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Short-Term Impacts of Fire and Post-Fire Restoration Methods on Soil Properties and Microbial Characteristics in Southern China

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Abstract: Wildfires and post-fire restoration methods significantly impact soil physicochemical properties and microbial characteristics in forest ecosystems. Understanding post-fire soil recovery and the impacts of various post-fire restoration methods is essential for developing effective restoration strategies. This study aimed to investigate how fire and soil depth influence soil physicochemical properties, enzymatic activities, and the structure of microbial communities, as well as how these factors change under different post-fire management practices. We sampled 0–10 cm (topsoil) and 10–20 cm (subsoil) in unburned plots, naturally restored plots, and two afforestation plots in southern China. The results showed that fire reduced topsoil soil moisture, nutrient levels, and microbial biomass. The variations in soil physicochemical properties significantly influenced microbial processes. Soil bulk density, nitrate, ammonium, carbon-to-nitrogen ratio, and availability of nitrogen, phosphorus, and potassium availability influenced soil enzyme activities. Soil pH, ammonium nitrogen, and the availability of nitrogen, phosphorus, and potassium were key factors shaping microbial composition. Fire altered the soil microbial communities by reducing the availability of nitrogen. Soil depth alleviated the impact of fire on the soil to some degree. Although artificial interventions reduced soil organic carbon, total nitrogen, and phosphorus, planting nitrogen-fixing species, such as *Acacia mangium*, promoted microbial recovery.

Keywords: wildfire effects; post-fire management; microbial activity; soil nutrients; phospholipid fatty acids



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1. Introduction

Among natural disturbances, wildfires are among the most disruptive to terrestrial ecosystems, yet the ongoing trend of global warming has heightened the risk of fires in humid tropical forests [1]. Fires severely affect land and forest biodiversity, resulting in habitat loss and contributing to climate change, with broad ecological, economic, and social consequences [2]. One of the most significant consequences of wildfires is soil erosion, which can obstruct vegetation regrowth, degrade water quality, deplete soil carbon

pools and nutrients in upland and riparian forests, and disrupt biogeochemical cycles [3]. Thus, developing effective post-disaster management strategies to mitigate these impacts is critical.

Soil is an irreplaceable resource (from a human perspective) and one of the most valuable assets for sustaining life [4]. Fires expose large areas of soil to air and sunlight, altering physical properties such as structure and humidity, which subsequently affect its chemical and biological characteristics [5]. Consequently, the physicochemical and biological properties of forest soil degrade, reducing their capacity to support ecosystems [6]. Research has documented how fire influences soil properties, including aggregate stability, texture, and porosity [7,8]. Nonetheless, the effects on soil properties can vary; for example, while some studies indicate that soil bulk density decreases after a fire [8], others have observed an increase [9]. Intense fires lead to nutrient loss through combustion and a decline in soil organic matter and total nitrogen [5]. Due to the uneven distribution of heat, the effects of fire on soil properties are often spatially heterogeneous and primarily limited to the upper several centimeters of soil [4]. The influences of fire on the properties and microbial characteristics in soil may diminish with increasing soil depth. Fire primarily affects the top layer of microorganisms, and studies have shown that fire only reduces dissolved organic carbon in 0–10 cm soil [10,11]. Research on subtropical forests indicates that the effect of fire on microbial biomass carbon largely depends on soil depth [12]. Therefore, studying the impacts of fire on soil at different depths can provide deeper insights into fire dynamics.

Alterations in soil physicochemical properties affect microorganisms, which are essential for maintaining soil function. Soil microbial biomass carbon and nitrogen directly reflect the microbial activity [13]. Research indicates that wildfires, through heat stress and organic matter combustion, drive microbial biomass reductions and nutrient loss in subtropical forest soils [14]. Enzymes such as β -glucosidase, N-acetyl-glucosaminidase, and acid phosphatase mediate C, N, and P acquisition, while peroxidase drives organic matter decomposition, underscoring the critical role of soil extracellular enzymes in biogeochemical processes [15,16]. Substrate utilization and microbial composition significantly influence enzyme activity, with hydrolytic enzymes declining after a fire [15]. Fire can directly kill microorganisms by increasing soil temperature and potentially influencing the size, composition, and recovery of microbial communities over a period [17,18]. The severity of these effects is influenced by factors including fire intensity, duration, soil depth, and host interactions [11,19]. Although bacteria and fungi vary in their fire resistance, bacteria are typically more adaptable to soil conditions following a fire [20]. Factors such as fire intensity and soil depth can significantly affect the direction and extent of microbial changes [10,21]. Nevertheless, the specific mechanisms through which fire impinges upon microbial communities and their functional capacities, such as enzyme activities, remain poorly understood [22]. Additional exploration is required to clarify the interrelationships between soil attributes and communities of microorganisms under various post-fire restoration methods.

Post-fire restoration methods, including artificial restoration and human intervention, also have an essential impact on ecosystem recovery. For instance, removing burned wood and subsequent afforestation can impact soil and microbial recovery, potentially causing more harm than the fire itself [23,24]. Charcoal formed during incomplete combustion can enhance the water-holding ability of soils in subtropical regions [25]. The preference for tree species for afforestation, such as those capable of nitrogen fixation, can accelerate ecological restoration, improve soil properties, and promote microbial activity [26]. Although a great deal of research has emphasized forest fires in northern and Mediterranean regions [18,27], limited research has explored the impacts of subtropical wildfires and the efficacy of various post-fire restoration practices in these regions.

This research explores how fire and post-fire restoration methods influence soil properties, enzymatic activities, and microbial community structure at various soil layers within a subtropical forest. Specifically, we address three research questions: (1) What are the impacts of fire and post-fire restoration methods on soil physicochemical properties, enzyme

activities, and microbial community composition? (2) How do these impacts vary with soil depth? (3) Through what pathways does fire affect microbial community structure? We assume that fire causes a decrease in soil nutrients and microbial biomass and that these impacts are moderated by soil depth. Additionally, we hypothesize that afforestation with nitrogen-fixing species will promote faster microbial recovery. To test these hypotheses, we employed structural equation modeling (SEM) to elucidate the immediate and subsequent impacts of wildfire on microbial communities.

2. Materials and Methods

2.1. Study Area

This research was executed in a subtropical forest on Ling Yun Mountain in Guangdong Province, South China, to examine the impacts of wildfire and restoration methods after fire on physicochemical properties and microbial characteristics in soil. A forest fire affected the region from 5 December to 9 December 2019, burning a total area of 924.63 hectares. The pre-fire vegetation was dominated by *Pinus massoniana* and *Eucalyptus*, with 93.2% of the area being plantations. The climate of the study area is defined by monsoons, featuring a precipitation peak from April to September and a drought period from October to March. The yearly rainfall ranges from 1400 to 1956 mm, with an average temperature of 23 °C per year. The highest altitude of the region is 400 m above sea level, and the soil is primarily laterite derived from granite rock [28].

