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Crown-fire severity is more important than ground-fire severity in determining soil fungal community development in the boreal forest

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Abstract

1. Wildfire shapes the structure, dynamic and functioning of boreal forests. With predicted warmer and drier summers, increased incidence and intensity of crown-fires may affect plant–soil interactions with consequences for post-fire fertility and forest productivity.

2. We assessed how severity of crown- and ground-fire in boreal pine forests affected post-fire responses of soil fungal communities and their associated enzyme activities, and how variation in fire severity interacts with salvage (post-fire) logging in impacting soil fungi.

3. Crown fire-induced tree mortality had a stronger impact on fungal biomass and community composition than did ground-fire-induced loss of soil organic matter. Severe crown-fire led to replacement of ectomycorrhizal- and litter-associated fungi by stress-tolerant ascomycetes. Elevated activities of hydrolytic enzymes in burned areas were correlated with root-associated ascomycetes and moulds, suggesting opportunistic exploitation of labile organic substrates. Fire did not, however, increase the abundance of more potent basidiomycete decomposers in the organic layer, nor did it enhance organic matter oxidation by fungal peroxidases, indicating that the potential for major post-fire losses of carbon due to stimulated decomposition is limited. Rather, peroxidase activity was low in burned areas, likely reflecting the absence of ectomycorrhizal fungi. Post-fire salvage logging induced larger shifts in fungal communities in areas with low crown-fire severity.

4. *Synthesis.* Historically, boreal pine forests have been shaped by low-severity ground-fires. Our study highlights a risk that increasing occurrence of high-severity crown-fire as climate warms will have detrimental effects on mycorrhizal-mediated

functions that are pivotal for maintaining organic matter turnover, soil fertility and forest resilience.

1 | INTRODUCTION

Wildfire is a natural disturbance that shapes the structure, dynamics and functioning of boreal forests worldwide (Barnekow et al., 2008; Engelmark, 1999; Rogers et al., 2015; Wardle et al., 2003). Effects of fire are highly dependent on fire characteristics, which vary in space and time when forests burn (Keeley, 2009). A wildfire may predominantly act as a crown-fire in which most trees die, as a surface fire where only the understorey vegetation and the litter layer are burned, or as a severe ground-fire where a major part of the organic topsoil is consumed. The degree to which soil organic matter is combusted varies depending on fire intensity and duration. Historically, most fires in Fennoscandian boreal forests have been ground- or surface fires of low intensity, rather than stand replacing crown-fires (Rogers et al., 2015; Schimmel & Granstrom, 1997). Large trees (in particular *Pinus sylvestris*) usually survive these fires, and a significant portion of the organic layer is left intact below the uppermost charcoal layer (Schimmel & Granstrom, 1996). The fire regime of boreal forests is expected to be more severely affected by future changes in temperature and precipitation than that of temperate forests (Aakala et al., 2018; Drobyshev et al., 2014). As climate change continues, and summers become warmer and drier, both the frequency and magnitude of fires in coniferous forests are expected to increase (Krawchuk et al., 2009; Seddon et al., 2016). Between 2014 and 2019, Sweden has experienced the most serious wildfires in modern history in terms of burnt area and economic loss (Swedish Civil Contingencies Agency, https://ida.msb.se). Changes in fire type (crown- vs. ground- or surface-fire), intensity (the energy output from a fire), severity (the impact of fire measured as tree mortality and/or organic matter loss) and frequency may, potentially, alter the structure, productivity and successional dynamics of boreal forest ecosystems by shifting feedbacks between plants, microbes and the abiotic soil environment (Clemmensen et al., 2013, 2015; Johnstone et al., 2010).

The introduction of a large-scale forestry focused on timber production has changed the Fennoscandian forest landscape greatly over the last century, by introducing extensive clear-cutting, establishment of even-aged monocultures and efficient suppression of wildfires (Östlund et al., 1997; Siitonen, 2001; Svensson et al., 2018; Zackrisson, 1977). Furthermore, large forest fires usually involve ecosystem management after the fire such as salvage logging, which is the practice of logging trees following fire or other natural disturbances, with the objectives of retrieving wood and timber and facilitating rapid regeneration by planting. Still, salvage logging remains a highly controversial topic (Lindenmayer et al., 2012), in part because post-fire ecological succession is strongly influenced by the biological legacies remaining after natural disturbance, and the alteration of post-fire plant and fungal communities through salvage logging may detrimentally affect long-term forest development (Donato et al., 2006; Leverkus et al., 2018).

Effects of forest fires on fungal communities have been reported from several chronosequence studies (Holden et al., 2013; Sun et al., 2015; Yang et al., 2020) that mainly focused on the long-term development of communities after the disturbance. Variation in short-term responses in fungal communities related to reliable measurements of fire severity and post-fire logging and the underlying mechanisms remain to be investigated (Dahlberg et al., 2001; Holden et al., 2016; Reazin et al., 2016; Salo & Kouki, 2018). Fire can have both direct effects on soil fungi and indirect effects mediated by loss of vegetation and soil organic matter or changed soil pH and nutrient availability (Chen & Cairney, 2002; Day et al., 2019; Hart et al., 2005). Furthermore, consequences of post-fire salvage logging for fungal communities have been poorly studied, but are likely to depend highly on fire severity (Royo et al., 2016).

Responses of soil fungi to fires of different types and severities and to their post-fire management are fundamental to post-fire development of coniferous ecosystems because fungi are main drivers of organic matter dynamics and nutrient cycling (Sinsabaugh & Follstad Shah, 2012). In particular, production of extracellular oxidative enzymes by Agaricomycetes plays a key role in regulating organic matter turnover and nutrient cycling (Kyaschenko, Clemmensen, Karltun, et al., 2017; Stendahl et al., 2017). Ectomycorrhizal fungi are essential for post-fire establishment, growth and survival of trees by improving uptake of limiting nutrients and water (Smith & Read, 2008). Disturbance of the symbiosis may influence seedling establishment and stand structure (Duhamel et al., 2019; Nara, 2006; Simard, 2009) as well as long-term forest fertility and productivity (Clemmensen et al., 2013, 2015). After a fire, ectomycorrhizal fungi can persist on root tips of surviving trees, or as resistant structures, such as sclerotia or spores in the soil (Baar et al., 1999; Glassman et al., 2015). Following severe fires, or salvage logging, where most trees are killed or removed and the organic layer is largely combusted, fungal inoculum is reduced and recolonization depends on air-, soil- or animal-borne spores and inoculum residing deeper in the mineral soil (Dahlberg, 2002; Glassman et al., 2015; Stendell et al., 1999).

One of the main concerns about boreal wildfires are losses of carbon (C) and nitrogen (N) from the system. In addition to direct losses of C by combustion, fungal communities can contribute to

post-disturbance release of soil C via decomposition of organic matter and mineralization and leaching of N. Boreal forest soils are vertically stratified with an almost entirely organic layer (hereafter referred to as the 'mor layer', equivalent to the O-horizon) on top of the mineral soil. Different fungal guilds occupy distinct vertical niches in the mor layer, as a result of differences in C acquisition and competitive exclusion (Bödeker et al., 2016). While saprotrophs dominate in freshly deposited, cellulose-rich above-ground litter on the surface, mycorrhizal fungi dominate in the underlying, well-decomposed mor layer, where tree roots abound, as well as in the mineral soil (Lindahl et al., 2007). With direct access to host-derived carbohydrates, most ectomycorrhizal fungi have lost their capacity for decomposition during evolution (Kohler et al., 2015). Competitive exclusion of saprotrophic Agaricomycetes from the deeper organic horizon by ectomycorrhizal fungi may therefore hamper decomposition, resulting in accumulation of organic matter (Averill et al., 2014; Kyaschenko, Clemmensen, Karltun, et al., 2017). By disrupting the competitive dominance of ectomycorrhizal fungi in the mor layer, it is possible that severe crown-fires as well as salvage logging may trigger proliferation of saprotrophs and thereby accelerate decomposition of the remaining organic matter that was not directly combusted by the fire—the so-called 'Gadgil effect' (Averill & Hawkes, 2016; Fernandez & Kennedy, 2016; Gadgil & Gadgil, 1971, 1975; Kyaschenko, Clemmensen, Hagenbo, et al., 2017).

