

Article

Effect of Forest Fires on the Alpha and Beta Diversity of Soil Bacteria in Taiga Forests: Proliferation of Rare Species as Successional Pioneers

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Abstract: Forest fires are among the most influential drivers of changes in forest soil bacterial diversity. Nevertheless, little is known regarding the effects of forest fires on maintaining the complex interactions that preserve forest ecosystem stability. Therefore, this study characterized alterations in soil bacterial community composition and diversity within taiga forests subjected to varying disturbance intensities. Particularly, this study examined the bacterial community within a *Larix gmelinii* fire-burnt site in Daxinganling, analyzing the changes in bacterial community structure and function across light, moderate, and heavy fire-burnt sites, as well as a control sample site, utilizing Illumina MiSeq technology. Through an assessment of bacterial community diversity and soil physicochemical properties (moisture content (MC), pH, microbial biomass carbon (MBC), organic carbon (SOC), total nitrogen (TN), available nitrogen (AN), available phosphorus (AP), and available potassium (AK)), we explored the influence of the soil microenvironment on the soil bacterial community structure at the burnt site under different disturbance intensities. Our findings demonstrated that (1) there was no significant change in the Chao index of soil bacteria in the burnt site under different disturbance intensities, whereas the Shannon index decreased significantly ($p < 0.05$) and the Simpson index increased significantly ($p < 0.05$) in the burnt site under light and moderate disturbance. (2) The relative abundance of dominant phyla, such as Proteobacteria, Proteobacteria, and Actinobacteriota, did not change significantly in the fire-burnt site under different disturbance intensities, whereas rare species, such as *Acidipila*, *Occallatibacter*, and *Acidibacter*, experienced a significant increase in relative abundance at the genus level. (3) The results of principal coordinates analysis (PCoA) and canonical correlation analysis (CCA) revealed significant differences in the Beta diversity of soil bacteria in the fire-burnt site under varying interference intensities. The Beta diversity of soil bacteria exhibited significant differences ($p = 0.001$), with MC, pH, TN, AN, and AK identified as significant influencing factors. (4) FAPROTAX functional prediction analyses were conducted to assess the changes in soil bacteria involved in Cellulolysis, Chemoheterotrophy, and Aerobic_Chemoheterotrophy in the fire-burnt site, with the relative abundance of bacteria involved in Chemoheterotrophy being significantly increased ($p < 0.05$) under different disturbance intensities. Collectively, our findings demonstrated that different disturbance intensities caused by fires significantly affected the Alpha diversity, Beta diversity, and functional abundance of soil bacterial communities in taiga forests, with MC, pH, TN, AN, and AK being identified as key influencing factors. Additionally, the presence of numerous rare species suggests their role as pioneer communities in the succession of soil bacterial communities.

Keywords: soil bacteria; taiga forests; fire-burnt site; community structure; rare species



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1. Introduction

Forest fires are a major disruptor in forest ecosystems, impacting approximately 1% of the world's forests each year [1]. Fire disturbances affect the maintenance of forest biodiversity, climate regulation, and water retention to varying degrees [2]. The impacts of forest fires are generally known to be dual. For example, the burning of surface litter and trees causes soil erosion [3,4], thereby altering the physicochemical properties and nutrient availability of topsoil [5–7] and the biosphere [8]. However, forest fires can also promote and improve the material cycle and energy flow and ecosystem structure of forest ecosystems. Firstly, forest fires accelerate the decomposition of apoptotic material and promote nutrient cycling, thus promoting forest growth and development [9]. Secondly, forest fire reduces pests and diseases, improves forest land hygiene, and favors the growth and development of forest trees [10].

Soil bacteria are an important component of soil ecosystems and are the main driver of soil nutrient cycling, playing a key role in maintaining energy flow and material cycling [11,12]. Environmental factors are significant drivers of soil bacterial composition and diversity differences, with different factors selectively impacting soil bacteria. For instance [13], the pH can influence the composition, chemical properties, and utilization efficiency of soil substrates, thereby affecting bacterial community composition and diversity [14]; MC affects soil aeration and oxygen content, influencing bacterial respiration and metabolism [15]; SOC serves as an essential energy source for bacteria, directly affecting their growth and metabolism [16]; soil N can influence bacterial involvement in N fixation and nitrification processes [17]; and AP and AK affect bacteria capable of decomposing organic P and K or competing for P and K resources, indirectly leading to changes in bacterial community structure. Studies have shown that forest fires can exert direct or indirect lethal effects on soil bacteria [18,19]. High temperatures and the heat from fires can directly eliminate soil bacteria [20], in addition to causing nutrient loss from the soil by disrupting its structure, resulting in the death of certain bacteria or their inability to survive due to environmental stress [21]. Moreover, soil bacteria respond positively to ecological recovery after fire disturbance. The original “vegetation–soil–microorganism” interaction is disrupted during the process of community stabilization after a forest fire. Bacteria invade plant roots through mycelia, forming symbiotic structures, and absorb or fix nitrogen in the soil, ensuring that plants and soil nitrogen remain unaffected by forest fires. This, in turn, promotes the recovery of forest ecosystems post-fire disturbance [22].

