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

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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 postfire 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 1 year after fire and 8 unburned plots. High-throughput sequencing (MiSeq, ITS) revealed 2,034 fungal operational taxonomic units. 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.

KEYWORDS
disturbance, functional groups, global change, mycorrhizas, saprotrophs, Taiga Plains, understory

1 | INTRODUCTION

While boreal forests are disturbance-adapted, historical disturbance regimes are changing, particularly toward 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, Baltzer, Cumming, et al., 2018; Walker 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 prefire structure, possibly impacting ecosystem functions, such as ectomycorrhizal colonization of plants (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 et al., 2018; 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 colonization of plants to recover to prefire 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 4 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 prefire 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 postfire 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 Quebec, 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 postfire 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 postfire 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 1 year following fire after the largest wildfire event recorded in boreal forests of the Northwest Territories (NWT) of Canada, which occurred in 2014 (Canadian Interagency Forest Fire Centre, 2014). We focused 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: (a) What are the key drivers of postfire fungal community structure, in terms of richness, diversity, and composition of total fungi, mycorrhizas, and saprotrophs? We hypothesized 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). (b) What is the relationship between mycorrhizal communities and understory plant communities? We hypothesized that the composition of the postfire 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.

2 | METHODS

2.1 | Study region

In 2014, boreal regions in the NWT, Canada experienced a large fire event with 2.85 million ha burning (Walker, Baltzer, Cumming, et al., 2018; Walker et al., 2018a). Our study focused 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, while patches of jack pine 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, NWT, 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 & Climate Change Canada, 2018).

2.2 | 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 (Figure 1); 39 in four 2014 burn scars and 8 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 et al., 2018a; Walker, Baltzer, Cumming, 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 to 12 km.

At each plot, we established two 30 m parallel transects 2 m apart running from 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 5 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 1 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 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 in Walker, Baltzer, Cumming, et al. (2018) and Walker 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, Baltzer, Cumming, et al., 2018; Walker et al., 2018a). In burned black spruce-dominated plots, burn depth was based on measurements of the height of adventitious roots above the residual SOL on 10 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 prefire SOL depth and burn depth (Walker, Baltzer, Cumming, 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
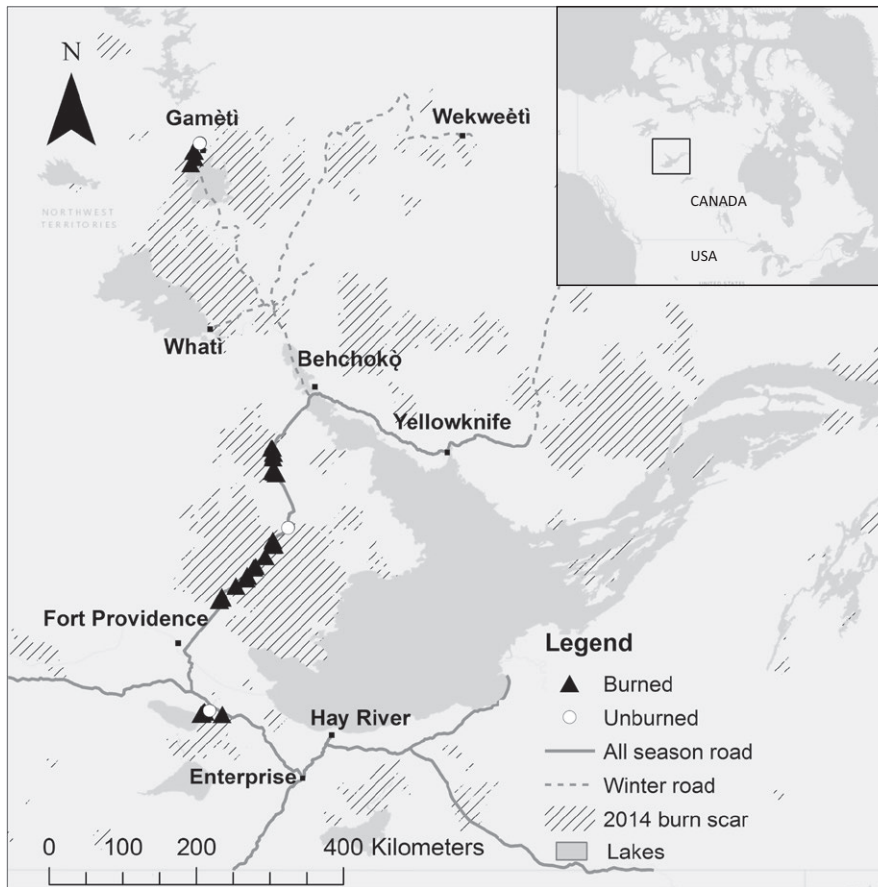
FIGURE 1 Location of 47 plots where soil samples were collected for analysis of soil fungal communities 1 year after fire in boreal forest stands of black spruce and jack pine on the Taiga Plains in the Northwest Territories, Canada. Black triangles show plots that burned in 2014, white circles show plots that did not burn in 2014 (unburned). Hashed areas show 2014 burn scars and dark gray areas represent water bodies. The minimum distance between plots was 100 m

