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RESEARCH ARTICLE

The temporal and spatial response of soil fungal community composition and potential function to wildfire in a permafrost region in Canada

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Abstract

1. The permafrost regions of the boreal forest store a large amount of carbon, which can be affected by ecological disturbance, especially the interference of forest fires. Understanding the dynamic responses of the post-fire soil fungal community is essential for predicting soil carbon dynamics.
2. We used a post-fire chronosequence (areas with 3, 25, 46 and >100 years post fire [ypf]) in Canadian boreal forests with continuous permafrost to examine the responses of fungal communities and fungal genes associated with biogeochemical cycling to fire in the surface and near-surface permafrost layers (0–5, 5–10 and 10–30 cm depth). We hypothesized that as the forest recovers from fire, the fungal communities and functional genes associated with biogeochemical cycling will also recover temporally and spatially, which will in turn affect soil carbon storage.
3. Our results demonstrate that the fire has long-term effects on fungal communities and functions in the surface and near-surface soils. The fungal species richness in the 0–5 and 5–10 cm soil layers increased with time since fire, which required at least 46 years to recover to pre-fire levels. Ascomycota in each of the soil layers in the recently burned area (3 ypf) and ericoid mycorrhizas *Oidiodendron maius* in the 10–30 cm soil layer in the control area were recognized as indicator taxa.
4. The examination of functional genes revealed that the diversity of potential genes and the expression of genes related to carbon degradation (e.g. *chitinase*, *cellobiase*, *exoglucanase* and *endoglucanase*) in recently burned area increased in the surface soil, whereas, decreased in the deep soil, suggesting the fire affect the loss of carbon differently in the surface and deep soils in the early stages after fire.

Yue-mei Zhang and Zhao-lei Qu equally contributed to the work.

5. In conclusion, the fires significantly altered the fungal communities and functional genes related to carbon storage along the soil vertical gradients and along the post-fire chronosequence.

KEYWORDS
functional gene expression profile, fungal community structure, permafrost soil, temporal and soil vertical gradient response, wildfire

1 | INTRODUCTION

Boreal forests account for about 50% of the total carbon (C) pool in global forest ecosystems (Malhi et al., 1999) and about 80% of them are located in upland soils, of which the great majority grow in environments underlain by different types of permafrost (Helbig et al., 2016). Global climate change has led to permafrost thawing (Baltzer et al., 2014) and frequent wildfires (Walker et al., 2019), that impact the global C cycle and have a positive feedback loop to the climate change, that is, permafrost thawing and frequent wildfires cause warming, which further accelerates permafrost thawing and frequent wildfires. In boreal forests, the soil microbes, especially fungi, play an important role in the C cycle by affecting the decomposition of organic matter and the nutrient cycle of plants (Boberg, 2021; Talbot et al., 2008). Ectomycorrhizal fungi form pervasive reciprocal symbiosis with trees and ground vegetation in boreal forests (Sun et al., 2015). Many species of ground vegetation can additionally form symbioses with ericoid mycorrhizal fungi. Mycorrhizal fungi obtain fixed C from their host plants in exchange for mineral nutrients, such as phosphorus and nitrogen, which positively affect plant growth (Smith & Read, 2010). Mycorrhizal fungi are known drivers of soil C sequestration and particle aggregation and have a significant impact on the composition of microbial and plant communities (Genre et al., 2020).

Boreal forest wildfires occur more frequently and are more severe due to increasing global temperatures, decreased precipitation and longer fire seasons (Balshi et al., 2009). Wildfires cause soil to heat up to 100–700°C (Certini, 2005), which has a fatal effect on fungi at the soil surface (Cairney & Bastias, 2007), with mortality occurring as temperatures surpass 60°C (Hart et al., 2005). The high soil temperatures can also affect the fungal reproduction ability and hinder their ability to recover after a fire (Bárcenas-Moreno & Bååth, 2009; Glassman et al., 2016). Meanwhile, wildfires do also indirectly affect soil microbial communities via ground plants and litter burning, or via changing the soil physical and chemical properties (Köster et al., 2021). The reduction in the ground shade and nutrients (Bhatnagar et al., 2018; Treseder et al., 2004) can reduce the abundance of soil fungi that prefer wetter soils (Dooley & Treseder, 2012). The wildfires increase the soil hydrophobicity, soil temperature and dryness after fire (O'Donnell et al., 2009), causing volatilization of the soil nutrients (Dooley & Treseder, 2012) and decreasing the quality and quantity of soil C (Waldrop & Harden, 2008). The ash deposits after a fire can increase soil pH (Certini, 2005; Switzer et al., 2012), and together with the above-ground changes in vegetation will affect the soil fungal community. Understanding how the fungal communities respond to wildfires and post-fire environment changes is critical to predicting soil C dynamics.

In boreal forests, the occurrence of fire will lead to C loss because fires burn plant biomass, moss layer, a portion of the humus pool and a portion of the total C stored in the organic layer (Deluca & Boisvenue, 2012). Meanwhile, the burning of the organic layer affects the soil fungal communities and function related to organic matter degradation (Sun et al., 2015). Fire also indirectly increases the activity of microbiome by increasing soil temperature and moisture (O'Donnell et al., 2011). Furthermore, the increase in soil pH post-fire reduces the richness and diversity of mycorrhizal fungi (Day et al., 2019; Zhou et al., 2019a), which shifts the soil microbial communities from fungal to bacterial dominance (Aaltonen et al., 2019). In turn, these changes affect the soil organic matter (SOM) decomposition, and the cycling of C, nitrogen and phosphorus (Zhou et al., 2019a). Many studies have investigated the short-term effects of wildfires on soil microbial communities (Pulido-Chavez et al., 2021). A few studies have also assessed the long-term effects of fire on the fungal communities in humus (0.5–1.0 cm) or top soil layer (0–10 cm) along a post-fire chronosequence in boreal forest (Holden et al., 2013; Sun et al., 2015). The fungal communities between soil depths in these studies, however, have not been evaluated. Studies have shown that the negative effects of fire on microbial biomass can remain for ~15 years in boreal forests (Dooley & Treseder, 2012) and ectomycorrhizal colonization required up to 15 years to return to pre-fire levels (Treseder et al., 2004). The composition and structure of the ectomycorrhizal community had stabilized 41 years after the wildfire, in jack pine stands in northeastern Alberta of Canada (Visser, 1995).

