Cite as: Day NJ, Dunfield KE, Johnstone JF, Mack MC, Turetsky MR, Walker XJ, White AL, & Baltzer JL (2019) Wildfire severity reduces richness and alters composition of soil fungal communities in boreal forests of western Canada. *Global Change Biology* 25: 2310-2324. DOI: 10.1111/gcb.14641

Wildfire severity reduces richness and alters composition of soil fungal communities in boreal forests of western Canada

Authors: Nicola J. Day[1], Kari E. Dunfield[2], Jill F. Johnstone[3,4], Michelle C. Mack[5], Merritt R. Turetsky[2], Xanthe J. Walker[5], Alison L. White[1‡], Jennifer L. Baltzer[1]

Addresses:

[1] Wilfrid Laurier University, Waterloo, Ontario, Canada

[2] University of Guelph, Guelph, Ontario, Canada

[3] University of Saskatchewan, Saskatoon, Saskatchewan, Canada

[4] University of Alaska Fairbanks, Fairbanks, Alaska, USA

[5] Northern Arizona University, Flagstaff, Arizona, USA

‡ Present address: Ontario Ministry of Natural Resources and Forestry, Peterborough, Ontario, Canada

Corresponding author: Nicola J. Day. Email: njday.ac@gmail.com. Phone +1 519 362 9855

Running head: Wildfire impacts on soil fungi

Keywords: disturbance; functional groups; global change; mycorrhizas; saprotrophs; understory; Taiga Plains

Abstract

Wildfire is the dominant disturbance in boreal forests and fire activity is increasing in these regions. Soil fungal communities are important for plant growth and nutrient cycling post-fire but there is little understanding of how fires impact fungal communities across landscapes, fire severity gradients, and stand types in boreal forests. Understanding relationships between fungal community composition, particularly mycorrhizas, and understory plant composition is therefore important in predicting how future fire regimes may affect vegetation. We used an extreme wildfire event in boreal forests of Canada's Northwest Territories to test drivers of fungal communities and assess relationships with plant communities. We sampled soils from 39 plots one year after fire and eight unburned plots. High throughput sequencing (MiSeq, ITS) revealed 2034 fungal operational taxonomic units (OTUs). We found soil pH and fire severity (proportion soil organic layer combusted), and interactions between these drivers were important for fungal community structure (composition, richness, diversity, functional groups). Where fire severity was low, samples with low pH had higher total fungal, mycorrhizal, and saprotroph richness compared to where severity was high. Increased fire severity caused declines in richness of total fungi, mycorrhizas, and saprotrophs, and declines in diversity of total fungi and mycorrhizas. The importance of stand age (a surrogate for fire return interval) for fungal composition suggests we could detect long-term successional patterns even after fire. Mycorrhizal and plant community composition, richness, and diversity were weakly but significantly correlated. These weak relationships and the distribution of fungi across plots suggest that the underlying driver of fungal community structure is pH, which is modified by fire severity. This study shows the importance of edaphic factors in determining fungal community structure at large scales, but suggests these patterns are mediated by interactions between fire and forest stand composition.

Introduction

While boreal forests are disturbance-adapted, historical disturbance regimes are changing, particularly towards intensified fire activity (Gauthier, Bernier, Kuuluvainen, Shvidenko, & Schepaschenko, 2015; Kasischke & Turetsky, 2006; Soja et al., 2007). Resilience relies on past ecological legacies that have shaped the structure and function of the system (Johnstone et al., 2016). For example, while fires often induce complete mortality of trees, many understory plants have buried rooting structures that are protected from fire to allow rapid resprouting (Greene & Johnson, 1999; Schimmel & Granström, 1996). There is evidence that shifting disturbance regimes have altered plant communities in boreal forests (Gauthier et al., 2015; Johnstone et al., 2010), but we know much less about how large fire events impact fungal communities (Holden, Rogers, Treseder, & Randerson, 2016; Treseder, Mack, & Cross, 2004). Given that up to 66% of soil carbon (C) in boreal forests can combust in large fire events (Rogers et al., 2014; Walker, Rogers, et al., 2018a), projected increases in fire frequency and severity and losses of soil organic matter are likely to have important impacts on microbial communities with flow-on effects on ecosystem functions, such as C cycling and storage (Kranabetter, Haeussler, & Wood, 2017).

Soil fungal communities are central for effective functioning of boreal forests through their roles in nutrient cycling as decomposers (saprotrophs; Allison & Treseder, 2011) and formation of mutualistic relationships (mycorrhizas; Smith & Read, 2008), for example. Mycorrhizal symbioses can determine growth and survivorship of individual plants (Bever, Platt, & Morton, 2012; Smith & Read, 2008), which play into the myriad of interactions that determine plant community structure. Many boreal forest fungi are fire-adapted or fire-dependent, possessing heat-resistant structures such as thick-walled sclerotia like those developed by morel mushrooms, *Morchella* (Dahlberg, Schimmel, Taylor, & Johannesson, 2001; Greene, Hesketh, & Pounden, 2010), or surviving in spore banks (Glassman, Levine, DiRocco, Battles, & Bruns, 2016) or buried roots (Hewitt, Bent, Hollingsworth, Chapin, & Taylor, 2013). However, fires can modify soil fungal community structure and induce fruiting bodies of ectomycorrhizal and saprotrophic fungi in boreal forests (Dahlberg et al., 2001; Greene et al., 2010; Treseder et al., 2004). Heat can also alter competitive dynamics among fungal taxa (Carlsson, Edman, Holm, & Jonsson, 2014). In addition, strong vertical stratification of soil fungi observed in some boreal forests (Clemmensen et al., 2015; Lindahl et al., 2007; Taylor et al., 2014) means that combustion of upper soil layers may

expose compositionally distinct communities from deeper soils. These fire-modified fungal communities could take many years to return to pre-fire structure, possibly impacting ecosystem functions, such as ectomycorrhizal colonisation (Treseder et al., 2004) and decomposition rates (Holden, Gutierrez, & Treseder, 2013). Understanding the impact of large fire events on soil fungal community structural attributes, such as richness, diversity, composition, functional groups, and relationships with plant communities, can provide insight on how boreal forests may be impacted by an altered fire regime.

Edaphic factors are important drivers of fungal community structure but are modified by fire. Soil pH (Högberg, Bååth, Nordgren, Arnebrant, & Högberg, 2003; Sun et al., 2015), moisture (Taylor et al., 2014; Toljander, Eberhardt, Toljander, Paul, & Taylor, 2006), and nutrient availability, particularly nitrogen (N; Allison & Treseder, 2011; Kyaschenko, Clemmensen, Karltun, & Lindahl, 2017), are correlated with fungal community structure in boreal regions and globally (Tedersoo et al., 2014). The denaturation of organic acids during fire increases soil pH (Certini, 2005), which may provide a short-term niche for some fungi in acidic boreal soils. Moreover, soil C and moisture changes with time since fire were correlated with soil fungal community structure in an Alaskan chronosequence (Holden et al., 2013). Thus, while we know that changes in edaphic factors induced by fire could impact fungal communities in boreal forests, the interactions and relative importance of various edaphic factors across stand types and along gradients of fire severity have not been explored.

Mycorrhizas, particularly ectomycorrhizas that are common in boreal forests, have been shown to decline after fire compared to other fungal groups in boreal forests (Holden et al., 2016; Sun et al., 2015). It may take up to 15 years for ectomycorrhizal colonisation to recover to pre-fire levels (Treseder et al., 2004). Moreover, species-specific interactions between plant and fungal taxa mean that differential survival of particular fungal taxa could greatly impact plant growth and survival and, hence, plant community structure (Bever et al., 2012; De Bellis, Kernaghan, Bradley, & Widden, 2006). For example, distinct ectomycorrhizal groups were identified on different plant species in Alaska just four years after fire (Bent, Kiekel, Brenton, & Taylor, 2011). The immediate effect of fire on mycorrhizal fungi could impact plant recovery after severe fires due to plant-soil feedbacks (Bever et al., 2012). Similarly, saprotrophs can have affinities to particular types of plant litter in boreal forests (Sterkenburg, Bahr, Brandström Durling, Clemmensen, & Lindahl, 2015;

Treseder et al., 2014). It can take up to 12 years for boreal soils to recover to pre-fire decomposition rates (Holden et al., 2013), even though saprotrophs are often abundant after fire (e.g., Sun et al., 2015). Recovery in key ecosystems following fire may therefore reflect succession in both fungal and plant community structure (Clemmensen et al., 2015; Taylor et al., 2010; Visser, 1995).

While we have some understanding of post-fire relationships between fungal communities and dominant canopy species in the boreal forest, we have little knowledge of relationships with understory plant communities, where the majority of plant diversity lies. Strong relationships between fungal and understory plant composition have been observed in Alaska (Taylor et al., 2014) and in Québec, where plant understory composition accounted for 25% of variation in fungal composition in a culture-based study (De Bellis, Kernaghan, & Widden, 2007). These relationships were found in the absence of recent fire but suggest that we may see high plant species richness if there is high mycorrhizal species richness due to the greater number of mutualists during the critical post-fire regeneration stage. Previous studies show that plant species establishing within the first few years of fire are likely to be retained in the system for at least the first decade of forest regeneration (Day, Carrière, & Baltzer, 2017; Johnstone et al., 2004), so the availability of mycorrhizas post-fire could have long-term implications for plant community structure. There is a need for greater understanding of the impact of large fire events on fungal communities and relationships with understory plant communities.

Here, we quantitatively assess drivers of fungal community structure and their relationships with regenerating plant communities one year following fire after the largest wildfire event recorded in boreal forests of the Northwest Territories of Canada, which occurred in 2014 (Canadian Interagency Forest Fire Centre, 2014). We focussed on subarctic forests in dominant and mixed stands of black spruce (*Picea mariana*) or jack pine (*Pinus banksiana*) in burned and unburned areas on the Taiga Plains. We address two questions: (1) What are the key drivers of post-fire fungal community structure, in terms of richness, diversity and composition of total fungi, mycorrhizas, and saprotrophs? We hypothesised that fire severity, measured as proportion soil organic layer (SOL) combustion, would have a greater impact on fungal community structure than edaphic factors or stand conditions due to mortality of many fungal groups with more severe burning (Bergner, Johnstone, & Treseder, 2004; Holden et al., 2016). (2) What is the relationship between mycorrhizal communities and understory plant communities? We hypothesised that the

composition of the post-fire fungal community would reflect the understory plant composition due to species-specific interactions between mycorrhizas and plants (Bent et al., 2011). Our study provides an improved understanding of the impacts of fire × environment interactions on fungal communities and the implications for associated understory plant community structure across a landscape of different stand types.

Methods

Study region

In 2014, boreal regions in the Northwest Territories (NWT), Canada experienced a large fire year with 2.85 million ha burning (Walker, Rogers, et al., 2018a). Our study focussed on the mid-boreal and subarctic forests of the Taiga Plains, which are undulating with limited variation in topography and elevation (Ecosystem Classification Group, 2009). These forests are dominated by black spruce (*Picea mariana*), while patches of jack pine (*Pinus banksiana*) and trembling aspen (*Populus tremuloides*) occur in well-drained areas that have thinner organic layers (Ecosystem Classification Group, 2009). All of these canopy species are mycorrhizal (Wang & Qiu, 2006). The closest weather station with consistent records is in Yellowknife, Northwest Territories, showing a mean annual temperature of -4.3°C and mean monthly temperatures ranging from -25.6°C in January to 17°C in July with annual precipitation of 289 mm (averages 1981-2010; Environment and Climate Change Canada, 2018).

Field methods

All field measures were taken during June-August 2015. Sampling occurred at 47 permanently-marked plots within 1 km of road or boat access between 60.94 and 64.15°N (Fig. 1); 39 in four 2014 burn scars and eight in forested areas that did not burn in 2014. We selected burned plots from a larger set of plots to represent gradients of fire severity, moisture, and stand type (see Walker, Rogers, et al., 2018a; Walker, Baltzer, et al., 2018). Plots that did not burn in 2014 were comparable to the burned plots in terms of stand type and moisture class (Table S1). The minimum

distance between plots was 100 m; distances between burned and unburned plots ranged from 3-12 km.

At each plot, we established two 30 m parallel transects 2 m apart running south to north (total plot area was 60 m^2). Soil was collected for analysis of fungal communities at 0, 12, and 24 m along the east transect for a total of 141 samples (47 plots × 3 samples per plot). Samples were collected to a depth of 5 cm; most were from the organic horizon (112 samples) except where there had been complete combustion to expose mineral soil (29 samples). Each sample was approximately 10 × 10 × 5 cm and sampling equipment was disinfected with Clorox wipes between samples. Soil samples were kept on ice in the field, frozen within five days, and shipped to the University of Guelph, Ontario, Canada.

The identity of each vascular plant species was determined in 1 m^2 square quadrats adjacent to each soil sample. The most frequently occurring plant species one year following fire were dwarf scouring rush (*Equisetum scirpoides*), conifer seedlings (jack pine and black spruce that are difficult to distinguish in the first year of growth), and *Salix* spp. Detailed information on understory plant communities is provided in White (2018) and Table S2.

We measured fire severity as the proportion soil organic layer (SOL) combusted. This was calculated using measurements in the 2014 burned plots and calibrated using measurements from plots that had no record of burning in the NWT (prior to 1965). Full details and data are available (Walker, Baltzer, et al., 2018; Walker, Rogers, et al., 2018a, 2018b). Briefly, at 10 points along the two transect lines at regular intervals we measured residual SOL depth in burned plots and total SOL depth in unburned plots. We obtained up to 20 measurements of SOL depth per plot by also measuring points beside trees in the surrounding plot area to account for potential heterogeneity (see Walker, Rogers, et al., 2018a; Walker, Baltzer, et al., 2018). In burned black spruce-dominated plots, burn depth was based on measurements of the height of adventitious roots above the residual SOL on ten trees per plot. In plots where only jack pine was present, burn depth was based on moisture class-specific estimates of residual SOL compared to SOL depth in unburned plots. Proportion SOL combusted was calculated using these estimates of pre-fire SOL depth and burn depth (Walker, Baltzer, et al., 2018). All unburned plots were assigned proportion SOL combusted of zero. All burned plots experienced some SOL combustion at the plot-level even where burning was patchy (Table S1).

