

REVIEW

Fire as a Dynamic Ecological and Evolutionary Force

Wildfire impacts on root-associated fungi and predicted plant–soil feedbacks in the boreal forest: Research progress and recommendations

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Abstract

1. Root-associated fungi play a critical role in plant ecophysiology, growth and subsequent responses to disturbances, so they are thought to be particularly instrumental in shaping vegetation dynamics after fire in the boreal forest. Despite increasing data on the distribution of fungal taxonomic diversity through space and time in boreal ecosystems, there are knowledge gaps with respect to linking these patterns to ecosystem function and process.
2. Here we explore what is currently known about postfire root-associated fungi in the boreal forest. We focus on wildfire impacts on mycorrhizal fungi and the relationships between plant–fungal interactions and forest recovery in an effort to explore whether postfire mycorrhizal dynamics underlie plant–soil feedbacks that may influence fire-facilitated vegetation shifts.
3. We characterize the mechanisms by which wildfire influences root-associated fungal community assembly. We identify scenarios of postfire plant–fungal interactions that represent putative positive and negative plant–soil feedbacks that may impact successional trajectories. We highlight the need for empirical field observations and experiments to inform our ability to translate patterns of postfire root-associated fungal diversity to ecological function and application in models.
4. We suggest that understanding postfire interactions between root-associated fungi and plants is critical to predict fire effects on vegetation patterns, ecosystem function, future landscape flammability and feedbacks to climate.

KEYWORDS

Arctic, climate change, community assembly, dark septate endophytes, ectomycorrhizal fungi, ericoid mycorrhizal fungi, subarctic, succession

1 | BACKGROUND: POSTFIRE PLANT–SOIL FEEDBACKS IN THE BOREAL FOREST

Interactions between plants and soil biota after wildfire have the potential to shape vegetation patterns and ecosystem function in

the boreal forest. Plant–soil feedbacks encompass interactions among plants, rhizosphere microbes and abiotic soil conditions that influence plant growth and diversity, and thus regulate ecosystem dynamics (Bever et al., 2012; van der Putten et al., 2013). Plant–soil feedbacks can be positive, where plants accumulate biota that

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are beneficial for their growth, for example mycorrhizal mutualists, or negative, where plants accumulate biota that reduce growth, such as pathogens (Bever et al., 2012; van der Putten et al., 2013). Plants can foster or inhibit specific soil biota through various exudates and metabolic by-products, alteration of soil conditions (nutrients, pH) and litter deposition (van der Putten et al., 2016; Veen et al., 2019). Critically, plant–soil feedbacks are species specific, so soil biota that exert positive growth effects on one plant species may exert negative growth effects on another species, which is why plant–soil feedbacks are considered a key mechanism underpinning species coexistence in plant communities (Bever et al., 2012; van der Putten et al., 2013). Disturbance events like wildfires alter the physical, chemical and biotic soil environment (Certini, 2005), providing new conditions for postfire communities of soil biota (Cairney & Bastias, 2007) and establishing vegetation to engage in plant–soil feedbacks that influence plant successional trajectories.

Root-associated fungi play key roles in plant–soil feedbacks making them a potentially critical determinant of ecosystem responses to fire disturbance and the effects of climate change. Root-associated fungi include mycorrhizal fungi of different guilds, for example, ectomycorrhizal, ericoid and arbuscular mycorrhizal fungi, along with other fungal guilds with less certain functional status for plants, for example, dark septate endophytes. We expect fungal communities to play a dominant role in plant–soil feedbacks in boreal forests because boreal trees universally form ectomycorrhizae. Wildfire disturbance, which has intensified with climate change, reorganizes the composition of root-associated fungi, which may, in turn, affect plant productivity and successional trajectories through plant–soil feedbacks. Because postfire forest composition influences the

ecosystem carbon storage capacity (Mack et al., 2021) and surface energy exchange (Betts & Ball, 1997), elucidating plant–soil feedbacks in the boreal forest, a biome with disproportionately large soil carbon stores, likely has important implications for predicting terrestrial feedbacks to the climate system.

We have a better understanding of above-ground postfire patterns and processes in the boreal forest than we do below-ground ecology. Historically, self-replacing successional trajectories have occurred following wildfires in the spruce and larch-dominated forests of North America and Eurasia (Alexander et al., 2018; Johnstone, Chapin, et al., 2010). However, alternative successional trajectories where deciduous or pine trees replace spruce are correlated with climate-induced changes in the wildfire regime (Baltzer et al., 2021; Johnstone, Hollingsworth, et al., 2010; Schulze et al., 2012). The roles of fungi in slowing or facilitating these transitions are poorly understood. However, studies documenting patterns of community assembly and succession of root-associated fungi after fire are accumulating in the boreal forest (Figure 1; Appendix S1, Table S1). Analyses to date provide insights into patterns of fungal diversity in relation to fire characteristics, vegetation composition and environmental variables (e.g. Dahlberg, 2002; Sun et al., 2015; Treseder et al., 2004). Most studies assessing fire impacts on fungi in the boreal forest are observational, assessing taxonomic changes in fungal community structure, abundance or biomass in soil (Figure 1; Figures S3–S5). Yet, the translation of root-associated fungal diversity to functional attributes that might predict outcomes of plant–soil feedbacks is limited by the challenge of measuring key fungal traits such as growth rate, residence time, tissue chemistry and others (Table 1). Instead, function has been inferred based on limited