To promote soil recovery, post-fire afforestation was implemented in March 2020. The burned areas were cleared of debris, including branches, weeds, and other materials, and native broadleaved tree species, mainly *Acacia mangium* and *Michelia macclurei*, were planted. Four sites were selected for study: the unburned area (UF), the natural recovery area (NRF), and two afforestation areas with different species (ARF1: *Acacia mangium* and ARF2: *Michelia macclurei*). Each site consisted of three plots, totaling 12 plots overall, each measuring 10 m × 10 m (Figure 1). The altitude, aspect, slope, and other details of the sites are provided in Table S1.

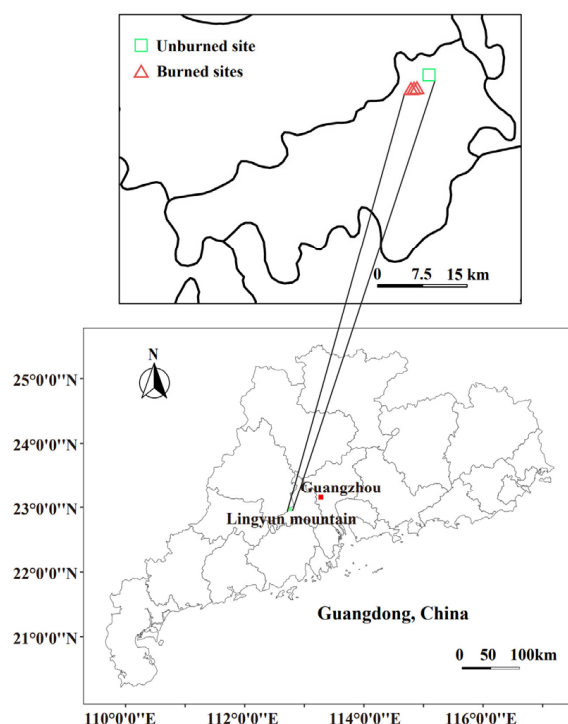


Figure 1. Map showing the study area and the location of the sample site on Ling Yun.

2.2. Soil Sampling and Chemical Analyses

Soil sampling was conducted in March 2022, 28 months after the fire. Within each plot, five soil cores were placed along an S-shaped sample from two depths: 0–10 cm of surface topsoil (0–10 cm) and 10–20 cm of deeper soil. A total of 120 subsamples were obtained. Five subsamples from an identical depth within every plot were blended to produce composite samples, which were promptly frozen in ice and delivered to the laboratory. Before being analyzed, the soil composite samples were sifted via a 2 mm mesh sieve.

The following methods were used to analyze the soil's physiochemical properties: bulk density, water retention, and porosity, which were quantified through the soaking method with a cutting ring [29]. Soil water content (SWC) was measured after drying soil samples in a 105 °C oven for a duration of 24 h. Soil pH was determined using a Sartorius PB-10 m with a soil-to-water proportion of 1:2.5. Total nitrogen (TN) and total phosphorus (TP) were assessed through the semi-micro Kjeldahl acid digestion technique [30] and molybdenum–antimony resistance colorimetric technique [31], respectively. Soil organic carbon (SOC) was measured using combustion analysis on soil samples that were air-dried [32]. Nitrate nitrogen (NO_3^- -N) and ammonium nitrogen (NH_4^+ -N) were quantified using copper cadmium reduction methods and indophenol blue colorimetry, respectively [33,34]. For available nitrogen (AN), potassium (AK), and phosphorus (AVP), AN was determined through the alkalosis diffusion approach (LY/T1229-1999), AK using flame photometry (GB7856-87), and AVP was measured via the molybdenum phosphor-blue colorimetric technique (GB7853-87).

2.3. Soil Microbial Biomass, Enzyme Activity and Microbial Characteristics Analyses

The chloroform fumigation–extraction technique was applied to measure microbial biomass carbon (MBC) and nitrogen (MBN) with a correction factor of 0.45 [35]. Enzyme activities included the N-acetyl-glucosaminidase (NAG) activity, which was measured following Deng and Popova [36]; β -glucosidase (BG) activity was estimated following Eivazi and Tabatabai [37]; and peroxidase (POD) activity was quantified with L-3,4-dihydroxyphenylalanine as a substrate [38]. Acid phosphatase (AP) was quantified following Tabatabai and Bremner [39].

Microbial communities were characterized via the phospholipid fatty acid (PLFA) technique [40]. In summary, 8 g of soil samples was freeze-dried and extracted using a chloroform–methanol–phosphate mixed buffer solution at a ratio of 1:2:8. The obtained lipids were separated into neutral, glycolipid, and polar lipids utilizing a silicic acid column with sequential elution using chloroform, acetone, and methanol. Total microbial biomass was determined based on the 66 different PLFAs detected in the samples. The PLFAs specific to different microbial groups were used to indicate general bacteria (GB), Gram-positive bacteria (G+), Gram-negative bacteria (G−), actinomycetes, general fungi (GF), arbuscular mycorrhizal fungi (AMF), and protozoa [41–44]. The calculation of the Shannon–Wiener diversity index (H) was performed [45].

2.4. Statistical Analyses

For each response variable (e.g., soil moisture, bulk density, enzyme activities), a one-way ANOVA was conducted to evaluate differences among plot types at each depth. Duncan's post hoc test was applied when significant results were obtained from ANOVA ($p < 0.05$). ANOVA was chosen for its robustness in comparing multiple groups and detecting differences in means. Levene's test was used to assess homogeneity of variance. Variables such as soil ammonia nitrogen, total nitrogen, carbon-to-nitrogen ratio, and acid phosphatase exhibited heterogeneity, as did nitrate nitrogen and total PLFAs in the surface soil, as well as organic carbon and available nitrogen in the deep soil. Welch's test was performed for these cases, followed by Tamhane's T2 post hoc test ($p < 0.05$). Similarly, the differences across various soil depths were also evaluated.

The Bray–Curtis dissimilarity metric was used to assess variation in microbial community composition among the four sites, with the results visualized using principal coordinate analysis (PCoA) implemented through the “ade4” package in R 4.3.2. Permutational multivariate analysis of variance (PERMANOVA) was applied to perform a quantitative evaluation of the joint impacts of wildfire and post-fire restoration methods on microbial community composition. Redundancy analysis (RDA) was conducted to reveal how environmental variables affect microbial communities. Structural equation modeling was employed to investigate the direct immediate and indirect subsequent impacts of fire on microorganisms and soil properties. All initial paths in the theoretical model were included, and insignificant paths were removed using d-separation criteria, and estimate indirect and total effects through the SEMEFF package [46].

