



Short-term response of soil bacterial and fungal communities to fire in rotational shifting cultivation, northern Thailand

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ABSTRACT

Soil microbial communities are ubiquitous and essential for the functioning of the soil system. The use of fire is a common practice in rotational shifting cultivation (RSC) to clear land after cutting vegetation for cultivation. However, three main questions remain unanswered: (1) What is more sensitive to fire between bacteria and fungi in RSC fields? (2) What kinds of bacterial and fungal taxa are resistant to fire in RSC fields? and (3) Does fire affect the complexity of soil microbial networks in RSC fields? To address these questions, surface soil samples (0–2 cm depth) were collected from sites with 10 years of fallow in Chiang Mai Province, northern Thailand, at three different time points: before burning (BB), 5 min after burning (AB), and 1 month after burning (AB-1 M). The results revealed that bacteria exhibited greater sensitivity to fire compared to fungi. After one month of burning, bacterial richness and diversity increased significantly and recovered more rapidly than fungi, likely due to the rise in soil pH post-fire. Heat-resistant bacteria and fungi were detected following the fire event. Specifically, within the bacterial community, the phylum Firmicutes exhibited a substantial increase of around 95 % (BB = 0.63 %, AB = 96.31 %), while the genera *Bacillus* (BB = 0.16 %, AB = 38.53 %), *Alicyclobacillus* (BB = 0.14 %, AB = 17.10 %), and *Aneurinibacillus* (BB = 0.03 %, AB = 10.48 %) showed over a tenfold increase after the fire. In the fungal community, the phylum Ascomycota (BB = 31.46 %, AB = 96.47 %) experienced a significant increase after the fire. At the genus level, *Penicillium* (BB = 4.99 %, AB = 54.14 %), *Aspergillus* (BB = 3.20 %, AB = 14.50 %), and *Hamigera* (BB = 0.02 %, AB = 10.07 %) displayed dominant increases in response to fire. Co-occurrence network analysis revealed that fungi tended to form more complex networks compared to bacteria. The complexity of both bacterial and fungal networks declined after the fire but rebounded significantly after one month. Our study underscores the significance of fire disturbance in shaping the dynamics of soil bacteria and fungi in RSC fields.

1. Introduction

Shifting cultivation, also known as swidden farming or slash-and-burn farming, is an agricultural technique that involves the clearing of an area using fire, followed by a short period of cultivation and subsequent fallow period (Pollini, 2014). This traditional farming practice has been passed down through generations (Maharjan et al., 2018). While shifting cultivation was once common in both America and Asia (Kingwell-Banham and Fuller, 2012; Burchfield, 2022), it is now primarily practiced in Asia and Southeast Asia, including countries such as India, Nepal, China, Thailand, and the Philippines (Rerkasem and Rerkasem, 1995; Rasul and Thapa, 2003). In Thailand, shifting cultivation is widely

practiced by indigenous peoples in the northern highlands. However, due to stringent forest protection laws, the clearing of primary forests and establishment of new settlements is prohibited. The existing areas where shifting cultivation is practiced in Thailand are referred to as rotational shifting cultivation (RSC) (Arunrat et al., 2022).

Fire is normally used to clear the land after cutting the vegetation for cultivation (Eastmond and Faust, 2006). Fire intensity, frequency, size, seasonality, type, and severity are crucial factors that interact and contribute to the characterization of fire regimes (Pausas and Keeley, 2014). High-severity fires have a more pronounced impact on soil parameters, leading to increased pH, reduced availability of phosphorus (P) and nitrogen (N), as well as a decrease in carbon (C) stock, when

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compared to low-severity fires (Elakiya et al., 2023). Fire exerts both indirect and direct influences on the prevalence of different microbial communities in the soil. Direct effects of fire occur as a result of heat transfer from the soil surface to lower depths (Cairney and Bastias, 2007). In addition, changes in soil properties such as pH, moisture content, soil nutrients, soil carbon, and soil temperature indirectly influence the presence and abundance of microbial groups (Certini, 2005). According to a meta-analysis on microbial responses to fire by Dooley and Treseder (2012), a reduction of approximately 33.2 % in bacterial abundance and 47.6 % in fungal abundance was observed following a fire. This review concludes that wildfires result in a greater reduction in microbial biomass than prescribed burns due to higher fire intensity.

The severity of the burn can impact the emergence of bacteria and fungi (Kennedy et al., 2015; Holden et al., 2016). Previous studies have indicated that fungi are more sensitive to fire compared to bacteria. Moreover, fungal growth rate is slower than bacteria after a fire (Sun et al., 2015; Zhou et al., 2020). In contrast, some genera in the phylum Ascomycota such as *Calyptrozyma*, *Coniochaeta*, *Oidiodendron*, and *Penicillium* and the phylum Basidiomycota *Naganishia* responded positively to fire in both low and high severity plots (Caiafa et al., 2023). The genus *Paraglomus* was dominant in burned soil under light, moderate, and heavy fire intensities in Taiga Forests, Northeast China (Cheng et al., 2023).

Soil microorganisms have a significant impact on soil properties and are involved in the decomposition of plant and animal residues, contributing to the formation of organic matter. However, the process of microbial decomposition is inhibited following a fire incident due to the impact of fire on the enzyme activities of microorganisms (Waldrop and Harden, 2008). Soil microbial communities can shift taxonomically with fire, which in turn can have an influence on the soil ecosystem, including factors such as seedling establishment and the recovery of vegetation and plants (Balsler and Firestone, 2005). The rate of recovery depends on the interaction of several factors, including soil hydrophobicity (Doerr et al., 2000), the intensity and frequency of precipitation, nutrient availability, and soil erodibility (Hinojosa et al., 2019; Rodriguez et al., 2017; Arunrat et al., 2023a). The study by Xiang et al. (2014) demonstrated that high fire intensity resulted in a reduction in bacterial diversity within one year after burning. However, it was observed that it took five to eleven years for the bacterial diversity to recover to pre-burning levels (Whitman et al., 2022). Fungi can require 12 to 24 years or more to recover to pre-fire levels, as indicated by previous studies (Treseder et al., 2004; Holden et al., 2013). Ectomycorrhizal fungal communities in the Russian Far East did not recover to pre-fire levels even 16 years after the fire (Miyamoto et al., 2021). Despite prescribed fire effects on bacteria and fungi being investigated in several areas, such as California grasslands (Glassman et al., 2023), Northern California mixed conifer forest (Fischer et al., 2023), and Great Smoky Mountains National Park, Southeastern, USA (Schwartz et al., 2016), the understanding of how soil bacteria and fungi respond to fire in RSC in Thailand is still lacking.