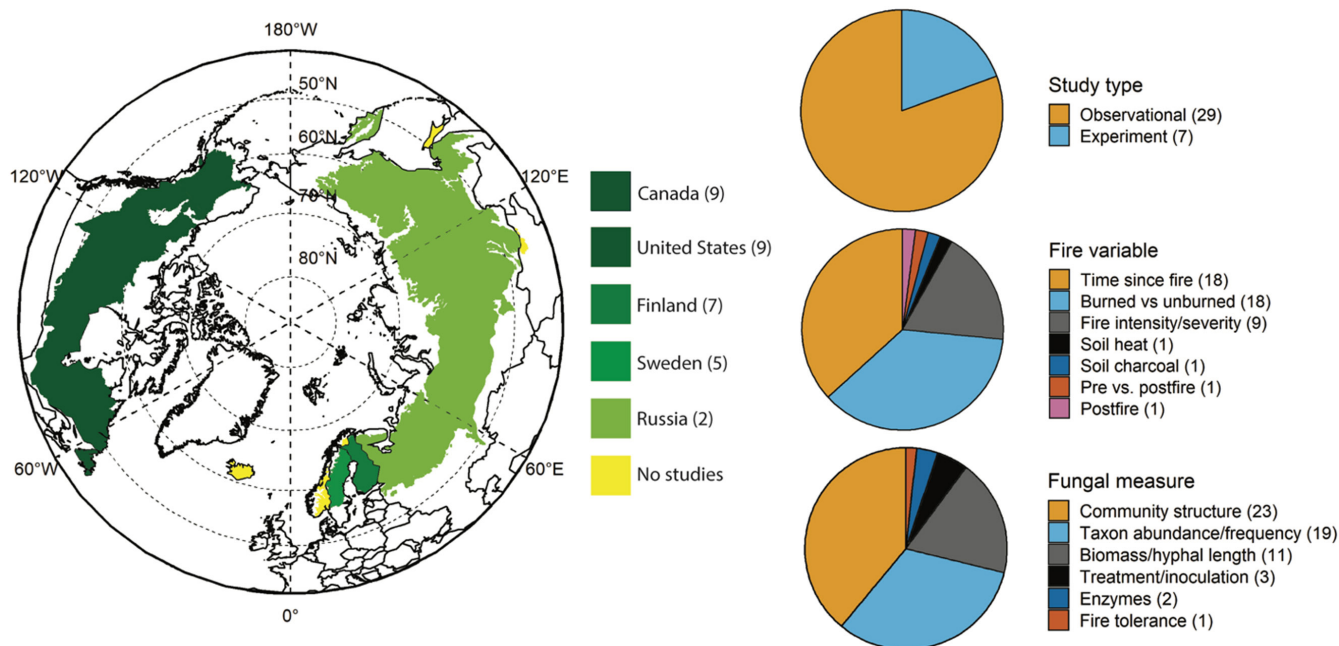


FIGURE 1 Map of the distribution of investigations of fire effects on mycorrhizal fungi in the boreal forest. Pie charts depict the types of investigations, fire variables addressed and fungal variables measured in response to fire. See Appendix S1 for further analysis and summary of literature

TABLE 1 Critical research priorities investigating fire effects on root-associated fungi and plant-soil feedbacks in boreal forests. We suggest long-term research priorities that can be addressed with short-term research goals through experimental and observational approaches that leverage currently feasible methodologies

Research priority	Key questions	Approach	Tools
Community assembly	<p>A Assess survival by resistant propagules after fire or heat</p> <p>B Measure spore dispersal distances and relate to spore traits</p> <p>C Test competition-colonization trade-offs</p>	<p>A Greenhouse bioassays of heated soil inoculum (or lab studies on culturable propagules)</p> <p>B Collect spores at different dispersal distances in burned and unburned areas and measure their traits, for example, size, shape, ornamentation</p> <p>C Experimentally introduce specific taxa or guilds with known combative-competitive life-history strategies</p>	<p>A Bioassays</p> <p>B Spore traps before and after fire</p> <p>C Axenic culture of specific fungi</p>
Traits	<p>A Measure traits linked to tolerance of disturbance or stress</p> <p>B Measure hyphal lengths and foraging distance from roots for fungi after fire</p> <p>C Test for relationships between traits and phylogenies</p> <p>D Relate ecological spectrum of generalism to specialism to traits</p>	<p>A Quantify melanin content, trehalose production, and heat-shock proteins, etc.</p> <p>B Measure spatial extent of genets</p> <p>C Develop or use technology or methods that simplify fungal trait measurements</p> <p>D Identify specificity of associations by taxon and relate to plant and fungal function</p>	<p>A HPLC and mass spectrometry for chemical signals</p> <p>B Couple microsatellites and spatial analysis</p> <p>B, C, Artificial intelligence technology to assess root-colonization rates (e.g. Evangelisti et al., 2021)</p> <p>C Genomic/transcriptomic-based studies for gene expression and phylogenetic relationships</p> <p>C, D, Recording fruiting body records in MyCoPortal (MyCoPortal, 2022) and R 'fungarium' (Simpson & Schilling, 2021)</p> <p>D Fun^{Fun}; FUNGuild (Nguyen et al., 2016)</p>
Generalist plant-fungal associations	<p>A Elucidate secondary successional dynamics</p> <p>B Test partner choice, for example, do hosts choose ericoid mycorrhizal fungi or dark septate endophytes, when ectomycorrhizal fungi are available?</p> <p>C Assess the impact of generalist versus specialist communities on plant performance and fitness</p>	<p>A Chronosequence or temporal studies of composition of bulk soil inoculum and plant-fungal associations</p> <p>B Experimentally manipulate timing and availability of different fungal taxa and guilds</p> <p>C Measure C costs and nutrient supplied to plants by different guilds, communities, or selected taxa</p>	<p>A Monitoring with destructive soil and root sampling over a time series</p> <p>B Experimental inoculation with field soil</p> <p>B, C, Axenic culture of specific fungi</p> <p>C Use biogeochemical tracers, for example, labelled isotopes or girdling, in conjunction with observations and/or manipulations of guild or taxonomic dominance</p>
Consequences for ecosystem function	<p>A Test roles of fungi in restoring soil C and N stocks</p> <p>B Test relationships between novel fungi and biogeochemical consequences</p> <p>C Scale impacts of root-associated fungi to the ecosystem level</p>	<p>A Inoculants in decomposition trials and long-term monitoring of soil C and N accumulation</p> <p>B Experimentally add specific fungal taxa or guilds to the field, mesocosm or glasshouse environment and monitor soil characteristics</p> <p>C Incorporate root-associated fungi into earth system models and dynamic vegetation models</p>	<p>A Experimental inoculation with field soil</p> <p>B Axenic culture of specific fungi</p> <p>C Cluster analysis based on phylogeny and/or traits. Represent fungi in vegetation dynamics by categorizing root-associated fungi into functional groups via a trait framework (e.g. effect traits sensu Lavorel & Garnier, 2002) or inferring function from plant or soil variables with applications in ecosystem process models</p>

understanding of the ecology of certain guilds or growth forms extrapolated from taxonomic identity.

Fungal trophic mode is used to deduce function and provides cursory insights into the outcomes of plant–fungal interactions. All fungi are heterotrophs, acquiring carbon from autotrophs, and are traditionally placed into three broad trophic categories: pathogens, decomposers and symbionts. However, some taxa seem to function in multiple trophic categories (Nguyen et al., 2016), such as harmless plant endophytes that transition to decomposers following tissue death (Chapela & Boddy, 1988a, 1988b). Thus, the context dependency of root-associated fungal trophic mode and subsequent effect on plant performance likely impacts postfire plant–soil feedbacks. *Here we explore the role of fire in structuring root-associated fungal communities, plant communities and use the plant–soil feedback framework to connect fire-driven shifts in root-associated fungal community structure and plant–fungal interactions with successional trajectories and ecosystem function. We identify knowledge gaps in our understanding of the mechanisms that underlie patterns of root-associated fungal diversity and response of host trees to plant–fungal interactions after fire. We finish by suggesting research priorities that would further our understanding in this area.*

2 | IMPACTS OF WILDFIRE ON VEGETATION AND ROOT-ASSOCIATED FUNGI IN THE BOREAL FOREST

The boreal forest is shaped by wildfire, which modulates its significant role in the global carbon cycle (Gauthier et al., 2015). With climate warming, changes in wildfire extent, severity and frequency (Wotton et al., 2017) are already underway. Fire or burn severity are typically measured by above-ground vegetation and below-ground soil organic matter consumption (Keeley, 2009). Increases in fire severity, in particular, may reduce carbon storage in the thick organic soil of the forest floor and redistribute it to trees (Mack et al., 2021) and the atmosphere (Walker et al., 2018, 2019), reshape the mosaic of deciduous and coniferous forests (Baltzer et al., 2021), and facilitate biome shifts such as the migration of boreal forest into tundra (Hewitt, Hollingsworth, et al., 2016; Landhausser & Wein, 1993). The biophysical changes in forest structure and biogeochemical processes affected by wildfire can influence the surface energy balance and carbon storage capacity, thus linking regional boreal forest processes to the global climate system.