To assess impacts of crown-fire and ground-fire (including surface fire) severity and their interaction with post-fire salvage logging on fungal communities, we selected 25 stands exposed to fire of contrasting severities in a 13,000 ha area impacted by wildfire in 2014 in south-central Sweden (Figure 1). Within each of the burned stands, we established sub-plots subjected to salvage logging or without post-fire management. We evaluated these impacts by sequencing fungal ITS2 amplicons and measuring soil enzyme activities.

We hypothesized that:

Hypothesis 1 *Fungal communities would respond differently to crown- and ground-fire severity, with ECM fungi more influenced by crown-fire-induced tree mortality and saprotrophic fungi more responsive to ground-fire-induced soil organic matter loss.*
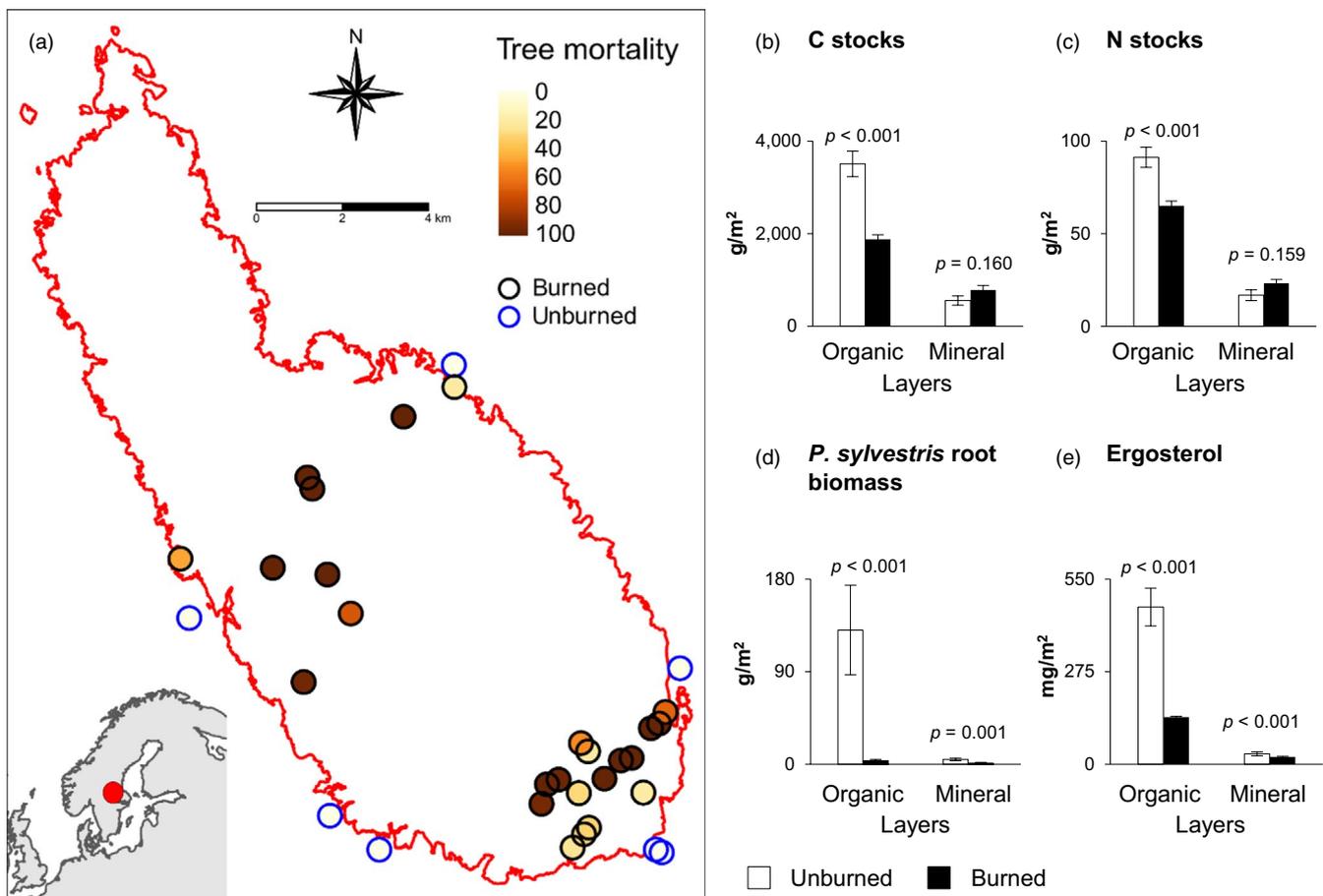
FIGURE 1 (a) Map of the 2014 wildfire in Västmanland, Sweden, showing the location of the 25 burned stands (black outer line) and the seven unburned reference stands (blue outer line). Circles corresponding to burned plots are coloured according to tree mortality, from yellow (low) to brown (high). $M \pm SE$ of (b) C stocks, (c) N stocks, (d) *Pinus sylvestris* root biomass per unit area and (e) fungal biomass per unit area measured as ergosterol in unburned stands and in burned (unlogged) stands in the organic mor layer and mineral soil. Comparisons between burned (unlogged) stands versus unburned stands in each soil layer were analysed by GLMs are indicated by *p* value. Data on *P. sylvestris* root biomass are in part extracted from Pérez-izquierdo et al. (2019)

Hypothesis 2 *Activities of soil enzymes involved in decomposition of post-fire soil organic residues would increase at higher tree mortality resulting from severe crown-fire, concurrent with relaxed ectomycorrhizal fungal competition and stimulation of saprotrophs.*

Hypothesis 3 *Post-fire salvage logging would induce larger shifts in fungal communities at lower crown-fire severity.*

In exploring these three hypotheses, our overarching goal was to provide insights into short-term changes of fungal communities with fire behaviour, crown-fire versus ground-fire, and its interaction with post-fire logging, to enable better prediction of ecosystem responses to future fire scenarios in Fennoscandian boreal forest subjected to climate change and post-fire management.

2 | MATERIALS AND METHODS

2.1 | Study sites and sampling

In July 2014, a fire outbreak in south-central Sweden (N 59°53′44″, E 16°11′27″), known as the Västmanland burn, affected more than 13,000 ha of boreal forest (Gustafsson et al., 2019). Before the fire, the forested area was dominated by commercial *Pinus sylvestris* plantation forest with stand ages between 40 and 60 years and a minor contribution of *Picea abies* and *Betula pendula*. The understorey consisted mainly of ericaceous dwarf shrubs (*Vaccinium vitis-idaea* and *V. myrtillus*) and mosses (*Pleurozium schreberi* and *Hylocomium splendens*). Within this area, we selected 25 burned stands with similar soil type, topographic position, management history (planted after harvest) and tree age (40–60 years). The stands (mean area 0.5 ha) represented a gradient in fire severity and were selected based on an active search supported by satellite photos, with the aim to maximize variation in both tree mortality and loss of below-ground organic matter. During stand selection, we made sure that stands affected by different fire severities were as evenly distributed throughout the study area as is possible (Figure 1). To test the interactive effects of salvage logging and fire severity on fungal communities, about half of the area of each of the 25 burned stands was logged immediately (a few days) after the fire, with a ground-based harvester as part of the fire rescue operation to prevent trees from blocking forest roads. Seven unburned stands, distributed around the study area within 500 m of the fire perimeter, were included as reference (Figure 1).

