



Host identity affects the response of mycorrhizal fungal communities to high severity fires in Alaskan boreal forests

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ABSTRACT

Ongoing climate change in the boreal forests of western North America is associated with wildfires which are increasing in extent and severity, thus impacting mycorrhizal fungal communities through fungal mortality and shifts in host species and age. We planted three native tree species, *Picea mariana*, *Picea glauca*, and *Populus tremuloides*, and non-native *Pinus contorta* var. *latifolia* at 22 post-fire sites, encompassing wide variation in fire severity and environmental gradients, across Interior Alaska. We characterized fungal community composition using Illumina MiSeq. Fire severity had a greater impact on fungal composition than the environmental variables we considered. There were large shifts in fungal Phyla and guilds with high severity, but these shifts were dependent on host tree species. We also found pine-specific fungi on *Pinus contorta* var. *latifolia*. These data suggest that shifts in mycorrhizal fungal communities from increases in fire severity may be exacerbated by associated changes in plant successional trajectories and host composition.

1. Introduction

All tree species in boreal forests are obligately mycorrhizal (Smith and Read, 2008), thus, these fungi must be considered when studying ecosystem responses to climate change and related disturbances. Across circumpolar boreal forests, warmer and drier conditions are driving increases in fire severity which has been linked to shifts in canopy and understory vegetation (Johnstone et al., 2010b; Shvidenko and Schepaschenko, 2013; Day et al., 2019). Wildfire impacts mycorrhizal fungi through heat-induced mortality and reduction of suitable hosts, or shifts in host composition and age (Neary et al., 1999; Taudière et al., 2017). Fire also impacts soil characteristics such as pH, moisture, and nutrient availability (e.g., Neary et al., 1999; Bodí et al., 2014; Hessburg et al., 2016), all of which can indirectly impact mycorrhizal fungal communities (e.g., Högberg et al., 2007; Erlandson et al., 2016; Glassman et al., 2017). Changes in mycorrhizal fungal communities induced by increasing fire severity could have important ramifications for ecosystem function. Mycorrhizal fungi are instrumental in supporting primary productivity (van der Heijden et al., 2008), serve as a major

conduit for carbon transfer from canopy to soil (Ruess et al., 2003), cycle or rearrange carbon and nitrogen stocks (e.g. Treseder and Allen, 2000; Read and Perez-Moreno, 2003; Clemmensen et al., 2013, 2015), and account for 17 times more diversity than plants in Interior Alaskan boreal forests (Taylor et al., 2014). Thus, understanding how increasing wildfire severity and associated shifts in forest tree composition impact mycorrhizal fungal community composition may help us understand climate change induced alterations to boreal forest structure and function.

Data from boreal and other forest ecosystems suggest wildfire often reduces ectomycorrhizal fungal colonization (Treseder et al., 2004; Dove and Hart, 2017) and diversity, shifts composition (e.g. Sun et al., 2015; Day et al., 2019; Pulido-Chavez et al., 2021), and lowers the potential of colonization via hyphal extension, making colonization via resistant or newly dispersed spores and other propagules more important (e.g. Bruns et al., 2002; Glassman et al., 2016). Despite decades of research on the general effects of fire on mycorrhizal fungi, relatively little is known about the more precise effects of fire characteristics (e.g. Sun et al., 2015; Holden et al., 2016; Reazin et al., 2016). The few

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studies of fire severity, defined as the loss of organic matter above and belowground (Keeley, 2009), have demonstrated that general fire effects, such as decreased richness, biomass, and low tolerance of Basidiomycota to fire are more pronounced with higher fire severity (e.g., Holden et al., 2016; Reazin et al., 2016; Day et al., 2019). These studies have been important in our understanding of how fungal communities may shift under higher fire severity, but have analyzed fungal communities from soil cores or from fungi colonizing bioassay seedlings of a single host species in simplified greenhouse conditions. Total soil fungal communities can contrast sharply with the subset on root tips (Koide et al., 2005) and do not necessarily capture the fungi directly involved in plant-fungal feedbacks. Additionally, most of these studies have examined fungi at broad taxonomic levels, potentially masking the effects on individual fungal species, which can have diverse functions within a genus (Chaverri and Samuels, 2013). Finally, while there is overlap among tree species in mycorrhizal associations, there is also strong evidence for host preference (Hortal et al., 2017; Bogar et al., 2019) and a negative relationship between ectomycorrhizal fungal community similarity and host taxonomic distance in boreal forests (Ishida et al., 2007; Bent et al., 2011).

Wildfire can filter fungal communities, which may limit partner discrimination between host and symbiont. The extent to which partner discrimination exists in disturbed environments is unknown. If partner discrimination is limited due to reduced abundance and diversity in fire filtered fungal communities, this could negatively impact host performance, as hosts often favor fungal partners that confer greater benefits and sanction cheaters (Hortal et al., 2017; Bogar et al., 2019). In contrast, partner discrimination post-fire could exacerbate fire induced changes in fungal communities when fire is accompanied by changes in plant composition as mycorrhizal fungal composition appears to be tightly linked to plant host identity (Martínez-García et al., 2015), and even genotype, within a single host species (Lamit et al., 2016). Host discrimination of fungal communities could be further modulated through priority effects (Kennedy et al., 2009) in which species that establish earlier gain a competitive advantage and influence the success of species that arrive later, and the impacts can persist for several generations (Hiscox et al., 2015; Debray et al., 2022). Either scenario could create positive plant-fungal-feedbacks during reforestation that may have important functional consequences.

Evidence suggests that greater fire severity in Interior Alaska is linked to *Populus tremuloides* and paper birch (*Betula neoalaskana*), breaking a 5000–7000 y old cycle characterized by black spruce (*Picea mariana*) self-replacement (Johnstone et al., 2010b; Scheffer et al., 2012; Hollingsworth et al., 2013). Black spruce has been theorized to retain its historic dominance due to its larger seed size allowing it to outcompete deciduous trees when the mossy organic layer is not fully combusted (Johnstone et al., 2010b). However, high severity fires can expose mineral soils where faster growing, but smaller seeded aspen and birch trees can thrive (Johnstone et al., 2010b). In addition to shifts in native host dominance, there is potential for expansion of non-native lodgepole pine (*Pinus contorta* var. *latifolia*) through escape from experimental timber plantations that are prevalent within the region and ongoing north-westward migration from the native range in Yukon, Canada (Johnstone and Chapin, 2003). There have been no native pines for >10,000 years in Interior Alaska (Lloyd et al., 2006). Along current range borders, lodgepole pine readily outcompetes black spruce after fire and maintains dominance as forest stands age (Johnstone and Chapin, 2003). Thus, fire may initiate the escape from plantations and augment spread from its current range. This is significant as pines often host fungi specific to the genus that are commonly co-introduced or established with the presence of pine (e.g. Hayward et al., 2015) and are currently undocumented in native Interior Alaskan boreal forests.

We sought to address how variation in fire severity, concomitant shifts in native host species, and range expansion of a non-native host may interact to alter the mycorrhizal fungal communities in the boreal forests of Interior Alaska. We took advantage of a large-scale regional

experiment studying the effects of fire severity on post-fire seedling success (Johnstone et al., 2010a; Mack et al., 2021) to analyze mycorrhizal fungal community composition on three native tree species, black spruce, white spruce (*Picea glauca*), and trembling aspen, as well as non-native lodgepole pine. We asked the following questions: (1) Are there relationships between fungal taxa and fire severity or other environmental variables expected to impact mycorrhizal composition? (2) Do variations in fire severity affect fungal communities of individual host species differently, thereby influencing fungal communities at the site level? (3) Does planted lodgepole pine host unique fungal partners that are not observed on native hosts?

2. Materials and methods

2.1. Site description

2004 was the largest fire year on record for Alaska, with over 2.7 million ha consumed (Wendler and Shulski, 2009; Wendler et al., 2011). Our study utilized 22 intensive study areas established within three major burn complexes from 2004: the Dalton Complex, the Taylor Complex, and the Boundary Fire Complex (Fig. S1) (Johnstone et al., 2009). These burn complexes are located in Interior Alaska and are bound by the Alaska Range (63°N) to the South, the Brooks Range and latitudinal treeline (67°N) to the North, the Dalton Highway (150°W) to the West, and the Alaska/Canada border (142°W) to the East. Interior Alaska has a continental climate characterized by a large differential in air temperature between summer and winter, relatively low precipitation (286 mm annual average) and discontinuous permafrost (Osterkamp and Romanovsky, 1999). In the spring of 2005, sites were surveyed, and several parameters were catalogued, including composite burn indices (Johnstone et al., 2020). Composite burn indices were determined from the ground as per methods from Key and Benson (2006). Braun-blauquet abundance measurements were taken for resprouting vegetation and are available through the Bonanza Creek LTER data catalog (Bernhardt, 2016; <https://doi.org/10.6073/pasta/0899340dabaa1f709c5c57e18222b875>). All sites were dominated by black spruce with occasional individuals of trembling aspen, white spruce, and paper birch prior to the 2004 fires. Pre-fire the sites ranged from wet, acidic, black spruce muskeg with understories dominated by *Eriophorum vaginatum* tussocks and acidic sphagna, to nonacidic dry forests with understories dominated by *Equisetum* and lichens (Hollingsworth et al., 2006; Johnstone et al., 2010b). The sites were chosen to maximize the range of burn severities, site moistures, topographic positions and geographic dispersion within the burn complexes (Johnstone et al., 2009).

