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Drivers of post-fire vascular plant regeneration in the conifer-dominated boreal forest of southern Northwest Territories

Alison White
alison.white25@yahoo.ca

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DRIVERS OF POST-FIRE VASCULAR PLANT REGENERATION IN THE CONIFER-DOMINATED BOREAL FOREST OF SOUTHERN NORTHWEST TERRITORIES

by

Alison White
(BSc. Biology, Dalhousie University, 2005)
(B.Ed. Queen's University, 2011)

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ABSTRACT

In recent years, climate warming has led to an increase in the severity and frequency of naturally occurring fires in boreal ecosystems globally. In 2014, an unprecedented 3.4 million hectares of boreal forest burned in the Northwest Territories (NWT). While much research has focused on post-fire succession of serotinous tree species such as *Picea mariana* (black spruce) and *Pinus banksiana* (jack pine), the understory community of vascular plants play an important role in ecosystem functioning but less is known about the response of this component of the system to changing fire regimes. Regeneration strategies such as the ability to resprout from underground rhizomes or disperse an abundance of seeds following fire are examples of plant traits that are adapted to fire regimes and have supported patterns of early recovery of boreal plant communities. Environmental factors such as surficial moisture and soil substrate conditions can also impact post-fire community assembly. Vascular plant community responses to changing fire severity and frequency will shape patterns of succession; understanding changes in these patterns in vascular plant assembly immediately following disturbance will enable future predictions to be made regarding forest recovery. Understanding the patterns of early recovery of plant communities is of interest both for humans and wildlife that depend on self-recovery of vegetation in this region.

During the summer of 2015, information was collected on the presence of plant species and their regeneration modes in 212 sample plots throughout the NWT. Our objectives were to 1) quantify the role of environmental variables and fire characteristics on taxa richness and regeneration traits following an extreme wildfire event; and 2) characterize and investigate vascular plant species composition immediately following fire, with a view to understanding the environmental variables and plant traits underlying post-fire assembly processes.

We found that plant community recovery in the southern boreal forest of the NWT is rapid and dominated primarily by rhizomatic species present pre-fire. Our findings suggest that environmental characteristics influenced patterns of community assembly across multiple spatial scales. Poorly drained areas with greater surficial moisture and associated soil characteristics strongly supported self-replacement of plant communities.

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CHAPTER 1. GENERAL INTRODUCTION

1.1 The boreal forest

The boreal forest stretches across the northern circumpolar regions of Alaska, much of northern Canada, Russia, Scandinavia as well as parts of Scotland (NRC 2005). For the most part, the boreal forest exists above 50° north latitude and is part of the biome also known as Taiga (NRC 2005). Climate in the Taiga region tends to have long, extremely cold winters and short, warm summers, resulting in a brief growing season; there are also strong seasonal fluctuations in air temperature and day length (Bonan and Shugart 1989). Permafrost (ground that stays below 0°C for two or more consecutive years; Muller 1947) distribution is also tightly linked to climate and is an important control on subsurface characteristics such as soil temperature, moisture, subsurface hydrology, biogeochemistry, rooting zone depth and microtopography (Woo 1992). This vast expanse of woodland comprises one third of the world's total forested landscape covering approximately 1.3 to 1.5 million square kilometres (Dudley *et al.* 1998). Undisturbed boreal forest ecosystems are important global carbon sinks containing more than 30% of all carbon present in the terrestrial ecosystems (Kasischke 2000).

Canada is home to 28% of the world's boreal forests (NRC 2017) and the wildlife that inhabit this ecosystem. It is important to the Canadian economy and livelihoods of many northern Canadian communities (Dudley *et al.* 1998; Nelson *et al.* 2008). In Canada, the boreal forest is dominated by closed and open canopy coniferous forests of *Picea* spp. (spruce) and *Pinus* spp. (pine). The boreal forest has low diversity despite its size, which can be attributed to harsh climatic conditions and limited solar energy driven by its northern distribution; the boreal forest supports approximately 300 vascular plant species from upwards of 47 families in North America (La Roi 1967). The boreal forest's composition is generally described by the dominance of conifers underlain by low shrubs, herbaceous vegetation, mosses and lichens. Many species of vascular plants are common across all areas of the boreal forest, for example, while shrubs and trees are generally of the same genera. In the North American boreal forest, *Pinus banksiana* Lamb. (jack pine) and *Picea mariana* (Mill) BSP (black spruce) (Brouillet *et al.* 2013) are the two most widespread and dominant coniferous species (Arseneault 2001); other common dominant conifers include *Picea glauca* (Moench) Voss (white spruce) and *Larix laricina* (Du Roi) K. Koch (tamarack). Common deciduous trees and shrubs include *Betula papyrifera* Marsh. (paper birch), *Betula neoalaskana* Sargent (Alaska paper birch), *Populus tremuloides* Michx (trembling aspen), *Populus balsamifera* Linnaeus (balsam poplar), *Betula glandulosa* (glandular birch) and many species of *Salix* (willow). Understory shrubs common to this area include *Vaccinium vitis-idaea* (lingonberry), *Vaccinium uliginosum* (bog bilberry), *Arctostaphylos uva-ursi* (bear berry), *Ledum groenlandicum* (Labrador tea) and *Rosa acicularis* (prickly rose). Common herbs include *Rubus chamaemorus* (cloud berry), *Linnaea borealis* (twinflower), *Cornus canadensis* (bunchberry) and *Hedysarum alpinum* (alpine hedysarum).

Although dominant trees and stand types are a main focus of ecological research in the boreal forest, an important component of forest biodiversity is the community of understory plants, which have a strong influence on the overall forest structure and contribute immensely to forest ecosystem functioning (Nilsson and Wardle 2005). The diversity of plants in the understory for example, can increase total resource uptake by plants and subsequently lower nutrient loss within an ecosystem (Hooper and Vitousek 1997). Many environmental characteristics present in stands such as the presence of permafrost and cold, acidic soil are moderated in part by the understory plant species composition (Bonan 1992; Fisher *et al.* 2016) further emphasizing the importance of this component of the ecosystem. Although diversity of the understory community in the boreal forest is considered low in comparison to more temperate and tropical forests, there is still much to be understood concerning the life history and phenology of many boreal understory species. A deeper understanding of boreal community dynamics is required to address concerns for biodiversity conservation and forest management in a changing climate. Ecosystem services such as subsistence for human-wellbeing in the form of edible plants and unique habitats that support wildlife will be sensitive to variation in understory species composition. Such understanding would also enable predictions of future forest changes that are important to wildlife through improved understanding of changing habitat conditions.

1.2 Wildfire in the boreal forest

The boreal forest is adapted to natural disturbances such as pest outbreaks, drought and wind damage, which naturally range in frequency and scale; these non-stand replacing disturbances help to maintain heterogeneity by creating a mosaic of stands that are perpetually in different stages of regeneration across the landscape (Antos and Parish 2002; Burton *et al.* 2008). The major driver of ecological processes within the boreal forest however, is wildfire, which is a stand replacing disturbance mechanism that ultimately dictates dominant patterns of succession and tree species distribution; dominant patterns of tree distribution can further dictate regional and local fire regimes depending on the flammability of the successional vegetation (Payette 1992; Cumming 2001; Stocks *et al.* 2003; Keeley 2009). From an ecological perspective, wildfires are considered beneficial for the ecosystem as they renew the forest by aiding in the release of nutrients that support plant growth (MacLean *et al.* 1983), destroy pests and diseased trees (McCullough *et al.* 1998) and help to open the canopy enhancing penetration of sunlight to the forest floor (Hart and Chen 2006). Large expanses of even-aged stands throughout the boreal biome provides evidence of periodic wildfire events (Payette 1992; Stocks *et al.* 2003).

Combined factors characterizing an ecosystem's fire history in a given area are collectively known as the fire regime (Heinselman 1981). The fire regime comprises the frequency (number of fires per unit time in a given area; Payette 1992), intensity (heat energy release), size, pattern and severity (combustion of above and belowground biomass during fire; Van Wagner 1983) of a particular fire. The general temporal and spatial patterns of fire behaviour and effects over multiple fire cycles (decades to centuries) determine the fire regime in a given ecosystem. Fire regime and behaviour vary depending on factors such as vegetation type, fuel structure, stand age and successional stage (i.e., present age-class structure of the forest is particularly important to understanding its past fire history for example; Van Wagner 1978). Climate and weather patterns, topography and landscape patterns (such as temporal and spatial variation in habitat type, soil type, etc.) also influence fire behaviour (Taylor and Skinner 2003; Wotton *et al.* 2010).

Forest fire regimes in Canada differ across the country; the eastern boreal forests, for example, tend to be characterized by longer fire intervals (~150 years) and lower severity. In western Canada, fires are often extensive in size, severe (Stocks *et al.* 2003), and more frequent (~50-150 years) (Payette 1992; Bergeron and Dansereau 1993; Larsen 1997; Chipman and Johnson 2002). An examination of the spatial distribution of all Canadian fires >200 hectares in the 1980s showed that by far the greatest area burned was in the boreal region of west-central Canada (Stocks *et al.* 1996). Furthermore, the Taiga Plains and Taiga Shield Ecozones in northwestern Canada experience some of the highest annual rates of burn relative to the area of forest available, in comparison to other ecozones across Canada (Burton *et al.* 2008). These higher burn rates can be attributed to a combination of fire-prone ecosystems, extreme fire weather, lightning activity and reduced levels of protection throughout the region (Stocks *et al.* 1996) due to low human population densities.

Wildfires can also occur throughout the growing season. Following snow-melt in spring, for example, fuel types are highly flammable, as deciduous trees have not yet flushed and herbaceous ground cover and conifer foliage often has low moisture content, resulting in an active if short-lived 'spring fire season' (Lewis and Ferguson 1988; Kasischke and Turetsky 2006). Later in the growing season, deep moss layers and peat soils common in *P. mariana* stands can become dry and highly flammable during summer droughts as well as during the early fall as vegetation becomes dormant, resulting in severe crown fires (Payette 1992). Furthermore, depth to the water table, which is also important for the preservation of deep organic layers (Harden *et al.* 2006) lowers through the growing season, likely leading to a combination of longer droughts, increased availability of fuel (Kasischke and Turetsky 2006) and greater potential for smouldering combustion (Van Wagner 1987; Peter 1992; Miyanishi and Johnson 2002).

The rate of combustion and overall fire behaviour is influenced heavily by the chemical and physical characteristics of the vegetation present (Ward 2001), with high moisture content within fuels impeding the rate of combustion (Nelson 2001), indicating a strong influence of vegetation on fire regime. Fuels are often classified as ground fuels (highly decomposed and partially decomposed organic material in contact with the inorganic layer), surface fuels (recently fallen and partially decomposed twigs and etc.) and crown fuels (canopies of mostly coniferous trees) (Payette 1992; Nelson 2001). Ladder fuels such as saplings, arboreal lichens and dead lower branches within conifer forests enable vertical movement of fire from surface fuels into the canopy (Payette 1992). *Picea mariana* stands typically experience high severity crown fires that result in complete crown mortality, but often vary in severity at the soil level (Miyanishi and Johnson 2002). The spread of fire is determined mainly by factors such as weather (including wind direction and speed), topography, fuel quantity and fuel moisture content (Nelson 2001). There is usually considerable interest in the flaming front or zones of fire where the combustion is primarily flaming. Smouldering combustion is also common in large litter layers of the boreal forest under limited oxygen conditions (Weber 2001) and limited fuel moisture (Peter 1992). Smouldering combustion can lead to substantial combustion of biomass after the flaming front has passed with implications for regeneration processes.

1.3 Community assembly: plant traits, fire and the environment

The structure of the boreal forest can be thought of as a mosaic of stands in various stages of growth and recovery following disturbance; this process of change in the structure and composition of a community is known as succession. Species in the boreal forest are adapted to regular wildfire; successional patterns are determined by species adaptations to various fire regimes (Keeley *et al.* 2011). In warmer, conifer dominated forests for example, thick bark and self-pruning strategies (the bottom branches of coniferous trees are dropped), are adaptations that ensure less impact on individuals of that species in different fire regimes. Regeneration strategies are an example of plant traits that can be adapted to certain fire regimes such as seeds that germinate in response to smoke and heat (Bond and van Wilgen 1996), providing a fitness advantage to plants that possess those traits in fire-prone environments (Keeley *et al.* 2011).

In the much colder environment of high-latitude boreal forests, growth is limited, stand replacing fires are common and species adaptations to fire differ from that of more southerly forested ecosystems. Dominant tree species in the boreal zone of northern Canada such as *P. banksiana* and *P. mariana*, have serotinous cones (canopy stored seeds depend on heat-induced release); therefore, the cones are able to withstand heat and provide an abundant seed source immediately following fire if they are not completely burned. The serotinous characteristics of these tree species can lead to the sustained presence of serotinous species over generations of disturbances as these species are able to self-replace throughout disturbance cycles (Lamont and Enright 2000; Buma *et al.* 2013).

Additionally, some plants have the ability to resprout from belowground vegetative structures that remain protected in the soil. Likewise, the establishment of deep seedbanks that persist within the soil and germinate following fire is another example of regeneration strategies that ensure high plant and propagule survival rates following fire in the boreal (Rowe 1983; Wang and Kemball 2005). Residual organisms and plant structures that are available and successful following past disturbances provide a biological legacy that ensures successful regeneration through future disturbances (Franklin *et al.* 2000; Johnstone *et al.* 2016). In general, there are two common post-fire regeneration strategies that plants use in the boreal forest: 1) regrowth from above or belowground vegetative structures such as woody stems or rhizomes (underground stems that grow horizontally, putting out lateral shoots and adventitious roots at intervals) and 2) seed dispersal (movement of seeds away from the parent plant (Lyon and Stickney 1976). In the boreal forest rhizomes are generally able to survive high temperatures from fire (Granström and Schimmel 1993; Schimmel and Granström 1996). Off-site seed-dispersal or on-site seeds can survive the disturbance in the form of canopy seedbanks (serotinous conifers) or soil seedbanks as well.

Dispersed seed from plants can also form dormant seedbanks that reappear following disturbance (Bond and van Wilgen 1996); species with thick, hard seed coats such as *Rosa* spp. and *Corydalis* spp. are known to maintain persistent, fire dependent seed pools in Alaska, for example (Viereck 1973). *Corydalis sempervirens* has been known to maintain viable seedbanks for up to eighty years (Fyles 1989) and have seeds that are dispersed within proximity to the parent plant by ants (Sprengelmeyer and Rebertus 2015). Other early successional species that can be represented in persistent seedbanks and are known to germinate following fire include *Geranium bicknellii* (northern cranesbill) and *Dracocephalum parviflorum* (Lyon and Stickney 1976). The mechanism by which seedbanks are germinated is not always clear; *Geranium bicknellii* has been shown to require exposure to high temperatures for dormancy release and likely relies on fire to do so (Granström and Schimmel 1993). Other studies on post-fire seedbank germination suggest heat, smoke and light trigger germination (or a combination of these) depending on the species (Abrams and Dickmann 1982; Archibold 1989; Granström and Schimmel 1993; Read *et al.* 2000)

Plants are not always limited by one regeneration mode, however. Early post-fire plant communities are often suspected to be a combination of species that have survived the fire, species that have re-colonised from undisturbed forest, or both (Bond and van Wilgen 1996). Examples of variation in regeneration modes among boreal plants include common resprouters such as *Vaccinium vitis-idaea* and *Ledum groenlandicum*. Trees and shrubs such as *P. tremuloides*, *Alnus* spp. and *B. papyrifera* can proliferate successfully from underground structures that survive fire, but also from small, light-weight, wind-dispersed seeds capable of traveling over a kilometre from their source (Dyrness *et al.* 1986; Zasada 1986). It is expected that these multi-modal species have the potential to be successful under varying disturbance conditions. For example, the graminoid *Calamagrostis canadensis* (Michx.) PB (bluegrass), is one of the most abundant post-fire herbaceous species owing to quick-growing underground root systems coupled with successful seed dispersal by wind (Dyrness *et al.* 1986). Studies on the biology of *Epilobium angustifolium* (fireweed), a successful coloniser following fire, have shown 100% seed viability of samples taken in Quebec and grown in warm, moist conditions in the laboratory (Jobidon 1968), and that a single plant may yield as many as 80 000 seeds per year (Salisbury 1962). The prolific nature of this species, supplemented with its ability to produce rhizomatically, makes its post-fire success inevitable. Since many studies focus on forest recovery in terms of canopy trees, further understanding of the drivers of regeneration strategies of understory plants in varying fire conditions and environmental conditions is required. Understory vegetation exerts strong controls on aboveground and belowground processes such as patterns of succession and the proportion of a stand's net primary productivity (Chapin 1983). Furthermore, understory vegetation accounts for the species diversity and subsequent functional diversity within stands (Roberts 2004, Nilsson and Wardle 2005). Predicting ecological responses of early recovering vascular plants, including both understory and tree species, will help determine forest recovery and the subsequent functioning of future forests.

Overall, regeneration strategies have been selected for by past fire conditions, ultimately facilitating the resilience of particular understory communities and enabling future generations to thrive following fire (Keeley *et al.* 2011). This resilience is a component of the ecosystem's resilience or the ability for a system to persist and absorb change and disturbance while maintaining relationships between populations or system variables (Holling 1973). It is thought that the ability of plants to re-establish post-fire is mainly influenced by the amount of organic soil that is consumed during fire, and the extent of damage or loss of belowground structures (Schimmel and Granström 1996). For slow growing, rhizomatic regenerators, future generations do particularly well in areas where organic soil is left substantially intact (i.e., following low severity fires) or where rooting depths extend below the depth of burn (Schimmel and Granström 1996). The resilience of the understory community is not solely dependent on fire behaviour however. The physical environment is tightly coupled with vegetation composition and will, therefore, play a role in both fire behaviour and post-fire community assembly.

Pre-fire plant community structure is governed heavily by soil conditions in northern boreal forests, where organic soil layers are particularly important for determining abiotic conditions that contribute to vegetation, decomposition and carbon balance across these landscapes (Harden *et al.* 2006; Fisher *et al.* 2016). Variation in species composition across interior Alaska has been attributed in part to site drainage in relation to topography, for example (Hollingsworth *et al.* 2006). Indeed, in some cases, pre-fire site characteristics and environmental gradients are more important than fire severity in determining patterns of post-fire community assembly (Chipman and Johnson 2002; Hart and Chen 2006; Boiffin *et al.* 2015). Furthermore, resprouter dominance has been known to increase along moisture gradients (Smith *et al.* 1993), and diversity and species richness have been found to increase downslope where moisture and nutrients are suspected to be more available (Chipman and Johnson 2002). There is a need to develop our understanding of the role of fire characteristics, environmental conditions and the regenerative abilities of the understory communities to better predict species composition and vegetative responses in varying fire regimes.

1.4 Environmental characteristics, stand type and fire behaviour

Environmental gradients across the landscape are often reflected in dominant stand type, which is strongly influenced by soil conditions in particular (Fosberg *et al.* 1996). Canadian boreal forests demonstrate substantial differences in soil conditions and associated forest type; organic soil depths in unburned *P. mariana* stands are often much greater than *P. banksiana*-dominated stands, for example (Letang and de Groot 2012; Walker *et al.* 2017 in press). Soil temperature and moisture conditions are affected by organic soil depths and soil bulk density, further influencing stand composition through seedbed conditions (Letang and de Groot 2012).

Many factors contribute to the accumulation of organic soil depths and the *P. mariana* stands that are supported by them; these factors include the presence or absence of permafrost, low decomposition rates, cold soil temperatures and a surplus of moisture (van Cleve *et al.* 1983; Bonan and Shugart 1989). Organic layer accumulation leads to a rise in the water table, subsequently creating high soil moisture conditions in *Sphagnum*-rich, *P. mariana* stands in particular (Fenton *et al.* 2006). Low-lying, poorly drained areas with *P. mariana* dominance also support understory species that grow well in wet, nutrient poor, acidic conditions such as *Ledum groenlandicum* and *Equisetum* spp. (horsetails).

Pinus banksiana-dominated stands on the other hand, are moisture limited, with shallow organic soil depths and low fuel loads (Letang and de Groot 2012). *Pinus banksiana*-dominated stands and their associated understory species perform well in well-drained areas on ridgetops and upland sites with course, gravelly to sandy soils (Carroll and Bliss 1982; Pinno and Errington 2016; Day *et al.* 2017). Species common in drier substrates include the shrub *Rosa acicularis* and the herb *Linnaea borealis*.

It is likely then, that stand type combined with the environmental conditions conducive to stand type, will influence fire behaviour and vegetation. In *P. mariana*-

dominated stands in particular, the combination of deep organic soils that tend to be cold and maintain high moisture levels year-round (as a result of high water tables) have the potential to resist fire and maintain permafrost, for example (Harden *et al.* 2006). It is safe to say that moisture holding capacity of soils and the associated water table depth are important in determining how a fire burns and how a community returns. The deeper the organic layers, the more likely that the legacies of thermal and nutrient cycling governed by fire and revegetation will be maintained, for example (Harden *et al.* 2006).

1.5 Boreal forest and climate change

Over the past century, the boreal forest has experienced climate change (IPCC 2013), exemplified by warming trends that have been most apparent. In the past 75 years, northwestern Canada has warmed at 2-3 times the global average (Zhang *et al.* 2000). Temperatures are projected to rise by an additional 2–11°C by 2100 (IPCC 2013). The impacts of such rapid warming are still not completely known. Higher latitudes are particularly sensitive to warming temperatures given the effects of warming on hydrological processes such as snow melt, permafrost thaw, precipitation and evapotranspiration in the boreal forest (Settele *et al.* 2014). Evidence of rising temperatures, increased precipitation (Chapin *et al.* 2000), increased evapotranspiration and subsequent decreased fuel moisture have been documented (Wotton *et al.* 2010). Increased evapotranspiration has led to drought stress in some areas (Stocks *et al.* 2000), including evidence of drought stress in trees (Barber *et al.* 2000; Walker *et al.* 2015).

Weather conditions conducive to fire such as warming temperatures, increased drought conditions and increased fire ignitions from lightning have already brought about variation in the temporal and spatial scales of naturally occurring wildfire in recent years (Soja *et al.* 2007). In the past 50 years, for example, there has been a strong increase in the annual area burned in western North America (Kasischke *et al.* 1995; Gillett *et al.* 2004; Soja *et al.* 2007), which has been attributed to climate warming (Stocks *et al.* 2000; Soja *et al.* 2007; Macias Fauria and Johnson 2008). Continued altered fire regime and behaviour in response to changing climate and weather are predicted in the future (Amiro *et al.* 2008, DeGroot *et al.* 2013), including increases in area burned and fire frequency (Kasischke and Turetsky 2006; Krawchuk *et al.* 2009). Increases in the length of fire seasons are also predicted (Wotton and Flannigan 1993; Wotton *et al.* 2017). The trend towards larger areas of the boreal forest burning since the 1970s (Soja *et al.* 2007) has recently been exemplified in fire seasons in western Canada. In the past five years alone, we have seen three unprecedented fire years; in 2014, the Northwest Territories experienced an extremely large fire year with approximately 3.4 million hectares burned. Similarly, Saskatchewan saw 1.7 million hectares burned in 2015 (CIFFC 2014) and most recently, British Columbia surpassed provincial historical records in 2017 (BC Wildfire Service). Combined, this evidence points to the fact that the fire regime is changing necessitating improved understanding of the response of boreal vegetation to these changes.

In relation to vegetation, changes in fire characteristics such as severity and frequency can affect community regeneration patterns and influence the future composition of the boreal forest (Hollingsworth *et al.* 2006; Johnstone and Chapin 2006a). Severe fires in Alaska, for example, have shifted *P. mariana*-dominated stands toward dominance by deciduous broadleaf species; severe fires have exposed mineral soil seedbeds upon which small-seeded, wind-dispersed species such as *P. tremuloides* can readily establish and out-compete slower-growing *P. mariana* (Johnstone and Chapin 2006b) Evidence increasingly points to the early establishment of the long-term understory community in the first few years following wildfire, therefore, fire characteristics and environmental conditions for early colonisers immediately following a fire are thought to determine the successional trajectory of the stands (Johnstone and Chapin 2006a; Johnstone, Hollingsworth, *et al.* 2010; Hollingsworth *et al.* 2013; Day *et al.* 2017). Knowledge of these changes in varying stand conditions involving *P. banksiana*, *P. mariana* and a mixture of the two is not well understood, especially as climate warming continues and fire regimes continue to change.

Variable fire characteristics such as fire severity and frequency, can affect post-fire regeneration as a function of mode of regeneration (Rowe 1983; Schimmel and Granström 1996; Wang and Kemball 2005; Johnstone, Hollingsworth, *et al.* 2010; Hollingsworth *et al.* 2013). Since rooting depths and mode of regeneration differ among species, the depth of consumption of the organic soil layer will impact the way that plants regenerate and the assemblage of species that return following fire (Flinn and Wein 1977; Schimmel and Granström 1996). Plants that rely on re-sprouting from underground will have less success in environments where organic layer thickness is severely reduced by combustion (Schimmel and Granström 1996; Johnstone, Chapin, *et al.* 2010) since many species rooting systems are within the organic layers (Flinn and Wein 1977, see Chapter 3, **Figure 3.2**). *Vaccinium vitis-idaea* for example, has a surficial rooting system extending only 2-3cm belowground (Schimmel and Granström 1996) while *Ledum groenlandicum* (Labrador tea) rhizomes are found at 15-30cm depth (Dyrness *et al.*

1986). Systematic differences in rooting depth may, therefore, result in differential responses of rhizomatous species to the depth of soil burning; deeper root systems, especially those at the interface between organic soil and mineral soil would be expected to be at an advantage to survive particularly severe fires (Schimmel and Granström 1996). In Strong and La Roi's study in central Alberta (1983), eight of the eleven coniferous stands studied had 50% of root mass within a 15cm zone, the bulk of which generally occurred within 5cm of the forest floor, further suggesting the vulnerability of many species to soil combustion. On the other hand, a low severity fire in moist organic soil may result in limited combustion of surface fuels with little effect on deeply buried plant parts, which will promote the regeneration of the pre-fire community (Schimmel and Granström 1996).

Colonisation from seed may be enhanced after relatively deep burning fire, both for species with a soil seedbank and those that disperse from off-site seed sources if the depth of burn destroys belowground root systems and exposes mineral soil (Bond and van Wilgen 1996; Johnstone and Chapin 2006b; Johnstone, Hollingsworth, *et al.* 2010). With very severe burns however, seed banks in the soil may be destroyed allowing for dispersers to have better establishment with increasing depth of burn, since dormant seed banks are typically concentrated at the interface of organic and mineral soils (Schimmel and Granström 1996). It should be noted, however, that some species may be tolerant of high temperatures associated with fire. Indeed, *Rubus idaeus*, *Geranium bicknellii* and *Galium triflorum* were found to be significant indicator species in intensely burned patches in a *P. tremuloides* dominated forest in Alberta; the author attributed their regeneration from seedbanks (Lee 2004), suggesting that some seedbanks are capable of regenerating following severe fires given their tolerance to high heat or heat and smoke serve to enhance germination (Bond and van Wilgen 1996). *Geranium bicknellii* has been shown to require high temperatures for dormancy release as mentioned earlier (Granström and Schimmel 1993). Literature on the specifics of boreal seedbank biology is limited, however; further understanding of how individual species are successful components of the understory following fire is needed.

Similarly, more frequent fires may alter the potential for seedbanks to re-establish successfully over time as seeds are depleted from the seedbank and not given sufficient time to re-establish. The same may be said about the ability for underground, rhizomatic tissue to be depleted with frequent fires as moist, organic soil and the community supported by this soil takes time to accumulate.