A mature stand in the boreal forest that has not burned recently (~110–180 years) has an overstorey of ectomycorrhizal trees (*Picea mariana* (Mill.), *Picea glauca* (Moench) Voss, *Betula* species, *Larix* species or *Pinus banksiana* Lamb.) and an understorey of ectomycorrhizal deciduous tall or dwarf shrubs (e.g. *Alnus viridis* (Chaix) DC. ssp. *crispa* (Aiton) Turrill, *Salix* spp., *Betula nana* L.) and ericoid mycorrhizal deciduous and evergreen shrubs (e.g. *Rhododendron groenlandicum* Oeder., *Vaccinium* spp.) with few arbuscular mycorrhizal hosts (Day, White, et al., 2020; Hollingsworth et al., 2006; Paulson III et al., 2021). Beyond the dominant mycorrhizal fungal

guilds (ectomycorrhizal, ericoid mycorrhizal, arbuscular mycorrhizal fungi), dark septate endophytes, with putatively mycorrhizal function (Jumpponen, 2001; Jumpponen & Trappe, 1998; Mandyam & Jumpponen, 2005; Newsham, 2011), are ubiquitous throughout the cold, high-latitude environments (Newsham et al., 2009; Timling & Taylor, 2012) and have been observed frequently in bulk soils and on root systems of boreal plants (DeVan, 2019; Hewitt et al., 2017; Hewitt, Chapin III, et al., 2020; Hewitt, DeVan, et al., 2020). The boreal forest treeline, the ecotone with tundra, marks a biogeographic boundary from dominance by ectomycorrhizal fungi to ericoid mycorrhizal fungi (Read, 1991). The mycorrhizal boundary collocated with the northern treeline has been hypothesized to influence fire-facilitated biome shifts of boreal forest into tundra and associated trajectories of landscape flammability (Hewitt, Bennett, et al., 2016); yet these interactions have not been fully explored.

Postfire boreal plant successional trajectories are largely determined within a decadal time frame following fire (Johnstone et al., 2004; Johnstone, Hollingsworth, et al., 2010). This showcases the importance of ecological factors that determine community assembly and successional trajectories: dispersal, establishment and growth of both plants and soil biota. In severe fires, the organic soil layers can be completely combusted to reveal high-quality seedbeds by exposing deeper mineral soils (Brown et al., 2015; Greene et al., 2004, 2007). Wildfire characteristics related to the degree of organic soil combustion and plant survival strongly influence the legacy of prefire root-associated fungi (Dahlberg et al., 2001; Perez-Izquierdo et al., 2021). The community structure of postfire root-associated fungi is thus modulated by context dependencies associated with wildfire characteristics, vegetation and edaphic factors (e.g. Day et al., 2019; Taylor et al., 2010; Treseder et al., 2004; Whitman et al., 2019).

3 | POSTFIRE FUNGAL COMMUNITY ASSEMBLY

We can start to draw some general patterns of postfire fungi in boreal forests from the few studies where information on fungal distributions have been gathered (Appendix S1; Table S1). However, there is a regional bias in studies of postfire mycorrhizal fungi in boreal forests, with over half from northwestern Canada and Alaska (Figure 1). Fire has been shown to alter the root-associated fungal inoculum potential, taxonomic and functional composition across different levels of classification (guilds, phyla, genera, etc.). Fungal species richness consistently declines with fire in the boreal forest (Day et al., 2019; Sun et al., 2015), as it does in other biomes (Dove & Hart, 2017). Generally, ascomycetes increase after fire relative to basidiomycetes and mycorrhizal fungi decline relative to decomposers or pathogens (Holden et al., 2016; Rodriguez-Ramos et al., 2021; Sun et al., 2015). Ericoid mycorrhizal fungi show variable responses to fire impacts: relative abundance and richness are reduced in response to burning compared to unburned sites but show a positive response to crown-fire severity across burned sites (Perez-Izquierdo

et al., 2021), while their relative abundance shows little change with increasing time after fire (Sun et al., 2015). Arbuscular mycorrhizal fungi appear to be more resilient to fire than ectomycorrhizal fungi globally (Xiang et al., 2015); work in the boreal forest supports this. In a chronosequence study in Alaska, arbuscular mycorrhizal fungi colonization rates, hyphal lengths and glomalin levels at 3 years after fire were comparable to older burns (Treseder et al., 2004). In contrast, colonization by ectomycorrhizal fungi took 15 years to recover to prefire levels (Treseder et al., 2004). These findings in the boreal forest support broader conclusions that colonization by mycorrhizal fungi can be relatively resilient to fire in many biomes (Dove & Hart, 2017; Xiang et al., 2015) where fungi persist but composition can shift dramatically (Figure 3, Hewitt et al., 2013, 2017).

Postfire root-associated fungal communities are composed of those that are stimulated by fire, survive in the soil or in association with plants that are not killed, or disperse from unburned patches within or beyond the edge of a burn scar (Figure 2, Table 1). In Fennoscandian boreal forests, for example, at least 80 fungal species are thought to be fire dependent and 40 taxa produce sporocarps exclusively after fire (Dahlberg, 2002), suggesting wildfire creates niches that favour reproduction in certain taxa, although these are not considered to be mycorrhizal fungi. A few studies have been able to document shifts in the dominance of fungal taxa with serendipitous pre- and postfire sampling in the same location (Baar et al., 1999; Taylor & Bruns, 1999). A series of studies has led to a distinction between 'early-stage' ectomycorrhizal fungi, which rapidly colonize isolated seedlings via spores, and 'late-stage'

ectomycorrhizal fungi, which seem to require support from more mature trees and colonize roots most effectively via mycelial extension, that is, vegetative growth (Last et al., 1987; Mason et al., 1983). This distinction is relevant to postfire scenarios, particularly stand-replacing fires where seedlings are needed to replace canopy trees. Variation in 'early-stage' and 'late-stage' status likely helps explain why fungal communities after fire are compositionally different from areas that burned many decades earlier (Jonsson, Dahlberg, Nilsson, Zackrisson, & Karen, 1999; Visser, 1995). While direct observations are lacking (Figure 1), we infer that some fungi can survive fires in boreal forests because heat-resistant fungi are present in unburned areas (Day, Cumming, et al., 2020) and late-successional stage fungi are often present in burned areas (Hewitt et al., 2017; Jonsson, Dahlberg, Nilsson, Kårén, & Zackrisson, 1999).

