the primary source of soil nutrients, accumulates largely in the topsoil. A decrease in temperature because elevation decreases soil evaporation and the soil respiration rate, leading to changes in pH and SOC concentrations [3,5,40]. Importantly, we found that the aforementioned results decreased with increasing soil depth, except for the soil pH. These differences might be associated with differences in organic matter input, nutrient availability, climate type, and litter decomposition [41]. Previous studies have reported inconsistent soil physiochemical property patterns at various elevations [20,21,39]. Overall, these results might reveal a different influence of elevation on soil characteristic factors.

The activity of soil enzymes is an important indicator of the health status and microbial activity of a soil, and these enzymes are prone to fast turnover and high susceptibility to quick responses to variations in elevation and the soil environment [42–44]. In this study, we observed a significant effect of elevation on S-UE, S-S, S-ACP, and S-CAT, with the lowest values occurring from 2100–2400 m asl, whereas there was no significant difference in S-ACP and S-CAT and a slight increase in S-UE at elevations ranging from 600–2100 m asl. The results are consistent with this hypothesis, and these results have both similarities and

differences with those of previous studies [42,45,46]. This discrepancy could be caused by the diverse vegetation cover, plant root exudates, and climatic regimes at specific elevations because soil enzyme activities are very susceptible to environmental signals [17,22,24,27]. In addition, we observed that soil enzyme activity decreased with increasing depth in the soil layer at the same elevation, which was in accordance with the results of previous studies [27,46]. This might be because of the abundant litter return, good hydrothermal, and aeration conditions at the soil layer surface, which provide an appropriate living environment and many nutrient substances for microorganism growth; meanwhile, microbial metabolism is vigorous, leading to a relatively high active matter concentration [46,47]. Additionally, elevation directly affects the changes in soil enzyme activities by affecting soil characteristics, such as pH, SOC, and soil aggregates. In summary, elevation has a profound effect on soil physicochemical characteristics and enzyme activity in Fanjing Mountain, and this effect also plays a crucial role in the formation of soil microbial diversity and the shaping of ecological functions in Fanjing Mountain.

4.2. Differential Responses of Microbial Structures Across Elevation Sites

Here, we researched soil microbial diversity and community structure at different elevation sites. Although the trends in bacterial and fungal abundance and diversity exhibit single-peak patterns with elevation, the trends in bacterial diversity were not significant at all elevations, which might indicate that elevation does not directly affect bacterial diversity but has an indirect influence via other environmental factors [5,12]. These results support our hypothesis that there is a strong elevational influence on microbial diversity, especially fungal diversity. Our results were similar to those of several previous studies, for example, at different elevation sites on Mount Kilimanjaro in East Africa and Sygera Mountain (Tibet, China) [30,35]. However, Yang et al. [41] reported that the alpha-diversity and fungal richness of soil bacteria first decreased and then increased with elevation in southern Himalaya. This is likely because the relative contributions of elevational influences on microbial diversity rely primarily on their relative effects on the soil environment. Additionally, the soil bacterial diversity was greater than the fungal diversity. These findings are in line with those of Yang et al. [41], who suggested that the different microbial niches in the Fanjing Mountain differ with elevation. In brief, the inconsistency of soil microbial diversity patterns at different elevation sites may be due to varying environmental factors induced by elevation.

The dominant phyla of the soil bacterial communities along the elevational gradient were the same, consisting of Acidobacteria, Pseudomonadota, and Chloroflexi. This finding is basically consistent with those of previous studies [3,7,41]. Several previous studies have shown that Acidobacteria are oligotrophic bacteria that can degrade complex lignin and cellulose and provide nutrients for the soil [34]. Pseudomonadota contain a variety of metabolic nitrogen-fixing bacterial species and are involved in a variety of biochemical cycles [35]. These results suggested that the bacterial populations of these phyla have strong adaptability. In addition, for fungal communities, the dominant fungal phyla were Ascomycota and Basidiomycota, with Ascomycota accounting for greater relative abundance at higher elevations and Basidiomycota accounting for greater relative abundance at lower elevations. Previous studies have demonstrated that Basidiomycota have the capacity to degrade aliphatic/protein and Ascomycota are common saprophytic bacteria in soil that can decompose refractory organic matter and play a considerable role in the soil nutrient cycling process and the function and stability of soil microorganisms [3,35]. We speculate that the advantage of Basidiomycota at lower elevations could be correlated with their capacity to degrade complicated lignocellulose components because the vegetation species structure at relatively low elevations is more complicated and the soil litter layer is thicker in Fanjing Mountain. In contrast, Ascomycota can utilize more resources and are more resistant to environmental pressures, increasing its survival benefit at high elevations [5,35]. Together, these results indicated that, to a large extent, elevation determined