The species that comprise microbial communities can be either dominant or rare [23]. Dominant species play a vital role in ecosystems, exhibiting strong responses to environmental changes under extreme conditions and interacting with other species. They possess a higher resource utilization capacity and typically occupy a substantial portion of the ecological niche space, contributing to ecosystem balance and stability through increased stability and asynchrony [24]. Rare species are equally crucial for species coexistence and biodiversity maintenance in forest ecosystems. They form diverse coexisting assemblages with dominant species through non-random competition, avoiding excessive direct inter-species competition. Rare species also regulate soil nutrient efficiency and equilibrium through functional microorganisms and influence habitat selection of both dominant and rare species, thereby modulating plant–soil feedback mechanisms [25].

The Daxinganling region stands out as one of the areas in China experiencing an increasing number of forest fires, both in frequency and scale. This surge in fires has particularly impacted the larch, a prominent vegetation type in the Daxinganling region, severely altering the landscape pattern of the local forest ecosystem and diminishing its role as an ecological barrier [26]. Current research on fire damage in the Daxinganling forest primarily focuses on spatial and temporal changes in burned sites [27], the stability of soil aggregates, organic carbon characteristics post-vegetation restoration in burned sites [28], changes in the spatial distribution pattern of larch natural forests in burned sites [29], and the impact of soil carbon fractions in the tundra zone of burned sites [30]. Research on the diversity of soil microbial community structures is scarce, with existing

studies on the Daxinganling Mountains' burned areas often employing traditional biological methods. For example, Cheng et al. [31] used phospholipid fatty acids (PLFAs) to study the impact of different burning intensities and recovery times on soil microbial communities, while Sun et al. [32] used microscopy to examine the effects of varying burn intensities on arbuscular mycorrhizal fungi. Given the large number and variety of soil microbes, traditional microbial culturing methods fall short of reflecting the true state of soil microbiota, missing the majority of microbes and failing to capture the full scope of microbial structure and function. Illumina MiSeq sequencing technology, known for its high throughput, sensitivity, and repeatability, is now widely applied in microbial research for its ability to systematically and comprehensively analyze the structural characteristics and functions of soil microbial communities [33,34].

Therefore, using Illumina MiSeq sequencing analysis technology, this study focused on a fire-burned site from June 2010 to analyze differences in the community structure of soil bacteria, exploring the response patterns of soil bacterial communities to environmental changes in fire-burned areas. This aims to reveal the mechanisms of interaction between recovery in fire-burned sites and the soil bacterial community, providing scientific evidence for their interrelation.

2. Materials and Methods

2.1. Study Area

The experimental site was established in the Huzhong National Nature Reserve in Heilongjiang ($122^{\circ}42'14''$ – $123^{\circ}18'05''$ E, $51^{\circ}17'42''$ – $51^{\circ}56'31''$ N; Figure 1). The study area is located in Cretaceous acidic volcanic rock stratum, encompassing 4 soil orders, 4 soil types, and 11 subcategories, among which brown coniferous forest soil is a zonal soil developed under cold-temperate coniferous forests. The litter layer beneath the forest is thick, with low base saturation, and the soil is acidic; originating from acidic parent rock, it features a thin coarse layer conducive to leaching, with a noticeable process of soil podzolization [35]. The reserve features gentle topography, an elevation ranging from 847 to 974 m, and a mean annual temperature of -4°C . The region experiences a mean annual precipitation of 458.3 mm, a mean annual relative humidity of 71%, and a mean annual evaporation of 911 mm. The reserve encompasses 41 species of woody plants, including 4 trees and 37 shrubs, with an average diameter at breast height (DBH) exceeding 1 cm. Additionally, there are 127 species of herbaceous plants, representing 21 families and 39 genera. The protected area is primarily characterized as a cold-temperate-zone coniferous forest, where the dominant species is *Larix gmelinii*. Overall, the reserve is predominantly a cold-temperate coniferous forest, with *Larix gmelinii* as the dominant species [26].

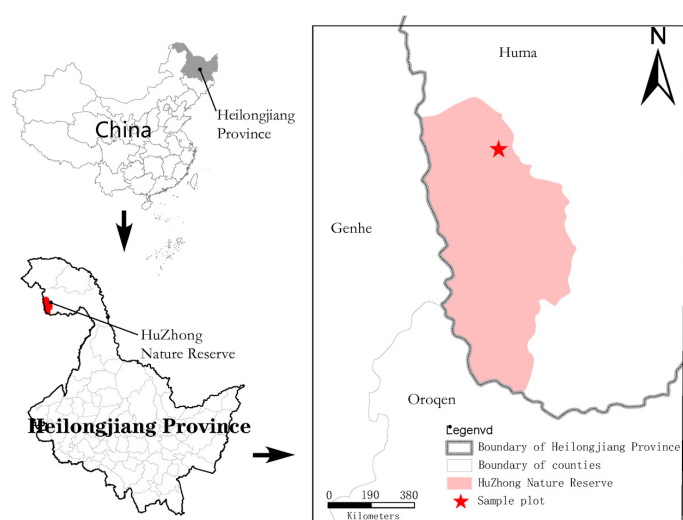


Figure 1. Location of experimental plots.

