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Distinct fungal successional trajectories following wildfire between soil horizons in a cold-temperate forest

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Summary

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Key words: cold-temperate forests, community succession, ectomycorrhizal fungi, extracellular enzymes, fungal biomass, saprotrophs, soil horizons, wildfire chronosequence.

- Soil fungi represent a major component of below-ground biodiversity that determines the succession and recovery of forests after disturbance. However, their successional trajectories and driving mechanisms following wildfire remain unclear.
- We examined fungal biomass, richness, composition and enzymes across three soil horizons (Oe, A1 and A2) along a near-complete fire chronosequence (1, 2, 8, 14, 30, 49 and c. 260 yr) in cold-temperate forests of the Great Khingan Mountains, China. The importance of soil properties, spatial distance and tree composition were also tested.
- Ectomycorrhizal fungal richness and β -glucosidase activity were strongly reduced by burning and significantly increased with 'time since fire' in the Oe horizon but not in the mineral horizons. Time since fire and soil C : N ratio were the primary drivers of fungal composition in the Oe and A1/A2 horizons, respectively. Ectomycorrhizal fungal composition was remarkably sensitive to fire history in the Oe horizon, while saprotroph community was strongly affected by time since fire in the deeper soil horizon and this effect emerged 18 years after fire in the A2 horizon.
- Our study demonstrates pronounced horizon-dependent successional trajectories following wildfire and indicates interactive effects of time since fire, soil stoichiometry and spatial distance in the reassembly of below-ground fungal communities in a cold and fire-prone region.

Introduction

Wildfire is one of the most severe disturbances to natural forests globally (Millar & Stephenson, 2015; Seidl *et al.*, 2017). Ongoing climate change (e.g. warming and drying) is expected to increase the extent, frequency and severity of forest fires (Taufik *et al.*, 2017; Holden *et al.*, 2018; Walker *et al.*, 2019). Increasing wildfire will lead to rapid carbon (C) losses (Bowman *et al.*, 2013; Walker *et al.*, 2018) and subsequent impacts on soil processes (Ludwig *et al.*, 2018), vegetation succession (Cai *et al.*, 2013), trophic structure of soil fauna (Butenko *et al.*, 2017) and microbial community composition (Prendergast-Miller *et al.*, 2017).

Soil-inhabiting fungi are among the most important components of terrestrial habitats as they influence the functioning, stability and development of ecosystems (Peay *et al.*, 2016; Baldrian, 2017). Saprotrophic fungi decompose organic materials and maintain forest C cycling (Snajdr *et al.*, 2011), whereas mycorrhizal fungi promote seedling establishment and mineral nutrition of plants (Smith & Read, 2008). In particular, ectomycorrhizal (EcM) fungi dominate large tracts of high-latitude forests (Tedersoo *et al.*, 2014) and serve as important partners for regenerating forest trees after severe disturbances, such as

clearcutting and wildfire (Treseder *et al.*, 2004; Glassman *et al.*, 2016; Hewitt *et al.*, 2017; Duhamel *et al.*, 2019). Some EcM fungi also have a high capability to decompose organic materials by Fenton chemistry or manganese-dependent peroxidases. By competing with saprotrophic fungi for soil nitrogen (N), they may exert a major influence on the balance of soil C and N pools in forests (Averill *et al.*, 2014; Lindahl & Tunlid, 2015; Smith & Wan, 2019). Consequently, better understanding of spatial and temporal patterns of soil fungi and their functional guilds (e.g. EcM fungi and saprotrophs) is pivotal to predicting variation in biodiversity and functioning of forest ecosystems and informing management issues under global climate change scenarios.

Fungal succession – the sequential replacement of fungal taxa following natural or anthropogenic disturbances (*sensu* Prach & Walker, 2011; Chang & Turner, 2019) – is becoming a vital interactive theme of fungal ecology and disturbance ecology, especially in forest ecosystems (Baldrian, 2017). For example, soil fungal communities dramatically shifted in Norway spruce forests during the 4 yr following an insect outbreak; fungal biomass decreased and mutualistic fungi were replaced by saprotrophs (Stursova *et al.*, 2014). Wilhelm *et al.* (2017) found that soil fungal communities had long-term responses to clearcutting

for decades after harvest; the relative abundances of drought-tolerant and heat-tolerant taxa increased, while EcM fungal diversity decreased. Nevertheless, comprehensive studies on soil fungal succession in wildfire chronosequences are relatively limited (Cairney & Bastias, 2007; McMullan-Fisher *et al.*, 2011; Taudiere *et al.*, 2017), especially in East Asia. Existing studies suggest that, in the short-term (e.g. < 5 yr), soil fungal communities respond strongly to wildfire, with the most prominent changes being a transition from dominance of Basidiomycota to Ascomycota, and fire severity, stand age, pH, soil moisture and C:N ratio being considered the underlying drivers of these changes (Waldrop & Harden, 2008; Reazin *et al.*, 2016; Day *et al.*, 2019). In the long term (e.g. decades to centuries), soil fungal communities experience regular dynamics following wildfire, with gradual replacement of Ascomycota by Basidiomycota and recovery of EcM fungal abundance; dominant plant species, litter C:N ratio, soil pH and C content have been identified as the underlying drivers of these dynamics (Sun *et al.*, 2015; Duhamel *et al.*, 2019). For the longer timescale (e.g. millennia), cord-forming EcM basidiomycetes decline, while ericoid mycorrhizal (ErM) ascomycetes still dominate in late-successional forests, with the recalcitrant soil C pool enlarging (i.e. humus accumulation) (Clemmensen *et al.*, 2015).

While the litter and humus horizons are sometimes completely consumed by intense fires, the underlying mineral horizons are less affected by C loss and high temperature. The subsoil may harbor a large resistant spore bank that provides a legacy for soil fungal succession following wildfire (Glassman *et al.*, 2016). Only a few studies on fire chronosequences have assessed different soil horizons; these studies indicate a stronger response of soil fungal communities to wildfire in the organic horizon than in mineral horizons, at least in boreal forests (Waldrop & Harden, 2008; Holden *et al.*, 2013).

Here, we surveyed fungal biomass and extracellular enzymes as well as diversity and composition of fungal taxa and functional guilds across three soil horizons (Oe, A1 and A2) along a long-term fire chronosequence (1, 2, 8, 14, 30, 49 and *c.* 260 yr). We tested the following hypotheses:

(1) Fungal composition, rather than biomass, diversity and extracellular enzymes, strongly responds to fire history. Changes in biomass, diversity and extracellular enzymes are expected to be less pronounced because of complementary performance of pyrophilous fungi (McMullan-Fisher *et al.*, 2011) and functional redundancy in forest soil fungal communities (Talbot *et al.*, 2014; Truong *et al.*, 2019).

(2) Fire history and covarying soil properties are the main drivers of soil fungal community shifts, with different effects depending on soil horizon. We predicted that the effect of time since fire on fungal communities would be strongest in the Oe horizon and decrease with soil depth.

We performed this study in the Great Khingan Mountains (50°10'–53°33'N, 121°12'–127°00'E), which harbor the largest and oldest contiguous cold-temperate forest in China. The Great Khingan Mountains are the southernmost of Taiga forests in the northern hemisphere, storing a disproportionately large amount of C. For the last 2500 yr, the EcM trees *Larix gmelinii* and

Betula platyphylla have firmly colonized this cold-temperate forest region (Zhao *et al.*, 2016). Over the past decades, however, wildfires have been disturbing this region, resulting in dramatic losses of net primary production and changes in tree composition (Wang *et al.*, 2001; Cai *et al.*, 2013). It was estimated that the overall fire occurrence density would increase by 30–230% by the end of this century in the Great Khingan Mountains (Liu *et al.*, 2012).

Materials and Methods

Study area and field sampling

The study area was under the jurisdiction of Genhe forestry bureau in northeastern China. The area harbored *Larix gmelinii* Rupr. and *Betula platyphylla* Suk. mixed forest, the most widespread forest type in the Great Khingan Mountains. Dominant understory plants included *Ledum palustre* L. (Ericaceae; ErM plants), *Rhododendron dauricum* L. (Ericaceae; ErM plants), *Vaccinium vitis-idaea* L. (Ericaceae; ErM plants), *Pyrola calliantha* Andres (Ericaceae; partial mycoheterotroph plants) and *Deyeuxia angustifolia* Vickery (Poaceae; AM plants). Based on the forest fire records of the Genhe forestry bureau (1962–2016 yr), a fire chronosequence of burned forests (BF) from 1 to *c.* 260 yr after fire was reconstructed (viz. BF2016, BF2015, BF2009, BF2003, BF1987, BF1968 and PF-primary forests), and four neighboring unburned controls (UC) of the more recently burned forests (viz. UC2016, UC2015, UC2009 and UC2003) were identified (Fig. 1). The primary forest site harbored several *c.* 260-yr-old *Larix gmelinii*, so we regarded this site as naturally regenerated *c.* 260 yr after fire. Climate and topography differed little in the sampling area, and some basic information of each site (based on different fire history) is summarized in Table 1.