We identified every tree in the 60 m^2 plot area to assess stand composition. In the burned stands, fallen trees killed by fire were included in this census in order to estimate pre-fire stem densities for each species. Stand type in burned and unburned stands was characterised as the proportion of total stems that were black spruce in the plot area; since there were only two dominant tree species, this metric provides a continuous variable representing a gradient between the dominance of black spruce to that of jack pine.

We estimated stand age to indicate the minimum time since fire prior to 2014. In boreal forests there is often near complete mortality of trees and rapid germination of tree seedlings in the few years following fire (Greene & Johnson, 1999), meaning that stand age provides a good estimate of the time since the previous fire and may be considered a measure of fire return interval. We collected basal tree discs or cores as close to the ground as possible but above the root collar of five trees of each dominant conifer species representing the dominant size class in the plot. Stand age was estimated by preparing and sanding tree cores and discs using standard dendrochronology techniques to count rings for an estimate of minimum tree age (Cook & Kairiukstis, 1990). Detailed decisions on stand age are in Walker, Baltzer, et al. (2018).

Lab methods

We measured a range of edaphic factors known to influence soil microbial community composition. We used standard soil assays to measure pH, total C, and total N (Hendershot, Lalande, & Duquette, 2008). For DNA extraction, frozen soil samples were thawed at 4°C for up to three days to mitigate dramatic changes that may have occurred if rapidly thawed. Thawed soils were homogenised prior to subsampling. We followed the standard protocol from the MoBio Powersoil Kit (MoBio Laboratories, Solana Beach, CA, USA) using 250 mg of starting material except that the first incubation with the proprietary protein precipitant (solution C2) was increased to 10 minutes to optimise purity. DNA was stored at -20°C and shipped to the Canadian Centre for Computational Genomics - Montréal Node for Illumina (MiSeq) sequencing using primers ITS1F (Gardes & Bruns, 1993) and ITS2 (White, Bruns, Lee, & Taylor, 1990).

A nested PCR approach was used to prepare the samples for MiSeq. The first PCR attached the MID tags and amplified fungal DNA, and the second PCR added barcodes and adapters. The initial PCR was run in 25 µl volumes with 2.5 µl buffer (10X with $MgCl_2$), 10 mM

deoxyribonucleotide triphosphate, 1.5 μM of each primer, and 1 U Hotstart Taq polymerase. The PCR consisted of 96°C for 15 minutes, 33 cycles at 96°C for 30 s, 58°C for 30 s, 72°C for 60 s, followed by 2°C for 10 min. The product was diluted 1/100 for the second PCR in 20 μl volumes at 95°C for 10 minutes, followed by 15 cycles at 95°C for 15 s, 60°C for 30 s, 72°C for 60 s, and 72°C for 3 min. DNA concentrations were measured by Qubit and standardized to equal concentrations prior to sequencing.

Bioinformatics processing

Bioinformatics processing was performed by McGill University and Génome Québec Innovation Centre (Montreal, Québec, Canada). Several quality control steps were applied to 14,841,340 paired-end reads (MiSeq Reagent Kits v2). Paired-end reads <250 bp were discarded. Reads with an average quality score <30, reads with more than 10 undetermined bases (Ns), and reads with 10 or more low-quality nucleotides (scores <20) were discarded. Contaminants (adapters, barcodes, PhiX) and MID tags were removed and flanking regions of SSU and 5.8S were trimmed using Duk v. 2013-04-15 (http://duk.sourceforge.net/). At this point, only paired-end reads were retained. A total of 13,424,680 paired-end reads passed the control quality steps and were assembled using FLASH (Magoc & Salzberg, 2011). A total of 10,469,018 sequences (77.98%) were successfully assembled. Initial clustering at 100% similarity removed duplicate sequences, followed by clustering at 99% similarity in DNACLUST (Ghodsi, Liu, & Pop, 2011). Clusters with fewer than three sequences were discarded and chimeras were removed using UCHIME *de novo* followed by UCHIME reference (Edgar, Haas, Clemente, Quince, & Knight, 2011). Resulting clusters were clustered once more at 97% similarity to obtain operational taxonomic units (OTUs) in DNACLUST and clusters containing fewer than three sequences were removed for a total of 6,251,059 sequences packed in 4,182 clusters.

OTUs were assigned to taxonomic lineages by classifying each cluster with the Ribosomal Database Project (RDP) with 100 bootstraps (Wang, Garrity, Tiedje, & Cole, 2007), using UNITE v.01.12.2017 (Kõljalg et al., 2013; USDA, 2017). This was run using “AssignTaxonomy” in DADA2 v.1.8.0 (Callahan et al., 2016) run in R v.3.5.1(R Core Development Team, 2018). Taxonomic names were assigned at each taxonomic level where RDP classifier bootstrap confidence values were greater than 0.8. Taxonomic labels below genus were not assigned due to

these relatively short sequences that make it difficult to accurately delineate to species level. We further removed three samples with very low reads (<5000 sequences) and rare OTUs that occurred in two or fewer of these 138 samples. The resulting dataset had a mean of 42,999 reads per sample (range 4,316-191,316) and 266 OTUs per sample (range 62-627). Sequences were deposited to DDBJ/ENA/GenBank under the accession KBZF00000000 of BioProject PRJNA447993.

We used the FUNGuild database to assign each OTU to probable functional groups (guilds) based on published literature (Nguyen et al., 2016). Further analyses of functional groups only retained OTUs in taxa with confidence levels of 'probable' or 'highly probable' in guild assignments. We pooled all mycorrhizas that were detected (ectomycorrhizas, ericoid mycorrhizas, and orchid mycorrhizas) and calculated the number and abundance of OTUs in each functional group in each sample.

Statistical analyses

All analyses were conducted in R version 3.5.1 (R Core Development Team, 2018) with packages where specified. Data arrangements, basic calculations, and graphs were performed using package tidyverse (Wickham, 2017) with extensions in egg (Auguie, 2017).

What are the key drivers of fungal community structure?

Each sample was randomly subsampled to 4,300 reads (retained 593,400 of 6,096,239 reads; "rarefy", package vegan). To assess drivers of fungal composition, we ran a permutational analysis of variance (PERMANOVA; Anderson, 2001) on the modified Raup-Crick dissimilarities with variables fire severity, soil pH, soil C:N, stand age, stand type, and interactions fire severity × pH and fire severity × C:N. The Raup-Crick metric reduces the effect of α diversity on β diversity by estimating probabilities that sampling units have OTUs in common, with the probability of an OTU occurring being proportional to its observed frequency and then tested against null models through permutation (Chase, Kraft, Smith, Vellend, & Inouye, 2011). We restricted the 999 permutations within plots to account for the nested sampling design (function "adonis", package vegan; Oksanen et al., 2017). We visualised fungal community structure using principal co-

ordinates analysis (PCoA) on 138 samples specifying the modified Raup-Crick dissimilarity on presence-absence data ("raupcrick", package vegan).

We further investigated the underlying structure of fungal communities by decomposing β diversity (β_{sor}: Sorensen dissimilarity) into its two components to infer underlying drivers of fungal biodiversity in these samples: nestedness (β_{nes}) and turnover (β_{sim}), where $\beta_{sor} = \beta_{nes} + \beta_{sim}$ (Baselga, 2010). High nestedness occurs where OTU composition of low richness samples are subsets of species from higher richness samples (*sensu* Baselga, 2010). We expect high nestedness if fire is the main underlying driver of fungal communities because the fungi present after the fires would comprise a subset of the pre-fire community. Alternatively if nestedness is low and turnover is high, this suggests that fire is less important for the underlying structure of fungal communities ("beta.multi", package betapart; Baselga & Orme, 2012).

We used six response variables as further metrics to understand drivers of fungal communities: diversity and richness of total fungal OTUs, mycorrhizas, and saprotrophs. Here, OTU richness is the number of unique fungal OTUs in a sample and we used Shannon's diversity ("diversity", package vegan). We developed five candidate generalised linear mixed-effects models in the information-theoretic framework to explicitly test hypotheses of the effects of burn, stand conditions, edaphic factors, and burn × edaphic factors on richness and diversity (Table 1; Supplementary Methods; Burnham & Anderson, 2002; Anderson, 2008). For each response we also tested the null model with no predictors, and the full model with all predictors (Anderson, 2008). Plot was a random effect in all models to account for the spatially nested sampling. Models with plot nested within burn scar showed qualitatively similar results so we display the plot-only random effect models for parsimony. Richness models were run as a negative binomial response ("glmer.nb", packae lme4 Bates, Maechler, Bolker, & Walker, 2015) and diversity models were run with a continuous response ("lmer", package lme4). All predictors were uncorrelated ($r < 0.5$) and were centred and standardised prior to inclusion.

The order of models of the candidate set was determined by AICc. This is used to calculate the weight (i.e., the probability) of each model in the candidate model set for the data, provided by w_i (Anderson, 2008). We used model-averaged parameter estimates and unconditional confidence intervals to assess the importance of each predictor using ("modavg", package AICcmodavg Mazerolle, 2017). This calculates the weighted mean coefficient value across all models, where the weight is w_i; variables were considered important if the 95% confidence interval did not cross

zero (Anderson, 2008). Estimates from this function can be biased away from zero (Cade, 2015) but were unable to use the shrinkage version due to our interaction terms. Therefore, we further assessed relationships by calculating model-averaged predictions ("modavgPred", package AICcmodavg; Mazerolle, 2017). Marginal R^2m (fixed effects only) and conditional R^2c (fixed and random effects) were calculated for each model ("r.squaredGLMM", package MuMIn; Nakagawa & Schielzeth, 2013; Barton, 2017). All models were run with 137 samples across 47 plots due to omission of one sample with high soil C:N having undue leverage. Results were qualitatively the same when an outlier in total fungal richness was removed so we present the models with this outlier included.

What is the relationship between mycorrhizal communities and understory plant communities?

We focussed on presence-absence responses for both plants and fungi because we did not have abundance information for the plants. Firstly, we performed a correlation test for rarefied mycorrhizal OTU richness and plant species richness with 999 permutations; this was repeated for Shannon's diversity. Secondly, we tested for differences between quadrats in terms of mycorrhizal composition and plant composition using a Mantel test. We used matrices of presence-absence data of mycorrhizal and plant composition and modified Raup-Crick dissimilarities using 999 permutations ("raupcrick" and "mantel", package vegan). All analyses were run at the quadrat level to be able to link the fine-scale information on mycorrhizal communities with fine-scale information on adjacent plant communities. Three quadrats contained zero plant species in 2015 so we omitted these for a total of 135 samples as it is not possible to determine dissimilarities with empty sites.

Results

Overview of fungal communities

The total number of sequences per sample was not strongly correlated with fire severity (proportion SOL combusted), suggesting no bias in sampling effort along the range of severity

(Fig. S1). The species accumulation curve for the 2034 fungal OTUs across 138 samples reached an asymptote and indicated that all OTUs were detected by ~60 samples (Fig. S2). Fewer than half of the 2034 OTUs were identified to genus using the UNITE database and RDP classifier (728 OTUs). A further 113 were only able to be assigned to family, 54 to class, 270 to order, 119 to phylum, and 750 OTUs could only be assigned to Kingdom. Most of the OTUs were in Ascomycota (791 OTUs), with fewer in Basidiomycota (422 OTUs) and some in Mortierellomycota (50 OTUs) and Chytridiomycota (10 OTUs), with other phyla represented in minor ways (4 in Mucoromycota, 4 in Rozellomycota, 1 in Entomophthoromycota, 1 Monoblepharomycota, and 1 in Olpidiomycota). At the order level, most OTUs were in Helotiales (325 OTUs) and Agaricales (143 OTUs). The most frequent and abundant OTU was *Calyptrozyma* sp. (Fig. S3), followed by two OTUs that matched *Geopyxis carbonaria*. OTUs matching *Oideodendron* were also common (Fig. S3). Many of the most common OTUs were in both burned and unburned samples (Tables S3-S6).

Only 600 of the 2034 OTUs were assigned to a functional group; the majority of OTUs had unknown functional group (Table 2). Of those assigned to functional group, saprotrophs were the most common. Of the mycorrhizal OTUs, ectomycorrhizas were the most frequent and abundant followed by ericoid mycorrhizas.

What are the key drivers of fungal community structure?

The PERMANOVA showed that soil pH and fire severity were the most important drivers of fungal composition, with pH explaining one-third of the variation in composition (Table 3). When the PERMANOVA was restricted to include only samples from burned plots, pH and fire severity continued to explain the greatest variation (Table S7). Our decomposition of β diversity showed that total β diversity (β_{sor}) was 0.99. Of this, 99% (0.98) was accounted for by spatial turnover (β_{sim}), with only 1% (0.01) accounted for by nestedness (β_{nes}).

The first two axes of the PCoA explained 14.1% of the variation in fungal OTU composition and clearly showed the importance of pH as the dominant driver of composition followed by fire severity (axis 1: 9.6%; axis 2: 4.5%; Fig. 2). OTUs that were highly positively correlated with the first PCoA axis (increasing pH) included root endophytes such as *Exophiala* sp., Chaetothyriales sp., and *Cladophialophora* sp. (Table S8). Those that were negatively correlated included

386 endophytic taxa *Serendipita*, Myxotrichaceae, and Sebacinales. Those OTUs associated with the
387 second PCoA axis (increasing fire severity) included *Phoma* and *Cladosporium*, as well as the
388 cosmopolitan genus *Penicillium.* OTUs in *Cladophialophora* sp. were correlated with lower fire
389 severity (Table S8).

390 Overall, our results across richness and diversity metrics showed that fire severity and soil
391 pH were key drivers of fungal community structure. Mean fungal OTU richness per sample was
392 105 (SD 43; range: 37-337) and mean Shannon's diversity was 0.69 (SD 2.53; range: 0.73-3.87).
393 According to the model weights, the models most supported by the data were the burn × edaphic
394 model followed by the burn model and the full model (Table 4). All richness models had low R^2
395 values, showing poor fit and the diversity models had slightly higher R^2. For both richness and
396 diversity, the random effects accounted for a large amount of variation in the models, as shown by
397 the R^2_c being at least twice that of the R^2_m (Table 4). This suggests high variability in OTU richness
398 and diversity within plots for samples that were only 12 m apart. The null, edaphic, and burn
399 models all had weights of zero or near-zero, which shows that these models were very poor for
400 explaining OTU richness and diversity compared to the other models. The richness models run
401 with only samples from burned plots similarly showed the burn × edaphic model and the burn
402 model were the most highly weighted (Table S9), suggesting that results were not driven by an
403 unburned vs. burned effect. Using model averages, the 95% confidence intervals did not cross zero
404 for fire severity, where OTU richness and diversity declined with increased severity (Fig. 3a,d;
405 Table S10). The interaction between fire severity and pH was only important for richness; where
406 pH was high and severity was low, there was greater total fungal richness than where pH was high
407 and severity was high (Fig. 3a).