Meanwhile, the soil depth acts as an ecological filter of soil properties, and the heterogeneous environments affect the soil fungal diversity, composition and function along the vertical profile (Xu et al., 2021). In boreal forest, the fungal communities differed significantly in the soil profile, with saprophytic fungi dominating the litter layer, while mycorrhizal fungi were more dominant in the deeper layers (McGuire et al., 2013; Santalahti et al., 2016). Fire leads to the loss of litter in the soil surface and changes the physical properties of soil, leading to permafrost thaw and an increase in the depth of the active layer (the seasonally freezing and thawing layer above the permafrost), exposing previously frozen SOM to decomposition (Jiang et al., 2015). Therefore, we hypothesized that the occurrence

of fire would lead to a decrease in the diversity of fungal communities related to the C cycle in the soil surface and an increase in the deeper active layer.

In this study, four forest areas were selected in the continuous permafrost region of northern Canada, which had recovered 3 years (3 ypf), 25 years (25 ypf), 46 years (46 ypf) and >100 years (control) after a wildfire. The study aims to investigate the temporal and soil vertical gradient dynamics of soil fungal communities and their potential functions after the fire, and to assess the long-term effects of forest fires on the fungal community in the permafrost region. We hypothesized that with the forest regrowth after the fire, the soil fungal community composition and the function will recover to pre-fire level and the post-fire response of the soil fungal community might differ between soil depths.

2 | MATERIALS AND METHODS

2.1 | Study areas

The study areas were located in a continuous permafrost zone in the Yukon and the Northwest Territories (66°22′N – 67°26′N and 136°43′W – 133°45′W respectively), in Canada. The areas are characterized by long, cold winters, with an annual average temperature of −8.8°C (mean air temperatures well below 0°C from October to April), and an average annual precipitation of 248 mm (Köster et al., 2017). The altitude of the terrain in the region ranges from 150 to 600 m above sea level and the soil is formed from Cretaceous sandstones covered by ice-rich fluvial and clay-rich colluvial deposits, with continuous permafrost underneath (Zhou et al., 2020). The dominant tree species consist of black spruce (*Picea mariana* [Mill.] Britton, Sterns and Poggenburg), white spruce (*Picea glauca* [Moench] Voss) and the ground vegetation is comprised of lingonberry (*Vaccinium vitis-idaea* L.), cloudberry (*Rubus chamaemorus* L.), bog bilberry (*Vaccinium uliginosum* L.) and *Rhododendron groenlandicum* Oeder. More detailed information on the area was described previously (Zhou et al., 2020).

2.2 | Sample collection

The soil samples were collected in July 2015. The measurements were carried out in a forest post-fire chronosequence consisting of forest areas burned in 2012 (3 ypf), 1990 (25 ypf), 1969 (46 ypf) and >100 years ago (100 ypf, set as control) along the Dempster Highway in Northern Canada. Wildfire history was determined based on Canadian government GIS data (http://www.geomaticsyukon.ca/data) and the forest age of the control was determined by taking increment cores from the largest tree in the sampling plot using an increment borer (Zhou et al., 2020). Three sampling lines per forest age class were established. The lines were at least 200 m apart from each other and consisted of three sample plots (20 × 20 m) that were 50 m apart from each other (Köster et al., 2017). The forests burned >100 years ago were used as controls, which were placed next to each burned forest area. One soil pit was excavated within every sample plot, and the soil samples were collected from three different soil depths including 0–5 cm (surface soil layer), 5–10 cm (middle soil layer) and 10–30 cm (deep soil layer), that measured from the soil surface excluding the litter layer. In total, 107 samples (4 forest areas × 3 sampling lines × 3 sampling plots × 3 depths, with one sample missing) were available for analysis.

In summer, the active layer thickness of the control area was 28.0 ± 2.0 cm, while that of the 3 ypf was much deeper (101.0 ± 9.0 cm). Thus, soil samples at the 10–30 cm layer in the control were on near-surface permafrost layers, and those in the remaining forest areas were on the active layer. The thickness of the organic layer in the control was 16.0 ± 1.4 cm, but declined to 5.3 ± 1.2 cm in 3 ypf (Zhou et al., 2020). As a result, soils collected from 5 to 10 cm layer in 3 ypf were mineral soils, while those in the remaining areas were organic soils (Zhou et al., 2020). All samples were transported in liquid nitrogen (−180°C) with a dry shipper. Each sample was divided into two subsamples. One was stored in a 2-ml Eppendorf vial (stored at −80°C in the laboratory until further analysis) from homogenized soils for DNA extraction. Another was used for the determination of physical and chemical properties (stored at 4°C in the laboratory until further analysis). The soil properties and vegetation characteristics of each forest area were measured and described previously (Köster et al., 2017; Zhou et al., 2019b). Briefly, we estimated the permafrost depths using a linear regression model of the temperature in the mineral soil against the depths. Soil pH was analysed using a glass electrode (Standard pH meter, Radiometer Analytical) in 35 ml soil suspensions, consisting of 10 ml of the soil sample and 25 ml of ultrapure Milli-Q water (left overnight to stand after mixing). The soil water content was measured using a soil moisture sensor (Thetaprobe ML2x, Delta-T Devices Ltd) connected to a data reader (HH2 moisture meter, Delta-T Devices Ltd). The soil organic C and N were measured using a total organic C analyser (Shimadzu TOC-V CPH, Shimadzu Corp.). Inorganic phosphorus was measured using the ammonium molybdate–malachite green method on a 96-well microplate. We used the chloroform fumigation extraction (CFE) method to estimate soil microbial biomass C, N and P contents. Ground vegetation biomass was measured at four 0.20 × 0.20 m^2 subplots per plot. The tree biomasses were calculated based on the tree diameter and height (details on environmental factors are listed in Table S1).

2.3 | DNA extraction, Illumina MiSeq sequencing and data processing

Genomic DNA was extracted from a 0.25 g (fresh weight) soil sample after homogenization using NucleoSpin Soil genomic DNA kit (Macherey-Nagel GmbH & Co. KG) following the manufacturer's instructions. The DNA concentrations were quantified using the Qubit 2.0 Fluorometer (Thermo Fisher Scientific) and were diluted

to 10 ng μl^{-1} with nuclease-free water. The DNA was subjected to PCR amplification of the fungal Internal Transcribed Spacer 2 (ITS2) region by using the fungus-specific primers gITS7 and ITS4 (Ihrmark et al., 2012) containing partial TruSeq adapter sequences at the 5′ ends (ATCTACACTCTTTCCCTACACGACGCTCTTCCGATCT and GTGACTGGAGTTCAGACGTGTGCTCTTCCGATCT respectively). The PCR reactions were performed in triplicate in a 20 μl mixture containing 4 μl of 5 × FastPfu Buffer, 2 μl of 2.5 mM dNTPs, 0.8 μl of each primer (5 μM), 0.4 μl of FastPfu Polymerase, 0.2 μl of BSA and 10 ng of template DNA, and the process was as follows: 3 min of denaturation at 95°C, 36 cycles of 30 s at 95°C, 30 s for annealing at 55°C and 45 s for elongation at 72°C, and a final extension at 72°C for 10 min. The PCR products were checked from a 2% agarose gel, and then further purified. The PCR amplicons were sequenced using the pair-ended (PE-300) Illumina MiSeq Platform at the Institute of Biotechnology, University of Helsinki. The raw reads were deposited into the NCBI Sequence Read Archive (SRA) database with Accession Number: PRJNA780219 (Zhang et al., 2022).