All sampling occurred during a short time interval (August 23–September 2 in 2017) to avoid the effects of seasonality. At each site (burned forests or unburned controls), we established four 30 × 30 m plots at least 30 m apart (Fig. 1). The maximum distance between plots was 138 km in the entire study. The pairwise distance between plots of burned forests and unburned controls ranged from 0.2 to 3.3 km. At each plot, three 20 × 20 cm soil samples were collected *c.* 14 m apart along the diagonal of the plot. We removed litter and divided soil samples into Oe (degraded organic/humic soil: *c.* 3–6 cm depth), A1 (mineral soil: 0–10 cm) and A2 (mineral soil: 10–20 cm) horizons. Three 20 × 20 cm soil samples of each horizon were homogenized as one composite sample to represent the 900 m² plot; each of the four plots within the same site represented one kind of fire history (Fig. 1). In total, we collected 132 soil samples (11 sites × four plots × three horizons). Sampling equipment (shovels and knives) was disinfected with Clorox wipes (Oakland, CA, USA) between plots. We recorded larch : birch ratio within each plot, based on the number of stems of living trees (diameter at breast height > 3 cm). All samples were taken back to the laboratory in ice bags within 12 h. After sieving through a 2 mm mesh, each sample was divided into two subsamples: one was stored at 4°C

Fig. 1 The sampling map of the Great Khingan Mountains, China. PF, primary forests; BF, burned forests; UC, unburned controls. The number behind BF and UC were the year of fire occurrence. In each fire history, four 30 × 30 m plots were established at least 30 m apart. In each plot, three 20 × 20 cm soil samples of each horizon were homogenized as one composite sample to represent an independent sample. The upper-right and lower diagrams show the within-site and among-site scales, respectively. Owing to the long regeneration following wildfire, the unburned controls of BF1987 and BF1968 were not found. The elevation data came from the srtm 90 m digital elevation data (<http://srtm.csi.cgiar.org/>).

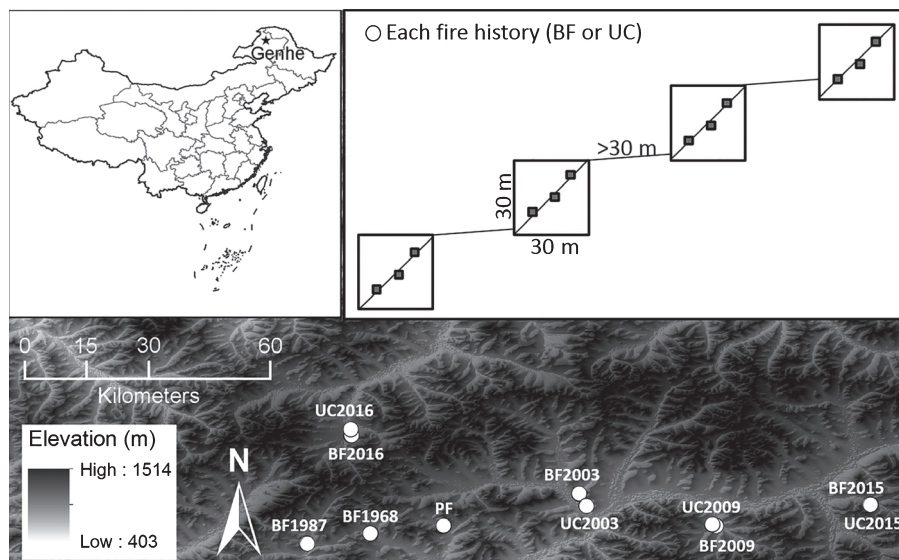


Table 1 The geography, topography, climate and vegetation of each site based on different fire histories.

	PF	BF1968/BF1987	BF2003/BF2009/BF2015/BF2016	UC2003/UC2009/UC2015/UC2016
No. of plots	4	4/4	4/4/4/4	4/4/4/4
Time since fire (yr)	~260	49/30	14/8/2/1	–
Latitude (°N)	50.9423–50.9427	50.9032–50.9258	50.9421–51.1405	50.9444–51.1542
Longitude (°E)	121.4953–121.4968	121.1949–121.3361	121.2920–122.4334	121.2913–122.4343
Elevation (m)	845–853	839–855	807–938	779–906
Slope (°)	8	7–10	4–12	5–8
MAT (°C/yr)	–4.4	–4.3	–4.7–4.4	–4.6–4.4
MAP (mm yr ^{–1})	536.3	522.2–528.7	536.3–565.5	530.8–564.4
Larch : birch ratio	0.3–3.9	0.8–5.6	1.4–55.0	2.2–20.0
Dataset 1			↙	
Dataset 2	↘	↘	↘	↘

PF, primary forests; BF, burned forests; UC, unburned controls. The number behind BF and UC were the year of fire occurrence. MAT, mean annual temperature; MAP, mean annual precipitation. Dataset 1 included the pairwise burned and unburned plots ($n = 32$) to compare the difference between burned forests and unburned controls, while dataset 2 included a fire chronosequence ($n = 28$) to explore the shift with time since fire. Slope was measured by App VELUX, and MAT and MAP were derived from the WORLDCLIM v.2 at 30 arcsecond resolution (www.worldclim.org).

to measure soil properties, ergosterol and extracellular enzymes, and the other was stored at -40°C for DNA extraction.

Measurements of soil properties

Altogether 27 soil variables were measured for all samples, including soil moisture, pH, total C (TC), total N (TN), C : N ratio, N : P ratio, soil organic C (SOC), nitrate N (NO_3^- -N), ammonium N (NH_4^+ -N), dissolved organic N (DON), dissolved organic C (DOC), available K, available P, available Ca, available Mg, available Al, available Fe, available Mn, available Mo, total K, total P, total Ca, total Mg, total Al, total Fe, total Mn and total Mo. Soil moisture was measured gravimetrically. Soil pH was measured using a Thermo Orion-868 pH meter (Thermo Orion Co., Waltham, MA, USA) in a suspension of 20% soil and 80% water. TC and TN were determined with a C–hydrogen–N (CHN) elemental analyzer (2400 II CHN elemental analyzer; PerkinElmer, Boston, MA, USA). SOC was determined according to the method of Zou *et al.* (2015). NO_3^- -N, NH_4^+ -

N, DON and DOC were measured using a total organic C and total N analyzer (Shimadzu, Kyoto, Japan). An ICP Optima 8000 (Perkin-Elmer, Waltham, MA, USA) was used to measure the total and available contents of K, P, Ca, Mg, Al, Fe, Mn and Mo. Before that, Mehlich 3 (Zbiral & Nemeč, 2000) and a three-acid-system (nitric acid, perchloric acid and hydrofluoric acid) were used to extract the available and total nutrients, respectively. In addition, four soil physical properties were determined for the mineral horizons (A1 and A2), including bulk density and proportions of clay, silt and sand. The proportions of clay, silt and sand were measured on a Laser Particle Sizer LS13320 (Beckman, Brea, CA, USA).

Measurements of fungal biomass and extracellular enzymes

Ergosterol content of freeze-dried samples was measured within the first week after sampling as a proxy for fungal biomass. Ergosterol was extracted from samples using cyclohexane, 10% KOH

and methanol (Koster *et al.*, 2014) and filtered (pore size 0.22 μm), followed by measurements on a HPLC-1260 (Agilent, Santa Clara, CA, USA) using 5 μm SB-C18 columns 250 \times 4.6 mm (Agilent). The injection volume was 20 μl , and the flow rate of methanol was 0.8 ml min^{-1} . We detected ergosterol at 286 nm UV light at 30°C column temperature.

Five extracellular enzymes were assayed using an iMark microplate absorbance reader (Bio-Rad, Hercules, CA, USA). Briefly, β -glucosidase was assayed using p-nitrophenyl β -D-glucopyranoside (pH = 4.5); laccase was assayed using 2,2'-azinobis-3-ethylbenzothiazoline-6-sulfonic acid (pH = 4.5); Mn-peroxidase was assayed using 3-methyl-2-benzothiazolinone hydrazone and 3,3-dimethylaminobenzoic acid with Mn and H_2O_2 (pH = 4.5); urease was assayed using urea with Nessler solution (pH = 5.0, Ruiz-Herrera & Gonzalez, 1969); acid phosphatase was assayed using para-nitrophenylphosphate (pH = 4.5, Hui *et al.*, 2013). Three replicates were performed for each sample.

Sequencing and bioinformatics

Total DNA of each sample was extracted from 0.5 g soil using a FastDNA[®] Spin kit (Bio 101, Carlsbad, CA, USA) according to the manufacturer's instructions. The extracted DNA was amplified by targeting the fungal internal transcribed spacer 2 (ITS2) rDNA region using the primer pair ITS3 and ITS4 (White *et al.*, 1990) equipped with unique barcodes. The volume of the PCR amplification system was 20 μl , containing 0.4 μl FastPfu Polymerase (TransGen Biotech, Beijing, China), 2 μl DNA template (5 $\text{ng } \mu\text{l}^{-1}$), 0.8 μl each of 5 μM forward and reverse primers, 1.2 μl of 20 mg l^{-1} BSA (Takara, Shiga, Japan), 4 μl of 5 \times FastPfu Buffer (TransGen Biotech, Beijing, China), 2 μl 2.5 mM dNTPs and 8.8 μl sterile water. The amplification condition consisted of one cycle of 95°C for 3 min, 38 cycles of 94°C for 30 s, 55°C for 30 s and 72°C for 45 s, and a final extension at 72°C for 10 min. The amplicons were sequenced using the Illumina MiSeq platform PE300 (Illumina Inc., San Diego, CA, USA) following Yang *et al.* (2017). The raw sequencing data were submitted to Sequence Read Archive (SRA) under the BioProject accession code PRJNA 480528.