3. Results

3.1. Impacts of Fire, Soil Depth, and Post-Fire Restoration Methods on Soil Physiochemical Properties

Post-fire restoration methods significantly affected most soil physical properties, except for bulk density (BD) (Table 1). Soil water content (SWC) and field water content (FWC) were higher in the unburned plots versus other plots. Nonetheless, no statistically significant difference was found in SWC and FWC between the UF and NRF, while both were significantly different from the afforestation plots (ARF1 and ARF2). There were no significant variations detected within the two afforestation plots for SWC, FWC, and capillary porosity. Fire tends to increase BD, but no significant variations in BD were found between the different post-fire restoration sites. After the fire, the reduction in SWC, FWC, and capillary porosity was less pronounced in the subsurface layer (10–20 cm) than in the topsoil layer (0–10 cm).

Table 1. Soil physical properties at different depths under different sites. Data reported are average \pm SE; SE indicates the standard error derived from 3 replicate measurements. Varied lowercase letters reflect significant variations in sites ($p < 0.05$); there was no significant difference with the same letter. SWC: soil water content; FWC: field water content; CP: capillary porosity; BD: bulk density; UF: unburned forest; NRF: burned but naturally regenerating forest; ARF1: burned but afforestation restored with *Acacia mangium*; ARF2: burned but afforestation restored with *Michelia macclurei*.

	Depth (cm)	Sites				<i>p</i> Depth
		UF	NRF	ARF1	ARF2	
SWC (%)	0–10	16.85 \pm 0.32 a	15.67 \pm 0.21 a	10.87 \pm 1.17 b	12.01 \pm 1.26 b	0.700
	10–20	15.91 \pm 0.56 a	15.98 \pm 0.13 a	11.41 \pm 0.82 b	13.8 \pm 0.7 ab	
FWC (%)	0–10	20.04 \pm 1.35 a	17.53 \pm 0.72 a	11.42 \pm 1.04 b	12.24 \pm 0.67 b	0.611
	10–20	17.74 \pm 0.75 a	16.15 \pm 0.35 a	12.34 \pm 0.09 b	11.94 \pm 1.55 b	
CP (%)	0–10	39.95 \pm 0.53 a	39.38 \pm 0.73 ab	31.34 \pm 1.15 c	35.17 \pm 1.51 bc	0.234
	10–20	37.47 \pm 1.42 a	37.43 \pm 1.01 a	31.99 \pm 1.29 ab	30.88 \pm 1.55 b	
BD (g cm ⁻³)	0–10	1.19 \pm 0.01	1.31 \pm 0.07	1.41 \pm 0.05	1.48 \pm 0.03	0.787
	10–20	1.18 \pm 0.01	1.47 \pm 0.04	1.37 \pm 0.07	1.44 \pm 0.01	

Soil chemical properties varied significantly with fire and post-fire restoration methods (Table 2). Fire tends to increase soil pH, with no significant variations noted between post-fire restoration sites. Fire significantly reduced the contents of total phosphorus, available phosphorus, and available potassium in the surface soil. It also reduced the contents of soil organic carbon, total nitrogen, and available nitrogen, especially in the 0–10 cm of topsoil. Soil organic carbon and total nitrogen in the 10–20 cm of deeper soil were less affected by wildfire. Total nitrogen, phosphorus, and available nitrogen levels were significantly high in the NRF than the afforestation plots, yet no significant change was detected between the two afforestation strategies. Notably, NO₃⁻-N levels were highest in ARF2 plots. Overall, nutrient levels (SOC, TN, TP, AN, AK, AVP, NO₃⁻-N, NH₄⁺-N) were lower in deeper

soil across all sites, and the impacts of fire on deeper soil chemistry properties were less pronounced compared with topsoil (Table 2).

Table 2. Soil chemical features at various depths under different sites. Data reported are average \pm SE; SE indicates the standard error derived from 3 replicate measurements. Varied lowercase letters reflect significant variations in sites ($p < 0.05$); there was no significant difference with the same letter. SOC: soil organic carbon; TN: total nitrogen; TP: total phosphorus; NH_4^+ -N: ammonium nitrogen; NO_3^- -N: nitrate nitrogen; AN: available nitrogen; AVP: available phosphorus; AK: available potassium; UF: unburned forest; NRF: burned but naturally regenerating forest; ARF1: burned but afforestation restored with *Acacia mangium*; ARF2: burned but afforestation restored with *Michelia macclurei*.

	Depth (cm)	Sites				<i>p</i> Depth
		UF	NRF	ARF1	ARF2	
pH	0–10	4.26 \pm 0.03	4.37 \pm 0.05	4.4 \pm 0.01	4.36 \pm 0.04	0.947
	10–20	4.26 \pm 0.03	4.34 \pm 0.05	4.41 \pm 0.01	4.35 \pm 0.04	
SOC (g kg ⁻¹)	0–10	25.96 \pm 3.44 a	19.1 \pm 0.77 ab	11.18 \pm 3.31 b	9.61 \pm 0.9 b	0.031
	10–20	15.16 \pm 2.82 a	11.83 \pm 0.9 a	7.05 \pm 0.37 a	7.06 \pm 0.44 a	
TN (g kg ⁻¹)	0–10	2.51 \pm 0.27 ab	2.24 \pm 0.08 a	1.8 \pm 0.15 ab	1.47 \pm 0.06 b	0.004
	10–20	1.55 \pm 0.28 a	1.66 \pm 0.03 a	1.2 \pm 0.07 a	1.38 \pm 0.08 a	
TP (g kg ⁻¹)	0–10	0.6 \pm 0.02 a	0.28 \pm 0.02 b	0.18 \pm 0.01 c	0.15 \pm 0.01 c	0.694
	10–20	0.53 \pm 0.02 a	0.25 \pm 0.02 b	0.16 \pm 0.01 c	0.15 \pm 0.01 c	
C/N	0–10	10.25 \pm 0.31	8.54 \pm 0.28	6.05 \pm 1.51	6.52 \pm 0.5	0.349
	10–20	9.79 \pm 0.67	7.16 \pm 0.65	5.89 \pm 0.10	5.13 \pm 0.18	
N/P	0–10	4.22 \pm 0.53 b	8.13 \pm 0.74 a	9.98 \pm 0.37 a	10.11 \pm 0.83 a	0.185
	10–20	3 \pm 0.64 c	6.71 \pm 0.53 b	7.36 \pm 0.38 b	9.42 \pm 0.21 a	
NH_4^+ -N (mg kg ⁻¹)	0–10	5.11 \pm 0.59	2.52 \pm 0.22	2.74 \pm 0.25	2.39 \pm 0.08	0.117
	10–20	3.06 \pm 0.23	2.14 \pm 0.07	2.38 \pm 0.23	2.48 \pm 0.03	
NO_3^- -N (mg kg ⁻¹)	0–10	1 \pm 0.08 a	0.86 \pm 0.07 a	1.78 \pm 0.29 a	0.86 \pm 0.04 a	0.019
	10–20	0.62 \pm 0.04 b	0.68 \pm 0.02 b	1.06 \pm 0.13 a	0.51 \pm 0.06 b	
AN (mg kg ⁻¹)	0–10	155.9 \pm 8.29 ab	124.42 \pm 3.06 a	79.76 \pm 9.24 b	67.25 \pm 5.6 b	0.034
	10–20	104.84 \pm 10.35 ab	98.99 \pm 2.94 a	50.47 \pm 2.08 b	42.85 \pm 2.94 b	
AVP (mg kg ⁻¹)	0–10	22.11 \pm 2.25 a	9.37 \pm 1.02 b	11.9 \pm 1.55 b	8.47 \pm 0.32 b	0.024
	10–20	12.14 \pm 1.24 a	6.57 \pm 0.7 b	8.35 \pm 0.71 b	4.49 \pm 0.96 b	
AK (mg kg ⁻¹)	0–10	5.56 \pm 0.41 a	3.31 \pm 0.32 b	3.88 \pm 0.19 b	3.71 \pm 0.34 b	0.074
	10–20	4.14 \pm 0.44 a	3.21 \pm 0.39 a	2.92 \pm 0.11 a	3.35 \pm 0.25 a	