included in this census in order to estimate prefire stem densities for each species. Stand type in burned and unburned stands was characterized 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 disks 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 disks using standard dendrochronology techniques to count rings for an estimate of minimum tree age (Cook & Kairiukstis, 1990). Detailed decisions on stand age are given in Walker, Baltzer, Cumming, et al. (2018).

2.3 | Laboratory 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 3 days to mitigate dramatic changes that may have occurred if rapidly thawed. Thawed soils were homogenized prior to subsampling. We followed the standard protocol from the MoBio Powersoil Kit (MoBio Laboratories, Solana Beach, CA) using 250 mg of starting material except that the first incubation with the proprietary protein precipitant (solution C2) was increased to 10 min to optimize 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 polymerase chain reaction (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 mmol/L deoxyribonucleotide triphosphate, 1.5 µmol/L of each primer, and 1 U Hotstart Taq polymerase. The PCR consisted of 96°C for 15 min, 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 min, 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.

2.4 | Bioinformatics processing

Bioinformatics processing was performed by McGill University and Génome Québec Innovation Centre (Montreal, Quebec, 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 small subunit ribosomal DNA 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 Fast Length Adjustment of SHort reads (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.

Operational taxonomic units 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 (<5,000 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.

2.5 | 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).

2.5.1 | 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 visualized fungal community structure using principal coordinates 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 prefire 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 for diversity we used Shannon's index ("diversity," package vegan). We developed five candidate generalized 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; Data S1; Anderson, 2008; Burnham & Anderson, 2002). 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

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 was omitted due to outlying soil C:N. The range and units of each variable are presented in Table S1. Fire severity is the proportion of the soil organic layer combusted

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

Note: Detailed hypotheses are given in Data S1.

run with a continuous response ("lmer," package lme4). All predictors were uncorrelated ($r < 0.5$) and were centered and standardized prior to inclusion.

The order of models of the candidate set was determined by corrected Akaike information criterion (AIC_c). 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 (CIs) 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% CI did not cross zero (Anderson, 2008). Estimates from this function can be biased away from zero (Cade, 2015) but we 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^2_m (fixed effects only) and conditional R^2_c (fixed and random effects) were calculated for each model ("r.squaredGLMM," package MuMIn; Barton, 2017; Nakagawa & Schielzeth, 2013). 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.

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

We focused on presence–absence responses for both plants and fungi because we did not have abundance information for the plants. First, we performed a correlation test for rarefied mycorrhizal OTU richness and plant species richness with 999 permutations; this was repeated for Shannon's diversity. Second, 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.

3 | RESULTS

3.1 | 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 (Figure S1). The species accumulation curve for the 2,034 fungal OTUs across 138 samples reached an asymptote and indicated that all OTUs were detected by ~60 samples (Figure S2). Fewer than half of the 2,034 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 in 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. (Figure S3), followed by two OTUs that matched *Geopyxis carbonaria*. OTUs matching *Oideodendron* were also common (Figure S3). Many of the most common OTUs were in both burned and unburned samples (Tables S3–S6).

Only 600 of the 2,034 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.