We merged the paired-end reads using FLASH (Magoc & Salzberg, 2011). QIIME 1.9.0 (Caporaso *et al.*, 2010) and CUTADAPT 1.9.1 (Martin, 2011) were used for quality filtering, trimming and chimera removal. Altogether 3817 700 sequences passed quality filtering (parameters: minlength = 280, maxambigs = 0, phred quality threshold = 30). We removed the flanking large ribosomal subunit (LSU) and 5.8S gene sequences using ITSx 1.0.11 (Bengtsson-Palme *et al.*, 2013) and removed putative chimeric sequences by a combination of *de novo* and reference-based chimera checking (Edgar *et al.*, 2011). The remaining sequences were clustered into operational taxonomic units (OTUs) at 97% similarity threshold based on the USEARCH algorithm (Edgar, 2010). Taxonomy was assigned to each OTU by using the Ribosomal Database Project (RDP) Classifier with minimum confidence of 0.8 (Wang *et al.*, 2007). The UNITE v.7.2 (<http://unite.ut.ee>) release for QIIME served as the reference database for fungal taxonomy (Koljalg *et al.*, 2013).

After removing singletons and nonfungal reads, we retained 3670 862 fungal sequences assigned to 5887 OTUs from 504 genera. The functional guilds were assigned using the FUNGUILD pipeline (Nguyen *et al.*, 2016). The data distribution of functional guilds is summarized in Supporting Information Table S1. In order to analyze fungal diversity and composition at the same sequencing depth, samples were subsampled to 12 323 sequences (i.e. the minimum number of sequences among 132 samples).

Statistical analyses

The study was divided into two datasets that were analyzed separately (Table 1). Dataset 1 treated burned and unburned plots in a paired manner to examine overall burning effects on fungal biomass, diversity, enzymes and composition ($n = 32$ in each horizon). Dataset 2 included a fire chronosequence (*viz.* seven stages after fire), which was used to examine temporal changes in fungal biomass, diversity, enzymes and composition after fire ($n = 28$ in each horizon). We partitioned the analyses by soil horizon because of the overriding effects of horizon on soil properties, fungal biomass, diversity, composition and enzymes (Fig. S1; Table S2). In addition, the analyses of fungal diversity and composition were performed for the two dominant guilds (*viz.* EcM fungi and saprotrophs) separately. The number of observed OTUs was used as proxy for fungal richness (i.e. α -diversity), whereas Bray–Curtis dissimilarity (following Hellinger transformation) between each sample pair was used to quantify differences in community composition between samples (i.e. β -diversity). All statistical analyses were conducted in R 3.5.2 (R Core Team, 2018).

To analyze dataset 1 (paired burned and unburned plots), linear mixed-effects models (LMMs) were fitted using the LME4 package (v.1.1-21; Bates *et al.*, 2015) to quantify burning effects on soil properties, fungal biomass, diversity, enzymes, and the relative abundances of fungal classes and functional guilds, with site as a random factor. The significance of each LMM was tested by the function 'Anova' in CAR 3.0-3 (Fox & Weisberg, 2019) and adjusted for multiple comparisons by the function 'p.adjust' in STATS 3.5.2 (R Core Team, 2018). Marginal (m) and conditional (c) R^2 were calculated by the function 'r.squaredGLMM' in MUMIN 1.43.6 (Bartón, 2019). Marginal R^2 (R_m^2) represents the variance explained by fixed effects (i.e. the burning effects), whereas conditional R^2 (R_c^2) represents the variance explained by both fixed and random effects. Nonmetric multidimensional scaling (NMDS) analyses were performed using the VEGAN package (v.2.5-3; Oksanen *et al.*, 2018) to illustrate the differentiation in community composition of total fungi, EcM fungi and saprotrophs between burned and unburned plots. The relationship between the decline in community similarity with increasing geographic distance (distance decay) was tested for communities of total fungi, EcM fungi and saprotrophs in burned and unburned plots, respectively (Nekola & White, 1999). The distance decay models were also applied separately at the within-site (< 1 km, the upper right diagram in Fig. 1) and among-site (20–80 km, the lower diagram in Fig. 1) scales. For recently burned forests, we also considered the spatial distribution of fire history by

testing variation in dissimilarities of time since fire among each burned site as a function of increasing geographic distance. In addition, response ratio analyses (Luo *et al.*, 2006) were performed to determine specific fire-responding OTUs. Before analysis, we set a threshold of 60% frequency to screen OTUs. In other words, only OTUs found in at least 10 samples in both burned forests and unburned controls were analyzed.

For dataset 2 (fire chronosequence), LMMs were performed to analyze effects of time since fire on soil properties, fungal biomass, diversity, enzymes as well as the relative abundances of fungal classes and functional guilds, with site as a random factor. Specifically, we first used corrected Akaike information criterion (AICc) to identify the best mixed-effects model from linear, quadratic and cubic polynomial models (Tables S3–S6). We then calculated the associated parameters for each best model, such as P , R_m^2 and R_c^2 , as described earlier. After P adjustment, the predicted fitted values for the significant relationships were illustrated by the function ‘ggpredict’ in GGEFFECTS (v.0.14.1; Lüdecke, 2018). In addition, we used the function ‘manyglm’ in MVABUND (v.4.0.1; Wang *et al.*, 2012) to test how each OTU varied with the increasing time since fire, focusing on species with > 60% frequency. Nonmetric multidimensional scaling (NMDS) analyses were performed in VEGAN to illustrate the community shifts of total fungi, EcM fungi and saprotrophs along the time since fire gradient. To quantify the drivers behind fungal community shifts following wildfire and identify the effects of time since fire on fungal composition when accounting for the spatially nested design and soil heterogeneity, generalized dissimilarity modeling (GDM; Ferrier *et al.*, 2007) was performed using the GDM package (v.1.3.11; Manion *et al.*, 2018). Before GDM, Mantel tests ($P < 0.05$) were performed in VEGAN to identify candidate drivers from a full set of variables that included 27 soil properties, larch : birch ratio, geographic distance matrix and time since fire in the Oe horizon, and 31 soil properties, larch : birch ratio, geographic distance matrix and time since fire in the A1 and A2 horizons, respectively (Tables S7–S9). We quantified the contribution of

each variable to turnover in fungal communities in two ways. We used the ‘gdm.varImp’ function to estimate overall variable importance as the percentage change in deviance explained between models fitted with permuted and unpermuted variables. As such, we estimated the exclusive contribution of each primary driver to the total deviance explained as total deviance explained \times variable importance (%). We also used the sum of the I-spline coefficients for each variable as a measure of the magnitude of compositional variation along each gradient, with greater sums indicating relatively more turnover associated with that variable (Fitzpatrick *et al.*, 2013). The I-splines from the fitted GDM were extracted using the ‘isplineExtract’ function and plotted to show variation in the rate of compositional turnover of total fungi, EcM fungi and saprotrophs along the primary environmental gradient, holding all other covariates constant (Fitzpatrick *et al.*, 2013).

All data were tested for normality by Shapiro–Wilk normality test, as implemented in STATS 3.5.2 (R Core Team, 2018). When necessary, data (fungal biomass, richness, enzymes, soil properties, larch : birch ratio and time since fire) were logarithm- or square-root-transformed before the LMMs and GDM.

Results

Fungal biomass, richness and extracellular enzymes

Fungal biomass was significantly reduced by burning in the A1 horizon in dataset 1 (Table 2). Total fungal richness did not differ between burned and unburned plots in the Oe ($P_{adj} = 0.520$), A1 ($P_{adj} = 0.971$) and A2 ($P_{adj} = 0.678$) horizons, but EcM fungal richness was significantly lower in burned forests than in unburned controls in the Oe horizon (Table 2). There was no significant difference in EcM fungal richness among horizons ($P = 0.306$). The activity of β -glucosidase was also significantly reduced by burning in the Oe horizon (Table 2).

Fungal biomass and saprotroph richness were not affected by time since fire in any horizon, as analyzed by LMMs for dataset 2

Table 2 Results of linear mixed-effects models for the burning effects on fungal biomass, richness and enzymes with site as a random factor, based on dataset 1.

	Oe				A1				A2			
	P_{adj}	β_{fixed}	R_m^2	R_c^2	P_{adj}	β_{fixed}	R_m^2	R_c^2	P_{adj}	β_{fixed}	R_m^2	R_c^2
Fungal biomass	0.325	−15.97	0.115	0.430	< 0.001	−0.64	0.396	0.396	0.323	−0.24	0.116	0.430
Total fungal richness	0.520	−62.31	0.039	0.479	0.971	1.00	0.000	0.126	0.678	17.06	0.016	0.066
EcM fungal richness	< 0.001	−33.56	0.378	0.434	0.138	−0.25	0.195	0.535	0.179	−13.00	0.162	0.299
Saprotrophs richness	0.520	−17.25	0.038	0.676	0.971	0.38	0.000	0.009	0.853	1.50	0.001	0.001
β -glucosidase	0.011	−19.31	0.342	0.503	0.513	−0.24	0.072	0.404	0.589	−1.12	0.035	0.408
Laccase	0.093	−62.47	0.162	0.341	0.513	−17.15	0.035	0.408	0.452	−17.99	0.112	0.459
Mn-peroxidase	0.093	−2.57	0.129	0.172	0.513	−0.93	0.019	0.153	0.913	−0.05	0.000	0.000
Urease	0.397	−0.18	0.049	0.234	0.513	−0.28	0.054	0.658	0.589	−2.07	0.051	0.536
Acid phosphatase	0.974	0.01	0.000	0.731	0.513	0.63	0.020	0.020	0.369	−1.71	0.140	0.305

P_{adj} , P values after adjustment based on Benjamini–Hochberg procedure; β_{fixed} , estimate of fixed effect (i.e. estimate of burning effect); R_m^2 , the variance explained by fixed effects; R_c^2 , the variance explained by both fixed and random effects. Dataset 1 included the pairwise burned and unburned plots ($n = 32$ in each horizon). Significant P_{adj} values are in bold. Urease and acid phosphatase in Oe were log-transformed; β -glucosidase, urease, fungal biomass and EcM fungal richness in A1 were log-transformed; urease and fungal biomass in A2 were square-root-transformed and logarithm-transformed, respectively.