Ultimately, a complex feedback between climate, soil interactions, forest type and understory composition controls overall ecosystem functioning in the boreal forest. Patterns of forest cover have shown to strongly reflect the interactions between disturbance regime and species regenerative potential (Payette 1992; Suffling 1995). The impacts of species-level losses or changes within an ecosystem through wildfire may have far-reaching impacts that alter forest ecosystem functioning (Weber and Stocks 1998; Nilsson and Wardle 2005). The deciduous trajectory in parts of Alaska is a dramatic alternative to the conifer-dominated boreal forests because of changes in litter production, decomposition, lower organic soil accumulation and warmer soils that characterize deciduous forests (Johnstone, Chapin, *et al.* 2010). Furthermore, the high moisture content in deciduous forest fuels will reduce the amount of crown fire and total fuel consumption during wildfire events, although the degree to which future boreal fuel load and fuel type will change is still unknown (de Groot *et al.* 2013). Lost or altered forest cover and associated understory vegetation from changing fire regimes can hinder carbon sequestration in both trees and forest soils and can affect the capacity of the boreal forest to function as a carbon sink (Kasischke 2000).

1.6 Importance and rationale of research

Changes to current or future fire regimes can be expected to have pronounced effects on boreal plant species composition with implications for boreal forest functioning (Weber and Stocks 1998; Burton *et al.* 2008). Given the vast expanse of the boreal forest as well as its importance to ecological processes at local and global scales, understanding the future composition and function of this ecosystem is essential in light of biodiversity conservation, forest management and community adaptation. The unprecedented fire year in 2014 in the NWT provided a timely opportunity to examine drivers of understory species richness, community assembly and plant species composition following an extensive disturbance in an understudied part of the boreal forest of western Canada.

By linking species traits with composition and environment (including fire characteristics) this comprehensive approach draws important conclusions on the ecological processes that drive community assembly following extensive wildfire. This work helps build upon monitoring efforts addressing the recovery of high latitude forests following fire, enabling decisions to be made regarding land use planning for humans and wildlife, and resource development in fire-dominated ecosystems where unprecedented fire regime changes are predicted.

1.7 Objectives and hypotheses

In this thesis, my goals were to: (1) quantify the role of environmental variables and the severity and frequency of fire on vascular plant taxa richness and regeneration traits following an extreme wildfire event; and (2) characterize and investigate vascular plant species composition immediately following fire, with a view to understanding the environmental variables and plant traits underlying post-fire assembly processes.

I hypothesized that taxa richness and the potential for resprouting would decline with increased severity and frequency because of limitations on regeneration from underground rhizomes in heavily consumed organic soils and in young stands that have not had the chance to re-establish understory communities or organic soil depths following the last disturbance. In more severe burns, species with multiple regeneration modes such as those capable of aerially seeding and storing seedbanks would be more likely to establish. However, in the most severe fires it was expected that aerial dispersers would be the most successful.

1.8 Thesis Overview

The first chapter of this thesis is a general introduction to the boreal forest and the role of wildfire as the main agent of disturbance throughout the boreal forest ecosystem. The chapter then investigates how vascular plant communities are able to re-establish following wildfire, and the role of environmental characteristics in governing vegetation and fire characteristics. The impacts of climate change on the natural fire regime is then investigated. The chapter concludes with potential consequences of a changing fire regime on the recovery of the vascular plant community and the long-term implications of these changes.

The second chapter has been formatted in preparation for submission as a manuscript to a scientific journal. This manuscript is co-authored with Nicola Day, Xanthe Walker, Jill Johnstone, Steve Cumming, Michelle Mack, Merritt Turetsky and my supervisor Jennifer Baltzer. My role in this research project included leading field data collection and data processing such as identifying species in the field and mounting plant specimens for the Wilfrid Laurier Herbarium. My role also extended to leading data analyses and writing and revising the thesis. The manuscript outlines the immediate drivers of understory community assembly following extensive wildfires spanning two ecozones in the NWT. We found a strong environmental legacy associated with surficial moisture and soil characteristics to be driving post-fire taxa richness and community assembly. This environmental legacy enables the biological legacy of plant traits that drive compositional differences following fire across both ecozones and stand types.

The third and final chapter of this thesis discusses the contributions of this research to monitoring efforts addressing the recovery of high latitude forests following fire. I investigate how our findings compare to other fire ecology studies looking at drivers of post-fire vegetation recovery in boreal forests around the world and suggest further rationale behind the resilience we are seeing in these forests in response to a severe wildfire event. To this end, I introduce some novel rooting depth data as a case study to highlight the environmental variability and subsequent vegetation legacy across the landscape. The chapter also touches upon the inherent relationships between people and the environment in the NWT and the role of fire in their livelihood and future. The chapter points out the integrative approach of this project and potential future research directions. Lastly, the chapter concludes with a summary of the thesis.

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CHAPTER 2. ENVIRONMENTAL LEGACIES DRIVE POST-FIRE VASCULAR PLANT RECOVERY IN SUB-ARCTIC BOREAL FOREST

2.1 Abstract

The boreal forest is adapted to regular wildfire with fire characteristics playing a key role in post-fire plant community assembly. The frequency and severity of fire provides a filter for successful plant regeneration strategies, such as the ability to resprout from belowground tissue. Understanding how fire characteristics and other environmental variables impact the mechanisms of vascular plant establishment may enable us to predict plant regeneration responses to changing fire regimes in the face of climate change. This is important given that the understory community of vascular plants plays an important role in ecosystem function. In 2014, an unprecedented 3.4M ha of boreal forest burned in the Northwest Territories (NWT). The 2014 fire provided an opportunity to investigate the drivers of vascular plant taxa richness, community assembly and plant species composition using taxonomic and trait-based methods. We established 212 permanent plots across the Taiga Plains and Taiga Shield Ecozones. A range of abiotic and biotic variables were measured, including depth of organic layer, fire severity and pre-fire stand composition throughout conifer-dominated stands. Species presence and modes of regeneration of vascular species were recorded. Our generalized findings demonstrated that belowground regeneration of the plant community was most common across both ecozones. Poorly drained areas with greater surficial moisture and associated soil characteristics enabled a proportionally greater representation of species regenerating from rhizomes across multiple spatial scales. Lower severity fires resulted in greater post-

fire taxa richness; post-fire plant communities following more severe fires had proportionally greater representation of species regenerating via seed dispersal and seed bank. Our findings suggest the vascular plant community composition in the southern boreal forest of the NWT demonstrates self-recovery following fire disturbance, as a result of moisture conditions and soil substrate legacy effects.

2.2 Introduction

Stand-replacing wildfires are a common form of disturbance in the western boreal forest of North America with average fire return intervals ranging between 50-150 years (Payette 1992; Bergeron and Dansereau 1993; Larsen 1997). The boreal forest is highly resilient to this disturbance agent, having the ability to reorganise into the same structure and function following fire (Holling 1973; Gunderson 2000), with stand self-replacement a common successional trajectory (Johnstone and Chapin 2006a). However, warming trends have been pronounced in this region in recent decades at a rate that is 2-3 times the global average (Zhang *et al.* 2000). This has led to an increase in fire frequency and severity (Kasischke and Turetsky 2006), a pattern that is predicted to continue in the future (Amiro *et al.* 2009; de Groot *et al.* 2013; Wotton *et al.* 2017). Such changes are expected to impact understory community assembly and vegetation patterns (Hollingsworth *et al.* 2013). Greater understanding of how vascular plant communities assemble and are maintained at local and landscape scales is necessary to predict changes to ecosystem successional patterns and functional diversity with changing fire regimes.

Plant traits are an important component determining the rate and trajectory of post-fire plant community assembly, with different fire characteristics selecting for different regeneration strategies (Keeley *et al.* 2011; Hollingsworth *et al.* 2013). Current boreal plant regeneration strategies have evolved under past fire conditions; patterns in plant communities and species distributions within the boreal forest are therefore reflected in the processes of forest recovery and succession following large-scale disturbances (Loucks 1970; Heinselman 1981). For example, the serotiny (heat induced release of long-term canopy stored seeds) of dominant conifers that comprise the canopy of mature forests is an important mechanism ensuring stand self-replacement over repeated cycles of wildfire, especially in mature stands (Johnstone and Chapin 2006a). Residual organisms and plant structures that are available and successful following past disturbances provide a biological legacy that ensures successful regeneration following future disturbances (Franklin *et al.* 2000; Johnstone *et al.* 2016). Dominant tree species in the boreal forest such as *Pinus banksiana* Lamb. (jack pine) and *Picea mariana* (Miller) B.S.P. (Brouillet *et al.* 2013) (black spruce) have cones that open following high heat exposure for example and provide a seed source immediately following fire. Adaptive strategies of plants in the understory community also ensure high plant and propagule survival rates following fire (Rowe 1983; Wang and Kemball 2005). Specifically, understory plant regeneration may occur from on-site seeds that survive the disturbance (i.e., cone and seed banks), or from resprouting from deeply buried vegetative structures (Lyon and Stickney 1976).

Given predicted changes in fire regime, colonisation from seed may be enhanced after relatively deep burning fire, both for species with a soil seedbank and those that disperse from off-site seed sources if the depth of burn destroys belowground root systems and exposes mineral soil (Bond and van Wilgen 1996). With very intense burns however, seed banks in the soil may be destroyed allowing for dispersers to have better establishment with increasing depth of burn (Schimmel and Granström 1996). There is a need to improve our understanding of the functional mechanisms driving changes in post-fire plant species composition and consequently, species richness in boreal plant communities to predict responses of these communities to altered fire characteristics.

Fire severity (combustion of above and belowground biomass during fire) coupled with frequency, size, intensity, type (ground vs. canopy) and season of burn are all considered important processes governing ecosystem recovery, structure and function following fire (Van Wagner 1983) and naturally influence stand-level and landscape vegetation patterns (Bergeron and Dansereau 1993). Of these processes, soil burn severity, or the depth of burn in surface soil organic layers (Van Wagner 1983), is often attributed to having the greatest impact on post-fire plant communities because of the concentration of regeneration potential in the organic layer in the form of regenerative tissues and seedbanks (Schimmel and Granström 1996; Hollingsworth *et al.* 2013; Pinno and Errington 2016). Previous studies looking at post-fire species richness in the boreal forest showed that species richness can decline in severely burned areas (Hollingsworth *et al.* 2013; Pinno and Errington 2016). Patterns and processes underlying plant traits such as plant phenology and seed biology in the boreal forest are still poorly understood following various fire regimes. Furthermore, given the dominant role of fire in the boreal landscape, it is often difficult to decipher between pre-existing environmental characteristics and changes to the environment caused by fire.

Indeed, environmental characteristics inherent to the site such as site productivity, seedbed condition and soil moisture (often associated with topography), have been shown to be important in forest regeneration following fires (Greene *et al.* 1999; Hollingsworth *et al.* 2006; Johnstone, Chapin *et al.* 2010). Biotic and abiotic environmental conditions act as ecological filters, selecting for plant communities that are successful following disturbance (Keddy 1992). Not surprisingly, plant species richness and diversity are often studied following fire since changes in soil composition, light and nutrient regimes are rapid during this time (Hart and Chen 2006), all of which factor heavily on vegetation growth (Chipman and Johnson 2002; Hollingsworth *et al.* 2006). Previous studies looking at post-fire species richness in the boreal forest showed that species richness can increase in lower topographic positions where moisture and nutrients may accumulate (Chipman and Johnson 2002).

Deciphering between the role of environmental characteristics and fire characteristics is even more challenging when you consider their interaction and ability for one to influence the other. For example, poorly drained sites with deep organic soils prior to fire provide excellent environmental conditions for slow growing, stress-tolerant species capable of rhizomatic regeneration from above and belowground tissue (Grime 1977; Schimmel and Granström 1996; Lavorel and Garnier 2002). These same site conditions may also provide the cool, moist conditions to protect these sites from deep burning and the effects of increased fire severity or frequency (Johnstone and Chapin 2006b). Developing new understanding about the role of fire characteristics, environmental conditions and the plant traits associated with community assembly in response to an altered fire regime, will improve our ability to model and predict species composition and vegetative responses in the future.

Throughout the summer of 2014 extensive wildfires burned approximately 3.4 million hectares of boreal forest in the Northwest Territories (NWT) of Canada, spanning the Taiga Plains and Taiga Shield Ecozones (CIFFC 2014). The unprecedented fire year provided the opportunity to examine the potential for severe wildfire to impact post-fire vascular plant regeneration processes spanning two ecozones across a gradient of *P*.

banksiana and *P. mariana*-dominated stands and ask questions about the relative importance of environmental gradients versus fire characteristics in shaping post-fire community assembly. The study objectives were to: (1) quantify the role of environmental variables and the severity and frequency of fire on vascular plant taxa richness and regeneration traits following an extreme wildfire event; and (2) characterize and investigate vascular plant species composition immediately following fire, with a view to understanding the environmental variables and plant traits underlying post-fire assembly processes.

Our findings enable us to identify compositional patterns in plant communities from a combination of plant functional traits and environmental filters that are thought to structure post-fire landscapes in this region and their relationship with fire severity. By linking species traits with composition, environmental characteristics and fire characteristics this comprehensive approach draws important conclusions on the ecological processes that drive community assembly following extensive wildfire in the NWT.

2.3 Materials and Methods

2.3.1 Study Area

This study was conducted across a broad geographical range within the NWT, spanning two low subarctic ecozones: The Taiga Plains Low Subarctic (LS) Ecozone and the Taiga Shield LS Ecozone. Both ecozones have short, cool summers and long, cold winters. Average annual temperatures in Hay River (60.8162°N, -115.7854°W) and Yellowknife (62.4540°N, -114.3718°W) are -2.5°C and -4.3°C, respectively; average annual precipitation is 336mm and 228mm, respectively (Environment Canada 2017).

The climate within this region is representative of much of our study area though we had study plots that extended North of Yellowknife. The Taiga Plains LS comprises the central third of the Taiga Plains and is a mix of undulating glacial till plains and peatlands with permafrost in wetter areas (Ecosystem Classification Group 2007). This area is characterised by open, slow growing, forest dominated by *P. mariana* and *P. banksiana* that extend to the northern edge of the boreal forest (Ecosystem Classification Group 2008). The Taiga Shield LS in the eastern part of the NWT has hilly bedrock with thin boulder till overlain in places by layers of clay, sand, gravel and boulders. Study regions in both ecozones are underlain by discontinuous permafrost, which is defined by ground that stays perennially below 0°C for two or more consecutive years (Muller 1947) and covers between 50% and 90% of the landscape (Brown and Pewe 1974).

2.3.2 Site selection

Between May and August 2015, 212 permanent plots were established across a 400km latitudinal range covering seven burn complexes from the 2014 fire season, ranging from Kakisa in the South to Gamètì and Wekweètì in the North (**Figure 2.1**). For accessibility purposes, most of the sampling plots were established within 1km of roads or edges of water bodies. To reduce bias, random sampling locations were generated from geospatial data to encompass an array of different strata across the seven burn complexes creating a stratified, random sampling design (Cumming in preparation, **Appendix Table 1**). Strata were comprised of the following: 1) 2014 date of burn information determined from MODIS fire progression maps (late season vs. early season burn). We assumed that late season burns would be more severe due to the typically greater availability of fuel at the end of season (Kasischke and Turetsky 2006); 2) pre-fire dominant stand type based on Land Cover Map of Canada 2005 (LCC05), produced from 250m spatial resolution MODIS data (Latifovic *et al.* 2004) and Forest Resource Inventory (FRI) when available, which maps the distribution and abundance of forest tree species to a spatial resolution of 2-10ha (Cumming *et al.* 2015). Land cover classes were common, conifer-dominated classes and represented different stand densities in the sampling landscape. Pre-fire vascular plant species composition was not available and could only be speculated based on dominant stand type and associated environmental conditions. These strata ensured that we captured a range of conifer-dominated forest types in our sampling; and 3) fire history (areas with fire records since 1960 vs. those that had no record of fire since 1960) allowing us to sample stands ranging widely in fire return interval. Each random sampling location was assigned a moisture classification based on the mineral soil texture and presence or absence of permafrost (Johnstone *et al.* 2008; **Appendix Figure 1**)To help understand the impacts of site moisture conditions on fire severity and subsequent growing conditions for regenerating plants, two other locations were selected to span the local moisture gradient, within 500m of the first randomly chosen coordinate (i.e., within a single MODIS pixel). A site was considered the conglomeration of all three plots (i.e., moisture classes were nested within strata).

2.3.3 Data collection and calculation; vegetation

In 2015, elevation, GPS coordinates, slope and aspect were measured at each sampling plot and two parallel 30m transects were established, running from south to north. The point of origin at the western-most transect was permanently marked for future sampling (**Appendix Figure 2**).

Along the eastern-most transect, five 1m^2 quadrats were established at 6m intervals along the transect line with the first quadrat placed at the origin. To characterize regeneration of plant communities after a fire, the presence of each vascular species was documented in each quadrat. Unknown specimens were collected at least 1m away from the transect to be verified at a later date, however, species that were very small or unidentifiable were grouped by genus. To characterize seedbed conditions within each quadrat, ground cover of each of the following categories was recorded to the nearest percent within each vegetation quadrat: organic soil cover, mineral soil cover, litter, charcoal, ash, standing water, burned and unburned feathermoss, lichens, burned and unburned sphagnum, rock, woody debris, *Marchantia* spp. (a common liverwort post-fire) and *Ceratadon* spp. (a common moss post-fire). Variables that were thought to possibly be conditionally dependent were combined. Since *Marchantia* spp. and *Ceratadon* spp. are common early colonising bryophytes and are often found together, for example, we clumped these in our analyses into a "bryophyte" category. A Pearson's correlation matrix was conducted (**Appendix Table 14**). Rock and organic cover were removed because of correlations with organic soil cover and mineral soil cover, respectively. Variables that were present in trace amounts (i.e. ash) were not considered for the candidate models. The variables considered to support excellent seedbed conditions following fire were used in the final candidate models: mineral soil cover, bryophyte and charcoal. As all 2015 Taiga Plains sampling occurred early in the growing season, we revisited these sites in May 2016 to assess whether the spring 2015 presence data represented the full vascular species composition of the first post-fire growing season. They were revisited again in August 2016 to capture the changes in species presence in the second growing season.

We determined the regeneration strategy of plants that were present in each quadrat by excavating individuals of each sampled species closest to the North and South ends of the sampling transects or at least 1m away from the quadrats to minimize disturbance. Regeneration mode was categorized on a scale of 1-4: 1) survival intact, 2) regeneration from seed, 3) aboveground regeneration such as resprouting from a stump or log and 4) belowground resprouting from root/rhizomatous tissue. Aboveground resprouting and survival following fire were rarely recorded in our plots and were consequently removed from the analysis (i.e., survival intact was found at < 10 of our 209 plots) leaving only two categorical variables: regeneration from seed and regeneration from belowground resprouting. All information collected on plant regeneration was collected in the first growing season post-fire between the end of May and end of August 2015.

The majority of vascular plants were identified to species; 61% on the Taiga Plains and 70% on the Taiga Shield, respectively. All specimens were verified at the National Herbarium of Canada. Specimens that could not be identified to species were allocated to genus. All *Equisetum* spp. except *Equisetum scirpoides*, were classified to the genus level given the difficulty in deciphering among species immediately following disturbance when reproductive structures are typically not present. Similarly, all conifers of the *Pinus* and *Picea* genera were identified to genus in the first sampling season to avoid misidentification of such small individuals. *Carex* spp. were identified at the genus level to avoid misidentification as many of the samples taken had not reached maturity but were mature enough to decipher perigynia. The presence of genus-level identification within the dataset lead us to discuss taxa richness instead of species richness throughout. For simplification, we refer to the *Betula* genus as being *Betula neoalaskana* Sargent (Alaska paper birch) on the Taiga Shield and *Betula glandulosa* (glandular birch) on the Taiga Plains as the tree form was dominant on the Taiga Shield and the shrub form was dominant on the Taiga Plains. We recognize the issues of identifying the leaves of this genus at early life stages given similar leaf morphologies and hybridisation of *Betula* spp. in the region (Johnsson 1945; Jarvinen *et al.* 2004) but use these species names to decipher between the tree and shrub forms of this genus in general. A full species composition list for the Taiga Plains and Taiga Shield can be found in **Appendix Table 2** and **Appendix Table 3**). Nomenclature followed Porsild and Cody (1980) to remain consistent with field guide nomenclature from Johnson *et al.* (1995) except for *Salix* spp., which were identified as *Salix* A-H morphospecies based on their leaf phenotypic traits (**Appendix Table 5**). To avoid redundancy, all tree species names are abbreviated after the first use; all other understory species maintain their full names throughout. Tree names were updated using the Database of Vascular Plants of Canada (VASCAN) (Brouillet *et al.* 2013). A large portion of collected voucher specimens are now located in the Wilfrid Laurier University Herbarium in Waterloo, Ontario, Canada (vouchers # 1-95).

2.3.4 Data collection and calculation; environmental and fire characteristics

Trees that were originally rooted between the two 30m transects (spanning 2m) were assessed for aboveground fire severity by visually assessing canopy consumption (cone and branches) using a categorical scale from 0-3 based on Johnstone *et al.* 2008 (**Appendix Table 4**). The consumption index followed: 0=no consumption; cones uncharred with many live, green needles remaining; 1=low consumption; cones 0-33% charred with few needles and small twigs remaining; 2=moderate consumption; cones 34-66% charred with few small twigs and many branches remaining; 3=high consumption; 67-100% charred cones or none remaining with most lower canopy branches consumed. To create a continuous variable representing above ground consumption (tree consumption), we averaged the branch consumption rankings at each plot; cone rankings were excluded from this calculation because of the difficulty deciphering the absence of cones as a result of burning vs. absence pre-fire.

Burn depth was assessed by measuring organic soil consumption as a measurement of the distance from the highest 1-3 adventitious roots on *P. mariana* trees to the forest floor (Boby *et al.* 2010). Adventitious roots are produced as organic soil accumulates ensuring access to surficial soil resources (LeBarron 1945); the remnants of adventitious roots are visually evident after burning (Kasischke and Johnstone 2005; Boby *et al.* 2010). To create the burn depth variable in *P. mariana* stands, a correction was applied to the adventitious root height measurements to account for the fact that adventitious roots are not located at the surface of the soil (~4 cm; Walker *et al.* 2017 in press). In *P. banksiana*-dominated stands where adventitious roots are not present, the residual organic layer depth was subtracted from the estimates of organic layer depths specific to site moisture classes in stands that burned prior to 1960 (n=36 control plots in strata named Control Group (CG) 1, CG 2 and Control Shield (CS); Walker *et al.* 2017 in press).

All trees originally rooted between the two 30m transects that were ≥ 1.3m in height were measured for diameter at breast height (DBH; 1.3m); these measurements included snags that were dead at the time of fire and fallen trees that were killed by fire. The basal diameter of trees < 1.3m tall were also measured. Tree density (stems m^{-2}) and basal area (m^2 ha^{-1}), were calculated as measures of stand structure. Basal area was calculated from stem diameter at breast height or base if less than 1.3m in height ($BA = \pi(DBH/2)^\wedge 2$).

In order to create a continuous stand age variable (estimate of time since last fire), we collected tree cores and cookies of the dominant coniferous tree species in the pre-fire tree canopy ($n = 5$ per dominant species). Cookies or cores were taken as close to the tree stem base as possible to minimize bias in estimating tree ages (Vasiliauskas and Chen 2002). Samples were sanded with a belt sander and palm sander using progressively finer grit (200-600 grit). The polished samples were then scanned at 3800 dpi and the images imported and counted in Cybis CooRecorder v.7.8 (Larsson 2006) or WinDendro 2009 (Regent Instruments Canada Inc. 2009). For cross-sectional samples, tree rings were counted twice at 90° angles while in tree cores, rings were counted on both sides of the core. Seventeen samples did not show evidence of the pith; where the pith was not sampled, the minimum count was taken from as close as possible to where there was some evidence of the pith. Where there was no evidence of any pith, rings were counted until a subjective point, such as a break in a core. If the two counts had >5% discrepancy due to unclear ring definition from compaction, they were manually recounted. We did not cross-date annual growth rings because samples were taken for a coarse estimate of stand age (time since last fire), not to infer any information regarding within year growth or to interpret information from individual tree rings. When aging stands, we assumed tree ages would cluster around the date of the last major fire event (pulse of post-fire recruitment). When >50% of trees fell within 10-20 years of each other, a plot was assumed to have arisen from one fire event and the maximum tree age was used to age the stand. Where there was weak evidence for a specific stand age, samples from the other plots within the site were consulted to support a decision. Sites without a dominant cluster were further inspected; maximum or median tree age was used so that whichever was picked was consistent with age of nearby plots.

2.4 Data Analysis

All analyses were performed using R v.3.3.1 (R-Development Core Team 2016). All statistical analyses were conducted separately for the Taiga Plains and Taiga Shield due to differences in the timing of measurements that occurred systematically between the two ecozones. Species area curves created using the “rarefaction” method in the vegan package version 2.4-1 (Oksanen *et al.* 2017) ensured sampling saturation was achieved on the Taiga Plains and Taiga Shield despite sampling these ecozones at different times during the summer of 2015; this addressed sample-size bias in taxa richness assessments to allow direct comparison of post-fire taxa richness in the two ecozones (Gotelli and Colwell 2010; Oksanen *et al.* 2017).

Since we sampled the Taiga Plains early in the spring of 2015 and some of the specimens were very small, we were concerned we did not fully capture the first growing season of the vascular plant community in our first sampling period. To ensure we chose the most accurate sampling period representing the first growing season, a Mantel test with Pearson's correlation of coefficient was used on the three separate sampling periods (Spring 2015, Spring 2016 and Fall 2016) on the Taiga Plains (Mantel 1967; Legendre and Legendre 1998) using the vegan package (Oksanen *et al.* 2017). The Mantel test is a permutational test that computes the relationship between two distance matrices while testing the statistical significance of matrix correlations. We used the Sorenson distance indicating binary data and used 1000 permutations. The Mantel test examined if there were any temporal differences in species composition at different sampling times. Results from our Mantel tests for the Taiga Plains indicated that species composition in Spring 2015 was not significantly different from Spring 2016 since it was significantly correlated with the Fall 2016 matrix ($r = 0.70$, $P \leq 0.05$). Subsequently, we chose to use the Spring 2015 data as representative of the first growing season post-fire.

Of the original 212 plots, we removed one site on the Taiga Shield that was missing stand age data, for a total of 209 plots; 125 and 84 plots on the Taiga Plains and Taiga Shield, respectively. There was one outlier in the Taiga Plains data (ZF46-1A), which was a plot that exhibited a higher quantity of mineral soil cover than other plots, but it was retained in the analyses since it was considered a true representation of the high mineral soil and charcoal content at this site post-fire. Significant findings did not change as a result of this outlier.

Principal Coordinates Analysis (PCoA) was used to investigate species compositional differences among stand types and between ecozones. PCoA is a distance-based ordination method used to visualize patterns in data and allows for the use of data that is not continuous (Gower 1966). PCoA was calculated using species presence/absence data by plot, specifying the Sorenson distance for the similarity matrix. Sorenson distances are suggested for binary data (Grace and McCune 2002; Legendre and Legendre 2012) and were calculated using 'vegdist' in vegan (Oksanen *et al.* 2017). The PCoA was run using function 'cmdscale' in base R. Species scores were calculated to produce a supporting species ordination using the 'wascores' function in the vegan package.

2.4.1 Modelling post-fire regeneration modes and taxa richness

We used Generalized Linear Mixed Effects Models (GLMMs) to quantify the role environmental characteristics and fire characteristics on taxa richness and mode of regeneration following fire. GLMMs allow for the incorporation of random effects (plot nested within site nested within burn) with non-normal, multivariate data (Burnham and Anderson 2002; Zuur *et al.* 2010; Mazerolle 2016). GLMMs were run at the plot-level for regeneration modes and at the quadrat-level for taxa richness since fine-scale predictors were available (i.e., the number of taxa in each quadrat, % cover variables and residual organic depths). Quadrat-level analyses were thought to be more telling of variability that can occur at finer scales following fire in these stands and the nested design was accounted for in these analyses. Analysis of taxa richness at the plot-level was conducted for comparison purposes; results are included in **Appendix Table 6** and **Appendix Table 7**. Continuous predictor variables included: plot basal area, tree consumption, burn date (day of year), residual organic depth, burn depth, stand age, percent mineral soil cover, percent charcoal cover and percent bryophyte cover. In addition, dominant stand type and moisture class were included as categorical predictor variables (**Appendix Table 8**).