3.1 | In situ survival of fungi

Root-associated fungi can survive in patches that remain unburned or on host plants that survive burning. Rootstock can survive fire to resprout, which is the dominant regeneration strategy of boreal forest understorey species (Day, White, et al., 2020; De Grandpré et al., 1993; Hollingsworth et al., 2013). Mycorrhizal fungi surviving in unburned patches can provide a source of inoculum for regenerating plants in temperate forests (Brunns et al., 2002). In the boreal forest, ectomycorrhizal fungi that survive on resprouting plants can colonize seedlings of other species (Hewitt et al., 2017; Jonsson,

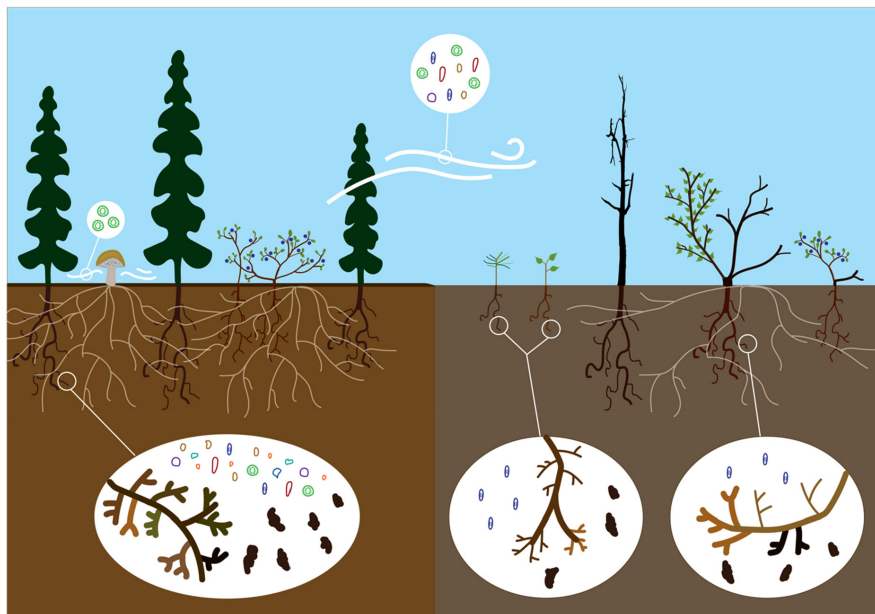


FIGURE 2 Graphical representation of prefire (left) and postfire (right) root-associated fungal inoculum. The prefire inoculum is hosted by live overstorey ectomycorrhizal trees and ecto- and ericoid mycorrhizal understorey shrubs. There is a highly diverse and abundant source of vegetative fungal biomass, that is, mycelium, along with sclerotia and a diverse and abundant spore bank. The postfire inoculum has limited vegetative growth from mycelium associated with resprouting vegetation that survived fire or hosts at the edge of the burn scar. The spore bank and the mycelial sources of inoculum are reduced in abundance and diversity; yet, some heat-resistant and pyrophilic spores and sclerotia may germinate. Overall, the composition of root-associated fungi has been strongly filtered and diversity and richness reduced by the fire and the postfire conditions. Spores are dispersed from adjacent unburned areas

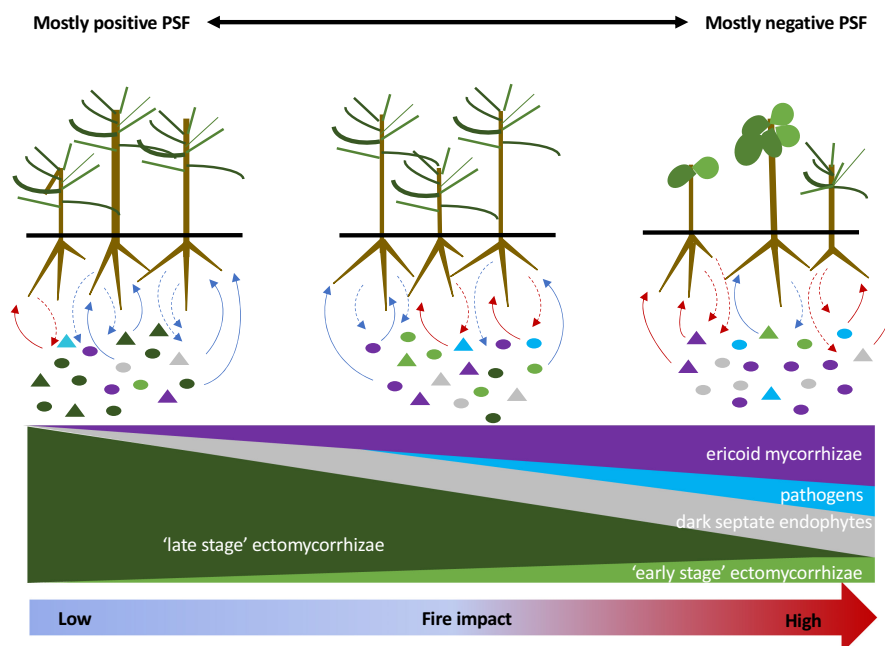


FIGURE 3 Conceptual diagram of wildfire impacts on major guilds and functional groups of root-associated fungi of conifer and deciduous seedlings in the boreal forest and predicted plant–soil feedbacks (PSFs) immediately after fire. Increasing fire impact is due to higher severity of burning, repeat burning occurrence or greater fire size, which impact sources of inoculum (Figure 2). Shifts in relative abundance of the fungal groups and effects on plant performance are informed by studies of roots and bulk soil. Dominance of fungal groups is depicted by colour and shape of the soil biota which corresponds with the coloured wedges. Reference to ‘early-stage’ ectomycorrhizal fungi, corresponds with taxa that rapidly colonize seedlings via spores, whereas ‘late-stage’ ectomycorrhizal fungi, corresponds with taxa in association with mature trees that colonize seedling roots via mycelial extension. Blue arrows indicate predicted positive PSF, red arrows indicate negative PSF. Solid arrows indicate impacts that have been studied, while dashed arrows are hypothesized relationships. Adapted from Mariotte et al. (2018). We expect as fire impact increases and the postfire root-associated fungal community shifts in direct relation to fire effects, there will be greater potential to alter plant–soil feedbacks; this could lead to a breakdown of positive conifer–soil feedbacks and facilitate a shift to negative conifer–soil feedbacks, potentially facilitating a transition to dominance by deciduous trees that is often observed after severe fires

Dahlberg, Nilsson, Kårén, & Zackrisson, 1999). The importance of resprouting plants for mycorrhizal inoculum may explain the lower fungal colonization in seedlings after fire in glasshouse studies compared to field studies (Dove & Hart, 2017; Hewitt, Hollingsworth, et al., 2016). Some nonmycorrhizal, pyrophilous fungi have recently been shown to associate with bryophytes as endophytes (Raudabaugh et al., 2020), suggesting nonvascular plants may also be an important source of fungal propagules after fire.