2.2. Sample Plot

Sample plots were set up and sampled in July 2019 year. The sample plots were located in the Daanling cold-temperate coniferous forest fire site of 2010 and were categorized into three distinct fire intensities: light (L), moderate (M), and heavy (H). Control plots (CK) were also designated in adjacent areas with same site conditions, ensuring similar conditions except for variations in fire intensity; the specific division is described in Table 1. Each sample plot, including three plots of 20 m × 20 m, underwent sampling using a 5-point mixed sampling method. Soil samples were collected from a depth of 0–20 cm, excluding surface layers of withered material and humus [24]. After thorough mixing and removal of debris and rhizomes, the samples were sieved through a 2 mm sieve and stored in a cold place for further use. Part of the samples was utilized for soil bacterial DNA extraction, whereas the remainder was dedicated to determining soil physical and chemical properties; refer to previous literature for specific measurements [36].

Table 1. Classification of different fire intensities [36].

Fire Intensity	The Proportion of Wood Burned to Death by Fire	Height of Blackening of Tree Trunks
L (light)	<30%	<2 m
M (moderate)	30%~70%	2 m~5 m
H (heavy)	>70%	>5 m

2.3. Determination of Physicochemical Properties of Soil

Soil microbial biomass carbon (MBC) was determined by the fumigation–extraction method [37], soil pH by a soil–water ratio (m/m) of 2.5:1 [38], soil moisture content (MC) by the drying method [39], available potassium (AK) by flame photometry, total nitrogen (TN) by the semi-micro Kjeldahl method [40], soil organic carbon (SOC) using a C-N analyzer (Jena-2100S, Analytik Jena AG, Jena, Germany) [41], available phosphorus (AP) by sodium hydrogen carbonate (NaHCO₃) extraction colorimetric method [40], and alkali-hydrolyzable nitrogen (AN) by the alkali distillation method [40].

2.4. Soil Bacterial DNA Extraction and Sequencing

Soil bacterial genomic DNA was extracted using the Fast DNA[®] Spin Kit for Soil (MP Biomedicals, Irvine, CA, USA) according to the manufacturer's instructions, and the concentration was assessed using an ultra-micro spectrophotometer (NanoDrop2000, Thermo, Waltham, MA, USA). Illumina MiSeq sequencing was then conducted after confirming that the samples met the amplification requirements. The 338F and 806R primer pair was then used to amplify the V3–V4 region of bacterial 16S rDNA. The amplification system consisted of 4 µL of 5× TransStart FastPfu buffer, 2 µL of 2.5 mM dNTPs, 0.8 µL of upstream primer (5 µM), 0.8 µL of downstream primer (5 µM), and 0.8 µL of TransStart. The amplification protocol consisted of a pre-denaturation step at 95 °C for 5 min, followed by 30 cycles at 95 °C for 1 min, 52 °C for 1 min, and 72 °C for 1 min, and a final extension at 72 °C for 10 min [42,43]. The PCR amplification products were detected through electrophoresis on a 2% agarose gel, followed by elution, purification, and recovery. Illumina MiSeq was performed by Shanghai Meiji Biomedical Technology Co. The data information of the optimized sequences will be uploaded to the NCBI SRA database (sequence number: PRJNA1039144).

2.5. Sequencing Data Processing and Statistics

The sequencing data underwent denoising utilizing the DADA2 (Divisive Amplicon Denoising Algorithm) method within QIIME2 (v2022.2). Subsequently, sequences were clustered at a 100% similarity level to generate amplicon sequence variants (ASVs). Representative sequences of ASVs were annotated using the RDP classifier (v1.9.1) software, based on the Silva 16S rRNA taxonomic database. We used the Venn Diagram package of software R-3.3.1 to calculate the ASVs number and relative abundance of soil samples.

Using Alpha diversity indices to represent soil bacterial diversity, the Alpha diversity indices (Chao, Shannon, and Simpson, according to Formulas (1)–(3)) were calculated using Mothur (v.1.30.2) [42,43].

$$S_{chao} = S_{obs} + \frac{n_1(n_1 - 1)}{2(n_2 + 1)} \quad (1)$$

$$H_{shannon} = - \sum_{i=1}^{S_{obs}} \frac{n_i}{N} \ln \frac{n_i}{N} \quad (2)$$

$$D_{simpson} = \frac{\sum_{i=1}^{S_{obs}} n_i(n_i - 1)}{N(N - 1)} \quad (3)$$

where S_{obs} is the actual number of observed species (such as ASV); n_1 is the number of species (such as ASVs) containing only one sequence; n_2 is the number of species (such as ASVs) containing only two sequences; n_i is the number of sequences contained in the i -th species (such as ASV); and N is all sequence numbers.

Using the “vegan” and “ggplot” packages in R-3.3.1, a principal coordinates analysis (PCoA) employing the Bray–Curtis distance algorithm was conducted to analyze the Beta diversity of the soil bacterial communities in the burnt sites with different disturbance intensities. The similarity or difference between bacterial community groups was tested using Adonis. Changes in soil physicochemical properties, bacterial diversity indices, and the relative abundance of bacterial communities were identified via one-way ANOVA utilizing the SPSS 25.0 software. Significant differences between data sets were assessed using Duncan’s method. The Pearson correlation algorithm was employed to analyze the relationships between bacterial diversity, relative abundance, and physicochemical properties. Additionally, canonical correspondence analysis (CCA) was used to reveal the main physicochemical factors influencing the bacterial community. Finally, the FAPROTAX (v1.2.1) software was used to predict the ecological functions of soil bacteria [42,43].