Exploratory scatter plots and box plots were created to assess normality and potential outliers in all variables to be used in our models (Zuur *et al.* 2010). All continuous predictor variables associated with the initial candidate models were normalized and tested for collinearity by constructing a Pearson's correlation matrix (**Appendix Table 9**). R-values where $0.3 < r < 0.5$ between two variables are thought to demonstrate a weak relationship (Moore *et al.* 2013). However, given the noise within ecological data, we assumed typically "weak" relationships to be important; all correlation values ≥ 0.35 were considered correlated and removed from the analyses. Burn depth was positively correlated with stand age in both ecozones and was subsequently removed from the analyses. Burn depth was also correlated with residual organic depths on the Taiga Plains. The categorical variable, moisture class was also removed because of a strong correlation with residual organic layer thickness. Residual organic layer thickness was log-transformed to meet normality. Since we did not include burn depth in our GLMMs, residual organic depths were recognized as representive of both site conditions and fire severity; we included residual organic depth in our Seedbed Model given its important determinant of seedbed quality.

A priori candidate models (Anderson 2008) were used to test specific hypotheses about combinations of predictors that might be most important in predicting post-fire community assembly and taxa richness. These models were: 1) Fire Characteristics, 2) Stand Characteristics, and 3) Seedbed Conditions (**Table 2.1**).

We also included the full model (all predictors) and the null model (random term only) in our suite of candidate models. GLMMs were performed with the "lme4" (Bates *et al.* 2015) package and the multi-model averaging package “AICcmodavg” (Mazerolle 2016) to select the candidate model based on the lowest second order Akaike Information Criterion (AICc). We modeled the number of taxa in each quadrat (i.e. taxa richness) using a Poisson distribution (log link). We also modeled the proportion of plants regenerating from seed at each plot using a binomial distribution (logit link). Mode of reproduction was modelled as a binomial response that described the probability of a plant reproducing from seed as a measure of the proportion of plants reproducing from seed compared to rhizome at each plot. *A priori* contrasts were used to compare the categorical variable dominant stand type; *P. banksiana*-dominated stands were the reference stand for all models (Crawley 2007). We quantified the proportion of observed variance explained by the fixed effects (marginal R^2) and both fixed and random effects (conditional R^2) of the lowest AICc candidate models for the Poisson and binomial distributions using the package “MuMIn” (Barton 2015); the calculation of change in variance in this package followed Nakagawa and Schielzeth (2013). Regression estimate plots were created using the “coefplot2” package (Bolker 2012).

2.4.2 Species composition; environmental characteristics, fire characteristics and species traits

To understand environmental variables and plant traits underlying assembly processes and species composition, we combined two complementary multivariate techniques: RLQ and the Fourth Corner statistic using the “ade4” package (Dray and Dufour 2007). The RLQ summarizes the joint multivariate structure of three matrices: (R) environmental variables, (L) community composition and (Q) species-level functional traits (Legendre *et al.* 1997; Dray and Legendre 2008). In summarizing the relationship between these three matrices, RLQ analysis assigns scores to samples, species, traits, and environmental variables along orthogonal axes based on permutation tests and produces a graphical summary of the main structures.

The Fourth Corner analysis then takes the weighted row scores from the RLQ matrices and statistically tests the relationships between environmental variables and species traits one trait and one environmental variable at a time (Dray and Legendre 2008; Dray *et al.* 2014). The Fourth Corner analysis uses the site scores of the species ordination as row weights for the R matrix and species scores of the sites ordination as row weights for the Q matrix. Applying the fourth-corner tests to the output of the RLQ analysis is a new approach recommended by Dray *et al.* (2014).

In testing bivariate associations in the Fourth Corner analysis, P-values were calculated using the default permutation model (named model 6 by Dray *et al.* 2014), linking matrices L and Q. This combined approach corrects for type I error rates (Dray *et al.* 2014). We conducted 49, 999 random permutations of sites and species in testing the null hypothesis that the distribution of species with fixed (i.e., site-independent) traits is not influenced by environmental conditions, with model 4, which links the matrices L and R and tests the null hypothesis that the species composition of sites with fixed environmental conditions is not influenced by the species traits. Due to multiple tests on environmental variables, the P-values were corrected by the false discovery rate method (FDR; Benjamini and Hochberg 1995; Dray *et al.* 2014). RLQ and Fourth Corner analyses were also conducted at the plot-level for comparison purposes; results can be found in **Appendix Table 10**.

In the RLQ and Fourth Corner analyses the same fire characteristics, pre-fire stand characteristics and seedbed condition variables were used in the R matrix as comprised the set of GLMM candidate model predictors. The continuous variables were: burn date, stand age, tree consumption, basal area, residual organic depth, percent charcoal cover, percent mineral soil cover and percent bryophyte cover. We used the continuous variable representing the proportion of each tree species in each stand type instead of the dominant stand type variable to refine the analysis. The estimated proportion of the dominant tree species pre-fire was calculated as the density of stems per m^2 of $60m^2$ sampled area. Since RLQ is an ordination, we included additional correlated variables that were excluded from our GLMM models. These additional variables included moisture class (categorical) and burn depth (continuous). A complete description of variables used in the RLQ and Fourth Corner analyses can be found in **Appendix Table 8**.

Species life-history traits used in the Q matrix were compiled from field measurements, observations and literature sources, and were used as predictors of species composition post-fire. Broadly speaking the selected traits followed Noble and Slatyer (1980), who suggested that species "vital attributes" play an imperative role in succession following disturbance. These vital attributes include: (1) persistence of a species during and after disturbance; (2) the ability to establish and grow to maturity in the developing community; and (3) the time taken for the species to reach critical life stages. The five life history traits we used were: 1) the proportion of each individual regenerating from seed in each quadrat, 2) growth form (shrubs, forbs, trees, graminoids, seedless vascular plants, 3) seed dispersal mode (wind, animal), 4) life span (annual, biennial, perennial) and 5) leaf persistence (evergreen, deciduous). For a detailed description and rationale of the life history traits used in the RLQ analyses, see **Appendix Table 11**.

We used dummy variables to code nominal-scale categorical variables in the traits and environmental matrices with the number of dummy variables representing a single attribute being equal to the number of levels (categories) in that variable minus one (Zar 2010). The level for each categorical variable that was chosen as the default state was the level represented by the greatest frequency in the sample. For each dummy variable, the state for the variable could either be 0 or 1. For a list of all variables and the default levels used in the matrices, see **Appendix Table 10.**

In our Taiga Plains data, the community matrix (L: *m* x *k*) represented 102 taxa (*k*) at 591 quadrats (*m*). The environmental matrix (R: *m* x *p*) displayed information about the 17 environmental variables (*p*) at the 591 quadrats (*m*). The traits matrix (Q: *k* x *n*) described 9 life history traits (n) of the same 102 taxa (k). In our Taiga Shield data, the community matrix (L: *m* x *k*) represented 43 taxa (*k*) at 380 quadrats (*m*). The environmental matrix (R: *m* x *p*) displayed information about the 17 environmental variables (*p*) at the 380 quadrats (*m*). The traits matrix (Q: *k* x *n*) described 9 life history traits (n) of the same 43 taxa (k). The community matrix (L) was analysed and generated scores through correspondence analysis (CA) (Hirschfeld 1935). Correspondence analysis is like Principal Component Analysis but allows for the use of discrete variables (in this case the presence or absence of plant species). The R and Q matrices were analysed, and scores were generated from Hill-Smith Principal Components Analysis, which is a form of Principal Components Analysis that allows for mixed continuous and categorical variables (Hill and Smith 1976).

2.5 Results

During the 2015 sampling period, we recorded a total of 79 species (including trees) and 43 genera (plants we could not identify to species) of vascular plants in 38 families on the Taiga Plains. On the Taiga Shield we recorded 30 species and 13 genera from a total of 17 families. The majority of plots were in stands dominated by *P. mariana* or *P. banksiana*, with a small group of plots in stands designated “other”, which were dominated by *Larix laricina* (Du Roi) K. Koch (tamarack) on the Taiga Plains and *Picea glauca* (Moench) Voss (white spruce) on the Taiga Shield. On the Taiga Plains, the majority of the sites dominated by *L. laricina* were located in young stands in our most southerly fire perimeters (SS33 and ZF20), in mesic-subhygric and subhygric conditions.

2.5.1 General vascular plant composition

The PCoA of vascular plant species composition revealed a clear differentiation in community structure based on ecozone. The first two axes of the PCoA explained 22.19% of the total variation (axis 1: 13.41%; axis 2: 8.78%), and predominantly distinguished differences in species composition on the basis of ecozone and stand type, respectively (**Figure 2.2**). Species composition differences were most notable between *P. banksiana* and *P. mariana* -dominated stands on the Taiga Plains where prolific seeders in the Asteraceae family were more common in the *P. banksiana*-dominated stands and species associated with slow-growing, hardy rooting systems such as *Ribes* spp. and *Rubus* spp.

were more common in *P. mariana* stands (**Figure 2.3**). Complete lists of species documented in each ecozone can be found in **Appendix Table 2** and **Appendix Table 3**.

Of the entire species pool, we recorded information on regeneration modes for 64 species and 33 taxa that could only be identified to genus; this effort represented 31 families on the Taiga Plains. We recorded information on regeneration modes for 27 species and 13 taxa that could only be identified to genus, representing 16 families on the Taiga Shield. Reproduction from rhizome was the most common mode of regeneration in both ecozones (**Figure 2.4** and **Appendix Table 13**). On the Taiga Plains, 90% of measured species regenerated from rhizomes at least once in our dataset, demonstrating the importance of this mode of regeneration following fire. Common species that predominantly regenerated from rhizome on the Taiga Plains included *Rosa acicularis*, *Galium boreale*, *Potentilla fruticosa* and *Ledum groenlandicum*. On the Taiga Shield, 81% of measured species reproduced rhizomatically at least once in our data. The species that reproduced solely sexually on the Taiga Plains and Taiga Shield were either rare (occurring in five plots or less) or are not known to reproduce from rhizome. These species were similar across both ecozones and included; *Viola* spp., *Corydalis* spp. and Pinaceae seedlings. *Geranium bicknellii* and *Dracocephalum parviflorum* also regenerated from seed, but were found mainly on the Taiga Plains. Some species such as *Alnus crispa, Epilobium angustifolium, B. neoalaskana, Betula glandulosa* and *Cyperaceae* spp. exhibited both regeneration modes at multiple transects indicating the potential for concurrent sexual regeneration (seed dispersal and/or seedbank germination) and vegetative regeneration (resprouting).

2.5.2 Predictors of post-fire taxa richness and community assembly

Species rarefaction curves approached saturation in both ecozones (**Figure 2.5**) suggesting that our sampling efforts were adequate to characterize the post-fire community. Quadrat-level and plot-level taxa richness was similar in both ecozones, however, the Taiga Plains exhibited greater taxa richness overall (**Figure 2.5**, **Appendix Table 2**, **Appendix Table 3**). On the Taiga Plains, the average vascular plant taxa richness in each quadrat was 5.9 and 11.4 taxa in each plot. On the Taiga Shield the average number of taxa in each quadrat was 4.2 and 7.6 taxa in each plot. Average taxa richness per site was 21.9 on the Taiga Plains and 13.6 on the Taiga Shield respectively.

Variation in taxa richness was best predicted by the Seedbed Conditions model ($R^2_{marginal}$ =0.05; $R^2_{conditional}$=0.54) on the Taiga Plains and the Full model ($R^2_{marginal}$ =0.40; $R^2_{conditional}$ =0.51) on the Taiga Shield (**Table 2.2**, **Table 2.3, Figure 2.7**). Within the Seedbed Conditions model of our GLMM analysis, residual organic layer was a significant positive predictor of taxa richness in both ecozones. On the Taiga Shield, *P. mariana*-dominated stands had significantly greater taxa richness compared to *P. banksiana* or *P. glauca*-dominated stands, which corresponds closely with residual organic layer thickness as *P. mariana* tends to inhabit sites with a thicker organic layer (**Figure 2.6**).

Taxa richness GLMMs that were analysed at the plot-level demonstrated variations on the initial findings when compared to the quadrat-level analysis, however the role of seedbed conditions, namely greater residual organic soil depths, remained an important indicator of taxa richness across the landscape (**Appendix Table 6**). Variation in taxa richness was best predicted by the Seedbed Conditions model in both ecozones (**Appendix Table 7**). Fine-scale seedbed indicators such as bryophyte and mineral soil were no longer significant on the Taiga Plains, but became significant on the Taiga Shield (**Appendix Table 6**). Greater variation was explained by fixed effects when modelled at the plot-level on the Taiga Plains ($R^2_{marginal}$ =0.10; $R^2_{conditional}$ =0.47) compared to the quadrat level indicating substantial within-plot variation in composition.

Variation in the proportion of plants regenerating from seed was best predicted by full models on both the Taiga Plains ($R^2_{marginal}$ =0.05; $R^2_{conditional}$=0.05) and the Taiga Shield ($R^2_{marginal}$ =0.21; $R^2_{conditional}$ =0.23) (**Table 2.4**. **Table 2.5**, **Figure 2.8**). Again, seedbed conditions had a significant impact on regeneration modes in both ecozones as did the burn date; both ecozones saw an increase in the proportion of plants regenerating from seed in areas with thinner residual organic layer and those that burned later in the season. On the Taiga Plains specifically, we saw an increase in the proportion of plants regenerating from seed in the presence of early-colonising bryophytes (*Marchantia* spp. and *Ceratadon* spp.) and in stands dominated by *L. laricina* (**Figure 2.7**). Seedbed conditions important to the proportion of plants reproducing from seed on the Taiga Shield included exposed mineral soil and low charcoal cover. Similar to the taxa richness models, stand characteristics were also important in community assembly on the Taiga Shield; the proportion of plants regenerating from seed on the Taiga Shield increased in stands with greater basal area and aboveground tree consumption. There were proportionally fewer plants reproducing from seed in *P. mariana* and *P. glauca*-dominated stands (**Figure 2.8**).

2.5.3 Trait-environment relationships and species composition

Our RLQ analyses demonstrated a strong gradient of environmental constraints on vascular plant composition organised by pre-fire stand type and moisture class; the Taiga Plains and Taiga Shield demonstrated similar, significant trait-environment relationships mediated by species in the RLQ analyses (**Figure 2.9, Figure 2.10**). The first two axes of the RLQ analysis captured 82.8% and 11.0% of the trait-environment projected inertia on the Taiga Plains and 84.5% and 9.8% on the Taiga Shield (**Table 2.6**). Correlations between traits and environmental variables were 0.32 and 0.18 for axis 1 and 2, respectively on the Taiga Plains and 0.50 and 0.25 for axis 1 and 2, respectively on the Taiga Shield (**Table 2.6**).

Compositional patterns in the vascular plant community of the stands were determined mainly by the pre-fire proportion of each dominant tree type present (*P. mariana* and *P. banksiana*) in conjunction with site moisture class and residual organic layer thickness (**Figure 2.9, Figure 2.10**). On the Taiga Plains in general, stands dominated by *P. banksiana* trees tended to be in dry, xeric sites with sandy to gravelly soils with an understory of herbs such as *Vicia* spp., *Galium* spp., *Linnaea borealis* and *Calamagrostis canadensis*. *Picea mariana*-dominated stands were predominantly located in mesic and subhygric conditions that are often associated with low lying, poorly-drained areas with greater accumulation of organic matter. These stands had a vascular plant composition that was strongly related to greater residual organic soil layers that would have accumulated over time and subsequently tended to be in older age classes (**Figure 2.9**). Species associated with this stand type were *Equisetum* spp., graminoids such as *Oryzopsis* spp., taxa from the *Liliaceae* family, *Campanula rotundifolia* and *Salix* spp. Species that appeared to do well across many moisture classes regardless of stand type in our data included slow growing, rhizomatous species such as *Ledum groenlandicum, Arctostaphylos uva-ursi* and taxa from the *Rosaceae* family.

Species composition on the Taiga Shield Ecozone was also strongly influenced by the pre-fire forest type. Similar to the Taiga Plains, stands with a greater pre-fire proportion of *P. banksiana* tended to be located in dry, xeric conditions with sandy to coarse-textured soils. Short-lived herbs such as *Geranium bicknellii, Corydalis sempervirens* and *Epilobium glandulosum* were present in these dry conditions. Species of the *Poaceae* family were not particular to any specific moisture class or stand type as they appeared at the origin of the species ordination **(Figure 2.10**). As proportional representation of pre-fire *P. mariana* increased, graminoids became more common, most commonly *Calamagrostis* spp. and *Carex* spp. as did *Salix* spp. For further information on stand differences, please see **Appendix Table 12**.

Our Fourth Corner analysis revealed that the composition of post-fire plant communities was mainly influenced by the regeneration mode trait. In both ecozones, the Fourth Corner statistic differentiated plants regenerating from seed as being significantly positively associated with charcoal, mineral soil and bryophyte cover (productive seedbed conditions), burn date, the pre-fire proportion of *P. banksiana* trees in the stand and drier soil moisture categories (**Table 2.7**). A negative association was found between the aforementioned significant trait and the proportion of *P. mariana* trees in the stand, sub-hygric plots and residual organic thickness on the first axis (**Table 2.7**) indicating that these sites were dominated by resprouting species. The seedless vascular growth form

(*Equisetum* spp.) differed in its associations in each ecozone as well. On the Taiga Plains, presence of *Equisetum* spp. was positively associated with residual organic layer thickness, depth of burn, and wet site moisture classes associated with pre-fire *P. mariana* dominance. In contrast, on the Taiga Shield, *Equisetum* spp. were positively associated with the same environmental variables as plants reproducing from seed, which may be indicative of differing rhizome/rooting depths of this growth form or responses of different species since this taxon was grouped by genus in these two ecozones.

Specific findings unique to the Taiga Plains included a negative association between burn depth and the proportion of plants regenerating from seed on the first axis. Burn depth was correlated with residual organic depth, consequently greater burn depths were present in areas of greater residual organic depths (**Table 2.7**). Plants with wind dispersed seed were differentiated on the second axis and were significantly positively associated with bryophyte cover (**Table 2.7**).

Unique to the Taiga Shield, the Fourth Corner statistic differentiated plants regenerating from seed as being positively associated with the proportion of *P. glauca*-dominated stand type, as well as in older stands with increased basal area on the first axis. Also on the first axis, shrubs were positively associated with residual organic layer thickness, stand age, the proportion of *P. mariana* trees in the stand and sub-hygric plots. No traits or environmental variables were significantly differentiated on the second axis for the Taiga Shield results (**Table 2.7**)

When the RLQ and Fourth Corner analysis was conducted at the plot-level, the role of moisture class coupled with stand type was highlighted again in relation to species composition on theTaiga Shield. On the Taiga Plains, however, there were no significant species traits associated with the environmental variables at the plot-level (**Appendix Table 10)**.

2.6 Discussion

Despite the NWT boreal forest experiencing wildfire that extended across an unprecedentedly large spatial extent in 2014, this study indicates an overarching environmental legacy associated with surficial moisture conditions and soil characteristics. This environmental legacy ultimately drives post-fire taxa richness, community assembly and the traits that determine compositional differences following fire in this region. Combined results of our analyses demonstrated strong relationships between species composition, traits, regeneration mode and taxa richness in relation to seedbed quality in particular. These findings are telling of a stronger, underlying driver of post-fire taxa richness and community assembly relating to site moisture, which is also driving some differences observed between stand types and species composition as well (**Figure 2.9**, **Figure 2.10**). These findings are surprising in that large-scale disturbances like the 2014 wildfires are expected to trigger abrupt forest transitions (Johnstone *et al.* 2016), however, the vulnerability of plant communities in a changing fire regime may be more dependent on regional variation than we anticipated.

Despite distinct ecozone conditions and associated compositional differences (**Figure 2.2, Figure 2.3**), there were consistent and similar findings in terms of post-fire plant assembly. In our GLMM results, regardless of the model selected, variables associated with seedbed conditions were consistent drivers of both taxa richness and community assembly (**Figure 2.7, Figure 2.8**). Previous research has similarly demonstrated that edaphic factors in combination with climate are primary drivers influencing patterns in species diversity and richness in southwestern Yukon (Paudel *et al.* 2016). Local conditions such as water and nutrient availability as well as substrate heterogeneity have demonstrated a stronger effect than climate on understory richness throughout other parts of Canada (Bartels and Chen 2010; Zhang *et al.* 2014). The presence of colonising bryophytes in combination with mineral soil exposure, served as important indicators of seedbed quality in this study as well. *Ceratadon* spp. and *Marchantia* spp. are known to grow in areas of high light availability (Skutch 1929; Brassard and Chen 2006), high mineral soil content and in moist microsites (Hollingsworth *et al*. 2013), all excellent conditions for plants regenerating from seed that require rapid access to surficial moisture and light in early establishment phases (Hart and Chen 2006; Johnstone and Chapin 2006b).

Our findings supported the notion that fire severity is important to community assembly in this region as well. This finding is similar to other studies of large fire events that have found post-fire vegetation in boreal landscapes to be driven primarily by fire severity (Bernhardt *et al.* 2011; Hollingsworth *et al.* 2013; Pinno and Errington 2016). Our findings are consistent with some aspects of studies documenting community assembly following fire, for example, high plant and propagule survival rates following fire were linked with residual organic soil depths as has previously been demonstrated by Schimmel and Granström (1996), while exposed mineral soil provided an excellent environment for seed germination similar to the findings of Johnstone, Hollingsworth, *et al.* 2010. We recognize the inherent relationship between controlling characteristics of moisture and organic layer depth on fire behaviour (Miyanishi and Johnson 2002); fire behaviour inevitably leads to post-fire seedbed conditions. Since we did not include information on the proportion of organic material combusted in our GLMMs, and residual organic depth was included in our Seedbed Model, we have interpreted findings from our GLMMs as telling of environmental conditions as opposed to fire characteristics, however the residual organic seedbed variable represents information about both site conditions and fire severity. The large proportion of plants reproducing from rhizome in both ecozones was telling of the importance of this mode of regeneration following fire in this region, as well as the availability of organic soil to maintain these structures and support re-establishment of vascular plants.

Unique to our study was the consistent presence of ephemeral, early successional, seedbank species such as *Geranium bicknellii*, *Dracocephalum parviflorum* (Lyon and Stickney 1976; Anderson and Romme 1991) and *Corydalis* spp. (Viereck and Schandelmeier 1980), that were telling of the seedbed conditions following fire in both ecozones (**Figure 2.7, Figure 2.8**). Most species regenerating solely from seed in this study were from soil seedbanks while recruitment from aerial dispersers was more limited and highly variable. Therefore, despite the 2014 fires being the most widespread on record for this region, seedbanks were present and viable in the soil following the extensive disturbance. These findings were surprising given the expectation that seedbank species do well in light to mid-severity fires (Schimmel and Granström 1996; Wang and Kemball 2005), which further indicates that the 2014 fires were either not extremely severe, or that species reproducing from seedbank in this study are adapted to severe fire conditions. For example, *Dracocephalum parviflorum* has been documented as being present following severe fires in a more southerly system (Orr 1970) suggesting that tolerance of the seeds of some of these species to extreme heating may be high. Available literature on the seed biology of these species is limited, however, given the general success of seedbank species like *Dracocephalum parviflorum, Geranium bicknellii* and *Corydalis* spp. following fire, it is suspected that these species form deeply buried seedbeds in varying fire cycles, which is characteristic of early successional species (Grandin and Rydin 1998; Lee 2004; Hollingsworth *et al.* 2013). At the same time, an important characteristic of early successional forbs is their large proportion of annual production devoted to seeds (Grime 1977). Observations from a colleague collecting conifer seeds in the first growing season following the 2014 fires indicated that there was an abundance of *Dracocephalum parviflorum* seeds in the seed rain collected (K. Reid, observation). Likewise, *Epilobium angustifolium* has been estimated to yield as many as 80 000 seeds per year and be capable of drifting 2-3 km in the wind (Salisbury 1962; Solbreck *et al.* 1987). A combination of seedbank survival and prolific seed dispersal following fire is likely the combination that enables some forbs to do so well in the first stages following fire in the southern NWT, especially in seedbed conditions with exposed mineral soil.

Our decision to analyse ecozones separately was validated by our PCoA results, whereby there was a distinct division between ecozones based on the number of species, the types of species and to some degree, stand type (**Figure 2.2 and Figure 2.3**). These findings support the GLMM results that demonstrated stand type as a more important driver of taxa richness and community assembly on the Taiga Shield in particular (**Table 2.3 and Table 2.5**). Our GLMM results for taxa richness demonstrated a large discrepancy between the variation explained by the fixed effects in the two ecozones (Shield $R^2_{marginal}$=0.40; Plains $R^2_{marginal}$ =0.05). The large difference between the marginal R^2 values suggests that the nested sampling design had a disproportionately larger influence on the Taiga Plains. This is possibly indicative of the variability in environmental conditions expressed across plots and burn complexes on the Taiga Plains. This notion is further supported in our plot-level analysis whereby marginal R^2 increased to 10% (**Appendix Table 7**). The Taiga Shield and the Taiga Plains differ dramatically in geomorphological histories, soils development and parent materials (Ecological Stratification Working Group 1996). It can be said that the Taiga Shield has more limiting environmental conditions; it is typically known as a harsh environment with areas of bare ground and rock, thin boulder till and bedrock interspersed with fine-grained sediment (Ecosystem Classification Group 2008). Strata on the Taiga Shield were mostly sparse or low-density mixed, conifer stands (**Appendix Table 1**). The Taiga Plains on the other hand, is a mix of undulating glacial till plains and peatlands (Ecosystem Classification Group 2007) and strata on the Taiga Plains exemplified more of a gradient from *P. mariana* dominant to *P. banksiana*-dominant stands. Greater contrast in environmental conditions on the Taiga Shield were likely an important reason stand type was a more important driver of taxa richness and community assembly and why we see less plant diversity on the Taiga Shield in general.

For the most part, our RLQ and Fourth Corner analyses supported relationships found in our GLMM analyses; the assembly of post-fire plant communities in both ecozones was driven mainly by reproductive traits selected for in association with residual organic soil thickness and pre-fire stand type (**Figure 2.9Figure 2.9**, **Figure**

2.10). The role of moisture class coupled with stand type was highlighted in relation to species composition in the RLQ and Fourth Corner results in particular. Where burn depth was low, for example, we saw an increase in the proportion of each species reproducing from seed, namely forbs, in xeric, *P. banksiana*-dominated stands. On the other hand, slow growing, rhizomatous species such as shrubs were found in deep residual organic layers in stands dominated by *P. mariana*. This stark contrast indicates that *P. banksiana* forests potentially offer better substrates for seedling establishment (Duchesne and Sirois 1995), whereas *P. mariana* stands maintain an organic soil layer that inhibits seed germination and provides conditions for a strong legacy-effect of species composition following fire (Johnstone and Chapin 2006b), which can also be thought of as tfhe biological legacy of the system (Franklin *et al.* 2000; Johnson *et al.* 2016). This notion is also supported by greater residual organic depths in stands with a greater proportion of *P. mariana* (**Figure 2.9, Figure 2.10**).