3.2 | 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

TABLE 2 Assignments of 2,034 fungal operational taxonomic units (OTUs) to functional groups according to FUNGuild in 138 samples from boreal forests, Northwest Territories, Canada. For each functional group, the number of taxa, number of OTUs (unique sequence clusters), and number of sequences is shown. All functional groups were assigned at the 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
Lichenized	3	3	38
Fungal parasites	3	4	1,300
Unassigned	115	1,434	281,628
Total	282	2,034	593,400

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%; Figure 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 endophytic taxa *Serendipita*, Myxotrichaceae, and

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

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

The mean mycorrhizal OTU richness per sample was 21 (*SD* 13; range: 0–63) and the mean Shannon's diversity was 1.42 (*SD* 0.70; range: 0–2.68). The most probable model for mycorrhizal richness was the burn × edaphic model followed by the full and edaphic models (Table 4). For mycorrhizal diversity, the burn model followed by the burn × edaphic model were most probable (Table 4). These two models were also the most probable when only ectomycorrhizas

TABLE 3 Results from permutational analysis of variance with modified Raup–Crick dissimilarity on 2,034 fungal operational taxonomic units (OTUs) from 137 samples from boreal forests, Northwest Territories, Canada, assessing variation of fungal community composition explained by predictor variables. Permutations were restricted within plots with 999 permutations. Fire severity is the proportion of the soil organic layer combusted

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		

Note:. Variables in bold are significant at *p* < 0.05.
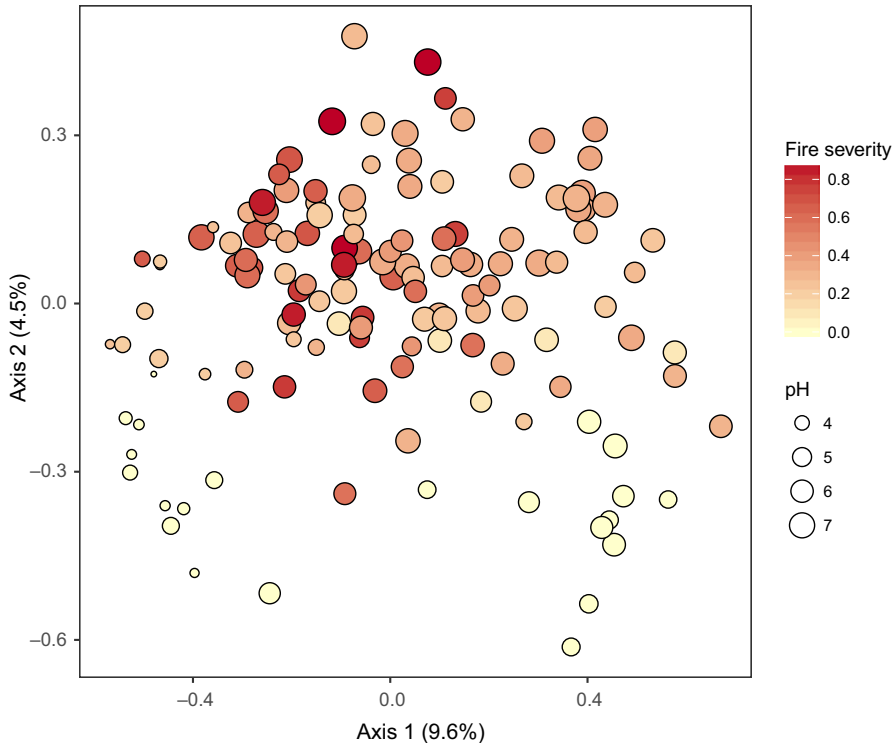Abbreviations: MS, mean sum of squares; SS, sum of squares.

FIGURE 2 Site scores for principal coordinates analysis ordination with presence–absence data for 2,034 fungal operational taxonomic units 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 fungal composition explained by each axis. The size of each point represents soil pH and the shading indicates fire severity (proportion soil organic layer combusted), which were shown to explain the most variation in fungal composition from the permutational analysis of variance (Table 3)

were considered (Table S11). All of these models had poor fit (low R^2) and there was high variation between samples within plots. Model averages showed that mycorrhizal richness and diversity both declined with increasing severity (Figure 3b,e; Table S10). Mycorrhizal richness declined with 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 (Figure 3b,e).

The mean saprotroph OTU richness per sample was 26 (*SD* 13; range: 4–62) and the 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 (Figure 3c; Table S10). None of the measured parameters were important drivers of saprotroph diversity (Table S10).