Numerous previous studies have examined the changes in soil

bacterial communities and fungi immediately after a fire in the short-term (1 year) (e.g., Sáenz de Miera et al., 2020; Qin and Liu, 2021; Day et al., 2019), as well as in the long-term (>10 years) (e.g., Treseder et al., 2004; Kipfer et al., 2011; Orumaa et al., 2022) following a forest fire occurrence. However, the important questions still remain unanswered: (1) how do soil bacterial communities and fungi respond to fire in RSC? and (2) which genera exhibit high tolerance to fire and fast-growing at early-month recovery after a fire?. This is because early post-fire recovery plays a crucial role in ecosystem restoration and resilience. The period immediately after a fire is critical for the regeneration of vegetation, establishment of new plant communities, and recovery of the overall ecosystem. This stage is characterized by significant alterations in resource availability, such as soil nutrients and organic matter, and substantial changes in the soil and microbial communities. Therefore, the aim of this study is to investigate the impact of fire on soil bacterial communities and fungi, as well as their recovery during the early-month period. We hypothesized that: (H1) immediate burning would lead to a greater reduction in fungal compared to soil bacterial communities due to slower growth and the loss of living plants (Holden et al., 2016; Zhou et al., 2020), (H2) the abundance of heat-resistant bacteria and fungi would be more pronounced after the fire, as some bacteria and fungi species possess heat-resistant spores (Glassman et al., 2016; Tu et al., 2021), and (H3) fire could lead to a reduction in the complexity of bacterial and fungal networks, and this reduction may recover within one month due to alterations in soil physiochemistry and enzyme activity (Yang et al., 2020; Papatheodorou et al., 2023). These hypotheses were formulated to explore the specific impacts of fire on soil microbial communities and to understand the dynamics of different microbial groups during the initial stages of post-fire recovery. Our findings provide an understanding of the processes and factors that drive early post-fire recovery, which is essential for effective post-fire management and conservation strategies.

2. Materials and methods

2.1. Study areas and site selection

The study area is located in Ban Mae Pok, Ban Thab Subdistrict, Mae Chaem District, Chiang Mai Province, Northern Thailand. The annual rainfall ranged from 1105 to 2688 mm, with the rainy season occurring from May to October. The winter season spanned from October to February, with minimum temperatures ranging from 3.2 to 22.1 °C. The summer season took place from February to April, with maximum temperatures ranging from 35 to 40 °C. Soils with slopes >35 % in Thailand were classified as slope complex soil series (LDD, 1992). The topsoil (0–10 cm) consisted of sandy loam, with soil pH ranging from 5.87 to 6.65. The organic matter content varied from 2.75 % to 5.53 % (Arunrat et al., 2022). The dominant tree species in the area include *Pterocarpus macrocarpus* Kurz, *Xylia xylocarpa* (Roxb.) Taub, and *Lithocarpus ceriferus* (Arunrat et al., 2023a).

A field with a 10-year fallow period in RSC (referred to as RSC-10Y)



Fig. 1. The RSC-10Y field at different time points.

was selected for the study because it was the community's field cycle for this year (2023). The field had previously used for upland rice cultivation and was left fallow for 10 years. In 2023, the RSC-10Y field (18°22'44.5"N, 98°11'45.3"E; elevation 789 m a.s.l; slope gradient 32 %) was cleared, burned, and used for cultivating upland rice again.

2.2. Experimental design, fire measurements and soil sampling

The field boundary was initially identified by the community leaders and members, followed by the implementation of a firebreak. Burning was conducted in May 2023 at 16.00–18.00 pm. The fire temperature during burning was measured using an infrared thermometer.

In the RSC-10Y field, we established ten transects spaced 50 m apart, originating from the highest point of the slope and extending to the lowest point. Along each transect, we marked five replicate plots for soil sampling along the slope. At each plot (10 × 10 m) within each transect, soil samples were collected at a depth of 0–2 cm (surface layer). Subsequently, soil samples from the five plots were combined to create one composite sample per transect. This design helps mitigate the impact of soil nutrient variation along the slope caused by erosion processes (Arunrat et al., 2023b), which could otherwise influence the richness and diversity of soil bacteria and fungi. Around 100 g of soil was placed into zip-lock plastic bags and stored at –20 °C for DNA extraction purposes. Moreover, approximately 1 kg of soil was placed into a plastic bag for the analysis of soil physical and chemical properties. Soil sampling was conducted at three different time points: before burning (May 2023), 5 min after burning (May 2023), 1 month after burning (June 2023) (Fig. 1). Each plot of soil sampling, the soil temperature and soil moisture were recorded at a depth of 2 cm with a Thermocouple Type K and a soil moisture meter, respectively.

2.3. Soil physicochemical properties analysis

Soil bulk density was determined by measuring the dry weight of the soil sample in a steel soil core after drying at 105 °C for 24 h. Hydrometer method was used to determine soil texture. Soil pH was measured using a pH meter (1:1 solids in water) (National Soil Survey Center, 1996). Electrical conductivity (ECe) was measured by determining the saturation paste extracts using an EC meter (Soil Survey Staff, 2014). Total nitrogen (TN) was analyzed using the micro-Kjeldahl method (Soil Survey Staff, 2014). Ammonium nitrogen (NH₄-N) and nitrate–nitrogen (NO₃-N) were measured by the KCl extraction method (Soil Survey Staff, 2014). The exchangeable calcium (exch.Ca), magnesium (exch.Mg), and potassium (exch.K) values were determined using atomic absorption spectrometry with NH₄OAc pH 7.0 extraction (Jones, 2001; Thomas, 1982). Available phosphorus (avail.P) was measured using the molybdate blue method (Bray II extraction) (Jones, 2001; Bray and Kurtz, 1945). Organic carbon (OC) was determined by potassium dichromate (K₂Cr₂O₇) in sulfuric acid (Jones, 2001; Walkley and Black, 1934) and converted to organic matter (OM) by multiplying by 1.724.

2.4. DNA extraction and sequencing

DNA was extracted from approximately 0.25 g of soil using the DNeasy PowerSoil Pro DNA Kit (Qiagen, USA). For bacterial analysis, the DNA samples were amplified on the hypervariable V3-V4 region of the 16S rRNA gene using primers 341F (5'-CCTAYGGGDBGCWSCAG) and 805R (5'-GGACTACNVGGGTHCTAAT-3') (Klindworth et al., 2013). For fungal analysis, the ITS1 regions were amplified using ITS1F (5'-CTTGGTCATTTAGGAAGTAA-3') and ITS2R (5'-GCTGCGTTCTTCATCGATGC-3') primers (Gardes and Bruns, 1993). The amplification condition included an initial denaturation step 2 min at 98°C, followed by 30 cycles of 98 °C for 20 s, 60 °C for 30 s, and 72 °C for 60 s, followed by a single step final extension step at 72 °C for 1 min. Subsequently, 16S and ITS amplicons were purified using sparQ

Puremag Beads (QuantaBio, USA) and indexed using 2.5 µl of each Nextera XT index primer in a 50 µl PCR reaction, followed by 10 cycles of PCR condition above. The final PCR products were cleaned, pooled and diluted to final loading concentration at 4 pM. The PCR products were subsequently sequenced on the Paired-end Illumina Miseq platform (2 × 250 bp) at the Omics Sciences and Bioinformatics Center of Chulalongkorn University (Bangkok, Thailand). The raw sequence data for the 16S rRNA and ITS genes were deposited in the National Center for Biotechnology Information (NCBI) under the accession number PRJNA1001269.

2.5. Bacterial taxonomic and functional identification

The sequences were analyzed using QIIME2 v. 2022.2 (Bolyen et al., 2019). Bacterial and fungal primers were removed using cutadapt v. 4.0 (Martin, 2011). Raw sequence data underwent quality filtering, merging, and removal of chimeras using the DADA2 plugin (Callahan et al., 2016). Amplicon sequence variants (ASVs) containing fewer than 2 sequences were excluded from the dataset to mitigate potential sequencing errors. The remaining sequences were taxonomically classified using the Silva database (Pruesse et al., 2007) for bacteria and the UNITE database (Abarenkov et al., 2021) for fungi. Bacterial and fungal-associated functions were predicted using PICRUSt2 (Douglas et al., 2020). Specifically, we focused on 11 enzymes involved in the carbon and nitrogen cycle, namely Nitrogenase, Nitrate reductase, Chitinase, β-glucosidase, Xylan 1,4-β-xylosidase, Cellulase, Alpha-N-acetylglucosaminidase, Endo-1,4-β-xylanase, Amidase, Urease, and Pectin lyase (Arunrat et al., 2023c).