In May 2016, 22 months after the fire, we established paired circular plots with 10 m radius: one plot in the logged area and one plot in the unlogged area of each of the burned stands. In addition, we set up a similar plot in each of the seven unburned reference stands. In each of the unlogged burned plots, we recorded the proportion of trees that had been killed by the fire within the 10 m radius area. From four randomly placed 16 cm diameter circular areas, we collected dried and weighted litter that had fallen after the fire. We further assessed the compositional coverage of understorey vegetation in each unlogged plot in eight 0.5 × 0.5 m randomly located squares within the 10 m radius area as frequencies of species (presence/absence) across twenty five 10 × 10 cm partitions, and expressed the results as the average frequency in the eight squares.

We collected 25 soil cores (each 3 cm in diameter) at 5-meter intervals in a 20 × 20 m grid (centred on the 10 m radius area) in each of the logged and unlogged plots of the burned stands as well as in the unburned stands. The cores were split into the organic mor layer (including litter) and mineral soil (uppermost 5 cm, when present). We sampled the full mor layer and measured the depth in the sampling holes. Upon collection, we removed all green plant parts and lichens and pooled samples from the same horizon within each plot. In some cases, <25 samples (minimum 18 for both mor layer and mineral soil) were pooled, if the entire mor layer was consumed in the fire or if mineral soil was lacking (mor layer overlying rock). Overall, we collected two composite samples per plot (25 burned stands × 2 logging treatments +7 unburned stands = 57 plots × 2 horizons = 114 composite samples in total), which were freshly weighed and kept at −20°C. Aliquots were freeze-dried and ball-milled for further analyses.

2.2 | Soil analysis and enzymatic activities

To estimate remaining pools of C and N in the mor layer, we analysed each soil sample for total C and N content using an Isotope ratio mass spectrometer (DeltaV, Thermo Fisher Scientific) coupled to an elemental analyzer (Flash EA 2000, Thermo Fisher). We determined soil water content gravimetrically as the difference in soil weight before and after freeze-drying. We calculated the total C stock of the mor layer as the C content (%) × mor dry mass (g/m^2), based on the added area of the 25 sampling cores (in cases when less than 25 mor samples were collected, the full area of the 25 cores was still used to calculate C stocks). We measured soil pH in a 1:3 (w:v) soil-to-deionized water slurry using a 744 pH meter (Metrohm).

We extracted ergosterol from the soil to determine total fungal biomass (Kyaschenko, Clemmensen, Hagenbo, et al., 2017; Nylund & Wallander, 1992). We quantified root biomass (g/m^2) of *P. sylvestris* and *Betula* sp. through quantitative real-time PCR (qPCR) on soil DNA extracts using specific primers according to Pérez-izquierdo et al. (2019).

To evaluate if fungal decomposition is stimulated more by crown-fire of greater severity (i.e. a Gadgil effect), we measured activities of selected hydrolytic and oxidative enzymes in samples from the mor layer of non-logged plots (*n* = 32) following the protocol of Kyaschenko, Clemmensen, Hagenbo, et al. (2017). We targeted three hydrolytic enzymes involved in cellulose and hemicellulose degradation: cellobiohydrolase (CBH), β-1.4-glucosidase (BG) and β-1.4-xylosidase (BXD), and two involved in nutrient mobilization: β-1.4-N-acetylglucosaminidase (NAG) and acid phosphatase (aP). We also assessed Mn-peroxidase activity to estimate enzymatic organic matter oxidation by Agaricomycetes (Kyaschenko, Clemmensen, Karltun, et al., 2017), and determined inhibition by comparing activity

of a known amount of horseradish peroxidase (Sigma-Aldrich) added to each sample (after heating to 100°C to remove native activity) with the activity in buffer.

2.3 | Fungal community analysis

To test if fungal communities respond differently to severity of crown-fires than to ground-fires, we extracted DNA from 2 ml of fine-ground material from each organic and mineral soil sample, following the protocol of Clemmensen et al. (2016). We amplified ITS2 markers using the forward primer gITS7 (Ihrmark et al., 2012) and the two mixed reverse primers ITS4 (75%; White et al., 1990) and ITS4arch (25%; Kyaschenko, Clemmensen, Hagenbo, et al., 2017) elongated with unique identification tags (Clemmensen et al., 2016). We optimized dilution of DNA extracts and cycle numbers for each sample to minimize PCR bias (Castaño et al., 2020). PCR amplifications were conducted in 50 µl reactions containing 0.05–0.5 ng of genomic DNA, polymerase buffer (ThermoFisher), 0.75 mM $MgCl_2$, 0.2 mM of dNTPs, 0.5 µM of gITS7, 0.3 µM of ITS4, 0.1 µM of ITS4arc and 0.5 U/µl of DreamTaq polymerase enzyme (ThermoFisher). The PCR conditions were as follows: 94°C for 5 min, followed by 28–31 cycles of 94°C for 30 s, 56°C for 30 s and 72°C for 30 s, with a final step of 72°C for 7 min. We purified three pooled PCR replicates from each sample with Sera-Mag magnetic carboxylate modified particles (Hydrophobic; GE Healthcare) and mixed equal concentrations into two composite pools, which we cleaned with the QIAquick PCR purification kit (QIAGEN GmbH). Adaptor ligation and Pacific Biosciences sequencing (Castaño et al., 2020) were performed by SciLifeLab (NGI) using 3 Sequel SMRT cells.

2.4 | Bioinformatic analysis

We used the bioinformatics pipeline SCATA https://scata.mykopat. slu.se (Ihrmark et al., 2012) to analyse raw sequences. Sequences were filtered by quality (accepting reads with length longer than 100 bp, mean quality higher than 20 and single base quality higher than 3), screened for primers (90% sequence similarity required) and identification tags, and complementary reversed when necessary. Sequences were then compared pairwise for similarity, using USEARCH (Edgar, 2013), and clustered into species hypotheses (SHs, Kõljalg et al., 2013), using single-linkage clustering with a 1.5% threshold distance for sequences to enter a SH and equal penalties for mismatch and gap extension. We obtained a total of 485,766 PacBio sequences after quality filtering (33.8% omitted) and removal of plant- and other non-fungal sequences (34% of high-quality sequences) which were clustered into 3,313 global SHs. Samples were, on average, represented by 4,337 (766–12,595) sequences from 268 (85–604) SHs. To enable taxonomic identification of SHs, the UNITE reference sequence database (Kõljalg et al., 2013) was included in the clustering, but we

also annotated sequences manually based on comparisons with the UNITE and NCBI databases with at least 98% similarity required for species-level identification. We assigned SHs to functional guilds based on taxonomic identity or similarity to database sequences recorded from well-defined substrates (i.e. cleaned roots or plant leaves), using the following functional groups: ectomycorrhizal fungi, ericoid mycorrhizal fungi, root-associated ascomycetes (excluding known ericoid and ectomycorrhizal taxa, but including two basidiomycete *Sebacina* species that accounted for 0.7% of the guild), saprotrophic soil ascomycetes, saprotrophic litter ascomycetes, saprotrophic basidiomycetes, moulds (Mortierellales, Eurotiales, Mucorales and Hypocreales), yeast-like [Saccharomycetales, Cystofilobasidiales, Filobasidiales, Leucosporidiales, Sporidiobolales, Taphrinales, Tremellales, Chaetothyriales with *Exophiala* and *Cladophialophora* anamorphs and Dothideales (*Hormonema* and *Aureobasidium*)] and plant pathogens. In total, we were able to assign 80% of the sequences to SHs within known taxa and functional guilds, with the remaining 20% assigned to SHs with unknown identity and/or function. Sequence data are deposited at NCBI-SRA under the accession number PRJNA592420.