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

There were 260 mycorrhizal OTUs and 78 vascular plant species 1 year after fire. There was a significant positive correlation between

mycorrhizal and plant species richness ($r = 0.34$; $t = 4.13$; $p < 0.05$; Figure 4a) and Shannon's diversity ($r = 0.34$; $t = 4.10$; $p < 0.05$; Figure 4b). The Mantel test showed weak but significant positive correlations between mycorrhizal and plant composition ($r = 0.12$; $p < 0.01$).

4 | 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, Bååth, Nordgren, Arnebrant, & Högberg, 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. Prefire 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 postfire plant community assembly.

TABLE 4 Results of corrected Akaike information criterion (AIC$_c$)-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 AIC$_c$, the change in AIC$_c$ relative to the best model, ΔAIC$_c$, the model weight, w_i, and the log-likelihood, Log(L), are given

Response variable	Model name	K	ΔAIC$_c$	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

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 (Figure 3). In contrast, this interaction was not important for either
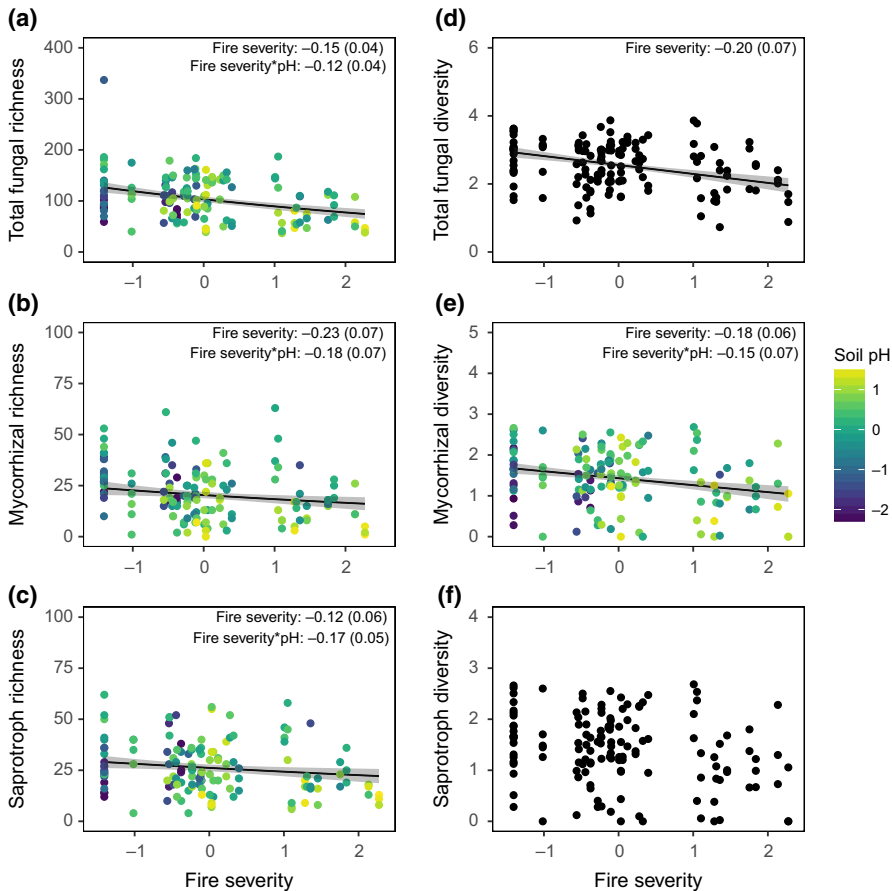
FIGURE 3 Relationships between response variables (model-average predictions) against fire severity estimated from candidate models for 2,034 fungal operational taxonomic units from 137 samples in boreal forests of the Northwest Territories, Canada. Fire severity against (a) total fungal richness, (b) 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. Gray areas around slope lines indicate 95% confidence intervals (95% CIs) based on the entire candidate model set. All variables were standardized and centered and plot was the random effect in all models. Model-averaged coefficients and *SE*s (in brackets) are given for variables for which the CIs do not overlap zero. Full outputs and CIs are presented in Table S10