3.2. Impacts of Fire, Soil Depth, and Post-Fire Restoration Methods on Soil Microbial Characteristics

Fire significantly diminished the content of microbial biomass carbon and nitrogen (MBC, MBN) in the topsoil (Figure 2). Recovery of MBC in ARF1 was significantly better than in NRF and ARF2 in the shallower soil, while post-fire restoration methods did not significantly affect MBC recovery in deeper soil (Figure 2a). MBN in topsoil was notably lower in post-fire plots than unburned plots (Figure 2b), and the content of MBC and MBN were higher in ARF1 plots in comparison with other post-fire plots. Fire had varying impacts on soil enzyme activities (Figure 3). The content of AP was higher in burned plots compared with unburned plots (Figure 3a), while the content of BG was higher in unburned plots (Figure 3b); however, the variation between AP and BG did not reach statistical significance. The content of NAG and POD decreased after the fire. NAG activity in ARF2 was significantly lower than in other plots (Figure 3c), although there was an absence of a significant difference in POD activity among different post-fire restoration methods (Figure 3d). Topsoil exhibited higher enzyme activity and microbial biomass than deeper soil. Generally, the average enzyme activity (AP, NAG, and POD) was higher in ARF1 plots in comparison to other post-fire plots.

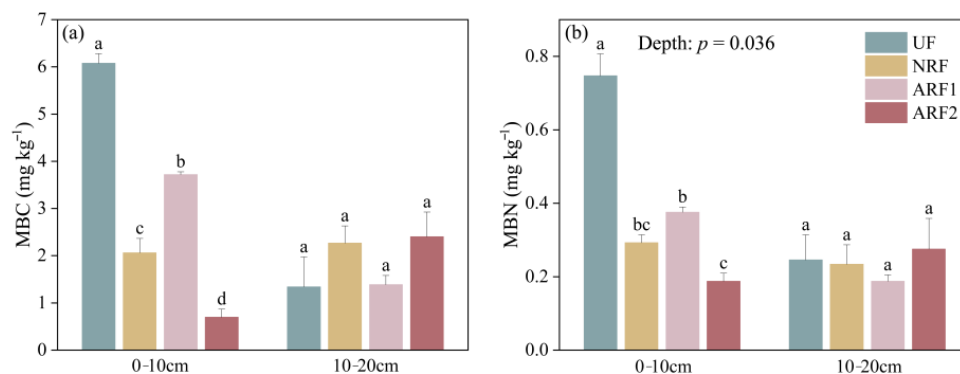


Figure 2. The content of microbial biomass carbon (MBC) (a) and nitrogen (MBN) (b) for unburned forest (UF), burned but naturally regenerating forest (NRF), and burned but afforestation restored with *Acacia mangium* (ARF1) and *Michelia macclurei* (ARF2) in different soil depths ($M \pm SE, n = 3$). Varied lowercase letters reflect significant variations in sites ($p < 0.05$); there was no significant difference with the same letter. Significant differences between soil depth ($p < 0.05$) have been marked in the figure.