The raw sequences were denoised, quality controlled and clustered into operational taxonomic units (OTUs) following the Standard Operation Procedure (SOP) in Mothur software version 1.39 (Schloss et al., 2009). Briefly, any chimeric and low-quality sequences with (i) ambiguous (N) bases, (ii) homopolymers longer than eight nucleotides, (iii) average quality score lower than 25, (iv) chimeras (using Chimera uchim in Mothur) and (v) fewer than 200 nucleotides were removed. Remaining high-quality sequences were pairwise aligned and classified into taxonomic groups with an 80% bootstrap confidence by using the mothur-formatted UNITE taxonomy reference database version 8.0 (UNITE Community, 2019). Sequences assigned to the plant chloroplast and nonfungal domain were filtered out. The sequences were further clustered to operational taxonomical units (OTUs) at 97% similarity (Schloss et al., 2009). Among these, the OTUs with less than one read across all samples were removed (Olesen et al., 2017; Tedersoo et al., 2010). In total 8,512,268 sequence reads were obtained after de-noising and quality control, with an average of 79,554 ± 37,768 (mean ± standard deviation, with the same convention used hereafter). The fungal community species richness (estimator Chao1; Chao, 1984), α-diversity index (Shannon index) and evenness (Shannon evenness; Shannon, 2001) were calculated with normalization data, in which the smallest size of the sequence number across all samples was used (18090).

2.4 | GeoChip 5.0 K

GeoChip 5.0 K is a comprehensive functional gene array related to microbial C, nitrogen, sulphur and phosphorus cycling, energy metabolism, and many other functions, for analysing the functional diversity, structure, potential metabolic activity and dynamics of microbial communities (Tu et al., 2014). In this experiment, 24 DNA samples were selected from 4 forest areas × 2 soil depths (0–5 cm and 10–30 cm) × 3 replicates per area/soil depth for GeoChip 5.0 K analysis. Briefly, the replicates were obtained from the pooled-genomic DNA sample of the three soil plots in each forest area. 100 ng of genomic DNA from the triplicates in each of the four areas was amplified by rolling circle amplification using the TempliPhi kit (GE Healthcare) and a modified protocol (Tu et al., 2014). Two micrograms of amplified genomic DNA was mixed with 3 μg μl^{-1} random primers, and then labelled with 15 μl of labelling master mix, after purification (QIAquick purification kit) and 45 min drying in a SpeedVac. Finally, hybridization on GeoChip 5.0 K microarray was done (Liang et al., 2010; Tu et al., 2014). The data were processed and normalized following Glomics Inc. standard protocols (removing outliers and data with low signal intensities according to the signal-to-noise ratio [SNR] < 2.0; He et al., 2007). The gene probes originating only from fungi were included in this analysis to match the fungal taxonomic analysis and that from bacteria, archaea and virus were excluded.

2.5 | Statistical analysis

One-way analysis of variance (ANOVA) with Tukey's HSD multiple range tests was used to test the significant differences in soil abiotic and biotic factors, α-diversity, dominant fungal taxa in communities and functional gene expression in each soil layer among the four forest areas and in each forest area between the soil layers using SPSS.26. We used linear regression to analyse the changes in fungal α-diversity, major phylum and the diversity of functional gene with post-fire chronosequence or soil depth. In the case of fungal community structure and functional gene expression profiles, principal coordinates analysis (PCoA) based on Bray–Curtis similarities at OTU level or at gene expression level was used as ordination method. To test how post-fire chronosequence and soil depth affected the fungal community structures and functional gene expression profiles, we used the permutational multivariate analysis of variance (PERMANOVA) by Bray–Curtis similarities after 9999 permutations with post-fire chronosequence, soil depth and their interaction as a fixed factor. A pair-wise test is performed to test for differences between groups of each factor and when the main effect is significant ($p < 0.05$). A distance-based linear model (DistLM) was used to test the correlation between the community or functional structure and the environmental variables (all variables are listed in Table S1). The PCoA, PERMANOVA and DistLM analyses were performed in PRIMER 7 (Anderson et al., 2008). To determine fungal taxa indicative of experimental treatments, we used indicator taxa analysis, which is a post-hoc test used to determine which fungal taxa are driving differences in community membership and abundance (Dufrêne & Legendre, 1997). We calculated and compared the indicator values (IndVal) among the four forest areas and among the soil layers with the multipath function in the INDICSPECIES package (Miquel De Caceres, 2016).

3 | RESULTS

3.1 | Temporal and spatial changes in fungal community α-diversity

The fungal species richness in the upper soil layers (0–5 and 5–10 cm) increased (R^2 = 0.305, R^2 = 0.373, Tables S2 and S3) throughout the forest succession, and was significantly higher in the 48 ypf and control (>100 ypf) areas than in the more recently burned area ($p < 0.05$, ANOVA; Figure 1a,d, Table S2). The fungal community diversity and evenness showed a similar pattern in the upper soil layers: the 25 ypf and 46 ypf areas had the lowest and highest values respectively, whereas the fungal diversity in the deep soil layer (10–30 cm) increased throughout the forest succession (Figure 1, Table S2). In the soil vertical space, the species richness in 46 ypf and control areas had the same trend of decreasing with soil layer.

3.2 | Temporal and spatial changes in fungal community structures

The sequences were assigned to 4019 OTUs after singleton removal across the four post-fire chronosequence areas. The shared and unique OTUs among the areas showed similar patterns in each of the three soil layers respectively (Figure 2). The four post-fire chronosequence areas shared 7.4%–10.3% of the total OTUs and the unique OTUs in each area increased after fire from 8.0% to 22.0% (Figure 2a–c). In addition, the 46 ypf and control areas shared the highest number of OTUs in all the three soil layers (0–5, 5–10 and 10–30 cm) respectively.