408 Mean mycorrhizal OTU richness per sample was 21 (SD 13; range: 0-63) and mean
409 Shannon's diversity was 1.42 (SD 0.70; range: 0-2.68). The most probable model for mycorrhizal
410 richness was the burn × edaphic model followed by the full and edaphic models (Table 4). For
411 mycorrhizal diversity, the burn model followed by the burn × edaphic model were most probable
412 (Table 4). These two models were also the most probable when only ectomycorrhizas were
413 considered (Table S11). All of these models had poor fit (low R^2) and there was high variation
414 between samples within plots. Model averages showed that mycorrhizal richness and diversity
415 both declined with increasing severity (Fig. 3b,e; Table S10). Mycorrhizal richness declined with
416 increasing pH (Table S10). The interaction between fire severity and pH was important for

mycorrhizal richness and could be considered as marginally important for diversity (upper confidence limit was exactly zero); where pH was high and severity was low, there was greater mycorrhizal richness or diversity than where pH was high and severity was high (Fig. 3b,e).

Mean saprotroph OTU richness per sample was 26 (SD 13; range: 4-62) and mean Shannon's diversity was 1.32 (SD 0.58; range: 0.08-2.89). The most probable model for saprotroph richness was the burn × edaphic model followed by the full and burn models (Table 4). For saprotroph diversity, the most probable model was the burn model followed by the null, the burn × edaphic, and the edaphic models (Table 4). Again, these models had low R^2 values and showed there was high within-plot variation in saprotroph richness and diversity. Saprotroph richness declined with increased fire severity and there was a significant interaction between pH and fire severity; where pH was high and severity was low, there was greater saprotroph richness than where pH was high and severity was high (Fig. 3c; Table S10). None of the measured parameters were important drivers of saprotroph diversity (Table S10).

What is the relationship between mycorrhizal communities and understory plant communities?

There were 260 mycorrhizal OTUs and 78 vascular plant species one year after fire. There was a significant positive correlation between mycorrhizal and plant species richness ($r = 0.34$; $t = 4.13$; $P < 0.05$; Fig. 4a) and Shannon's diversity ($r = 0.34$; $t = 4.10$; $P < 0.05$; Fig. 4b). The Mantel test showed weak but significant positive correlations between mycorrhizal and plant composition ($r = 0.12$; $P < 0.01$).

Discussion

This study supports the hypothesis that increased wildfire activity and severity impact fungal community structure and could thereby influence patterns of plant recovery after fire in these boreal forests. Our results suggest that pH is the primary driver of fungal community composition upon which fire acts as a filter. Consistent with observations in boreal forests and globally, fungal composition was mainly related to pH of the surrounding soil (Högberg et al., 2003; Sun et al.,

2015; Tedersoo et al., 2014). These communities were then mediated by fire, where areas that experienced greater fire severity had lower richness and diversity of total fungi and mycorrhizas, and saprotroph richness. Pre-fire stand type and stand age explained variation in fungal composition, which suggests we could detect successional stages in fungal communities even after fires. We found weak but significant relationships between plant and mycorrhizal community structure. These results from the largest fire year on record in this region suggest that changes to the fire regime, in terms of severity and frequency, could act as a recurring filter on fungal communities to alter composition and ecosystem resilience, similar to plant communities (Johnstone et al., 2010). Moreover, intensification of fire disturbance could lead to declines in mycorrhizas with implications for post-fire plant community assembly.

We found that soil pH is an underlying determinant of fungal community structure in these boreal forests; fire interacts with pH to further influence community composition, richness, and diversity. Supporting prior research at a global scale (Tedersoo et al., 2014), pH was the main determinant of fungal community structure, accounting for one third of the variation in composition (Table 3) and there was high mycorrhizal OTU richness at low pH (Table S10). Moreover, total fungal communities were highly structured by turnover processes, shown by the decomposition of β diversity, which suggests low dispersal at the microsite scale at which we sampled (Baselga, 2010). These patterns suggest there has been environmental stability to support local specialization and our findings indicate that this stability is due to edaphic factors, particularly pH. This is highlighted by the importance of the interaction between pH and fire severity for richness of total fungi, mycorrhizas, and saprotrophs (Fig. 3). In contrast, this interaction was not important for either total fungal species or saprotroph diversity and had only a marginal effect on mycorrhizal diversity (Table S10). This, in combination with diversity of all groups declining with fire severity, suggests that pH is the underlying driver of which fungi are there before the fires and then fires cause declines in abundance and mortality of particular fungal groups. For example, fire severity did not impact diversity of saprotrophs, supporting the idea that mycorrhizas are more susceptible to fire than saprotrophs (Holden et al., 2016; Sun et al., 2015; but see Cutler et al., 2017). It is further possible that fire-induced increases in pH had a more negative impact on mycorrhizas, since this group had greater richness in more acidic soils (Table S10). Taxa associated with higher fire severity on the PCoA included *Phoma* and *Penicillium*, which can form sclerotia to confer resistance to harsh environmental conditions (e.g., Seifert et al.,

2004). In contrast, OTUs in the root-associated genus *Cladophialophora* were correlated with the lower end of fire severity and high pH, which was also found in black spruce forests in Alaska after fire (Hewitt et al., 2013).

The ability for us to detect long-term successional patterns in fungal composition in relation to pre-fire stand age, even in recently burned soils (Table 3), suggests that some proportion of fungi survived in the soil rather than colonising via aerial dispersal. This is further supported by the high turnover. Moreover, many of the most common fungi were in both burned and unburned samples (Tables S3-S6). Our study does not give us the ability to detect which fungi survived the fires and which ones dispersed after the fires but other studies have found ectomycorrhizas can survive fires in soil spore banks in coastal pine forests (Glassman et al., 2016) and they can survive in roots at latitudinal treeline (Hewitt, Chapin, Hollingsworth, & Taylor, 2017). Structures that are able to survive belowground where they are buffered from the extreme heat of the fire is a key adaptation to promote rapid reassembly of communities and enable ecosystem resilience through ecological legacies (Johnstone et al., 2016). At our plots, most plants survived the fires to regenerate from persistent belowground structures (91% of species; White, 2018) so these roots may provide mycorrhizas and fungal endophytes with protection from fires. Fungi could also survive in unburned patches within a stand. The idea that many fungi were able to survive fires is supported by some of our common taxa. For example, the ectomycorrhizal *Russula decolorans* is a late-succession species (Visser, 1995) but our study and Hewitt et al. (2013) found this species in recently burned areas suggesting that this species is able to survive fires. Moreover, little seems to be known of the ecology of the basidiomycete *Fayodia gracilipes* but we have been able to culture this species from heat-treated soils (unpublished data), implicating an increased ability to survive fire.

Boreal wildfires have been shown to "re-set" fungal succession to select for efficient nutrient cyclers after fire; fungi that stabilise C and N to support C sequestration become more abundant as time since fire progresses (Clemmensen et al., 2015). Under this scenario, increased fire frequency, or decreased fire return interval, could lead to losses of fungi important for C sequestration and de-stabilise boreal regions as a C sink, particularly with additive C losses under shorter fire intervals (Brown & Johnstone, 2011). We found many OTUs of the efficient nutrient cycling taxa known as cord forming fungi, such as *Cortinarius* and *Suillus*, distributed across

samples regardless of fire severity. This is interesting because while *Suillus* spp., which form ectomycorrhizas exclusively with pines, are commonly found in the years immediately after fire, *Cortinarius* spp. are thought to be vulnerable to disturbance and typically become more abundant in the decades after fire (LeDuc, Lilleskov, Horton, & Rothstein, 2013; Sun et al., 2015; Visser, 1995). Clearly there is a need to further examine relationships between fire frequency, fungal functional groups, and C storage in boreal forests.

Important relationships between fungal communities and understory plant communities are understudied in boreal forests (De Bellis et al., 2007; Taylor et al., 2014). Associations between mycorrhizal and plant communities may arise in the absence of biotic interactions if both communities are sensitive to the same environmental factors. Alternatively, the weak but significant associations we observed between fungal and plant communities in terms of composition, richness, and diversity (Fig. 4) may reflect generalist interactions or be due to the lack of detection of arbuscular mycorrhizal (AM) fungi, which commonly form associations with a number of boreal plants (Wang & Qiu, 2006). This suggests that both the number and identities of mycorrhizas after disturbances are important due to plant-mycorrhizal specificity that can shape plant communities (Bent et al., 2011; Bever et al. 2012; Klironomos, 2002). For example, the high frequency and abundance of multiple OTUs of the ericoid mycorrhizal genus *Oideodendron* corresponds with the high frequency of ericaceous shrubs, *Vaccinium vitis-idaea* and *Arctostaphylos rubra* (Table S2).

We found a ratio of fungal OTUs to plant species of 25:1 and 3:1 of mycorrhizal OTUs to plant species. The high variability in total fungal diversity and richness in different samples within plots, which were only 12 m apart, supports the idea of high levels of fungal diversity over fine spatial scales in boreal soils (Taylor et al., 2014; Toljander et al., 2006). Future studies could consider taking a greater number of samples per plot to better capture this relatively small-scale variation. Saprotrophs were the dominant functional group in these soils, although the majority of fungi were not assigned to functional group and our methods do not enable us to assess fungal activity or biomass. The FUNGuild database is an excellent resource but difficulties in assigning fungi to particular functional groups without context may limit our current ability to infer functionality. Although many plants in our system form AM fungal associations (Subphylum Glomeromycotina; Spatafora et al., 2016; Wang & Qiu, 2006), our inability to detect these fungi

is likely due to a combination of the system being ectomycorrhizal-dominated and primer bias. Even though the same primer pair has detected AM fungal sequences in low abundances at high latitudes (Gittel et al., 2014), recent work suggests that the ITS2 region may provide a reasonable estimate of AM fungal communities (Lekberg et al., 2018). We suggest further research into AM-fungal detection in boreal forests to better resolve these communities.

Our metric of fire severity, proportion SOL combusted, makes it difficult to disentangle effects of the impact of heat from the fire from the depth of the soil sample, which has been related to fungal composition in other boreal regions (Clemmensen et al., 2015; Lindahl et al., 2007; Taylor et al., 2014). We cautiously interpret that our patterns are due to fire. The mean pre-fire depth of the organic layer was 27 cm while the mean depth of burn was only 10 cm. Thus, most of our samples were in the organic horizon (comprised of organic material above the mineral soil horizon; 112/138) and those samples from the mineral horizon were not compositionally distinct (Fig. S4). However, our sampling was not explicitly undertaken to assess differences between horizons so there was charred organic matter in the 15 mineral horizon samples with could hinder strong conclusions about horizon differences here.

Fire severity was negatively correlated with soil moisture ($r=-0.60$), which is a limiting factor for microbial activity, fungal abundance, and ectomycorrhizal community structure and colonisation rates in boreal forests (Toljander et al., 2006; Waldrop & Harden, 2008). Relationships between fungal community structure and soil moisture could be accentuated under a changing fire regime due to interactions with permafrost thaw (Brown et al., 2015), which can modify plant-fungal interactions and decomposition (Jassey et al., 2018). In our study, ten plots were known to be underlain by permafrost containing ice in the top 2-3 m of soil (J Holloway & AG Lewkowicz, unpublished data); these plots were not compositionally distinct (Fig. S5). Our sampling immediately after fire may not have captured permafrost thaw-related changes in soil moisture and fungal communities because thaw occurs gradually in the years following fire and depends on the severity of the fire, climate, and soil conditions (Brown et al., 2015; Gibson et al., 2018; Waldrop & Harden, 2008). These interactions between disturbances and edaphic factors over long time periods need to be considered under scenarios of global change.

We found the common fungi in the Northwest Territories were comparable to other boreal regions. Pezizomycetes are known to fruit after fire and includes our most common sequence,

Calyptrozyma (Fujimura, Smith, Horton, Weber, & Spatafora, 2005; Smith et al., 2017). This was closely related to a sequence of fungus that colonised roots after fires in Alaska (Bent et al., 2011) but this genus is deemed not to be mycorrhizal according to FUNGuild. The ectomycorrhizal *Meliniomyces bicolor* was also found associated with roots of different hosts after fires in black spruce forests in Alaska (Bent et al., 2011; Hewitt et al., 2013). The Pezizomycetous *Geopyxis carbonaria* was among the most common taxa in our sequences and we often observed these distinctive orange cups on mineral soil associated with *Morchella*, a pattern also seen in British Columbia, Canada (Greene et al., 2010). However, *G. carbonaria* sequences were not highly correlated with the fire severity axis on the PCoA and was among the most frequent taxa in the unburned soils (Table S4), suggesting that it has survived in the soil through the fire disturbance. Similarly, the heat-resistant genus *Leohumicola* (Nguyen & Seifert, 2008) was common in both burned and unburned samples (Tables S3-S6).

Fungi in Helotiales were common, which is also the case in other parts of the boreal forest including Alaska (Taylor et al., 2014), Canada (Ontario; Asemaninejad, Thorn, & Lindo, 2017) and Sweden (Clemmensen et al., 2015; Lindahl et al., 2007). This includes *Oideodendron*, which was one of our most common taxa. This ericoid mycorrhizal fungus may also be a saprotroph (Rice & Currah, 2006) and is common in boreal forests and *Sphagnum* bogs (Kyaschenko et al., 2017; Sterkenburg et al., 2015; Thormann, Currah, & Bayley, 2004). There may be some fire adaptations in Helotiales, being common after fires in Sweden (Cutler et al., 2017) and colonising pine seedlings in heat-treated soils (Izzo, Canright, & Bruns, 2006). We further found many sequences of yeasts, including the recently described genus *Rhodosporidiobolus, Lipomyces,* and *Saitoella complicata*, and the psychrotolerant Leucosporidiales.