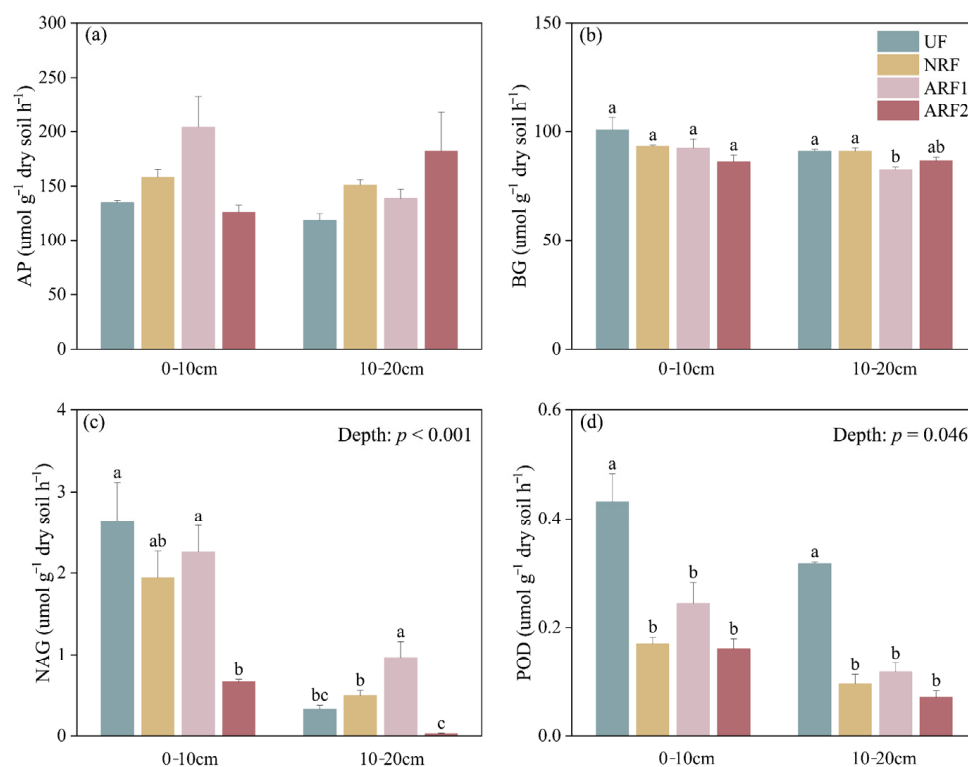


Figure 3. Microbial enzyme activity of acid phosphate (AP), β -glucosidase (BG), N-acetyl-glucosidase (NAG), and peroxidase (POD) (panels a–d, respectively) ($M \pm SE, n = 3$). Varied lowercase letters reflect significant variations in sites ($p < 0.05$); there was no significant difference with the same letter. Unburned forest (UF); burned but naturally regenerating forest (NRF); burned but afforestation restored with *Acacia mangium* (ARF1) and *Michelia macclurei* (ARF2). Significant differences between soil depth ($p < 0.05$) have been marked in the figure.

The average content of general bacteria, Gram-positive bacteria, Gram-negative bacteria, actinomycetes, and arbuscular mycorrhizal fungi PLFAs was lower in post-fire sites than unburned sites, while the highest content of general fungal and protozoa PLFAs was observed in NRF site (Table S2). The relative abundance of Gram-positive bacteria was the highest among the detected microorganisms, while fungi had a lower relative abundance (Figure 4). Fire reduced the proportion of AMF among the microbial community but increased

the ratios of actinomycetes and other microorganisms (Figure 4). The total phospholipid fatty acids (PLFAs) in the soil ranged from 8 to 33.66 nmol g⁻¹ (Figure 5a). ARF1 plots had higher average total PLFAs (14.34 nmol·g⁻¹) than NRF plots (13.38 nmol·g⁻¹), with lower PLFA levels in post-fire plots compared with unburned plots (Figure 5a). The Shannon–Wiener diversity index revealed significant differences in microbial diversity across different sites, with fire causing a general decline in diversity (Figure 5b). The fungi-to-bacteria ratio (F/B) tended to increase after the fire in most plots, except ARF2, though a significant increase was observed only in NRF (Figure 5c). The Gram-positive bacteria to Gram-negative bacteria ratio was higher in post-fire sites (Figure 5d). The Gram-positive bacteria to Gram-negative bacteria ratio was notably greater in ARF2 plots compared with other plots, while F/B was greater in NRF plots than in the afforestation area. PLFA content for various microbial groups decreased with soil depth, and the shift in microbial community composition was more pronounced in topsoil in comparison with the deeper soil (Table S2).

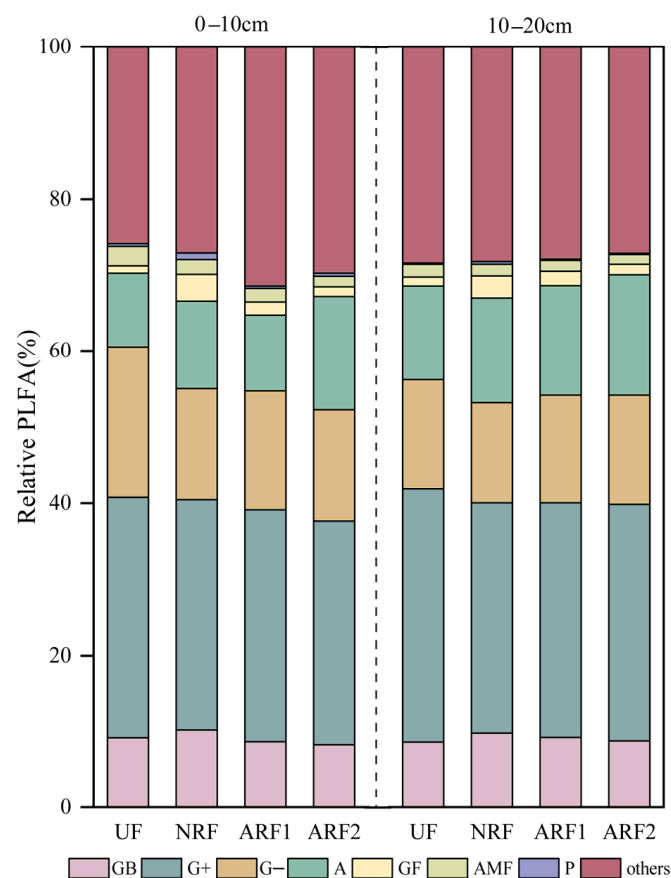


Figure 4. Relative content of soil microbial phospholipid fatty acids (PLFAs). G+: Gram-positive bacteria; G–: Gram-negative bacteria; A: Actinobacteria; AMF: arbuscular mycorrhizal fungi; P: protozoa; GF: general fungi, which are fungi other than AMF; GB: general bacteria, which are bacteria except for G+, G–, and A; others: other microbes. Unburned forest (UF); burned but naturally regenerating forest (NRF); burned but afforestation restored with *Acacia mangium* (ARF1) and *Michelia macclurei* (ARF2).