2.2. Study design and field sampling

In the summer of 2005, greenhouse-grown seedlings of black spruce, white spruce, trembling aspen, and lodgepole pine were planted in 22 sites. All seedlings were grown in a greenhouse under identical conditions at the Institute of Arctic Biology at the University of Alaska in Fairbanks, AK three months prior to planting in the field. Seedlings were germinated in sterilized vermiculite and later transplanted to Stuewe & Sons containers filled with a sterilized mix of vermiculite and peat moss. Seedlings were grown for a total of five months and were slowly acclimated to outdoor conditions during the last two weeks of growth by placing seedlings outdoors for increasing periods of time each day. Thus, it is possible some inoculum was transplanted with the seedlings, however, we found very strong site effects that would not occur if greenhouse fungi dominated the communities. Further, the fungi colonizing the seedlings were consistent with those from other post fire studies, suggesting any potential transplanted inoculum had little to no contribution to the overall community. Black spruce, white spruce, and aspen seed provenances were from Interior Alaska, while lodgepole pine seed provenances were from Yukon Territory, Canada. Due to the optimal

growing conditions in the greenhouse, the seedlings were equivalent to the size of 2–3 y old naturally established seedlings. Prior to planting, a subset of seedlings were inspected under a dissecting scope (10–40x) and assessed for the presence of root hairs (suggesting no mycorrhiza formation) versus swollen, branched tips with a mantle (any of which would suggest colonization). It should be noted that this form of examination may not have detected certain ascomycetes that may not produce a mantle, nor would it detect endophyte colonization. Each site included 10 blocks, with one seedling of each species planted in each block separated by approximately 15 cm; the blocks were spaced 5 m apart. In the summer of 2011 and 2013, seedlings in blocks 1–7 and 8–10 were destructively harvested, respectively. Seedlings were cut at their base and collected into contractor bags for subsequent analyses. In total, we used roots from 458 seedlings, with various numbers of replicates for each host and site, cumulative sample sizes can be found in Table S1. In both harvests, three lengths of roots up to 1 m long were carefully traced out from the root collar of each seedling and collected by gently digging around roots with gloved hands and trowels. Root sections were placed into plastic bags and stored in a cooler on ice for transport to the University of Alaska, Fairbanks, AK where they were gently rinsed with water and stored in stabilizing solution similar to RNALater™, solution methods are presented in detail in the supplemental materials. All environmental variables were measured at the site level. Environmental and fire characteristics were measured at the sites in 2005 and are described in detail elsewhere (Johnstone et al., 2009; Johnstone et al., 2010b). Full data for the burned sites can be accessed through the Bonanza Creek LTER data catalog (Johnstone & Hollingsworth, 2019; <https://doi.org/10.6073/pasta/824ee24090117c30930262374ea10a81>).

2.3. Molecular methods and bioinformatics

Twelve colonized root tips were chosen by random intercept methods from each seedling ($n = 458$) and pooled. Root tips were also inspected for their apparent health before harvest and flaccid, hollow, or very brittle root tips were excluded. Although twelve root tips provide only a sampling of the potential diversity of mycorrhizal fungi on a seedling, similar to other post-fire studies, the overall diversity was low (richness = 443 taxa, average seedling richness = 14), thus sequencing more root tips would not likely alter the ecological implications of the results. Furthermore, several sites contained very small seedlings (>0.5m tall) with small root systems, and seedlings often had poorly colonized root systems with few obviously colonized root tips. Lastly, due to the large number of seedlings, not all colonized root tips could be collected. Due to high rates of colonization by non-ectomycorrhizal taxa, a root tip was considered colonized if no root hairs were visible between 10–40x. Low ectomycorrhizal colonization made it difficult to assess total colonization rates, thus we do not present them. DNA was extracted from the pooled root tips using Qiagen DNeasy 96 Plant Mini Kit plates. RNase A and Proteinase K incubations for 15 min at 65 °C and 4 h at 50 °C, respectively, were performed prior to the manufacturer's protocol, which was then followed starting at step 9. Polymerase chain reaction (PCR) using ITS4_Fun and 5.8S_Fun (Taylor et al., 2016) was then used to amplify the ITS2 region and anneal the Nextera adaptors. After initial PCR, sequencing tags, Illumina adaptors, and Nextera adaptors were annealed in a second round of PCR and samples were pooled to roughly equal concentration as estimated by gel band brightness. The final library was cleaned and short fragments were removed using AMPure XP SPRI beads, following the manufacturer protocol (Beckman Coulter, Inc, Brea, CA). The library was quantified on a Qubit Fluorometer (Thermo-Fisher Sciences, Waltham, MA) and Bioanalyzer and sequenced on an Illumina MiSeq platform (Illumina, Inc., San Diego, CA) at the University of New Mexico, Clinical Translational Science Center. Detailed DNA extraction, PCR, library preparation, and sequencing methods are described in Supplemental Methods. Illumina sequences were processed using a combination of cutadapt and USEARCH

v9.2.64_i86linux64 following the UPARSE pipeline (Edgar, 2013). Full details and parameters can be found in the supplemental file. Taxonomy assignments were performed using constax (Gdanetz et al., 2017) using the Warcup ITS training data set (Deshpande et al., 2016). Taxonomic assignments were made to the lowest level that was identified with at least 80% confidence and consensus taxonomy was used for all downstream analyses. For all OTUs identified as *Suillus* sp., we performed a BLAST search on NCBI. The closest voucher specimen match for each OTU after removing putatively misidentified collections were used as an input for building a genus-wide ITS alignment and a maximum likelihood phylogenetic tree in Garli v0.0951 with default settings (Fig. S8) to better clarify species identity. Guild classification was estimated using FUNGuild (Nguyen et al., 2016) and refined using investigator knowledge. Guild assignments were only kept if the confidence was listed as 'highly probable' or 'probable' and no more than two guilds were assigned, otherwise the guild was listed as 'unknown'. *Melinomyces* was manually assigned as 'ericoid mycorrhizal' due to its dominance in the Operational Taxonomic Unit (OTU) table. Since we were most interested in mycorrhizal fungi, we subset the final OTU table to include only putatively mycorrhizal taxa. OTUs were considered putatively mycorrhizal if they fell into the following guild classifications: 'Arbuscular Mycorrhizal' (AM), 'Ericoid Mycorrhizal' (ERM), 'Ectomycorrhizal' (EMF), and 'Dark Septate Endophyte' (DSE). The reduced OTU table contained 443 OTUs and 458 seedling samples and can be accessed through the Bonanza Creek LTER data catalog (DeVan et al., 2022; <https://doi.org/10.6073/pasta/b346127a1e9372b83e2c554fef0ec55d>).

2.4. Statistics

As fire can directly and indirectly impact several environmental conditions that have been demonstrated to be important for fungal community composition, we wished to understand the impact of fire severity compared to other environmental gradients. Thus, prior to assessing the effects of fire severity on fungal communities, we tested the correlation strength of fungal communities with fire severity compared to other environmental gradients. This was tested by examining linear models of fire severity and environmental variables with relative abundances of various fungal groups and using the vegan envfit function to examine which variables most strongly correlated with total compositional dissimilarity. Understory and total composite burn index (CBI) and percent organic matter consumed were used as indices of 'fire severity' and tested independently in preliminary analyses. Since results were qualitatively similar for all burn indices, we chose to focus on analyses derived from total CBI because it provided the clearest patterns and it incorporates both soil surface and aboveground aspects of fire severity. All analyses were completed in R v 4.0.3 and figures were produced using the ggplot2 v 3.3.3 (Wickham, 2009) and ggpubr v 0.4.0 (Kassambara, 2020) packages.