2.5 | Statistical analysis

To relate fungal communities to understorey plant communities, we created a 'vegetation index' based on the first axis of a correspondence analysis (CA) of frequencies of plant species (Figure S1). To assess collinearity, we calculated Pearson correlations among all explanatory variables, that is, the proportion of alive trees, mor depth, C:N ratio, C stocks, soil pH, *P. sylvestris* litter mass, *P. sylvestris* and *Betula* root biomass and post-fire understorey vegetation present in the burned (unlogged) plots (Table S1). To relate fungal communities and enzymatic activities to above-ground fire severity, we created an index from the first axis of a principal component analysis (PCA) of the proportion of dead trees, *P. sylvestris* root biomass (negative sign) and *P. sylvestris* litter (negative sign), which were all strongly correlated with each other (Figure S2). Likewise, we used the first axis of a PCA of mor depth, soil C stocks and C:N ratio (all with negative sign) as an index of ground-fire severity (Figure S3). These two indices were not significantly correlated among the burned plots ($r = -0.05$; $p = 0.813$), enabling independent evaluation of effects of crown-fire and ground-fire.

To obtain graphical representations of differences in fungal community composition, we applied detrended correspondence analysis (DCA) to the data from all unlogged stands and with, or without, the unburned stands included as a reference. SH abundance data were Hellinger transformed before the analyses to account for taxa with many zeros and low count numbers, as well as for variation in sequencing depth (Legendre & Gallagher, 2001).

To compare soil variables [i.e. *P. sylvestris* and *Betula* root biomass, relative abundance of fungal functional guilds, fungal richness (of SHs), fungal biomass and enzymatic activities in the mor

layer] between burned unlogged stands and the unburned reference stands, we used GLMs, with separate analyses for the mor and mineral soil layers. To account for differences in sequencing depth, the model of fungal richness included the square root of the total number of sequences obtained per sample as a covariate (Tedersoo et al., 2014). We performed a *t* test to evaluate whether Bray–Curtis pairwise fungal community distances between burned plots and the unburned reference stands (average community) differed between the mor layer and the mineral soil.

To identify representative fungal SHs associated with fire, we conducted Indicator Species Analysis (with SHs > 100 reads; *p* < 0.05) using the function multipatt in the INDICSPECIES R package (Cáceres et al., 2013).

To address hypothesis 1, we tested the effect of different aspects of fire severity (i.e. the crown-fire severity index, the ground-fire severity index, *Betula* root biomass, pH and the understory vegetation index) on fungal community composition in the mor layer, using canonical correspondence analysis (CCA) among the burned, unlogged plots. The significance of each explanatory variable was tested individually, and conditionally by forward selection. To evaluate the linear effects of crown-fire and ground-fire severity on relative abundances of functional guilds, fungal biomass and fungal richness, we used GLMs separately for the mor and mineral soil layers. Residuals of each model were tested for normality by plotting against fitted values, normal Q–Q plots and Shapiro–Wilk tests, and variables were log or square root transformed when needed.

To address hypothesis 2, we tested for linear effects of crown-fire and ground-fire severity on enzyme activities using redundancy analysis (RDA) of Euclidean distances of the enzymatic activity matrix across burned, unlogged stands. Linear effects on individual enzymes were tested by GLMs. Overall, correlations between fungal community composition and enzyme activities were assessed with Mantel tests using Bray–Curtis dissimilarity for fungal abundances and Euclidean distance for enzyme activities. Tests were performed with, and without, inclusion of the unburned reference stands. Correlations between enzyme activities and fungal community composition were visualized by DCAs and evaluated by GLMs with each enzyme as response variable and square-root-transformed relative abundances of fungal guilds as explanatory variables.

To address hypothesis 3, we evaluated the effect of post-fire salvage logging on fungal community composition, using CCA without permutation among logged and non-logged burned stands (to account for the split-plot design). Univariate effects on edaphic and fungal variables (in mor layer and mineral soil) were evaluated by employing general linear mixed models (GLMM) with 'stand' as random factor in the LMERTEST R package (Kuznetsova et al., 2017). To relate logging effects on the mor-layer fungal community to fire severity, we used GLMs to assess correlations of pairwise Bray–Curtis distances between logged and unlogged stands with the crown-fire and ground-fire severity indices of the unlogged stands.

We used R version 3.5.2 (R Core Team, 2018) and CANOCO 5 (Microcomputer Power) for all analyses.

3 | RESULTS

3.1 | Comparison of unlogged burned stands and unburned reference stands

Fire-induced tree mortality varied from 20% to 100% among the burned stands (Figure 1a), and *P. sylvestris* root biomass in the burned stands were only 1%–15% of that in the unburned reference stands (Figure 1d), whereas *Betula* root biomass did not differ between unburned and burned stands (Table S2). Soil pH was higher in the burned stands (average 4.7) than in the reference stands (average 4.0), while total C and N stocks in the mor layer were, on average, decreased by 46% and 29% relative to the unburned stands (Figure 1b,c), and C:N decreased from 38 in unburned stands to 29 in burned stands (Table S2).

Fungal biomass in the mor layer of burned stands was on average 41% of that in the reference stands when expressed as a concentration (i.e. μg ergosterol per g soil; Table 1a), and 28% of the reference stands when expressed on an area basis (i.e. mg ergosterol per m^2; Figure 1e). Fungal community composition in the mor layer differed between the burned stands and unburned reference stands (Figure 2a), with guilds differing in their responses (Figure 3a). Relative abundances of ecto- and ericoid mycorrhizal species were 84% and 52% lower, respectively, in burned stands than in reference stands, while relative abundances of saprotrophic soil ascomycetes and yeasts were 65% and 40% higher, respectively (Table 1a). However, taking the decreased ergosterol levels following burning into account, it is unlikely that the relative increase in these two groups corresponded to an absolute increase in biomass. A species assigned to the genus *Calyptrozyma* (Leotiomycetes) was particularly abundant in burned plots and kept as a separate guild in subsequent analysis because of uncertain functional properties (Table S3). Notably, the relative abundance of saprotrophic basidiomycetes was not significantly different between burned and unburned stands.

The number of SHs within most of the functional guilds was significantly lower (by 33%–74% depending on guild) in the burned stands, except for saprotrophic litter ascomycetes and yeasts, for which richness was not significantly different, and for saprotrophic soil ascomycetes, which had 52% higher richness (Table 1a). However, several species were significantly more abundant in burned stands, most of which were saprotrophs and typically pyrofilous, such as *Sordaria fimicola*, *Pholiota highlandensis*, *Pyronema domesticum* and *Geopixis carbonaria*. Most of the identified indicator species for unburned conditions were ectomycorrhizal, with a high representation of *Russula* and *Cortinarius* species (Figure 2a). However, two ectomycorrhizal species, a *Sphaerosporella* sp. and *Laccaria oblongospora*, appeared as strong indicators of fire, with no sequences detected in the unburned stands (Table S3).

TABLE 1 Results (*t* values with *p* values in brackets) of GLMs testing the response of fungal communities to fire and correlations with crown-fire and ground-fire severity indices in (a) the mor layer and (b) the mineral soil. Significant values (*p* < 0.05) are indicated in bold