3. Results

3.1. Differences in Physicochemical Properties of Fire-Burnt Site Soils

The physicochemical characteristics of the soils of the burnt site under different disturbance intensities have been described before [36]; the physicochemical properties of the soil are shown in Supplementary Table S1.

3.2. Analysis of Differences in Soil Bacterial Diversity in Burnt Sites

As shown in Table 2, when compared to the control group, the Chao index of soil bacteria in the fire-burned site under different disturbance intensities did not exhibit significant changes. However, the Shannon index of soil bacteria exhibited a significant reduction ($p < 0.05$), with no significant difference in the Shannon index of the bacterial community among the soils of the fire-burned site under varying disturbance intensities. In contrast to the control group, the Simpson index of soil bacteria was significantly higher ($p < 0.05$) in the fire-burned site under light and moderate disturbance. These findings suggest that fire did not have a significant effect on the number of soil bacterial species but resulted in a reduction in the diversity and dominance of soil bacteria. Interestingly, the Alpha diversity of soil bacteria in the fire site under heavy disturbance recovered more quickly to the level before the fire.

Table 2. Alpha diversity of bacterial communities in soils with different fire intensities. Different marked letters indicate significant differences ($p < 0.05$; ANOVA).

Intensity	Chao	Shannon	Simpson
CK	920.88 ± 300.12 a	6.25 ± 0.30 a	0.004 ± 0.001 b
L	685.14 ± 44.06 a	5.64 ± 0.02 b	0.009 ± 0.000 a
M	798.76 ± 214.02 a	5.84 ± 0.16 b	0.008 ± 0.002 a
H	719.05 ± 49.96 a	5.97 ± 0.05 ab	0.005 ± 0.000 b

The results of the Beta diversity analysis of soil bacterial communities in the burnt site are illustrated in Figure 2. The explanatory power of the first axis reached 39.7%, the second axis reached 26.56%, and the cumulative explanatory power of the two reached 72.58%. A significant difference in soil bacterial community structure was observed between the fire group and the CK group (Adonis: $R = 0.9753$, $p = 0.001$). Specifically, the CK group was distributed in the first quadrant, the L and M groups in the second quadrant, and the H group in the third and fourth quadrants. These findings suggest that the Beta diversity of soil bacterial communities in the fire-burned sites under different disturbance intensities exhibited significant variations, with the structural composition of soil bacterial communities being more similar in the fire-burned sites under light and moderate disturbances.

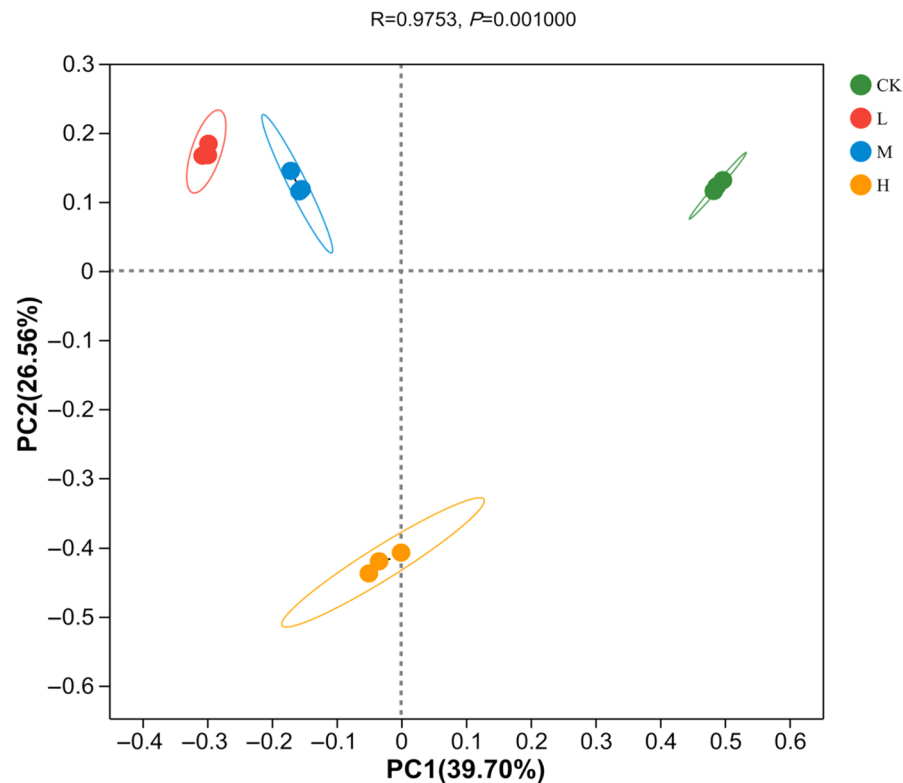


Figure 2. PCoA of bacterial communities in soil with different fire intensities.