Only fine spatial-scales (quadrat-level) displayed significant correlations between the traits and the environment on the Taiga Plains. This discrepancy between RLQ and Fourth Corner results at the plot versus quadrat-level suggests that the environmental variables used in this study explained a lower proportion of the species traits variance at broader scales than at finer scales on the Taiga Plains. Alternatively, other traits that we did not use may be associated with the distribution of species at broader scales. The occurrence of rare species on the Taiga Plains may also contribute to the lack of significant findings (**Appendix Table 10**). There were more rare taxa (≤ 5 occurences) in the Taiga Plains composition data than the Taiga Shield data. Since presence/absence data was used in the analyses, there were regular occurrences of zeros (absences) in the matrices. Multiple zeros combined with the variability of within plot environmental conditions (see GLMM results) suggests that the RLQ and Fourth Corner were unable to pick up on specific conditions at which species and their associated traits were significant at the plot-level.

We suggest that variance in post-fire community assembly in accordance with stand type reflects the overall differences in subsurface conditions inherently present in these stands; *P. mariana* and *P. banksiana*-dominated stands inhabit distinct moisture conditions and are qualitatively different regardless of successional stages (Larsen 1997). In their extensive study looking at forest floor depths across six ecozones in Canada, Letang and de Groot (2012) found that the dominant tree species influences both forest floor fuel loads and forest floor depths; *P. mariana*-dominated stands had approximately twice the forest floor depths as *P. banksiana*-dominated stands in five out of six ecozones studied. Walker *et al.* (2017 in press) recently confirmed these findings in our study region where organic soil depths in unburned *P. mariana*-dominated stands were greater than *P. banksiana*-dominated stands. Differences in depths of organic soil layers have been attributed to a surplus of moisture in cold, wet soils and low decomposition rates that subsequently support accumulation of organic matter over time in *P. mariana*-dominated stands (van Cleve *et al.* 1983; Bonan and Shugart 1989). *Pinus banksiana*-dominated stands on the other hand, have been found to be moisture limited, with shallow organic forest floor depths and subsequently lower fuel loads (Letang and de Groot 2012). Organic soil thickness and soil bulk density are known to be some of the most important characteristics affecting both soil temperature and moisture regime that in turn influence stand composition and the general ability for *P. banksiana* to outcompete *P. mariana* in well-drained soils (Letang and de Groot 2012).

Given the close relationship between soil properties and stand type, it can be argued that poorly drained sites with deeper organic soils prior to fire provided the environmental conditions for slow growing, rhizomatous species to re-establish pre-fire vegetation. In more northerly *P. mariana*-dominated stands, topography (drainage) is extremely important in determining species composition and vegetation patterns of late successional sites (van Cleve *et al.* 1983; Hollingsworth *et al.* 2006), which indicates that as long as moisture class is maintained to some degree, vascular plant communities in the northwestern boreal forests can maintain similar species composition through disturbance cycles, especially in stand types where moist organic material can re-establish over time. Indeed, it has been suggested from findings in Alaska that landscape positions providing cool, moist conditions may be relatively protected from the effects of increased fire severity or frequency (Johnstone and Chapin 2006b). This protection is likely linked to the shallow depth of the water table and its role in preserving cold, organic soil depths even through multiple fire cycles (Harden *et al.* 2006). This notion supports why pre-fire vegetation was more prominent in stands with greater organic soil depths on the Taiga Shield in particular, where *P. mariana*-dominated stands in this ecozone saw an increase in taxa richness and a decrease in plants reproducing from seed. Similarly, a recent study looking at taxa richness and time since fire in the Taiga Shield Ecozone also found taxa richness was greater in *P. mariana*-dominated stands, attributable, in part, to soil type in the stands in comparison to *P. banksiana*-dominated or mixed stands in the study; the authors interpreted soil type as a strong determinant of moisture holding capacity and drainage (Day *et al.* 2017). In contrast, it is quite likely that rhizomatous species were not as prevalent in *P. banksiana*-dominated stands pre-fire, which is why we did not find an abundance of rhizomatic species in these stands. Following a reconnaissance of three *P. banksiana* stand types in northeastern Alberta and southwestern Saskatchewan for example, Carroll and Bliss (1982) found a tall shrub layer absent from most stands studied and only ten species present in the shrub layer, indicative of lower rhizomatic regenerative potential in similar *P. banksiana*-dominated stands in our study. Similar to our findings, Carroll and Bliss (1982) also found greater species richness in the stand-type they documented as a mixture of *P. banksiana* and *P. mariana* trees.

Fire characteristics that did prove important in our GLMM models can be interpreted in relation to moisture and/or species composition related to stand types as well. The proportion of plants reproducing from seed at each plot increased in later season burns in both ecozones (**Figure 2.7**, **Figure 2.8**). These findings likely result from the combination of stand type and seed biology and/or phenology. In 2014, *P. banksiana*-dominated stands burned later in the season across both ecozones (**Appendix Figure 4**). The combination of dry, thin organic layers burning late in the season likely provided ideal seedbed conditions for germinating seeds the following spring (supported by our RLQ results), whereby more plants regenerated from seed in *P. banksiana*-dominated stands on the Taiga Plains and Taiga Shield (**Figure 2.9**, **Figure 2.10**). Late-season fires were likely beneficial for seedbank species, whereby extended light conditions, moisture and nutrients from snow melt the following spring (2015), provided previously buried seeds the opportunity to germinate and establish. Likewise, the early-season timing of seed dispersal of many boreal vascular species (FEIS 2017) may also support plants in dispersing seeds from neighbouring areas onto freshly burned sites in the spring following fire. A closer investigation into the increase of plants regenerating from seed in *L. laricina*-dominated stands demonstrated evidence of species that survived the fire in 2014 (i.e., survival intact) including *Salix* spp., *Betula glandulosa* and various graminoids that are known to flower in the spring (FEIS 2017). Conversely, earlier season fires in moister conditions might have given resprouting plants greater opportunity to take hold in the same year in which the fire occurred.

Overall, our results demonstrate that environmental conditions post-fire (which were likely influenced by moisture conditions pre-fire; Bernhardt *et al.* 2011) impose environmental legacies that have a strong influence in the southern boreal forests of the NWT where the 2014 wildfires were unprecedented in terms of areal extent, but apparently not severe in comparison to more northerly studies (Walker *et al.* 2017 in press).

2.7 Conclusion

Warmer temperatures and hotter, drier conditions are expected to extend the length of fire seasons, as well as increase the frequency, spatial extent and severity of fires in the northwestern boreal forest and elsewhere in Canada over the next century (Kasischke and Turetsky 2006; Girardin *et al.* 2013; Wotton *et al.* 2017). Understanding how forest plant communities assemble and are maintained at local and landscape scales is necessary to predict changes to ecosystem function associated with a changing fire regime.

Here we present strong evidence of the interacting effects of environmental legacies combined with species traits in determining local and regional-scale vascular plant community assembly patterns in the first year following extensive wildfire in the southern boreal forests of the NWT. We also found evidence for a role of fire characteristics in shaping these results, given the inherent linkages amongst vegetation legacies and fire behaviour. Our findings suggest the southern boreal forest of the NWT demonstrates resilience, as a result of moisture conditions and soil substrate legacy effects, which differ in comparison to similar post-fire studies in other areas of the western North American boreal forest.

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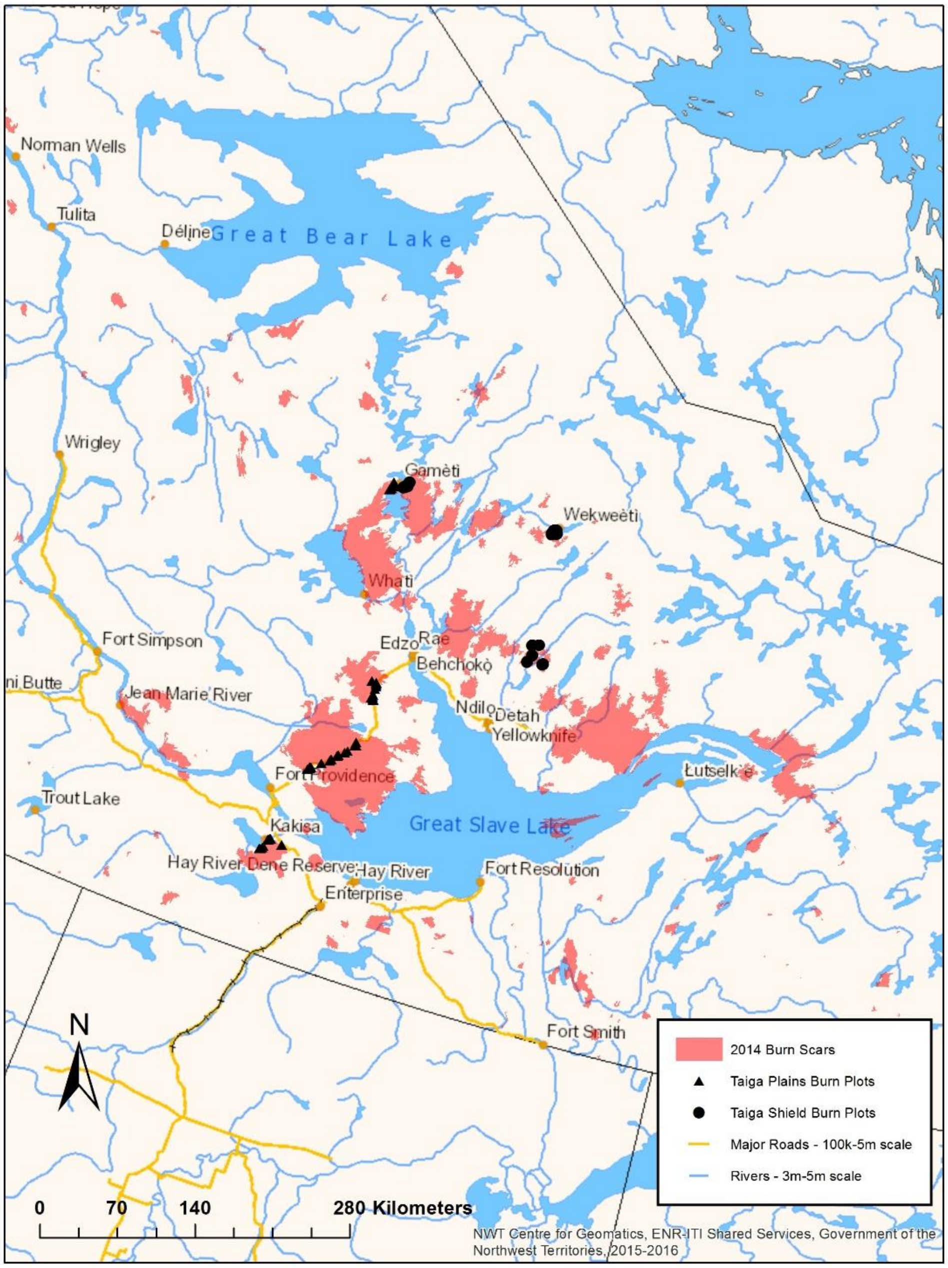
FIGURES



NWT Centre for Geomatics, ENR-ITI Shared Services, Government of the Northwest Territories, 2015-2016

Figure 2.1 Map of sampling areas within the Northwest Territories spanning two ecozones and encompassing seven burn complexes. Map shows sampled plots from the 2014 burns (n=209). True sample size is obscured given overlapping plots.

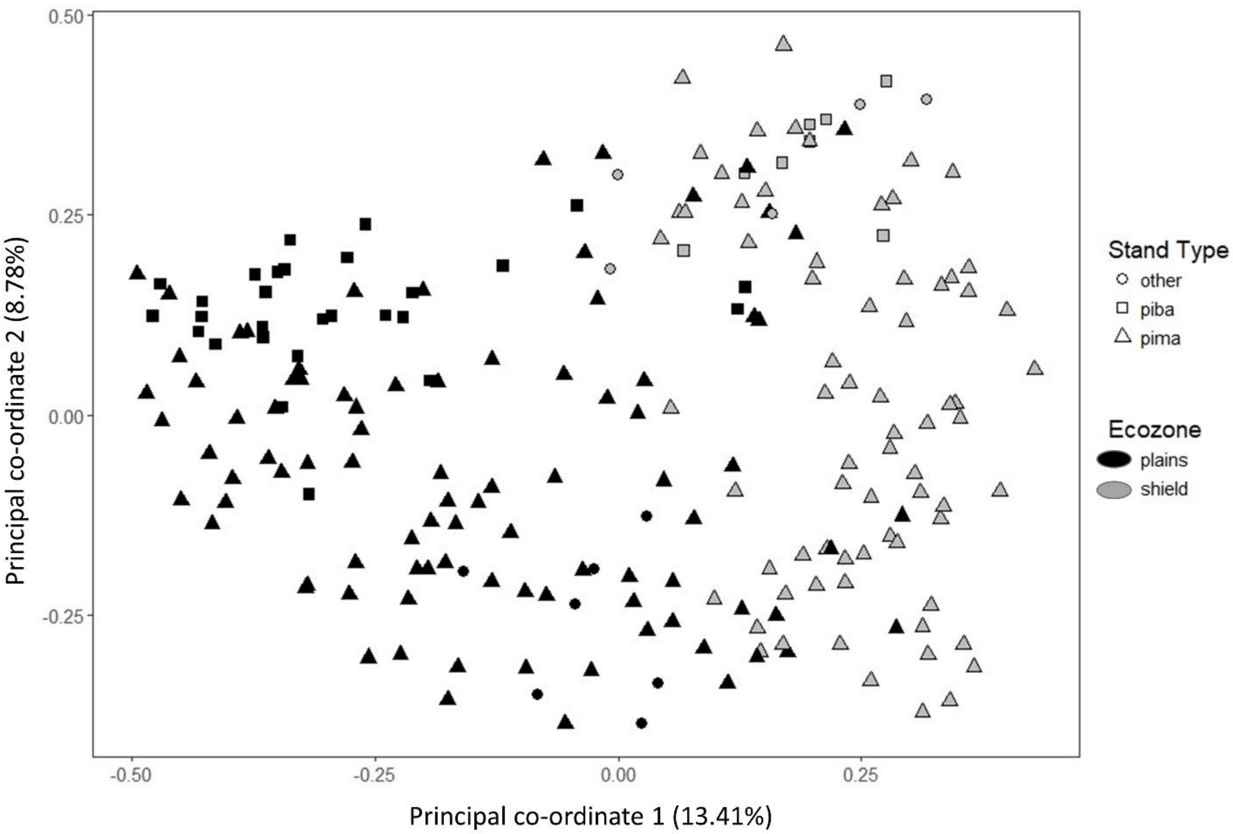


Figure 2.2 Plot scores for Principal Co-ordinates Analysis (PCoA) ordination with Sorenson distance. Values in brackets on the axes represent the amount of variation in species composition explained by each axis. Symbols denote pre-fire stand type and colour indicates ecozone. Stand types refers to dominant conifer present; other=*L. laricina* and *Picea* spp. on the Taiga Plains and *Picea glauca* on the Taiga Shield, piba=*Pinus banksiana*, pima= *Picea mariana*.

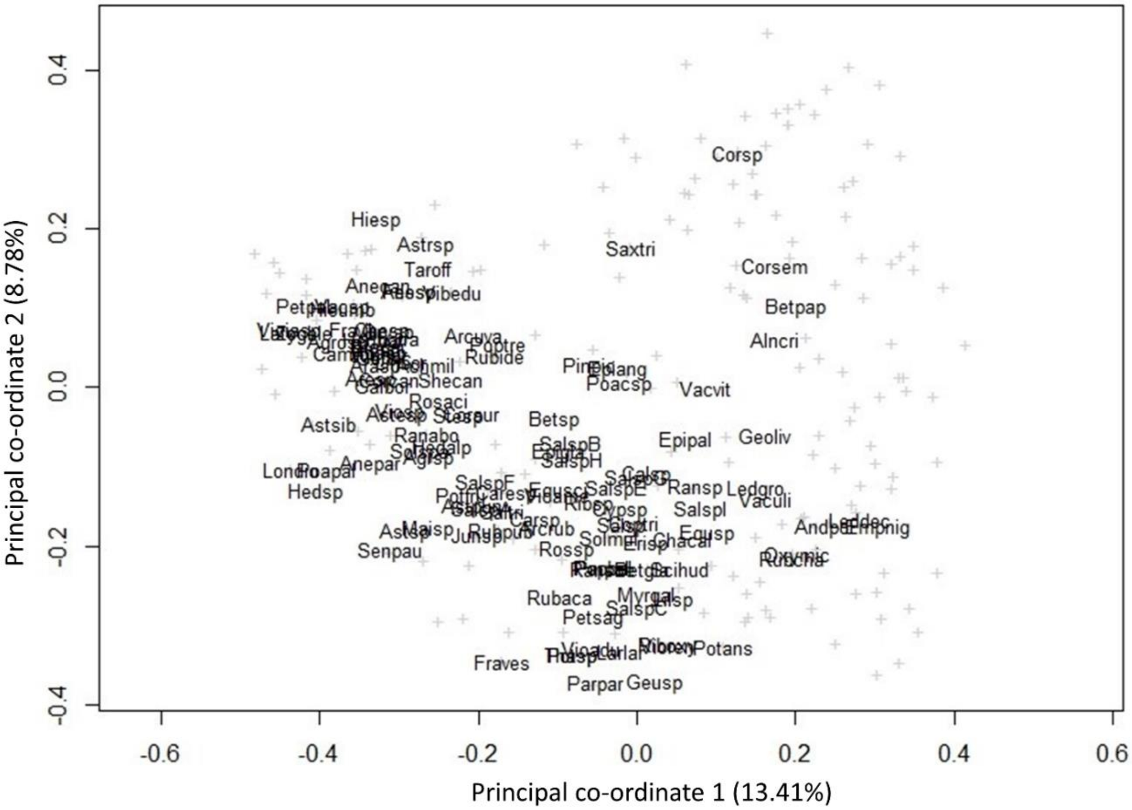


Figure 2.3 Species scores for Principal Co-ordinates Analysis (PCoA) ordination. Values in brackets on the axes represent the amount of variation in species composition explained by each axis. Grey crosses are site scores. See **Appendix Table 2** and **Appendix Table 3** for definitions of species codes.

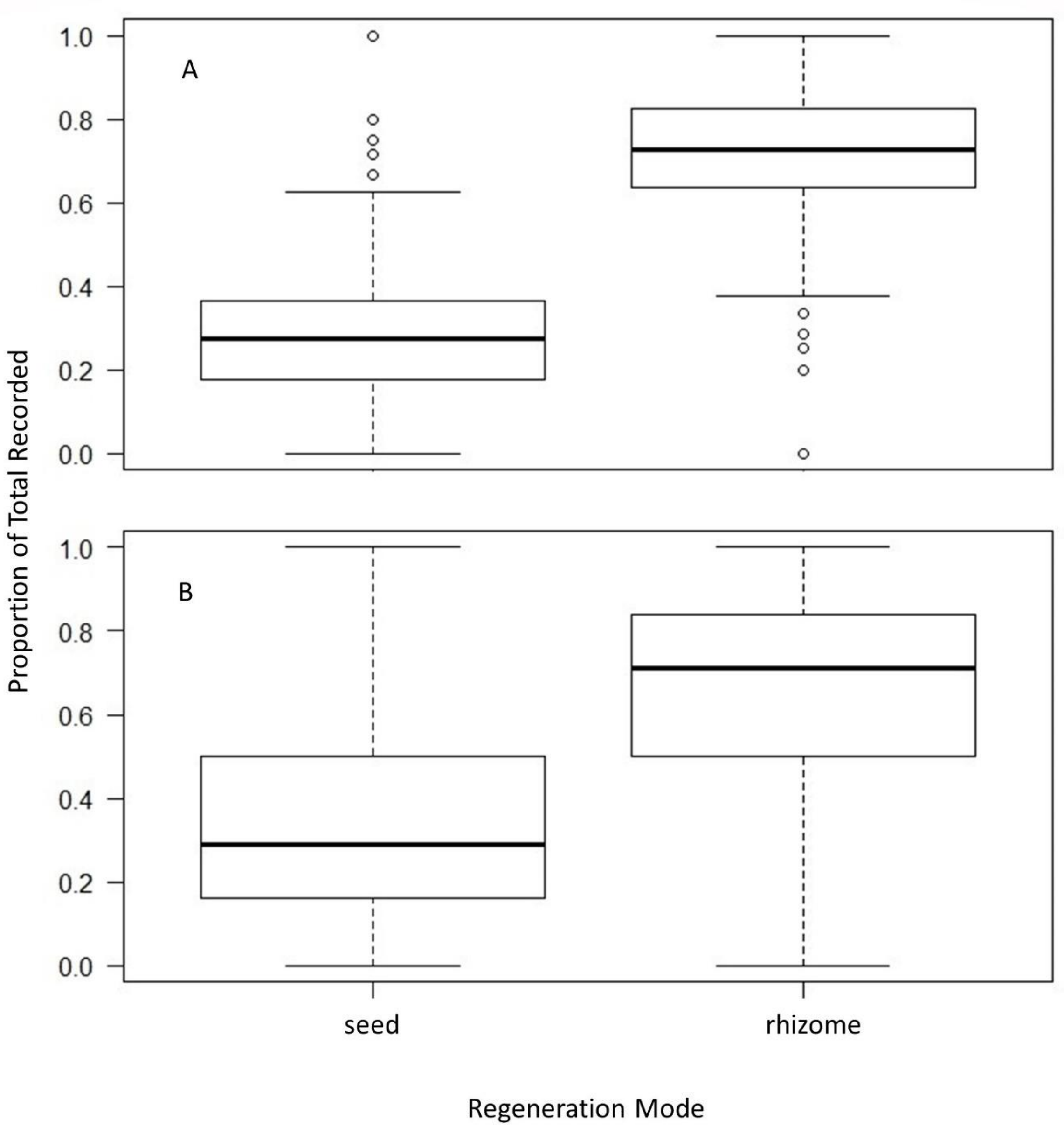


Figure 2.4 Boxplots showing the proportion of total taxa that were recorded regenerating from seed or rhizome (including those regenerating from both) on the Taiga Plains (n=105 taxa) (A) and Taiga Shield (n=43 taxa) (B). See also **Appendix Table 13.** Box =25th and 75th percentiles; horizontal line within the box represents the median. Whiskers are greater than +/- 1.5 times the interquartile range; circles represent outliers.

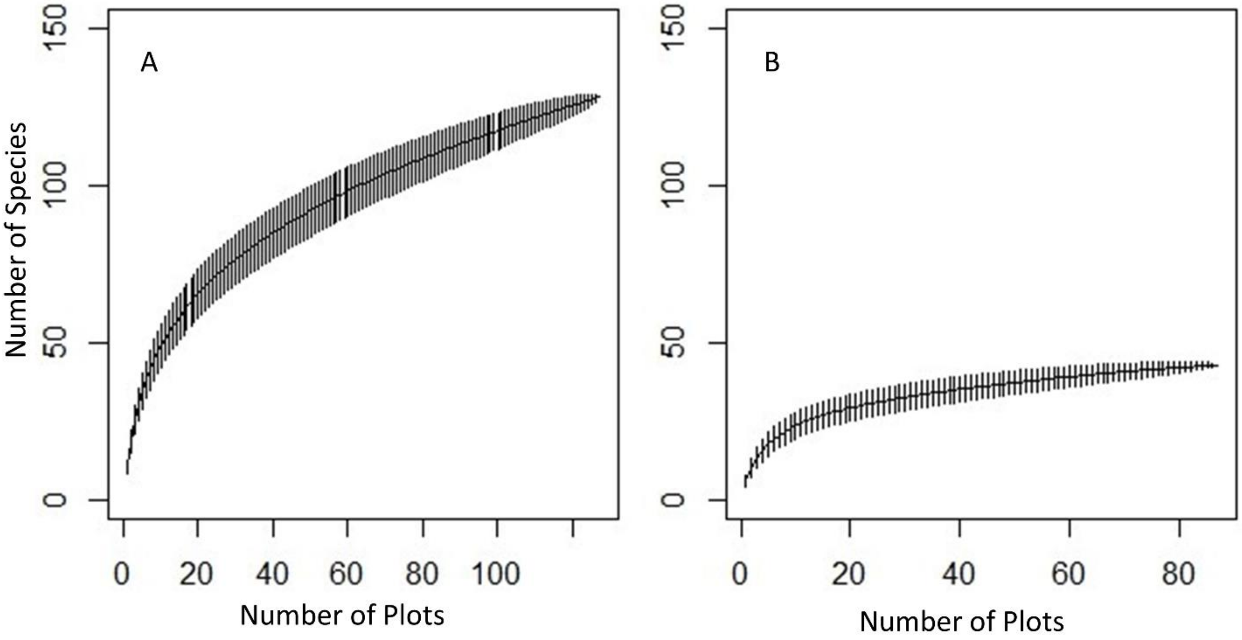


Figure 2.5 Species rarefaction curves comparing sampling effort in 2015 on the Taiga Plains (A) and Taiga Shield (B). The line represents the mean and perpendicular lines represent confidence intervals.