2.6. Statistical analysis

Statistical analyses were conducted using R (R Development Core, 2019) and the PAST program v. 4.03 (Hammer et al., 2001). One-way ANOVA and post hoc Tukey's HSD tests were performed to determine significant differences in soil properties with different time points (pre-burning, 5 min after burning, and 1 month after burning). Alpha diversity indices, including observed richness, Chao-1, Simpson, and Shannon indices, as well as the abundance of dominant genera and soil functions, were computed and statistically compared among timepoints (before burning, after burning 5 min and one month after burning) using repeated-measure ANOVA (for normally distributed data) or Friedman tests (for non-normally distributed data). Bacterial and fungal community compositions were analyzed and visualized through principal coordinate analysis (PCoA) based on Bray–Curtis distance. Differences in community compositions at each sampling time were assessed using repeated-measures permutational multivariate analyses of variance (PERMANOVA). A redundancy analysis (RDA) was employed to determine the influence of soil properties on bacterial and fungal community compositions. The significance of the correlation between these compositions was confirmed using the Mantel test. Alpha diversity indexes, ordination analysis, RDA and mantel test were performed in R using microeco package (Liu et al., 2021).

For network analysis, co-occurrence networks were constructed based on Spearman correlation. Correlations with $p < 0.05$ and correlation coefficients $|\rho| > 0.6$ were considered robust for generating the co-occurrence network (Zhao et al., 2022). The network was visualized using “Gephi” (Bastian et al., 2009). In this network, nodes represent genera, while edges or links represent connections between genera. Nodes were grouped into modules when they were highly connected within their own group. A network exhibits a modular structure when the modularity value exceeds 0.4. Network complexity was assessed based on the average degree, which signifies the average connections of each node with another unique node in the network (Zhao et al., 2022).

Table 1

Variation in soil properties: bulk density (BD) (Mg m^{-3}), electrical conductivity (EC_e) (dS m^{-1}), organic matter (OM) (%), organic carbon (OC) (%), total nitrogen (TN) (%), and proportion of sand, silt and clay (%).

Time point	pH (1:1)		EC _e		BD		OM		OC		TN		%Sand		%Silt		%Clay	
	Mean	Std	Mean	Std	Mean	Std	Mean	Std	Mean	Std	Mean	Std	Mean	Std	Mean	Std	Mean	Std
Pre-burning	4.97 ^a	0.18	0.14 ^a	0.02	1.33 ^a	0.04	6.68 ^a	0.46	3.88 ^a	0.27	0.25 ^a	0.05	24.57 ^a	3.87	48.30 ^a	1.68	27.13 ^a	3.11
5 min after burning	6.40 ^b	0.13	0.59 ^b	0.22	1.27 ^a	0.03	5.64 ^b	0.39	3.27 ^b	0.23	0.18 ^b	0.04	27.27 ^a	6.31	49.84 ^a	2.62	22.96 ^a	7.40
1 month after burning	6.45 ^b	0.17	0.46 ^b	0.09	1.27 ^a	0.02	5.62 ^b	0.43	3.26 ^b	0.25	0.17 ^b	0.03	29.31 ^a	5.68	47.82 ^a	3.20	22.87 ^a	7.39

^{a-b}denotes significant differences ($p < 0.05$).

Table 2

Variation in soil properties: available P (mg kg^{-1}); exchangeable K, Ca, and Mg (mg kg^{-1}), $\text{NH}_4\text{-N}$ (mg kg^{-1}), $\text{NO}_3\text{-N}$ (mg kg^{-1}), and C/N ratio.

Time point	Avail. P		Exch. K		Exch. Ca		Exch. Mg		$\text{NH}_4\text{-N}$		$\text{NO}_3\text{-N}$		C/N ratio	
	Mean	Std	Mean	Std	Mean	Std	Mean	Std	Mean	Std	Mean	Std	Mean	Std
Pre-burning	2.74 ^a	1.60	207.07 ^a	91.01	169.69 ^a	91.32	98.05 ^a	41.56	34.11 ^a	5.61	21.32 ^a	8.20	15.91 ^a	2.99
5 min after burning	27.52 ^b	20.21	298.67 ^b	48.42	718.19 ^b	223.58	226.02 ^b	55.03	55.42 ^b	26.96	4.27 ^b	3.67	18.73 ^b	3.88
1 month after burning	29.75 ^b	18.03	233.99 ^b	53.63	573.74 ^b	93.50	212.13 ^b	58.50	29.84 ^a	7.34	15.63 ^c	9.35	19.84 ^b	3.97

^{a-c}denotes significant differences ($p < 0.05$).

Table 3

Alpha diversity indexes of bacteria and fungi.

Site	Observed Richness	Chao-1	Shannon	Simpson
Bacteria				
Before burning	934.60 ± 103.31 ^a	970.98 ± 117.27 ^a	6.15 ± 0.09 ^a	0.9958 ± 0.0004 ^a
After burning (5 min)	206.00 ± 24.29 ^b	209.03 ± 26.58 ^b	3.60 ± 0.11 ^b	0.9211 ± 0.0072 ^b
One month after burning	1058.50 ± 285.63 ^a	1093.25 ± 308.96 ^a	6.27 ± 0.30 ^a	0.9962 ± 0.0011 ^a
Fungi				
Before burning	420.10 ± 31.27 ^a	435.30 ± 33.12 ^a	4.20 ± 0.09 ^a	0.9543 ± 0.0055 ^a
After burning (5 min)	123.00 ± 10.17 ^c	124.34 ± 11.11 ^c	2.53 ± 0.10 ^b	0.7648 ± 0.0240 ^c
One month after burning	263.40 ± 121.35 ^b	273.86 ± 121.59 ^b	3.13 ± 0.93 ^b	0.8536 ± 0.1070 ^b

^{a-c}denotes significant differences ($p < 0.05$).

3. Results

3.1. Soil physicochemical properties after fire

After 5 min of burning, the soils exhibited significantly lower levels of OM, OC, TN, and $\text{NO}_3\text{-N}$. Conversely, there were higher levels of pH, EC_e, soil nutrients (avail. P, exch. K, exch. Ca, exch. Mg), $\text{NH}_4\text{-N}$, and C/N ratio. However, no significant changes were observed in bulk density and soil texture after 5 min of burning. At 1 month after burning, soil parameters including pH, EC_e, avail. P, exch. K, exch. Ca, exch. Mg, and C/N ratio were higher than the pre-burning levels (Tables 1 and 2).

No significant differences in soil moisture were found among the three different time points. However, at a depth of 0–2 cm, a substantial increase in soil temperature was observed, rising from 25.5 °C before burning to 48.5 °C at 5 min after burning. During the burning process, the fire temperature in the litter layer ranged from 475.9 to 715.5 °C (Table S1).

3.2. Diversity, taxonomic distribution and community composition

3.2.1. Bacteria

A total of 505,170 high-quality and normalized bacterial sequences

were obtained in this study. These sequences were assigned to a total of 8129 ASVs. In total, 26 phyla, 70 classes, 115 orders, 177 families, and 294 genera were identified. As depicted in Table 3, all alpha diversity indices, including observed richness, Chao-1, Shannon, and Simpson's index, exhibited similar trends. The diversity significantly decreased after 5 min of burning. However, after 1 month, the diversity rebounded to similar levels as observed in the pre-burning site (Table 3).