3.3. Analysis of the Differences in Soil Bacterial Community Composition in the Fire-Burnt Site

As illustrated in Figure 3, at the phylum level, the predominant phyla of soil bacteria included Proteobacteria (32.68%–38.35%), Acidobacteriota (28.38%–33.49%), and Actinobacteriota (9.64%–13.21%). The relative abundance of the dominant phyla in the fire group did not exhibit a significant difference ($p > 0.05$) when compared with the control group. Regarding other phyla, including Proteobacteria, Acidobacteriota, Actinobacteriota, Chloroflexi, and Bacteroidota, the relative abundance did not differ significantly ($p > 0.05$) compared to the control group. However, within individual phyla, such as WPS-2, Gemmatimonadota, Planctomycetota, Myxococcota, Patescibacteria, and RCP2-54, the relative abundance showed a significant difference ($p < 0.05$) compared to the control.

The composition of the bacterial community at the genus level is detailed in Table 3, where the relative abundance of unidentified genera (42.88%–50.87%) and other genera (13.6%–22.46%) accounted for a relatively high proportion. The relative abundance of unidentified genera within the burnt group did not significantly differ from that of the control group ($p > 0.05$). However, the relative abundance of *Acidipila*, *Occallatibacter*, *Acidibacter*, *Pajaroellobacter*, *Acidocella*, *Tundrisphaera*, and *Chthoniobacter* in the burnt site was significantly higher compared to the control.

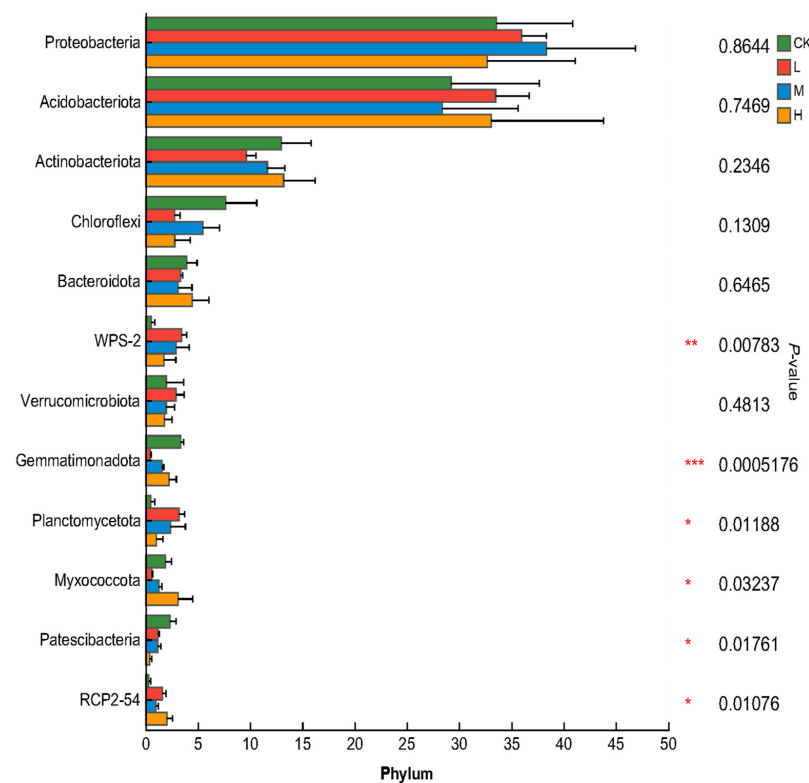


Figure 3. Bacterial community compositions at the phylum level. * $0.01 < p \leq 0.05$, ** $0.001 < p \leq 0.01$, and *** $p \leq 0.001$.

Table 3. Bacterial community compositions at the genus levels. Different marked letters indicate significant differences ($p < 0.05$; ANOVA).