The principal coordinates analysis (PCoA) showed that the four post-fire chronosequence areas in each soil layer and the three soil layers in each post-fire chronosequence area formed distinct fungal community structures, which was confirmed by PERMANOVA ($p < 0.01$, Figure 3a, Table S4). The pair-wise tests showed that in soil

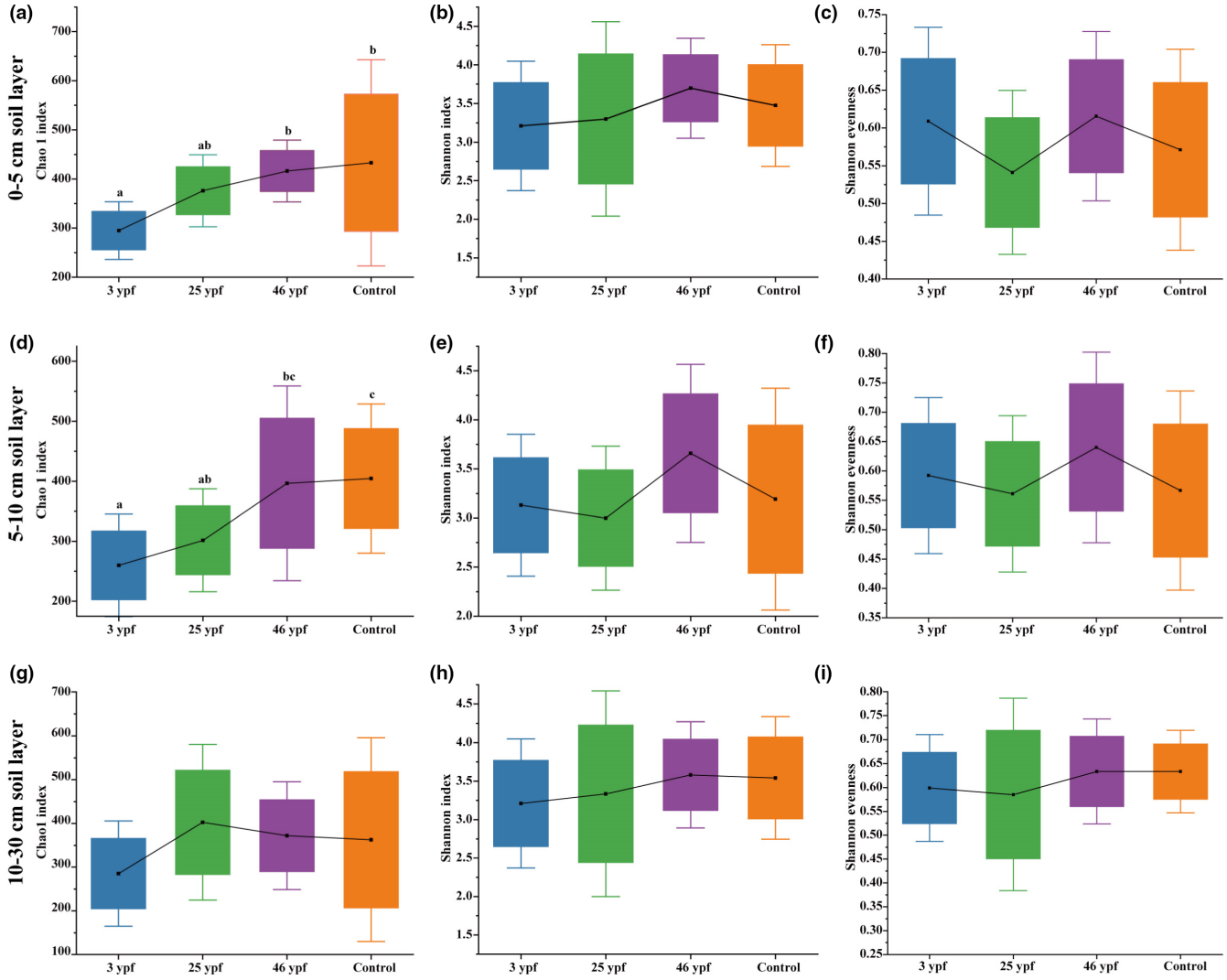

FIGURE 1 Fungal community richness (a, d and g), α-diversity (b, e and h) and evenness (c, f and i) in the 0–5 cm, 5–10 cm and 10–30 cm soil layer in the four post-fire chronosequence areas. Different letters in the figure represent the significant differences ($p < 0.05$) in each soil layer among the areas by ANOVA with Tukey's HSD multiple range tests. Boxes showing 25–75 percentiles, vertical lines showing the standard deviation (n = 9). Abbreviations: ypf, year-post-fire.