Fire impacts on soils may result in depth-specific survival of root-associated fungi and a strong reassortment of the community. In Interior Alaska, roughly 84% of fine root production occurs in the top 20cm of soil, with ~24% at 0–10 cm depth, and 57% at 10–20cm depth, dropping to 13% at 20–30cm and declining with increasing depth (Ruess et al., 2003). This suggests that a substantial proportion of root-associated fungal biomass may be eliminated by high severity fires that combust a large proportion of the organic horizon (Bergner et al., 2004). Within the top 20cm, ectomycorrhizal fungi vary in their depth and horizon preferences (Clemmensen et al., 2013; Lindahl et al., 2007), with some boreal ectomycorrhizal taxa occurring almost exclusively in upper (~20cm) mineral horizons (Taylor et al., 2010, 2014). Fungi in deeper organic and mineral soils may be protected from fire and increase in abundance after fire relative to those in the organic layer where most combustion occurs

(Walker et al., 2018). Extreme heating of the soil with high severity fires is generally restricted to the top few centimetres of mineral soil (Certini, 2005; Holden et al., 2013). Heat penetration, and therefore potential fungal survival, is likely determined by attributes that impact burn depth (Kreye et al., 2020), such as depth of prefire organic layer and soil moisture content (Walker et al., 2018). Depth-related fungal community reassortment has not been experimentally probed, to our knowledge (Figure 1). For example, because mycorrhizal fungi are vertically stratified, increased depth of burning with high severity fires may expose compositionally distinct fungal communities that can colonize seedlings as they establish on postfire soils.

We expect many root-associated fungi to be adapted to surviving fire in the boreal forest, based on results from other fire-dependent systems. However, experimental work that suggests the germination of spores is stimulated by heat, not ash, and that spores may survive dormant in soils for decades (Bruns et al., 2019; Peay, Bruns, & Garbelotto, 2010), such as the studies of *Rhizopogon olivaceotinctus*, an ectomycorrhizal fungus in California pine forests (Glassman et al., 2016; Peay et al., 2009), are lacking in the boreal forest. Despite no direct experimentation, observations suggest that root-associated fungi survive and emerge after fire. Clinical settings have provided some understanding of the molecular bases underlying heat resistance of spores or mycelia. In

general, thermotolerant fungi typically have less pigmentation than intolerant fungi (Mattoon et al., 2021). One exception to this is fungi with high amounts of melanin, which can confer heat and cold tolerance, among other attributes to tolerate abiotic and biotic stresses (Cordero & Casadevall, 2017; Malicka et al., 2022; Santos et al., 2021). Melanized endophytes have been shown to bolster heat tolerance in plants in inoculation studies (Redman et al., 2002), which suggests a functional role for the high colonization of dark septate endophytes observed on plants after fire (DeVan, 2019; Hewitt, Chapin III, et al., 2020; Horton et al., 1998). Heat shock proteins and trehalose play key roles in protecting cells of thermotolerant fungi (Mattoon et al., 2021; Tereshina, 2005). Interestingly, trehalose production is also thought to aid in cold tolerance in ectomycorrhizal *Hebeloma* spp. from northern high latitudes (Tibbett et al., 2002), so this carbohydrate may contribute to general stress tolerance in fungi. Molecular mechanisms of fungal survival after wildfires are not well understood (Figure 1, Table 1), particularly in the boreal forest, where we have yet to formally identify any heat-resistant mycorrhizal taxa (but see Day, Cumming, et al., 2020; Greene et al., 2010 for examples of nonmycorrhizal heat-resistant fungi).

3.2 | Postfire dispersal

Aerial dispersal of spores influences fungal community structure (Kivlin et al., 2014; Kobziar et al., 2018; Taudière et al., 2017), including ectomycorrhizal colonization of seedlings (Peay et al., 2012). At least some fungal propagules can survive in smoke and bacterial spore abundance declined with distance from fire in a study from Florida (Kobziar et al., 2018), presenting a possible mechanism for fungal community reorganization even while the fire is occurring. After fire, distance to an unburned edge is likely important for fungal taxa that rely on recolonization from beyond the burn (Peay, Garbelotto, & Bruns, 2010), as it is for dispersal-dependent plants (Johnstone et al., 2009). Small fungal spores can disperse further than large ones (Chaudhary et al., 2020; Golan & Pringle, 2017; Kivlin et al., 2014) and some ectomycorrhizal spores (e.g. *Suillus*) can disperse across multiple kilometres (Peay et al., 2012). In temperate forests, ectomycorrhizal taxa vary in their ability to disperse, germinate and establish (Nara, 2009). For the dispersal of fungi to play a relevant role in root associations, spores need to be able to survive environmentally challenging conditions, such as desiccation and solar radiation (Golan & Pringle, 2017). Indeed, a study in California showed environmental filtering was more important than dispersal limitation in soil fungal communities (Kivlin et al., 2014); yet, comparable studies on fungal dispersal in the boreal forest are lacking (Table 1).

3.3 | Environmental filters

Environmental filtering occurs when wildfire indirectly affects root-associated fungal communities by altering the conditions that shape

them. Heating of soils alters physical attributes like hydrophobicity, and chemical attributes like soil nitrogen and carbon pool sizes and molecular form, and pH (Certini, 2005; Doerr & Cerdà, 2005). As an example, fire generally causes an increase in soil pH through the combustion of organic acids and addition of ash (Certini, 2005; Day et al., 2019; Whitman et al., 2019). Soil pH was one of the main drivers of fungal community structure in several postfire boreal forest studies (Day et al., 2019; Sun et al., 2015; Whitman et al., 2019) and pH is a global driver of soil fungal distributions (Tedersoo et al., 2014). While soil fungi have a wide tolerance in pH (Wardle & Lindahl, 2014), fungal diversity often declines in highly alkaline soils (Delgado-Baquerizo et al., 2016; Rousk et al., 2010; Tedersoo et al., 2014). Soil pH may be an important moderating factor for early colonizing fungi postfire and may explain why in some cases pH is more important than fire severity itself for determining postfire fungal composition (Day et al., 2019). Thus, modifications of environmental characteristics by fire likely influence postfire fungal community assembly (Table 1).

The importance of fungal survival compared to dispersal after fires in the boreal forest, or in other systems, is unknown but is likely influenced by fire characteristics. Fire size, intensity and heterogeneity can impact the pool of potential colonizers and influence the importance of fire adaptation (Carlsson et al., 2012; Glassman et al., 2016) versus dispersal (Horton, 2017). Heat tolerance, a fire adaptation, may be a more important strategy in very large burned areas that are further from an unburned forest edge; whereas, dispersal may be a more common strategy of fungal colonizers in patchy burned areas or those closer to a forest edge and thus an inoculum source. Experimental efforts to assess mechanisms of root-associated community assembly are sorely needed (Figure 1, Table 1).