In conclusion, our study after a large wildfire event in subarctic boreal forests of the Northwest Territories of Canada supports prior research showing the importance of pH in determining underlying fungal community structure, which is then filtered by fire. These relationships may be mediated by pre-fire successional stand age (fire return interval), and stand type. Although we had high compositional turnover, we found evidence for correlations between mycorrhizal taxa and understory plants that could impact subsequent forest composition. Moreover, the interaction of fire with pH and potential long-term changes in factors important for microbial activity, such as changes in soil moisture due to permafrost thaw, suggests future

research could focus on assessing the longer term impacts of disturbance severity on soil microbial community structure. With increasingly large and frequent disturbance events anticipated with climate change, this study has enhanced our understanding of how large fire disturbances impact the soil microbial communities that drive ecosystem functioning.

Acknowledgements

This article is part of Project 170 of the Government of the Northwest Territories (GNWT) Department of Environment and Natural Resources Cumulative Impacts Monitoring Program (awarded to JLB). Additional funding for this research was provided by a Natural Science and Engineering Research Council (NSERC) Postdoctoral Fellowship to NJD, NSERC (Changing Cold Regions Network), Northern Scientific Training Program, a National Science Foundation DEB RAPID to MCM (grant #1542150), and NSERC Discovery to MRT. We thank the GNWT Aurora Research Institute (Research License 15879), the Ka'a'gee Tu First Nation, the Tłı̨chǫ Government, and the Wek'éezhìi Renewable Resources Board for their support of this research. The Wilfrid Laurier University-GNWT Partnership was instrumental in providing logistical support. We thank Canadian Centre for Computational Genomics - Montréal Node for running the MiSeq and bioinformatics, particularly P. Lepage, F. Lefebvre, E. Gonzalez, and P. Marquiz. We thank S. Cumming for contributions to sampling design, A. Sniderhan for making the map, J. Padullés Cubino for R code advice, and K. Reid and many students and technicians for field and lab assistance. We thank R. Hewitt for providing helpful comments on a manuscript draft and five anonymous reviewers whose suggestions greatly improved the manuscript.

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Tables

Table 1. List of candidate models and the effects they represent used to assess hypotheses of drivers of richness and diversity (Shannon's index) of total fungi, mycorrhizas, and saprotrophs across 137 samples from 47 plots in boreal forests. One of the 138 samples were omitted due to outlying soil C:N. The range and units of each variable are in Table S1. SOL: soil organic layer. Detailed hypotheses are in Supplementary Methods.

Model name	**Explanatory variables included**	**Effects represented**
Null	None	None
Burn	Proportion SOL combusted	Fire severity
Stand conditions	Proportion pre-fire black spruce Pre-fire stand age	Pre-fire stand type and time since last fire
Edaphic factors	Soil pH Soil C:N	Abiotic soil conditions
Burn × edaphic	Proportion SOL combusted × soil pH Proportion SOL combusted × soil C:N	Change in edaphic conditions with fire severity
Full model	Proportion SOL combusted Proportion pre-fire black spruce Pre-fire stand age Proportion SOL combusted × soil pH Proportion SOL combusted × soil C:N	As described above

915 Table 2. Assignments of 2034 fungal operational taxonomic units (OTUs) to functional groups
916 according to FUNGuild in 138 samples from boreal forests, Northwest Territories, Canada. For
917 each functional group the number of taxa, number of OTUs (unique sequence clusters), and
918 number of sequences is shown. All functional groups were assigned at genus-level.

Functional group	**No. taxa**	**No. OTUs**	**No. sequences**
Saprotrophs	111	291	184,634
All Mycorrhizas	33	260	106,745
Ectomycorrhizas	28	156	54,643
Ericoid mycorrhizas	2	49	34,107
Orchid mycorrhizas	3	55	17,995
Plant pathogens	11	24	17,337
Endophytes	4	13	1,655
Animal pathogens	3	5	63
Lichenised	3	3	38
Fungal parasites	3	4	1,300
Unassigned	115	1,434	281,628
Total	282	2,034	593,400

919

Table 3. Results from permutational analysis of variance (PERMANOVA) with modified Raup-Crick dissimilarity on 2034 fungal operational taxonomic units (OTUs) from 137 samples from boreal forests, Northwest Territories, Canada, assessing variation of fungal community composition explained by predictor variabless. Permutations were restricted within plots with 999 permutations. Fire severity is the proportion of the soil organic layer combusted. Variables in bold have significance at $P<0.05$.

Variable	Variation explained (%)	df	SS	MS	*Pseudo F*	*P*
pH	**32.82**	**1**	**4.66**	**4.66**	**121.88**	**0.002**
Fire severity	**14.34**	**1**	**2.04**	**2.04**	**53.24**	**0.003**
Stand age	**3.27**	**1**	**0.47**	**0.47**	**12.15**	**0.016**
Stand type	**2.21**	**1**	**0.31**	**0.31**	**8.20**	**0.028**
Fire severity × pH	5.51	1	0.78	0.78	20.46	0.230
C:N	4.42	1	0.63	0.63	16.43	0.102
Fire severity × C:N	2.80	1	0.38	0.38	9.98	0.102
Residuals	34.63	129	4.94	0.04	0.35	
Total	100	136	14.21	1.00		

Table 4. Results of AICc-based model selection assessing the drivers of richness and diversity (Shannon's index) of total fungi, mycorrhizas, and saprotrophs for 137 samples from boreal forests, Northwest Territories, Canada, with plot as the random effect. For each model the number of parameters, *K*, the sample size corrected Akaike information criterion, AICc, the change in AICc relative to the best model, ΔAICc, the model weight, w_i, and the Log-likelihood, Log(*L*) are given. R^2_m is the marginal R^2 (fixed effects only) and R^2_c is the conditional R^2 (fixed and random effects). See Table 1 and text for details of each model.

Response variable	Model name	K	ΔAICc	w_i	Log(L)	R^2_m	R^2_c
Total fungal richness	Burn × edaphic	8	0	0.73	-668.14	0.03	0.06
	Burn	4	3.09	0.15	-674.10	0.02	0.07
	Full	10	3.73	0.11	-667.70	0.03	0.06
	Null	3	10.11	0	-678.68	0	0.07
	Edaphic	5	13.73	0	-678.34	0	0.07
	Stand conditions	5	13.87	0	-678.42	0	0.07
Mycorrhizal richness	Burn × edaphic	8	0	0.70	-519.77	0.09	0.17
	Full	10	3.24	0.14	-519.08	0.09	0.17
	Edaphic	5	3.54	0.12	-524.87	0.05	0.15
	Burn	4	5.34	0.05	-526.85	0.04	0.14
	Null	3	13.27	0	-531.87	0	0.14
	Stand conditions	5	16.49	0	-531.34	0.01	0.14
Saprotroph richness	Burn × edaphic	8	0	0.65	-517.37	0.03	0.10
	Full	10	2.67	0.17	-516.39	0.04	0.10
	Burn	4	3.41	0.12	-523.49	0.01	0.10
	Null	3	6.00	0.03	-525.84	0	0.10
	Edaphic	5	7.41	0.02	-524.41	0	0.10
	Stand conditions	5	8.73	0.01	-525.07	0	0.09
Total fungal diversity	Burn × edaphic	8	0	0.67	-128.67	0.16	0.33
	Burn	4	2.28	0.22	-134.22	0.08	0.30
	Full	10	4.03	0.09	-128.37	0.17	0.34
	Null	3	7.69	0.01	-137.99	0	0.30
	Edaphic	5	9.93	0	-136.97	0.02	0.34
	Stand conditions	5	11.21	0	-137.61	0.01	0.30
Mycorrhizal diversity	Burn	4	0	0.70	-138.88	0.07	0.17
	Burn × edaphic	8	2.62	0.19	-135.78	0.12	0.20
	Null	3	5.49	0.05	-142.68	0	0.18
	Full	10	5.58	0.04	-134.94	0.13	0.20
	Stand conditions	5	8.31	0.01	-141.95	0.01	0.18
	Edaphic	5	9.12	0.01	-142.36	0.01	0.18
Saprotroph diversity	Burn	4	0	0.43	-111.23	0.04	0.36
	Null	3	1.02	0.26	-112.80	0	0.36
	Burn × edaphic	8	2.5	0.12	-108.07	0.09	0.38
	Edaphic	5	2.59	0.12	-111.45	0.02	0.37
	Stand conditions	5	4.19	0.05	-112.25	0.01	0.36
	Full	10	6.08	0.02	-107.55	0.10	0.37

Figures

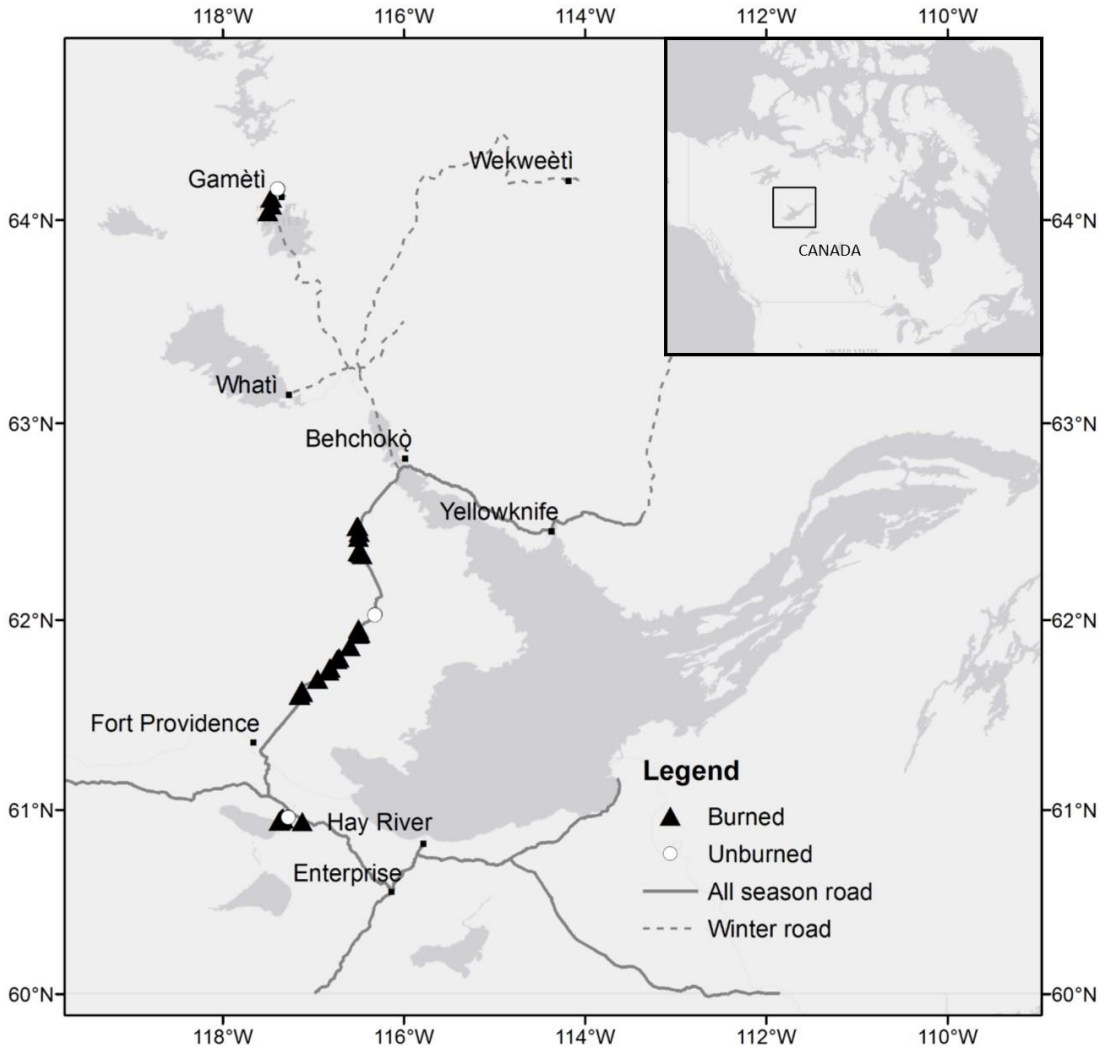
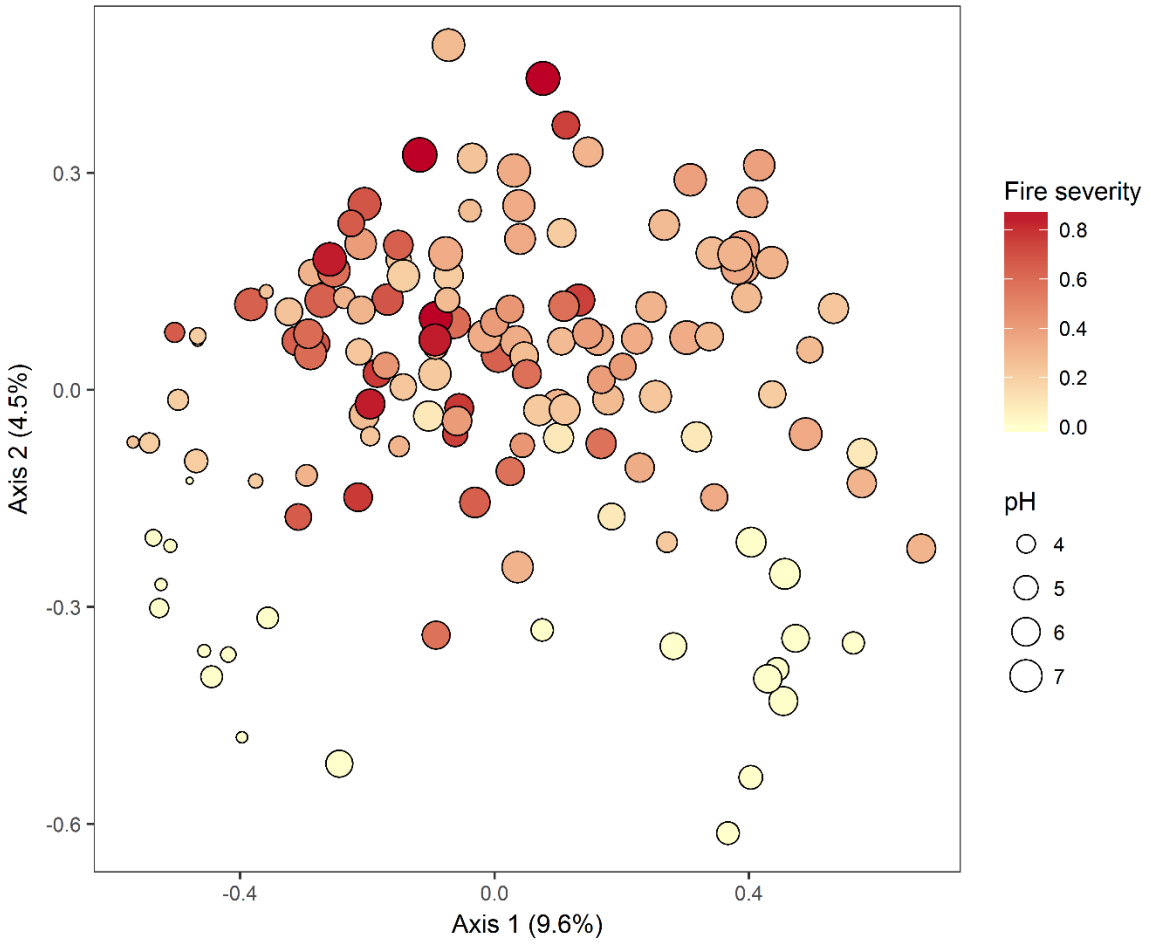


Fig. 1. Location of 47 plots where soil samples were collected for analysis of soil fungal communities one year after fire in boreal forest stands of black spruce and jack pine on the Taiga Plains in the Northwest Territories, Canada. Black triangles show plots that burned in 2014, white circles show plots that did not burn in 2014 (unburned). Hashed areas show 2014 burn scars and dark grey areas represent water bodies. The minimum distance between plots was 100 m.