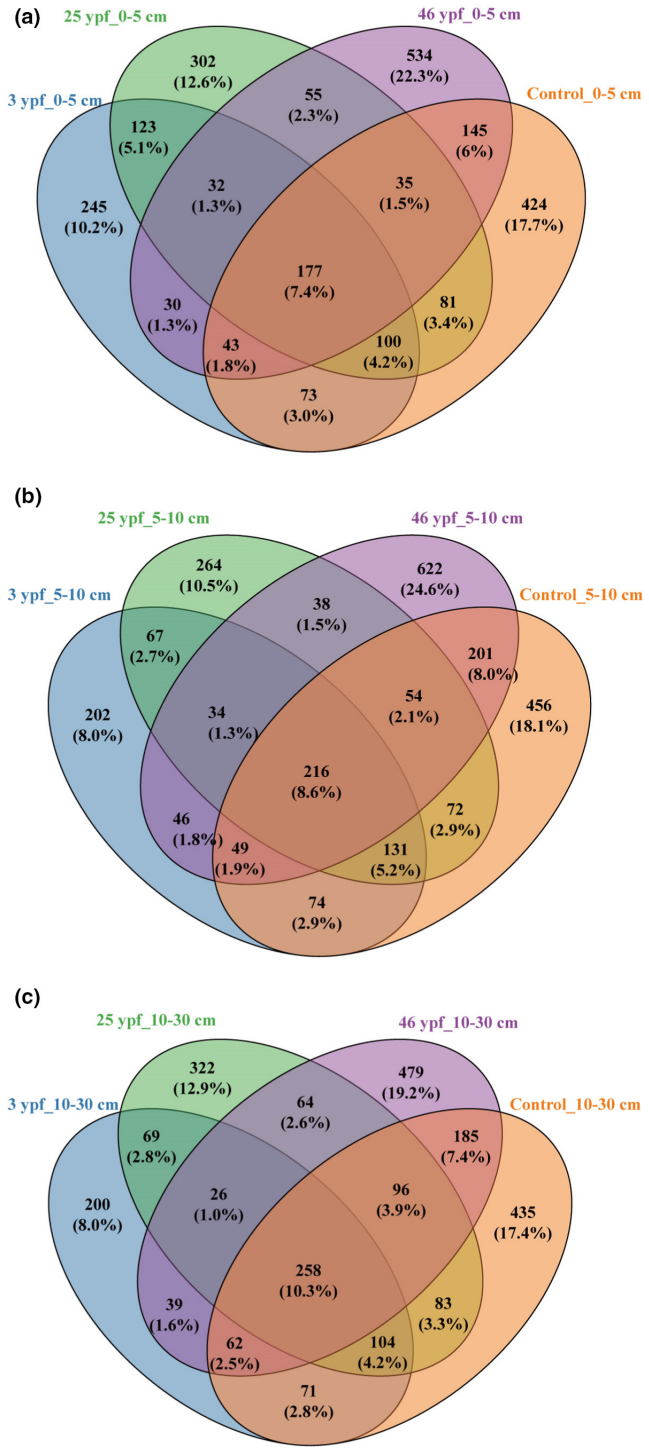

FIGURE 2 Venn diagram showing the unique and shared OTUs in the 0–5 cm (a), 5–10 cm (b) and 10–30 cm (c) soil layers in the four post-fire chronosequence areas. Abbreviations: ypf, year-post-fire.

vertical space, the 0–5 cm soil layer formed separate communities from other soil layers (5–10 cm and 10–30 cm) in each of the post-fire chronosequence areas. The three soil layers formed separate communities in the 46 ypf and control areas respectively. However, the community structures in 5–10 cm and 10–30 cm soil layer did not differ in 3 ypf area.

3.3 | Temporal and spatial changes in fungal community structures at taxonomic level

The indicator taxa analysis at phylum level revealed that Ascomycota was identified as indicator species in each of the three soil layers in the 3 ypf area ($p < 0.05$, Table S5). At genus level, in the 0–5 cm soil layer, *Calyptrozyma*, *Meliniomyces*, *Mycenae* and *Phialocephala* were indicators in the 3 ypf area. In 5–10 cm soil layer, *Calyptrozyma* and *Meliniomyces* were identified as indicator genera in the 3 ypf area and the control area respectively. In 10–30 cm soil layer, *Calyptrozyma* and *Serendipita* were identified as indicator genera in the 3 ypf area and the control area respectively. At the species level, in the 0–5 cm soil layer, *Exophiala xenobiotica* and *Russula suecica* were identified as indicator species in the 3 ypf area, and *Wilcoxina rehmii* as an indicator species in the 46 ypf area (Table S6). In the 10–30 cm soil layer, *E. xenobiotica*, *W. rehmii* and *Meliniomyces variabilis* were identified as indicator species in the 3 ypf, 46 ypf and control areas respectively. In 10–30 cm soil layer, *Russula suecica* and *W. rehmii* were identified as an indicator species in the 3 ypf and 46 ypf area respectively. *Oidiodendron maius* and *Solicoccozyma terricola* were the indicator species in the control area. In soil vertical space, in 3 ypf area, *Meliniomyces* was identified as an indicator genus in 0–5 cm soil layer. In 25 ypf area, *Oidiodendron* and *Pezoloma* were identified as indicator genera in 0–5 cm soil layer. In control area, *Cortinarius* and *Phialocephala* were identified as indicator genera in the 0–5 cm and 5–10 cm soil layers respectively. In the 0–5 cm soil layer, *O. maius* was identified as an indicator species in both the 3 ypf and 25 ypf areas. *M. variabilis* and *Pezoloma ericae* were as indicator species in the 25 ypf area. In the 5–10 cm soil layer, *Solicoccozyma terricola* was identified as indicator species in the 25 ypf area. In the 10–30 cm soil layer, *O. maius* was identified as indicator species in the 46 ypf area, while *E. xenobiotica*, *R. suecica* and *S. terricola* were used as indicator species in the control area. Details of the indicator species are listed in Tables S6 and S7.

3.4 | Temporal and spatial changes in fungal functional gene diversity and structure

In total, 4932 gene probes originating from fungi were detected from the surface layer (0–5 cm) and deeper layer (10–30 cm) across all the areas. These were involved in various metabolic processes, including the C, N, P and S cycle, metal homoeostasis, organic remediation, secondary metabolism and stress.

The diversity of functional gene (Shannon index) in each soil layer differed between the areas with time since fire. The diversity in 0–5 cm soil layer increased in 3 ypf and 25 ypf areas and decreased in older areas ($R^2 = 0.478$, Tables S2 and S3). In 10–30 cm soil layer, the 25 ypf area had higher diversity of functional gene than the 3 ypf and 46 ypf areas respectively ($p < 0.05$, ANOVA, Figure 4a, Table S2). In the soil vertical space, the diversity of functional gene in the 0–5 cm soil layer was higher than that in the 10–30 cm soil layer in 3 ypf and 46 ypf areas respectively; while the diversity of functional gene in