We used generalized dissimilarity models (GDMs), performed in the gdm package v 1.4.2.1 (Ferrier et al., 2007), to determine the importance of fire severity and other variables expected to structure mycorrhizal communities for each host species. These models identify the environmental gradients for which community dissimilarity is maximized between sites. We chose this approach as it overcomes nonlinear properties often found in ecological data and accounts for the nesting of individual samples within spatially clustered sites by incorporating geographic location as an environmental gradient. Before fitting GDMs, environmental variables were tested for correlation with each other (Table S14). When highly correlated (>0.85), the variable that either incorporated more environmental aspects or was more logical based on past research was kept while the other was removed. The final variable set for GDMs included: total CBI, estimated distance to the nearest unburned edge, pre-fire organic layer depth, soil texture class, pH, average of annual percent soil moisture measurements at a site over four years, post-fire residual organic layer depth, post-fire soil organic nitrogen content, slope angle, heat load index, the pre-fire proportion of black

spruce stems, and geographical location (latitude and longitude coordinates). The rationale for including each variable and their abbreviations can be found in Table 1. In brief, these models identify the environmental gradients that maximize community dissimilarity between sites. These models employ an extension of the Mantel approach, performing a regression with a link and a variance function of a single response variable matrix (pairwise site by species dissimilarity matrix) as a function of several explanatory matrices (Ferrier et al., 2007). GDMs fit nonlinear functions to the environmental variables using a linear combination of I-spline basis functions which the value of each survey site is calculated against. The absolute difference in value between sites is calculated for all pairs of sites from the I-spline basis functions. Finally, maximum likelihood estimation is used to fit coefficients to the I-spline basis functions using iterative non-negative least squares. Significance of the model is tested by comparing the deviance explained by the full model, with un-permuted environmental variables, to models where the environmental data are permuted a specified number of times using a bootstrapped p value. Variable significance is tested by repeating the above process but permuting one variable at a time and the importance quantified as percent change in deviance explained between a model fit with and without (unpermuted and permuted) the variable. Backward model selection was applied to remove variables until only significant predictors remained. Since twelve root tips may not fully represent a seedling's community composition, GDMs were run both with each seedling as an independent sample, and with fungal community composition averaged for each host by site, representing the fungal community from all root tips of a specific host species at each site. All subsequent analyses were performed only with each seedling as an independent sample as results were qualitatively similar during preliminary analyses.

NMDS ordinations and subsequent envfit and perMANOVA analyses were performed to visualize the data and test the effect of CBI, other measured environmental variables, and host on mycorrhizal fungal composition. These analyses were performed in addition to GDMs as they allowed examination of the overall mycorrhizal fungal composition (as opposed to host specific composition), and thus allowed us to test for differences between hosts which cannot be completed with GDM. Relativized OTU tables were used for NMDS analyses. The OTU tables were relativized in the phyloseq package v1.30.0 (McMurdie and Holmes, 2013) by dividing the read numbers for each OTU in a sample by the total number of reads in that sample, giving a relative abundance (RA), as opposed to rarefied abundance (McMurdie and Holmes, 2014). Stress plots and scree plots were generated using the vegan v2.5-7 (Oksanen et al., 2018) and goeveg packages v0.4.2 (Goral and Schellenberg, 2021) to determine the appropriate number of dimensions for all NMDS analyses by examining the fit and decline in stress with added dimensions. NMDSs were performed using a Bray-Curtis dissimilarity matrix of the relativized community data and environmental vectors (continuous quantitative site descriptors, i.e. pH, percent mortality, etc.) were plotted to maximize correlation of the points with the respective variables using in the vegan package. The averages of ordination scores for factor levels from envfit (categorical site descriptors, i.e. recruitment type, soil severity categories, etc.) were calculated and are shown in Table S2 perMANOVA analyses were used to statistically test whether the composition of mycorrhizal fungi was related to either total CBI or host; both simple and interaction models were run along with a model constraining the effects of total CBI by individual hosts in the vegan package. Significant test results were followed by post-hoc pairwise perMANOVA to determine which categories differed (Arbizu, 2020). Beta-dispersion of groups was compared by using the betadisp function in the vegan package.

To examine if specific taxonomic groups (Phyla or families), guilds, or diversity estimates changed predictably with fire severity, we constructed linear models of their relative abundance with measured CBI ($\text{lm}(\text{RA}_{\text{taxonomic group/guild}} \sim \text{total CBI})$ or $\text{lm}(\text{diversity metric}_{\text{Observed, Shannon, or Chao1}} \sim \text{total CBI})$). Normality of the residuals for all statistical

Table 1

Environmental variables considered in analyses, abbreviations, rationale for inclusion and the methods used to collect the data. Published data and detailed information can be found in the Bonanza Creek LTER data catalog (Johnstone et al., 2020; <https://doi.org/10.6073/pasta/824ee24090117c30930262374ea10a81>).

Variable	Abbreviation	Rationale for inclusion	Methods for variable measurement
Total CBI	Total CBI	Provides an estimate of burn severity that incorporates above and belowground metrics, as per Keeley, 2009.	Total CBI score was obtained by following standard procedures for the Composite Burn Index as per Key and Benson, 2006.
Estimated distance to nearest unburned edge	Est. dist. To burn edge	Represents a ranked distance to the nearest live stand of black spruce with greater than 100 trees, and thus the nearest likely source of fungal inoculum.	Distances <200m were paced, distances >200m were estimated visually and calibrated with measured road distances. To account for measurement error, distances were classified into eight semi-logarithmic classes. Break points were at 50, 100, 200, 400, 800, 1600, and 3000m.
Pre-fire organic layer depth	Pre-fire org.	Organic layer depth can influence the diversity and abundance of mycorrhizal fungi as they are strongly vertically stratified.	Pre-fire organic layer depth was estimated using adventitious root height as per Bobby et al. (2010)
Soil texture class	Soil texture	Soil texture influences fungal growth through influences on soil drainage, humus and base-cation related effects (Dickie et al., 2006)	Classes were estimated in the initial field assessment and ranked from coarse (1) to fine (5). 1 = sand, loamy sand, silty sand; 2 = loam, sandy loam, sandy silt; 3 = silt loam, clay loam, clayey silt loam; 4 = silt, silty clay loam, clayey silt; 5 = clay, silty clay, organics or frozen
pH	pH	pH, as it effects fungal growth, colonization, enzyme function, and realized niche space (Mahmood et al., 2003)	Average of four to five measurements taken from near-surface mineral soil samples
Average of annual percent soil moisture measurements	Moisture	Soil moisture demonstrated to influence ectomycorrhizal fungal diversity (Erlandson et al., 2016)	Average moisture as measured by time domain resonance probes over the course of 4 years.
Post-fire residual organic layer depth	Post ROM	Similar to pre-fire depth, this variable can effect fungal diversity.	Depth was measured at 11 random points along transect and averaged.
Post-fire soil organic	Post SON	N availability has been demonstrated to influence the	N content (kg/m^2) was determined using a Costech

(continued on next page)

Table 1 (continued)

Variable	Abbreviation	Rationale for inclusion	Methods for variable measurement
nitrogen content		structure of mycorrhizal fungal communities and implicated in declines of ectomycorrhizal fruiting bodies (Jiang et al., 2018; Lilleskov et al., 2002)	Elemental Analyzer (Costech Analytical, Los Angeles, California, USA).
Slope angle	Slope	Slope angle effects soil moisture, drainage, and radiation.	Slope in degrees measured by inclinometer
Heat load index	Heat load	Influences soil temperature which should effect fungal composition.	Heat load (unitless) was calculated from empirical equations from McCune, 2009). Eq2: $\ln(\text{heatload}) = -1.236 + 1.350 \cdot \cos(\text{lat}) \cdot \cos(\text{slope}) - 1.376 \cdot \cos(\text{aspect}) \cdot \sin(\text{slope}) \cdot \sin(\text{lat}) - 0.331 \cdot \sin(\text{lat}) \cdot \sin(\text{slope}) + 0.375 \cdot \sin(\text{aspect}) \cdot \sin(\text{slope})$.
Pre-fire proportion of black spruce stems	Proportion BS dens.	Reflects pre-fire forest composition and thus likely effects pre-fire fungal community composition.	Estimated by presence of charred tree stems, Boby et al. (2010).
Geographic location	Geographic location	May effect similarity of fungal communities through separation of niche space and dispersal limitation.	Latitude and longitude in decimal degrees measured by GPS (NAD 83 as datum)

tests with normality assumptions was assessed visually and quantitatively with a Shapiro-Wilk test when visual tests were unclear. When residuals for linear models did not meet normality assumptions 0.001 was added to the RA which was then log transformed. Homogeneity of variance assumptions were verified using Barlett’s test of homogeneity when appropriate. To control for the effect of host on the variation of taxonomic group RA/diversity estimates with CBI, we performed an ANCOVA using total CBI and host identity as the main effects as well as with an interaction between the variables; when significant, we tested pairwise comparisons in the multcomp package (Hothorn et al., 2008). Four diversity estimates (richness, Shannon, Simpson, Chao1) were calculated in the phyloseq package using rarefied data without replacement and OTUs no longer in the table after rarefaction were removed.