(Table S10). EcM fungal richness strongly increased with increasing time since fire in the Oe horizon ($\beta_{\text{fixed}} = 9.92$, $R^2_{\text{m}} = 0.407$; Table S10; Fig. 2), and total fungal richness showed a second-order polynomial fit with increasing time since fire in the A2 horizon ($\beta_{\text{fixed}} = 147.91$, $R^2_{\text{m}} = 0.274$; Table S10), namely, a strong decrease from 1 to 49 yr and a slight increase from 49 to 260 yr (Fig. 2). In the Oe horizon, variation in activity of β -glucosidase had a significant second-order polynomial relationship with time since fire, showing a strong increase within the first 14 yr after fire; Mn-peroxidase showed a third-order polynomial fit with increasing time since fire, namely, a decrease from 1 to 2 yr, an increase from 2 to 49 yr and a final decrease from 49 to 260 yr (Fig. 2). In the A1 and A2 horizons, the activity of urease varied significantly as a function of time since fire, matching the pattern of Mn-peroxidase in the Oe horizon (Fig. 2).

Fungal community composition

Based on dataset 1 (pairwise burned and unburned plots), the NMDS plot showed that soil fungal community composition significantly differed between burned and unburned plots, especially in the Oe horizon (Fig. 3). Of fungal classes and functional guilds, fire occurrence significantly enhanced the relative abundances of Eurotiomycetes ($\beta_{\text{fixed}} = 0.15$, $R^2_{\text{m}} = 0.411$), but reduced the relative abundances of Mucoromycetes ($\beta_{\text{fixed}} = -0.04$, $R^2_{\text{m}} = 0.169$), Saccharomycetes ($\beta_{\text{fixed}} = -0.01$,

$R^2_{\text{m}} = 0.321$) and Tremellomycetes ($\beta_{\text{fixed}} = -0.13$, $R^2_{\text{m}} = 0.230$) in the Oe horizon (Tables S11, S12). Moreover, response ratio analyses showed variation in the response of specific OTUs to wildfire (Table S13). In the Oe horizon, fire occurrence increased the relative abundances of nine OTUs, including five abundant OTUs belonging to *Penicillium* (Eurotiomycetes), three pathogenic fungal OTUs belonging to *Didymella boeremae*, *Gibberella tricineta* and *Ascochyta rabiei*, and one ErM fungal OTU – *Oidiodendron griseum*. Recent burning also suppressed 14 OTUs in the Oe horizon (e.g. two EcM fungal OTUs – *Cenococcum geophilum* and *Chloridium* sp., and two dark septate endophyte OTUs belonging to *Phialocephala fortinii*). In the mineral horizons, only 18 OTUs significantly responded to fire occurrence. In particular, the relative abundances in most of the fire-responding OTUs increased by burning in the A2 horizon, including one OTU of *Penicillium spinulosum*, one OTU of *Geminibasidium* sp., one OTU of *Phialocephala fortinii*, one OTU of *Solicoccozyma fuscescens*, one OTU of *Oidiodendron* sp. and four OTUs of unidentified Leotiomycetes or Ascomycota (Table S13).

In both burned forests and unburned controls, there were significant distance decay relationships for total fungi and saprotrophs in the Oe horizon. Relationships were much weaker in burned forests than in unburned controls, as shown by R^2 (Fig. 4a,g). Compared with the significant distance decay relationships of total fungi and saprotrophs in the A1 and A2

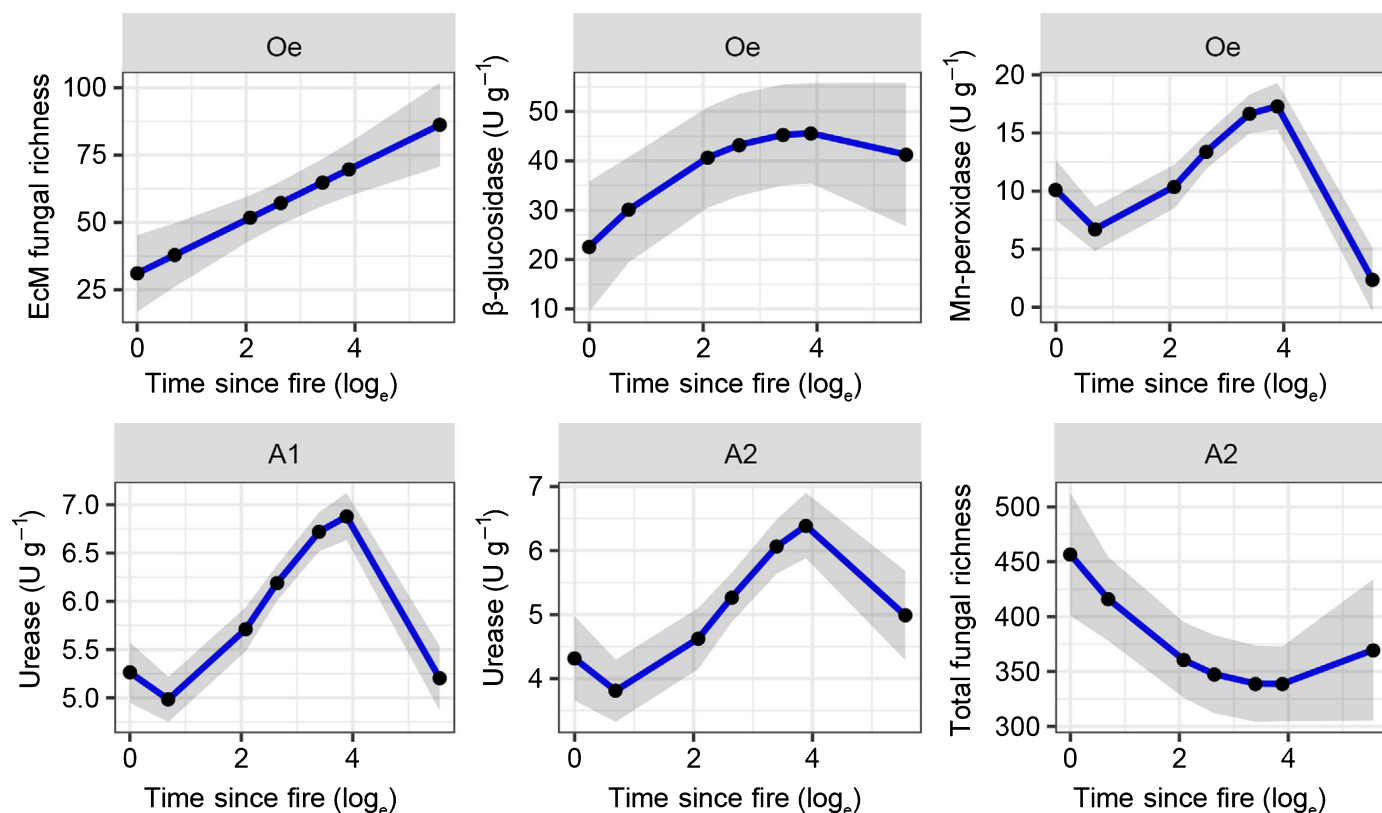


Fig. 2 The variation of fungal biomass, richness and enzymes along time since fire, as revealed by the marginal effects in linear mixed-effects models. Only the significant relationships are shown. The gray shaded areas show the 95% confidence interval of the fit. The details, including parameters, are summarized in Supporting Information Table S10. EcM, ectomycorrhizal.