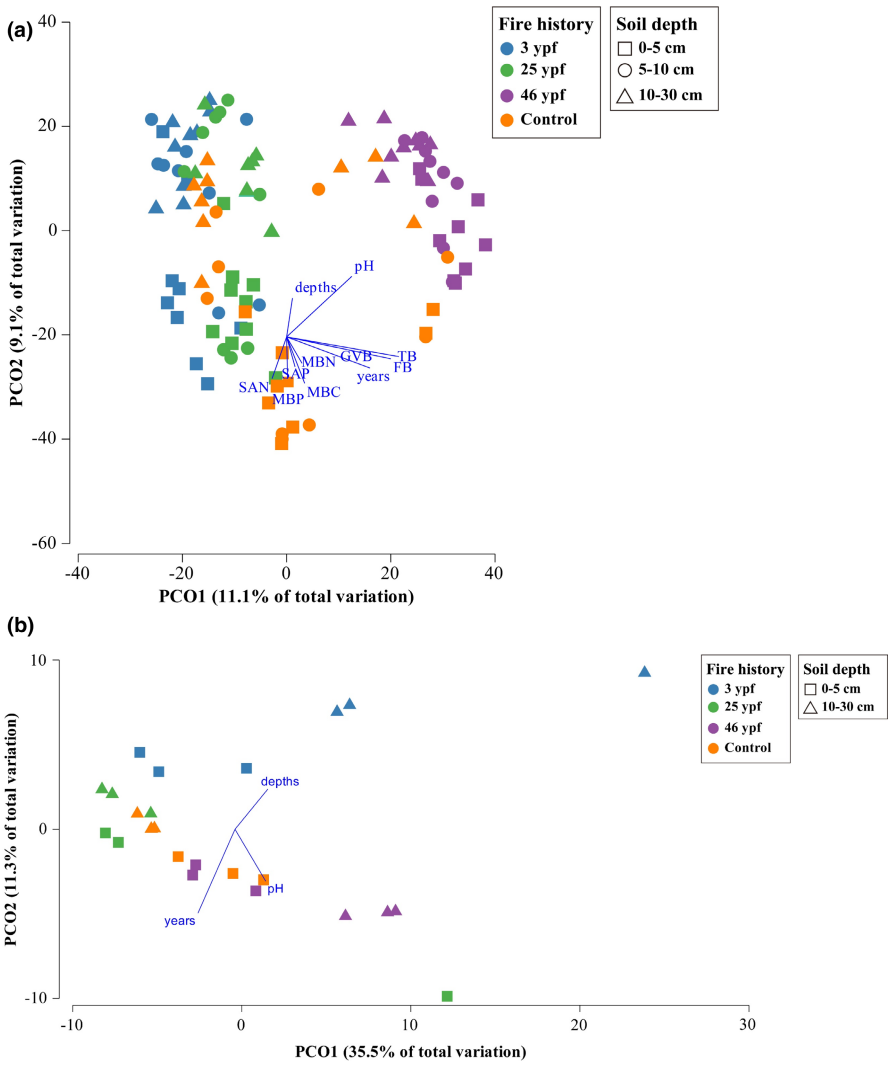

FIGURE 3 Principal coordinates analysis (PCoA) showing the fungal community structure (a) and the functional gene profile (b) based on the Bray–Curtis distances by using environmental factors as explanatory variables. Colour and symbol codes in the figure: blue represents samples of 3-year post fire (ypf), green represents samples of 25 ypf, purple represents samples of 46 ypf, and orange represents samples of the control; the square points represent samples of 0–5 cm soil layer, the circular points represent samples from 5 to 10 cm soil layer, and the triangular points represent samples from 10 to 30 cm soil layer. Abbreviations: TB, tree biomass; GVB, ground vegetation biomass; FB, foliage biomass; MBC, MBN and MBP are microbial biomass C, N and P contents; SAN and SAP are soil available N and P contents; FBR, fungal-to-bacterial ratio.

0–5 cm soil layer was lower than that in 10–30 cm soil layer in control area (Figure 4b, Table S2).

The functional gene expression differed between the 0–5 and 10–30 cm soil layers in each post-fire chronosequence area and among the post-fire chronosequence areas in the same soil layer (Figure S2). In the 0–5 cm soil layer, the genes of *acetyl xylan esterase*, *exoglucanase*, *pectate lyase* and *chitinase* of the soil organic matter degradation process had a higher gene expression in the 3 ypf areas, and then decreased 25 ypf and stabilized afterward (Figure 5a). In the 10–30 cm soil layer, the gene expression of *chitinase*, *cellobiase*, *exoglucanase* and *endoglucanase* genes for the C cycle process was significantly reduced in the 3 ypf areas, followed by a significant increase in the 25 ypf area, and then decreased afterward (Figure 5b). The *sulfite reductase* gene involved in sulphite reduction, the *sulfate permease* gene involved in sulphur assimilation and the *endopolyphosphatase* gene involved in polyphosphate degradation showed a similar trend, and the gene expression were lower in the 3 and 46 ypf areas, and higher in the 25 ypf and control areas (Figure 5c,d). The genes of *NADP-dependent glutamate dehydrogenase* and *glutamine synthetase* involved in ammonification differed in gene expression between the 0–5 and 10–30 cm soil layers in the 3 ypf area (Figure 5e).

The PCoA showed that the four post-fire chronosequence areas in the same soil layer and the two soil layers in each post-fire chronosequence area (except 25 ypf area) formed distinct functional gene expression profiles, which was confirmed by PERMANOVA ($p < 0.01$, Figure 3b, Table S5). The pair-wise tests (Table S5) showed that in 10–30 cm soil layer, the four post-fire chronosequence areas formed four gene expression profiles, but in 0–5 cm soil layer, only three gene expression profiles were formed (25 ypf area did not form an independent profile). In soil vertical space, the two soil layers (0–5 cm and 10–30 cm) formed separate gene expression profiles in each of the post-fire chronosequence areas, except in the 25 ypf area.

3.5 | Environmental factors contributing to fungal community structures and function

Many environmental parameters were strongly correlated with the fungal community structures and functional gene expression profiles (Figure 3a,b). DistLM analysis showed the fire history, soil depth, tree biomass and soil pH significantly correlated with the fungal community structures, while, the fire history was significantly