To test for differences in specific taxonomic groups, guilds, or diversity between hosts or binned CBI categories, we used Kruskal-Wallis tests in addition to or in place of standard ANOVA. In cases where ANOVA or Kruskal-Wallis showed significant differences, the Tukey or Dunn Kruskal Wallis multiple comparisons tests were performed to assess which groups were significantly different. Indicator species analyses were completed using the indicspc package v1.7.9 (Cáceres and Legendre, 2009) to assess the significance and strength of the association between particular OTUs and hosts or binned CBI categories.

3. Results

3.1. Illumina sequencing

Average and median read depth were 133,000 and 28,000 per seedling, respectively. When samples with less than 1000 reads were removed from analyses, read depth ranged between 1007 and 498,482. There were 2485 OTUs, of which 773 were confidently identified to guild and 443 were mycorrhizal. Despite making up less than a quarter of the OTUs, mycorrhizal OTUs accounted for 89% of the sequence read relative abundance (RA), and presumably some of the poorly identified fungi also fall in this category. The mycorrhizal OTUs included four phyla, 39 families, 58 genera, and 170 species. 133 OTUs were Ascomycota (R²63.03%), 299 Basidiomycota (R²36.97%), nine Glomeromycota (R²7.00e-4%), and two Mucoromycota (R²4.39e-4%). 288 OTUs were characterized as EMF (R²41.85%), 108 as ERM (R²44.96.1%), 38 as DSE (R²13.18%), and nine as AM (R² 7.00e-4%). Unprocessed sequence data are available through NCBI’s Sequence Read Archive (PRJNA806659). The final OTU table, reference sequences, taxonomic assignments, and environmental data are available through the Bonanza Creek LTER data catalog (DeVan et al., 2022; DOI:10.6073/pasta/b346127a1e9372b83e2c554fef0ec55d).

3.2. Importance of fire severity in predicting fungal community composition

The variables tested in our study (Table 1) were insufficient to explain variation in aspen fungal communities as GDMs were poorly fit. The full GDM model for aspen explained only 14.49% of the variation in fungal composition, the model deviance was 12.09%, and no variables were significant. Thus, further GDM details for aspen hosts are not presented here. In contrast, the measured environmental variables were sufficient to explain nearly a third or more of the mycorrhizal fungal community variance in full and backward selected minimal GDMs for all conifer hosts and had relatively low model deviance (<~10%) (Table 2). Black spruce mycorrhizal fungal communities were most strongly affected by total CBI, average soil moisture (measured by time domain reflectometry, TDR), and geographic location (Table 2). Lodgepole pine fungal communities were most strongly affected by total CBI, the proportion of pre-fire black spruce density (stems per square meter), pre-fire organic depth (cm), and geographic location (Table 2). Finally, white spruce fungal communities were most strongly affected by soil pH, moisture (average of three time domain reflectometry readings), and geographic location (latitude and longitude) (Table 2).

Total CBI, representing above and belowground fire severity (Keeley, 2009), was the most important variable for both black spruce and lodgepole pine fungal community dissimilarity between sites. When total CBI was permuted it reduced the explained variance by 62% for black spruce and 35% for lodgepole pine. Sites that experienced higher burn severities were more dissimilar (assessed by Bray-Curtis pairwise comparisons) from each other than were lower CBI sites; there appeared to be a threshold around CBI of 2.5 at which pairwise site dissimilarity increased drastically (Fig. 1). Total CBI did not significantly affect white spruce mycorrhizal fungal communities and was not retained in the minimal GDM. Instead, soil pH was the most important variable impacting white spruce mycorrhizal fungal communities, reducing the variance explained by 51% when permuted. White spruce fungal community pairwise dissimilarity steeply increased when sites compared had pH above 5.5. Average soil moisture was important for both black and white spruce fungal communities but had opposing trends. There were greater mycorrhizal fungal community dissimilarities between low moisture sites for black spruce and between high moisture sites for white spruce (Fig. 1). Soil moisture had a stronger effect on variation in white spruce compared to black spruce fungal communities, as there was higher maximum community dissimilarity shown by the maximum I-spline height reached (Fig. 1). Location measured by geographic

Table 2

Generalized dissimilarity model (GDM) results. The results for the full model, and models containing only significant variables are shown below. Variation in community composition explained by the full and minimal models are shown at the top, and importance for significant variables are shown in the table body. Variables that are insignificant for a particular host are denoted NA. Models were poor predictors of aspen fungal communities and are thus not shown.

Model results	Black Spruce		Lodgepole Pine		White Spruce	
	full 35.82%, $p < 0.01$, 6.75%	minimal 29.98%, $p < 0.01$; 7.36%	full 34.60%, $p = 0.05$; 5.77%	minimal 31.18%, $p < 0.01$; 6.07%	full 41.46%, $p = 0.01$; 9.58%	minimal 34.38%, $p < 0.01$; 10.74%
Predictor						
total CBI	28.96%, $p = 0.01$	62.12%, $p < 0.01$	20.51%, $p = 0.05$	35.46%, $p = 0.03$	4.21%, $p = 0.24$	NA
moisture	15.84%, $p = 0.02$	19.45%, $p = 0.03$	**	NA	7.16%, $p = 0.2$	42.45%, $p < 0.01$
soil texture	5.03%, $p = 0.3$	NA	3.69%, $p = 0.28$	NA	**	NA
slope	**	NA	**	NA	**	NA
heat load	**	NA	**	NA	**	NA
pH	0.51%, $p = 0.67$	NA	0.97%, $p = 0.43$	NA	7.03%, $p = 0.17$	51.28%, $p = 0.01$
pre-fire org.	1.41%, $p = 0.61$	NA	10.48%, $p = 0.21$	15.99%, $p = 0.1$	4.49%, $p = 0.32$	NA
post SON	**	NA	**	NA	**	NA
proportion BS dens	1.99%, $p = 0.32$	NA	5.22%, $p = 0.13$	21.91%, $p = 0.08$	2.98%, $p = 0.21$	NA
est. dist. to burn edge	**	NA	3.00%, $p = 0.29$	NA	**	NA
geographic location (latitude and longitude)	1.31%, $p < 0.01$	2.46%, $p < 0.01$	1.18%, $p = 0.04$	6.66%, $p = 0.01$	**	3.61%, $p < 0.01$

Model results present in the following order: the percent deviance explained, p values, and the model deviance. total CBI = total composite burn index, pre-fire org. = pre-fire organic matter depth in cm, post-fire SON = post-fire soil organic nitrogen content, proportion BS dens = proportion of black spruce density pre-fire (# per square meter), est. dist. to burn edge = estimated distance to burn edge. **= >0.1 change. minimal contains only variables with $p < 0.1$. Percent values in the body of the table represent variable importance which is calculated as the difference in variance explained by the full model and the model with the specific variable permuted.

coordinates impacted fungal composition for all three conifer hosts but was the least important variable for all three hosts.

Consistent with GDM models, the envfit function highlighted similar environmental variables important in explaining fungal community composition (Fig. 2, Table S2). Again, total CBI was the most important variable in determining variation in conifer mycorrhizal fungal communities ($R^2 = 0.16$, $p < 0.001$) (Table S2). The three-dimensional NMDS plot (stress = 0.199) showed a weak, but significant relationship between community composition and total CBI (perMANOVA: $R^2 = 0.027$, $p < 0.001$) (Fig. 2). Despite the importance of total CBI for community composition, total CBI did not correlate with any diversity metrics after rarefaction.

3.3. Fungal communities of aspen differ from conifers

Aspen mycorrhizal fungal communities had lower alpha diversity (Shannon) and beta dispersion ($p < 0.01$; betadisper), and hosted significantly different fungal communities from conifer hosts, described in detail below (Fig. 3A). Shannon diversity of fungal communities on aspen were lower than black spruce (Shannon diversity, $p = 0.027$; compared with Kruskal-Wallis and post-hoc Dunn test with Bonferroni adjustment) and lodgepole pine (Shannon, $p = 0.047$; compared with Kruskal-Wallis and post-hoc Dunn test with Benjamini-Hochberg adjustment) (Fig. S3; Tables S4 and S5). No other alpha diversity metrics were significantly different between any conifers. The Shannon diversity metric incorporates evenness but emphasizes richness.