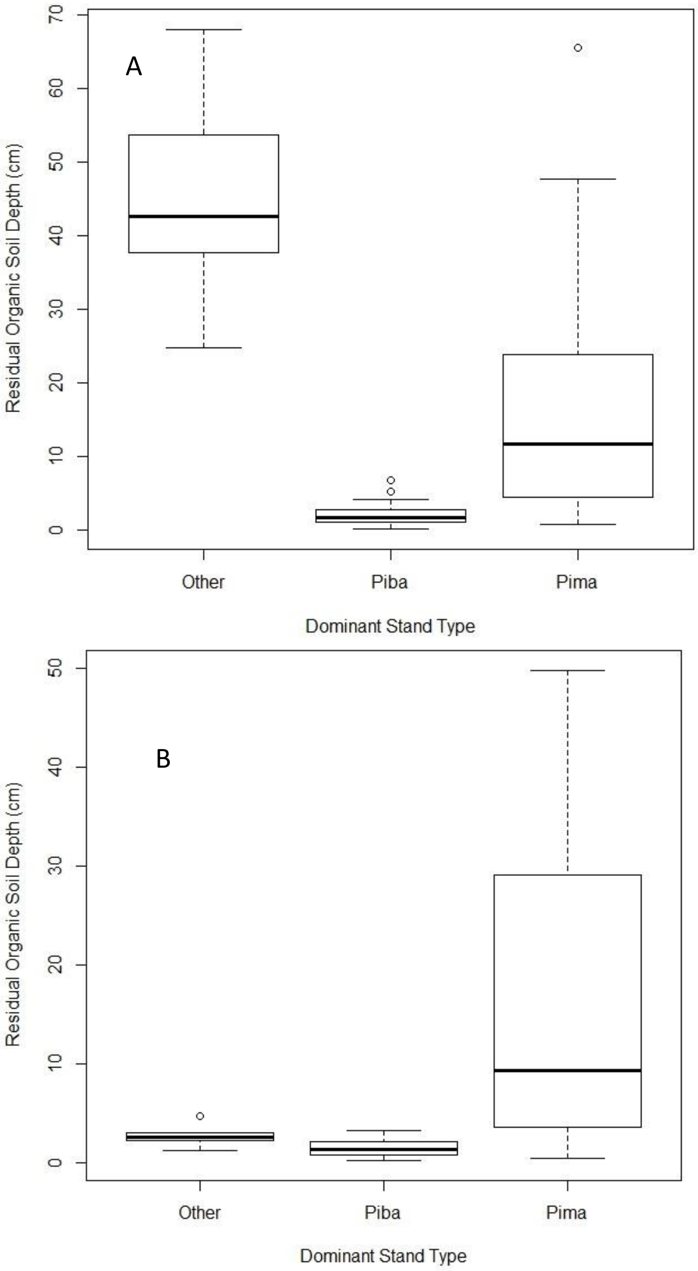


Figure 2.6 Boxplots showing Residual Organic Soil Depth (cm) in each Dominant Stand Type in plots on the Taiga Plains (n=125 plots) (A) and Taiga Shield (n=84 plots) (B). Box =25th and 75th percentiles; horizontal line within the box represents the median. Whiskers are greater than +/- 1.5 times the interquartile range; circles represent outliers. Stand type refers to dominant conifer present; Other=*Larix laricina* on the Taiga Plains and *Picea glauca* on the Taiga Shield; piba= *Pinus banksiana;* pima= *Picea mariana.*

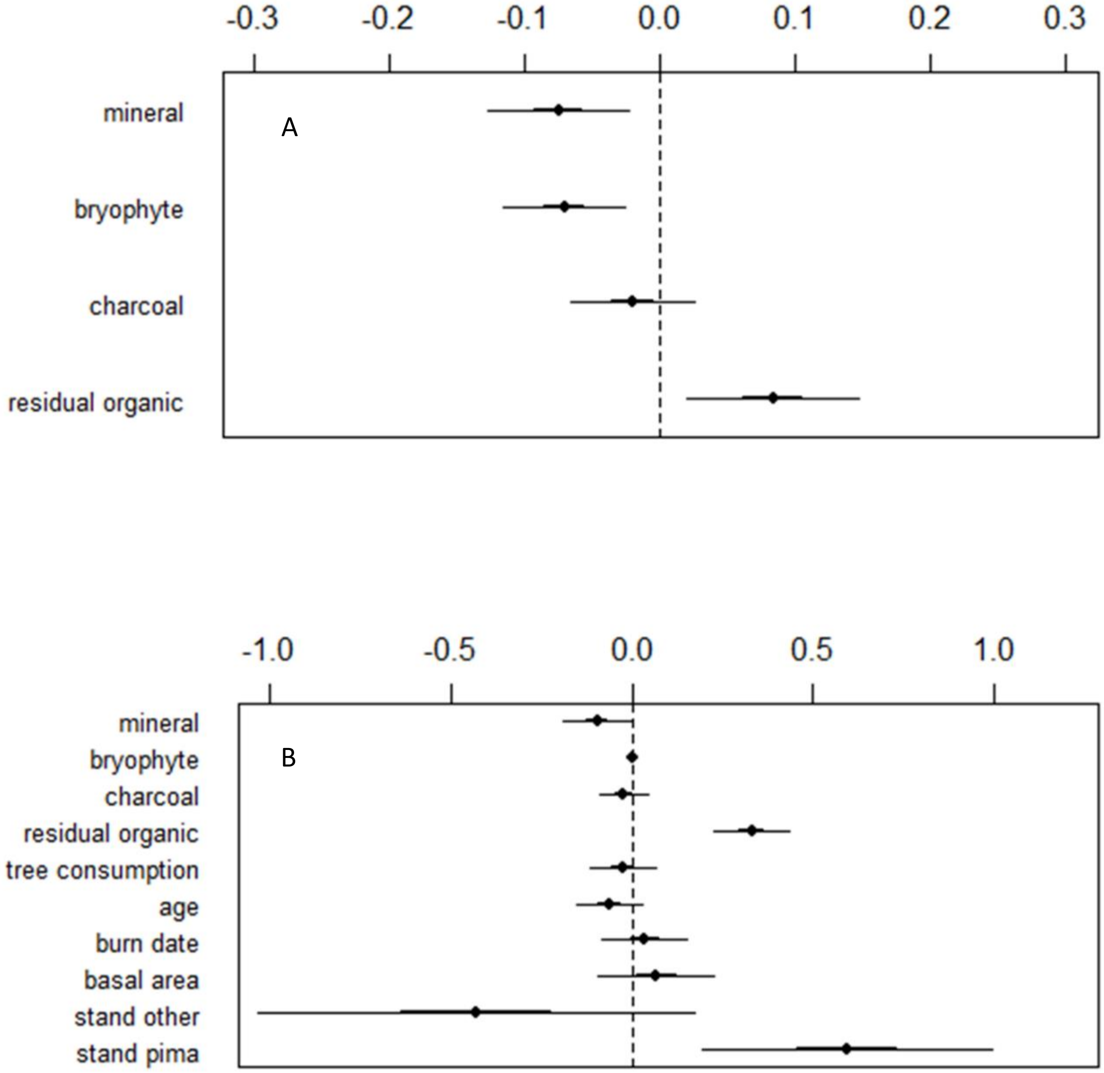


Figure 2.7 Regression estimates from the selected GLMM candidate model (lowest AICc model) of variation in post-fire taxa richness on the Taiga Plains (A) and Taiga Shield (B). Points represent the mean coefficient regression estimate. The dark line represents ±1 SD and the lighter line represents the 95% confidence intervals (2SD). All variables were standardized except the categorical variable representing stand type. On the Taiga Plains, $R^2_{marginal}$=0.05; $R^2_{conditional}$=0.54. On the Taiga Shield, $R^2_{marginal}$ =0.40; $R^2_{conditional}$ =0.51. Environmental variables include: mineral, bryophyte and charcoal=percent cover of exposed mineral soil, bryophyte (*Marchantia* spp. and *Ceratadon* spp.) and charcoal in each quadrat; residual organic=depth of post-fire residual organic soil (cm); tree consumption=average consumption of aboveground branches at each plot based on categorical values (see **Appendix Table 4**); age=average age of each stand/plot; burn date=calendar day of burn; basal area=total measured basal area (cm^2) of all species measured at each plot expressed on a per m^2 basis*;* stand types (pima, other) refers to dominant conifer present; other=*Larix laricina* on the Taiga Plains and *Picea glauca* on the Taiga Shield, pima= *Picea mariana.(*contrasted to *Pinus banksiana*). See **Table 2.3** for significance values.

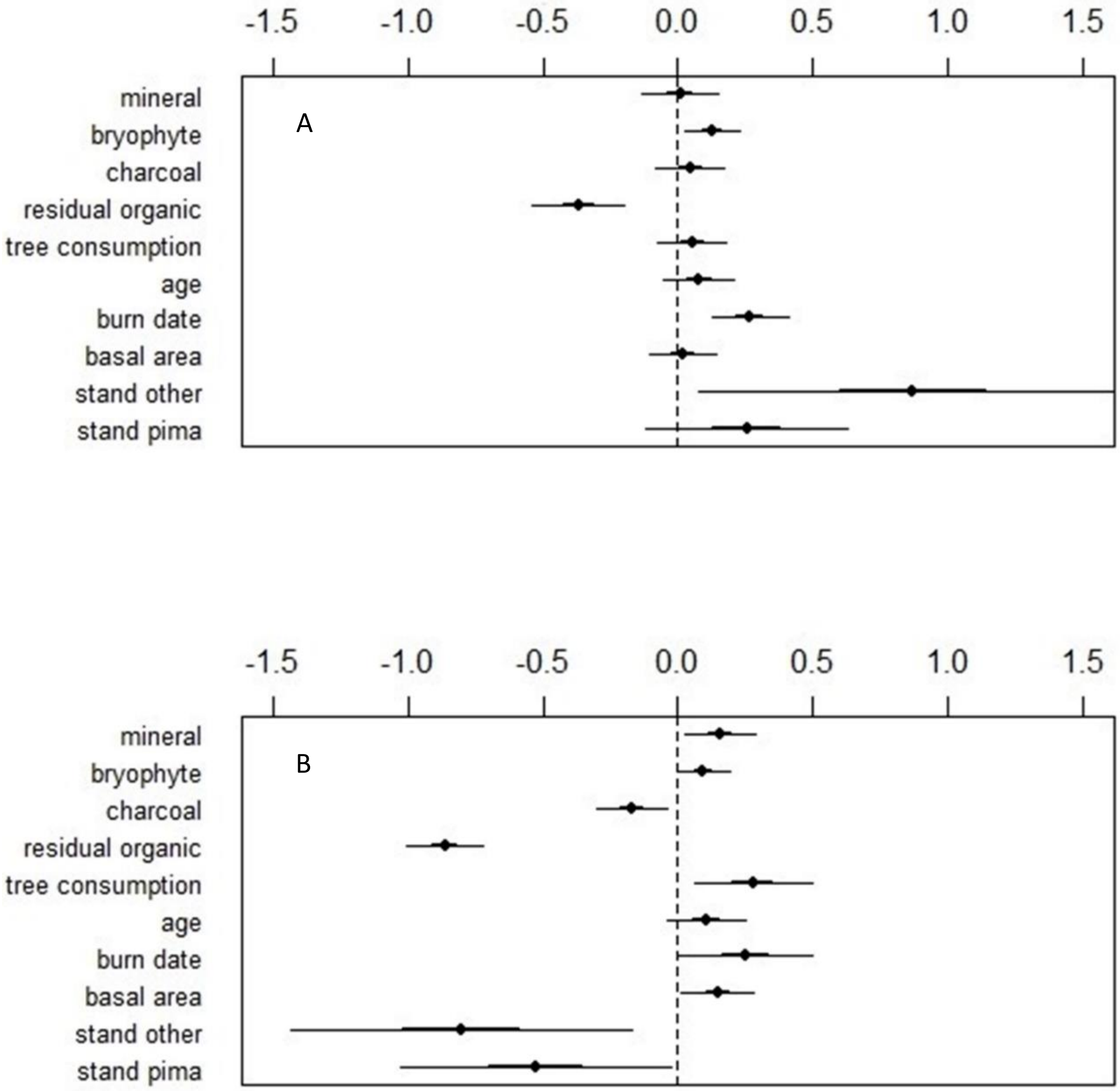
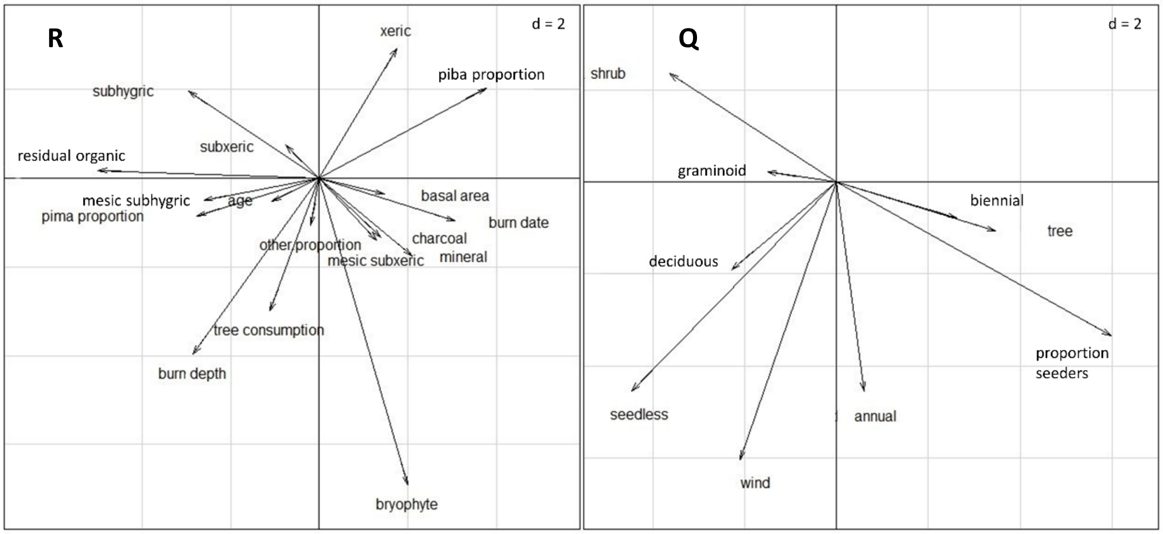


Figure 2.8 Regression estimates from the GLMM candidate model (lowest AICc model) of the variation in the proportion of plants regenerating from seed on the Taiga Plains (A) and Taiga Shield (B). Points represent the mean coefficient regression estimate. The dark line represents ±1 SD and the lighter line represents the 95% confidence intervals (2SD). All variables were standardized except the categorical variable representing dominant stand type. Environmental variables include: mineral, bryophyte and charcoal=average percent cover of exposed mineral soil, bryophyte (*Marchantia* spp. and *Ceratadon* spp.) and charcoal in each plot; residual organic=depth of post-fire residual organic soil (cm); tree consumption=average consumption of aboveground branches at each plot based on categorical values (see **Appendix Table 4**); age=average age of each stand/plot; burn date=calendar day of burn; basal area=total measured basal area (cm^2) of all species measured at each plot expressed on a per m^2 basis; stand types (pima, other) refers to dominant conifer present; other=*Larix laricina* and *Picea* spp. on the Taiga Plains and *Picea glauca* on the Taiga Shield, pima=*Picea mariana*.(contrasted to *Pinus banksiana*). See **Table 2.5** for significance values.


R
d = 2
xeric
piba proportion
subhygric
subxeric
residual organic
basal area
burn date
mesic subhygric
age
pima proportion
charcoal
mineral
other proportion
mesic subxeric
tree consumption
burn depth
bryophyte
Q
d = 2
shrub
graminoid
biennial
tree
deciduous
proportion seeders
seedless
annual
wind

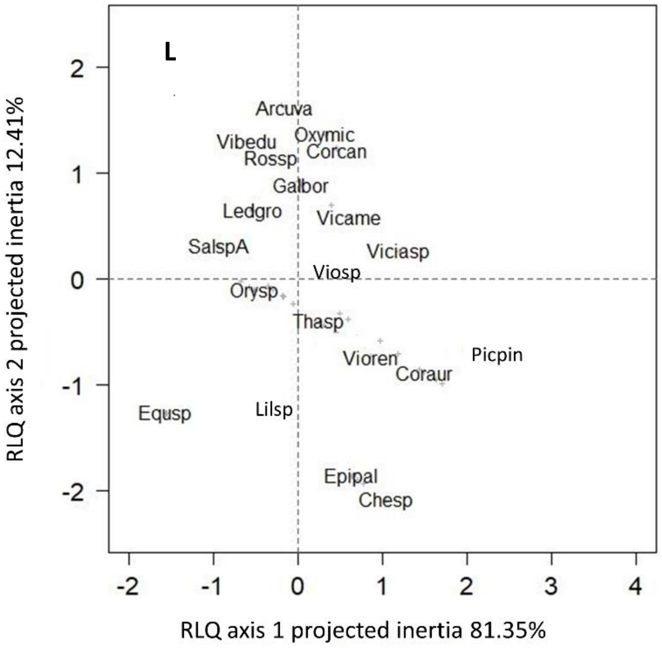
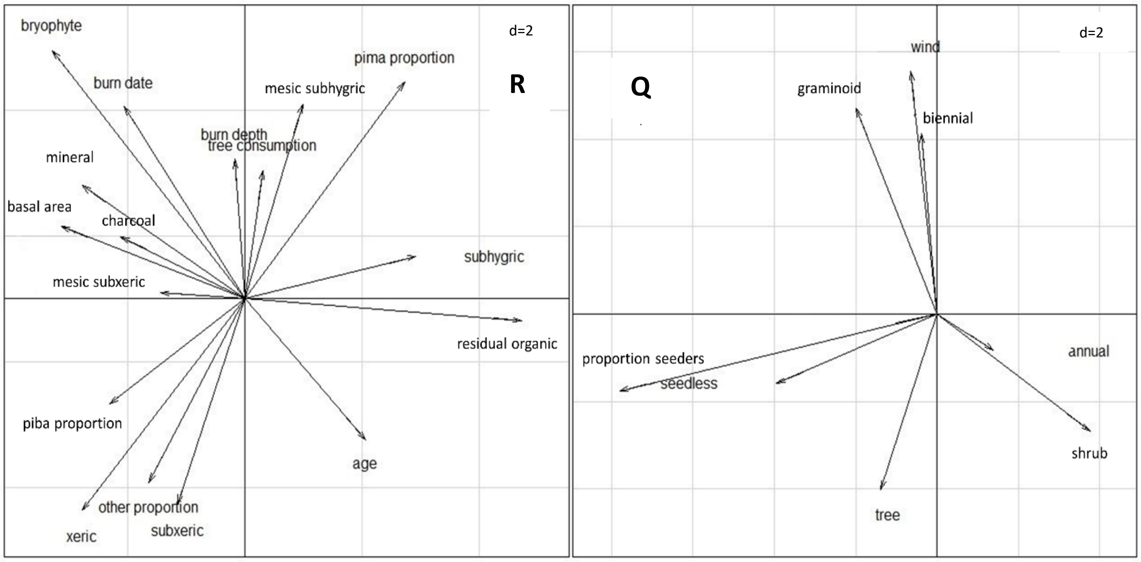

L
Arcuva
Vibedu
Oxymic
Rossp
Corcan
Galbor
Ledgro
Vicame
SalspA
Viciasp
Viosp
Orysp
Thasp
Vioren
Picpin
Coraur
Equsp
Lilsp
Epipal
Chesp
2
1
0
-1
-2
-2
-1
0
1
2
3
4
RLQ axis 2 projected inertia 12.41%
RLQ axis 1 projected inertia 81.35%

Figure 2.9 Results of the first two axes of RLQ analysis of the Taiga Plains data showing ordination of the first two axes of the coefficients for the environmental variables (R), coefficients for the traits (Q) and species ordination (L). Values in brackets on the axes of L represent the projected inertia (or variance in species and environmental scores captured) in each axis; d refers to grid-size. Environmental symbols in R: mineral, bryophyte, charcoal=percent covers exposed in each quadrat; burn date=calendar day of burn; basal area= total measured basal area (cm^2) of all species measured at each plot expressed on a per m^2 basis; piba, pima and other proportion= estimated proportion of dominant, pre-fire tree species based on density of stems per m^2 of 60 m^2 sample area where piba=*Pinus banksiana*, pima=*Picea mariana*, other=*Larix laricina*; xeric, subxeric, mesic subxeric, mesic, mesic subhygric and subhygric= ranking of plot moisture potential using the moisture class (**Appendix Figure 1**); age=stand age in years; residual organic=soil organic layer depth (cm) at each quadrat; burn depth=depth of burn (cm). Trait symbols in Q: proportion seeders=proportional representation of each species reproducing from seed at each plot; shrub, graminoid, seedless vascular, tree=growth forms based on general habit of growth (forb as default variable); deciduous=leaf persistence based on leaf type (evergreen as default variable); wind=seed dispersal mode (animal as default variable); annual, biennial=life span of each species (perennial as default variable). For species ordination (L) symbols have been jittered to reduce overlap, and only the most influential points on the axes are shown. For definition of species codes, see **Appendix Table 2**.


R
d=2
bryophyte
burn date
mesic subhygric
pima proportion
burn depth
tree consumption
mineral
basal area
charcoal
mesic subxeric
subhygric
residual organic
piba proportion
age
other proportion
xeric
subxeric
Q
d=2
wind
graminoid
biennial
proportion seeders
seedless
annual
shrub
tree

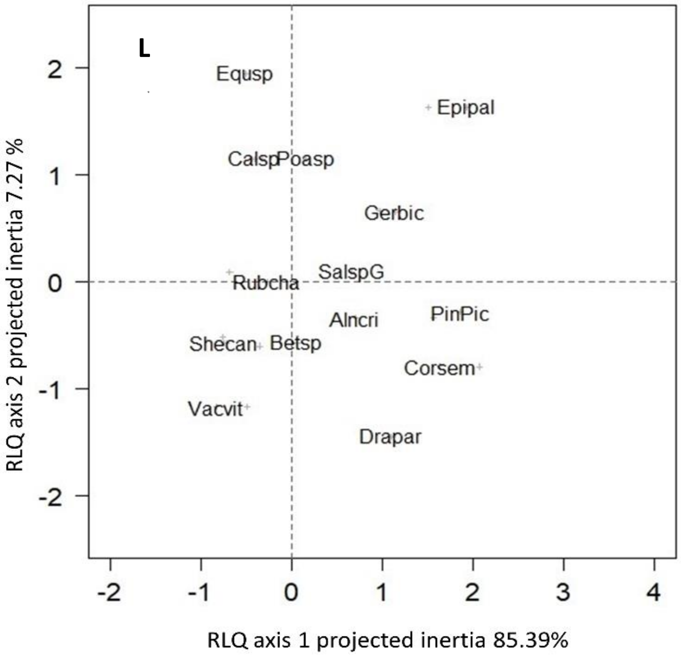

L
Equsp
Epipal
CalspPoasp
Gerbic
Rubcha
SalspG
Alncri
PinPic
Shecan
Betsp
Corsem
Vacvit
Drapar
2
1
0
-1
-2
-2
-1
0
1
2
3
4
RLQ axis 2 projected inertia 7.27 %
RLQ axis 1 projected inertia 85.39%

Figure 2.10 Results of the RLQ analysis of the Taiga Shield data showing ordination of the first two axes of the coefficients for the environmental variables (R), coefficients for the traits (Q), species ordination (L). Values in brackets on the axes of L represent the projected inertia (or variance in species and environmental scores captured) in each axis; d refers to grid-size. Environmental symbols in R: mineral, bryophyte, charcoal=percent covers exposed in each quadrat; burn date=calendar day of burn; basal area= total measured basal area (cm^2) of all species measured at each plot expressed on a per m^2 basis; piba, pima and other proportion= estimated proportion of dominant, pre-fire tree species based on density of stems per m^2 of 60 m^2 sample area where piba=*Pinus banksiana*, pima=*Picea mariana*, other=*Picea glauca;* xeric, subxeric, mesic subxeric, mesic, mesic subhygric and subhygric= ranking of plot moisture potential using the moisture class (**Appendix Figure 1**); age=stand age in years; residual organic=soil organic layer depth (cm) at each quadrat; burn depth=depth of burn (cm). Trait symbols in Q: proportion seeders=proportional representation of each species reproducing from seed at each plot; shrub, graminoid, seedless vascular, tree=growth forms based on general habit of growth (forb as default variable); deciduous=leaf persistence based on leaf type (evergreen as default variable); wind=seed dispersal mode (animal as default variable); annual, biennial=life span of each species (perennial as default variable). For species ordination (L) symbols have been jittered to reduce overlap, and only the most influential points on the axes are shown. For definition of species codes, see **Appendix Table 3.**

TABLES

Table 2.1 Summary of candidate models used in GLMMs to characterize variation in taxa richness and post-fire mode of regeneration.

Model Name	Predictor Variables	Scale (units)
Null	NA	NA
Fire Characteristics	Burn Date	Ordinal (day of year)
	Stand Age (age)	Continuous (years)
	Tree Consumption	Continuous (average of categorical values per plot)
Stand Characteristics	Dominant Stand Type: stand pima, stand other	Categorical
	Basal Area	Continuous (total basal area, cm^2) of all tree species expressed on a per m^2 basis
Seedbed	*Residual organic depth (residual organic)	Continuous (cm)
	*Percent charcoal cover (charcoal)	Continuous (%)
	*Percent bryophyte cover (bryophyte)	Continuous (%)
	*Percent mineral soil cover (mineral)	Continuous (%)
Full	All predictor variables listed	See Above

*Values were calculated at the quadrat level for taxa richness and at the plot level for regeneration mode. Random effects were burn complex, site and plot for taxa richness analysis; burn complex and plot for regeneration mode analysis. All predictor variables were standardized except dominant stand type; residual organic was log transformed and standardized.

Table 2.2 Ranking of the GLMM candidate models used to predict variation in taxa richness post fire on the Taiga Plains (A) and Taiga Shield (B), with the selected model (lowest AICc) in bold. Null model included with only the nested study areas as random effects: burn/site/plot. For each model (row headings) we reported: number of effects in each model(K), Log-likelihood (Log(L)), Akaike Information Criterion (AICc), change in AICc compared to lowest AICc model (ΔAICc), Akaike model weight (weight) and variance explained by fixed factors (marginal R^2) and both fixed and random factors (conditional R^2). Each model assumes a Poisson error structure and uses a logarithm link function.

A

Model	K	Log(L)	AIC_c	ΔAICc	weight	marginal R^2	conditional R^2
Seedbed	**8**	**-1379.95**	**2776.13**	**0.00**	**0.61**	**0.05**	**0.54**
Full	14	-1374.16	2777.03	0.90	1.00	0.11	0.52
Fire Characteristics	7	-1396.59	2807.35	31.22	1.00	0.04	0.53
Null	4	-1400.05	2808.16	32.02	1.00	0.00	0.54
Stand Characteristics	7	-1399.32	2812.83	36.69	1.00	0.00	0.55

B

Model	K	Log(L)	AIC_c	ΔAICc	weight	marginal R^2	conditional R^2
Full	**14**	**-820.58**	**1670.20**	**0.00**	**0.99**	**0.40**	**0.56**
Seedbed	8	-831.47	1679.29	9.09	0.01	0.27	0.51
Stand Characteristics	7	-844.10	1702.48	32.28	0.00	0.19	0.60
Null	4	-856.03	1720.15	49.96	0.00	0.00	0.59
Fire Characteristics	7	-855.71	1725.70	55.50	0.00	0.00	0.60

Table 2.3 The lowest AICc-selected candidate model describing variation in taxa richness on the Taiga Plains (Seedbed Model) (A) and Taiga Shield (Full Model) (B). Bold variables indicate a significant relationship with the response variable (taxa richness per quadrat). Table shows: Intercept, Burn Date=calendar day number, Age=stand age calculated from tree ring analyses, Tree Consumption=average consumption of aboveground branches at each plot based on categorical values, Stand Pima=dominant stand type classified as *P. mariana*, Stand Other=dominant stand type classified as mix of conifer species including *L. laricina* on the Taiga Plains and *P. glauca* on the Taiga Shield, Residual Organic=the depth of the soil organic layer remaining post-fire in cm, Charcoal=percent charcoal cover at each quadrat, Bryophyte=percent cover of *Marchantia* spp. and *Ceratadon* spp. at each quadrat, Mineral=percent cover of mineral soil exposed at each quadrat. See also **Table 2.1** and **Appendix Table 8** for a complete description of candidate models and variables used. Each variable was standardized; residual organic was log-transformed to meet a normal distribution.

A	Estimate	Std. Error	z-value	Pr(>|z|)
Intercept	1.580	0.111	14.178	2.00E-16
Residual Organic	**0.086**	**0.032**	**2.652**	**0.008**
Charcoal	-0.020	0.235	-0.890	0.373
Bryophyte	**-0.072**	**0.231**	**-3.138**	**0.001**
Mineral	**-0.074**	**0.026**	**-2.808**	**0.005**

B	Estimate	Std. Error	z-value	Pr(>|z|)
Intercept	0.860	0.183	4.702	2.58E-06
Stand Pima	**0.480**	**0.192**	**2.493**	**0.012**
Stand Other	-0.486	0.292	-1.666	0.095
Basal Area	0.067	0.077	0.876	0.380
Burn Date	0.030	0.056	0.535	0.592
Age	-0.068	0.044	-1.547	0.121
Tree Consumption	-0.038	0.044	-0.871	0.383
Residual Organic	**0.332**	**0.047**	**6.989**	**2.76E-12**
Charcoal	-0.030	0.033	-0.899	0.368
Bryophyte	0.031	0.026	1.201	0.229
Mineral	**-0.090**	**0.045**	**-2.006**	**0.045**

Table 2.4 Ranking of the GLMM candidate models used to predict variation in regeneration modes post- fire on the Taiga Plains (A) and Taiga Shield (B) with the supported model (lowest AICc) in bold. The Null model included with only the nested study areas as random effects: burn/site/plot. Response variable for all models was the proportion of plants regenerating from seed at each plot. For each model (row headings) we reported: number of effects in each model(K), Log-likelihood (Log(L)), Akaike Information Criterion (AICc), change in AICc compared to lowest AICc model (ΔAICc), Akaike model weight (weight) and variance explained by fixed factors (marginal R^2) and both fixed and random factors (conditional R^2). Each model assumes a Binomial error structure and uses a logit link function.