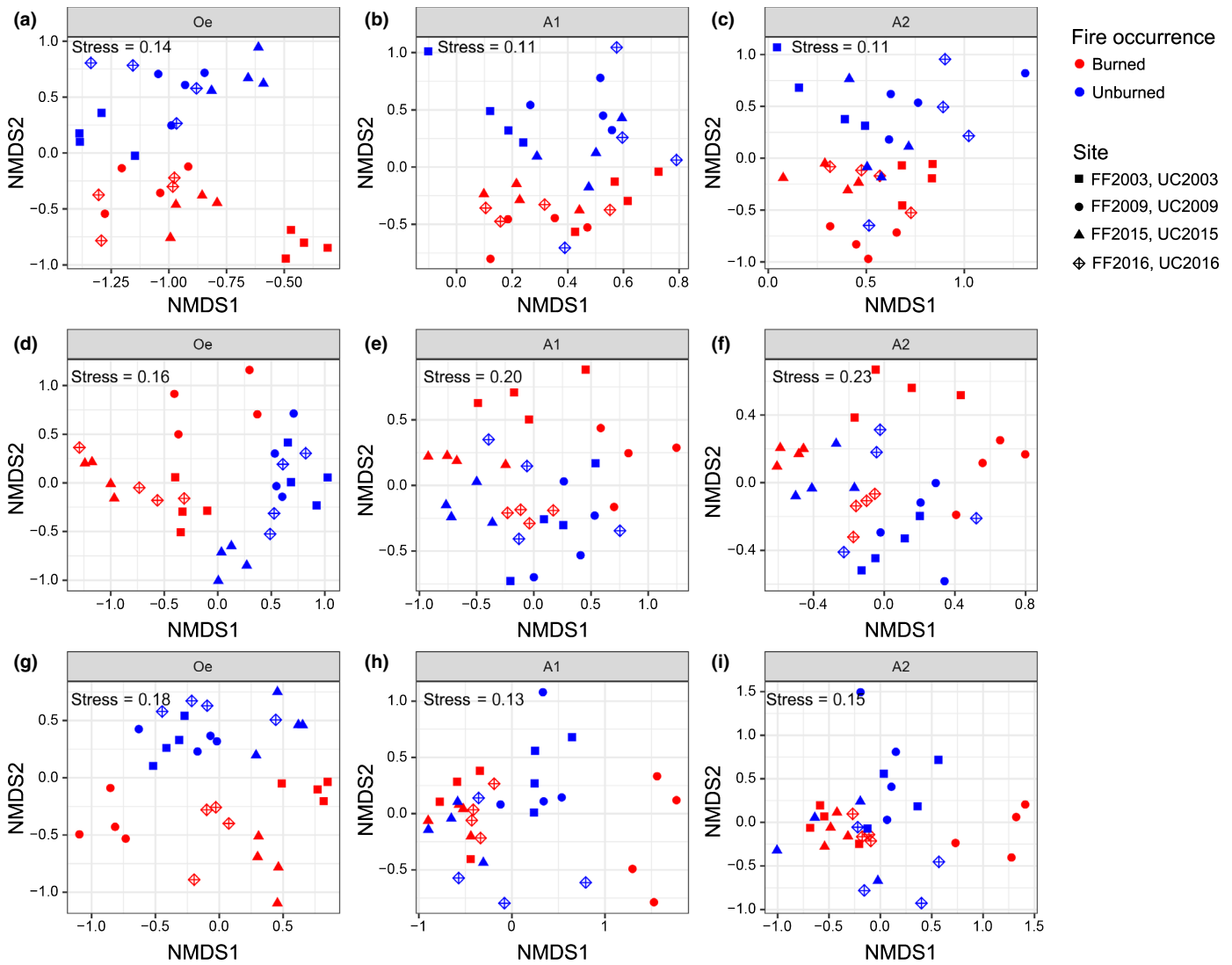


Fig. 3 The differentiation in community composition of total fungi (a–c), ectomycorrhizal (EcM) fungi (d–f) and saprotrophs (g–i) between pairwise (red) burned and (blue) unburned plots, with different sites distinguished by symbol. $n = 32$ in each horizon.

horizons of unburned controls, burned forests had no significant distance decay relationships in these two horizons (Fig. 4b–c, h–i). Similarly, there was a significant distance decay relationship for EcM fungi in the Oe horizon of unburned controls but not of burned forests (Fig. 4d). Furthermore, there were no significant distance decay relationships for total fungi at the within-site scale (< 1 km), regardless of whether it belonged to burned forests or unburned controls (Fig. S2a–c); however, the exception was that EcM fungi in the A1 horizon and saprotrophs in the Oe horizon in unburned controls had significant distance decay relationships at the within-site scale (Fig. S2e, g). At the among-site scale (20–80 km), total fungi, EcM fungi and saprotrophs across all soil horizons in burned forests exhibited an increase in similarity with increasing geographic distance (Fig. S3), namely, fungal community composition was more similar between more distant localities, which strongly coincided with variation in similarity of soil environment and time since fire with increasing geographic distance in recently burned forests (Fig. S4).

Based on dataset 2 (fire chronosequence), communities of total fungi, EcM fungi and saprotrophs varied considerably along the time since fire gradient across all soil horizons, and the variation seemed to be strongest in the Oe horizon (Fig. 5). With increasing time since fire, the relative abundances of Agaricomycetes, Geminibasidiomycetes and saprotrophs increased significantly, whereas the relative abundance of Eurotiomycetes monotonically declined in the Oe horizon (Figs S5 and S6; Tables S14 and S15). In addition, the relative abundance of Umbelopsidomycetes showed a U shape with increasing time since fire (Fig. S5), and that of ErM fungi showed a third-order polynomial fit with increasing time since fire in the Oe horizon (Fig. S6). In the A1 horizon, the relative abundances of lichenized fungi and OrM fungi showed a second-order polynomial fit with time since fire, strongly increasing during the late stage after fire (Fig. S6). In the A2 horizon, the relative abundance of Lecanoromycetes monotonically decreased with increasing time since fire, while that of Mortierellomycetes showed a time-lag

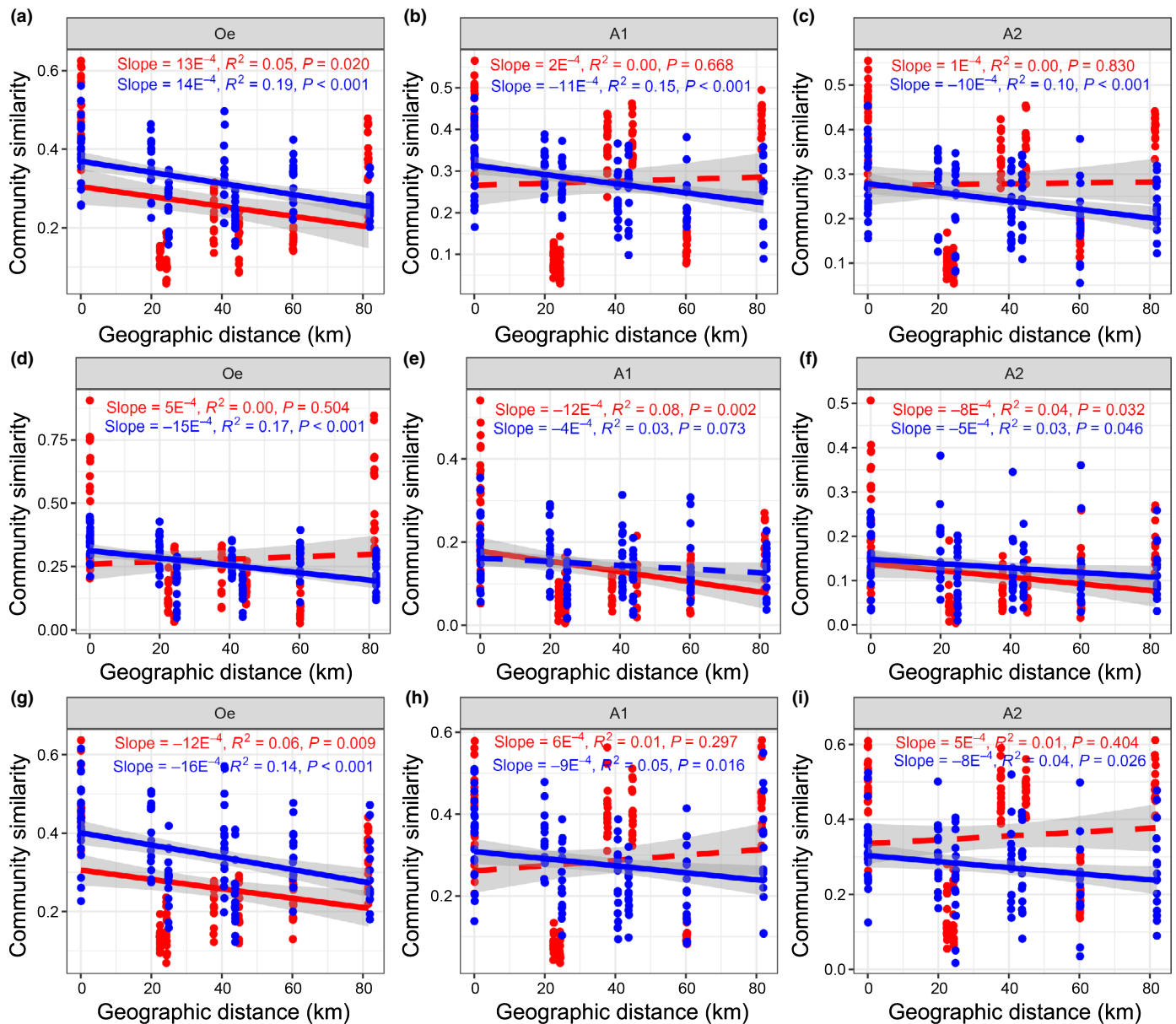


Fig. 4 Distance decay relationships of communities of total fungi (a–c), ectomycorrhizal (EcM) fungi (d–f) and saprotrophs (g–i) in pairwise (red) burned and (blue) unburned plots, respectively. Community similarity was represented by $1 - \text{Bray-Curtis dissimilarity distance}$. The gray shaded areas show the 95% confidence interval of the fit. $n = 32$ in each horizon.

increase after the 14th year post-fire (Fig. S5). In addition, the relative abundances of lichenized fungi and saprotrophs showed a U shape with increasing time since fire (Fig. S6). At the OTU level, we also observed several OTUs that significantly positively or negatively responded to time since fire (Table S16) and mostly in the Oe horizon. For example, six OTUs belonging to *Penicillium*, Eurotiomycetes and two pathogenic fungal OTUs belonging to *Didymella boeremae* and *Venturia hystrioides* significantly declined with increasing time since fire in the Oe horizon, and one dark septate endophyte OTU belonging to *Phialocephala fortinii* increased accordingly.