3.4. Evidence for host differentiation of fungal partners after fire

There were shared fungi among all hosts, but overall community composition was considered significantly different for all hosts except black and white spruce based on perMANOVA ($R^2 = 0.048$, $p < 0.001$) and post-hoc analyses (Fig. 3A, Table S6). There were several guild and taxonomic group differences among host seedlings. Aspen had higher relative abundance of Ascomycota and ericoid mycorrhizal fungal taxa and lower relative abundance of Basidiomycota and ectomycorrhizal fungal taxa compared to coniferous hosts (Fig. 3B and C). White spruce had lower relative abundance of Basidiomycota than lodgepole pine (Fig. 3B). Lodgepole pine had higher relative abundance dark septate endophytes than either aspen or white spruce (Fig. 3C). All coniferous hosts were dominated by ectomycorrhizal fungi, followed by ericoid

mycorrhizal fungi, then dark septate endophytes, while aspens were dominated by ericoid mycorrhizal fungi, ectomycorrhizal fungi, and then dark septate endophytes.

Indicator species analyses revealed several ectomycorrhizal fungi that were more common on aspens: three *Russula* species, *Inocybe lacera*, *Sebacina* sp., *Serendipita* sp., *Alnicola/Naucoria tantilla*, and *Cortinarius parvannulatus*. Black spruce had two indicator taxa: both of which were ectomycorrhizal fungi: *Hygrophorus pustulatus* and *Cortinarius* sp. Lodgepole pine had thirteen indicator taxa: nine, mostly non-native *Suillus* species (ectomycorrhizal), and four ericoid mycorrhizal fungal taxa: *Cadophora finlandica*, *Melinomyces* sp., and two *Pezoloma* species. White spruce had four indicator taxa, all of which were identified as *Amphinema* species (ectomycorrhizal). Black spruce had the greatest number of unique OTUs ($n = 53$), followed by white spruce ($n = 41$), lodgepole pine ($n = 38$) and aspen ($n = 28$). Full indicator species analysis results can be found in Table S12.

Evidence for an interaction between host and CBI was minimal. perMANOVA analyses showed a significant interaction between host and CBI (adonis: Bray-Curtis matrix ~ CBI*host), although the effect of the interaction term was weaker than either host or burn severity alone (host: $R^2 = 0.047$, $p < 0.001$, total CBI: $R^2 = 0.028$, $p < 0.001$, host*total CBI: $R^2 = 0.010$, $p = 0.009$) (Tables S8 and S9). When total CBI was constrained by host in perMANOVA (adonis: Bray-Curtis matrix ~ host: total CBI, strata = host), it had a slightly stronger effect than it did on its own ($R^2 = 0.072$, $p < 0.001$) (Table S8) and was only significant for coniferous hosts when examined on a single host at a time (Table S9). ANCOVA analyses examining the relationship of the relative abundances of phyla, guilds, families and individual taxa with CBI and host were significant for main effects (total CBI and host identity), but only OTU2 had a significant interaction effect ($p = 0.024$) (Table S10).

Due to the near zero read and relative abundances of Mucoromycota and Glomeromycota, Ascomycota and Basidiomycota relative abundance had nearly exact inverse linear relationships with CBI (Basidiomycota $\bar{R}^2$ CBI: adj. $R^2 = 0.022$, $p < 0.001$; Ascomycota $\bar{R}^2$ CBI: adj. $R^2 = -0.022$, $p < 0.001$) (Fig. S4, Table S11). This inverse relationship was nearly identical when using rarefied read counts and thus is not an artifact of relative abundance. Relatedly, ericoid mycorrhizal fungi relative abundance increased with CBI ($p < 0.01$, adj $R^2 = 0.018$), while ectomycorrhizal fungi relative abundance declined with CBI ($p < 0.01$, $R^2 = -0.016$) (Fig. S6, Table S11). However, the relationships between phylum and guild with CBI were weak and only significant on select

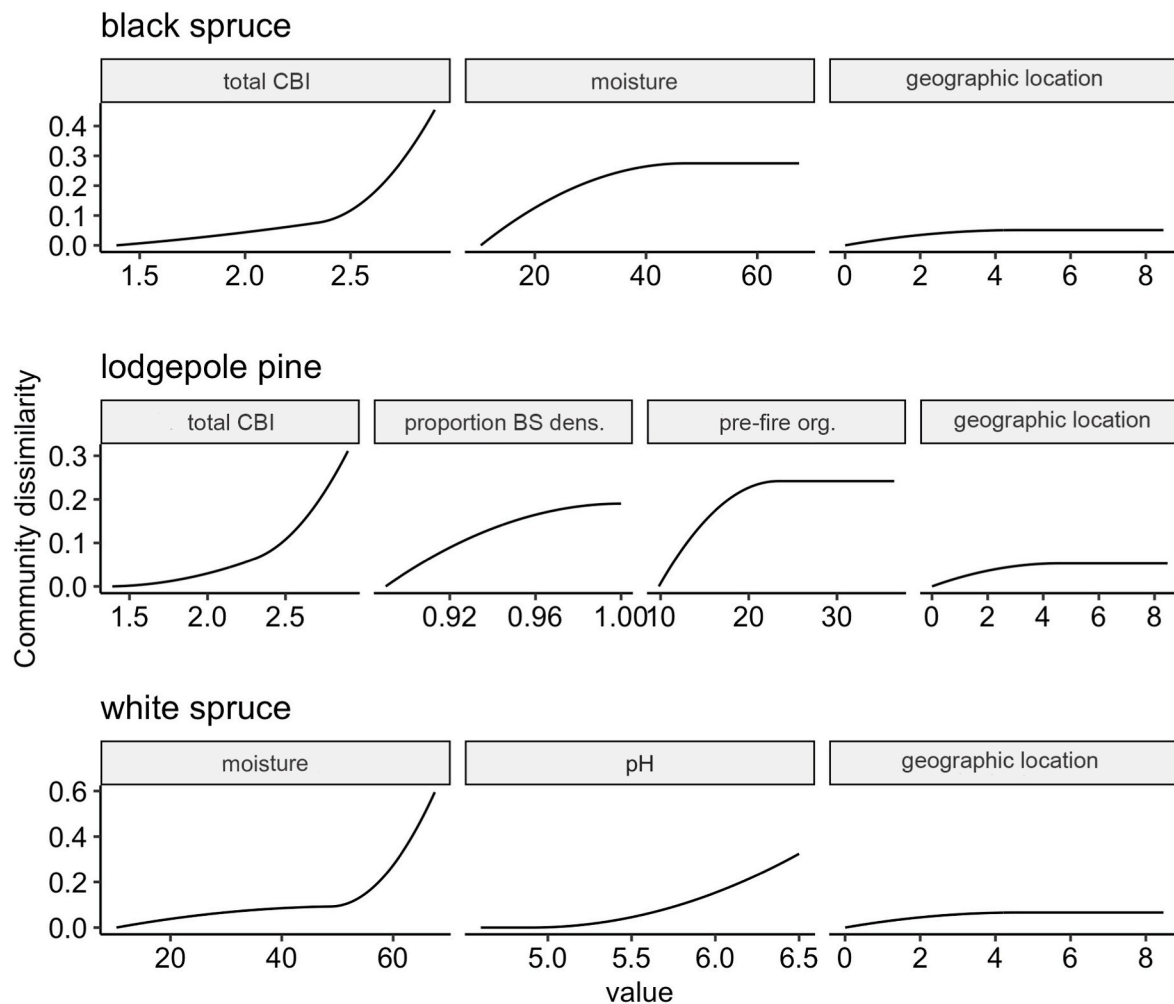


Fig. 1. I-splines for predictors kept in minimal general dissimilarity models that contained only significant variables. The x-axis shows the value of the predictor in original units, the y-axis shows fungal community dissimilarity (Bray-Curtis) as a function of the variable listed, while holding other variables constant. The maximum height of the I-splines corresponds with the maximum Bray-Curtis dissimilarity and slope indicates the rate of community turnover along the gradient. The variables are ordered from most to least important from left to right for each host species. CBI.total = total composite burn index, moisture = average of 3-time domain reflectometry measurements, PreFireOrg = pre-fire organic depth (cm), proportion BS dens = pre-fire proportion of black spruce density (number per square meter), geographic location = latitude and longitude coordinates.

coniferous hosts (Figs. S5 and S7, Table S11). All families and individual OTUs had a heavily right-skewed, zero-inflated, distribution of relative abundance and were transformed before linear regression ($\log(RA+0.01)$) or ANCOVA analyses.