945



946

947 Fig. 2. Site scores for principal co-ordinates analysis (PCoA) ordination with presence-absence
948 data for 2034 fungal operational taxonomic units (OTUs) in 138 samples from boreal forests,
949 Northwest Territories, Canada, specifying the modified Raup-Crick dissimilarity. Values in
950 brackets on the axes show the amount of variation in fungal composition explained by each axis.
951 The size of each point represents soil pH and the shading indicates fire severity (proportion soil
952 organic layer combusted), which were shown to explain the most variation in fungal composition
953 from the PERMANOVA (Table 3).

954

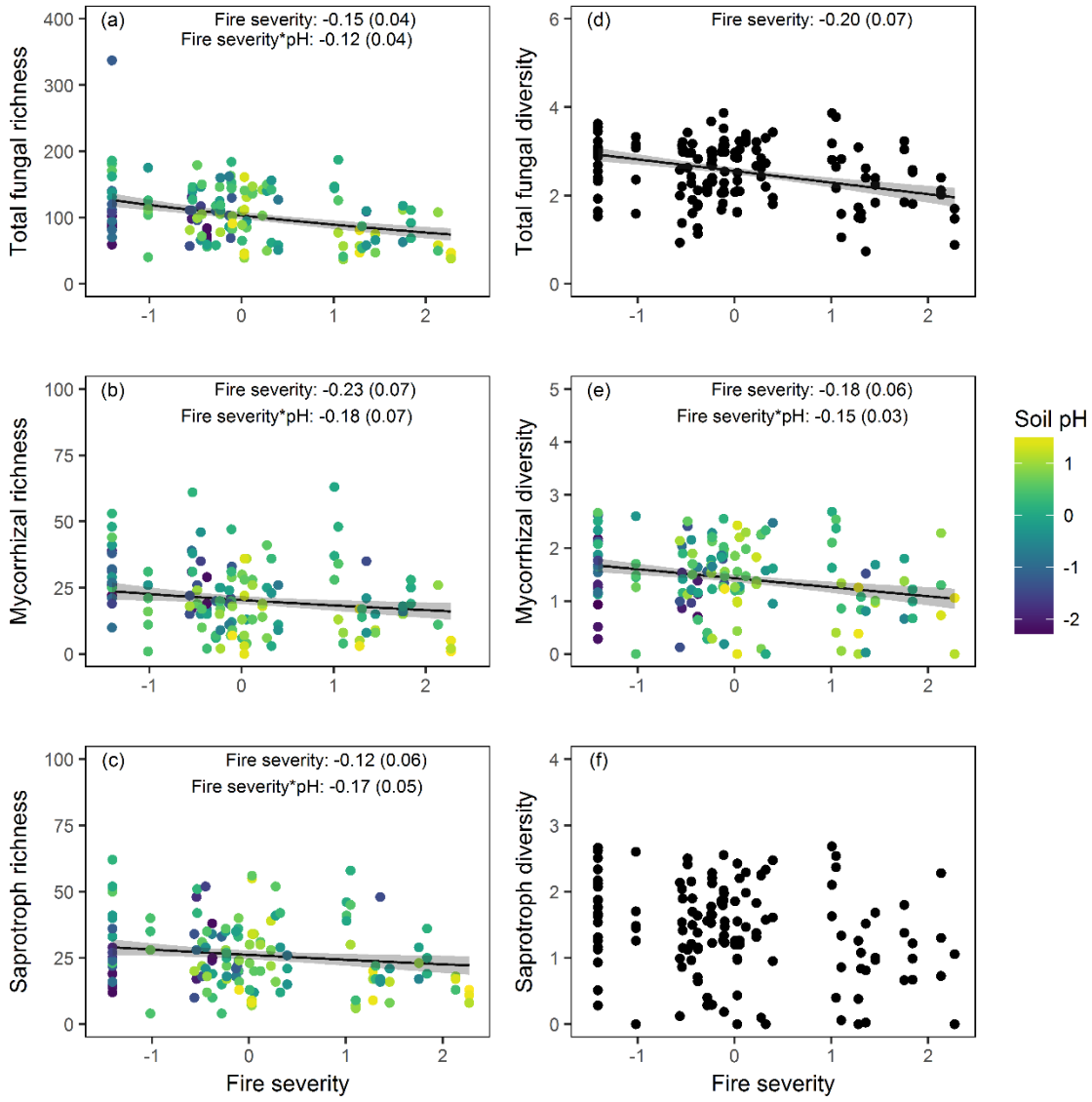
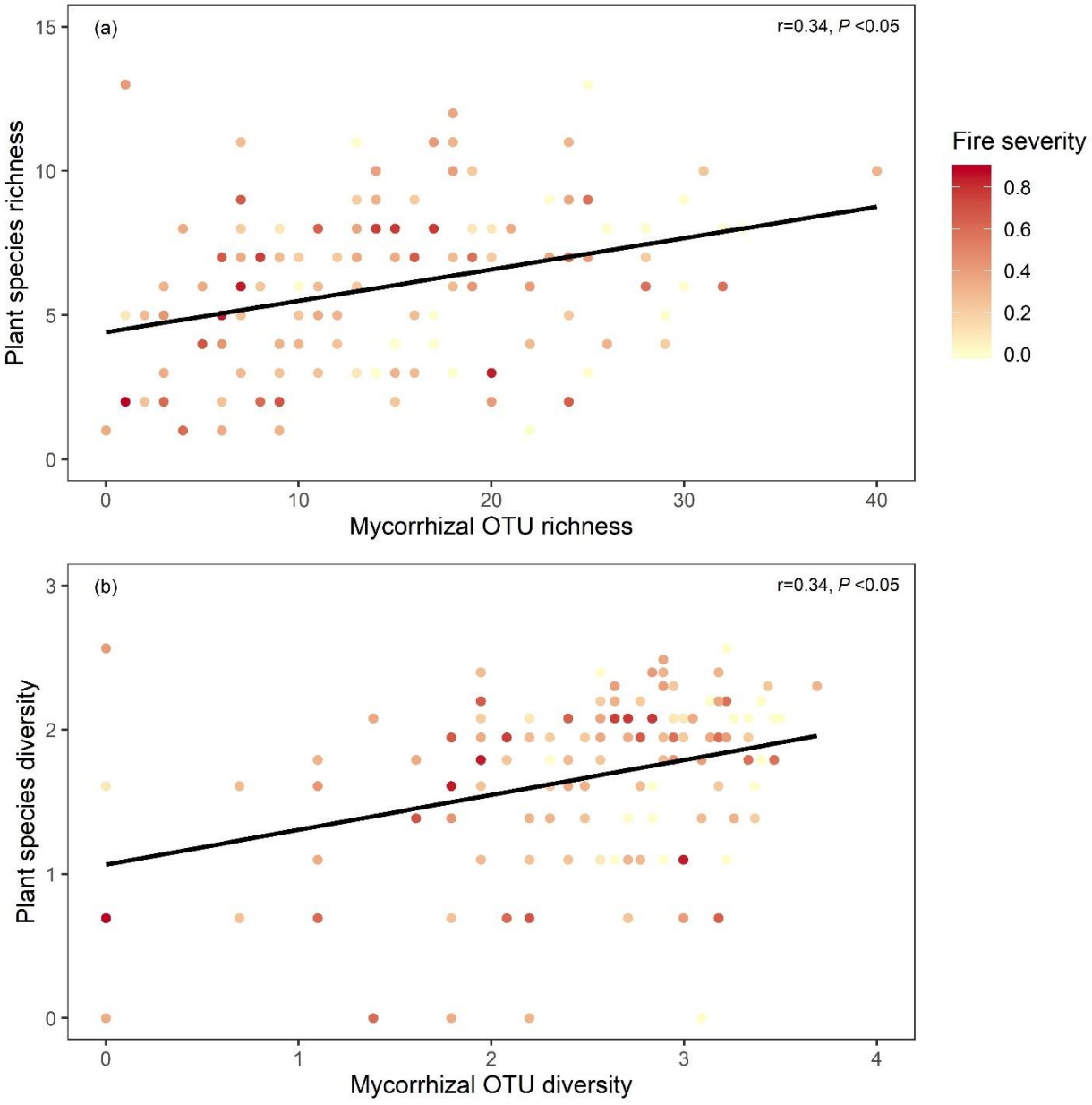


Fig. 3. Relationships between response variables (model-average predictions) against fire severity estimated from candidate models for 2034 fungal operational taxonomic units (OTUs) from 137 samples in boreal forests of the Northwest Territories, Canada. Fire severity against (a) total fungal richness, (b) mycorrhizal richness, (c) saprotroph richness, (d) total fungal diversity, (e) mycorrhizal diversity, and (f) saprotroph diversity. In (a), (b), (c), and (e) darker points indicate higher soil pH and lighter points indicate lower soil pH. Grey areas around slope lines indicate confidence intervals (95%) based on the entire candidate model set. All variables were standardised and centred and plot was the random effect in all models. Model-averaged coefficients and standard errors (in brackets) are given for variables for which the confidence intervals do not overlap zero. Full outputs and confidence intervals are presented in Table S10.

966



967

968 Fig. 4. Correlations between (a) mycorrhizal operational taxonomic unit (OTU) richness and
969 vascular plant species richness and (b) mycorrhizal OTU diversity and vascular plant species
970 diversity (Shannon's index) in 135 samples at 47 plots in boreal forests of the Northwest
971 Territories, Canada. The r and *P* values for permutation correlation tests are shown. Shading of
972 points indicates fire severity (proportion soil organic layer combusted). Three plots were omitted
973 due to having zero plant species present.

974

Supplementary Material: Wildfire severity reduces richness and alters composition of soil fungal communities in boreal forests of western Canada

Authors: Nicola J. Day, Kari E. Dunfield, Jill F. Johnstone, Michelle C. Mack, Merritt R. Turetsky, Xanthe J. Walker, Alison L. White, Jennifer L. Baltzer

Supplementary Tables

Table S1. Mean, minimum, and maximum values for predictor variables used in candidate models for 137 samples across 47 plots in boreal forests, Northwest Territories, Canada. SOL: soil organic layer.

Variable	Mean (range)		
	All samples	Burned	Unburned
Proportion of black spruce	0.75 (0, 1)	0.76 (0, 1)	0.69 (0, 1)
Stand age (years)	108 (58, 232)	107 (71, 232)	114 (58, 166)
Soil pH	5.86 (3.23, 7.62)	6.07 (3.36, 7.62)	4.66 (3.23, 6.51)
Soil C:N	30.76 (8.09, 120.62)	28.17 (8.09, 75.00)	44.35 (26.96, 120.62)
Soil moisture (gravimetric; %)	56.09 (5.19, 89.79)	55.11 (5.19, 81.35)	61.19 (17.53, 89.79)
Depth of burn (cm)	8.68 (0, 16.63)	10.35 (4.94, 16.63)	0 (0, 0)
Pre-fire SOL depth (cm)	27.30 (6.34, 85.00)	27.39 (6.34, 72.28)	30.57 (7.00, 85.00)
Fire severity (Proportion SOL combusted)	0.34 (0, 0.88)	0.40 (0.09, 0.88)	0 (0, 0)

Table S2. Plants recorded in 135 quadrats at 47 plots in boreal forests, Northwest Territories, Canada. There were three 1 × 1 m quadrats at each plot and soil samples for fungal community analysis were taken adjacent to each quadrat. Number of quadrats is the total number of quadrats where the plant species was present in 2015. Three quadrats did not have any plant species present.

Latin name	**Number of quadrats**
Equisetum scirpoides	61
Conifer seedling (black spruce/jack pine)	52
Salix sp. (morphotype A)	42
Cyperaceae sp.	42
Epilobium angustifolium	41
Rosa acicularis	39
Vaccinium vitis-idaea	36
Ledum groenlandicum	35
Potentilla fruticosa	32
Carex sp.	27
Calamagrostis sp.	27
Galium boreale	25
Geranium bicknellii	25
Linnaea borealis	25
Equisetum sp.	23
Betula glandulosa	21
Poaceae sp.	20
Arctostaphylos rubra	16
Cornus canadensis	15
Geocaulon lividum	14
Leymus sp.	12
Dracocephalum parviflorum	11
Rubus chamaemorus	11
Populus tremuloides	8
Salix sp. (morphotype H)	8
Salix sp. (morophotype F)	7
Picea mariana	7
Salix sp.	6
Corydalis aurea	6
Arctostaphylos uva-ursi	6
Salix sp. (morphotype B)	6
Oxycoccus microcarpus	6
Vaccinium uliginosum	5

Table S2. (cont.) Plants recorded in 135 quadrats at 47 plots in boreal forests, Northwest Territories, Canada. There were three 1 × 1 m quadrats at each plot and soil samples for fungal community analysis were taken adjacent to each quadrat. Number of quadrats is the total number of quadrats where the plant species was present in 2015. Three quadrats did not have any plant species present.