The most abundant phyla in the pre-burning site (BB) belonged to Verrucomicrobia (26.09 %), followed by Acidobacteria (20.64 %) and Chloroflexi (18.36 %). After 5 min of burning (AB), the Firmicutes phylum dominated the community, accounting for 96.31 % (an increase of approximately 95 %). However, the Firmicutes notably decreased after 1 month (AB-1 M), dropping from 96.31 % to 7.87 %. The dominant taxa in the AB-1 M site were Proteobacteria (29.19 %) and Actinobacteria (23.16 %) (Fig. 2a). At the order level, Chthoniobacterales (25.36 %) and Gemmatales (10.20 %) were the dominant orders in the BB. After 5 min of burning, Bacillales (93.06 %) became the dominant order, but after one month, the abundance of this taxon decreased to 7.18 %. Betaproteobacterales (10.72 %), Tepidiphraerales (8.67 %), and Bacillales (7.18 %) dominated the AB-1 M site (Fig. 2b).

Fig. 3a illustrates the abundant bacterial genera identified in this study. The most abundant genera in the BB were *Candidatus Udaeobacter* (14.41 %) and *Candidatus Xiphinematobacter* (10.94 %). However, after 5 min of burning, these two genera became rare taxa, with a relative abundance of <1 %. *Bacillus* (38.53 %), *Alicyclobacillus* (17.14 %), and *Aneurinibacillus* (10.48 %) increased by >10 times and became the dominant taxa in the AB time point. After one month, the abundance of the previously dominant genera in the AB site decreased to approximately 1–2 %. The dominant taxa in the AB-1 M site were *Geodermatophilus* (6.15 %), *Noviherbaspirillum* (4.57 %), and *Nocardioides* (4.63 %).

As depicted in Fig. 2c, the PCoA analysis explained 78.6 % of the variation in the bacterial community and indicated distinct differences in bacterial community composition across different sampling times. This observation was further confirmed by the PERMANOVA analysis, which demonstrated significant differences in bacterial community composition among the three sampling timepoints ($F = 49.52$, $p = 0.0001$).

3.2.2. Fungi

A total of 677,910 high-quality and normalized fungal sequences, assigned to 3189 ASVs, were obtained in this study. In total, 9 phyla, 33 classes, 79 orders, 190 families, and 424 genera were identified. As

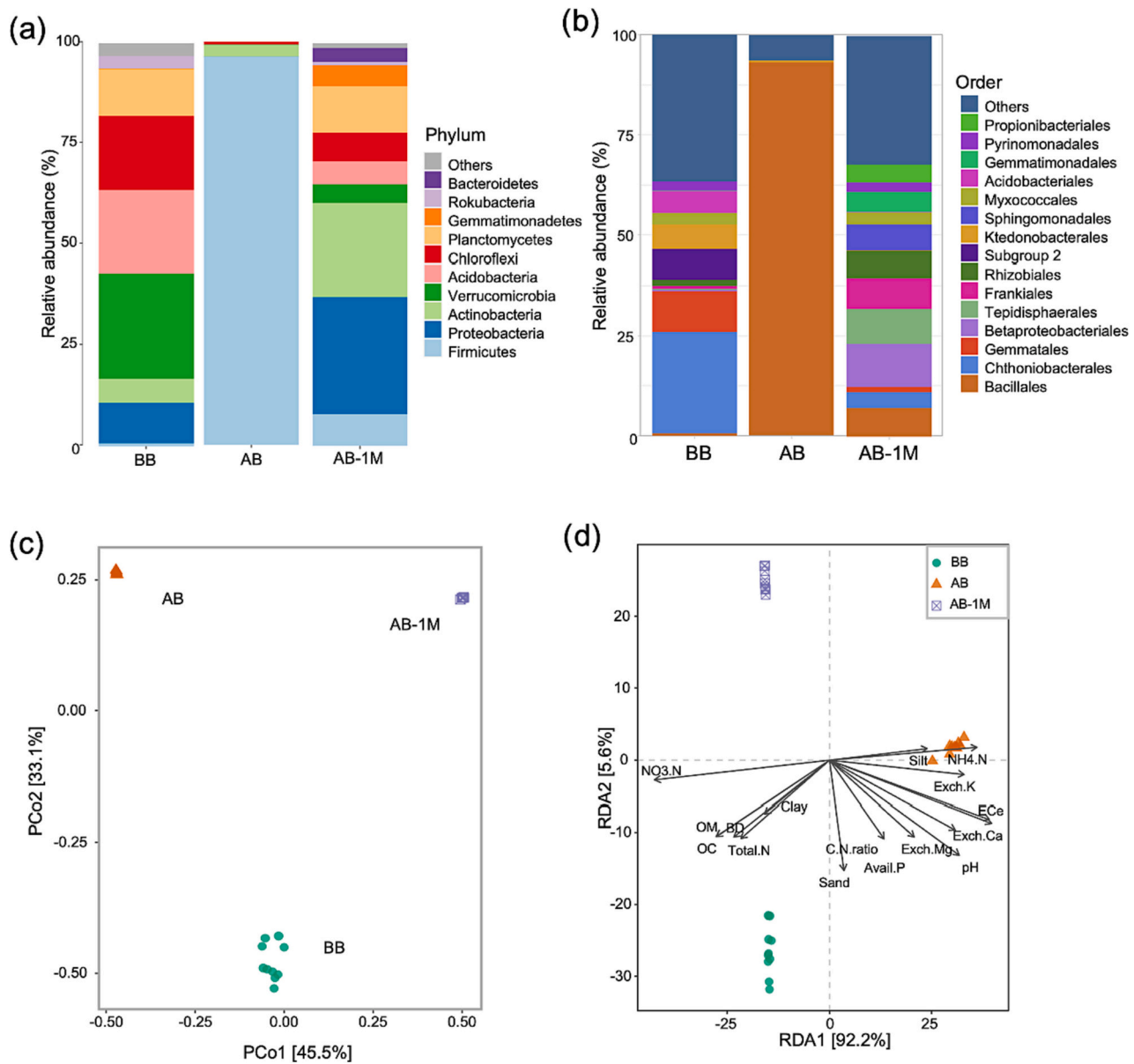


Fig. 2. Bacterial taxonomic distribution and community composition. Proportion of the most abundant bacteria at (a) Phylum and (b) order level. (c) PCoA analysis of bacterial community composition. (d) RDA analysis of bacterial community. BB = before burning; AB = After burning 5 min; AB-1 M = one month after burning.

indicated in Table 3, the observed richness, Chao-1, Shannon, and Simpson's diversity indices were significantly decreased after 5 min of burning. Subsequently, after one month, these diversity indices increased, although they did not reach the same levels as those observed before burning.

The most abundant phyla in the BB were Basidiomycota (53.91 %) and Ascomycota (31.45 %). Following 5 min of burning, the abundance of Ascomycota increased to 96.46 %, becoming the most dominant phylum at that time point. After one month, Ascomycota slightly decreased to 82.82 %, while Basidiomycota increased to 9.63 % (Fig. 4a). At the order level, the Basidiomycota_unidentified order (28.09 %) was the dominant order, followed by Eurotiales (13.04 %), Russulales (11.50 %), Agaricales (6.21 %), and Hypocreales (5.20 %). After 5 min of burning, the abundance of Eurotiales and Pezizales increased to 83.53 % and 8.57 %, respectively. In the AB-1 M, the dominant orders were Eurotiales (25.78 %), followed by Pezizales (24.49 %) and Hypocreales (10.12 %) (Fig. 4b).