	Burned versus unburned[a]	Correlation with fire severity[b]	
	t (*p* value)	Crown-fire severity	Ground-fire severity
(a) Mor layer			
Fungal biomass (µg ergosterol per g)	**−6.35 (<0.001)**	**−4.97 (<0.001)**	1.82 (0.083)
Fungal guilds (% of ITS amplicon)			
Ectomycorrhizal	**−7.77 (<0.001)**	**−3.84 (<0.001)**	0.25 (0.806)
Ericoid mycorrhizal	**−2.49 (0.016)**	**2.99 (0.007)**	0.16 (0.876)
Root-associated ascomycetes	0.087 (0.39)	−1.77 (0.092)	**−3.01 (0.007)**
Saprotrophic litter ascomycetes	0.01 (0.991)	**−6.32 (<0.001)**	0.38 (0.709)
Saprotrophic soil ascomycetes	**2.65 (0.013)**	−1.20 (0.245)	−0.33 (0.748)
Saprotrophic basidiomycetes	−1.8 (0.077)	−1.53 (0.141)	−1.32 (0.203)
Yeast-like	**2.8 (0.007)**	0.55 (0.587)	−0.75 (0.459)
Calyptrozyma	**5.61 (<0.001)**	**8.20 (<0.001)**	2.01 (0.058)
Mould	1.4 (0.166)	0.63 (0.535)	**−2.22 (0.038)**
Richness of fungal guilds (no of SHs)			
Total	**−4.25 (<0.001)**	**−6.61 (<0.001)**	−1.13 (0.271)
Ectomycorrhizal	**−9.16 (<0.001)**	**−3.21 (0.004)**	−0.85 (0.403)
Ericoid mycorrhizal	**−5.33 (<0.001)**	**−4.19 (<0.001)**	−1.54 (0.140)
Root-associated ascomycetes	**−3.67 (0.001)**	−2.08 (0.050)	−0.14 (0.891)
Saprotrophic litter ascomycetes	−0.78 (0.439)	**−6.41 (<0.001)**	−1.65 (0.115)
Saprotrophic soil ascomycetes	**6.14 (<0.001)**	**−2.33 (0.030)**	−0.48 (0.634)
Saprotrophic basidiomycetes	**−9.36 (<0.001)**	−1.87 (0.076)	−0.54 (0.593)
Yeast-like	−0.85 (0.402)	**−2.52 (0.021)**	−0.59 (0.563)
Mould	**−3.76 (<0.001)**	−1.24 (0.228)	0.63 (0.535)
(b) Mineral soil			
Fungal biomass (µg ergosterol per g)	**−6.49 (<0.001)**	**−2.39 (0.026)**	−0.83 (0.414)
Fungal guilds (% of ITS amplicon)			
Ectomycorrhizal	**−8.0 (<0.001)**	**−4.79 (<0.001)**	−1.19 (0.247)
Ericoid mycorrhizal	−0.57 (0.576)	−0.11 (0.911)	−1.61 (0.122)
Root-associated ascomycetes	−0.76 (0.455)	−0.50 (0.621)	**−2.39 (0.026)**
Saprotrophic litter ascomycetes	**2.74 (0.010)**	**−3.09 (0.006)**	−0.99 (0.333)
Saprotrophic soil ascomycetes	**5.39 (<0.001)**	−0.76 (0.458)	−1.01 (0.324)
Saprotrophic basidiomycetes	**2.75 (0.010)**	−0.12 (0.906)	0.47 (0.646)
Yeast-like	−0.16 (0.874)	**−3.00 (0.007)**	−0.30 (0.765)
Calyptrozyma	**3.78 (<0.001)**	**2.12 (0.045)**	**2.98 (0.007)**
Mould	**4.95 (<0.001)**	2.01 (0.057)	1.35 (0.191)
Richness of fungal guilds (no of SHs)			
Total	0.36 (0.719)	**−3.37 (0.003)**	0.19 (0.850)
Ectomycorrhizal	0.26 (0.799)	−1.30 (0.209)	0.30 (0.767)
Ericoid mycorrhizal	−0.60 (0.552)	**−2.72 (0.013)**	−0.31 (0.763)
Root-associated ascomycetes	−1.03 (0.314)	−1.70 (0.104)	−0.55 (0.592)
Saprotrophic litter ascomycetes	−1.17 (0.253)	**−2.90 (0.009)**	0.51 (0.613)
Saprotrophic soil ascomycetes	**2.97 (0.006)**	−1.24 (0.229)	0.56 (0.584)
Saprotrophic basidiomycetes	−1.02 (0.318)	**−2.78 (0.012)**	−0.87 (0.397)
Yeast-like	−1.06 (0.299)	−1.82 (0.084)	−0.95 (0.354)
Mould	−1.82 (0.079)	**−2.67 (0.015)**	−0.26 (0.801)

[a]Categorical differences between *n* = 7 unburned and *n* = 25 unlogged, burned stands.
[b]Correlations among *n* = 25 unlogged burned stands.