Prefire stand plant composition and diversity, tree density, stand age and land use correlates with fungal community structure in unburned stands (Day et al., 2019; De Bellis et al., 2006; Sun et al., 2015; Taylor et al., 2014), from which root-associated fungi may disperse. For instance, root-associated fungal composition on *Pinus contorta* Dougl. ex Loud var. *contorta* was influenced by the prefire relative proportion of *P. mariana* compared to other tree species in northwestern North America (DeVan, 2019). Another example from Sweden highlighted the importance of disturbance history, as prefire logging correlated with lower fungal diversity after fire compared to unlogged stands, despite having similar diversity prefire (Dahlberg et al., 2001). Information on which fungal taxa are present before fire aids in discerning which fungi can survive fire; yet, few studies have made pre- and postfire comparisons of fungal composition (Baar et al., 1999; Glassman et al., 2016) and to date the acquisition of prefire data in the boreal forest has been rare (Figure 1; Appendix S1). Pyrocosms and controlled burn plots may serve as practical alternatives to test the importance of prefire variables; however, unburned stands and prescribed burn characteristics will likely differ from those created during natural wildfire events based on stand characteristics, soil and weather.

3.4 | Competition

Although environmental characteristics and niche preferences probably influence the composition of root-associated fungi, arrival time is also likely to be important in determining success in the community (Table 1). For example, the first ectomycorrhizal fungus to colonize a seedling can determine the ability of others to colonize through priority effects (Kennedy et al., 2009). Early colonizing fungi are effective at resource acquisition and can exert competitive dominance over the later ones (Kennedy et al., 2009; Kennedy & Bruns, 2005). There is some evidence for competition–colonization trade-offs in root-associated fungi, although these studies were not carried out in a postfire context (Kennedy et al., 2011). Conjecturally, we believe there is a strong role for mycelial colonization of postfire seedlings when resprouting shrubs that support the mycelium are present (Bent et al., 2011; DeVan, 2019; Hewitt et al., 2017). In contrast, it seems that when resprouting shrubs are absent, fungi that are likely to be wind-dispersed, such as various ascomycetous dark septate endophytes and pathogens, take on a larger role in seedling colonization (Hewitt, Hollingsworth, et al., 2016). Communities of root-associated fungi, both mycorrhizal and endophytic fungi, are influenced by geographic distance, which suggests dispersal limitation, and structured by competition (Kennedy et al., 2011; Peay, Garbelotto, & Bruns, 2010; Wang et al., 2020). This indicates that suites of traits (good dispersal, ruderal) may follow expected patterns observed in macroecological studies (Peay et al., 2012). Thus, competition–colonization trade-offs may feature prominently in postfire community assembly. However, the relative importance of the actual structures responsible for postfire plant colonization (i.e. mycelium, resting propagules, wind-blown asexual or sexual spores) in the boreal forest have yet to be studied (Table 1).

4 | PLANT-FUNGAL INTERACTIONS IN RESPONSE TO FIRE

Fire results in generalist relationships between boreal seedlings and root-associated fungi (Table 1). This is apparent from observations of ectomycorrhizal host plants associating with several guilds of fungi and with generalist root-associated fungi taxa. While there is increasing evidence that ericoid mycorrhizal fungi can associate with ectomycorrhizal hosts from various ecosystems and states of disturbance (Grelet et al., 2009; Villarreal-Ruiz et al., 2004), their relative abundance increases on postfire ectomycorrhizal seedlings, possibly due to the rapid resprouting of ericoid host plants (Day, White, et al., 2020) and the limited inoculum and competition from ectomycorrhizal fungi after fire (DeVan, 2019; Hewitt, Hollingsworth, et al., 2016). Colonization of ectomycorrhizal seedlings by ericoid mycorrhizal fungi supports hypotheses that common mycorrhizal networks form between the two host types and that these may be important for postfire succession (Hewitt et al., 2017; Vrålstad, 2004). Dark septate endophytes are another common non-ectomycorrhizal fungal associate of postfire ectomycorrhizal hosts

(DeVan, 2019; Hewitt, Chapin III, et al., 2020; Horton et al., 1998) that appear to become more abundant when ectomycorrhizal fungal inoculum is reduced, particularly along gradients of fire severity (Hewitt, Hollingsworth, et al., 2016). Dark septate endophytes and many ericoid mycorrhizal fungi are highly melanized, a trait that may enhance their ability to survive fire or high solar radiation (Mattoon et al., 2021) if they disperse into a burn scar and may lend them a competitive advantage to opportunistically colonize ectomycorrhizal hosts. The high incidence of colonization of ectomycorrhizal hosts by nonectomycorrhizal fungi following fire can persist for at least 8 years in the boreal forest (DeVan, 2019), the same timeframe that forest successional trajectories are determined (Johnstone et al., 2004, 2020), and has been observed on ectomycorrhizal seedlings at the boreal-tundra ecotone immediately after fire (Hewitt et al., 2017). Multiple studies have shown a large fraction of shared fungal associates among *P. mariana*, *Populus tremuloides* Michx., *B. neolaskana* Sarg., *B. nana* and *P. glauca* following fire (Bent et al., 2011; DeVan, 2019; Hewitt et al., 2017). These common associates may be linked to reduced overall diversity of mycorrhizal fungi following fire, which in turn, through priority effects, dominate the communities of multiple host plants.

Generalism, the ability to associate with multiple hosts, may be an effective life-history strategy allowing root-associated fungi to persist through vegetation transitions after fire, while more specialist root-associated fungi may decline in the absence of appropriate hosts. For example, there are several fungi specific to Pinaceae that cannot establish without an appropriate host (Nuñez et al., 2009), and conversely, novel root-associated fungi may become established after fire with the introduction of a novel host (DeVan, 2019). *Alnus crispa* hosts specific root-associated fungi symbionts and this pattern persists after fire (Bent et al., 2011). Yet, *A. crispa* increases in abundance with wildfire (Lantz et al., 2010), perhaps because it can resprout and may not necessarily lose its root-associated fungi community. The generalist community of root-associated fungi observed after fire contrasts with observations of endophytic root-associated fungi in Arctic ecosystems where wildfire has not occurred and specialization based on host plant identity is strong (Abrego et al., 2020).

As in other ecosystems, the ability of boreal plants that must establish by seed and generally do not resprout to associate with a great diversity of fungal mutualists likely aids their persistent dominance in the system, even after disturbance has altered available mutualists. If fungi present after fire are more beneficial to one host than another, then these fungal associations may tip the competitive balance, at least in the short term, of one host over another. Furthermore, if fires are severe or large enough to drastically reduce inoculum, there is potential for seedlings lacking mycorrhizal partners to fail to establish. There is also potential for fungi present after fire to facilitate plant or fungal invasion. However, these ideas remain to be tested comprehensively in the postfire boreal environment (Table 1). The loss of native plants and fungi after fire can reduce competition and thus aid migrating or invading organisms. For example, *P. contorta* is slowly migrating towards the Alaskan boreal forest from Canada, and when planted

in Interior Alaskan boreal forests after fire it associates with several pine-specific fungi in the genus *Suillus*, which were previously undocumented in the region (DeVan, 2019). Fire assisted plant and fungal introductions can have important ecosystem consequences (Table 1). For example, *Suillus tomentosus*, found on *P. contorta* roots, has been demonstrated to host N-fixing bacteria (Paul et al., 2007) that could alter nutrient cycling in the nitrogen poor boreal forest, further influencing potential successional trajectories.