As depicted in Fig. 3b, the most abundant genera in the BB were *Russula* (10.80 %), followed by *Penicillium* (4.99 %), *Geminibasidium*

(4.43 %), and *Talaromyces* (3.98 %). After 5 min of burning, the abundance of *Penicillium*, *Aspergillus*, and *Hamigera* increased by 49.15 %, 11.30 %, and 10.05 %, respectively, making them the most abundant groups in the AB time point. Conversely, the abundance of *Russula* notably decreased. After 1 month, the abundance of *Penicillium* significantly decreased to 2.44 %, while the abundance of *Russula* remained unchanged. At the AB-1 M time point, *Lanprospora* (17.83 %) and *Aspergillus* (12.65 %) dominated the community.

As demonstrated in Fig. 4c, the PCoA analysis explained 84.3 % of the variation in the fungal community. The PCoA analysis revealed distinct separation in the fungal community composition at each sampling time, suggesting notable differences between fungal communities across time points. This observation was corroborated by the PERMANOVA analysis, which confirmed a statistically significant difference between the fungal community compositions at different sampling times ($F = 32.05, p = 0.0001$).

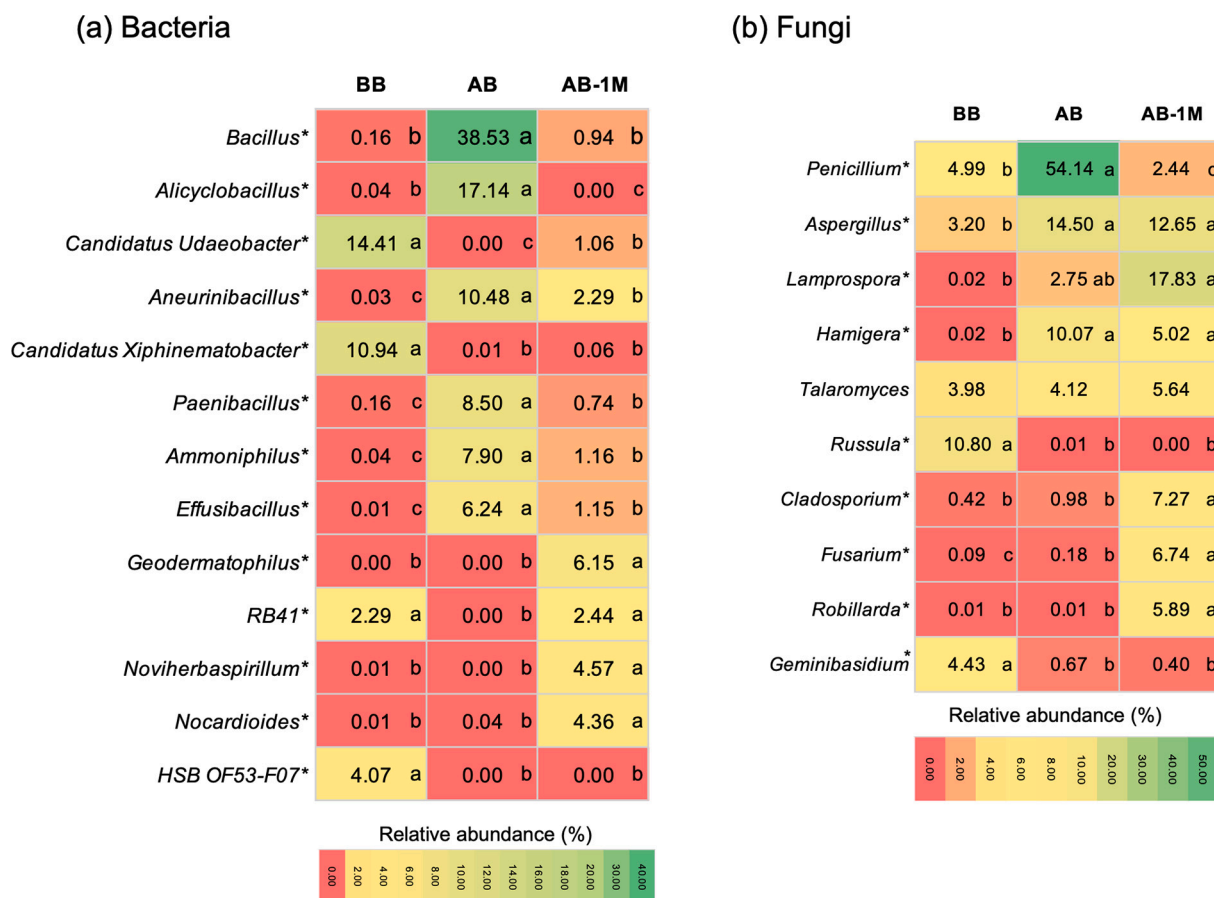


Fig. 3. The most abundance genera of (a) bacterial and (b) fungal community. Taxa with asterisk (*) were statistically different ($p < 0.05$). BB = before burning; AB = After burning 5 min; AB-1 M = one month after burning.

3.3. The effect of soil properties on bacterial and fungal community composition

The redundancy analysis (RDA) showed that the soil properties could explain 97.8 % and 77.5 % of the total variations in the bacterial and fungal community compositions, respectively (Figs. 2d and 4d). Mantel test revealed that pH, OM, OC, ECe, NO₃-N, Avail.P, Exch.K, Exch.Ca, Exch.Mg, TN and BD were significantly affected the community composition of both bacteria and fungi (Table 4). However, only pH presented a strong correlation among these variables (correlation coefficient > 0.7) (Table 4).

3.4. Network analysis

This study constructed separate networks for bacteria and fungi at each sampling time. As depicted in Fig. 5, each network exhibited a modular structure with modularity values exceeding 4. Notably, fungi consistently displayed more intricate networks compared to bacteria across all sampling times. When considering network complexity, indicative of a microbe's capacity to sustain its community under potential environmental perturbations, this study revealed a decline in the complexity of both bacterial and fungal networks after the initial 5 min of burning, followed by a substantial increase after one month (Fig. 5). Remarkably, the bacterial and fungal community in the AB time point emerged as the most vulnerable, indicating susceptibility to disruption from changing environmental conditions.

3.5. Predictive function

This study used PICRUST2 to predict enzyme that potentially

produced by the detected microbes. Here, we focus on soil enzymes involved in the carbon and nitrogen cycles. For bacteria, the abundance enzymes at before fire were β -glucosidase, cellulase, and amidase. The levels of β -glucosidase and nitrogenase enzymes exhibited a significant decrease after 5 min of burning, followed by a rebound to similar levels as the pre-burning period after one month (Fig. 6a).

For fungi, out of the 14 highlighted enzymes, only 9 were detected. Notably, the abundance of all detected enzymes, including Chitinase, β -glucosidase, Xylan 1,4- β -xylosidase, Cellulase, Endo-1,4- β -xylanase, and Pectin lyase, increased after 5 min of burning and then decreased to levels similar to those observed before the burning event after one month (Fig. 6b).