the soil microbial diversity and community composition, which could be one of the reasons for the complex biodiversity of Fanjing Mountain.

4.3. Effects of Soil Properties on the Soil Microbial Community

Many studies have investigated the relationships among soil physiochemical characteristics, soil enzyme activity, and soil microbial communities, but there is no consensus on this pattern or a consistent understanding of the factors driving it [21,31,45]. On the basis of the results of the Mantel test and RDA, TK, SC, and SACP strongly influenced the bacterial community composition, and TK, SA₁, SUE, and SOC substantially influenced the fungal community at the different elevation sites. Several previous studies have shown the alterations in TK and SOC could be affected by litter input and vegetation productivity, which likely shape the distinct microbial communities by supplying various resources for microbial growth [5,34,35]. In addition, our results also demonstrated that soil enzyme activity and soil aggregates can influence microbial community composition, to some extent, which is in line with the results of previous studies [11,42,48].

Generally, elevation strongly influences climatic properties (e.g., temperature and precipitation), therefore indirectly affecting soil microbial community composition [6,12,48]. Moreover, the variation in soil nutrients attracted by an increase in elevation may influence the soil microbial community structure indirectly [49,50]. Moreover, temperature is closely connected with soil enzyme activities and litter decomposition; thus, the influences of elevation on soil microbial diversity and communities can be reflected indirectly by alterations in soil characteristics (e.g., SOC, soil nutrients, and enzyme activity). Our findings provide a theoretical basis for protecting Fanjing Mountain ecology, vegetation restoration, and soil management. However, the primary limitation of the present work is that the narrow observable results obtained from this small-scale elevational study might not be applicable for large-scale elevational studies; thus, further investigations are needed.

5. Conclusions

This study revealed the different responses of soil properties and the microbial community along a continuous elevational gradient (600–2400 m asl) on Fanjing Mountain. Elevation significantly affects soil characteristics and enzyme activities, especially at the highest elevation. With increasing soil depth, they tended to decrease, resulting in surface aggregation. In addition, the soil bacterial and fungal community diversity presented a single-peak pattern with elevation. The predominant bacterial species were the phyla Acidobacteria, Pseudomonadota, and Chloroflexi and the genus *Candidatus Solibacter*, and *Rhodoplanes*. The phyla Basidiomycota and Ascomycota and the genus *Mortierella*, *Russula*, and *Sebacina* dominated the fungal communities. The soil SOC, TK, and enzyme activities (SC, SUE) were the main factors that drove the elevational distribution of the microbial communities. The soil microorganism community composition varied greatly among the elevations. The results of this study contribute to the understanding of the interactions among soil properties and microorganisms with increasing elevation, which provides insights into the influence of elevation on soil characteristics, microbial diversity, and communities in the Fanjing Mountain Forest ecosystem. In the future, we need to study how climate change will affect Fanjing Mountain ecosystems and continue to track the relationship between biological indicators and environmental change.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/f15111980/s1>, Figure S1: Soil profile at different elevations; Figure S2: Soil properties under the different elevation gradient. TK: Total potassium, EC: Electrical conductivity. Different capital letters indicate significant differences between different elevations in the same soil depth according to Tukey's HSD test. Different lowercase letters indicate significant differences between different soil depth in the same elevations. Bars indicate standard errors ($\pm$ SE, $n = 3$); Figure S3: PCA analysis of soil fungi community in different elevations.

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