Species Name	CK	L	M	H
<i>Norank</i>	0.43 ± 0.06 a	0.47 ± 0.01 a	0.51 ± 0.03 a	0.44 ± 0.08 a
<i>Others</i>	0.22 ± 0.03 a	0.14 ± 0.01 b	0.15 ± 0.01 b	0.16 ± 0.02 b
<i>Unclassified</i>	0.05 ± 0.01 a	0.04 ± 0.01 ab	0.06 ± 0.01 a	0.03 ± 0.01 b
<i>Bryobacter</i>	0.05 ± 0.01 b	0.03 ± 0 c	0.04 ± 0.01 bc	0.07 ± 0.01 a
<i>Granulicella</i>	0.01 ± 0.01 c	0.08 ± 0.01 a	0.04 ± 0.01 b	0.03 ± 0.01 bc
<i>Candidatus_Solibacter</i>	0.04 ± 0.01 b	0.02 ± 0 c	0.02 ± 0.01 c	0.05 ± 0.01 a
<i>Acidothermus</i>	0.01 ± 0 c	0.03 ± 0 b	0.03 ± 0 b	0.06 ± 0.01 a
<i>Roseiarcus</i>	0.01 ± 0 c	0.03 ± 0 a	0.02 ± 0.01 b	0.02 ± 0.01 b
<i>Mycobacterium</i>	0.02 ± 0 a	0.02 ± 0 a	0.01 ± 0 a	0 b
<i>Bradyrhizobium</i>	0.02 ± 0 a	0.01 ± 0 a	0.01 ± 0 a	0.02 ± 0.01 a
<i>Puia</i>	0.02 ± 0 a	0.01 ± 0 a	0.01 ± 0 a	0.01 ± 0.01 a
<i>Acidipila</i>	0 c	0.02 ± 0 a	0.01 ± 0 b	0.01 ± 0 c
<i>Mucilaginibacter</i>	0.01 ± 0 a	0.01 ± 0 a	0.01 ± 0.01 a	0.01 ± 0 a
<i>Occallatibacter</i>	0 c	0.02 ± 0 a	0.01 ± 0 b	0.01 ± 0 c
<i>Burkholderia-Caballeronia-Paraburkholderia</i>	0.01 ± 0 bc	0.02 ± 0 a	0.01 ± 0 b	0 c
<i>Candidatus_Udaeobacter</i>	0.02 ± 0.01 a	0 a	0.01 ± 0 a	0.01 ± 0.01 a
<i>Acidibacter</i>	0 c	0.01 ± 0 b	0 bc	0.02 ± 0 a
<i>Ellin6067</i>	0.02 ± 0.01 a	0 b	0 b	0 b
<i>Pajaroellobacter</i>	0 b	0 b	0.01 ± 0 ab	0.01 ± 0.01 a
<i>Gemmatimonas</i>	0.01 ± 0 a	0 b	0 b	0.01 ± 0 a
<i>Reyranella</i>	0.01 ± 0 a	0 b	0 b	0 b
<i>Rhodanobacter</i>	0.01 ± 0 a	0.01 ± 0 b	0 c	0 b
<i>Acidocella</i>	0 c	0.01 ± 0 b	0.01 ± 0 a	0 c
<i>RB41</i>	0.02 ± 0.01 a	0 b	0 b	0 b
<i>Haliangium</i>	0.01 ± 0 a	0 b	0 b	0.01 ± 0 a
<i>Candidatus_Koribacter</i>	0 a	0 a	0 a	0.01 ± 0.01 a
<i>Tundrisphaera</i>	0 b	0.01 ± 0 a	0 b	0 b
<i>Sphingomonas</i>	0.01 ± 0 a	0 b	0 b	0 b
<i>Chthoniobacter</i>	0 b	0.01 ± 0 a	0 b	0 b

3.4. Correlation Analyses of Factors Affecting Soil Bacterial Community Structure and Diversity in the Fire-Burnt Sites

As shown in Table 4, Shannon's index was significantly negatively correlated with AP ($p < 0.05$), whereas Simpson's index was significantly positively correlated with SOC ($p < 0.05$). The results showed that AP and SOC significantly reduced the diversity and dominance of soil bacteria.

Table 4. Correlation coefficients between soil environmental factors and soil bacteria diversity: * $0.01 < p \leq 0.05$.

Index	MC	pH	MBC	SOC	TN	AN	AP
Shannon	−0.36	0.04	−0.16	−0.44	−0.02	0.23	−0.69 *
Simpson	−0.01	0.26	0.21	0.66 *	−0.32	−0.54	0.53

As illustrated in Figure 4, the CCA for the levels of soil bacterial amplicon sequence variants (ASVs) revealed that CCA1 explained 24.67% of the structural differences in the soil bacterial communities in the fire-burnt site, while CCA2 explained 18.92%. The first two axes collectively accounted for 43.59% of the variation. The soil bacterial communities in the L and M groups exhibited a positive correlation with AP, SOC, and MBC. Conversely, the soil bacterial communities in the H group showed a positive correlation with AN, MC, and TN.

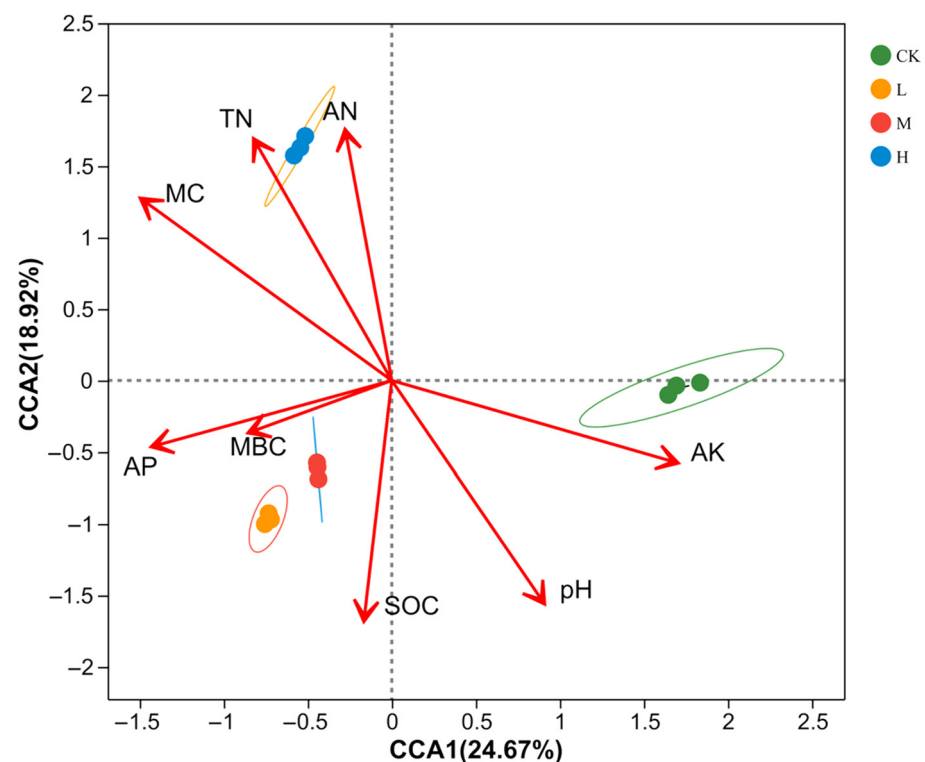


Figure 4. Canonical correspondence analysis (CCA) of soil bacteria community and environmental factors.