FIGURE 2 Variation in fungal community composition in the organic mor layer among (a) burned and unburned stands and (b) only burned stands, as visualized by sample (left) and species (right) plots of detrended correspondence analyses (DCA). The 59 most abundant taxa are shown. In the sample plots, circles are coloured according to the crown-fire severity index [from blue (low) to green (high)] and their size is inversely proportional to the ground-fire severity index (i.e. larger circles represent stands with more organic matter left). In the species plots, circle size is proportional to the average relative abundance of each species across all samples. DCA axes 1 and 2 explained 11.8% and 5.6%, respectively, of the total variation in (a), and 8.4% and 5.2%, respectively, of the total variation in (b). Names of species corresponding to the numbers are listed in Table S4
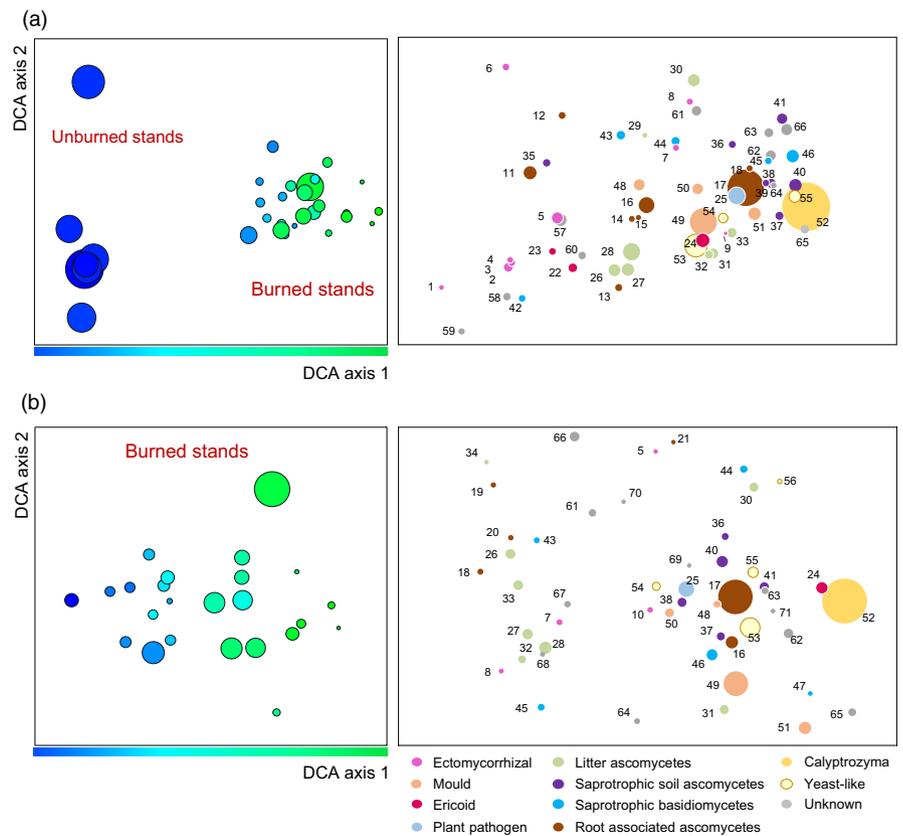
FIGURE 3 Variation in relative abundances of fungal guilds in the organic mor layer among (a) burned and unburned stands and (b) only burned stands, as visualized by sample (left) and species (right) plots of detrended correspondence analyses (DCA). In the sample plots, circles are coloured according to the crown-fire severity index [from blue (low) to green (high)] and their size is inversely proportional to the ground-fire severity index (i.e. larger circles represent stands with more organic matter left). In the species plots, circle size is proportional to the average relative abundance of each fungal guild across all samples. Vectors represent enzymatic activities (μmol gOM^{-1} s^{-1}) plotted in ordination space: CBH, cellobiohydrolase; BG, β-1.4-glucosidase; BXD, β-1.4-xylosidase; NAG, β-1.4-N-acetylglucosaminidase; aP, acid phosphatase; MnP, Mn-peroxidase. DCA axes 1 and 2 explained 67.1% and 5.2%, respectively, of the total variation in (a), and 63.4% and 3.5%, respectively, of the total variation in (b)
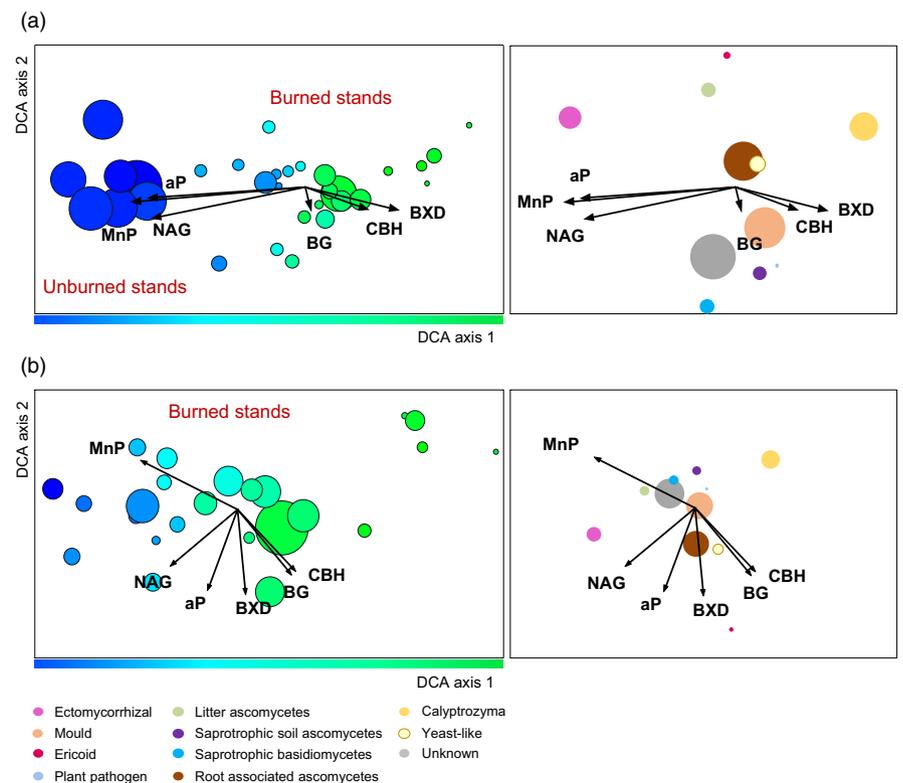
Activities of soil enzymes in the mor layer were correlated with fungal community composition across burned and unburned stands (Mantel test: $r = 0.50$; $p < 0.001$). The main effects of fire were an 83% reduction in MnP activity, a 64% reduction in NAG and a 69% reduction in aP, which mainly coincided with the loss of ectomycorrhizal fungi, and increases of one order of magnitude in activities of
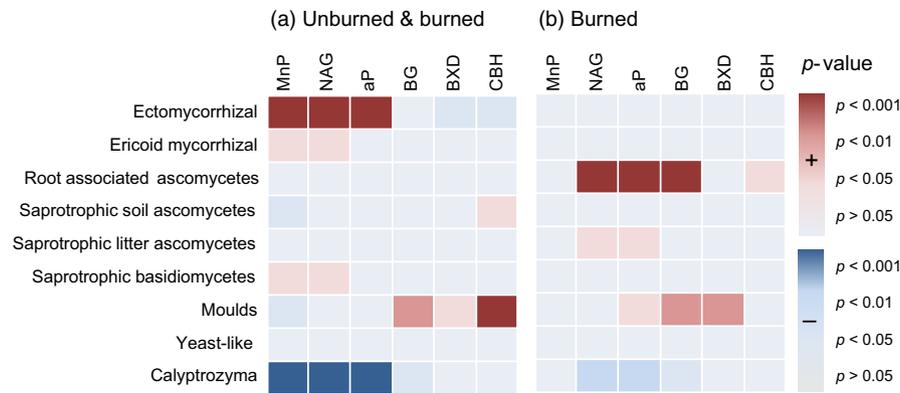
FIGURE 4 Heat map of correlations between relative abundances of different fungal functional guilds and enzymatic activities in the mor layer among (a) burned and unburned stands and (b) only burned stands, as analysed by GLMs. Red colour indicates positive correlation and blue negative correlations, with the intensity of colour increasing with the level of significance. CBH, cellobiohydrolase; BG, β-1.4-glucosidase; BXD, β-1.4-xylosidase; NAG, β-1.4-N-acetylglucosaminidase; aP, acid phosphatase; MnP, Mn-peroxidase

TABLE 2 Enzymatic activities in the mor layer ($M \pm SE$) of the burned ($n = 25$ burned, unlogged) and unburned ($n = 7$) forest stands used in this study. Values of t and p are derived from GLMs testing for comparisons between burned, unlogged stands versus unburned stands on enzymatic activities, t (p value). Significant values ($p < 0.05$) are indicated in bold

Enzyme activities (μmol gOM^{-1} s^{-1})	Burned	Unburned	t (p value)
Manganese peroxidase	0.06 ± 0.01	0.37 ± 0.09	**−6.59 (<0.001)**
N-acetylglucosaminidase	0.13 ± 0.01	0.37 ± 0.10	**−3.67 (<0.001)**
Phosphatase	0.39 ± 0.04	1.26 ± 0.31	**−3.85 (<0.001)**
β-glucosidase	0.40 ± 0.04	0.31 ± 0.08	0.72 (0.477)
Cellobiohydrolase	0.11 ± 0.02	0.03 ± 0.02	**2.82 (0.009)**
β-xylosidase	0.10 ± 0.02	0.02 ± 0.01	**2.99 (0.006)**

holocellulose hydrolysing enzymes (CBH and BXD), which correlated with the higher relative abundance of mould fungi (Figures 3a and 4a; Table 2).

Ergosterol levels were one order of magnitude lower in the mineral soil than in the mor layer, and significantly (70%) lower in the burned than in the unburned stands (30% lower in the mineral soil; Figure 1e). Fungal community composition in the mineral soil was clearly different from that in the mor layer (Figure S4) and significantly different between burned and unburned stands (CCA: variation explained, %=7.3; $p = 0.002$). Mineral soil communities were, however, less affected than mor-layer communities, as indicated by a significantly ($p = 0.001$) lower average Bray–Curtis distance between burned and unburned stands in the mineral soil (0.69 ± 0.01) than in the mor layer (0.75 ± 0.01). In the mineral soil, only the richness of saprotrophic soil ascomycetes was affected by fire, on average increasing from 5.6 to 11.4. Relative abundance of ectomycorrhizal fungi was 83% lower after fire while all the saprotrophic guilds but yeasts were relatively more abundant in the burned stands (Table 1b).

3.2 | Effect of crown- and ground-fire severity on fungal communities in unlogged stands

Among the burned plots, fungal biomass concentration in the mor layer was negatively correlated with crown-fire severity, but not with ground-fire severity (Table 1a). Fungal community composition

TABLE 3 Individual and cumulative effects of 'crown-fire severity index', 'ground-fire severity index', *Betula* root biomass, pH and an 'understorey vegetation index' on fungal community composition in the mor layer of burned stands ($n = 25$), as analysed by canonical correspondence analysis (CCA). Significant values ($p < 0.05$) are indicated in bold

	Individual effects		Cumulative effects[a]	
	Variation explained, %	p	Variation explained, %	p
Crown-fire severity	8.1	**0.005**	8.1	**0.002**
Ground-fire severity	4.9	0.135	4.9	**0.032**
Betula root biomass	5.1	0.073	4.7	0.090
pH	4.5	0.304	4.5	0.254
Understory vegetation index	5.6	**0.005**	4.4	0.344

[a]Forward selection of explanatory variables.

in the mor layer correlated significantly with both crown-fire and ground-fire severity, but the correlation with crown-fire severity was stronger (Figures 2b and 3b; Table 3). Fungal community composition was not significantly related to *Betula* root biomass or soil pH, and the correlation of fungal community with understorey

vegetation was only significant when crown-fire severity was not included in the model (Table 3). Relative abundances of ectomycorrhizal fungi and saprotrophic litter ascomycetes were negatively correlated with crown-fire severity, whereas opportunistic moulds and root-associated ascomycetes were negatively correlated with ground-fire severity. The relative abundances of ericoid mycorrhizal fungi, in particular *Pezoloma ericae* and *Calyptrozyma*, were positively correlated with crown-fire severity. Total fungal SH richness as well as richness of ectomycorrhizal fungi, saprotrophic litter and soil ascomycetes and yeasts were negatively correlated with crown-fire severity. Ericoid mycorrhizal fungal richness was negatively correlated with both crown- and ground-fire severity (Table 1a).