4. Discussion

4.1. Short-term effects of fire on soil microbial diversity and community composition

As shown in Table 3, the findings led to the rejection of the first hypothesis (H1). This study indicated that bacterial richness and diversity declined more than fungal after 5 min of burning. Our findings are in line with the study by Brown et al. (2019), which detected that bacteria are more sensitive to fire disturbance than fungi in the Southern Appalachian Mountains. In contrast, some previous research have reported that bacteria are more resistant to fire than fungi (Mabuhay et al., 2006; Pressler et al., 2019; Certini et al., 2021). We hypothesized that the opposite results may be due to differences in ecological types. Being the first investigation in RSC fields in Thailand, our findings highlight the need for a better understanding of the linkages between soil microbial community dynamics and disturbance activities in similar

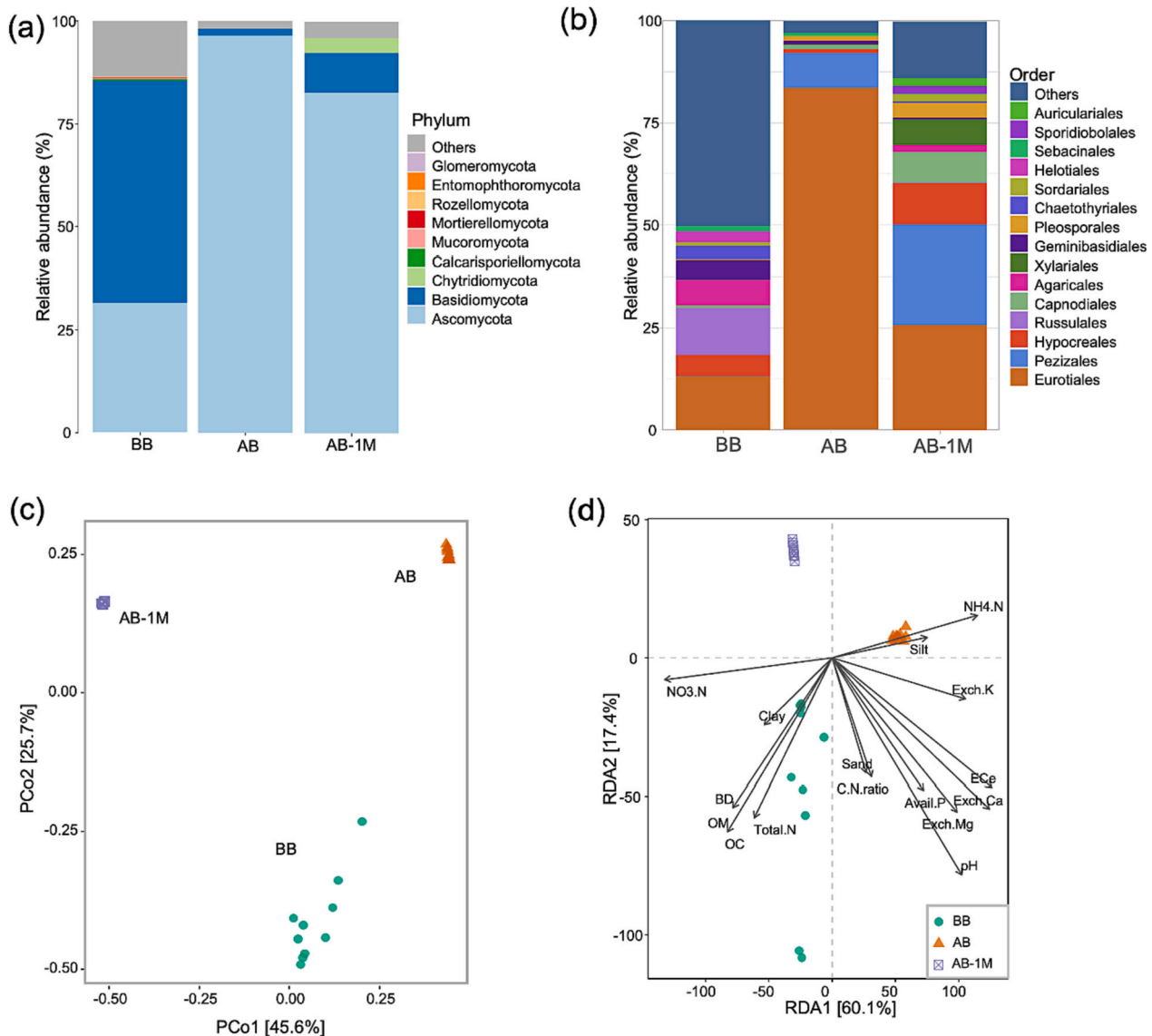


Fig. 4. Fungal taxonomic distribution and community composition. Proportion of the most abundant fungi at (a) Phylum and (b) order level. (c) PCoA analysis of fungal community composition. (d) RDA analysis of fungal community. BB = before burning; AB = After burning 5 min; AB-1 M = one month after burning.

ecological settings.

After one month of burning, bacterial richness increased significantly (+413.8 % to +423.0 %) and diversity showed a faster recovery (+8.2 % to +74.2 %) compared to fungi (Table 3). This recovery is attributed to the rise in soil pH after the fire (Table 1), as supported by the findings in Table 4, which demonstrate a strong correlation between soil pH and the community composition of bacteria and fungi. Similar to our findings, previous studies (Mabuhay et al., 2006; Rousk et al., 2010, and Bang-Andreasen et al., 2020) have also reported that bacteria tend to recover more rapidly after a fire than fungi, largely attributed to the increase in soil pH. Cruz-Paredes et al. (2021) stated that because bacteria have a cell membrane, pH generally influences the proton-driving force across the cell membrane. This can help explain why bacteria respond more strongly to changes in pH than fungi. Furthermore, an indirect factor contributing to the rapid re-colonization of bacteria is the increase in available nutrients resulting from the combustion of organic material after the fire (Table 2), which is consistent with the studies of Fernández et al. (1997) and Choromanska and DeLuca (2002). Fire leads to the loss of soil carbon and nitrogen through volatilization, while also releasing NH₄-N after the fire event (Choromanska and DeLuca, 2001). Additionally, a charcoal layer can form after the fire, which provides nitrogen

availability and pH regulation for bacteria (Wardle et al., 1998; Pietikäinen et al., 2000; DeLuca and Sala, 2006).

4.2. Abundance of heat-resistant bacteria and fungi post-fire

Our study successfully detected the abundance of pyrophilous microbes after the fire, thereby supporting the acceptance of the second hypothesis (H2). Pyrophilous microbes possess the ability to survive fires through mechanisms such as heat-resistant spores and sclerotia (Day et al., 2020; Smith et al., 2015). Fox et al. (2022) revealed that fires have a direct impact on fungal mortality. Changes in soil chemistries and structures, as well as the removal of hosts and substrates, indirectly affect fungal communities and composition. Furthermore, the survival of fire-resistant fungi often manifests in post-fire fungal communities, as those are typically protected by local refugia and spore banks. Some specific pyrophilous fungi, such as *Pyronema*, *Anthracoibia*, and *Pholiota carbonicola*, often appear after a fire. In the case of bacteria, the Firmicutes phylum increased by approximately 95 % (Fig. 2a), while the members of the genera *Bacillus*, *Alicyclobacillus* and *Aneurinibacillus* exhibited an increase of over 10 times after the fire (Fig. 3a). This is because Firmicutes have traits that resistant to fire and post-fire

Table 4
Mantel test presented correlation coefficient and significant values between soil properties and bacterial and fungal communities.