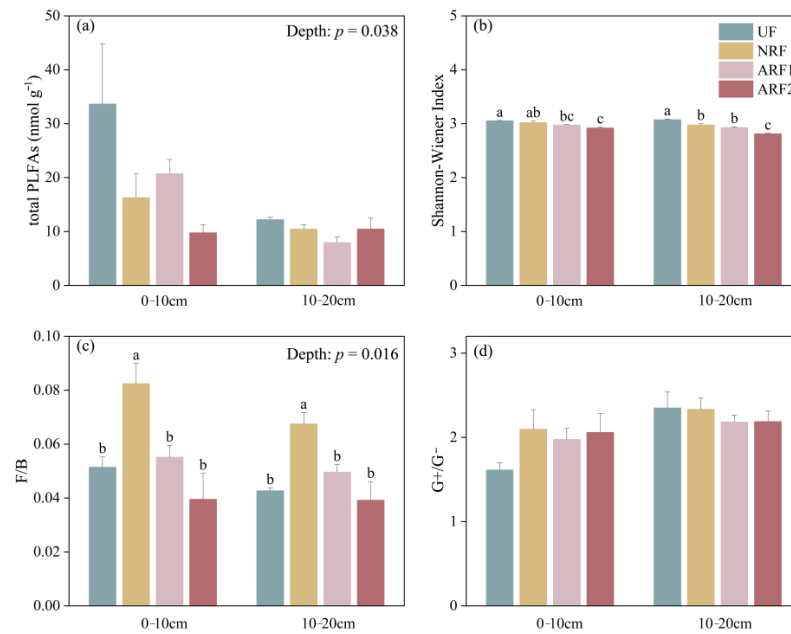


Figure 5. Total PLFAs (a), Shannon–Wiener diversity index (H, b), the ratio of Gram-positive bacteria to Gram-negative bacteria (G+/G−, c), and fungi to bacteria (F/B, d) ($M \pm SE$, $n = 3$). Varied lowercase letters reflect significant variations in sites ($p < 0.05$); there was no significant difference with the same letter. Unburned forest (UF); burned but naturally regenerating forest (NRF); burned but afforestation restored with *Acacia mangium* (ARF1) and *Michelia macclurei* (ARF2). Significant differences between soil depth ($p < 0.05$) have been marked in the figure.

3.3. Correlations of Soil Enzyme Activity and Microbial Community Composition with Soil Physicochemical Properties

PCoA revealed a marked distinction within the microbial community arrangement space (Figure 6). The primary and secondary axes explained 43.22% and 30.83% of the variance, respectively. PERMANOVA indicated significant dissimilarities in microbial community structure across different sites ($r^2 = 0.48$; $p = 0.001$) (Table S3). Fire significantly altered the microbial community composition, with differences observed between natural recovery and the afforestation plots (Table S3).

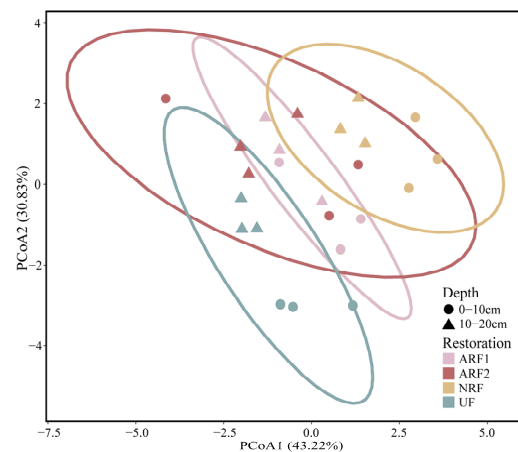


Figure 6. Principal coordinate analysis (PCoA) plots demonstrating microbial community composition. Sites are depicted using various colors, and soil depths are represented by shapes. Confidence ellipses at the 95% level were outlined for each site. Unburned forest (UF); burned but naturally regenerating forest (NRF); burned but afforestation restored with *Acacia mangium* (ARF1) and *Michelia macclurei* (ARF2).

Redundancy analysis (RDA) identified several soil properties that significantly influenced microbial activity and community composition. The primary and secondary axes elucidated 53.35% and 8.6% of the variability in microbial activity, and 67.77% of the total difference in microbial composition (Figure 7). Key soil physicochemical properties affecting microbial activities included bulk density (BD), nitrate nitrogen (NO_3^- -N), ammonia nitrogen (NH_4^+ -N), carbon nitrogen ratio (C/N), available nitrogen (AN), available phosphorus (AVP), and available potassium (AN) (Table S4). Variations in microbial community composition demonstrated a significant association related to soil pH, NH_4^+ -N, AK, AVP, and AN ($p < 0.05$) (Table S5). β -glucosidase, N-acetyl-glucosidase, peroxidase, microbial biomass carbon (MBC), and microbial biomass nitrogen (MBN) were positively associated with soil AN, AVP, AK, NH_4^+ -N, C/N, and SWC, and negatively associated with BD. In contrast, acid phosphate activity positively correlated with soil pH (Figure 7a, Table S4). Soil AVP, AN, and AK positively influenced total PLFAs and the PLFAs of diverse groups, while pH generally had a negative influence, except on protozoa (Figure 7b). Correlation analysis supported these findings (Figure S1), and a positive correlation was found between enzyme activity and the contents of MBC and MBN (Figure S1). The enzyme activity was positively correlated with the content of PLFAs in each group (Figure S2).

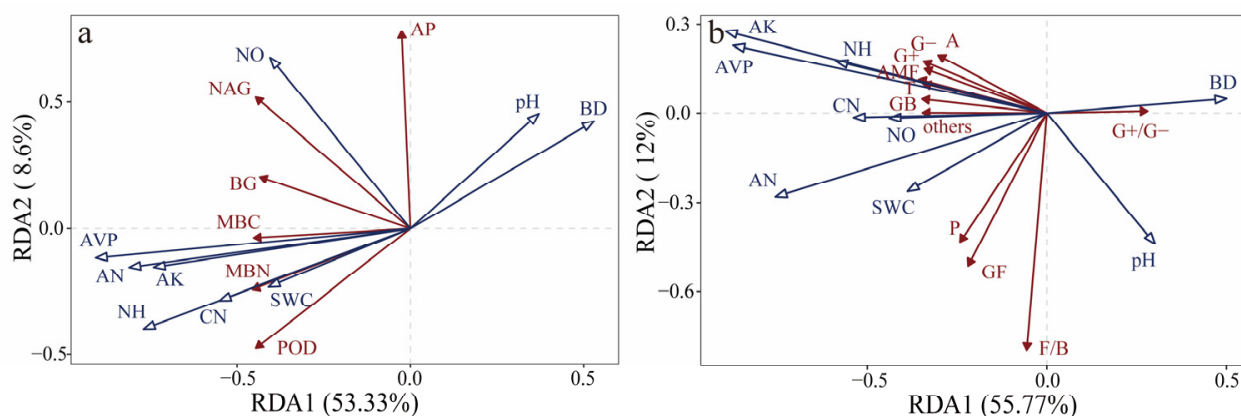


Figure 7. The association between microbial activity (a) community composition (b) and soil physicochemical properties based on redundancy analysis (RDA). Blue arrows indicate soil characteristics and red arrows indicate microbial activity/microbial community. AK: available potassium; AN: available nitrogen; AVP: available phosphorus; BD: bulk density; NO: NO_3^- -N; NH: NH_4^+ -N; CN: C/N ratio; SWC: soil water content; T: total PLFAs; MBC: microbial biomass carbon; MBN: microbial biomass nitrogen; AP: acid phosphate; BG: β -glucosidase; NAG: N-acetyl-glucosidase; POD: peroxidase; G+: Gram-positive bacteria; G-: Gram-negative bacteria; A: Actinobacteria; AMF: arbuscular mycorrhizal fungi; P: protozoa; GF: general fungi, which are fungi other than AMF; GB: general bacteria, which are bacteria except for G+, G-, and A; others: other microbes. Unburned forest (UF); burned but naturally regenerating forest (NRF); burned but afforestation restored with *Acacia mangium* (ARF1) and *Michelia macclurei* (ARF2).