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 prefire stand age, even in recently burned soils (Table 3), suggests that some proportion of fungi survived in the soil rather than colonizing 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 are 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 (N. J. Day, unpubl. 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 stabilize 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 destabilize boreal regions as a C sink, particularly with additive C losses under

FIGURE 4 Correlations between (a) mycorrhizal operational taxonomic unit (OTU) richness and vascular plant species richness and (b) mycorrhizal OTU diversity and vascular plant species diversity (Shannon's index) in 135 samples at 47 plots in boreal forests of the Northwest Territories, Canada. The *r* and *p* values for permutation correlation tests are shown. Shading of points indicates fire severity (proportion soil organic layer combusted). Three plots were omitted due to having zero plant species present
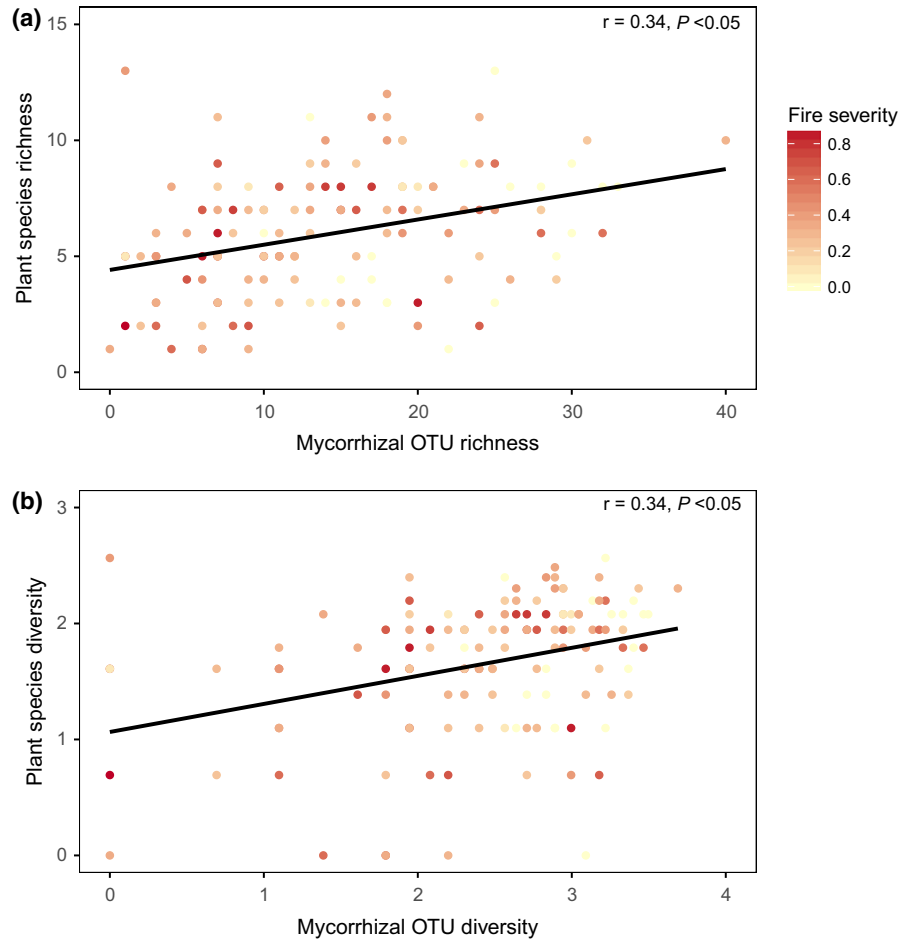
shorter fire intervals (Brown & Johnstone, 2011). We found many OTUs of the efficient nutrient cycling taxa known as cord forming fungi, such as *Cortinarius* and *Suillus*, distributed across samples regardless of fire severity. This is interesting because while *Suillus* spp., which form ectomycorrhizas 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 (Figure 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 prefire 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 (Figure 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 colonization 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, 10 plots were known to be underlain by permafrost containing ice in the top 2–3 m of soil (J. Holloway & A. G. Lewkowicz, unpubl. data); these plots were not compositionally distinct (Figure 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 NWT 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 colonized 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 *G. 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 after fire 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 colonizing 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 NWT 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 prefire 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.

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