The trends in relative abundance with CBI at broader levels of taxonomy were heavily influenced by the response of a few highly dominant OTUs to fire severity. The twenty most abundant taxa accounted for nearly 80% of the data, and 98% of the data was encompassed in the one hundred most abundant OTUs. We examined the relationships of the five most abundant taxa in the study. OTU2, *Thelephora terrestris*, was the second most abundant taxon in the study (overall $\bar{R}A11.26\%$), decreased with increasing CBI (Fig. 4, Table S11), and was likely a strong driver of the trends seen for both Basidiomycota and ectomycorrhizal relative abundance with CBI. OTU1, 417, and 3, all identified as *Pezoloma* spp., were the first, third, and fifth most abundant taxa across all burn sites (OTU1 overall $\bar{R}A17.90\%$; OTU417 overall $\bar{R}A9.46\%$; OTU3 overall $\bar{R}A7.56\%$). All three significantly increased with CBI, varying by host, and were likely the drivers of the positive trends in Ascomycota and ericoid mycorrhizal relative abundance with CBI. OTU5 (Fig. 4, Table S11), *Phialocephala fortinii* (overall $\bar{R}A9.22\%$) significantly declined with CBI; however, this relationship was only significant on the native hosts (Fig. 4, Table S11).

3.5. Lodgepole pine hosts pine-specific taxa previously undocumented in the region

There were 15 OTUs assigned to the genus *Suillus*, and all were found nearly exclusively on lodgepole pine (RA was low or near zero on all other hosts). The only *Suillus* species previously documented in Interior Alaska to our knowledge are *S. cavipes* and *S. grevillei* (associated with black spruce and larch) (López-Gutiérrez et al., 2008; ; Malcolm et al., 2008; Laursen and Seppelt, 2010; Laursen and McArthur, 2016), and *S. brevipes* (Laursen and Seppelt, 2010; Laursen and McArthur, 2016), but the latter has only been documented under stands of lodgepole pine in the coastal, Southeastern portion of the state where lodgepole pine occurs natively or where it has been planted in the region (Laursen, personal communication). *Suillus* was the fourth most abundant genus on lodgepole pine (11.94% by RA). OTU 20, *Suillus brevipes*, was by far the most abundant *Suillus* OTU ($\bar{R}A7.90\%$), followed by OTU32, *Suillus tomentosus* (1.64%), OTU1715, *Suillus brevipes* (1.05%), OTU85, *Suillus flavidus* (0.61%), OTU33, *Suillus pseudobrevipes* (0.48%), and OTU1836, *Suillus* sp. (0.25%). The other OTUs identified as *Suillus* made up less than a tenth of a percentage of the taxa on lodgepole pine. There was not a significant relationship between *Suillus* and CBI.

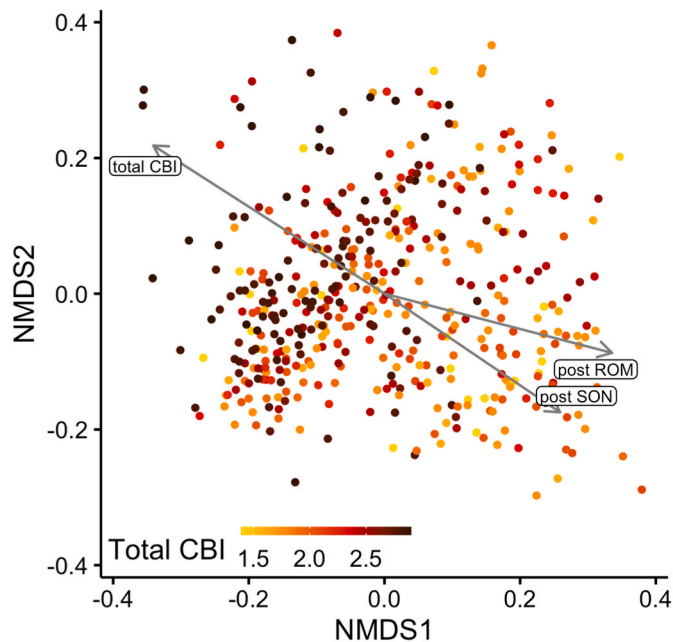


Fig. 2. The first two axes of the three-dimensional NMDS ordination (stress = 0.199) are shown. Each point represents fungal communities from 12 pooled root tips of each seedling. The input matrix was 443 taxa by 458 samples and the distance method used was Bray-Curtis. The NMDS showed clear directional change in mycorrhizal fungal community composition with total composite burn index (CBI). Envfit vectors were plotted on the ordination with arrow length proportional to their R^2 value (post ROM = residual organic matter depth, post SON = post-fire soil organic nitrogen, total CBI = total composite burn index). Only correlated continuous variables with an $R^2 \geq 0.10$ are shown on the ordination.

4. Discussion

In this study we identified relationships between fire severity and mycorrhizal fungal communities that differed among host species and were largely driven by changes in a few highly dominant fungal taxa. The importance of fire severity for mycorrhizal fungi was closely followed by soil organic nitrogen and residual organic matter, both of which are reduced by fire, and thus heavily associated with fire severity. Our study provides evidence of host differentiation in a post-fire scenario which, if this differentiation is tied to variable host benefits, has the potential to result in plant-fungal feedbacks that might play a role in disrupting a 5000–7000 y old cycle of black spruce self-replacement. Since these forests are obligately dependent on mycorrhizal fungi, which mediate some of the globe's largest carbon stocks (Clemmensen et al., 2013; Bradshaw and Warkentin, 2015) these changes could be far reaching.

A prior soil core study in the region found stark differences in mycorrhizal fungal communities between black spruce, white spruce, and early deciduous forests (Taylor et al., 2010). While we found substantial overlap of the four hosts' fungal communities (Fig. 3), they were significantly different, except for black and white spruce. Although host fungal communities were visually similar, the differences in the proportions of various taxa statistically set them apart. All our sites were dominated by black spruce pre-fire (90%–100% by stem density measured as number per square meter), thus, the post-fire fungal pool of survivors and short and medium-distance dispersers may have been limited to fungi that are common or abundant in black spruce forests. A key feature of many black spruce forests in Interior Alaska is a thick, mossy, organic understory that contributes to carbon storage, insulates permafrost, and fosters continued black spruce dominance due to seed traits (Johnstone et al., 2010b). Deep combustion of this layer, which happens only in severe fires, lends a competitive advantage to faster

growing birch, lodgepole pine, and aspen (Johnstone et al., 2010b). In our study, the latter two species hosted significantly different fungal communities compared to the communities colonizing black spruce. Fungal communities of black spruce and lodgepole pine were the most strongly affected by fire severity as per GDM, suggesting potential for post-fire plant-soil feedbacks after high severity fires that could possibly augment the establishment of lodgepole pine in forests previously dominated by black spruce. For example, high fire severity decreased the relative abundance of ectomycorrhizal fungi in favor of increases in dark septate endophytes and ericoid mycorrhizal fungi, in congruence with other studies (e.g. Horton et al., 1998; Bent et al., 2011; Hewitt et al., 2017), and these fungi have lesser known effects on host plant vitality. This shift was more pronounced for black spruce compared to lodgepole pine hosts. If dark septate endophytes and ericoid mycorrhizal fungi are less beneficial, as some species were found to be by Hewitt et al. (2020), they may reduce the ability of black spruce to compete with lodgepole pine after fire. However, this theory needs to be tested explicitly by measuring natural establishment post-fire rather than an outplant study where seedlings have artificially enhanced survival. Furthermore, high correlation of lodgepole pine fungal community composition with pre-fire black spruce density suggests lodgepole pine fungal communities are influenced by forest legacies that may be weakened by increasing fire severity. Reduction of black spruce adapted fungi may reduce competition and improve establishment success of fungi that are potentially more beneficial to lodgepole pine. However, we acknowledge that our study design does not allow us to separate the impacts of fire induced environmental changes from mycorrhizal communities on the two hosts.

As the only deciduous host in our study, aspens are the most phylogenetically distinct from black spruce and this was reflected in their post-fire mycorrhizal composition. Aspen hosted a lower alpha and beta diversity of fungi than coniferous species, which may similarly be due to prior dominance of black spruce in all our sites and the surrounding forests (Hollingsworth et al., 2013). Hosts and mycorrhizal fungi both display taxonomic preferences and participate in partner discrimination (Reinhart et al., 2012; Chen et al., 2017; Bogar et al., 2019), thus lower fungal diversity on aspen could reflect fewer compatible fungi prior to fire and those locally available to disperse into newly burned sites were likely adapted to black spruce. We found little variation in aspen hosts following fire, which explains the inability of our GDM models to predict turnover in fungal communities with any environmental variables measured. Low diversity aspen hosts were dominated by fungal taxa that increased in abundance at the highest fire severities on coniferous hosts. Aspen is common after fire and other disturbances (Bartos et al., 1994) and is a promiscuous host with the ability to form both arbuscular and ectomycorrhizal associations (Cripps, 2001). Thus, perhaps aspen is adapted to partner with fungi common in disturbed environments that are not as frequently reported on other ectomycorrhizal hosts in undisturbed ecosystems, such as ericoid mycorrhizal fungi, and this may contribute to its success in these contexts. However, these theories have not been explicitly tested to our knowledge.