A

Model	K	Log(L)	AIC_c	ΔAICc	weight	marginal R^2	conditional R^2
Full	**13**	**-216.08**	**461.49**	**0.00**	**0.67**	**0.05**	**0.05**
Seedbed	7	-223.96	462.89	1.40	0.33	0.03	0.03
Fire Characteristics	6	-230.6	473.93	12.44	0.00	0.02	0.02
Null	3	-241.19	488.58	27.09	0.00	0.00	0.01
Stand Characteristics	6	-239.49	491.70	30.20	0.00	0.00	0.03

B

Model	K	Log(L)	AIC_c	ΔAICc	weight	marginal R^2	conditional R^2
Full	**13**	**-557.46**	**1141.81**	**0.00**	**1.00**	**0.21**	**0.23**
Seedbed	7	-569.46	1153.19	11.38	0.00	0.17	0.20
Stand Characteristics	6	-682.35	1376.90	235.09	0.00	0.07	0.09
Fire Characteristics	6	-729.78	1471.77	329.96	0.00	0.01	0.05
Null	3	-737.27	1480.60	338.79	0.00	0.00	0.06

Table 2.5 The lowest AICc-selected candidate model describing variation in the proportion of plants regenerating from seed on the Taiga Plains (Full model) (A) and Taiga Shield (Full model) (B). Bold variables indicate a significant relationship with the response variable (proportion of plants regenerating from seed per plot). Table shows: Intercept; Burn Date=calendar day number; Age=stand age calculated from tree ring analyses; Tree Consumption=average consumption of aboveground branches at each plot based on categorical values (**see Appendix Table 4**); Stand Pima=dominant stand type classified as *P. mariana*; Stand Other=dominant stand type classified as a mix of conifer species including *L. laricina* on the Taiga Plains and *P. glauca* on the Taiga Shield; Residual Organic=the depth of the soil organic layer remaining post-fire, measured in cm; Charcoal=percent charcoal cover averaged across five quadrats at each plot; Bryophyte=percent cover of *Marchantia* spp. and *Ceratadon* spp. averaged across five quadrats at each plot; Mineral=percent cover of mineral soil exposed, averaged across five quadrats at each plot. Each variable was standardized; Residual Organic was log-transformed to meet a normal distribution. See also **Table 2.1** and **Appendix Table 8** for a complete description of candidate models and variables used. Each variable was standardized; Residual Organic was log-transformed to meet a normal distribution.

A	Estimate	Std. Error	z-value	Pr(>|z|)
Intercept	-1.213	0.159	-7.587	3.27E-14
Burn Date	**0.256**	**0.072**	**3.552**	**3.00E-04**
Age	0.076	0.066	1.141	0.253
Tree Consumption	0.045	0.063	0.721	0.470
Stand Pima	0.256	0.191	1.34	0.180
Stand Other	**0.854**	**0.411**	**2.079**	**0.037**
Basal Area	0.013	0.063	0.210	0.834
Residual Organic	**-0.362**	**0.087**	**-4.157**	**3.23E-05**
Charcoal	0.042	0.065	0.646	0.518
Bryophyte	**0.124**	**0.052**	**2.383**	**0.017**
Mineral	0.012	0.071	0.168	0.866

B	Estimate	Std. Error	z-value	Pr(>|z|)
Intercept	-0.01	0.328	-0.032	0.970
Burn Date	**0.251**	**0.125**	**1.995**	**0.046**
Age	0.108	0.073	1.477	0.139
Tree Consumption	**0.279**	**0.111**	**2.503**	**0.012**
Stand Pima	**-0.525**	**0.257**	**-2.041**	**0.041**

Stand Other	**-0.801**	**0.322**	**-2.484**	**0.012**
Basal Area	**0.149**	**0.068**	**2.176**	**0.029**
Residual Organic	**-0.861**	**0.071**	**-11.978**	**2.00E-16**
Charcoal	**-0.170**	**0.065**	**-2.593**	**0.009**
Bryophyte	**0.094**	**0.051**	**1.855**	**0.063**
Mineral	**0.155**	**0.065**	**2.367**	**0.017**

Table 2.6 Summary of the RLQ analysis for the Taiga Plains (A) and Taiga Shield (B). The table shows eigenvalues and percentages of projected inertia accounted for by the first two RLQ axes. Covariance refers to the covariance between the two new sets of factorial scores projected onto the first two RLQ axes (square root of eigenvalue); correlation refers to the correlation between the two new sets of factorial species scores projected onto the first two RLQ axes; cumulative inertia refers to the variance of each set of factorial scores computed in the RLQ analysis, both for the environment and for the traits.

A	Axis 1	Axis 2
Eigenvalues	0.632	0.096
% Projected Inertia	81.359	12.412
Covariance	0.795	0.310
Correlation	0.329	0.174
Cumulative inertia (environment)	3.340	5.101
Cumulative inertia (traits)	1.740	3.546

B	Axis 1	Axis 2
Eigenvalues	1.840	0.210
% Projected Inertia	85.391	7.272
Covariance	1.187	0.346
Correlation	0.500	0.216
Cumulative inertia (environment)	3.204	5.043
Cumulative inertia (traits)	1.750	3.141

Table 2.7 Results of Fourth Corner analysis showing all possible bivariate association between the environmental variables (y axis) and life history traits (x axis) on (A) the Taiga Plains and (B) the Taiga Shield. Significant (P-value≤0.05). Positive significant associations are represented in black; negative associations are in light grey; white indicates no relationship. Environmental variables include: Residual Organic=depth of post-fire residual organic soil (cm); Charcoal, Bryophyte and Mineral=average percent cover of exposed charcoal, bryophyte (*Marchantia* spp. and *Ceratadon* spp.) and mineral soil in each quadrat; Burn Date=calendar day of burn; Age=average age of each stand/plot; Pima, Piba and Other Proportion=proportion of dominant stand type based on stem density per m^2 of 60 m^2 sample area; Basal Area=total measured basal area (cm^2) of all species measured at each plot expressed on a per m^2 basis; Burn Depth=depth of burn (cm), moisture classes (Xeric, Subxeric, Mesic-subxeric, Mesic-subhygric, Subhygric)=ranking of plot moisture category based on moisture, soil type and permafrost presence (see Appendix Figure 1); Tree Consumption =average consumption of aboveground branches at each plot based on categorical values (see **Appendix Table 4**).Traits include: Proportion Seeders=the proportion of individuals of each species found reproducing from seed at each plot, Wind Dispersed=plants with seeds that are primarily dispersed by wind (default=animal); Evergreen=leaf persistence of each plant based on leaf type (default=deciduous); growth form (Graminoid, Seedless Vascular, Shrub, Tree)= grouped plants by growth form representing similarities in structure/function (default= Forbs); lifespan (Annual, Biennial)=life span of each species (default=perennial).See also **Appendix Table 8** for a complete description of environmental variables and **Appendix Table 11** for a complete description of life history traits.

A	Proportion Seeders	Wind Dispersed	Evergreen	Graminoid	Seedless Vascular	Shrub	Tree	Annual	Biennial
Residual Organic	▒				■				
Charcoal	■				▒				
Bryophyte	■	■			▒				
Mineral	■				▒				
Burn Date	■				▒				
Age									
Pima Proportion	▒				■				
Piba Proportion	■				▒				
Other Proportion									
Basal Area									
Burn Depth	▒				■				
Xeric									
Mesic-subhygric	▒				■				
Mesic-subxeric	■				▒				
Subhygric	▒				■				
Subxeric									
Tree Consumption									

B	Proportion Seeders	Wind Dispersed	Evergreen	Graminoid	Seedless Vascular	Shrub	Tree	Annual	Biennial
Residual Organic	▒				▒	■			
Charcoal	■				■	▒			
Bryophyte	■				■	▒			
Mineral	■				■	▒			
Burn Date	■				■	▒			
Age	▒				▒	■			
Pima Proportion	▒				▒	■			
Piba Proportion	■				■	▒			
Other Proportion	■				■	▒			
Basal Area	■				■	▒			
Burn Depth									
Xeric	■				■	▒			
Mesic-Subhygric									
Mesic-Subxeric	■				■	▒			
Subhygric	▒				▒	■			
Subxeric									
Tree Consumption									

CHAPTER 3. GENERAL DISCUSSION

This project provides insight into the mechanisms controlling post-fire vascular plant communities in the Taiga Plains and Taiga Shield Ecozones of the Northwest Territories (NWT). The NWT provides conditions for monitoring the large-scale response of the boreal forest in a changing climate, including the effects of future disturbance regime changes since this part of the boreal forest is largely intact and it experienced an unprecedentedly large fire year in 2014 (GNWT 2016). Findings from this work can build upon pan-boreal monitoring efforts addressing the recovery of high-latitude forests following fire and increase our understanding of the impacts of the extensive forest fires in times of climate change. Our findings showed this part of the boreal ecosystem has the ability to support and maintain ecological processes and the community of organisms that exist within the system.

One of the primary contributions of this project is the baseline dataset we established, including the creation of permanent sampling plots across the southern NWT landscape. Sustained monitoring of these plots will improve our understanding of the changes in post-fire plant species composition and richness through succession and future disturbances. This will enable decisions to be made regarding land use planning and resource development in fire-dominated ecosystems where fire regime changes are predicted.

Post-fire succession research such as this, also enables predictions of future forest changes that are important to wildlife through improved understanding of changing habitat conditions. Funding for part of this research was provided by the Government of the Northwest Territories' (GNWT) Cumulative Impact Monitoring Program (CIMP), with the intended focus of enabling predictions of long-term fire effects on wildlife habitat such as predictive *Rangifer tarandus* (caribou) habitat mapping within the forested areas of the Taiga Plains and Taiga Shield Ecozones. Cumulative effects of stressors such as drought and disturbance in the form of wildfire affects the habitat of *Rangifer tarandus groenlandicus* (barren ground caribou) and *Rangifer tarandus caribou* (woodland caribou), two caribou subspecies with partial ranges in the NWT, for example (GNWT 2016). Fire disturbance is likely to affect habitat availability for these caribou, where winter foraging grounds will potentially be avoided following fire (Joly *et al.* 2010). Overall, researchers will use these findings as part of the NWT-specific post-fire succession modules in the modelling program Spatial Discrete Event Simulation (SpaDES), which will help support decision making on future forest management for wildlife in the region (Chubaty *et al.* 2017).

3.1 Integrative Approach

This work formed part of a larger, trans-disciplinary examination of the aftermath of the 2014 forest fires in the NWT. Many individuals from various backgrounds and research institutions were involved in the development of the sampling design and protocols within the scope of this project including universities and the GNWT. Although the bulk of this study focused on forest ecology and botany, the integrative nature of the project included investigations into soil carbon, biogeochemistry, permafrost dynamics and site energy balance and relied heavily on the experience and expertise of multiple principle investigators. All of the investigations will feed into spatially explicit modelling efforts.

Associated with the integrative biology in this project is the inherent link between the biology and humans as inhabitants of the investigated landscape. For communities that still pursue traditional lifestyles, loss of diversity or shifts in species distributions in time and space could have consequences in terms of food security and land-use decisions. This project bridged the social component of the ecosystem we studied with our ecological findings. Indigenous communities in the NWT that have relied on hunting, trapping, gathering and the use of medicinal plants for generations could find their traditional use of and relationship with the land in this area changing with an altered fire regime. Caribou, for example, are historically an important wildlife resource and remain an important source for food, clothing, and cultural identity for Indigenous people in the NWT. Indigenous cultures are also connected to the land through trapping, fishing and harvesting berries such as *Vaccinium* spp. (blueberries and cranberries) and *Rubus chamaemorus* (cloud berry), all of which are an important part of northern Indigenous culture given their social and economic values. Understanding plant community response to fire and the associated impacts on wildlife will help prepare these communities for future conditions and support adaptation planning in association with services critical to human well-being in this subsistence region (Nelson *et al.* 2008).

Although I did not incorporate social impacts into the main body of work, during this project, I had the privilege to work with local community members including Indigenous communities, government workers and territorial park personnel throughout the NWT. In the summer of 2015 for example, a colleague and I participated in a Young Leaders' Summit, an initiative organised by Ecology North in which a group of young environmental professionals from across the Canadian north spent the day with us learning about forest ecology and the work we were doing in the NWT. Other outreach opportunities included a Fire Education Event with the Ka'a'gee Tu First Nation in Kakisa, which I helped to plan and where I spent the day with students, elders and social scientists teaching students how to conduct vegetation sampling and learning about fire ecology from scientific and traditional knowledge perspectives. My most recent contribution was helping to create an Educational Kit as part of a pilot project initiated by the GNWT to incorporate mapping tools such as ArcGIS into classrooms. I contributed documents to the kit to help support teachers and students wishing to establish permanent sampling plots, sample plants in the field and collect specimens for the creation of a classroom herbarium. All of these occasions have provided opportunities for informal discussions on the role of fire in a changing climate and occasions to connect with people from diverse backgrounds.

3.2 Significance

Since multiple interacting factors such as fire characteristics, climate variability, plant regeneration strategies and environmental characteristics interact to affect vegetation regeneration following fire, disentangling the relative influences of each can be challenging. This same complexity governing vegetation distribution and disturbance histories throughout the boreal forest makes predicting responses to disturbance such as wildfire difficult. This study is unique in that I demonstrate the consistent importance of seedbed quality and associated soil characteristics across multiple spatial scales. I was able to demonstrate consistent drivers of post-fire vascular plant communities across a large spatial scale whereby differences in results at the plot, stand and landscape levels are often common in similar work (De Grandpré *et al.* 1993; Turner and Romme 1994; Boiffin *et al.* 2015; Markham and Essery 2015). The results of the papers above combined with our results demonstrate the need to continue investigating post-fire succession in this region. Generalizing findings and making predictions may have limited power in extending to broader scales within the boreal forests of Canada and globally, which is partially why our hypotheses were incorrect when extending results from Alaska to expectations in the NWT. Specifically, our predictions regarding the role of fire in post-fire vascular plant recovery based on studies in western North America (Bernhardt *et al.* 2011; Hollingsworth *et al.* 2013; Pinno and Errington 2016) were not consistent with the results presented in Chapter 2.

In our results, poorly drained areas with greater surficial moisture, greater organic soil depths and *P.mariana*-dominated stand types enabled pre-fire plant communities to be maintained in the NWT. Furthermore, there was a greater representation of plants regenerating from belowground across the landscape, which led us to liken our findings to the ecological resilience of these ecozones, or the ability for a system to persist and absorb change and disturbance while maintaining relationships between populations or system variables (Holling 1973). These findings indicate that deep organic soil depths that are able to maintain moisture may have a higher threshold for resisting successional trajectory shifts as fire characteristics continue to change with a warming climate (Johnstone and Chapin 2006b). Overall, our results demonstrate that environmental conditions post-fire impose environmental legacies that have a stronger influence than fire characteristics in the southern boreal forests of the NWT.

As mentioned in Chapter 1 of this document, vegetation patterns are tightly linked with both topography and disturbance histories. Ecological resilience across the Taiga Plains and Taiga Shield Ecozones can also be attributed then, to a landscape that is adapted to large-scale fires (Burton *et al.* 2008), but also fires that are not particularly severe. Our results are comparable to a paper from eastern Canadian boreal forests where habitat characteristics such as stand type and gradients of moisture explained a higher proportion of variation in species composition following fire; these findings were consistent across multiple scales and the authors attributed findings to a low severity burn (Boiffin *et al.* 2015). Further evidence of the 2014 NWT fires not being severe was demonstrated by Walker *et al.* (2017 in press), in which a mean burn depth of 9.4cm was measured in *P. mariana*-dominated stands, approximately half the depth of burns in interior Alaska in recent years.

Despite the NWT being relatively flat, topography and geomorphological histories still played a strong role in patterns of vegetation and associated legacies. In a study looking at 3461 km^2 area within the mixed-wood boreal forest in western Canada, Bridge and Johnson (2000) found an important role of surficial geology and geomorphic processes in producing the upland mosaic pattern of species composition and stand types across the landscapes. Their findings included a section of forest in Saskatchewan, which is known to be a notoriously flat region. Therefore, we should not underestimate the role of the minimal topography in the NWT in maintaining the vegetative legacy I reported on.

The vegetative legacy and associated resilience that is demonstrated in this study is possibly a result of the high amount of landscape heterogeneity in our study region. Differing geomorphological histories and varying subsurface soil characteristics have already been extensively discussed. Stand characteristics, from age-classes to stand type and density were likewise, variable across both ecozones (**Appendix Table 1**). The landscape scale of our study, ultimately allowed us to capture a mixture of stand types, multiple moisture classes and stands in various stages of succession. Indeed, large scale fires are thought to promote landscape heterogeneity and biodiversity across the boreal forest more generally (Burton *et al.* 2008). Many ecological models have suggested that a diverse and heterogeneous ecosystem is more ecologically resilient to environmental stress as it has an increased ability to absorb disturbance without dramatic change to ecosystem properties and processes; such ecosystems may also recover more quickly (Holling 1973; Peterson *et al.* 1998; Gunderson 2000). Furthermore, forest ecologists have pointed out the role of spatial heterogeneity in the resilience of other ecosystems in warmer climates (Virah-sawmy *et al.* 2009; Levine *et al.* 2016).

To further support the power of a heterogeneous landscape that possibly contributes to the resilience in this region, I have chosen to present a case study to explore new data collected in 2016 that will help enhance our understanding of plant community resilience. The plant-edaphic interface is seldom examined, despite the importance of this area in influencing fire behaviour and the vegetative legacy of plant communities in particular. A combination of varying soil substrates, fire histories and rooting depths would be expected to contribute to the resilience demonstrated in the southern NWT.

3.3 Rooting depths of vascular plants in southern NWT: A case study

3.3.1 Overview

As laid out in Chapters 1 and 2 of this thesis, the impact of fire on rhizomatic tissue is dependent on the severity of the fire (organic soil combustion) and the depths at which rhizomatic tissue and seedbanks are stored (Schimmel and Granström 1996; Wang and Kemball 2005). This large-scale project has enhanced our understanding of the post-fire responses in the NWT, however, classifying regeneration modes into resprouters and seeders did not provide us with a full understanding of the depths of rooting structures in the plant communities and the predictive power such information could afford with future increased fire severity and frequency. It was hypothesized that the greater variability in rooting depths within plant communities, the greater the ability of pre-fire communities to re-establish under a range of fire characteristics.

Methods

In 2016, I conducted field work in affiliation with the 2014 fire project in a series of plots that burned prior to the 1960s in the southern region of the Taiga Plains. In these plots, I assessed secondary root and rhizome depths of persistent successional vascular plants at a series of control plots (n=48) including CG1 (control group) and CG2 (used for burn depth calibrations in the 2014 burn data) as well as CG3 near Hay River (**Figure 3.1**). At each control plot, I measured the rooting depth of as many species as possible that were present in the previous years' species presence data. I aimed for a minimum of three replicates per species, however, this was not always feasible since species I was looking for (those that were also present in post-fire communities) were not always present or abundant in the control plots (n=227 measurements). Belowground measurements were taken by carefully digging next to the rooting structure of each individual and measuring the depth (cm) from the first secondary root or first rhizome, stolon or bulb encountered to the top of the soil profile and noting the substrate in which the root was growing in (moss layer, fibric layer, humic layer and mineral soil layer).

A Shapiro Wilk test was used to assess the normality of the rooting depth data. A Fligner-Killeen test was used to assess homogeneity of variances of rooting depths in each moisture class. The Fligner-Killeen test is non-parametric, assesses medians and is sensitive to outliers (Conover *et al.* 1981; Crawley 2007).

3.3.2 Findings and comparisons to the literature

The majority of rooting structures were located in the upper organic layers of the soil profile (**Figure 3.2**). The rooting depth data was not normally distributed and was non-transformable (Shapiro Wilk: W=0.88, P-value<0.05). Variance in rooting depths was not significantly different across moisture classes (Fligner-Killeen: med chi-sq.=5.92, df=5, P-value=0.31) (**Figure 3.3**). Although there appears to be little variation in the general rooting zone of vascular plants in this region, general observations can still be made to support the idea that rooting depth variability is contributing to the landscape resilience seen in this region. There is, for example, variation among individual species rooting depths and the moisture classes in which the species were found in Tables 3.1.

Ledum groenlandicum, for example, had rhizomes ranging from 4-12cm belowground. The dwarf shrubs family *Vaccinium* spp. had roots ranging from ~3-11cm and were found growing in a range of moisture classes. Some herbs also demonstrated similar variation; the common forb *Hedysarum alpinum* had roots extending from 3.5-14.5cm in a range of moisture classes as well (**Table 3.1**). Furthermore, an inspection of the rooting depth outliers present in each moisture class (**Figure 3.3**), revealed that the outliers are incidences of deeper rooting depths ranging from 15-25cm. A closer inspection of the data indicated that these were different species from multiple growth forms. These findings potentially indicate that the species we sampled demonstrate the ability to regenerate in varying burn depths (**Figure 3.3**), however the bulk of plant community re-establishment in this region is likely dependant on relatively shallow organic soil combustion.

In comparison to other studies assessing root distributions in the boreal forest, our root depths initially appear relatively shallow (**Table 3.2**). Studies have shown that some vascular plant species such as *Rosa acicularis* and *Ledum groenlandicum* are capable of deep rooting structures (**Table 3.2**). Flinn and Wein (1977) found *Ledum groenlandicum* roots at a depth of 48cm and Strong and La Roi (1983) found rooting depths up to 140cm for the same species (**Table 3.2**). These studies did not necessarily restrict their assessment to the area in which the first secondary root or rhizome was encountered in the soil horizon and so the species reproductive abilities in the literature presented may be much shallower than the maximum rooting depths documented. Similar to our work, Strong and La Roi (1983) found rooting depths of many vascular plant species to be within 15cm of the ground surface in Alberta. They suggested the bulk of root systems are close to the forest floor because of warmer soil temperatures and possible mechanical limitations such as increased soil density with depth. It is also possible that shallow rooting depths provide a competitive advantage following early season nutrient pulses associated with spring snow melt (Pomeroy *et al.* 1999).

3.3.3 Conclusions and future suggestions

1) The shallow rooting depths and the presence of rhizomes in the humic and fibric layers of the soil profile that I present in the NWT supports the notion that the forests in this region are adapted to fire histories that are not severe. These observations also support our understanding that the 2014 fires were extensive in size, but not particularly severe since there was a greater frequency of plants reproducing from rhizome on the Taiga Plains and Taiga Shield Ecozones.
2) Shallow rooting systems are not unique to this region.
3) The variability of rooting depths within the upper organic layers of many vascular plant species likely contributes to the heterogeneity in the region, which likely contributes to the ecosystem resilience throughout multiple fire cycles, as was demonstrated in the 2014 fires.
4) Despite the inherent physical labour associated with gathering data on functional traits such as rooting depths, a greater understanding of the life history traits of plant species in relation to environmental gradients in this region is necessary. Consistent field measurement protocols are also imperative so that relationships between plant communities and the environment can be understood and compared across scales and studies.

3.4 Future directions

Although the boreal forest in the NWT demonstrated resilience to an extreme fire event, there should be caution in assuming the effects of rapid climate change will not alter the resilience of these ecozones in the near future. Continued monitoring to understand the thresholds at which forest types and underlying soil substrates will no longer be resilient to changing climate and associated acceleration of fire regimes is needed, especially in relation to subsurface conditions such as permafrost. Severe drought conditions combined with increased fire frequency could easily tip the threshold of this region and result in historically moisture-rich sites to burn more readily, as was observed in the 2014 fires. *Picea mariana*-dominated stands in mesic moisture classes will possibly experience the first and most drastic changes. *Picea mariana* forests at dry and moderately well-drained landscape positions were most vulnerable to complete combustion of the organic soil layer in 2014 (Walker *et al.* 2017 in press).

At the same time, further investigation into fire ecology of *P. banksiana*-dominated stands is required. If these forest types do not have the organic soil depths or moisture conditions necessary to protect a vegetative legacy, upland sites of the NWT may be at risk of depleting canopy and soil seedbanks as well as rhizomatic tissue more quickly (Bond and van Wilgen 1996). Successful vascular plant species under such conditions are likely to have the following attributes: fast-growing, capable of dispersing seeds long distances, persistent on the landscape (long life-span) and able to regenerate from multiple modes such as *Salix* spp. and *Betula* spp. of the shrub growth forms and *Calamagrostis* spp. of the graminoid growthform. Ruderal species that are known to proliferate easily and invade disturbed sites such as *Epilobium* spp. and *Taraxacum* *officinale* F.H. Wiggers (common dandelion) will also be at an advantage, presumably with reduced competition. Ultimately, these stands may shift to homogenized communities without the additional diversity that current vascular plant communities can provide across the landscape.

On a final note, this study focused on vascular plants, however, the role of non-vascular plant communities in supporting the maintenance of sub-surface moisture conditions through regular fire cycles is also important. Given the limited understanding of the role of non-vascular species in contributing to the resilience of vascular plant communities following fire, future research in this area would be beneficial to our understanding of legacy effects in the boreal forest as well.

3.5 Summary

The pressure of climate warming in northwestern Canada has led to more severe and frequent forest fires in the boreal forests of this region. The unprecedented fire year in 2014 provided the opportunity to examine the potential for severe wildfire to impact post-fire vascular plant regeneration processes spanning two ecozones across a gradient of *P. banksiana* and *P. mariana*-dominated stands. The community of vascular plant plants, which have a strong influence on the overall forest structure and ecosystem functioning, are less commonly the focus of post-fire succession studies. The 2014 fire provided an opportunity to investigate the drivers of taxa richness, community assembly and vascular plant species composition following an extensive disturbance event in the boreal forest of western Canada using taxonomic and trait-based methods. Our generalized findings demonstrated that vascular plant communities regenerating in the

NWT are resilient across both ecozones. I attributed these findings to landscapes that have increased subsurface moisture and organic soil depths that are able to override fire characteristics in supporting the compositional stability of vascular plant communities in this region. These findings are further summarised as the prevalence of an environmental legacy, which enables a vegetative legacy in the southern NWT.

3.5.1 Overall

a) The boreal forest is adapted to regular wildfire, which helps to shape landscape diversity and influence ecosystem processes such as succession. In recent years, climate change has warmed and dried parts of the boreal forest so that the severity and frequency of naturally occurring fires has increased.

b) Fire can drive selection for particular plant traits such as plant regeneration strategies, that are well suited to such wildfire. The fire regime plays a key role in plant community assembly post-fire; resilience of the pre-fire vascular plant community is possible if the fire is not severe and rhizomatic tissue is left in relatively intact.

c) Understanding how variations in fire severity and other environmental variables impact the mechanisms of vascular plant establishment may enable us to predict plant regeneration responses to changing fire regimes in the face of climate change. With increased fire severity, organic layer depth is severely altered, which has the potential to remove underground root systems that would otherwise resprout following a fire. An increase in fire frequency means regenerating stands will sustain multiple disturbances in a short period of time, potentially impacting future plant regenerations in the process.

d) The results of this research demonstrate the importance of maintaining data collection at permanent sampling plots across the NWT landscape and for modelling wildlife habitat and forest management practices in a changing climate.

3.5.2 Drivers of post-fire vascular plant communities in the NWT

a) Different surficial geology and geomorphological histories on the Taiga Pains and Taiga Shield produced different patterns of species composition and stand types across the landscape, with the Taiga Shield being less diverse than the Taiga Plains.

b) Despite these ecozone differences, environmental characteristics in both ecozones demonstrated the importance of seedbed quality and soil characteristics driving vascular plant regeneration immediately following fire.

c) Lower severity fires resulted in greater post-fire taxa richness; post-fire plant communities following more severe fires had greater representation of seed dispersal and seed bank species. *Picea mariana* stands on the Taiga Shield in particular, demonstrated post-fire residual organic soil depths conducive to increased taxa richness and the re-establishment of rhizomatic, pre-fire vegetative communities. Seedbank species did surprisingly well in the more severe burns implicating heat tolerance in these seeds.

d) Fire characteristics that did prove important to community assembly such as burn date (seasonal timing) and burn depth had an underlying association with pre-fire site conditions such as moisture and species composition/stand type.

e) I concluded that poorly drained areas with greater surficial moisture and associated soil characteristics enabled a pre-fire vegetative legacy to be maintained in the NWT. Maintained organic soil depths have a higher threshold for resisting successional trajectory shifts as fire regimes continue to change with a warming climate. We likened the subsurface conditions to the environmental legacy in this region.