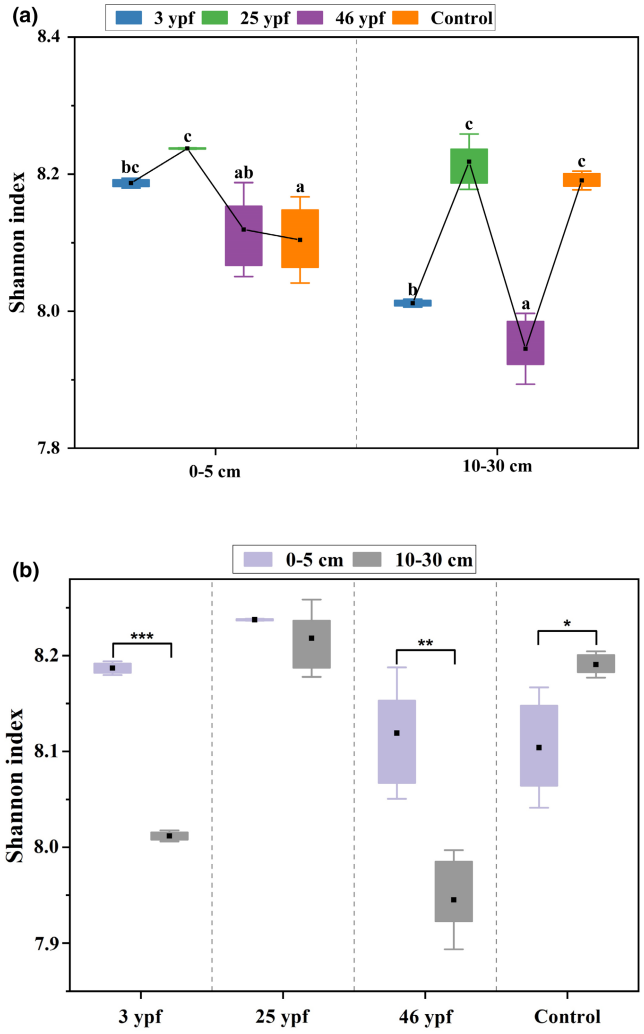

FIGURE 4 Principal coordinates analysis (PCoA) showing the fungal community structure (a) and the functional gene profile (b) based on the Bray–Curtis distances by using environmental factors as explanatory variables. Colour and symbol codes in the figure: blue represents samples of 3-year post fire (ypf), green represents samples of 25 ypf, purple represents samples of 46 ypf and orange represents samples of the control; the square points represent samples of 0–5 cm soil layer, the circular points represent samples from 5 to 10 cm soil layer, and the triangular points represent samples from 10 to 30 cm soil layer. Abbreviations: TB, tree biomass; GVB, ground vegetation biomass; FB, foliage biomass; MBC, MBN and MBP are microbial biomass C, N and P contents; SAN and SAP are soil available N and P contents; FBR, fungal-to-bacterial ratio.

correlated with the functional gene expression profiles (Table S8, $p < 0.05$ with DistLM analysis).

4 | DISCUSSION

Our study demonstrated that the fungal community structures in the same soil layer differed between the four post-fire chronosequence areas, suggesting that fire not only has a significant effect on soil fungal communities in the surface layer, which is consistent with previous studies (Sun et al., 2015), but also in the deeper layer. One exception is that in the 0–5 cm soil layer, the functional gene profiles in the 25 ypf area was not separated from other post-fire areas. The lack of separation in functional gene profiles may have been due to one plot in this grouping, which varied significantly from the others. Both the soil properties and above-ground vegetation can influence the soil fungal communities. With the forest recovery after fire, the above-ground vegetation becomes progressively more diverse, and both the mixing of plant litter and the interaction of root exudates may be important factors causing significant changes in soil physicochemical properties, such as pH, which may lead to an altered fungal community and function (Glassman et al., 2017; Tian et al., 2021). The soil vertical gradient itself is an important determinant of fungal community composition and dispersal (Lindahl et al., 2007; Upton et al., 2020). In addition, the fire also shifted the fungal community and function in soil vertical gradient as the surface (0–5 cm) and deep (10–30 cm) soil layers formed a separate community structure and functional gene profile in each post-fire chronosequence area.

The species richness in the upper soil layers (0–5 and 5–10 cm) in 46 ypf and control (>100 ypf) areas were similar with no significant difference between them, which were significantly higher than that in the more recently burned 3 ypf area. The similar result was also observed on microbial biomass in the same study areas that is, the soil microbial biomass C and nitrogen in the upper soil layers did not differ between the 46 ypf and control areas, which significantly increased from 3 ypf to 46 ypf areas (Zhou et al., 2019b), suggesting that the fungal communities in soil surface have recovered from fire in 46 ypf forests. The fungal species richness decreased significantly in the upper soil layer (0–5 and 5–10 cm depth) in the recently burned areas, which agrees with previous studies that fire reduces the fungal species richness (Dove & Hart, 2017). The reason for these results may be that fire likely eliminates fungal species that cannot withstand high temperatures directly (Baar et al., 1999; Horton et al., 1998), or indirectly reduce acid-loving or moisture-loving fungal community in soil by increasing soil pH and the hydrophobicity of soil in the humus layer (DeBano, 2000; O'Donnell et al., 2009) leading to soil drying (Peay et al., 2009). In addition, fires cause a reduction in vegetation and loss of hosts for mycorrhizal fungi (Rashid et al., 1997; Smith et al., 2005), resulting in a decline in mycorrhizal fungi. Subsequently, with the recovery of vegetation, the fungal diversity and species richness also gradually recover due to the increase in forest litter and nutrient input (Bárcenas-Moreno & Bååth, 2009).

Indicator taxa analysis is a post-hoc test used to determine which microbial taxa are driving differences in community membership and abundance in each experimental group (treatment; Bach et al., 2018). Ascomycota as a differential phylum in each soil layer in the 3 ypf area, was identified to be the dominant post-fire fungus, meaning they can respond rapidly to the fire, and colonize the areas within a few weeks after the fire and post-fire colonization can take up to 2 years after fire (Adamczyk et al., 2012;