5 | IMPACTS OF ROOT-ASSOCIATED FUNGI ON FOREST RECOVERY AFTER FIRE

Just as postfire host composition can influence root-associated fungal communities, the interdependent nature of these organisms is underscored by the potential for root-associated fungal composition to affect postfire successional trajectories by conferring variable outcomes to hosts, that is, plant–soil feedbacks. Despite commonly being thought of as mutualists, root-associated fungi exist on a spectrum from parasitic to mutualistic (Johnson et al., 1997), and these different outcomes for plant performance may be linked to fungal guild or taxon. Two independent outplant studies in Interior and Arctic Alaska found negative or neutral effects of ericoid mycorrhizal fungi or dark septate endophytes on *P. mariana* seedling growth but positive effects of the ectomycorrhizal fungus *Thelephora terrestris* (DeVan, 2019; Hewitt, Chapin III, et al., 2020). For example, endophytes *Cadophora finlandica* (C.J.K. Wang & H.E. Wilcox) and *Phialocephala fortinii* (C.J.K. Wang & H.E. Wilcox) were negatively correlated with growth of *P. mariana* seedlings (DeVan, 2019; Hewitt, Chapin III, et al., 2020). However, some ericoid fungi in the genus *Pezoloma* were positively associated with growth of *P. mariana*, *P. glauca* and *P. contorta*, suggesting biotic context dependency in the outcomes of plant–soil feedbacks (DeVan, 2019), specifically, different growth effects depending on host species. The functional impact of ericoid mycorrhizal fungi and endophytes on plant performance warrants further field investigation (Table 1) building on experimental inoculation studies (Reininger & Sieber, 2013). Furthermore, if root-associated fungi can promote changes in plant successional trajectories this could alter overall flammability of the landscape (Cumming, 2001; Hewitt, Hollingsworth, et al., 2016; Marchal et al., 2020).

Host plant identity can influence the plant response to root-associated fungi after fire. Fungal pathogens accumulated more rapidly on *Picea* compared to *Alnus* (Hewitt, Hollingsworth, et al., 2016), reducing plant biomass during the early establishment phase. Growth of *P. abies* and *P. sylvestris* was greatest when inoculated with soil biota from low-severity fire soil, whereas *B. pendula* Roth. growth was unaffected by inoculation with soil biota from different fire severities, suggesting low-severity fire favours conifer seedling regeneration and deciduous establishment is influenced by postfire abiotic conditions more so than root-associated fungi (Ibáñez et al., 2021). A study in the Northwest Territories of

Canada observed negative effects of seven heat-resistant fungi, with mostly decomposer identities, on the biomass of two conifers, *P. mariana*, *P. banksiana*, and overall negligible effects or weak positive associations with three taxa on deciduous, *B. papyrifera*, Marshall., seedling growth (Day, Cumming, et al., 2020). These glasshouse-based results transferred to the field, that is, there were weak but significant reductions in conifer seedling densities in the field where these fungal taxa were abundant (Day, Cumming, et al., 2020). Thus, fire activity that filters for heat-resistant taxa may cause declines in conifers and help push the system to a more broadleaf-dominated system that has been observed in many areas after fire in the North American boreal forest (Johnstone, Hollingsworth, et al., 2010) with important implications for ecosystem carbon allocation and future flammability. These patterns persist at the edge of the boreal forest, where at treeline there is variation in plant biomass and foliar traits that correlates with the composition of root-associated fungi (Hewitt et al., 2017; Hewitt, Chapin III, et al., 2020). Effects of various root-associated fungi on particular hosts can be modulated by abiotic and biotic contexts. For example, several ectomycorrhizal fungi had stronger positive effects on conifer seedling biomass at lower pH levels and when paired with particular other root-associated fungi after fire in Alaska (DeVan, 2019). These field results are supported by a laboratory study that found ectomycorrhizal diversity was correlated with shifts in allocation of biomass to roots and shoots as well as N and P status of *B. populifolia*, Marshall. seedlings (Baxter & Dighton, 2001). Together these studies demonstrate the species-specific outcomes from plant–fungal interactions and the potential for plant–soil feedbacks to influence successional trajectories and ecosystem function.

Biotic interactions among soil microbes also need to be considered in the quest to predict the result of postfire root-associated fungi–seedling interactions. Mycorrhizal helper bacteria are important for mycorrhizal function (Frey-Klett et al., 2007), but may be removed by fire (Whitman et al., 2019). Furthermore, the presence of other root-associated fungal species can change the outcome of a plant–fungal association. High relative abundance of *Meliniomyces* sp. resulted in a stronger positive effect of other root-associated fungi taxa on *P. contorta* and *P. glauca* seedlings in Interior Alaska following fire (DeVan, 2019). The context dependency of root-associated fungi–seedling interactions based on the full rhizosphere microbiome likely impacts vegetation establishment after fire and might be assessed through network or co-occurrence analyses; however, interpretations from these analyses remain difficult.

6 | SUMMARY: LINKING DIVERSITY TO FUNCTION WITH POSTFIRE PLANT–SOIL FEEDBACKS

In the boreal forest, our collective observations of postfire root-associated fungal diversity from soils and roots show reduced

ectomycorrhizal fungal inoculum (richness and abundance) compared to other constituents of the root-associated fungi, yet dark septate endophytes and ascomyceteous fungi that typically associate with ericaceous host plants are apparently abundant and available to colonize establishing ectomycorrhizal host plants (Figure 3). Shifts in the postfire root-associated community are shaped by characteristics of the wildfire (size, severity), the pre- and postfire environment, and in particular the persistence of sources of in situ vegetative inoculum. In the postfire context, we suggest that early plant hosts seem to be dependent on resprouting vegetation as a source of ectomycorrhizal symbionts; otherwise, they associate with ascomyceteous endophytes, some of which have been negatively associated with growth and other metrics of plant performance (DeVan, 2019; Hewitt, Chapin III, et al., 2020). Thus, fire may filter out beneficial taxa from the potential species pool, preventing or delaying associations with preferred partners (Hortal et al., 2017) that initiate the positive plant–soil feedback characteristic of mature ectomycorrhizal forests. Seedlings that by chance establish near resprouting vegetation and associate with refugial fungi connect to a more mature fungal community that has likely already been conditioned by partner choice, albeit via a different host species. This suggests there may ultimately be a positive ectomycorrhizal plant–soil feedback, a negative dark septate endophyte feedback and ericoid mycorrhizal plant–soil feedbacks that can be positive or negative depending on context and partner identities. Predictions about the future fire regime in the boreal forest include shorter fire return intervals, larger and more severe fires. These fire characteristics would likely result in greater mortality of host plants and thus fewer resprouters, with the postfire root-associated fungal community shifting towards one shaped more by dispersal, a reduction in ‘late-stage’ ectomycorrhizal taxa, and an increase in ‘early-stage’ ectomycorrhizal taxa, ericoid mycorrhizal fungi or endophytes. Although speculative, we suggest that these changes could tip the balance from positive to negative plant–soil feedbacks in these systems due to differences in growth promoting functions of the fungal partners. This could, in turn, set the stage for the establishment of novel vegetation communities.