Despite evidence for different host preferences post-fire, black and white spruce fungal communities were not significantly different, which contrasts with unburned forests in the region where they are distinct (Taylor et al., 2014), suggesting fire may reduce inoculum and contribute to homogenization of host fungal communities. However, whether increased overlap in fungal community composition between black and white spruce is due to reduction in inoculum from fire, or the fact that all burned sites were previously dominated by black spruce is untested. Similar phenomena have been observed in the Southwestern US, where piñon pine ectomycorrhizal fungal communities converged towards dominance of a few closely related taxa when subject to diverse stresses (herbivory, parasites, competing trees or drought) (Gehring et al., 2014). Our results suggest fire severity associated increases in aspen may cause a reduction in local fungal diversity, as aspens host

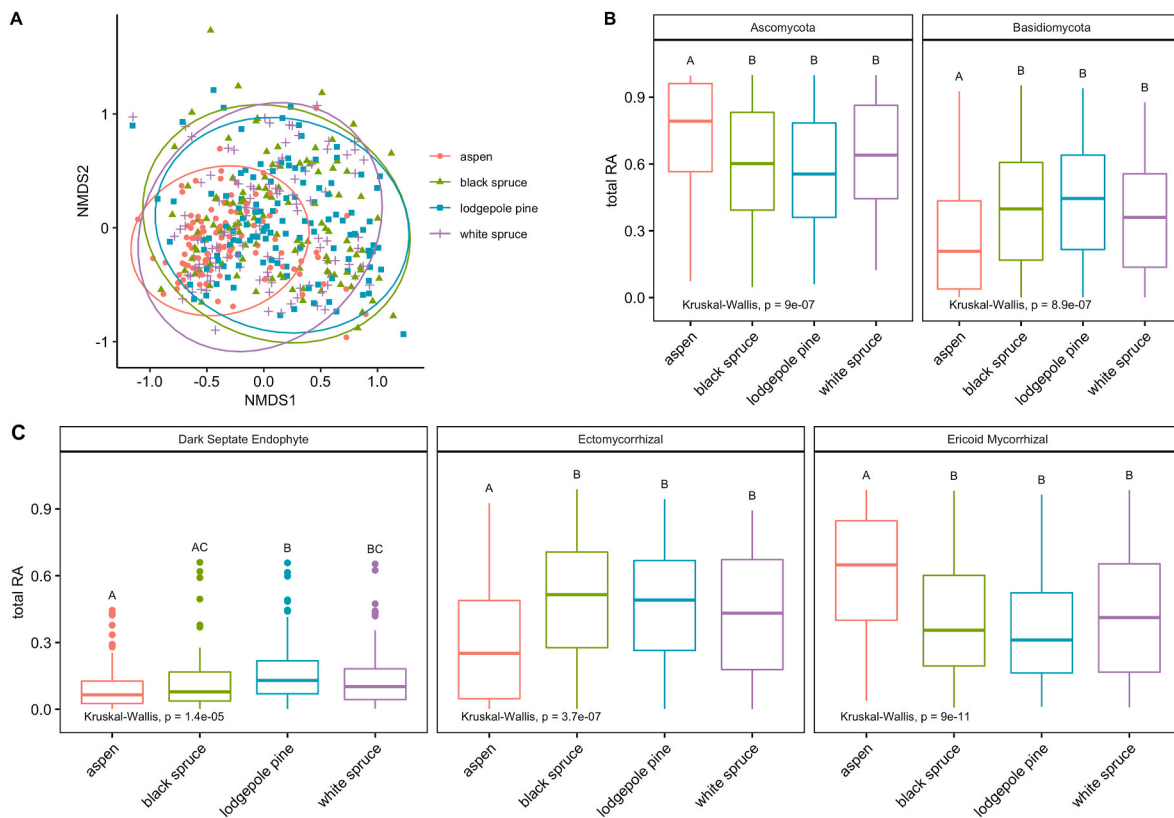


Fig. 3. (A) The same NMDS ordination as Fig. 2 is shown but colored by host tree species. Despite substantial overlap, there was a significant difference between hosts per perMANOVA ($R^2 = 0.047$, $p < 0.001$). Relative abundances (RAs) of various fungal groups were compared between host species using Kruskal Wallis tests with Dunn post-hoc analyses, $\alpha = 0.05$. Community composition is significantly different between all hosts except black and white spruce. Aspen had significantly lower dispersion compared to conifers ($p < 0.001$). (B) Aspen had significantly higher Ascomycota RA compared to conifer species. White spruce had nearly significantly higher Ascomycota RA compared to lodgepole pine ($p = 0.07$). Basidiomycota RA was significantly higher on conifers compared to aspen, and nearly significantly higher on lodgepole pine compared to white spruce ($p = 0.07$). (C) Ectomycorrhizal RA was significantly higher on conifers compared to aspen; conversely, ericoid mycorrhizal RA was significantly higher on aspen compared to conifers. Dark septate endophyte RA was significantly higher on lodgepole pine compared to aspen and black spruce.

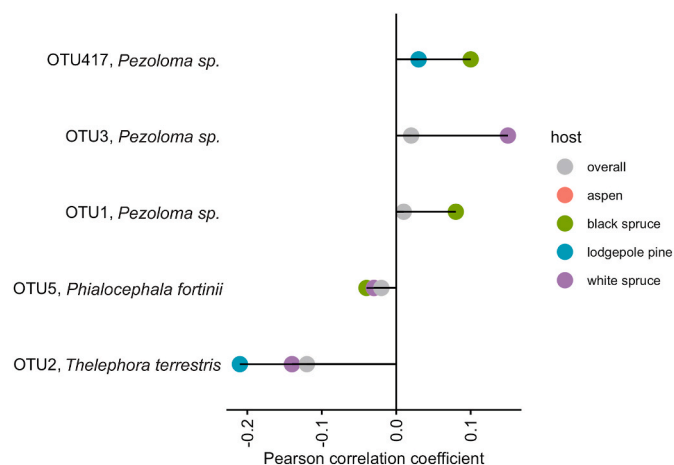


Fig. 4. Pearson correlation coefficients shown for five most abundant taxa where they had significant ($p < 0.05$) correlations with total composite burn index.

only a subset of the fungi found on coniferous hosts after fire. Additionally, increases in aspen and subsequent changes in mycorrhizal fungal communities could disrupt plant-fungal feedbacks that have likely been shaped by black spruce in Interior Alaska for millennia.

Phylum and guild level fungal compositional correlations with fire

severity observed in the current study were driven by strong responses of a few highly dominant taxa. These taxa accounted for large proportions of their respective phyla and guilds, and because they were relatively sensitive to fire severity, they drove the patterns observed at broader taxonomic levels. This was similar to the findings of Reazin et al. (2016), however the OTU level taxa driving broader patterns differed from ours, but this is likely due to differences in ecosystem type. Together, this underlines the importance of analyzing fungal communities at fine taxonomic levels since conclusions drawn from analyses on broad taxonomic levels may actually only reflect a single fungal species and opposing trends could be true for other species within the same broader taxonomic group or guild. This is especially important as closely related fungi can have diverse functions and generalizing from broader taxonomic levels may obscure the ability to link fungal structure to function. For example, the family Helotiaceae contains both ericoid mycorrhizal fungi and saprotrophs, among other guilds. In our study, where CBI ranged from 1.39 to 2.9, some of the fungal taxa with the highest relative abundances have commonly been identified in spore banks (i.e. *Cenococcum*, *Phialophora*, *Cadophora*, *Wilcoxina*, *Thelephora*) and are frequently found after fire in both temperate and boreal forests (Baar et al., 1999; Taylor and Bruns, 1999; Nguyen et al., 2012; Glassman et al., 2016). Similar taxa as found in this study were found on naturally regenerating seedlings in the same region four years after the 2004 fire season and were suggested to be widely and evenly distributed (Bent et al., 2011). Conversely, fungal genera that have previously observed as dominants in unburned Interior Alaskan black spruce forests (e.g. *Cortinarius*, *Tricholoma*, *Russula*) had notably low abundances (Taylor et al.,

2014). In combination with prior studies, our results show similarities in dominant taxa of post-fire fungal communities of multiple forest types after one, four, seven, and nine years post fire. This evidence for slow recovery is consistent with earlier studies that reported ectomycorrhizal colonization rates can take 15 y to recover, and community composition can require up to 41 years to stabilize following fire (Visser, 1995; Treseder et al., 2004). Since the mycorrhizal fungal community composition becomes more dissimilar with greater fire severity, it seems likely that increasingly severe fires could extend recovery time or prevent return to pre-fire fungal communities altogether, especially when fire is accompanied by shifts in forest tree composition, since fungal composition is so tightly linked to host identity (e.g. Ishida et al., 2007; Martínez-García et al., 2015).