Activities of soil enzymes were correlated with fungal community composition among the burned plots (Mantel test: $r = 0.35$; $p = 0.001$). Hydrolytic enzyme activities were significantly and negatively correlated with ground-fire severity (RDA: $F = 7.4$; $p = 0.006$) and positively correlated with the relative abundance of moulds, root-associated ascomycetes and saprotrophic litter ascomycetes (Figure 4b). Enzyme activities were not significantly related to crown-fire severity (RDA: $F = 2.4$; $p = 0.096$).

In the mineral soil, responses of fungal guilds to fire severity were generally similar to the responses observed in the mor layer. The relative abundances of ectomycorrhizal fungi, saprotrophic litter ascomycetes and yeasts were negatively correlated with crown-fire severity, and saprotrophic soil ascomycetes were negatively correlated with ground-fire severity. *Calyptrozyma* was positively correlated with both crown- and ground-fire severity. The number of fungal SH in the mineral soil was negatively correlated with crown-fire severity (Table 1b).

3.3 | Effects of salvage logging

Across the 25 burned stands, logging decreased *P. sylvestris* root biomass by 34% and increased soil pH from 4.7 to 5 while no significant effects were observed on soil water content, C:N ratio or C and N stocks in the mor layer (Table S2) or on fungal biomass and total fungal richness in the mor layer and mineral soil (Table S5). However, logging impacted fungal community composition significantly in both horizons (CCA mor layer: pseudo-$F = 1.5$, $p = 0.002$; CCA mineral soil: pseudo-$F = 1.2$, $p = 0.002$). The main observed effects of logging on the fungal community were a 24% increase in the relative abundance of yeasts, whereas root-associated ascomycetes and saprotrophic litter ascomycetes in the mor layer decreased by 17% and 45%, respectively. Ectomycorrhizal fungal SH richness decreased by 25% in mor layer and 29% in the mineral soil (Table S5a). Pairwise Bray–Curtis distances of mor-layer fungal communities between logged and unlogged stands were negatively correlated with crown-fire severity (Figure 5), indicating a stronger effect of salvage logging on fungal communities when post-fire tree survival was high. No correlation was detected with ground-fire severity ($t = 0.38$; $p = 0.705$).
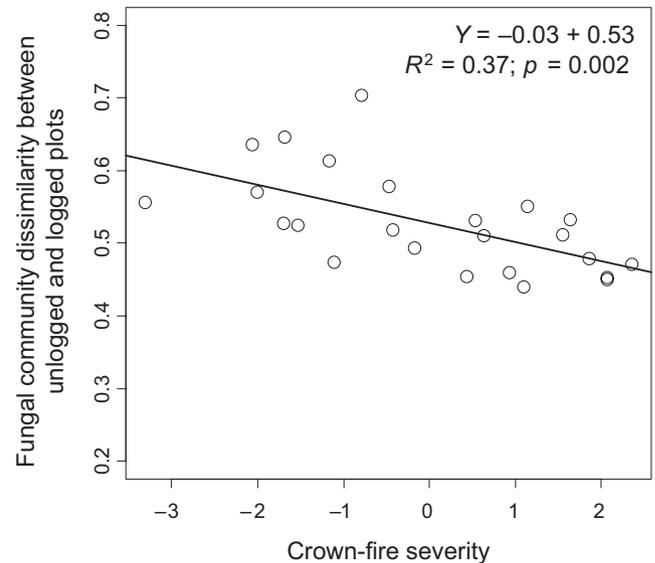
FIGURE 5 Correlation between Bray–Curtis pairwise distances of fungal communities in the organic mor layer of logged and unlogged burned plots from the same stand and crown-fire severity index as analysed by GLMs

4 | DISCUSSION

Most fires in Fennoscandian boreal forests have been reported to be ground- or surface-fires of low intensity that leave many surviving trees, rather than stand-replacing crown-fires (Schimmel & Granstrom, 1996). *Pinus sylvestris* has evolved particular traits, such as thick and non-flammable bark, that increase survival through low-intensity ground-fires (Rogers et al., 2015), and also grows high and self-prunes low branches, creating a gap between ground surface fuels and the canopy that reduces the onset of crown-fires (Keeley, 2012). In our study, we found that survival of *P. sylvestris* after fire played a key role in maintaining fungal biomass, diversity and community composition. As tree mortality and losses of soil organic matter deprived fungi of different sources of C substrates, crown-related and ground-related aspects of fire severity were associated with contrasting responses of the fungal community, as predicted in our first hypothesis.

The total fungal biomass as well as the relative abundance and richness of symbiotic ectomycorrhizal fungi declined with increasing crown-fire severity (Table 1). The ectomycorrhizal fungal genera *Cortinarius* and *Russula* that were abundant in the unburned stands were absent or of low abundance in all burned stands, in line with previous studies on fire chronosequences in boreal and hemi-boreal forests (LeDuc et al., 2013; Sun et al., 2015; Visser, 1995; Yang et al., 2020). In particular, *Cortinarius* species are specialized in the mobilization of organic N (Bödeker et al., 2014) and form large individuals that are likely to demand large quantities of host C. Moderate- to high-intensity fires convert part of the soil organic N to inorganic forms (Certini, 2005; Grogan et al., 2000), supposedly favouring disturbance-adapted ectomycorrhizal fungi with high affinity for inorganic N and lower C demand (LeDuc et al., 2013). In

post-fire chronosequences, ectomycorrhizal fungal richness has been found to increase linearly, concurrent with the recovery of above-ground vegetation (Duhamel et al., 2019; Hart et al., 2005; Yang et al., 2020).

The dominant role of ectomycorrhizal fungi in the soil community of boreal forests, and the sensitivity of these fungi to disruption of the below-ground C allocation by their host, is well recognized (Högberg et al., 2001; Sterkenburg et al., 2018). Although all stands in the present study were subjected to intense fire with severe effects on tree survival (root mortality always exceeded 85%), ectomycorrhizal fungi supported by trees in stands subjected to somewhat lower intensities of crown-fire could be of major importance for forest recovery (c.f. Nara, 2006). Most of the ectomycorrhizal fungal species that survived in burned stands in our study are common in fungal spore banks in boreal ecosystems (Glassman et al., 2015), although some of them (e.g. *Piloderma*) were highly abundant also in the unburned forests and could have survived as resistant propagules on the roots. *Suillus pseudobrevipes* was one of the most abundant colonizers in stands with higher tree survival, supporting previous studies that identified this wind-dispersed fungus as an opportunistic species and early post-fire colonizer (Glassman et al., 2015; LeDuc et al., 2013; Visser, 1995). Two ectomycorrhizal species, *Sphaerosporella* sp. and *Laccaria oblongospora*, recognized as pioneers in burned areas (Danielson, 1984; de Román & de Miguel, 2005), were not detected in the unburned stands but proliferated only after fire, probably from a sparse spore bank inoculum. In the mineral soil, the richness of ectomycorrhizal fungi was not significantly lower in the burned sites than in the unburned reference stands, and not related to tree mortality (Table 1), suggesting that the mineral soil may constitute a reservoir of ectomycorrhizal diversity, which may be of particular importance for post-fire seedling regeneration in stands where the ectomycorrhizal fungal communities in the mor layer are severely damaged (Dahlberg, 2002; Yang et al., 2020).