Latin name	**Number of quadrats**
Asteraceae sp.	5
Myrica gale	4
Shepherdia canadensis	4
Campanula rotundifolia	4
Scirpus hudsonianus	4
Liliaceae sp.	3
Rubus acaulis	3
Larix laricina	3
Anemone parviflora	3
Oryzopsis sp.	3
Zygadenus elegans	3
Ranunculus abortivus	3
Betula papyrifera	3
Ledum decumbens	3
Galium trifidum	2
Epilobium glandulosum	2
Rubus pubescens	2
Hedysarum alpinum	2
Phacelia franklinii	2
Andromeda polifolia	2
Agrostis sp.	2
Petasites palmatus	2
Empetrum nigrum	2
Petasites sagittatus	1
Viola adunca	1
Rosaceae sp.	1
Caryophyllaceae sp.	1
Ribes sp.	1
Erigeron sp.	1
Chamaedaphne calyculata	1
Potentilla anserina	1
Solidago multiradiata	1
Lonicera dioica var. *glaucescens*	1

997 Table S2. (cont.) Plants recorded in 135 quadrats at 47 plots in boreal forests, Northwest
998 Territories, Canada. There were three 1 × 1 m quadrats at each plot and soil samples for fungal
999 community analysis were taken adjacent to each quadrat. Number of quadrats is the total number
1000 of quadrats where the plant species was present in 2015. Three quadrats did not have any plant
1001 species present.

Latin name	**Number of quadrats**
Aster sp.	1
Aster puniceus	1
Poa palustris	1
Rubus ideus	1
Maianthemum sp.	1
Parnassia parviflora	1
Juniperus horizontalis	1
Stellaria sp.	1

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Table S3. The 20 most frequent fungal operational taxonomic units (OTUs) in samples from burned (n=116) areas from boreal forests, Northwest Territories, Canada. OTU number is unique to this dataset. Species hypotheses and blast results from the UNITE database are shown (UNITE Community 2017). Functional group assignment is from FUNGuild with confidence probable or highly probable. Shaded rows denote OTUs that were in frequent or abundant in both burned and unburned samples.

Number of samples	OTU number	Species hypothesis match	Reference sequence	E value	Percent identity	Functional group
113	367290	*Calyptrozyma* sp. SH199123.07FU	HM164559	5.00E-129	99.6	Unassigned
111	233670	Venturiaceae sp. SH219667.07FU	KF617760	5.00E-124	98.42	Saprotroph
106	825100	*Geopyxis carbonaria* SH216567.07FU	KU932495	1.00E-125	99.2	Unassigned
102	918678	Fungi sp. SH191316.07FU	KU581211	1.00E-130	100	Unassigned
93	982916	*Penicillium* sp. SH207148.07FU	KC818327	1.00E-130	100	Unassigned
90	778360	*Scutellinia* sp. SH193566.07FU	KJ028787	5.00E-114	98.3	Saprotroph
88	639932	*Mortierella alpine* SH183634.07FU	KP714627	2.00E-128	99.6	Unassigned
87	586433	*Acephala* sp. SH204986.07FU	KM068384	1.00E-130	100	Unassigned
87	1034337	Hyaloscyphaceae sp. SH196224.07FU	KP889806	1.00E-129	100	Saprotroph
84	297682	Helotiales sp. SH196478.07FU	KU176259	1.00E-130	100	Unassigned
84	477356	*Oidiodendron* sp. SH216998.07FU	KF156314	5.00E-129	99.6	Mycorrhiza (Ericoid)
83	207357	*Fimetariella rabenhorstii* SH203402.07FU	KU516462	3.00E-121	98.02	Endophyte
82	324349	*Oidiodendron* sp. SH217001.07FU	FJ553111	2.00E-118	97.23	Mycorrhiza (Ericoid)
82	492925	Pezizomycetes sp. SH202424.07FU	JQ761544	2.00E-98	96.76	Unassigned
81	526543	*Saitoella complicata* SH220498.07FU	KY105295	8.00E-127	99.21	Unassigned
77	536836	*Trichoderma* sp. SH177687.07FU	KF617954	2.00E-128	100	Unassigned
77	755882	*Anthracobia* sp. SH1543265.08FU	MG663263	4.00E-125	98.06	Unassigned
77	899505	*Penicillium* sp. SH182483.07FU	KP714560	1.00E-130	100	Unassigned
74	369074	*Lipomyces* sp. SH201431.07FU	KT923624	3.00E-126	99.6	Unassigned
73	538943	*Cladosporium* sp. SH1572792.08FU	MH399503	4.00E-130	100	Saprotroph
73	951735	Fungi sp. SH1528207.08FU	MH019902	1.00E-115	99.57	Unassigned

Table S4. The 20 most frequent fungal operational taxonomic units (OTUs) in samples from unburned (n=22) areas from boreal forests, Northwest Territories, Canada. OTU number is unique to this dataset. Species hypotheses and blast results from the UNITE database are shown (UNITE Community 2017). Functional group assignment is from FUNGuild with confidence probable or highly probable. Shaded rows denote OTUs that were in frequent or abundant in both burned and unburned samples (top 20).

Number of samples	OTU number	Species hypothesis match	Reference sequence	E value	Percent identity	Functional group
22	443531	*Oidiodendron* sp. SH216991.07FU	KP889961	4.00E-125	98.81	Mycorrhiza (Ericoid)
21	586433	*Acephala* sp. SH204986.07FU	KM068384	1.00E-130	100	Unassigned
21	982916	*Penicillium* sp. SH207148.07FU	KC818327	1.00E-130	100	Unassigned
18	297682	Helotiales sp. SH196478.07FU	KU176259	1.00E-130	100	Unassigned
18	367290	*Calyptrozyma* sp. SH199123.07FU	HM164559	5.00E-129	99.6	Unassigned
18	453680	Helotiales sp. SH1523356.08FU	KP889801	1.00E-130	98.86	Unassigned
18	749225	Myxotrichaceae sp. SH1564449.08FU	JQ513895	6.00E-134	99.25	Saprotroph
18	825100	*Geopyxis carbonaria* SH216567.07FU	KU932495	1.00E-125	99.2	Unassigned
18	1034337	Hyaloscyphaceae sp. SH196224.07FU	KP889806	1.00E-129	100	Saprotroph
17	477356	*Oidiodendron* sp. SH216998.07FU	KF156314	5.00E-129	99.6	Mycorrhiza (Ericoid)
17	580765	*Cladophialophora chaetospira* SH1529632.08FU	HQ871874	2.00E-134	97.19	Saprotroph
17	1000985	*Oidiodendron* sp. SH1564463.08FU	HM488481	6.00E-134	99.62	Mycorrhiza (Ericoid)
16	324349	*Oidiodendron* sp. SH217001.07FU	FJ553111	2.00E-118	97.23	Mycorrhiza (Ericoid)
16	941073	*Oidiodendron* sp. SH217001.07FU	JQ666681	5.00E-129	99.6	Mycorrhiza (Ericoid)
16	972589	Leucosporidiales sp. SH1524317.08FU	KP889379	2.00E-133	97.83	Unassigned
15	823855	Fungi sp. SH1529602.08FU	KF617296	4.00E-141	98.93	Unassigned
14	259440	*Mortierella* sp. SH1607997.08FU	MF423520	9.00E-127	99.21	Unassigned
14	345336	*Meliniomyces bicolor* SH1523753.08FU	EU292532	3.00E-132	99.61	Mycorrhiza (Ecto)
14	593961	Chaetothyriales sp. SH1557298.08FU	FJ554031	1.00E-146	98.32	Unassigned
14	639932	*Mortierella alpina* SH183634.07FU	KP714627	2.00E-128	99.6	Unassigned
14	918678	Fungi sp. SH191316.07FU	KU581211	1.00E-130	100	Unassigned
14	920035	*Cladophialophora* sp. SH1529591.08FU	JF519467	2.00E-143	98.62	Saprotroph

Table S5. The 20 most abundant fungal operational taxonomic units (OTUs) in samples from burned (n=116) areas from boreal forests, Northwest Territories, Canada. OTU number is unique to this dataset. Species hypotheses and blast results from the UNITE database are shown (UNITE Community 2017). Functional group assignment is from FUNGuild with confidence probable or highly probable. Shaded rows denote OTUs that were in frequent or abundant in both burned and unburned samples (top 20).

Number of samples	OTU number	Species hypothesis match	Reference sequence	E value	Percent identity	Functional group
644970	367290	*Calyptrozyma* sp. SH199123.07FU	HM164559	5.00E-129	99.6	Unassigned
392598	825100	*Geopyxis carbonaria* SH216567.07FU	KU932495	1.00E-125	99.2	Unassigned
244690	297682	Helotiales sp. SH196478.07FU	KU176259	1.00E-130	100	Unassigned
213580	233670	Venturiaceae sp. SH219667.07FU	KF617760	5.00E-124	98.42	Plant Pathogen
131878	148590	Leucosporidiales sp. SH1522748.08FU	KP889411	2.00E-138	99.63	Unassigned
130527	210980	*Fayodia gracilipes* SH1553066.08FU	KC176299	5.00E-170	100	Saprotroph
113575	253574	*Leohumicola* sp. SH1564438.08FU	EU292662	3.00E-131	100	Saprotroph
113541	750039	*Geminibasidium* sp. SH1563152.08FU	FJ553582	2.00E-138	99.27	Saprotroph
113403	632101	*Russula decolorans* SH1538837.08FU	FJ845432	6.00E-144	100	Mycorrhiza (Ecto)
108601	492925	Fungi sp. SH1552003.08FU	KY651112	2.00E-138	97.57	Unassigned
108573	778360	*Scutellinia* sp. SH193566.07FU	KJ028787	5.00E-114	98.3	Saprotroph
85749	586433	*Acephala* sp. SH204986.07FU	KM068384	1.00E-130	100	Unassigned
83205	1034337	Hyaloscyphaceae sp. SH196224.07FU	KP889806	1.00E-129	100	Saprotroph
77194	593609	*Humicolopsis cephalosporioides* SH1522924.08FU	KY065165	3.00E-137	100	Unassigned
69679	477356	*Oidiodendron* sp. SH216998.07FU	KF156314	5.00E-129	99.6	Mycorrhiza (Ericoid)
69287	982916	*Penicillium* sp. SH207148.07FU	KC818327	1.00E-130	100	Unassigned
63711	401034	Cortinariaceae sp. SH1503722.08FU	KP889889	3.00E-173	99.12	Mycorrhiza (Ecto)
59219	531099	Leucosporidiales sp. SH1522759.08FU	KF617682	8.00E-128	98.1	Unassigned
55583	1000985	*Oidiodendron* sp. SH1564463.08FU	HM488481	6.00E-134	99.62	Mycorrhiza (Ericoid)
54012	931721	*Rhodosporidiobolus* sp. SH1560099.08FU	KF617362	3.00E-102	93.41	Unassigned

Table S6. The 20 most abundant fungal operational taxonomic units (OTUs) in samples from unburned (n=22) areas from boreal forests, Northwest Territories, Canada. OTU number is unique to this dataset. Species hypotheses and blast results from the UNITE database are shown (UNITE Community 2017). Functional group assignment is from FUNGuild with confidence probable or highly probable. Shaded rows denote OTUs that were in frequent or abundant in both burned and unburned samples (top 20).

Number of samples	OTU number	Species hypothesis match	Reference sequence	E value	Percent identity	Functional group
67398	443531	*Oidiodendron* sp. SH216991.07FU	KP889961	4.00E-125	98.81	Mycorrhiza (Ericoid)
53464	354692	Myxotrichaceae sp. SH1564437.08FU	KT759217	6.00E-134	99.25	Saprotroph
46137	586433	*Acephala* sp. SH204986.07FU	KM068384	1.00E-130	100	Unassigned
32665	1034337	Hyaloscyphaceae sp. SH196224.07FU	KP889806	1.00E-129	100	Saprotroph
20777	823855	Fungi sp. SH1529602.08FU	KF617296	4.00E-141	98.93	Unassigned
19736	980851	*Clavaria sphagnicola* SH1648143.08FU	HQ211954	8.00E-163	100	Saprotroph
19250	806593	*Meliniomyces* sp. SH1523783.08FU	KF617237	6.00E-129	98.85	Mycorrhiza (Ecto)
18373	401034	Cortinariaceae sp. SH1503722.08FU	KP889889	3.00E-173	99.12	Mycorrhiza (Ecto)
15778	684224	*Serendipita* sp. SH1577333.08FU	KC965991	2.00E-148	98.65	Mycorrhiza (Orchid)
14838	253574	*Leohumicola* sp. SH1564438.08FU	EU292662	3.00E-131	100	Saprotroph
14805	135135	Fungi sp. SH1565778.08FU	EU292599	3.00E-137	98.56	Unassigned
14773	1028724	Fungi sp. SH1544332.08FU	JF300744	2.00E-134	100	Unassigned
13226	775149	Sebacinaceae sp. SH1544470.08FU	JQ420980	2.00E-159	100	Unassigned
12894	345336	*Meliniomyces bicolor* SH1523753.08FU	EU292532	3.00E-132	99.61	Mycorrhiza (Ecto)
12616	148590	Leucosporidiales sp. SH1522748.08FU	KP889411	2.00E-138	99.63	Unassigned
12179	858844	*Sarcodon* sp. SH1642778.08FU	KF617227	2.00E-169	99.39	Mycorrhiza (Ecto)
10541	461129	Lecanoromycetes sp. SH1566020.08FU	KM504464	0	99.52	Unassigned
10126	646099	*Lactarius* sp. SH1519106.08FU	KU861471	4.00E-161	99.37	Mycorrhiza (Ecto)
9921	988038	Hyaloscyphaceae sp. SH1523001.08FU	FJ475776	7.00E-133	100	Saprotroph
9396	920035	*Cladophialophora* sp. SH1529591.08FU	JF519467	2.00E-143	98.62	Saprotroph

Table S7. For samples from burned plots only, results from permutational analysis of variance (PERMANOVA) with modified Raup-Crick dissimilarity on 2034 fungal operational taxonomic units (OTUs) from 137 samples from boreal forests, Northwest Territories, Canada, assessing variation of fungal community composition explained by predictor variabless. Permutations were restricted within plots with 999 permutations. Fire severity is the proportion of the soil organic layer combusted. Variables in bold have significance at $P<0.05$.