Overall, GDM explained a large proportion of the variation in community composition for total fungi, EcM fungi and

saprotrophs, with a total deviance explained of 71.4%, 54.9% and 66.7%, respectively (Table 3). Specifically, time since fire was the strongest driver of total fungal community shifts in the Oe horizon, exclusively explaining 5.0% of the deviance; C : N ratio was the strongest driver of total fungal community shifts in the A1 and A2 horizons, exclusively explaining 44.3% and 48.1% of the deviance, respectively. As was the case for total fungi, variation in EcM fungal community composition in the Oe horizons was primarily driven by time since fire, which exclusively explained 12.3% of the deviance. By contrast, available Mg and $\text{NO}_3^- \text{-N}$ were the strongest driver of EcM fungal community shifts in the A1 and A2 horizons, respectively. Similar to total fungi, variation in saprotroph community composition was also

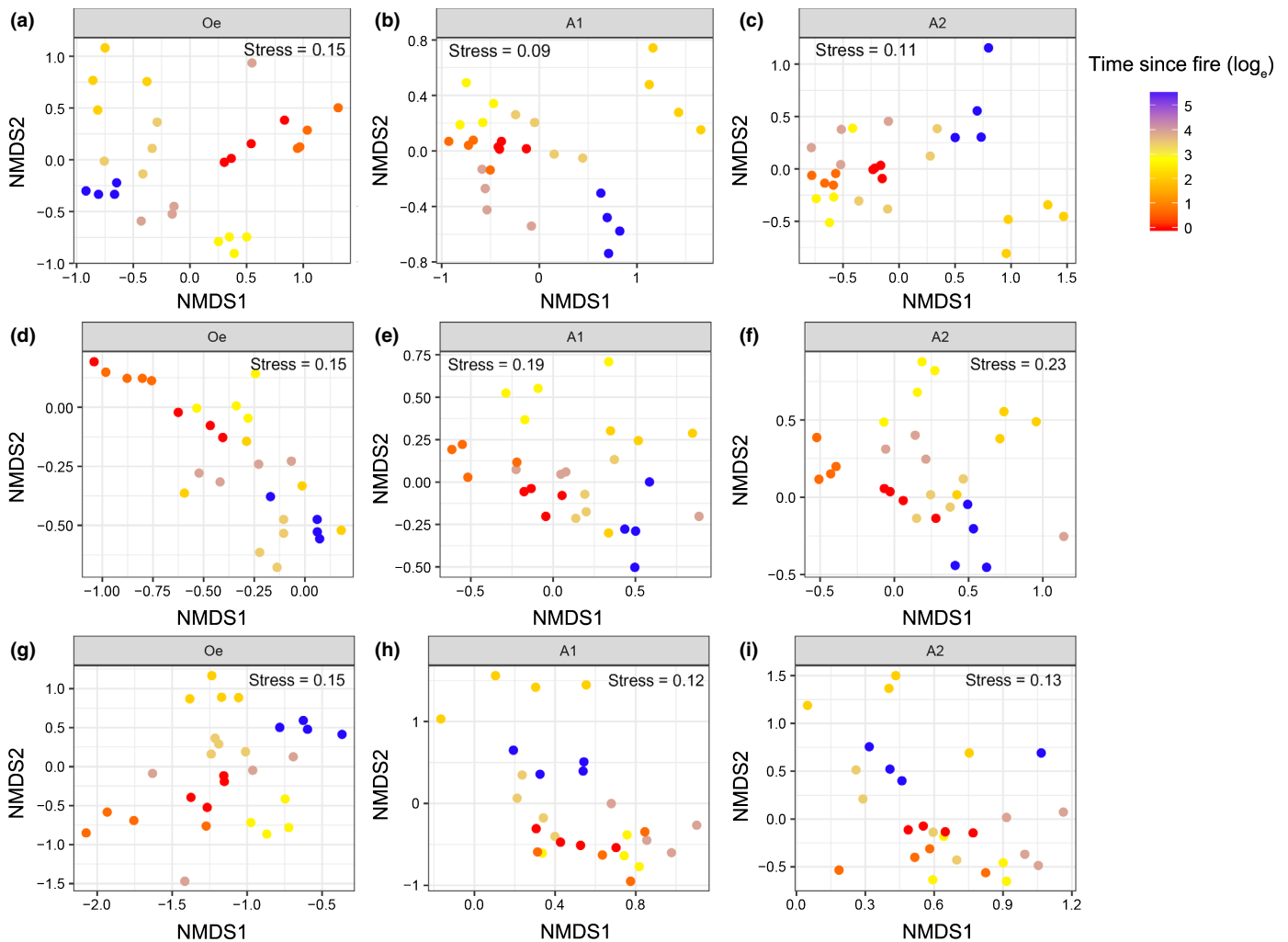


Fig. 5 Community shifts of total fungi (a–c), ectomycorrhizal (EcM) fungi (d–f) and saprotrophs (g–i) in a fire chronosequence. Time since fire (yr) was log-transformed and shown in a color gradient. $n = 28$ in each horizon.

strongly associated with C : N ratio in the A1 and A2 horizons, which exclusively explained 54.9% and 10.7% of the deviance, respectively. By contrast, geographic distance was the strongest driver of saprotroph community composition in the Oe horizon. Of note, time since fire also exclusively explained 8.6% of the deviance in saprotroph community shifts in the A2 horizon, which was the second strongest driver following C : N ratio in that horizon.

Based on best model-fitted I-splines of C : N ratio (Fig. 6), community compositional turnover of total fungi varied dramatically in the low C : N ratio interval and approached an asymptote after a C : N ratio of $c. 25$. In addition, there was distinct variation in patterns of community turnover for EcM fungi and saprotrophs along the C : N ratio gradient (e.g. EcM fungi: cubic functions fitted in Oe and A2; saprotrophs: quadratic functions fitted in Oe and A2). I-splines of time since fire in the best GDMs indicated that variations in community turnover were strongly guild- and horizon-dependent (Fig. 6). In the Oe horizon, communities of total fungi, EcM fungi and saprotrophs varied along the time since fire in a similar manner, but the variation magnitudes dramatically varied among fungal guilds

(coefficient of EcM fungi = 0.88; coefficient of total fungi = 0.38; coefficient of saprotrophs = 0.21). Saprotrophic fungal community turnover started from the first year after fire in the Oe horizon but from the third and 18th years after fire in the A1 and A2 horizons, respectively, after accounting for covariant environmental predictors and geographic distance. Conversely, time since fire explained more deviance of saprotroph community turnover in the deeper soil horizon in GDM (Oe, 1.3%; A1, 2.5%; A2, 8.6%; Table 3).

Discussion

Effects of fire occurrence

Here we found that burning effects on fungal richness were only pronounced for the EcM fungal guild and only so in the Oe horizon (Table 2), which was consistent with the findings in other recent studies (Salo & Kouki, 2018; Day *et al.*, 2019; Owen *et al.*, 2019). In the Oe horizon, the mean OTU richness of EcM fungi declined by > 40% in recently burned forests compared with that in unburned controls, and burning individually

Table 3 The drivers of fungal community shifts in a fire chronosequence determined by generalized dissimilarity modeling.

	Total fungi			EcM fungi			Saprotrophs		
	Coefficients	Variable importance	P	Coefficients	Variable importance	P	Coefficients	Variable importance	P
Oe									
Time since fire		Deviance explained = 74.1%		Deviance explained = 61.1%			Deviance explained = 69.5%		
(log _e)	0.38	6.8	<0.001	0.88	20.2	<0.001	0.21	1.8	0.028
Total Ca	0.36	4.5	<0.001	0.45	4.3	<0.001	0.44	5.3	<0.001
Geographic distance	0.26	4.3	<0.001	0.17	1.0	<0.001	0.41	9.8	<0.001
C : N ratio	0.48	2.9	<0.001	0.59	4.5	<0.001	0.47	2.6	0.009
Available P	0.20	2.5	<0.001	–	–	ns	0.46	8.0	<0.001
DON	0.29	2.3	0.009	0.59	6.0	<0.001	–	–	ns
Available Mn	0.25	1.8	0.037	0.37	3.4	0.009	–	–	ns
pH	0.34	1.7	0.018	–	–	ns	0.49	2.6	0.046
Available Mo	0.18	1.4	0.009	0.27	1.8	0.018	0.38	3.8	0.009
(log _e)									
SM	–	–	ns	0.28	2.0	0.009	–	–	ns
Total Mo	–	–	ns	0.88	8.4	<0.001	–	–	ns
A1									
	Deviance explained = 76.2%			Deviance explained = 52.0%			Deviance explained = 70.8%		
C : N ratio	0.82	58.1	<0.001	0.45	13.1	0.028	1.06	77.5	<0.001
pH	0.41	3.8	<0.001	–	–	ns	0.47	8.0	<0.001
Total K	0.28	3.7	<0.001	–	–	ns	–	–	ns
Available Mg	0.30	2.6	<0.001	1.19	38.1	<0.001	–	–	ns
(log _e)									
Geographic distance	–	–	ns	0.41	16.3	<0.001	–	–	ns
Time since fire	–	–	ns	–	–	ns	0.22	3.6	<0.001
(log _e)									
A2									
	Deviance explained = 64.0%			Deviance explained = 51.7%			Deviance explained = 59.9%		
C : N ratio	0.91	75.1	<0.001	0.58	11.2	<0.001	0.62	17.9	<0.001
Total Mg	0.44	16.8	<0.001	0.67	14.2	<0.001	–	–	ns
Available Ca	0.37	9.9	<0.001	0.45	11.8	<0.001	0.31	11.4	<0.001
NO ₃ ⁻ -N (sqrt)	–	–	ns	1.31	25.3	<0.001	0.50	5.1	0.009
Geographic distance	–	–	ns	0.22	4.2	<0.001	–	–	ns
Time since fire	–	–	ns	–	–	ns	0.23	14.3	<0.001
(log _e)									

DON, dissolved organic nitrogen; SM, soil moisture; NO₃⁻-N, nitrate nitrogen; log_e, natural log transformation; sqrt, square-root-transformation; ns, not significant. Fitted permutations = 109. n = 28 for each horizon. The strongest drivers are in bold.