3.5.3 Significance

a) The Taiga Plains and Taiga Shield Ecozones of the NWT have the ability to support and maintain ecological processes, including the community of plants that exist within the system as climate and associated fire regime changes.

b) The mechanisms controlling post-fire vascular plant species composition and taxa richness in this boreal region are largely governed by environmental characteristics such as moisture class, soil texture and associated stand types.

c) The results from this study demonstrate that a changing climate has not interfered with the recovery of vascular plant communities following fire in this region.

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FIGURES

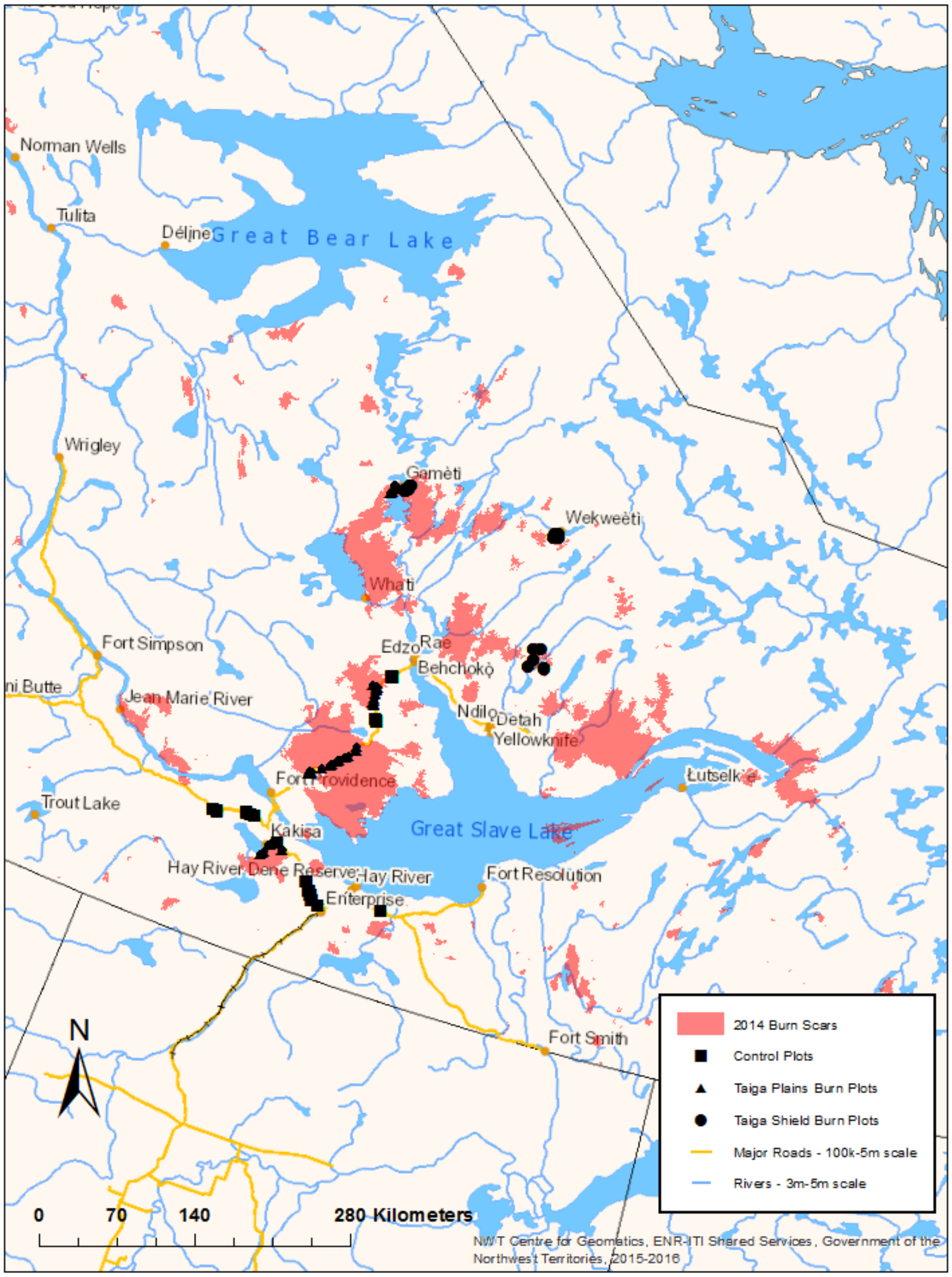


Figure 3.1 Map of sampling areas within the Northwest Territories spanning two ecozones and encompassing seven burn complexes. Map shows sampled plots from the 2014 burns (n=209) and unburned control plots sampled for species rooting depth measurements (n=48). True sample size is obscured given overlapping plots.

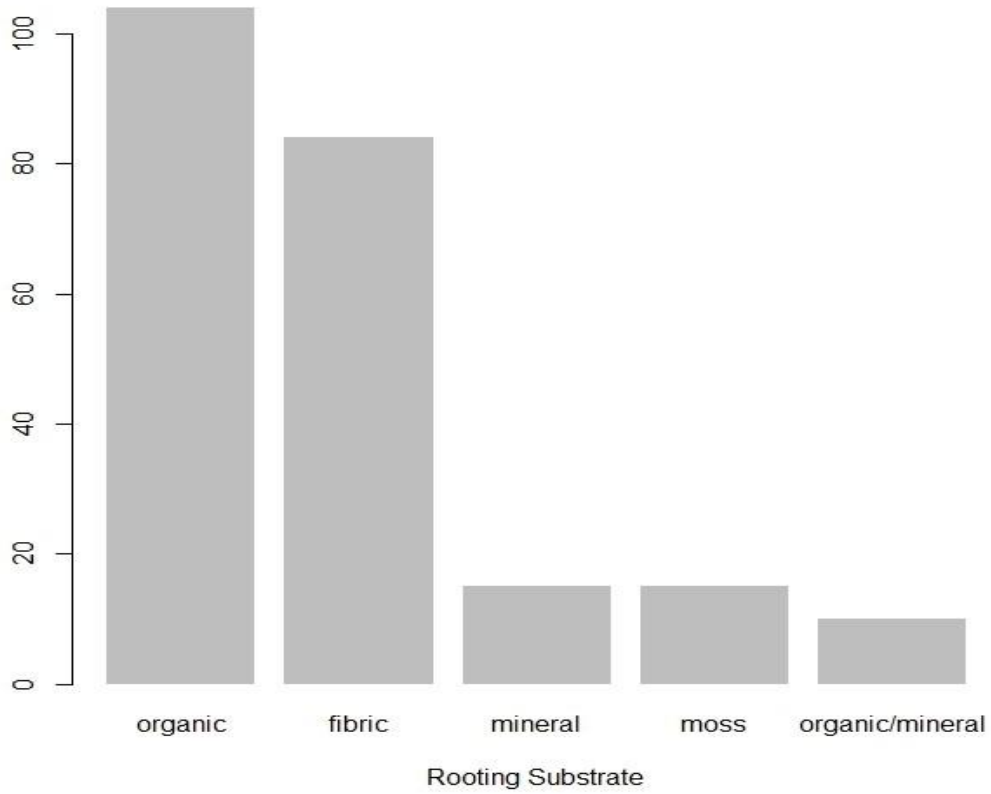


Figure 3.2 Frequency of rooting substrates of species pool sampled in unburned sites in southern NWT in 2016 (n = 227). Humic=decomposed organic soil; fibric=undecomposed material; mineral=mineral soil; moss=live moss; mineral/humic =transition area at which decomposed organic soil appeared to combine with the mineral soil layer.

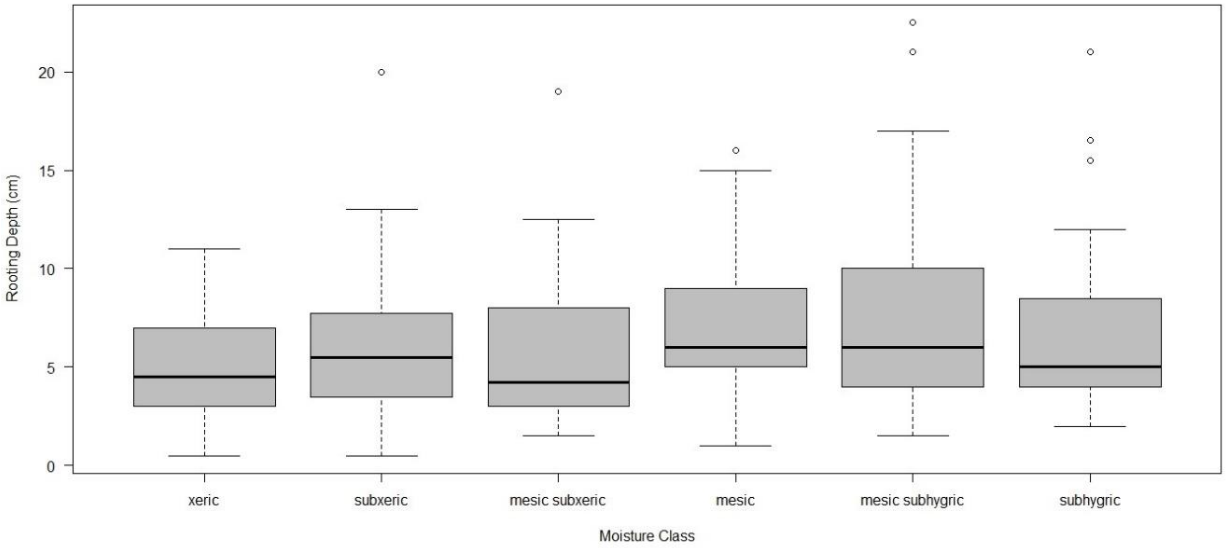


Figure 3.3 Boxplot showing Rooting Depths (cm) of vascular plants (n=227) measured across six moisture classes. Box =25th and 75th percentiles; horizontal line within the box represents the median. Whiskers are greater than +/- 1.5 times the interquartile range; circles represent outliers. Moisture classes range from dry (xeric) to wet (subhygric) and are based on **Appendix Figure 1** (Johnstone *et al.* 2008). Rooting depths were measured in 2016 in a southern NWT chronosequence of stands that burned prior to the 1960s (n=48 control plots). Data was not normal and non-transformable. Variance is not significantly different based on medians (Fligner-Killeen: med chi-squared=5.92, df=5, P-value=0.31).

TABLES

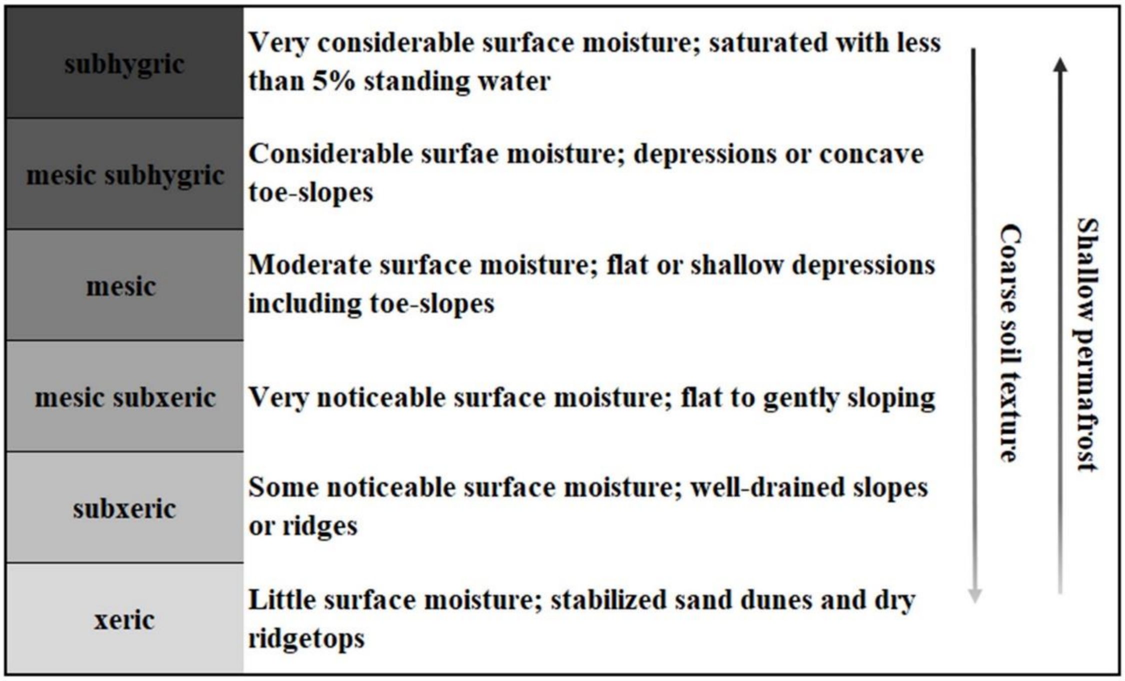
Table 3.1 Table showing range and mean rooting depths of a subset of species on the Taiga Plains Ecozone grouped by growth form. Dominant moisture class is in accordance with the 2014 sampling protocol (Johnstone *et al.* 2008) (see **Appendix Figure 1**).

Species Code	Mean Rooting Depth (cm)	Range (cm)	Number of Samples	Dominant Moisture Class
Graminoids				
Carex spp.	4.5	1-6	7	range
Poa spp.	5.0	3-8	4	range
Shrubs				
Rosa acicularis	9.1	6-13	3	dry
Ledum groenlandicum	9.0	4-12	4	wet
Arctostaphylos uva-ursi	3.2	0.5-5.5	5	dry
Myrica gale	12.8	11-16.5	3	wet
Potentilla fruticosa	8.0	4.5-15	3	range
Vaccinium uliginosum	6.0	3-11	3	range
Vaccinium vitis-idaea	6.1	3-10.5	3	range
Arctostaphylos rubra	6.0	3.5-12	4	range
Andromeda polifolia	3.3	2-5.5	7	range
Empetrum nigrum	3.1	2.5-4.5	3	range
Shepherdia canadensis	6.8	5-10	4	range
Forbs				
Rubus pubescens	4.7	3.5-7	4	range
Linnaea borealis	4.0	3-5	3	dry
Cornus canadensis	3.3	0.5-7	3	range
Zygadenus elegans	9.6	7-15	4	range
Epilobium angustifolium	6.0	3-12	4	range
Achillea millefolium	5.6	2-9	4	range
Anemone parviflora	5.6	3.5-7.5	3	range
Campanula rotundifolia	7.8	5.5-10	3	range
Galium trifidum	5.1	3-8	4	range
Geocaulon lividum	5.6	3.5-9	4	range
Hedysarum alpinum	7.9	3.5-14.5	5	range
Seedless Vasculars				
Equisetum scirpoides	8.2	2.5-16	5	range
Equisetum variegatum	2.6	1.5-4	3	range

Table 3.2 Literature review of mean and range of rooting depths of various boreal vascular plants grouped by growth form. Stand type refers to the dominant stand as described by the authors; Picmar=*Picea mariana*; Pinban=*Pinus banksiana;* Psemen=*Pseudotsuga menziesii* (Douglas fir) and Mixed=deciduous species mixed with either Pinban or Picmar. NA indicates missing information for that reference.

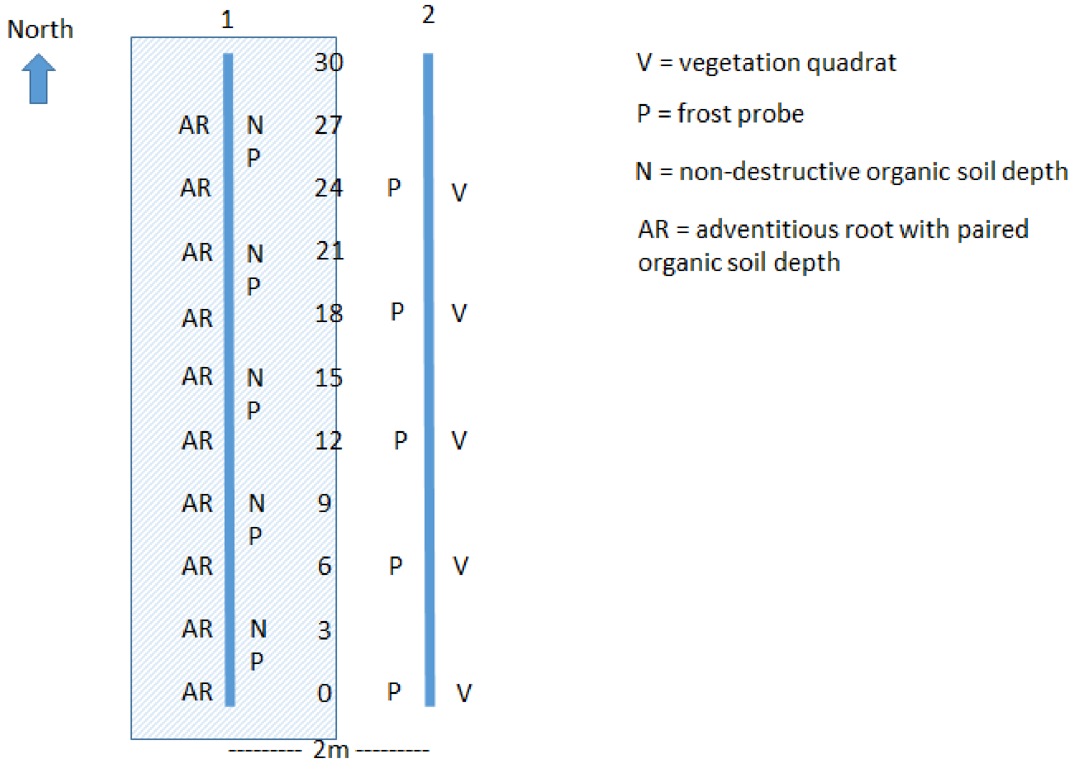
Species	**Study Location**	**Stand Type**	**Rooting Depth (cm)**	**Range(cm)**	**Source**
Shrubs					
Rosa acicularis			NA	0-20	Fire Effects Information System (FEIS 2017)
Rosa acicularis	AB	Pinban	96.66	30-140	Strong and La Roi 1986
Rubus pubescens	AB	Pinban	14	NA	Strong and La Roi 1986
Ledum groenlandicum	AB	Picmar	27	27	Strong and La Roi 1986
Ledum groenlandicum	NB	Mixed, Picmar	45	40-48	Flinn and Wein 1977
Ledum groenlandicum	NA		NA	15-50	Hebert and Thiffault 2011
Ledum groenlandicum	Alaska	Picmar	NA	15-30	Dyrness *et al.* 1986
Arctostaphylos uva-ursi	AB	Pinban	122.5	110-135	Strong and La Roi 1986
Vaccinium vitis-idaea	AB	Pinban	10.33	5-17	Strong and La Roi 1986
Vaccinium vitis-idaea	Sweden		NA	2-3	Schimmel and Granström 1996
Vaccinium vitis-idaea	AB	Mixed	NA	19-23	Smith 1962
Forbs					
Linnaea borealis	AB	Pinban	9	NA	Strong and La Roi 1986
Cornus canadensis	AB	Pinban Picmar	17.5	9-13	Strong and La Roi 1986
Cornus canadensis	NB	Mixed	8	6-13	Flinn and Wein 1977
Cornus canadensis	BC	Psemen	NA	5-13	McLean 1969
Epilobium angustifolium	BC	Psemen	NA	1.5-5	McLean 1969
Epilobium angustifolium	NB	Mixed	3.66	2.5-5	Flinn and Wein 1977

APPENDIX

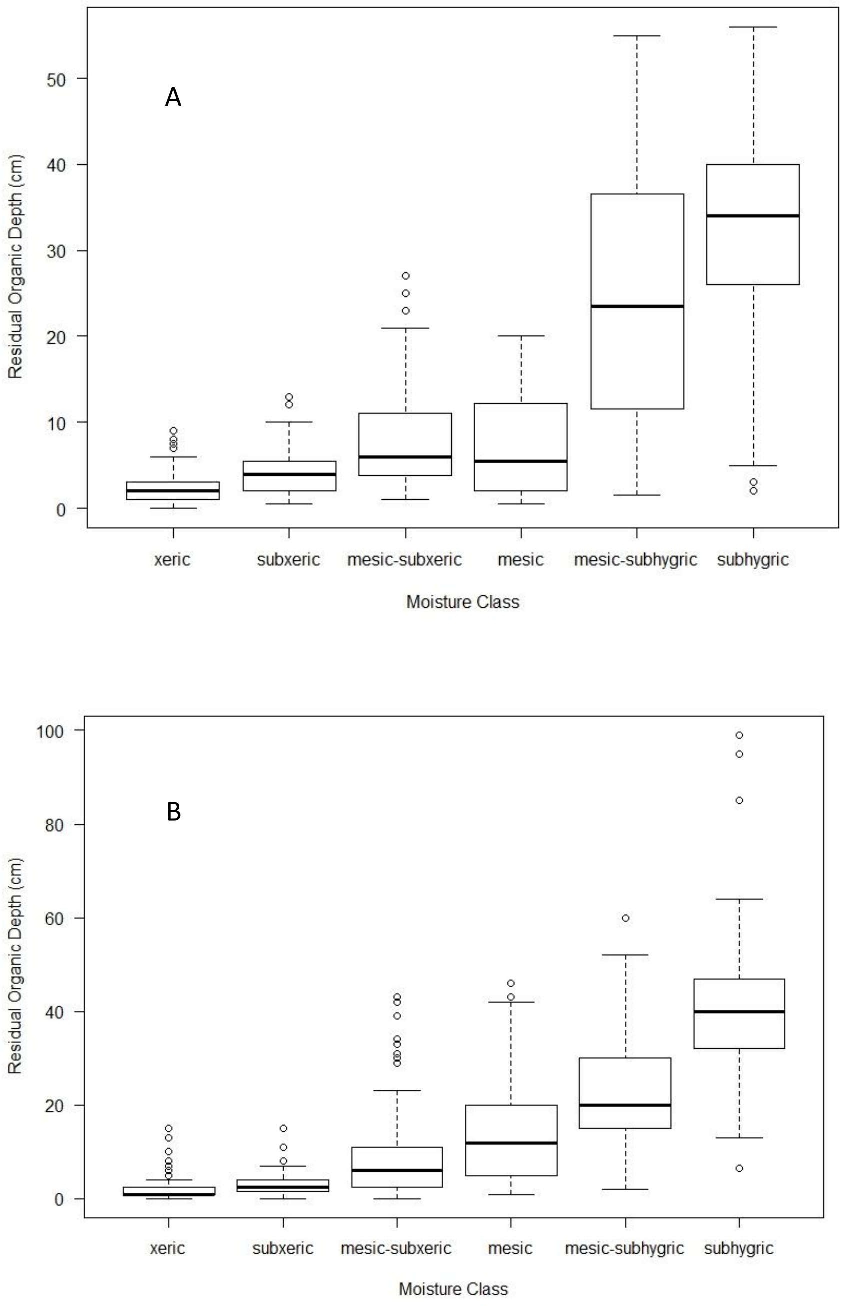


subhygric	Very considerable surface moisture; saturated with less than 5% standing water
mesic subhygric	Considerable surfae moisture; depressions or concave toe-slopes
mesic	Moderate surface moisture; flat or shallow depressions including toe-slopes
mesic subxeric	Very noticeable surface moisture; flat to gently sloping
subxeric	Some noticeable surface moisture; well-drained slopes or ridges
xeric	Little surface moisture; stabilized sand dunes and dry ridgetops

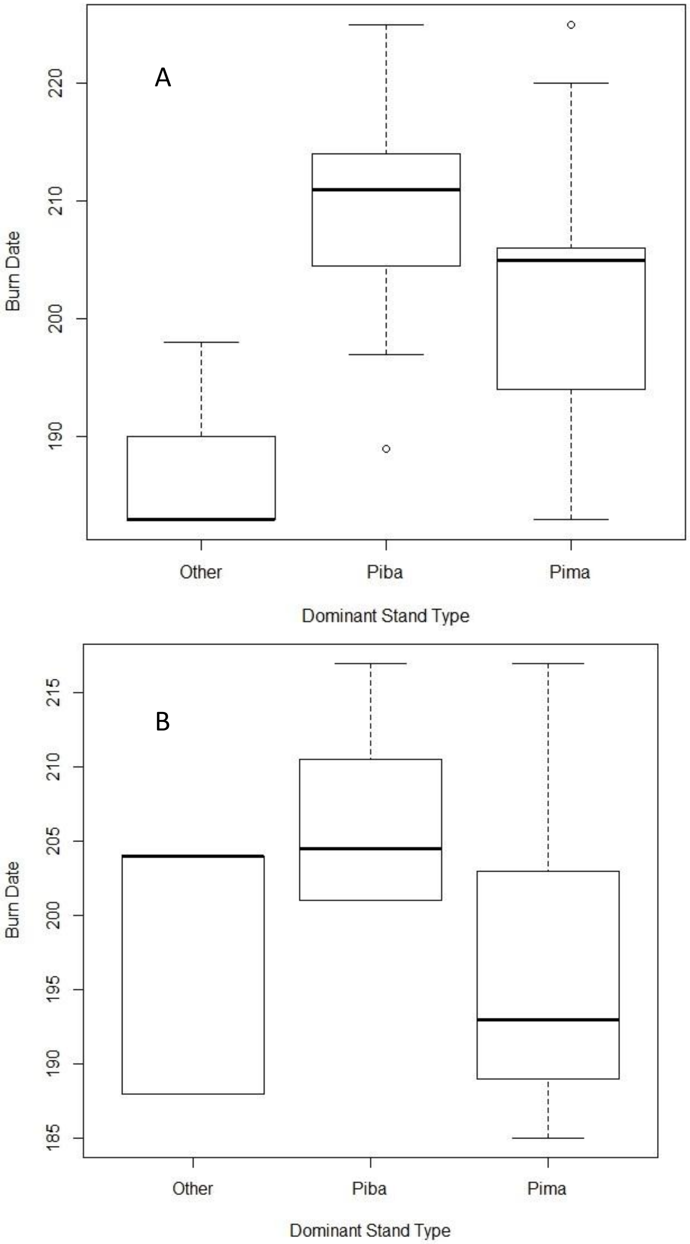
Appendix Figure 1 Pictograph used to identify and label moisture classes across multiple strata in the NWT Taiga Plains and Taiga Shield Ecozones. Image modified from Johnstone *et al.* 2008. At each site, we sampled across the available moisture classifications and classified plots according to this key.



Appendix Figure 2 Diagram outlining sampling protocol in 2015 field season. Each plot consisted of two parallel transects of 30m in length. Transect 1 was used to characterize pre-fire stand composition and density and aboveground biomass consumption. Along transect 1, loss of organic soils was measured using the adventitious root (AR) method (Boby *et al.* 2010). Maximum thaw depth was measured at three-meter intervals, alternating along each transect. Vegetation (V) data were collected along transect 2.



Appendix Figure 3 Boxplots showing Residual Organic Depth (cm) in each Moisture Class of plots (n=125) on the Taiga Plains (A) and Taiga Shield (n=84) (B). Box =25th and 75th percentiles; horizontal line within the box represents the median. Whiskers are greater than +/- 1.5 times the interquartile range; circles represent outliers. Moisture classes range from dry (Xeric) to wet (Subhygric) and were based on **Appendix Figure 1** from Johnstone *et al.* 2008.



Appendix Figure 4 Boxplots showing Burn Date (day of year) in each dominant stand type on the Taiga Plains (n=125) (A) and Taiga Shield (n=84) (B). Box =25th and 75th percentiles; horizontal line within the box represents the median. Whiskers are greater than +/- 1.5 times the interquartile range; circles represent outliers. Other=*Larix laricina*; Piba=*Pinus banksiana*; Pima=*Picea mariana*.