As shown in Table 5, soil MC, pH, TN, AN, and AK had highly significant ($p < 0.01$) effects on the bacterial community composition of soil.

Table 5. Influence of soil physicochemical properties on the Beta diversity of bacterial communities. Diversity: * $0.01 < p \leq 0.05$, ** $0.001 < p \leq 0.01$, and *** $p \leq 0.001$.

Index	R ²	p-Value
MC	0.9374	0.001 ***
pH	0.7852	0.002 **
MBC	0.1995	0.347
SOC	0.6831	0.011 *
TN	0.8537	0.007 **
AN	0.7596	0.01 **
AP	0.5413	0.026 *
AK	0.783	0.009 **

3.5. Prediction of Bacterial Functionality of Soil

As shown in Figure 5, the main functional classifications within the soil in the experimental sample plots were Cellulolysis (2.39%–17.23%), Chemoheterotrophy (32.13%–42.07%), and Aerobic Chemoheterotrophy (31.66%–41.84%), and the functional composition of the bacterial community in the soil was altered by fire burning. The functional composition of the soil bacterial community was altered by fire burning, in which Cellulolysis was highly significant ($p < 0.001$). Moreover, Chemoheterotrophy and Aerobic Chemoheterotrophy were highly significant ($p < 0.001$) and higher ($p < 0.01$) than that of the control group with the increase in fire-burning intensity.

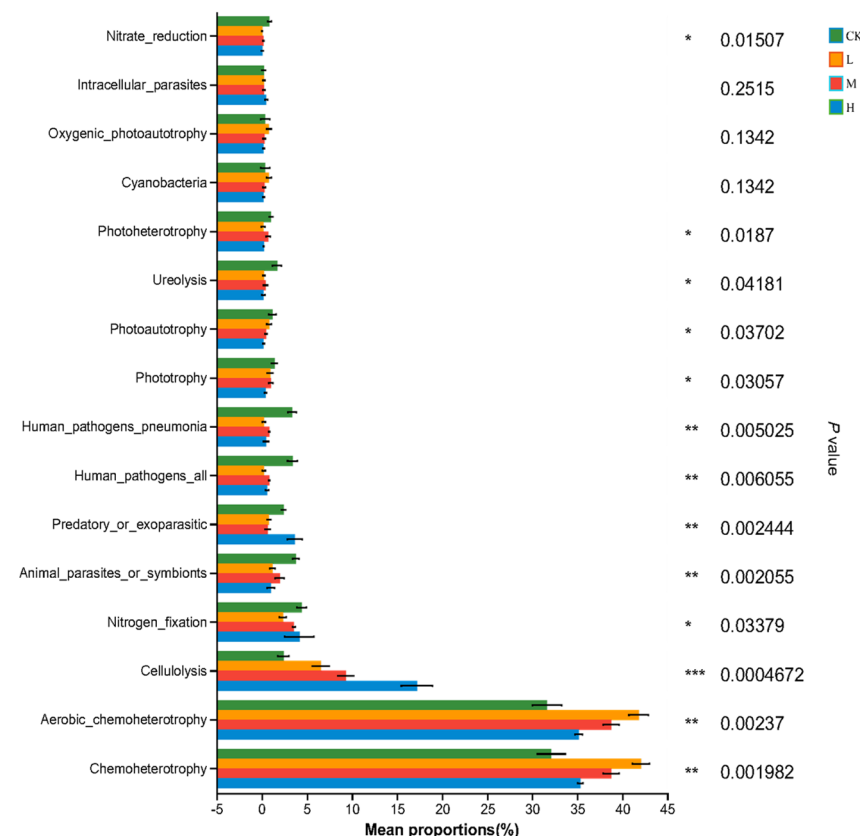


Figure 5. Prediction of FAPROTAX function of soil bacteria under different fire disturbance conditions: * $0.01 < p \leq 0.05$, ** $0.001 < p \leq 0.01$, and *** $p \leq 0.001$.