We did not find any relationship with alpha diversity or richness with fire severity which is contrary to previous studies that have reported declines in ectomycorrhizal fungal biomass, respiration, colonization, diversity, and abundance following fires of varying severity (Dahlberg et al., 2001; Reazin et al., 2016; Day et al., 2019). However, it is notable that our study took place 5–7 y after planting and there may have been differences in diversity at an earlier time point. Further, the sites in our study all experienced stand-replacing fires, whereas in most of the previously cited studies most fires were non-stand-replacing. Fire in the boreal forest often results in near complete mortality of trees, likely resulting in a drastic reduction in ectomycorrhizal fungal inoculum. However, resprouting vegetation post-fire may act as an important refugium for root-colonizing fungi. Recovery of post-fire vegetation was sampled in a subset of our sites and showed higher average coverage of ericaceous hosts as compared to ectomycorrhizal hosts at every burn site surveyed, and no ectomycorrhizal seedlings were found at the site with the highest total CBI (TC29) (Fig. S2, Table S3) (Bernhardt, 2016). The increase of ericoid mycorrhizal fungal relative abundance with total CBI suggests that the lack of naturally regenerating or surviving ectomycorrhizal hosts (black spruce or ectomycorrhizal shrubs) and thus ectomycorrhizal fungi at sites experiencing higher burn severities, could reduce competition experienced by ericoid mycorrhizal fungi and allow them to colonize seedlings that are typically ectomycorrhizal. Similarly, Hewitt et al. (2017) documented fungal community overlap between naturally regenerating ectomycorrhizal seedlings and resprouting ericoid shrubs following a tundra fire, and posited that resprouting ericoid shrubs serve as a potential hub of inoculum for ectomycorrhizal seedlings. Ericoid mycorrhizal fungi colonizing seedlings via mycelial expansion from resprouting shrubs may have a competitive advantage due to priority effects (Kennedy et al., 2009) and are also better adapted to phenolics produced by their ericaceous hosts than are typical ectomycorrhizal fungi (Pellissier, 1993; Souto et al., 2000; Mallik, 2003), which could bolster their presence and longevity following fire. Increases in ericoid mycorrhizal fungi at the expense of ectomycorrhizal fungi could have far-reaching effects for ecosystem function. For example, ericoid mycorrhizal fungi are hypothesized to contribute to greater carbon storage due to their recalcitrant, often melanized, biomass and have greater nitrogen mobilizing capabilities, while ectomycorrhizal fungi, especially basidiomycete species that produce rhizomorphs, may be more efficient at transporting nutrients long distances (Read and Perez-Moreno, 2003; Clemmensen et al., 2015). Thus, increasing mortality of black spruce with higher fire severities may spur the loss of ectomycorrhizal fungi, opening niche space for ericoid mycorrhizal and other opportunistic fungi that have the potential to augment establishment of other host tree species and alter nutrient cycling dynamics.

Lodgepole pine had substantial overlap in fungal community composition with all the native host species, suggesting that its establishment and potential range expansion could be facilitated by local fungal taxa. However, lodgepole pine was preferred by several fungi based on indicator species analysis, including members of the genus *Suillus*, which contains many species that occur solely on the genus *Pinus* (Molina and Horton, 2015; Liao et al., 2016), and have not previously

been documented in Interior Alaska (Laursen and Seppelt, 2010; Taylor et al., 2014; Laursen and McArthur, 2016). There was a surprising diversity, geographic spread, and overall abundance of the genus *Suillus* on lodgepole pine seedlings, and these fungi were dominant on pines regardless of burn severity. This suggests, cointroduction or revitalization of dormant *Suillus* propagules has already occurred and could be augmented by either escape from experimental plantations or by natural migration. The decline in ectomycorrhizal taxa with fire severity compared to the lack of a relationship of *Suillus* with fire severity suggests suilloid fungi are less affected by fire than other ectomycorrhizal taxa and may serve as drivers of pine expansion and invasion in Interior Alaska, consistent with previous work in other biomes (Policelli et al., 2019).

The source of inoculum for *Suillus* in Interior Alaska is unknown. However, we note that all the seedlings were greenhouse grown in Fairbanks, Alaska, and did not exhibit visible colonization when planted. Greenhouse contamination would thus be unlikely to explain the diversity of *Suillus* species recovered on pine seedlings. Furthermore, *Suillus* sporocarps are abundant in lodgepole pine plantations throughout Alaska (DeVan, personal observation), suggesting that plantations may be one source of inoculum. Despite prior evidence for limited dispersal abilities in the genus (e.g. Galante et al., 2011; Peay et al., 2012; Branco et al., 2017), *Suillus* was found on seedling roots across most of our sites, including ones that were separated by hundreds of kilometers from the nearest plantation. *Suillus granulosus* and other previously undocumented mycorrhizal fungi in Interior Alaska have been recorded with pines planted at least nine km from the closest native stand, which, along with our data provides support for longer distance dispersal potential in the genus (Urcelay et al., 2017). Because pine was present in Interior Alaska ~10,000 y ago (Matthews, 1970), an alternative hypothesis may be posited: ancient *Suillus* propagules could be preserved in permafrost soils and become reactivated with thaw (which is promoted by severe fires) and establish due to presence of an appropriate host, lodgepole pine (Chapin et al., 2006; Bellemain et al., 2013). Pither and Pickles (2017) recently proposed a ‘paleosymbiosis’ hypothesis that migrating hosts could associate with fungi that have been inactive for millennia and suggested this is particularly plausible in regions with favorable preservation conditions such as permafrost. Regardless of the source of inoculum, our results suggest that the introduction and spread of lodgepole pine can lead to explosions of *Suillus* populations nearly anywhere in Interior Alaska, and along with pine, these populations have the potential to significantly alter forest structure and function. For example, the tuberculate structures formed by *Suillus tomentosus* and *Pinus contorta* host diazotrophic bacteria that have 150–800 fold higher nitrogenase activity compared to other EMF-bacterial combinations (Frey-Klett et al., 2007; Paul et al., 2007, 2012). Since many boreal forests are strongly nitrogen limited (Hobbie et al., 2002), co-introduction of *S. tomentosus* could lend a competitive advantage over native hosts and alter ecosystem nitrogen dynamics.

To our knowledge, this study is the first to reveal host-specific dynamics of fungal community dissimilarity in response to increasing fire severity. These dynamics could, in turn, influence successional trajectories in the Interior Alaskan boreal forest. Aspen and lodgepole pine forests support very different understory structure and vegetation in comparison to black spruce forests (Chapin et al., 2006). Recent work further highlights a correlation of fungal and understory plant species diversity, suggesting cascading ramifications of altered fungal diversity (Day et al., 2019). Severe fires promote dominance of native aspen (Johnstone et al., 2010b; Shenoy et al., 2011; Kelly et al., 2013) and create opportunities for recruitment and expansion of non-native lodgepole pine (Johnstone and Chapin, 2003). Aspen and lodgepole pine in turn associate with distinct fungi and may functionally alter the local environment. Increasing aspen dominance is predicted to exert a negative feedback on fire frequency and intensity due to its lower flammability (Barrett et al., 2011; Mann et al., 2012). In contrast, lodgepole pine is highly flammable and fire-adapted (Brown, 1975), and

thus perhaps has the greatest potential to alter both native fungal communities and fire regimes in boreal forests. The dependence of global carbon stocks on these forests and the importance of these fungi in mediating these stocks makes these findings a valuable contribution to our understanding of boreal ecosystem responses to increasing wildfire severity.

Declaration of competing interest

We have no conflicts of interest to disclose. Please address correspondence regarding this manuscript to Rae DeVan (m.rae.dev@unh.edu). Below we have provided the names and contact information for five suggested reviewers along with a data availability statement. Thank you for your consideration of this manuscript.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.funeco.2022.101222>.

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