Variables	Bacteria		Fungi	
	Correlation coefficient	<i>p</i>	Correlation coefficient	<i>p</i>
pH	0.7676	0.0016*	0.7169	0.0018*
OM	0.4801	0.0016*	0.4226	0.0018*
OC	0.4781	0.0016*	0.4205	0.0018*
ECe	0.6759	0.0016*	0.5732	0.0018*
NH ₄ -N	-0.0561	0.8570	-0.1411	0.9980
NO ₃ -N	0.3286	0.0016*	0.2125	0.0064*
Avail.P	0.3798	0.0016*	0.4024	0.0018*
Exch.K	0.1522	0.0276*	0.1532	0.0267*
Exch.Ca	0.5817	0.0016*	0.4846	0.0018*
Exch.Mg	0.3808	0.0016*	0.3311	0.0018*
TN	0.2578	0.0016*	0.2998	0.0018*
BD	0.2730	0.0016*	0.2767	0.0018*
Sand	-0.0049	0.5109	-0.0084	0.5717
Silt	0.0401	0.2446	0.0840	0.1095
Clay	0.0841	0.0840	0.0684	0.1246
C/N ratio	0.0727	0.1342	0.1671	0.0267*

* denote significant differences ($p < 0.05$).

environment such as thermotolerant, endospore, reduces nitrogen, solubilizes phosphate (Pulido-Chavez et al., 2023). In fungi, the Ascomycota phylum increased to 96.46 % after the fire and became the most abundant, replacing the Basidiomycota phylum that was dominant before the fire (Fig. 4a). At the genus level, *Penicillium*, *Aspergillus*, and *Hamigera* exhibited dominant increases following fire disturbance (Fig. 3b). The presence of Ascomycota after fires has been observed in various areas, including Pinaceae forests (Xiang et al., 2014), Spanish shrublands (Pérez-Valera et al., 2018), Mediterranean shrublands (Livne-Luzon et al., 2021), Eucalyptus ecosystems (Ammitzboll et al., 2022), and Cleveland National Forest in southern California (Pulido-Chavez et al., 2023). Specifically, Ascomycota *Penicillium* has a high ability to capitalize on the increased availability of nutrients and carbon, as it is a common saprotrophic fungus in terrestrial ecosystems (Lumley et al., 2011).

In order to identify the genera displaying rapid growth during the early-month recovery after a fire, our study found that Proteobacteria and Actinobacteria were the most abundant one month after burning, whereas Firmicutes notably decreased from 96.31 % to 7.87 % (Fig. 2a). This shift might be influenced by physiological traits such as nutrient mineralization affinity and aromatic hydrocarbon degradation capabilities (Fischer et al., 2021; Steindorff et al., 2021). *Geodermatophilus*, *Noviherbaspirillum* and *Nocardioidea* were the three most dominant taxa during the early-month recovery after a fire (Fig. 3a). Pulido-Chavez et al. (2023) also reported a similar finding, observing an increase in the abundance of Proteobacteria *Noviherbaspirillum* over time in response to wildfires within fire-adapted chaparral shrublands in southern California. As for the rapid colonization of fungi in the early stages following the fire, Ascomycota *Penicillium* remained dominant but slightly decreased, while Basidiomycota increased to 9.63 % (Fig. 4a), indicating that fungi respond slowly to changes in soil physiochemical properties. However, the relative abundance of Ascomycota, specifically *Penicillium*, after the fire, can be attributed to its role as a fast colonizer owing to highly abundant spore production. Additionally, certain *Penicillium* species are capable of degrading polycyclic aromatic hydrocarbons (PAHs) generated from combustion processes (Leitão, 2009). It should be noted that an increase in relative abundance may not necessarily indicate an increase in the total abundance of individuals.

4.3. Effects of fire on microbial enzymes and network complexity

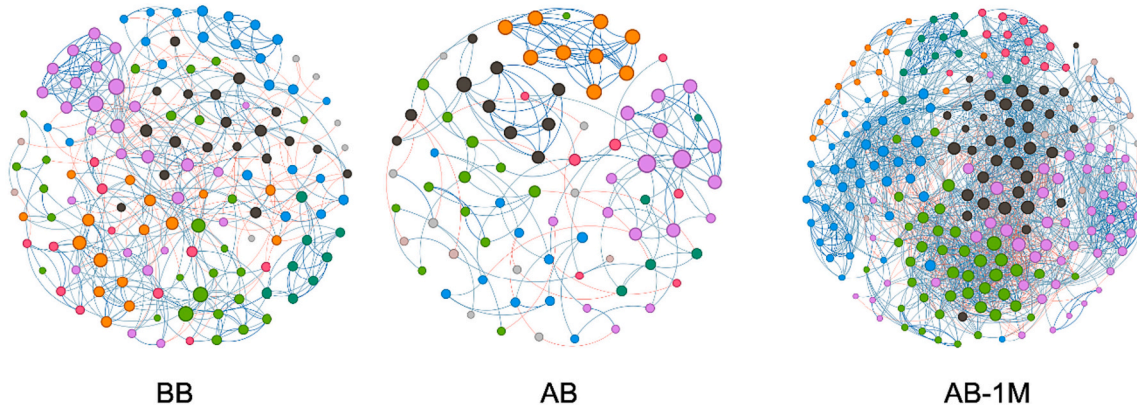
Soil microorganisms regulate the carbon and nutrient transport, maintaining a balance between terrestrial ecosystems and global climate

change (Gougoulias et al., 2014). Fire is a significant contributor to global climate change, impacting soil microbial communities and thereby affecting their role in the carbon and nutrient dynamics of terrestrial ecosystems (Dooley and Treseder, 2012). This is due to the substantial alteration of soil enzyme activity caused by fire (Pei et al., 2023). In our study, β -glucosidase was the primary microbial enzyme that exhibited a significant decrease after burning and returned to the same level after one month (Fig. 6a and b). This is attributed to the loss of organic matter and the mortality of microorganisms in the soil caused by fire (Eivazi and Tabatabai, 1988). Additionally, there is an increase in β -glucosidase activity with the addition of organic amendments (García-Ruiz et al., 2008). Our study revealed that Proteobacteria and Actinobacteria were dominant one month after the fire (Fig. 2a). These groups are known to catalyze nitrification, promoting recovery through biogeochemical nitrogen cycle processes (Shridhar, 2012; Tyc et al., 2017). Meanwhile, Ascomycota and Basidiomycota fungi were detected after one month of fire (Fig. 4a), capable of forming mycorrhizal symbiosis with plants, thereby benefiting plant nutrition absorption and regrowth (Toju et al., 2013).

To test the third hypothesis (H3), we conducted co-occurrence network analysis to assess the impact of fire disturbance on the complexity of bacterial and fungal networks. The results support the acceptance of the third hypothesis, indicating that the complexity of bacterial and fungal networks decreased after the fire and then experienced a dramatic increase one month later. Interestingly, we observed that fungi exhibited a more complex network than bacteria, with a higher average degree (Fig. 5). The presence of more complex and interconnected fungal communities in our study area may indicate a higher efficiency of biochemical transmission and a greater potential to withstand loss and recover after external environmental perturbations such as fire. On the other hand, bacterial communities may be more vulnerable, which is supported by the findings in Table 3, where bacterial richness and diversity declined more than fungal richness and diversity after the fire. Vos et al. (2013) and Chen et al. (2017) have demonstrated that fungi are generally more closely associated with plants' roots due to their ability to provide nutrients during symbiotic relationships. Certain fungi are obligate plant root symbionts, endophytes, and even pathogens (Peay et al., 2013; Mommer et al., 2018). This is because fires consume plants and litter, removing specific habitats and substrates. The mortality of plants leads to the disappearance of plant-associated fungi, indicating that fungi on tree roots will die if host trees are killed by fire. However, the survival of fungi can change in terms of physiology, growth, and community composition due to alterations in environmental conditions (Fox et al., 2022). This suggests that fungi are more influenced by the plant community, whereas bacteria are more closely linked to soil properties (Delgado-Baquerizo et al., 2018). As shown in Fig. 5, fire causes the reduction of the network topological characteristics (nodes, links, and average degree) of the fungal and bacterial taxa. One month after the fire, however, the complex networks of fungi and bacteria exhibited a significant increase, surpassing their pre-fire levels. This suggests that the post-fire environment provided ample substrate and diverse habitat for colonization, thereby enhancing the connectivity of both fungal and bacterial communities. This is further confirmed by the Mantel test (Table 4), which indicates a strong correlation between soil properties and bacterial and fungal communities.