4. Discussion

4.1. Effects of Fire on the Alpha Diversity of Soil Bacteria

The impact of fire on soil physicochemical properties induces changes that lead to the disappearance or reduction of certain bacterial species, significantly influencing the

Alpha diversity of soil bacteria [44]. Previous studies have demonstrated that SOC and phosphorus play direct or indirect roles in the survival and reproduction of microorganisms primarily by affecting the soil carbon cycle [45], with AP and SOC being significantly correlated with notable changes in soil bacterial Alpha diversity [46,47]. In this study, the species diversity and dominance of soil bacteria exposed to fire were significantly reduced, exhibiting a significant negative correlation with AP and a significant positive correlation with SOC, which is consistent with previous findings [48–50]. The reduction of soil bacterial diversity and dominance can be attributed, on one hand, to the inhibitory effect of excess AP on microbial osmotic pressure, cell expansion pressure, ionic balance, and stomatal movement [51]. On the other hand, excess AP may form insoluble compounds with other nutrient elements (e.g., Zn and Fe), reducing the effectiveness of elemental phosphorus and inhibiting the growth and metabolism of soil bacteria [52]. The reduction of SOC decreased the excitation of soil carbon, diminishing the organic carbon mineralization rate, slowing down organic carbon conversion [53], and weakening soil microbial respiration [54], ultimately reducing soil microbial activity and metabolic efficiency [55]. This, in turn, inhibits the recovery of soil bacterial communities.

The substantial reduction in soil bacterial diversity and dominance in the fire-affected site observed in this study can be primarily attributed to the direct lethal impact of forest fires and the destructive effects of high temperatures on bacterial cell structure and function, resulting in a decline in their diversity [20]. Additionally, forest fires intensify competition for nutrients and resources among soil bacterial communities, creating a scenario where some species demonstrate heightened resistance to disturbances and enhanced competitiveness for survival, driven by numerical superiority. Consequently, the relative scarcity of soil nutrients post-fire further exacerbates the mortality rates of weaker colonies, contributing to a decrease in the diversity of soil bacterial communities [56]. In this study, the restoration of the number of species, diversity index, and dominance index of soil bacteria in fire-damaged sites under heavy disturbance to pre-fire levels aligns with previous findings [44]. This recovery may be attributed to the substantial burning of plant and apoplastic material under heavy fire disturbance, which accelerates the influx of nutrients and enhances nutrient content in the soil [57]. This, in turn, promotes the growth and metabolism of soil bacteria and expedites the recovery process of soil bacterial communities [58].

4.2. Effects of Fire on the Structural Composition of Soil Bacterial Communities

After forest fires, heterogeneous changes occur in the local or soil micro-regional environments, impacting the structural composition of soil bacterial communities [50]. The present study revealed significant differences in the soil physicochemical properties of fire-burned sites, with MC, pH, TN, AN, and AK having highly significant effects on the soil bacterial community structure and altering Beta diversity, consistent with previous research [44,59]. Among them, changes in MC led to alterations in physical properties such as soil porosity and aeration [60], which, in turn, affected the species and numbers of aerobic and anaerobic microorganisms in the soil [61,62]. Moreover, changes in MC also led to changes in pH, conductivity, and nutrients (TN, AN, and AK) [63–66] and other chemical properties, and the decomposition of these organic materials and the release of nutrients provided the carbon and energy sources required by soil bacteria to synthesize cellular materials [67]. Additionally, the supply of sufficient nutrients improved the activity of soil bacteria to a certain extent [68], thus promoting their growth and reproduction.

Differences in the thermal sensitivity and environmental adaptation of soil bacteria contribute to changes in the community structure of dominant and rare species in fire-burned sites [50]. Although no significant differences were observed among the dominant bacterial taxa, several rare species exhibited significant changes, including an increased relative abundance of species such as *Acidipila*, *Occallatibacter*, and *Acidibacter* after the fire, which was attributed to rapid organic matter decomposition and nutrient release, providing abundant resources for soil bacteria growth [69,70]. The emergence of rare taxa such as *Microgenomates* and *Allokutzneria* after fire burning may result from their superior heat

tolerance, facilitating faster adaptation to the post-fire soil environment and contributing to their proliferation [24,58,71].

The life history response and ecological niche partitioning hypotheses suggest that rare bacterial taxa adopt r-strategy life histories, exhibiting fast growth rates and rapid responses to nutrient inputs post-fire, occupying unutilized resources and vacant ecological niches as pioneer communities [72,73]. As post-fire vegetation and soil recover, certain species regain advantages in resource utilization and competition, thereby dominating the microbial community [74]. In turn, rare species tend to occupy the edge of the ecological niche, forming a distribution pattern that minimizes competition with dominant species by utilizing limited resources [75].

5. Conclusions

In this study, we found that forest fires altered the community structure and diversity of soil bacteria, MC, pH, TN, AN, and AK, which are the key factors influencing the structural changes in soil bacterial communities. This study explores the structure of soil bacterial communities in burned areas and their influencing factors, offering an initial analysis of the impact of fire on soil microbes and the environment. However, the influence of fire on the material cycle of forest ecosystems is complex, particularly with the large influx of biochar post-burn, which may induce a “carbon priming effect”, carbon–nitrogen (C-N) coupling, and the redistribution of other elements. It also encompasses changes and possibly the reconstruction of biotic communities, such as soil microbes and soil fauna. These issues require a further in-depth investigation to fully understand the impact of fire on forest ecosystems, providing essential data and theoretical support for the restoration of damaged ecosystems.

Supplementary Materials: The following supporting information can be downloaded at <https://www.mdpi.com/article/10.3390/f15040606/s1>, Table S1: Soil physicochemical properties of different fire intensities. Different marked letters indicate significant differences ($p < 0.05$; ANOVA).

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