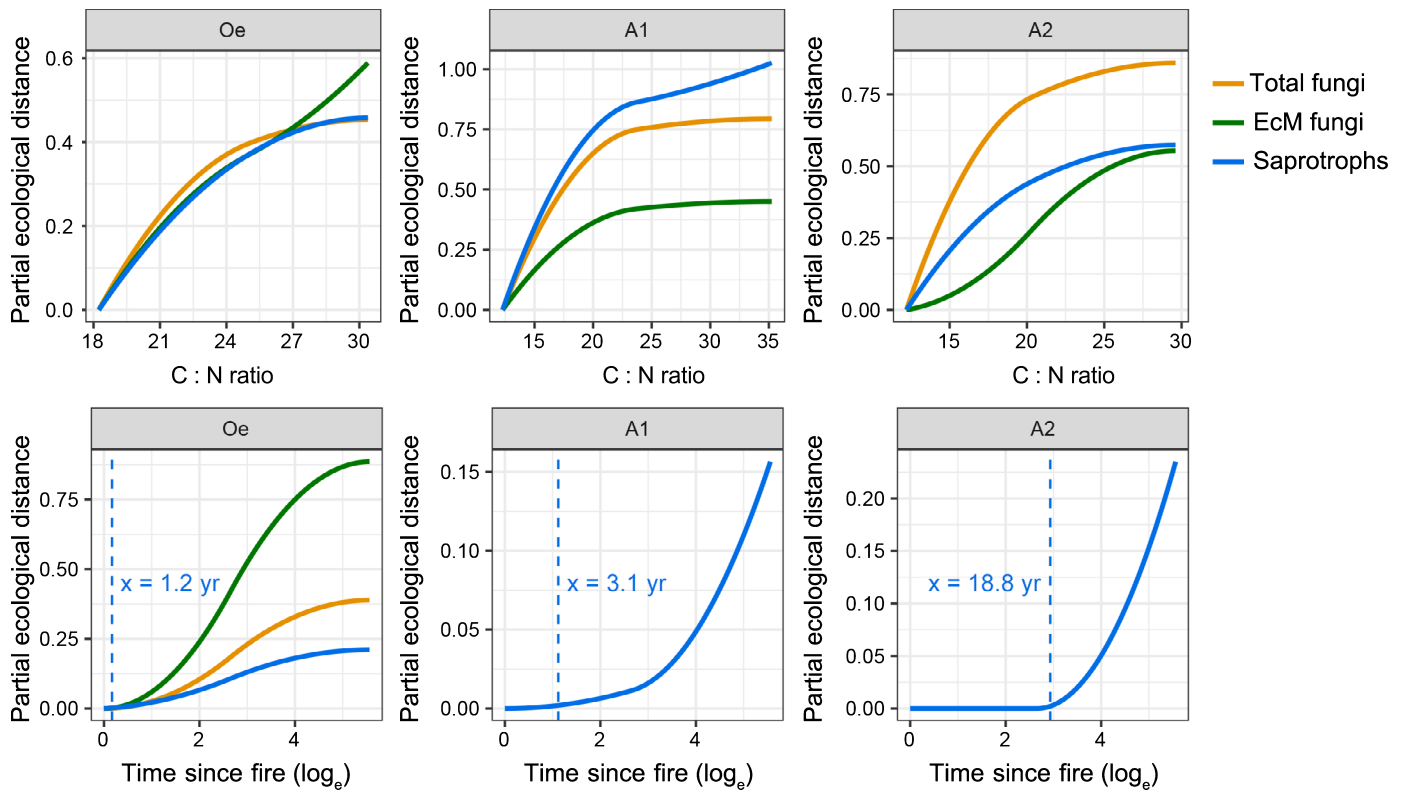


Fig. 6 The best model-fitted l-splines of carbon : nitrogen (C : N) ratio and time since fire showing the variation of fungal community turnover along the primary environmental gradient. In diagrams of time since fire, the thresholds of saprotroph community turnover are shown as the vertical dashed blue lines. Before the thresholds, saprotrophs community turnover was < 1% of the overall turnover. EcM, ectomycorrhizal.

explained 37.8% of the variation in EcM fungal richness (Table 2). The observed decline in EcM fungal richness may be related to the fire-induced mortality of EcM plant hosts (larch and birch), especially in the first few years after burning. In ponderosa pine forests of California, Glassman *et al.* (2016) reported significant reduction of EcM fungal richness in the soil spore bank within 1 month after fire. In the oak-pine woodland of Mississippi, EcM fungal richness significantly decreased in wildfire plots compared with that in prescribed burned plots and unburned plots; the activities of laccase, peroxidase and *N*-acetyl- β -D-glucosaminidase significantly decreased in wildfire plots accordingly (Rasmussen *et al.*, 2018). In this study, fire occurrence also significantly decreased the activities of β -glucosidase in the Oe horizon (Table 2), which may be attributable to the combined changes in quantity and quality of plant litter (Toberman *et al.*, 2014) and the reduced EcM fungal richness (this study; Phillips *et al.*, 2014). Additionally, burning is thought to affect the composition of soil organic matter that produces new C compounds resistant to oxidation and biological degradation (González-Pérez *et al.*, 2004). The aforementioned processes may correspond to declined turnover of soil organic matter, mitigating C losses during the early stage after fire. Specifically, the difference of soil properties between burned forests and unburned controls is shown in Notes S1 and Table S17.

Changes in community composition are the most frequently observed effect of wildfire on soil fungi (McMullan-Fisher *et al.*, 2011; Taudiere *et al.*, 2017). In this study, burning effects on

fungal composition (including EcM fungi and saprotrophs) were pronounced in upper soils (Fig. 3). In the Oe horizon, fire occurrence significantly enhanced the relative abundance of Eurotiomycetes, but decreased the relative abundances of Mucoromycetes, Saccharomycetes and Tremellomycetes (Table S11). Within the Eurotiomycetes class, five abundant OTUs assigned to *Penicillium* exhibited a significant positive response to fire occurrence and accounted for 7.56% of total sequences in the Oe horizon (Table S13). In a recent study on fungal communities and fire severity, Day *et al.* (2019) found that the relative abundances of several OTUs identified as *Penicillium* significantly increased with increasing fire severity, and some *Penicillium* species have been reported to form sclerotia to resist harsh environments and survive high temperatures in laboratory conditions (McGee *et al.*, 2006). In addition, we observed that the relative abundances in some pathogenic fungi OTUs increased by burning, and symbiotic fungi like dark septate endophytes and EcM fungi were suppressed in the Oe horizon (Table S13). Taken together, these results suggest that burning may have a negative impact on forest health and tree growth by the modification of specific plant-associated taxa in the short term.

Variations in a fire chronosequence

Consistent with the strong effects of fire occurrence on EcM fungal richness, EcM fungal richness monotonically increased with

time since fire in the Oe horizon, showing an increase from 37 OTUs per plot in the first year after fire to 81 OTUs per plot 260 yr after fire (Fig. 2). Visser (1995) found that mycorrhizal fungal richness significantly increased in a fire chronosequence from 6 to 122 yr after wildfire in jack pine stands of Canada. In pine forests of Europe, Franco-Manchon *et al.* (2019) showed that mycorrhizal fungal taxa were impacted more severely by wildfire than were saprotrophic taxa. The linear increase in EcM fungal richness can be assumed to be correlated with the recovery of above-ground plants (Day *et al.*, 2019; Duhamel *et al.*, 2019). In addition, total fungal richness showed a second-order polynomial fit with increasing time since fire in the A2 horizon, namely, a decrease from the first year after fire to the 49th year after year, and a slight increase after 49 yr (Fig. 2). As far as we know, this pattern has not been reported before and may indicate complicated dynamics of fungal richness that depend on long-term processes in deeper soils (Higuera, 2015). Different from the monotonic increase in EcM fungal richness, the activities of β -glucosidase and Mn-peroxidase significantly varied as a function of time since fire and with different nonlinear patterns in the Oe horizon (Fig. 2), suggesting some asynchronies between soil enzymes and fungal richness during forest recovery processes. In addition, the variation of soil properties with time since fire is shown in Notes S2, Table S18 and Fig. S7.

Shifts in community composition along the fire chronosequence were also pronounced in the Oe horizon (Fig. 5), coinciding with a significant increase in the relative abundances of Agaricomycetes and Geminibasidiomycetes, and a decline in Eurotiomycetes (Fig. S5). Of note, Agaricomycetes and Eurotiomycetes were the most abundant fungal classes, except for Leotiomycetes in the Oe horizon, accounting for 13.38% and 15.19% of total sequences, respectively. Previously, numerous studies have reported gradual replacement of Ascomycota by Basidiomycota in the fungal succession following wildfire (Holden *et al.*, 2013; Sun *et al.*, 2015; Reazin *et al.*, 2016). Hewitt *et al.* (2013) even proposed that late-stage fungi in a fire chronosequence might be K-strategists with a slow growth rate, large mycelia and long life span, characteristic of saprotrophic and EcM Basidiomycota (Vincenot & Selosse, 2017). Here, most taxa in Agaricomycetes belonging to the typical saprotrophic and EcM Basidiomycota (Martin *et al.*, 2016) exhibited monotonic increases in their relative abundance with increasing time since fire (Fig. S5). Corresponding to the increase in relative abundances of several *Penicillium* OTUs by burning, six OTUs belonging to *Penicillium* significantly decreased with increasing time since fire (Table S16). It implies that some pyrophilous fungal taxa like *Penicillium* in Eurotiomycetes may be gradually replaced along a fire chronosequence.