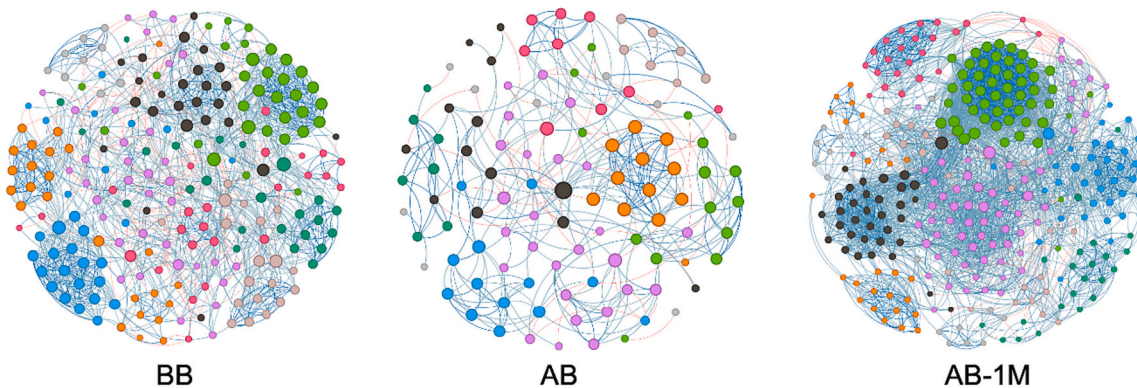
The bacterial co-occurrence network exhibited a higher degree of modularity compared to fungi (Fig. 5), suggesting that bacteria possess a greater ability to form sub-communities, which reflects a high level of niche differentiation (Faust and Raes, 2012). This phenomenon could be attributed to the rapid decomposition rates of litter in tropical rainforests, which result in ample soil nutrient availability and foster soil bacterial niche differentiation (Zhang et al., 2019). Our study highlights that the changes in the complex interactions and co-occurrence patterns among bacterial and fungal taxa were driven by external environmental factors.

(a) Bacteria



	No. of Node	No. of link	Average degree	modularity value
BB	137	474	6.91	1.092
AB	82	174	4.34	0.841
AB-1M	218	2169	19.9	1.012

(b) Fungi



	No. of Node	No. of link	Average degree	modularity value
BB	224	1308	11.68	0.844
AB	110	336	6.11	0.904
AB-1M	295	3688	25.00	0.625

Fig. 5. The co-occurrence network of (a) bacteria and (b) fungi in different samples. Network diagrams with nodes colored according to ecological clusters (Modules). Node (each genus) were grouped into module into modules when they were highly connected within their own group but much less connected outside the group. BB = before burning; AB = After burning 5 min; AB-1 M = one month after burning.

5. Conclusion

Our study revealed that bacteria exhibit greater sensitivity to fire disturbance compared to fungi. This was evidenced by the decline in bacterial richness and diversity, surpassing the reduction observed in fungi, after burning. Following one month of burning, bacterial richness increased significantly, and its diversity exhibited a faster recovery when compared to fungi. This recovery can be attributed to the rise in soil pH post-fire. Notably, the abundance of heat-resistant bacteria and fungi were detected after the fire event. Specifically, within the bacterial community, the Firmicutes phylum saw a substantial increase of around 95 %, while the genera *Bacillus*, *Alicyclobacillus*, and *Aneurinibacillus* exhibited over a tenfold increase after the fire. In contrast, among fungi, the Ascomycota phylum witnessed a significant surge after the fire, overtaking the previously dominant Basidiomycota phylum.

Furthermore, at the genus level, *Penicillium*, *Aspergillus*, and *Hamigera* displayed dominant increases in response to fire disturbance. Based on our co-occurrence network analysis, fungi exhibited a propensity for more complex networks compared to bacteria. Notably, the complexity of both bacterial and fungal networks diminished after the fire but rebounded significantly after one month. It should be noted that further research involving more RSC fields and long-term investigation is necessary to conclusively confirm our findings in this study.

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.apsoil.2024.105303>.

CRediT authorship contribution statement

Noppol Arunrat: Writing – review & editing, Writing – original draft, Methodology, Investigation, Funding acquisition, Formal analysis,

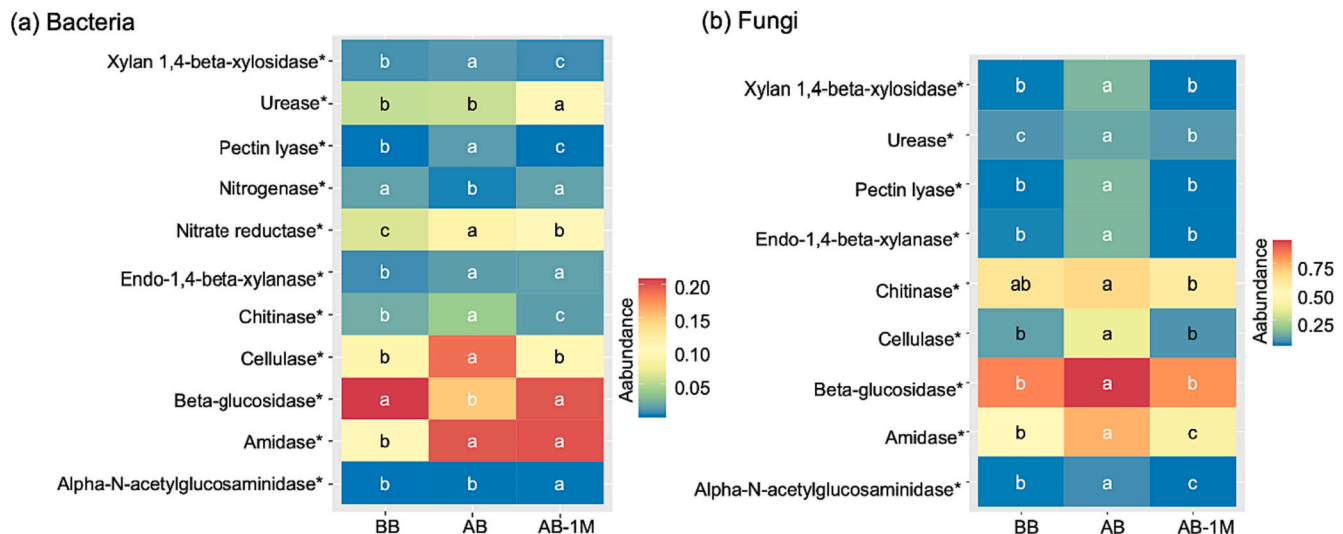


Fig. 6. Heatmap shows the mean abundances of enzymes that potentially produced by (a) bacteria and (b) fungi. BB = before burning; AB = After burning 5 min; AB-1 M = one month after burning. Function with asterisk (*) were statistically different ($p < 0.05$).

Data curation, Conceptualization. **Chakriya Sansupa:** Writing – review & editing, Writing – original draft, Methodology, Formal analysis. **Sukanya Sereenonchai:** Writing – original draft, Methodology, Investigation, Conceptualization. **Ryusuke Hatano:** Writing – original draft, Supervision, Methodology, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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