Ascomycetes colonizing freshly fallen litter from heat and smoke damaged trees thrived in stands with low crown-fire severity (Table 1; Figure 2). This observation partly contradicts the predictions of our first hypothesis that responses of saprotrophs to fire would be driven mostly by the loss of C in the mor layer. On the other hand, severe ground-fire, resulting in high losses of mor C and associated reductions in the quality of the remaining organic matter, reduced the abundance of both non-mycorrhizal root-associated fungi and moulds (Table 1), the latter of which live on easily accessible constituents of the organic layer (e.g. mycorrhizal mycelium). Activities of cellulolytic enzymes (BG, BXD and CBH) increased after the fire and were positively correlated with the increase in both these fungal groups (Figures 3b and 4b), and negatively related to ground fire severity. Higher abundance of root-associated ascomycetes after less severe ground-fire was also related to higher activities of N and P mobilizing enzymes (Figure 4b). Ascomycetes that establish as endophytes in roots have been proposed to possess significant decomposer capabilities and proliferate as saprotrophs on hydrolysable compounds from dead roots and mycelium following high tree mortality (Kohout et al., 2018; Lindahl et al., 2010).

However, exploitation of dead roots, mycelium and other resources that become available after fire is conditional on incomplete consumption of the organic layer, explaining the negative correlation of fungal opportunists and hydrolytic enzymes with ground-fire severity. Decomposition of organic material by opportunistic species after the fire will probably last only until easily decomposable compounds are depleted and is not likely to involve major losses of mor layer C from the system.

Burning that involves a combination of high crown- and ground-fire severity had a drastic effect on fungal biomass and community composition (Table 1; Figure 2). In severely burned stands, black yeasts (*Exophiala* and *Cladophialophora*) and a *Calyptrozyma* species dominated the DNA pool. Black yeasts inhabit stressful, oligotrophic niches that are often rich in aromatic compounds (Hoog et al., 2006). Interestingly, the same *Calyptrozyma* species was found to be the most abundant species after a big boreal forest wildfire in Canada (Day et al., 2019), as well as in oligotrophic polluted arsenic mines (Volant et al., 2016). These stress-tolerant, oligotrophic fungi are seemingly favoured by relaxed competition from other fungi after the fire and probably survive through living on residual charcoal that is normally enriched in aromatic hydrocarbons (Kaal et al., 2009; Prenafeta-Boldú et al., 2006).

Although some saprotrophic litter basidiomycetes were able to grow after fire, including species previously recognized as fire adapted (e.g. *Pholiota highlandensis*), this guild of particularly potent decomposers did not increase in relative abundance in response to the fire-induced decline of ectomycorrhizal fungi, even though most stands had large amounts (varying from 1 up to 69%) of C remaining in the mor layer (Table 1; Figure 2). Manganese peroxidases, which mediate the energy-demanding oxidation of lignin and other complex aromatic macromolecules, and thus control organic matter turnover in boreal forests (Kyaschenko, Clemmensen, Karltun, et al., 2017; Stendahl et al., 2017), were not stimulated by any aspect of fire-severity (Figure 3). Thus, we found little support for our second hypothesis that crown-fire-induced loss of ectomycorrhizal competition would trigger proliferation of saprotrophic basidiomycetes and thereby accelerate decomposition of the remaining, more recalcitrant organic matter, in analogy to the Gadgil effect (Fernandez & Kennedy, 2016; Gadgil & Gadgil, 1971, 1975). Sterkenburg et al. (2018) found that saprotrophic basidiomycetes were unable to exploit organic matter in the mor layer following removal of ectomycorrhizal fungi by root severing and proposed that extensive saprotrophic exploitation of the mor layer was prevented by a low-energy return from decomposition of material with a low proportion of hydrolysable compounds. Similarly, no increases in decomposition were observed after a bark beetle attack on a spruce forest (Štursová et al., 2014). On the contrary, Kyaschenko, Clemmensen, Hagenbo, et al. (2017) observed an increase in saprotrophic basidiomycetes after clear-cutting. These contrasting results bring into question the generality of the Gadgil effect and call for better understanding of context dependencies.

While our second hypothesis predicted that fire would stimulate decomposition of organic residues, we instead observed that

activity of Mn-peroxidases across all burned stands was 83% lower after burning compared to the unburned reference stands (Table 2; Figure 3a). Manganese peroxidases have evolved exclusively within the Agaricomycetes and are mainly produced by saprotrophs (Kohler et al., 2015) but also by some ectomycorrhizal taxa (Bödeker et al., 2014; Kyaschenko, Clemmensen, Hagenbo, et al., 2017; Talbot et al., 2013) with a supposed key role in the mobilization of organic N (Lindahl & Tunlid, 2015; Zak et al., 2019). A major reduction in Mn peroxidase activity during the first years after fire might restrict further post-fire losses of C from the soil, at least in the short term (c.f. Holden et al., 2013). Similarly, activities of hydrolytic enzymes that mobilize N (NAGs) and P (aP) from organic matter were also lower (~66%) in fire-affected stands, aligned with the lower relative abundance of ectomycorrhizal fungi (Table 2; Figure 3a). These findings support the idea that certain ectomycorrhizal fungi (e.g. *Cortinarius* spp.) actively drive organic matter decomposition and associated nutrient cycling in boreal forests (Lindahl & Tunlid, 2015) and that this function is largely lost after severe crown-fire. Similarly, Sterkenburg et al. (2018) found a major reduction in Mn peroxidase and NAG activities after disruption of mycorrhizal root links, whereas Kyaschenko, Clemmensen, Karltun, et al. (2017) (in boreal forest) and Entwistle et al. (2018) (in nemoral forest) instead found that high peroxidase activity and organic matter turnover were linked mainly to ligninolytic saprotrophs.

In line with our third hypothesis, post-fire salvage logging induced larger shifts in fungal communities in stands with more alive trees compared to stands where most trees were killed by crown-fire (Figure 5). As expected, logging mainly affected fungi that are dependent on relatively recently fixed C, including ectomycorrhizal fungi and saprotrophic litter ascomycetes. In turn, the dying mycelia of these fungi after logging probably induced the observed increase in yeasts that utilize these mycelia (Lindahl et al., 2010). Thus, salvage-logging tended to shift fungal communities of less severely burned plots towards those characteristic of plots that had been subjected to more severe fire (Purdon et al., 2004). Because survival of trees after fire is key in maintaining fungal biomass and diversity, avoiding or reducing the extent of salvage logging in areas with surviving trees could serve as an effective strategy to reduce the impact of the fire.

In conclusion, fungal biomass and diversity appear to be more sensitive to severe crown-fires than to the historically prevalent ground-fires, and our findings suggest that the survival of *Pinus sylvestris* after fire plays a key role in maintaining fungal communities. As crown-fires are expected to become more frequent with climate change (Drobyshev et al., 2014), our study highlights a risk of detrimental effect on mycorrhizal-mediated functions that are pivotal for maintaining organic matter turnover, soil fertility and forest recovery. However, although fire promoted opportunistic saprotrophs, we did not find clear evidence that the stimulation of fungal decomposition after wildfire would pose a major threat to post-fire carbon storage below-ground. Furthermore, our study provides new insights into ecosystem responses to future fire scenarios in the Fennoscandian boreal forest that are likely to result from climate change, and information to better perform policy-making decisions about the environmental consequences of salvage logging under contrasting burning scenarios.

AUTHORS' CONTRIBUTIONS

M.-C.N. conceived the project together with B.D.L., K.E.C. and D.A.W.; M.-C.N., G.G. and J.S. selected the forest stands and B.D.L., K.E.C., M.-C.N., and D.A.W. performed the data collection; L.P.-I. performed the laboratory work and data analyses; L.P.-I. wrote the first draft of the manuscript, and all authors contributed substantially to revisions.

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/1365-2745.13529.

DATA AVAILABILITY STATEMENT

Data were deposited in the Sequence Read Archive (https://www.ncbi.nlm.nih.gov/bioproject/PRJNA592420).

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SUPPORTING INFORMATION

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