7 | FUTURE DIRECTIONS

We have provided a synthesis of what is broadly known about postfire root-associated fungal communities, plant–fungal interactions and the potential for plant–soil feedbacks in boreal forests. Our evaluation of the state of knowledge (Figure 1) suggests an urgent need to be able to better link described patterns of postfire mycorrhizal diversity to function. We suggest this may be achieved by forging connections between observational, experimental and modelling studies that are focused on multiple fire variables (e.g. severity, pre- vs. postfire), and incorporate compositional and most importantly, functional measurements (community amplicon sequencing and functional profiling). Here, we outline some of the areas we consider fundamental to building a better understanding of mechanisms and functions of fungi in postfire environments. We identify knowledge

gaps, future directions of study and highlight methods and tools to aid these investigations (Table 1).

7.1 | What are the mechanisms underlying community assembly of root-associated fungi?

While we know some of the taxonomic identities of postfire fungi in the boreal forest, we know far less about the mechanisms that are responsible for these patterns, especially the ways by which fungi colonize roots after fires. Circumstantial evidence suggests that some ericoid fungi are able to capture new postfire roots via vegetative mycelial spread from roots of ericaceous shrubs that resprout after fire (DeVan, 2019; Hewitt et al., 2017; Hewitt, Chapin III, et al., 2020). However, data to directly document fungal survival on resprouting shrubs and mycelial extension are lacking. Similarly, there is circumstantial evidence to suggest that dark septate endophytes and pathogens may rapidly colonize burnt soils via wind-dispersed spores (Hewitt, Hollingsworth, et al., 2016), but this has yet to be demonstrated empirically in the boreal forest. Furthermore, our understanding of the influence of in situ inoculum sources relative to germination from a spore bank or dispersal by spores and their impacts on host plants has a strong regional bias from the North American boreal forest (Figure 1). To build a solid ecological foundation for understanding postfire plant–fungal dynamics, we advocate for a combination of simultaneous observational and experimental work on the mechanisms of dispersal and root colonization (Table 1). Some possibilities to address mechanisms of postfire community assembly include:

1. Bioassay soil inoculum potential to assess survival by resistant propagules;
2. Trap spores to identify propagules that disperse in after fire;
3. Test competition–colonization trade-offs by experimentally introducing ‘late-stage’ fungi, known to be strong competitors to determine if they displace ericoid fungi and dark septate endophytes commonly associated with postfire seedlings.

7.2 | Which functional traits are important to fungal community assembly in postfire environments?

Bolstering records of taxonomic distributions and improving our understanding of how these taxa can be classified into a traits framework is a key data gap in the boreal forest (Table 1). Fungal traits related to dispersal, dormancy and propagule survival will likely have predictive power with respect to postfire community assembly, as discussed above. In contrast, we do not yet have any conceptual framework that would allow us to predict postfire community assembly in terms of a ‘fungal economic spectrum’ of fast versus slow growth strategies (Andrews & Harris, 1986) nor ‘effect traits’ such as extracellular enzymes (Figure 1) that might influence biogeochemical cycles (Crowther et al., 2014).

Linking fungal traits to function has progressed with the recent development of the Fun^{Fun} database, which assigns traits to fungi according to their taxonomy (Zanne et al., 2020). This builds on the FUNGuild database, which assigns fungal taxa into functional groups (Nguyen et al., 2016). While we are excited about the potential uses of these tools, we are limited by the lack of fungal trait knowledge from the boreal forest. In terms of fungal distributions postfire, the 'fungarium' R package, which is based on sporocarp collections in MyCoPortal (2022), has been used to link fungal taxa to fire over space and time (Simpson & Schilling, 2021). However, sparse sporocarp records from many regions of the boreal forest may preclude its usefulness in this biome. We therefore suggest future studies of postfire fungal traits should:

1. Measure traits that confer broad tolerance to disturbance, for example, melanin content, trehalose production and heat-shock proteins;
2. Calculate fungal hyphal lengths and foraging distance from roots after fire;
3. Test for relationships between traits and phylogenies to improve phylogenetic predictions of function and community assembly;
4. Quantify the degree of fungal generalism or specialism in plant-fungal interactions after fire in the boreal forest and how this relates to traits;
5. Develop or take advantage of technology or methods that simplify fungal trait measurements, for example, artificial intelligence technology to assess time-consuming traits, that is, root-colonization rates (Evangelisti et al., 2021).

7.3 | What are the functional consequences of generalist plant-fungal associations after fire?

A better understanding of the influence of postfire root-associated fungi on host plant performance and dominance would elucidate whether plant-soil feedbacks strongly shape vegetation structure and biogeochemical cycling in the boreal forest (Table 1). Although generalism appears to be a common strategy after fire, there are differential benefits to plant performance based on root-associated taxonomic composition. We must consider whether the successional dynamics that ensue for root-associated fungal communities support the hypothesis that there are more specialized fungi with greater time since disturbance as host plant diversity increases, or whether greater fire severity or reduced fire return interval and a subsequent reduction of the extant community could result in few specialist fungi and a persistent generalist community. We suggest the following approaches to address this knowledge gap:

1. Monitor bulk soil inoculum and plant-fungal associations over time to evaluate successional dynamics after fire;
2. Test partner choice, for example, do hosts choose ericoid mycorrhizal fungi or dark septate endophytes, when ectomycorrhizal

fungi are available, through the manipulating of the timing and availability of fungi provisions;

3. Measure C costs and nutrients supplied to plants by different guilds, generalist communities, or selected suites of symbionts using tracers like labelled isotopes or girdling in conjunction with observations and/or manipulations of guild or taxonomic dominance.

7.4 | What are the consequences for ecosystem function if there are shifts in root-associated fungi after fire?

Biogeochemical consequences of shifts in fungal community after fire are unknown but could manifest through variation in the traits of the fungal community (Table 1). Fungal biomass can represent a significant fraction of soil organic matter (Clemmensen et al., 2013) and fungal taxa with different traits, that is, melanin, vary in biomass (Hobbie & Agerer, 2010) and production (Ekblad et al., 1995). However, there is a paucity of data that have quantified these variables to date. We again need observational and experimental work that would place fungal taxa in a fungal economic spectrum traits framework to inform ecosystem process rates. This would allow for exciting applications in Earth system models and dynamic vegetation models through data-model integration that could, for example, reduce uncertainty in model estimates of terrestrial C and N stocks. To link postfire root-associated fungi to ecosystem function, we need to:

1. Measure biogeochemical traits: tissue chemistry, pools (standing biomass, production) and life-span;
2. Test the roles of fungi in restoring soil carbon and nitrogen stores with decomposition inoculation trials and long-term monitoring of soil carbon and nitrogen accumulation;
3. Explore the ability of novel fungi, for example, *Suillus*, to spur unanticipated biogeochemical consequences;
4. Incorporate root-associated fungi into process and earth system models.

AUTHOR CONTRIBUTIONS

Rebecca E. Hewitt, Nicola J. Day, M. Rae DeVan and D. Lee Taylor conceived the ideas and designed the methodology; Rebecca E. Hewitt led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data presented in the manuscript are summarized in Table S1.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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