SEM explained 61%, 37%, and 96% of the changes in microbial diversity, bacterial PLFA, and fungal PLFA content, separately. Fire exerted a direct positive relationship with bulk density while negatively affecting available nitrogen (Figure 8). Indirectly, fire adversely affected microbial diversity, bacterial PLFA content, and fungal PLFA content through its influence on the soil's available nitrogen. The soil's available nitrogen had both direct and indirect positive impacts on fungal PLFA content (Table S6).

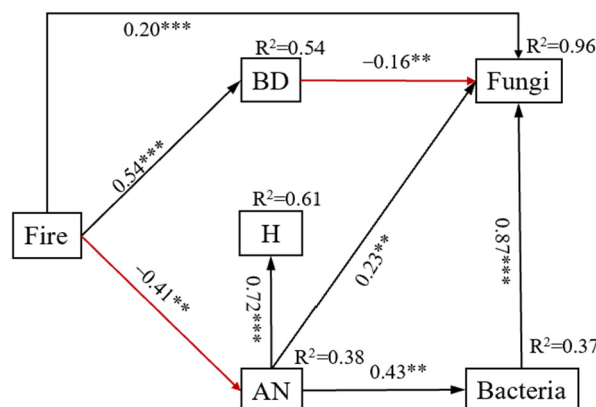


Figure 8. Structural equation models examining the relationships between fire, soil physicochemical properties, and the microbial community ($X^2 = 11.53$, $p = 0.173$, $df = 8$). The numbers associated with the arrows signify standardized path coefficients. Black and red arrows represent positive and negative effects, respectively. R^2 values indicate the percentage of variance accounted for by each endogenous variable. ** $p < 0.01$ and *** $p < 0.001$. AN: available nitrogen; BD: bulk density; H: Shannon–Wiener diversity index.

4. Discussion

4.1. Effects of Fire on Soil Physical and Chemical Properties

Our findings confirm that wildfires significantly alter soil physicochemical properties, particularly in the topsoil. Soil water content and field capacity decreased after the fire, primarily due to the loss of organic matter, soil structure damage, and increased evaporation, which collectively reduced soil moisture. High temperatures caused soil structure damage to the soil, with ash clogging pore spaces, resulting in reduced capillary porosity and an increase in bulk density [47,48]. The elevation in soil pH, attributed to ash deposition, the loss and denaturation of organic acids, and mineral transformation, supports our hypothesis that fire directly affects soil chemical properties [6].

The observed reductions in the content of soil organic carbon (SOC) and total nitrogen (TN) are consistent with findings that wildfires volatilize organic matter, leading to significant nutrient loss [49]. While previous studies have reported increased soil phosphorus levels after fires [50], we found a decrease, suggesting that phosphorus volatilization may occur at high temperatures, depending on soil characteristics [51]. Additionally, reductions in SOC have been linked to changes in microbial composition and population size, increased carbon mineralization rates due to elevated pH, and carbon dissolution following fire events [52]. Nitrogen loss may also result from the release of N into the atmosphere as nitrous oxides, increased uptake and leaching associated with post-fire plant growth, and ash erosion [50,53]. Furthermore, the increased nitrate levels observed in plots with *Acacia mangium* underscore the role of nitrogen-fixing species in influencing soil nitrogen availability during early recovery. These species can convert atmospheric nitrogen, thereby contributing to the soil nitrogen cycle [54].

4.2. Effects of Fire on Soil Enzymatic Activities and the Structural of Microbial Communities

Fire significantly diminished the content of microbial biomass carbon and nitrogen (MBC, MBN), particularly in surface soils (0–10 cm), supporting our hypothesis that fire adversely affects microbial biomass. Variation in soil organic carbon (SOC), total nitrogen (TN), and MBC, MBN was positively associated, and microbial activity depended strongly on substrate availability [55], indicating that fire indirectly affects microbial biomass by altering soil carbon and nitrogen. This reduction in MBC and MBN is likely a result of the direct thermal destruction of microbial cells and the removal of carbon and nitrogen sources essential for microbial growth [56]. Changes in soil enzyme activities after the fire further support the idea that soil enzymes are highly sensitive to fire-induced variation in the soil environment [16,57]. Interestingly, we observed a differential response among soil enzymes:

while phosphatase activity increased after the fire, reflecting potential microbial adaptation to phosphorus scarcity, β -glucosidase activity declined across all plots, possibly due to a decrease in labile carbon substrates [58,59]. Furthermore, soil available P is positively correlated with the activity of the N-acquiring enzyme (NAG) in the soil, suggesting that the availability of phosphorus can trigger the increase in the augmentation of nitrogen nutrient effectiveness [60]. A reduction in SOC and TN would impede the growth and activity of microorganisms [13,61]. The reduction in soil MBC and MBN resulting from the fires directly reflected the decline in soil microbial activity. Soil enzymes are primarily derived from microorganisms [13]. It can thus be surmised that the reduced soil carbon and nitrogen levels observed in the fire sample may be a contributing factor to the observed decline in extracellular enzyme activity. Moya et al. [62] have previously reported that while the poor nutrient availability and reduction in the carbon mineralization rate following fires may delay the recovery of microbial activity, the collection of soil carbon and nitrogen stocks during the succession process may lead to an increase in enzyme activity.