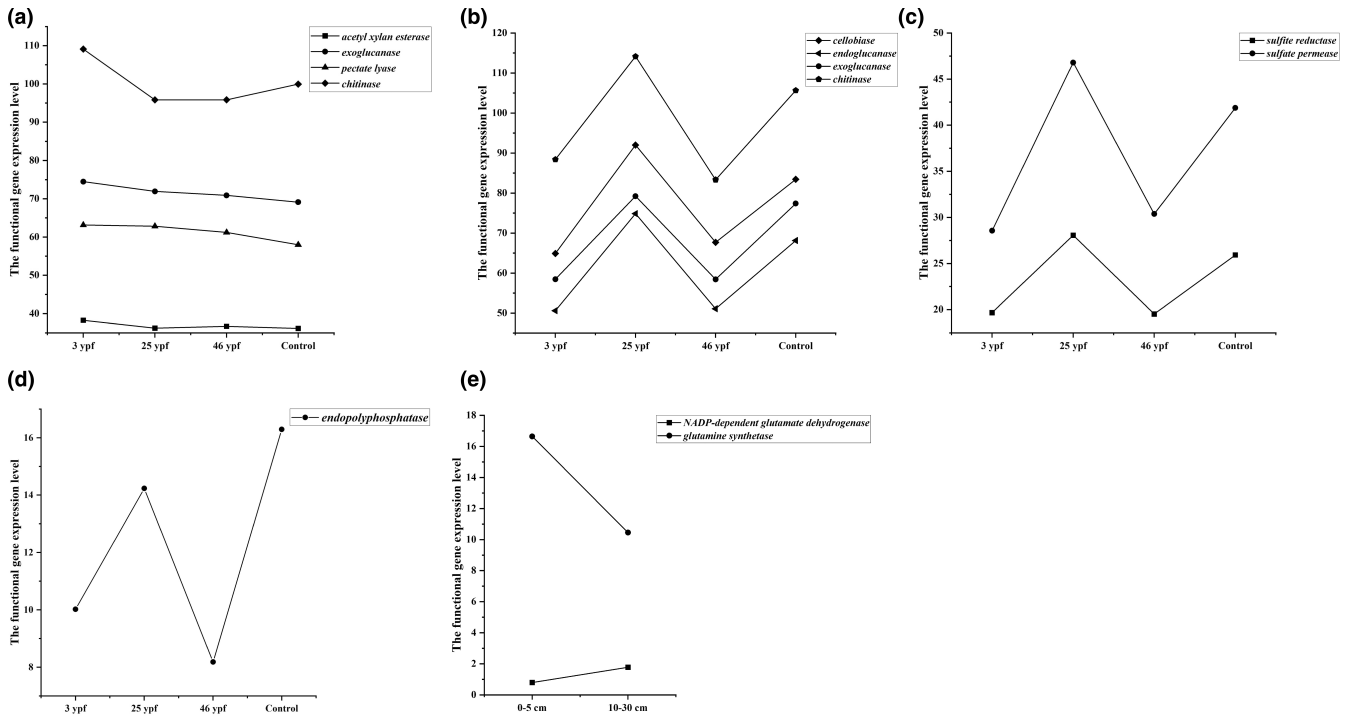

FIGURE 5 The significantly expressed genes involved in C cycle in the 0–5 cm soil layer (a), C cycle in the 10–30 cm soil layer (b), S cycle in the 10–30 cm soil layer (c), P cycle in the 10–30 cm soil layer (d) in the four post-fire chronosequence areas, and N cycle in the 3 ypf site (e) in the two soil layers. Abbreviations: ypf, year-post-fire.

Reazin et al., 2016). As compared to control areas, *Calyptrozyma* exhibited higher relative abundance in the 3 ypf area. This was attributed to the fact that most members in *Calyptrozyma* have higher tolerance to fire, and can survive through living on residual charcoal that is normally enriched in aromatic hydrocarbons (Pérez-Izquierdo et al., 2021). *Oidiodendron maius* is an ericoid mycorrhiza and forms associations with the roots of ericoid plants, which can improve host plant growth by aiding plant uptake nutrient uptake (Douglas & Smith, 1989). *Vaccinium* vitis-idaea L., *V. uliginosum* L. and *Rhododendron groenlandicum* Oeder are the common ericoid shrubs in the studied areas, and they disappeared for a while because of fire. With the restoration of plantation after fire, *O. maius* became an indicator species in the deeper soil layer in the control area. In addition, *E. xenobiotica* was an indicator species in the upper soil layers (0–5 cm and 5–10 cm) in the 3 ypf area. *E. xenobiotica*, a relatively common group of pathogens, is frequently found in habitats rich in monoaromatic hydrocarbons and alkanes (De Hoog et al., 2006). It can be enriched as an opportunistic species in the early post-disturbance stages when alkanes and aromatic compounds are abundant and the entire forest ecosystem is unstable after experiencing fire disturbance. Subsequently, as the ecosystem stabilizes over a longer period of time after wildfire, the relative abundance of this taxon group decreases to a much lower level and remains stable.

The genes associated with soil organic matter degradation had a higher expression level in the surface soil layer (0–5 cm) in the recently burned area (3 ypf) compared with other areas. Studies have shown that forest burning introduces large amounts of C-rich material to the soil surface as litter from dead trees (Harden et al., 1997; Harmon et al., 1990). The increase in C-rich material after fire may have favoured the aggregation of fungi and thus contribute to the increase in the expression level of genes related to cellulose and hemicellulose degradation in the surface litter. The death of a large number of fungal mycelium caused by fire can also lead to the increase in chitin in the soil (Williams & Robinson, 1981), thus, the expression of chitin degradation genes was more abundant in the 3 yfp areas (0–5 cm). Compared with the surface soil layer, the changes in the expression level of functional genes in deep soil layer (10–30 cm) were more significant. The reason might be due to the occurrence of the fire causing the deep soil to melt, and the refreezing of the deep soil as the time between fires increases, thus causing significant changes in the functional genes in the deep soil layer. In the deep soil layer, the expression level of genes (*cellobiase*, *endoglucanase*, *exoglucanase* and *chitinase*) involved in the soil organic matter degradation was significantly reduced in the recently burned areas (3 ypf) and was increased in the 25 ypf areas, which showed a similar pattern as the fungal species richness along with the fire history. Fungi in deep soils are affected by the root secretions of plants in addition to the soil physicochemical properties compared to those in surface (Baumert et al., 2018). Therefore, we expected that in the early post-fire stages, the fungal acquisition of carbonaceous material secreted by plant roots decreases due to the reduction of vegetation, and as the plants recover, this carbonaceous material increases and in turn the degradation of C by fungi is enhanced. Apart from this, high fungal mortality in the recently burned areas

(3 ypf) was also a cause for the reduction of fungi associated with organic matter degradation in the deeper layer. Therefore, higher expression of organic matter degradation-related genes in surface soils of the early post-fire stages may cause a reduction in C storage in surface soils, and conversely, lower expression in their deeper layers may bring an increase in C storage.

In conclusion, our study highlighted the long-term and soil vertical spatial effects of fire on soil fungal communities in boreal forest. Our findings indicate that fire has long-term impacts on fungal community composition in surface and near-surface soils, in which the fungal richness in surface soils was significantly reduced and may take at least 46 years to return to pre-fire levels. The effect of fire on fungal diversity was more pronounced in the surface soil layer, while that on functional genes was more pronounced in deep soil. In addition, changes in soil fungal community composition after fire resulted differences in functional genes, especially those related to organic matter degradation. The expression of genes associated with C degradation was significantly increased in the surface soil in recently burned area compared to areas burned long time ago, while the opposite was observed in the deep soil, suggesting that the fire affects C storage differently along soil depths and along post-fire time. It is necessary to construct a framework to study the specific role of the soil microbiome in post-fire forest recovery and nutrient cycling to better understand the impact of natural disturbances on forests.

AUTHOR CONTRIBUTIONS

Jussi Heinonsalo, Hui Sun and Jukka Pumpanen conceived the ideas and designed the methodology; Jukka Pumpanen, Kajar Köster and Frank Berninger collected the samples; Jussi Heinonsalo, Hui Sun, Jukka Pumpanen and Kajar Köster received the funding; Outi-Maaria Sietiö, Xuan Zhou, Frank Berninger, Yue-mei Zhang and Zhao-lei Qu analysed the data; Yue-mei Zhang and Zhao-lei Qu wrote the manuscript. All authors contributed critically to the draft of the manuscript and gave final approval for publication.

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CONFLICT OF INTEREST

All the authors declare that there is no conflict of interest related to this work.

DATA AVAILABILITY STATEMENT

The raw sequences were submitted to the National Center for Biotechnology Information (NCBI) with access No. PRJNA780219 (Zhang et al., 2022). https://www.ncbi.nlm.nih.gov/bioproject/PRJNA780219.

APPROPRIATE LICENCES AND PERMITS

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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