Variable	**Variation explained (%)**	**df**	**SS**	**MS**	***Pseudo F***	***P***
Soil pH	32.85	1	3.12	3.12	132.57	0.001
Fire severity	12.09	1	1.15	1.15	48.79	0.001
Stand age	7.47	1	0.71	0.71	30.16	0.001
Proportion black spruce	3.27	1	0.31	0.31	13.21	0.008
Fire severity × soil pH	5.74	1	0.54	0.54	23.15	0.013
Soil C:N	7.03	1	0.67	0.67	28.38	0.001
Fire severity × soil C:N	5.05	1	0.48	0.48	20.36	0.001
Residuals	26.5	107	2.52	0.02	0.27	
Total	100	114	9.49	1.00		

Table S8. Fungal operational taxonomic units (OTUs) most highly correlated with the first two axes of the principal co-ordinates analysis, showing the OTU number unique to this study, the closest taxon match and species hypothesis number in the UNITE database, and the correlation with the axis (R). For each axis, the 10 OTUs that were most positively and negatively correlated are shown.

Axis 1 (increasing pH)				**Axis 2 (increasing fire severity)**			
OTU	**Taxon**	**Closest UNITE match**	**R**	**OTU**	**Taxon**	**Closest UNITE match**	**R**
79340	*Exophiala* sp.	SH1635779.08FU	0.56	828813	*Phoma* sp.	SH1547057.08FU	0.55
593961	Chaetothyriales sp.	SH1557298.08FU	0.54	538943	*Cladosporium* sp.	SH1572792.08FU	0.53
161978	*Cladophialophora* sp.	SH1529665.08FU	0.54	318017	Pleosporaceae sp.	SH1573995.08FU	0.52
680831	Mortierellaceae sp.	SH1607998.08FU	0.51	492925	Fungi sp.	SH1552003.08FU	0.47
360122	*Phialocephala lagerbergii*	SH1545864.08FU	0.49	899505	*Penicillium* sp.	SH1529989.08FU	0.46
1027794	Fungi sp.	SH1509519.08FU	0.48	719894	*Penicillium* sp.	SH1529984.08FU	0.45
738447	*Mortierella antarctica*	SH1650287.08FU	0.48	233670	Venturiaceae sp.	SH1626886.08FU	0.45
376575	Leotiomycetes sp.	SH1564439.08FU	0.47	375108	*Sporobolomyces gracilis*	SH1575132.08FU	0.44
977357	*Phialocephala lagerbergii*	SH1545864.08FU	0.47	473778	*Coniochaeta navarrae*	SH1645224.08FU	0.43
639932	*Mortierella alpina*	SH1650284.08FU	0.47	526543	*Saitoella complicata*	SH1514739.08FU	0.43
639451	Fungi sp.	SH1608144.08FU	-0.53	580765	*Cladophialophora chaetospira*	SH1529632.08FU	-0.55
775149	Sebacinaceae sp.	SH1544470.08FU	-0.48	749225	Myxotrichaceae sp.	SH1564449.08FU	-0.53
354692	Myxotrichaceae sp	SH1564437.08FU	-0.48	988429	Fungi sp.	SH1529602.08FU	-0.48
806593	*Meliniomyces* sp.	SH1523783.08FU	-0.47	500832	*Oidiodendron* sp.	SH1564449.08FU	-0.46
99776	*Serendipita* sp.	SH1577449.08FU	-0.47	1003704	*Phylliscum* sp.	SH1632783.08FU	-0.45
587434	Venturiaceae sp.	SH1626953.08FU	-0.44	920035	*Cladophialophora* sp.	SH1529591.08FU	-0.45
171505	Hyaloscyphaceae sp.	SH1544284.08FU	-0.41	366390	Herpotrichiellaceae sp.	SH1529793.08FU	-0.45
461129	Lecanoromycetes sp.	SH1566020.08FU	-0.40	443531	*Oidiodendron* sp.	SH1564449.08FU	-0.45
549089	*Oidiodendron* sp.	SH1564437.08FU	-0.40	304006	Fungi sp.	SH1529602.08FU	-0.45
145390	Helotiales	SH1522948.08FU	-0.40	762166	*Cladophialophora chaetospira*	SH1529584.08FU	-0.43

Table S9. Using samples from only burned plots, results of AICc-based model selection assessing the drivers of fungal operational taxonomic unit (OTU) richness for 115 samples from boreal forests, Northwest Territories, Canada, with plot as the random effect. For each model the number of parameters, *K*, the sample size corrected Akaike information criterion, AICc, the change in AICc relative to the best model, ΔAICc, the model weight, w_i, and the Log-likelihood, Log(*L*) are given. See Table 1 and text for details of each model.

Response variable	**Model name**	**K**	**ΔAICc**	w_i	**Log(L)**
Total fungal richness	Burn × edaphic	8	0	0.47	-565.59
	Burn	4	0.16	0.43	-570.17
	Full	10	4.03	0.06	-565.23
	Null	3	6.32	0.02	-574.32
	Edaphic	5	7.63	0.01	-572.81
	Stand conditions	5	10.25	0	-574.12

Table S10. Model-averaged parameter estimates, unconditional standard errors, and 95% unconditional confidence intervals (lower; upper) for each predictor variable incorporated into candidate models for total fungal, mycorrhizal, and saprotroph richness and diversity (Shannon's index) for 2034 fungal OTUs in 137 samples from boreal forests, Northwest Territories, Canada. Unconditional confidence intervals that do not overlap zero are shown in bold. See Table 1 and text for details of each model. Fire severity is the proportion soil organic layer combusted.

Response variable	Variable	Model-averaged estimate (β)	Unconditional standard error	95% confidence interval
Total fungal richness	**Fire severity**	**-0.15**	**0.04**	**-0.24, -0.06**
	Stand type	0.02	0.04	-0.05, 0.11
	Stand age	0.02	0.04	-0.06, 0.10
	pH	-0.01	0.04	-0.09, 0.08
	C:N	0.03	0.04	-0.05, 0.10
	Fire severity × pH	**-0.12**	**0.04**	**-0.20, -0.03**
	Fire severity × C:N	0	0.03	-0.06, 0.06
Mycorrhizal richness	**Fire severity**	**-0.23**	**0.07**	**-0.36, -0.09**
	Stand type	-0.03	0.07	-0.17, 0.10
	Stand age	0.07	0.07	-0.06, 0.20
	pH	**-0.18**	**0.07**	**-0.31, -0.05**
	C:N	0.08	0.06	-0.05, 0.20
	Fire severity × pH	**-0.18**	**0.07**	**-0.31, -0,04**
	Fire severity × C:N	0	0.05	-0.10, 0.09
Saprotroph richness	**Fire severity**	**-0.12**	**0.06**	**-0.23, -0.01**
	Stand type	-0.03	0.05	-0.13, 0.08
	Stand age	0.07	0.05	-0.03, 0.17
	pH	-0.04	0.05	-0.14, 0.06
	C:N	0.05	0.05	-0.05, 0.14
	Fire severity × pH	**-0.17**	**0.05**	**-0.27, -0.07**
	Fire severity × C:N	0.01	0.04	-0.07, 0.08

Table S10. (cont.) Model-averaged parameter estimates, unconditional standard errors, and 95% unconditional confidence intervals (lower; upper) for each predictor variable incorporated into candidate models for total fungal, mycorrhizal, and saprotroph richness and diversity (Shannon's index) for 2034 fungal OTUs in 137 samples from boreal forests, Northwest Territories, Canada. Unconditional confidence intervals that do not overlap zero are shown in bold. See Table 1 and text for details of each model. Fire severity is the proportion soil organic layer combusted.

Response variable	Variable	Model-averaged estimate (β)	Unconditional standard error	95% confidence interval
Total fungal diversity	**Fire severity**	**-0.20**	**0.07**	**-0.33, -0.06**
	Stand type	0.04	0.07	-0.08, 0.17
	Stand age	0.09	0.06	-0.11, 0.14
	pH	0.04	0.07	-0.10, 0.18
	C:N	-0.06	0.07	-0.19, 0.07
	Fire severity × pH	-0.10	0.07	-0.24, 0.04
	Fire severity × C:N	-0.02	0.05	-0.12, 0.07
Mycorrhizal diversity	**Fire severity**	**-0.18**	**0.06**	**-0.31, -0.06**
	Stand type	0.08	0.06	-0.04, 0.21
	Stand age	0.00	0.06	-0.12, 0.12
	pH	-0.06	0.07	-0.20, 0.08
	C:N	-0.02	0.07	-0.16, 0.11
	Fire severity × pH	**-0.15**	**0.07**	**-0.29, 0.00**
	Fire severity × C:N	0.01	0.05	-0.09, 0.11
Saprotroph diversity	Fire severity	-0.11	0.06	-0.24, 0.01
	Stand type	-0.01	0.07	-0.13, 0.12
	Stand age	-0.06	0.06	-0.19, 0.06
	pH	0.10	0.06	-0.02, 0.22
	C:N	0.05	0.05	-0.06, 0.16
	Fire severity × pH	-0.03	0.06	-0.16, 0.10
	Fire severity × C:N	0.02	0.04	-0.06, 0.10

Table S11. Results of AICc-based model selection assessing the drivers of ectomycorrhizal fungal diversity (Shannon index) for 137 samples from boreal forests, Northwest Territories, Canada, with plot as the random effect. For each model the number of parameters, *K*, the sample size corrected Akaike information criterion, AICc, the change in AICc relative to the best model, ΔAICc, the model weight, w_i, and the Log-likelihood, Log(*L*) are given. See Table 1 and text for details of each model.

Response variable	Model name	K	ΔAICc	w_i	Log(L)
Ectomycorrhizal diversity	Burn × edaphic	8	0	0.49	-132.00
	Burn	4	1.11	0.28	-136.97
	Full	10	3.10	0.10	-131.24
	Null	3	3.22	0.10	-139.08
	Stand conditions	5	6.24	0.02	-138.46
	Edaphic	5	7.34	0.01	-139.01

Supplementary Figures

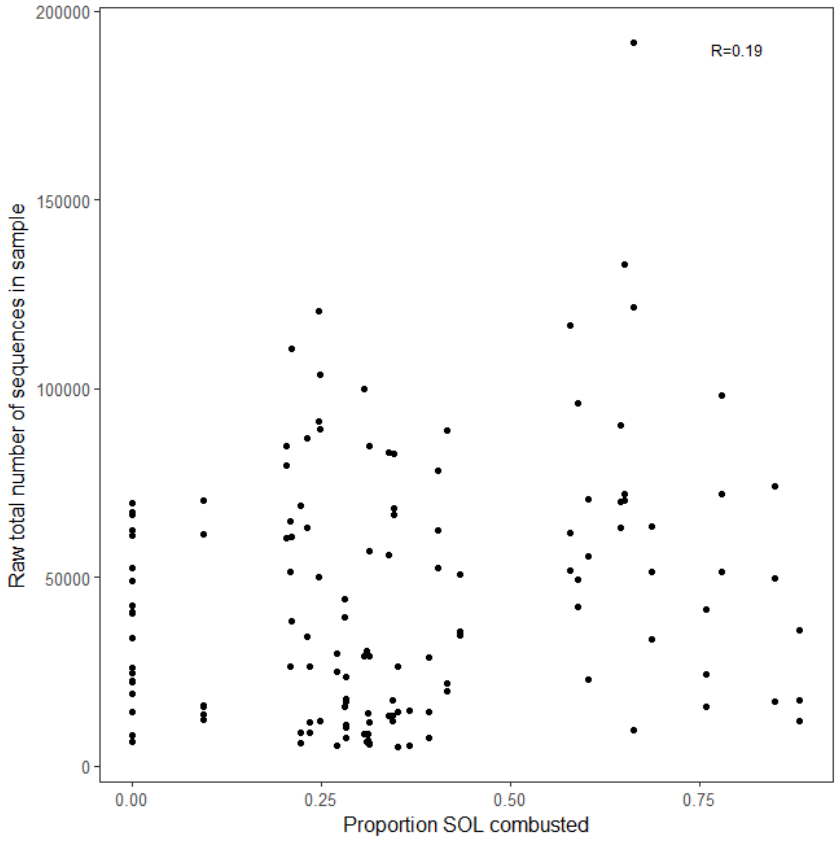

Fig. S1. Relationship between proportion soil organic layer (SOL) combusted (fire severity) and the total number of sequences per sample based on raw reads for 138 samples from boreal forests, Northwest Territories, Canada.

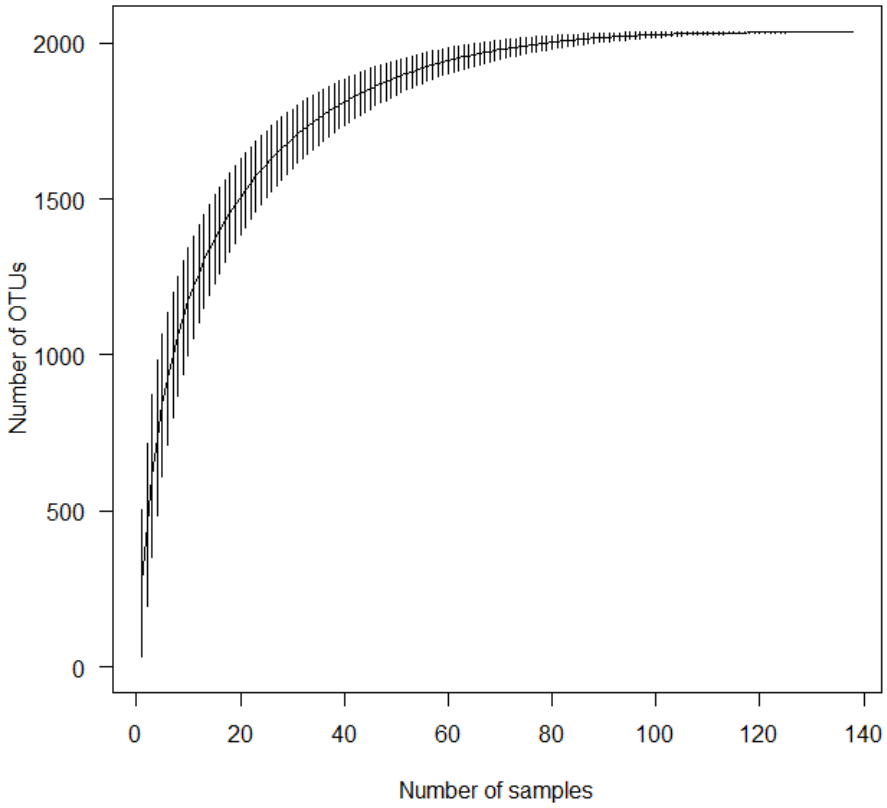

Fig. S2. Species accumulation curve of 2034 fungal operational taxonomic units (OTUs) in 138 samples from boreal forests, Northwest Territories, Canada, showing means and standard deviations based on 999 permutations.