Drivers of fungal succession

Consistent with our hypothesis, we found significant covariation between edaphic variables and fungal communities following wildfire. In particular, C:N ratio was the strongest predictor of total fungi and saprotrophs across mineral soil horizons; C:N ratio was also retained as a significant factor in all GDM models

(Table 3). Previously, most studies have reported a strong effect of soil pH on fungal community composition under fire scenarios (Hewitt *et al.*, 2013; Day *et al.*, 2019); however, few studies have pointed out the pronounced role of C:N ratio in fungal community shift along a fire chronosequence (but see Clemmensen *et al.*, 2015). The soil C:N ratio reflects the state of nutrient availability and the extent of N limitation. Fungal taxa and guilds have different C and N requirements (e.g. some require more C sources, while others prefer more N; Grosso *et al.*, 2016; Smith & Wan, 2019), reflecting varied optimal nutrient stoichiometry (Cleveland & Liptzin, 2007).

The importance of spatial predictors in explaining fungal composition is in agreement with nearly all studies assessing geographical effects (Bahram *et al.*, 2013; Talbot *et al.*, 2014). Here, using pairwise comparisons of recently burned and unburned plots, we go further and demonstrate that burning can diminish distance decay relationships in fungal communities, especially in the mineral soil horizons (Fig. 4). At the within-site scale (< 1 km), only EcM fungal communities in the A1 horizon and saprotrophic fungal communities in the Oe horizon showed significant distance decay relationships in unburned controls but not in burned forests (Fig. S2). After removing the points of within-site variation, we were surprised to observe increases in community similarity with increasing geographic separation for total fungi, EcM fungi and saprotrophs across all soil horizons in burned forests at the among-site scale (Fig. S3). At the among-site scale, dissimilarities of fire histories (i.e. differences in time since fire) declined with increasing geographic distance in burned forests (Fig. S4); namely, fire histories were more similar between localities that are more distant. Accordingly, dissimilarities of fire-induced soil properties also declined with increasing geographic distance in recently burned forests (Fig. S4). Therefore, this spatial distribution pattern of fire histories primarily drives the lack of distance decay relationships in this study.

Last but not least, we demonstrate that fire history is an important factor that drives soil fungal distribution in this cold and fire-prone region. Time since fire was identified as the strongest driver of compositional turnover in total fungi and EcM fungi in the Oe horizon, exclusively explaining 5.0% and 12.3% of the deviance, respectively, whereas time since fire only explained 1.3% of the deviance of saprotroph communities in the Oe horizon (Table 3). Consistent with other studies (Franco-Manchon *et al.*, 2019), our results indicate that EcM fungal communities are more sensitive to fire history than saprotroph communities in the organic horizon, in terms of both composition and richness (Table S10). It is likely that the strong variation in EcM fungal communities as a function of time since fire is related to the recovery of above-ground vegetation (e.g. the increase in EcM tree biomass of larch and birch). Other factors, such as plant community succession following wildfire, may also drive soil fungal community shifts in a long-term fire chronosequence (Hewitt *et al.*, 2013; Clemmensen *et al.*, 2015). Community turnover of saprotrophs rapidly started from the first year after fire in the Oe horizon, and started from the third and 18th years after fire in the A1 and A2 horizons, respectively (Fig. 6). Although the slowest response of saprotroph community composition to wildfire was

observed in the A2 horizon, time since fire explained a large deviance (8.6%) of saprotroph community composition in this horizon, when accounting for other covaried environmental predictors (Table 3). The observed lag effect of time since fire cannot be detected by classical multivariate ANOVAs (Anderson & Walsh, 2013) and distance-based redundancy analyses (McArdle & Anderson, 2001), and provides a novel insight into the long-term successional trajectories for below-ground biota following wildfire, especially in the deeper soil horizons (Chang & Turner, 2019).

The main limitation of our study is the lack of information about fire severity. Cai *et al.* (2013) suggested that large burned patches in cold-temperate forests of the Great Khingan Mountains exhibited heterogeneity in burn severity owing to variations in site conditions and fuel loading. Indeed, fire severity is an important factor affecting fungal diversity and composition (Salo & Kouki, 2018; Day *et al.*, 2019). In particular, whether fire occurrence significantly affected soil fungal communities or not might be highly dependent on fire severity (Owen *et al.*, 2019). Nevertheless, we focused on the long fire history effects in this study. Another limitation was that we did not consider post-fire vegetation dynamics in the herb and shrub layers as well as the variation in living tree biomass. In this study, the relative abundances of ErM fungi and OrM fungi varied considerably with time since fire in the Oe and A1 horizons, respectively (Fig. S6). Their changes may be correlated with the different successional trajectories in Ericaceae and Orchidaceae plant communities following wildfire. In addition, the increase in EcM tree biomass with increasing time since fire may determine the significant changes in EcM fungal richness and communities in this study.

In conclusion, our study revealed significant effects of fire history on soil fungal composition across organic and mineral horizons in cold-temperate forests of the Great Khingan Mountains. Soil nutrient stoichiometry, time since fire and spatial factors together explained a large proportion of variation in fungal composition, which strongly depended on soil horizon and fungal guild. Communities (incl. richness) of EcM fungi were remarkably sensitive to fire history in the upper soil horizon, compared with those of saprotrophs. By contrast, time since fire explained significant variation in community composition of saprotrophs in the deeper soil horizon, and this effect was characterized by a time-lag – emerging 18 yr after fire. Considering the ecosystem services of soil fungi in forests, the observed strong context-dependent responses of soil fungi to wildfire will greatly benefit our understanding of ecosystem-level consequences of burning and trajectories of recovery.

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Author contributions

HC and JZ conceived the study. TY, XLin and PL did the sampling work. TY, XLin, YJ, X Liu, YN and YS performed the experiments and analyzed the data. TY, LT, MCF and HC wrote the manuscript. All authors read and approved the final manuscript.

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Fig. S1 Patterns of fungal community composition among soil horizons.

Fig. S2 Distance decay relationships of communities of total fungi (a–c), EcM fungi (d–f) and saprotrophs (g–i) at the within-site scale (< 1 km) in pairwise burned forests and unburned controls.

Fig. S3 Distance decay relationships of communities of total fungi (a–c), EcM fungi (d–f) and saprotrophs (g–i) at the among-site scale (20–80 km) in pairwise burned forests and unburned controls.

Fig. S4 The among-site variation in dissimilarities of time since fire and soil environment along geographic distance in burned forests.

Fig. S5 The variation of relative abundances in fungal classes along time since fire, as revealed by the marginal effects in linear mixed-effects models.

Fig. S6 The variation of relative abundances in functional guilds along time since fire, as revealed by the marginal effects in linear mixed-effects models.

Fig. S7 The variation of soil properties along time since fire, as revealed by the marginal effects in linear mixed-effects models.

Notes S1 The difference in soil properties between burned forests and unburned controls.

Notes S2 The variation of soil properties along the time since fire.

Table S1 Assignments of 5887 fungal OTUs to functional guilds in this study.

Table S2 The variation of soil properties, fungal biomass, richness and enzymes among soil horizons.

Table S3 The comparison between linear and nonlinear models for the effects of time since fire on fungal biomass, richness and enzymes with site as a random factor, based on corrected Akaike information criterion for small datasets.

Table S4 The comparison between linear and nonlinear models for the effects of time since fire on the relative abundances of fungal classes with site as a random factor, based on corrected Akaike information criterion for small datasets.

Table S5 The comparison between linear and nonlinear models for the effects of time since fire on the relative abundances of fungal guilds with site as a random factor, based on corrected Akaike Information Criterion for small data sets.

Table S6 The comparison between linear and nonlinear models for the effects of time since fire on soil properties with site as a random factor, based on corrected Akaike information criterion for small datasets.

Table S7 The Spearman's product-moment correlation (r) between total fungal composition (Bray–Curtis distance) and candidate variables in a fire chronosequence.

Table S8 The Spearman's product-moment correlation (r) between EcM fungal composition (Bray–Curtis distance) and candidate variables in a fire chronosequence.

Table S9 The Spearman's product-moment correlation (r) between saprotrophic fungal composition (Bray–Curtis distance) and candidate variables in a fire chronosequence.

Table S10 Results of linear mixed-effects models for the effects of time since fire on fungal biomass, richness and enzymes with site as a random factor, based on dataset 2.

Table S11 Results of linear mixed-effects models for the burning effects on the relative abundances of fungal classes with site as a random factor, based on dataset 1.

Table S12 Results of linear mixed-effects models for the burning effects on the relative abundances of fungal guilds with site as a random factor, based on dataset 1.

Table S13 The response ratios of soil fungal communities to fire occurrence in the Oe, A1 and A2 horizons at the OTU level.

Table S14 Results of linear mixed-effects models for the effects of time since fire on the relative abundances of fungal classes with site as a random factor, based on dataset 2.

Table S15 Results of linear mixed-effects models for the effects of time since fire on the relative abundances of fungal guilds with site as a random factor, based on dataset 2.

Table S16 The variation of each soil fungal taxa along time since fire, as revealed by model-based analysis of multivariate abundance data.

Table S17 Results of linear mixed-effects models for the burning effects on soil properties with site as a random factor, based on dataset 1.

Table S18 Results of linear mixed-effects models for the effects of time since fire on soil properties with site as a random factor, based on dataset 2.

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