Our study revealed discernible alterations in the structure of the soil microbial community in the aftermath of a fire, showing that the overall PLFAs, bacterial, and fungal contents all decreased after fire. Moreover, soil microbial diversity decreased after fire, and the reduction in microbial abundance and diversity could have caused a deterioration of ecosystem function [63]. Bacterial and fungal declines differed, except for a rise in fungal content and a drop in bacterial content in the NRF plots, resulting in a post-fire change in the proportion of fungi to bacteria in the plots. The increase in fungi (especially AMF) in the NRF may have been due to P limitation, mycorrhizal fungi being more abundant in sites more limited by soil nutrients, fire-induced substrate changes, and competitor mortality, which can stimulate positive fungal responses [64,65]. When contrasted with Gram-negative bacteria, Gram-positive bacteria feature a cell wall that is markedly thicker and stronger [66], which enables them to better survive in resource-limited environments and withstand environmental stresses. This might account for the elevation of the ratio of Gram-positive bacteria to Gram-negative bacteria in shallow soil post-fire. The higher relative abundance of actinomycetes in post-fire plots may be related to the fact that the spores they formed were highly resistant to fire [67]. Principal coordinate analysis (PCoA) indicated distinct changes in microbial community composition under different management strategies. The results indicate that soil pH and the nutrient accessibility in the soil exert a considerable influence on soil microbial structure, which is in agreement with previous research that soil microbes are linked to variation in available nitrogen, and the sustained reduction in microbial activity may result from the loss of carbon–nitrogen binding after the fire [68]. Fire directly and indirectly drives changes in soil bacteria and fungi through environmental factors. SEM further revealed that the effect of fire on the content of bacteria and fungi and the Shannon–Wiener diversity index is mainly through available nitrogen. Studies have shown that variations in the structure of bacterial and fungal communities are associated with alterations in nitrogen pools [69]. Increasing nitrogen availability can support the expansion and reproduction of microbial communities, enhancing microbial biomass, and affect fungal diversity. Available nitrogen may be a key factor affecting microbial metabolic potential and functional genes [70,71]. Increased soil bulk density by fire negatively affected the PLFA concentration in fungi, with reports indicating that soil bulk density contributed to the reduction in the PLFA concentration in bacteria, fungi, and overall microorganisms [72].

4.3. Implications for Depth

Whether it is the increase in pH after fire or the decrease in soil nutrients (SOC, TN, TP, etc.), the changes in deep soil were smaller than those in shallow soil, indicating that the impact of fire decreases with increasing depth. Although the overall soil PLFAs content decreased by 21.14% on average, the decrease was lower than that in the topsoil layer (53.66% on average). Microorganisms were usually more affected in the topsoil because the temperature was usually greater in the topsoil. Fire experiments showed that the soil depth

difference was 5 cm, and the temperature difference could be more than 100 °C [73]. Soil nutrients decrease with soil depth. Similarly, soil enzyme activity and microbial content also decrease as soil depth increases, which is connected to the decline of soil organic matter and nutrients. Wu et al. [61] believe that their reduction will inhibit the development of microorganisms and change soil enzyme activity. The results illustrated that the effect of fire on soil diminished with an increase in soil depth. A fire study about *Pinus tabulaeformis* forests in North China showed that organic matter moderated the arrangement of microbial communities with increasing depth. Fire not only directly affected the microbial community in the topsoil but also affected the deeper soil over an extended period [10].

4.4. Implications for Post-Fire Management Strategies

Our results highlight important implications for post-fire restoration methods in subtropical forests. The microbial biomass and microbial activity in the *Acacia mangium* plantation plots recovered better than other post-fire plots, consistent with the research results of *Acacia mangium* in Eucalyptus plantation. *Acacia mangium* is an N₂ fixing species, which can increase MBC, regulate soil microbial characteristics, and increase the concentration of C and N in soil active components [74]. Therefore, the total PLFAs and F/B in ARF1 plots are closer to those of the unburned sample plot, indicating that planting *Acacia mangium* is conducive to the post-fire recovery of soil microorganisms. However, our findings also caution against immediate after-fire practices, including timber harvesting and site preparation, which can degrade soil properties by reducing moisture and nutrient availability and disturbing soil structure [23]. Prior research has shown that harvesting increases soil community diversity [75]. However, this study found the microbial diversity in the natural recovery plots showed no significant difference to that in the ARF1 plots, demonstrating that the impacts of soil compaction and harvesting on microbial diversity could be offset by cultivating *Acacia mangium* to a certain extent. To optimize ecosystem recovery, we recommend delaying interventions until natural vegetation begins to recover, typically 1 or 2 years after the fire [10,76]. During this period, strategies should focus on enhancing structural complexity at the forest floor, retaining deadwood to protect soil and improve nutrient availability, and minimizing soil compaction to promote microbial and soil health [10,77]. In the long-term, post-fire restoration strategies for subtropical China should focus on the restoration of vegetation and consider the use of nitrogen-fixing trees in artificial reforestation efforts, such as *Acacia mangium*.

While our study provides ponderable insights into the effects of fire and post-fire restoration methods on soil and microbial dynamics, additional research is required to comprehend the long-term effects of various restoration methods across varied subtropical ecosystems. Further research ought to explore the interactive impacts of fire severity, soil depth, and management interventions on microbial functional traits and their roles in ecosystem functions, providing a more comprehensive understanding of soil resilience and recovery after fire.

5. Conclusions

Our findings demonstrate that wildfires significantly alter soil physicochemical properties and microbial community composition, with impacts varying by soil depth and post-fire restoration methods. We found that fire reduced soil nutrients (SOC, TN, AN), leading to declines in microbial biomass carbon and nitrogen, NAG, POD activities, and the content of microbial groups (PLFAs). Key factors influencing microbial community structure included soil pH and the availability of nitrogen, phosphorus, and potassium. Fire indirectly affected soil microbial composition by altering soil physical properties and nitrogen availability. Soil depth mitigates the effect of fire on soil, as nutrients, microbial activities, and microbial content decline with increasing depth. Our findings highlight the importance of selecting appropriate post-fire restoration methods to promote ecosystem recovery. While interventions like logging exacerbate soil degradation, afforestation with nitrogen-fixing species, such as *Acacia mangium*, enhances microbial recovery. We strongly

recommend prioritizing nitrogen-fixing species in post-fire landscapes and delaying interventions until natural vegetation recovery is evident, to optimize soil health and enhance ecosystem resilience. However, this study focused solely on the early recovery stages of soil properties, leaving long-term trends uncertain. Future research should explore the interactive effects and underlying mechanisms of fire severity, soil depth, and management interventions on microbial functional traits and their contributions to ecosystem functions.

Supplementary Materials: The following supporting information can be downloaded at <https://www.mdpi.com/article/10.3390/fire7120474/s1>, Figure S1: Heat map of Spearman correlation coefficients for measures of microbial activity and microbial composition vs. soil properties associated with the UF, NRF, ARF1, and ARF2 sites; Figure S2: Heat map of Spearman correlation coefficients for microbial activity vs. microbial composition measures with the UF, NRF, ARF1, and ARF2 sites; Table S1: General description of the control and burned sites; Table S2: Changes in PLFAs content of various microbial groups in sites with fire and post-fire management in different soil layers; Table S3: Significance analysis of fire and post-fire management on soil microbial community composition; Table S4: Permutation test for redundancy analysis (RDA) for microbial activity under the final model; Table S5: Permutation test for redundancy analysis (RDA) for microbial community composition under the final model; Table S6: Indirect and total effects from structural equation models exploring the interactions between fire, fungal content, soil properties, Shannon-Wiener diversity index and bacterial content.

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