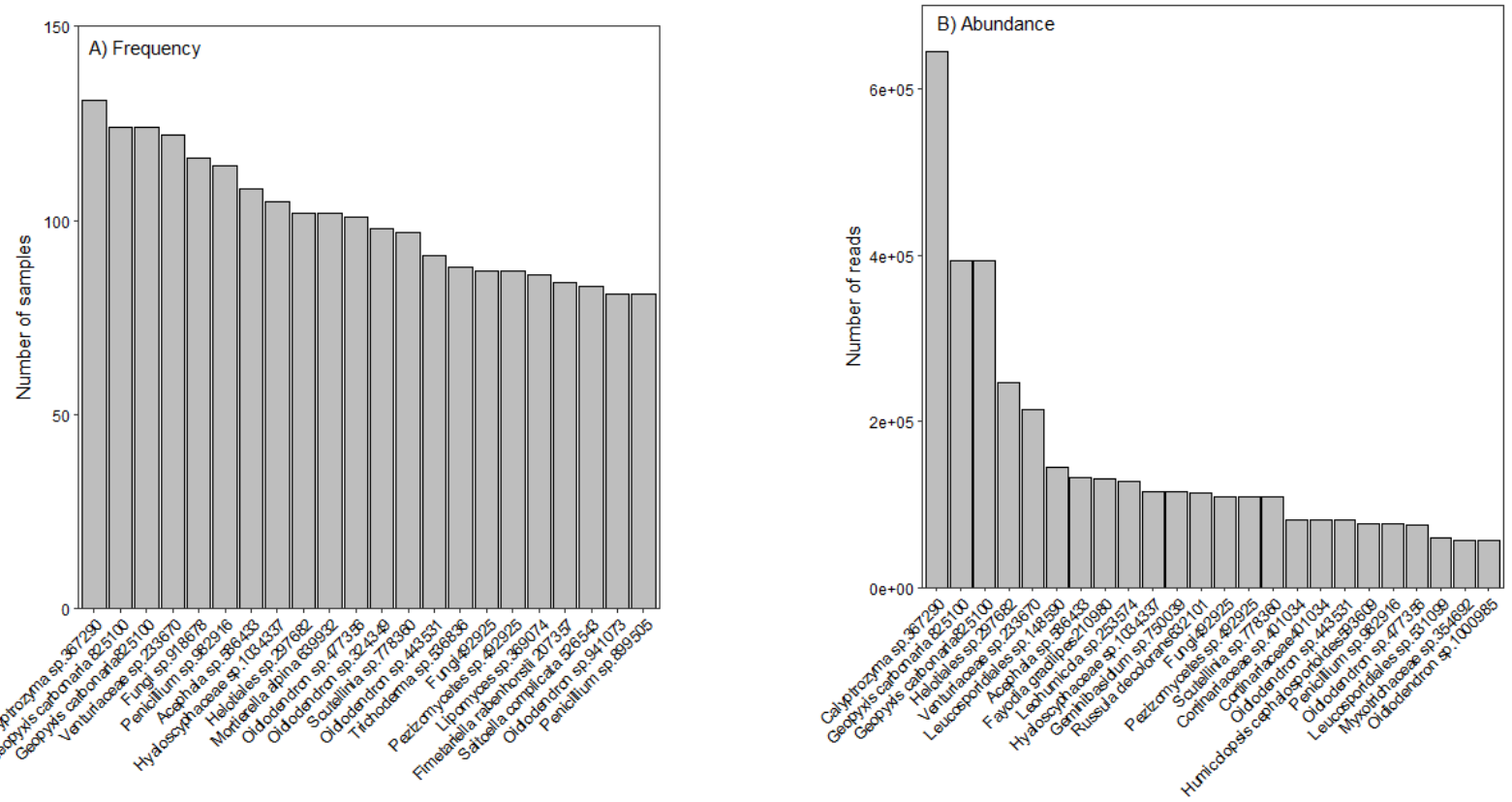

Fig. S3. Bar graphs of the 20 most frequent fungal OTUs in plots in (A) and abundant OTUs (B) for 2034 fungal operational taxonomic units (OTUs) in 138 samples from boreal forests, Northwest Territories, Canada. For full information on OTUs see Tables S3 & S4.

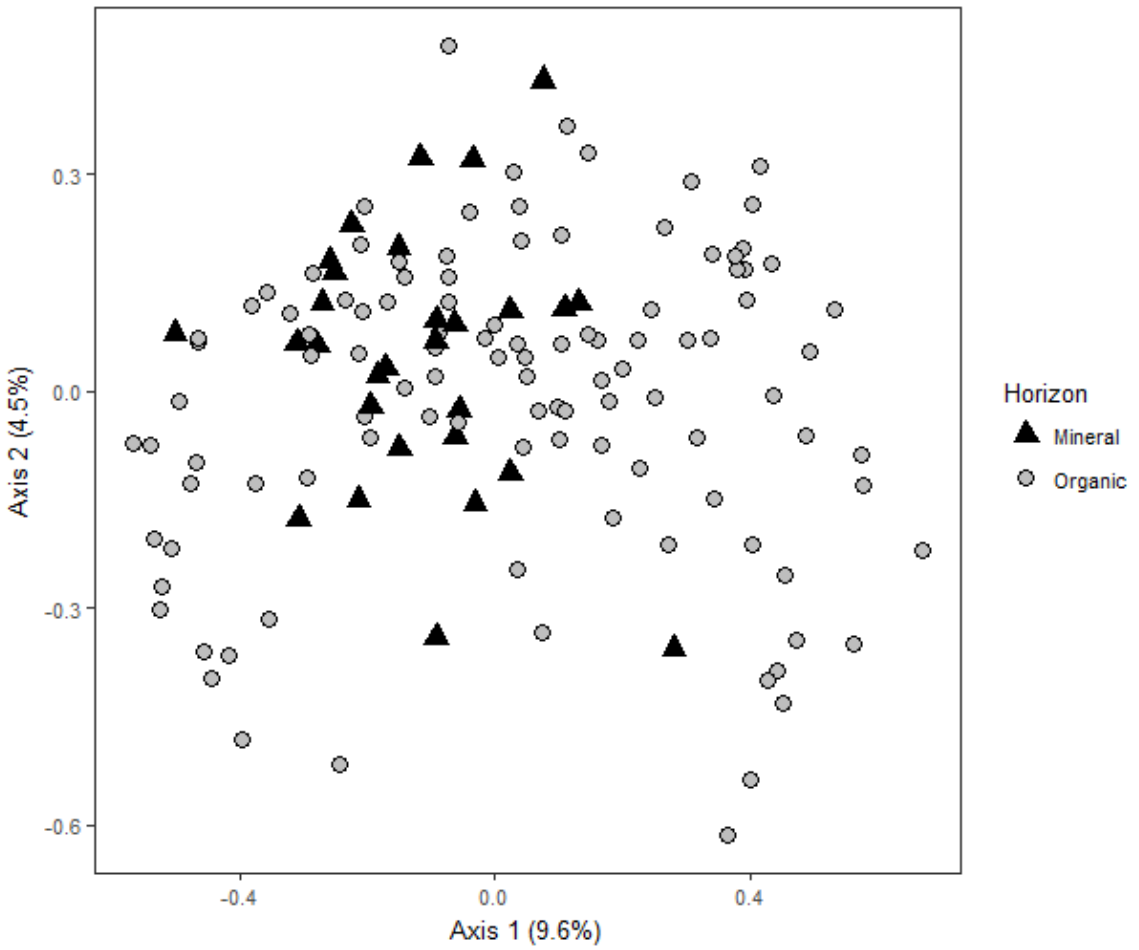

Fig. S4. Site scores for principal co-ordinates analysis (PCoA) ordination with presence-absence data for 2034 fungal operational taxonomic units (OTUs) in 137 samples from boreal forests, Northwest Territories, Canada, specifying the modified Raup-Crick dissimilarity. Values in brackets on the axes show the amount of variation in OTU composition explained by each axis. Black triangles show samples from the mineral horizon and grey circles show samples from organic the horizon.

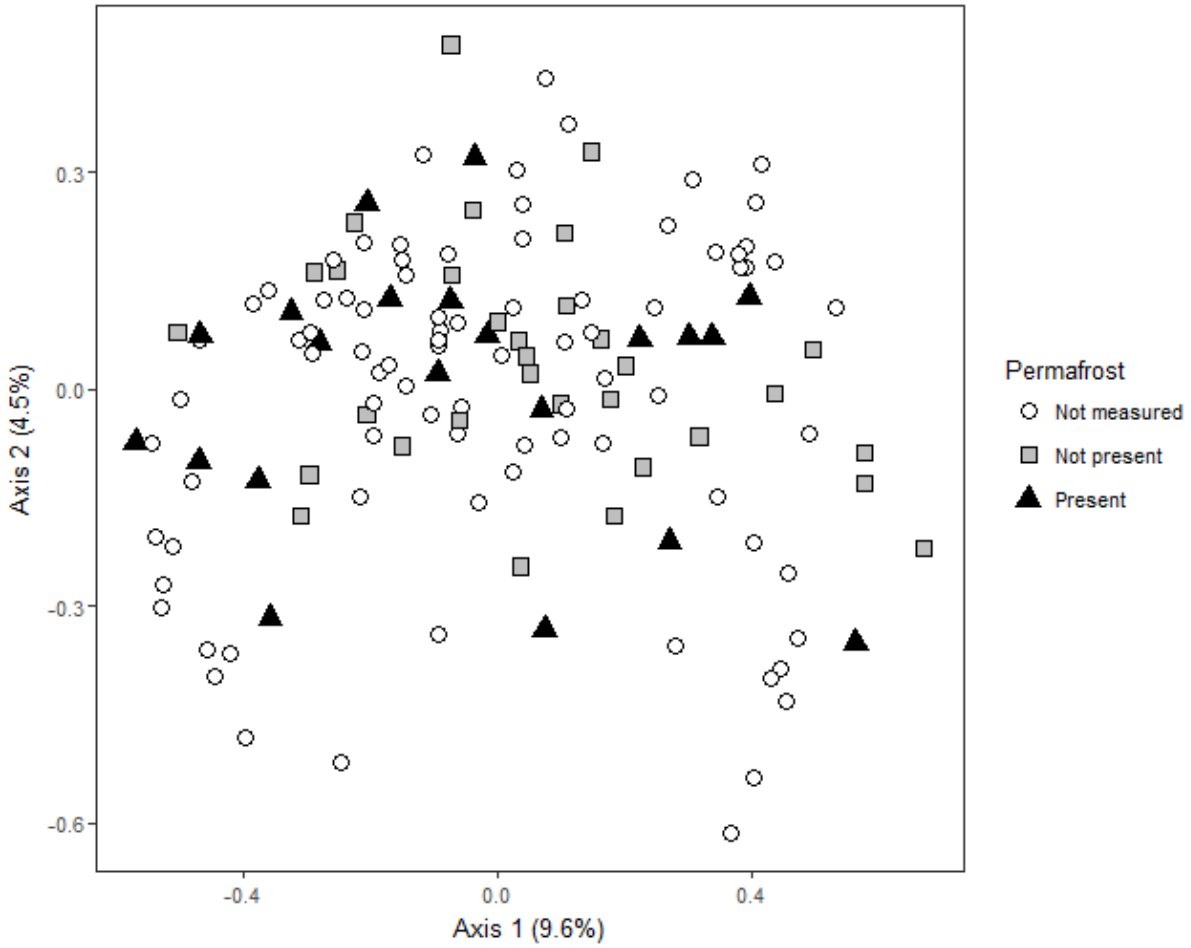

Fig. S5. Site scores for principal co-ordinates analysis (PCoA) ordination with presence-absence data for 2034 fungal operational taxonomic units (OTUs) in 137 samples from boreal forests, Northwest Territories, Canada, specifying the modified Raup-Crick dissimilarity. Values in brackets on the axes show the amount of variation in OTU composition explained by each axis. Samples from plots where permafrost containing ice was detected using electrical resistivity tomography (ERT) are shown by black triangles, plots where permafrost containing ice was not found by digging soil pits or ERT in the top 2-3 m of soil are shown by grey squares, and plots where the presence of permafrost was not measured are shown by white circles.

Supplementary Methods

Hypotheses of drivers of changes in richness and diversity of total fungi, mycorrhizas, and saprotrophs

We had specific hypotheses for the impact of each of our measured predictors on fungal community structure (Table 1). We expected total fungal richness and diversity to decline with increased fire severity due to fire-induced mortality of many taxa. Since saprotrophs have been shown to increase in abundance after fire in boreal forests (Dahlberg et al., 2001), we expected areas of greater fire severity to have greater richness and diversity of saprotrophs. The sensitivity of ectomycorrhizas to fire (Treseder et al., 2004) meant we expected lower mycorrhizal richness and diversity with increased fire severity. We further expected diversity of mycorrhizas and saprotrophs to differ in different stand types due to different litter substrates and plants associated with different stands (Day, Carrière, & Baltzer, 2017; Purdon, Brais, & Bergeron, 2004), however, we did not expect differences in total fungal richness. We expected fungal richness and diversity to increase with stand age representing fungal community change after fires. Long-term successional changes have been documented in fungal communities along chronosequences (Clemmensen et al., 2015; Sun et al., 2015; Visser, 1995) so we expected there to be an increase in mycorrhizas and declines in saprotrophs with stand age (Sun et al., 2015; Treseder et al., 2004). In terms of edaphic factors, while saprotrophs may increase in richness and diversity in soils with low C:N due to increases in microbial activity and decomposition, and mycorrhizas may decline, the opposite could occur under high C:N due to competitive interactions among these functional groups (Clemmensen et al., 2015; Gadgil & Gadgil, 1971). pH is a key determinant of microbial activity due determining nutrient availability, and is important for determining fungal community structure globally (Tedersoo et al., 2014). Therefore, we expected that fungal richness and diversity would increase as pH increased towards neutral. Since soil characteristics can be modified by fire (Certini, 2005), we also expected soil C:N and pH to interact with fire severity to impact richness and diversity of total fungi, mycorrhizas, and saprotrophs (Shenoy, Kielland, & Johnstone, 2013; Sun et al., 2015).

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