Appendix Table 1 Table of sample sites and strata based on ecozone. Pre-fire vegetation= *Picea mariana* (Pima), *Pinus banksiana* (Piba) or a combination of the two (mixed). When Forest Resource Inventory (FRI) was available, dominant species was used for site selection; Canadian Landcover Class (LCC05) information was used otherwise.

Burn ID	Burn Name	Ecozone	Pre-fire vegetation	Pre-fire forest density	Burn season	Re-burned ?	# of Sites	# of plots
SS033	Kakisa	Taiga Plains	*Pima*	Medium	early	no	4	12
			Pima	Low	early	no	2	6
			Pima	Medium	early	yes	2	3
			Pima	Low	early	yes	2	4
ZF020	Central	Taiga Plains	*Pima*	FRI	early	no	4	11
			Pima	FRI	late	no	3	9
			Piba	FRI	early	no	3	9
			Piba	FRI	late	no	4	10
ZF046	Northern	Taiga Plains	*Piba*	FRI	early	no	3	9
			Piba	FRI	early	yes	3	9
			Piba	FRI	late	no	3	9
			Piba	FRI	late	yes	3	9
ZF035	Gamètì West	Taiga Plains	mixed	Sparse	mid	no	3	9
			mixed	Medium	mid	no	3	9
			mixed	Low	mid	no	3	9
ZF044	Gamètì East	Taiga Shield	mixed	Medium	early	no	3	9
			mixed	Low	early	no	3	9
			mixed	Low	late	no	3	9
ZF026	Wekweètì	Taiga Shield	mixed	Medium	early	no	3	9
			mixed	Low	early	no	3	9
			mixed	Sparse	early	no	3	9
			mixed	Sparse	early	yes	3	9
ZF104	Discovery Mine	Taiga Shield	mixed	Medium	mid	no	2	4
			mixed	Low	mid	yes	2	4
			mixed	Medium	mid	yes	4	8
			mixed	Low	mid	no	4	8

Appendix Table 2 Species composition data on the Taiga Plains. NA indicates specimens identified to family. Nomenclature follows Porsild and Cody (1980).

Family	Species Code	Species Latin Name
Asteraceae	Achmil	*Achillea millefolium*
Poaceae	Agrosp	*Agrostis* spp.
Poaceae	Agrsp	*Agropyron* spp.
Betulaceae	Alncri	*Alnus crispa*
Ericaceae	Andpol	*Andromeda polifolia*
Ranunculaceae	Anecan	*Anemone canadensis*
Ranunculaceae	Anepar	*Anemone parviflora*
Ranunculaceae	Anesp	*Anemone* spp.
Caryophyllaceae	Arasp	*Arabis* spp.
Ericaceae	Arcrub	*Arctostaphylos rubra*
Ericaceae	Arcuva	*Arctostaphylos uva-ursi*
Caryophyllaceae	Aresp	*Arenaria* spp.
Asteraceae	Asteraceaesp	NA
Asteraceae	Astersp1	*Aster* spp.
Asteraceae	Astpun	*Aster puniceus*
Fabaceae	Astragalussp	*Astragalus* spp.
Asteraceae	Astsib	*Aster sibiricus*
Betulaceae	Betgla	*Betula glandulosa*
Betulaceae	Betpap	*Betula neoalaskana*
Betulaceae	Betsp	*Betula* spp.
Poaceae	Calsp	*Calamagrostis* spp.
Campanulaceae	Camrot	*Campanula rotundifolia*
Cyperaceae	Carexsp	*Carex* spp.
Caryophyllaceae	Carsp	NA
Ericaceae	Chacal	*Chamaedaphne calyculata*
Chenopodiaceae	Chesp	*Chenopodium* spp.
Ranunculaceae	Coptri	*Coptis trifolia*
Fumariaceae	Coraur	*Corydalis aurea*
Cornaceae	Corcan	*Cornus canadensis*
Fumariaceae	Corsem	*Corydalis sempervirens*
Lamiaceae	Drapar	*Dracocephalum parviflorum*
Onagraceae	Epiang	*Epilobium angustifolium*
Onagraceae	Epigla	*Epilobium glandulosum*
Onagraceae	Epipal	*Epilobium palustre*
Equisetaceae	Equsci	*Equisetum scirpoides*
Equisetaceae	Equsp	*Equisetum* spp.
Asteraceae	Erisp	*Erigeron* spp.

Poaceae	Fessp	*Festuca* spp.
Rosaceae	Fraves	*Fragaria vesca*
Rosaceae	Fravir	*Fragaria virginiana*
Rubiaceae	Galbor	*Galium boreale*
Rubiaceae	Galtri	*Galium trifidum*
Santalaceae	Geoliv	*Geocaulon lividum*
Geraniaceae	Gerbic	*Geranium bicknellii*
Rosaceae	Geusp	*Geum* spp.
Fabaceae	Hedalp	*Hedysarum alpinum*
Fabaceae	Hedbor	*Hedysarum boreale*
Fabaceae	Hedsp	*Hedysarum* spp.
Asteraceae	Hieraciumsp	*Hieracium* spp.
Asteraceae	Hieumb	*Hieracium umbellatum*
Cupressaceae	Junhor	*Juniperus horizontalis*
Pinaceae	Larlar	*Larix laricina*
Fabaceae	Latoch	*Lathyrus ochroleucus*
Ericaceae	Leddec	*Ledum decumbens*
Ericaceae	Ledgro	*Ledum groenlandicum*
Poaceae	Leysp	*Leymus* spp.
Liliaceae	Lily1	NA
Caprifoliaceae	Linbor	*Linnaea borealis*
Caprifoliaceae	Londio	*Lonicera dioica var. glaucescens*
Asparagaceae	Maisp	*Maianthemum genus*
Myricaceae	Myrgal	*Myrica gale*
Poaceae	Orysp	*Oryzopsis asperifolia*
Ericaceae	Oxymic	*Oxycoccus microcarpus*
Celastraceae	Parpal	*Parnassia palustris*
Ranunculaceae	Parpar	*Parnassia parviflora*
Asteraceae	Petpal	*Petasites palmatus*
Asteraceae	Petsag	*Petasites sagittatus*
Hydrophyllaceae	Phafra	*Phacelia franklinii*
Pinaceae	PinPic	NA
Poaceae	Poasp	*Poa* spp.
Salicaceae	Popbal	*Populus balsamifera*
Salicaceae	Poptre	*Populus tremuloides*
Rosaceae	Potans	*Potentilla anserine*
Rosaceae	Potfru	*Potentilla fruticose*
Rosaceae	Potsp	*Potentilla* spp.
Ranunculaceae	Ranabo	*Ranunculus abortivus*
Ranunculaceae	Ransce	*Ranunculus sceleratus*
Ranunculaceae	Ransp	NA
Grossulariaceae	Ribes	*Ribes* spp.

Grossulariaceae	Riboxy	*Ribes oxyacanthoides*
Rosaceae	Rosaci	*Rosa acicularis*
Rosaceae	Rossp	NA
Rosaceae	Rubaca	*Rubus acaulis*
Rosaceae	Rubcha	*Rubus chamaemorus*
Rosaceae	Rubide	*Rubus idaeus*
Rosaceae	Rubpub	*Rubus pubescens*
Juncaceae	Rush1	NA
Salicaceae	Salsp1	*Salix* spp.
Salicaceae	SalspA	*Salix* spp.
Salicaceae	SalspB	*Salix* spp.
Salicaceae	SalspC	*Salix* spp.
Salicaceae	SalspD	*Salix* spp.
Salicaceae	SalspE	*Salix* spp.
Salicaceae	SalspF	*Salix* spp.
Salicaceae	SalspG	*Salix* spp.
Salicaceae	SalspH	*Salix* spp.
Salicaceae	SalspI	*Salix* spp.
Cyperaceae	Scihud	*Scirpus hudsonianus*
Asteraceae	Senpau	*Senecio pauperculus*
Elaeagnaceae	Shecan	*Shepherdia canadensis*
Asteraceae	Solmul	*Solidago multiradiata*
Asteraceae	Solspa	*Solidago spathulata*
Caryophyllaceae	Stelon	*Stellaria longifolia*
Caryophyllaceae	Stesp	*Stellaria* spp.
Asteraceae	Taroff	*Taraxacum officinale*
Ericaceae	Vacsp	*Vaccinium* spp.
Ericaceae	Vaculi	*Vaccinium uliginosum*
Ericaceae	Vacvit	*Vaccinium vitis-idaea*
Caprifoliaceae	Vibedu	*Viburnum edule*
Fabaceae	Vicame	*Vicia Americana*
Fabaceae	Viciasp	*Vicia* spp.
Violaceae	Vioadu	*Viola adunca*
Violaceae	Violasp	NA
Violaceae	Vioren	*Viola renifolia*
Melanthiaceae	Zygele	*Zygadenus elegans*

Appendix Table 3 Species composition data on the Taiga Shield. NA indicates specimens identified to family. Nomenclature follows Porsild and Cody (1980).

Family	Species Code	Species Latin Name
Betulaceae	Alncri	*Alnus crispa*
Ericaceae	Andpol	*Andromeda polifolia*
Ericaceae	Arcrub	*Arctostaphylos rubra*
Ericaceae	Arcuva	*Arctostaphylos uva-ursi*
Betulaceae	Betgla	*Betula glandulosa*
Betulaceae	Betpap	*Betula neoalaskana*
Betulaceae	Betsp	*Betula* spp.
Poaceae	Calsp	*Calamagrostis* spp.
Cyperaceae	Carexsp	*Carex* spp.
Ericaceae	Chacal	*Chamaedaphne calyculata*
Ranunculaceae	Coptri	*Coptis trifolia*
Fumariaceae	Coraur	*Corydalis aurea*
Fumariaceae	Corsem	*Corydalis sempervirens*
Fumariaceae	Corsp	*Corydalis* spp.
Lamiaceae	Drapar	*Dracocephalum parviflorum*
Ericaceae	Empnig	*Empetrum nigrum*
Onagraceae	Epiang	*Epilobium angustifolium*
Onagraceae	Epigla	*Epilobium glandulosum*
Onagraceae	Epipal	*Epilobium palustre*
Equisetaceae	Equsci	*Equisetum scirpoides*
Santalaceae	Geoliv	*Geocaulon lividum*
Geraniaceae	Gerbic	*Geranium bicknellii*
Ericaceae	Leddec	*Ledum decumbens*
Ericaceae	Ledgro	*Ledum groenlandicum*
Poaceae	Leysp	*Leymus* spp.
Caprifoliaceae	Linbor	*Linnaea borealis*
Ericaceae	Oxymic	*Oxycoccus microcarpus*
Pinaceae	PinPic	NA
Poaceae	Poasp	*Poa* spp.
Salicaceae	Poptre	*Populus tremuloides*
Grossulariaceae	Ribes	*Ribes* spp.
Rosaceae	Rosaci	*Rosa acicularis*
Rosaceae	Rubcha	*Rubus chamaemorus*
Salicaceae	Salsp1	*Salix* spp.
Salicaceae	SalspA	*Salix* spp.
Salicaceae	SalspE	*Salix* spp.
Salicaceae	SalspG	*Salix* spp.

Salicaceae	SalspH	*Salix* spp.
Salicaceae	SalspI	*Salix* spp.
Cyperaceae	Scihud	*Scirpus hudsonianus*
Elaeagnaceae	Shecan	*Shepherdia canadensis*
Ericaceae	Vaculi	*Vaccinium uliginosum*
Ericaceae	Vacvit	*Vaccinium vitis-idaea*

Appendix Table 4 Stand-level consumption classification system used to assess canopy consumption by assessing cone and tree branches. Classification=the categorical number given after assessment of each tree. Adapted from Johnstone *et al.* 2008.

Classification	Cone	Tree
No consumption (0)	0% charred	Live with green needles remaining
Low (1)	0-33% charred	Few needles, most small twigs remaining
Moderate (2)	34-66% charred	Few small twigs, many branches
High (3)	67-100% charred or no cones remaining	Most branches and cones consumed

Appendix Table 5 Salix identification key describing eight morphospecies used in the field based on leaf phenotypic traits.

Morphospecies Name	Description of phenotypic traits
Salix A	leaves serrated leaves not hairy at maturity (tomentose) no white, powdery or waxy substance on leaf underside
*Salix B	leaves not serrated leaves hairy at maturity no white, powdery or waxy substance on leaf underside
Salix C	leaves not serrated leaves not hairy at maturity no white, powdery or waxy substance on leaf underside
SalixE	leaves not serrated leaves not hairy at maturity powdery or waxy substance on leaf underside
Salix F	leaves serrated leaves hairy at maturity no white, powdery or waxy substance on leaf underside
Salix G	leaves serrated leaves hairy at maturity powdery or waxy substance on leaf underside
Salix H	leaves not serrated leaves hairy at maturity powdery or waxy substance on leaf underside
Salix I	leaves serrated leaves not hairy at maturity powdery or waxy substance on leaf underside

* Salix D = B. These have been combined into Salix B in the data; all others have maintained their original name.

Appendix Table 6 The lowest AICc-selected candidate model describing variation in taxa richness on the Taiga Plains (Seedbed Model) (A) and Taiga Shield (Seedbed Model) (B). Bold variables indicate a significant relationship with the response variable (taxa richness per plot). Table shows: Intercept, Residual Organic=the depth of the soil organic layer remaining post-fire (cm), Charcoal=percent charcoal cover at each quadrat, Bryophyte=percent cover of *Marchantia* spp. and *Ceratadon* spp. at each quadrat, Mineral=percent cover of mineral soil exposed at each plot. See also **Table 2.1** and **Appendix Table 8** for a complete description of candidate models and variables used. Each variable was standardized; residual organic was log-transformed to meet a normal distribution.

A	Estimate	Std. Error	z-value	Pr(>|z|)
Intercept	2.28	0.113	20.105	2.00E-16
Residual Organic	**0.069**	**0.024**	**2.841**	**0.004**
Charcoal	-0.005	0.063	-0.083	0.933
Bryophyte	-0.018	0.043	-0.414	0.678
Mineral	-0.062	0.048	-1.270	0.204

B	Estimate	Std. Error	z-value	Pr(>|z|)
Intercept	1.960	0.042	45.86	2.00E-16
Residual Organic	**0.398**	**0.055**	**7.13**	**1.02E-12**
Charcoal	-0.031	0.060	-0.53	0.598
Bryophyte	**0.157**	**0.050**	**3.09**	**0.002**
Mineral	**-0.142**	**0.070**	**-2.04**	**0.041**

Appendix Table 7 Ranking of the GLMM candidate models used to predict variation in taxa richness post-fire (plot-level) on the Taiga Plains (A) and Taiga Shield (B), with the selected model (lowest AICc) in bold. Null model included the nested study areas as random effects: burn/site. For each model (row headings) we reported: number of effects in each model(K), Log-likelihood (Log(L)), Akaike Information Criterion (AICc), change in AICc compared to lowest AICc model (ΔAICc), Akaike model weight (weight) and variance explained by fixed factors (marginal R^2) and both fixed and random factors (conditional R^2). Each model assumes a Poisson error structure and used a logarithm link function.

A

Model	K	Log(L)	AIC_c	ΔAICc	weight	marginal R^2	conditional R^2
Seedbed	**7**	**-365.01**	**744.98**	**0.00**	**0.73**	**0.10**	**0.47**
Full	13	-358.93	747.13	2.16	0.25	0.19	0.51
Null	3	-373.70	753.60	8.62	0.01	0.00	0.37
Fire Characteristics	6	-370.74	754.19	9.21	0.01	0.09	0.40
Stand Characteristics	6	-371.65	756.01	11.04	0.00	0.02	0.43

B

Model	K	Log(L)	AIC_c	ΔAICc	Weight	marginal R^2	conditional R^2
Seedbed	**7**	**-194.74**	**404.96**	**0.00**	**0.62**	**0.57**	**0.57**
Full	13	-187.36	405.91	0.95	0.38	0.61	0.61
Stand Characteristics	6	-221.32	455.74	50.77	0.00	0.29	0.29
Null	3	-240.10	486.50	81.54	0.00	0.00	2.73
Fire Characteristics	6	-239.81	479.70	87.74	0.00	0.00	0.00

Appendix Table 8 Description of codes and environmental variables used in GLMM models and RLQ analyses. Code=names used in ordination graphs; Variable=the actual name of the variable used; Scale=type of data used; Description=detailed information on how the variable was obtained.

Code	Variable	Scale	Description
Basal Area	Total basal area	Continuous	Total measured basal area (cm^2) of all species measured at each plot expressed on a per m^2 basis. Basal area was calculated from stem diameter at breast height or base if less than 1.3m in height (area of each tree=π(DBH/2)^2.
Stand Pima Stand Piba Stand Other	Dominant stand type	Categorical	Based on dominant coniferous tree species at each plot, *P. mariana*, *P. banksiana,* Other= *L. laricina* (Taiga Plains)*; P. glauca* (Taiga Shield).
**Pima Proportion **Piba Proportion **Other Proportion	Proportion of dominant stand type	Continuous	Estimated proportion of dominant, pre-fire tree species based on density of stems per m^2 of $60m^2$ sample area. Estimate includes all trees and saplings that were alive at the time of the 2014 fires. Pima=*P. mariana*, piba=*P. banksiana,* other=*L. laricina* and *Picea* spp. on the Taiga Plains and *P. glauca* on the Taiga Shield.
Tree Consumption	Average above ground tree consumption	Continuous	Average per plot of ranked tree consumption variables: blank=snag pre-fire, 0=none, alive and no consumption; 1=low, only needles consumed, most small twigs remaining; 2=moderate, with few needles and small twigs remaining but many branches; 3=high, most of the aboveground canopy except the central trunk and branch stubs consumed, NA=for all the unburned plots (see **Appendix Table 4**).
Burn Date	Burn date	Continuous	Date of Burn (calendar day) measured from daily fire progression maps (Cumming 2017); pixel-based approach (roughly 500m x 1km).
*Xeric, *Subxeric *Mesic-subxeric *Mesic *Mesic-subhygric *Subhygric	Moisture class	Categorical	Ranking of plot moisture potential using the moisture class (Appendix Figure 1; Johnstone *et al.* 2008). Values range from dry (Xeric) to wet (Subhygric) and are also affiliated with soil texture and the presence of permafrost.
Residual Organic	Residual Organic Soil	Continuous	Mean of organic layer depth (cm) measured at 10 points along the transect.

	Depth		
Age	Stand Age	Continuous	Based on ~5 basal samples (cookies and cores) taken per dominant tree species per plot. This variable is the mean number of rings counted based on 2 measurements.
*Burn Depth	Burn Depth	Continuous	Depth of burn calculated by 1) adventitious root height and the associated offset for *P. mariana* sites OR 2) subtracted residual organic layer depth from the control plots average soil organic layer depth associated with each moisture class in control *P. banksiana* stands.
Mineral	Percent Mineral Soil Cover	Continuous	Percent cover of exposed mineral soil in each quadrat.
Charcoal	Percent Charcoal Cover	Continuous	Percent cover of burnt wood that remained as charcoal in each quadrat.
Bryophyte	Percent Bryophyte Cover	Continuous	Percent cover of *Marchantia* spp. (liverwort) and *Ceratadon* spp.(common post-fire moss) in each quadrat.

*Variables accompanied with an (*) were included in RLQ analyses, but not GLMMs because of correlations.

**The proportion of dominant tree species was used in the RLQ analysis instead of the categorical dominant stand type used in the GLMMs.

Appendix Table 9 Pearson's correlation matrices of continuous environmental variables considered for all analyses of Taiga Plains data (A) and Taiga Shield data (B). Bold numbers indicate the cut-off at which we assumed an important correlation (≥0.35). Burn Date=calendar day of burn; Age=stand age in years; Basal Area=total measured basal area (cm^2) of all species measured at each plot expressed on a per m^2 basis; Residual Organic=soil organic layer depth (cm) at each plot; Charcoal, Bryophyte, Mineral=mean percent covers exposed in each plot; Burn Depth=depth of burn (cm); Tree Consumption=average consumption of aboveground branches at each plot based on categorical values (see Appendix Table 4).

A	Burn Date	Age	Basal Area	Residual Organic	Charcoal	Bryophyte	Mineral	Burn Depth	Tree Consumption
Burn Date	1								
Age	-0.21	1							
Basal Area	-0.14	0.11	1						
Residual Organic	-0.33	-0.03	-0.07	1					
Charcoal	0.07	-0.07	0.04	-0.14	1				
Bryophyte	0.01	0.04	0.03	0.01	0.02	1			
Mineral	0.16	-0.05	-0.02	**-0.35**	0.26	-0.02	1		
Burn Depth	-0.34	**0.48**	-0.02	**0.40**	-0.10	0.14	-0.20	1	
Tree Consumption	-0.03	0.12	0.09	0.06	0.02	0.03	0.01	0.23	1

B	Burn Date	Age	Basal Area	Residual Organic	Charcoal	Bryophyte	Mineral	Burn Depth	Tree Consumption
Burn Date	1								
Age	-0.28	1							
Basal Area	-0.07	0.28	1						
Residual Organic	-0.14	0.21	-0.18	1					
Charcoal	0.23	-0.14	0.14	-0.16	1				
Bryophyte	0.23	-0.09	0.12	-0.09	0.00	1			
Mineral	0.16	-0.12	0.10	-0.26	0.10	0.13	1		
Burn Depth	-0.21	**0.46**	0.27	0.34	-0.08	0.06	-0.01	1	
Tree Consumption	-0.19	0.06	0.05	0.07	0.00	-0.10	-0.05	0.22	1

Appendix Table 10 Results of Fourth Corner analysis showing all possible bivariate association between the environmental variables (y axis) and life history traits (x axis) on (A) the Taiga Plains and (B) the Taiga Shield. Significant (P-value≤0.05). Positive associations are represented in black; negative associations are in light grey; white indicates no relationship. Environmental variables include: Residual Organic=depth of post-fire residual organic soil (cm); Charcoal, Bryophyte and Mineral=average percent cover of exposed charcoal, bryophyte (*Marchantia* spp. and *Ceratadon* spp.) and mineral soil in each quadrat; Burn Date=calendar day of burn; Age=average age of each stand/plot; Pima, Piba and Other Proportion=proportion of dominant stand type based on stem density per m^2 of 60 m^2 sample area; Basal Area=total measured basal area (cm^2) of all species measured at each plot expressed on a per m^2 basis; Burn Depth=depth of burn (cm), moisture classes (Xeric, Subxeric, Mesic-subxeric, Mesic-subhygric, Subhygric)=ranking of plot moisture category based on moisture, soil type and permafrost presence (see Appendix Figure 1); Tree Consumption =average consumption of aboveground branches at each plot based on categorical values (see Appendix Table 4).Traits include: Proportion Seeders=the proportion of individuals of each species found reproducing from seed at each plot, Wind Dispersed=plants with seeds that are primarily dispersed by wind (default=animal); Evergreen=leaf persistence of each plant based on leaf type (default=deciduous); growth form (Graminoid, Seedless Vascular, Shrub, Tree)= grouped plants by growth form representing similarities in structure/function (default= Forbs); lifespan (Annual, Biennial)=life span of each species (default=perennial).See **Appendix Table 7** for a complete description of environmental variables and **Appendix Table 8** for a complete description of life history traits.

A	Proportion Seeders	Wind Dispersed	Evergreen	Graminoid	Seedless Vascular	Shrub	Tree	Annual	Biennial
Residual Organic									
Charcoal									
Bryophyte									
Mineral									
Burn Date									
Age									
Pima Proportion									
Piba Proportion									
Other Proportion									
Basal Area									
Burn Depth									
Xeric									
Mesic-subhygric									
Mesic-subxeric									
Subhygric									
Subxeric									
Tree Consumption									

B	Proportion Seeders	Wind Dispersed	Evergreen	Graminoid	Seedless Vascular	Shrub	Tree	Annual	Biennial
Residual Organic	▒				■	■	▒	▒	▒
Charcoal	■				▒	▒	■	■	■
Bryophyte	■	■	▒	■	▒	▒	■	■	■
Mineral	■				▒	▒	■	■	■
Burn Date	■				▒	▒	■	■	■
Age									
Pima Proportion	▒				■	■	▒	▒	▒
Piba Proportion	■				▒	▒	■	■	■
Other Proportion	■				▒	▒	■	■	■
Basal Area	■				▒	▒	■	■	■
Burn Depth		■	▒	■		▒			
Xeric	■				▒	▒	■	■	■
Mesic-Subhygric									
Mesic-Subxeric									
Subhygric	▒				■	■	▒	▒	▒
Subxeric									
Tree Consumption									

Appendix Table 11 Description of life history traits of vascular plants used in RLQ and Fourth Corner Analyses. Trait Code=the terminology found on associated ordination graphs; Trait=the functional trait being measured; Scale=whether the trait was continuous or categorical; Description=a description of how the trait information was calculated; Rationale=reasoning for including trait in analyses; Source=where and when the trait data was collected.

Trait Code	Trait	Scale	Description	Rationale	Source
Proportion Seeders	Proportion of individuals of each species regenerating from seed	Continuous	Total number of observations of each species regenerating from seed	Ability to establish post-fire, especially on severely burned sites.	Field data collected in 2015
Shrub, Graminoid, Seedless Vascular, Tree, Forb	Growth Form	Categorical; forbs as baseline state for modelling	Plants categorized by similar morphology and general habit of growth	Ability to persist (survive) fire based on regeneration strategy and/or phenology.	Literature (Johnson 1995, USDA)
Wind, Animal	Seed Dispersal Mode	Categorical; animal as baseline state	Primary mode of seed dispersal for each species (wind, animal)	Ability to establish; wind-dispersed seeds more likely to quickly disperse and be abundant (Grime 1977).	Field observation and fruit type
Annual, Biennial, Perennial	Duration	Categorical; perennial as baseline state	Life span of each species (annual, biennial or perennial)	Time to maturity and ability to establish. Annuals and biennials grow quickly, disperse seeds rapidly and spread quickly (Grime 1977).	Literature (Johnson 1995, FEIS 2017)
Deciduous Evergreen	Leaf Persistence	Categorical; evergreen as baseline state	Based on leaf type (deciduous or evergreen)	Time to maturity and ability to establish. Deciduous leaves have a short period of leaf production with high potential productivity. Deciduous species often have lightweight, wind-dispersed seeds (Grime 1977; Lavorel and Garnier 2002).	Literature (Johnson 1995, FEIS 2017)

Appendix Table 12 Summary of general stand characteristics in each ecozone. Table shows mean± standard deviation and standard error of variables on the Taiga Plains (n=125 plots) and Taiga Shield (n=84 plots). Burn Date=calendar day of burn; Age=stand age; Basal Area=total measured basal area of all species measured at each plot expressed on a per m^2 basis; Residual Organic=soil organic layer depth at each plot; Burn Depth=depth of burn; Tree Consumption=average consumption of aboveground branches at each plot based on categorical values (see **Appendix Table 4**).

	Taiga Plains		**Taiga Shield**	
Variable	Mean± Standard Deviation	Standard Error	Mean± Standard Deviation	Standard Error
Burn Date (day)	202.26 ± 10.98	0.98	196.72 ± 8.87	0.96
Age (years)	104.12 ± 43.04	3.84	101.52 ± 51.11	5.57
Basal Area (cm^2/ m^2)	17.09 ± 9.50	0.85	8.77 ± 5.90	0.64
Residual Organic (cm)	14.06 ± 15.03	1.34	13.41 ± 14.56	1.58
Burn Depth (cm)	9.59 ± 3.58	0.32	10.67 ± 3.23	0.34
Tree Consumption (averaged categorical scale; 0-3)	2.08 ± 0.76	0.06	1.49 ± 0.56	0.06

Appendix Table 13 Frequency table showing the proportion of total taxa found regenerating from seed only, rhizome only or taxa that exhibited both regernation strategies.

	Seed	Rhizome	Both	Total taxa
Taiga Plains	9	60	36	105
Taiga Shield	7	24	12	43

Appendix Table 14 Pearson's correlation matrix of percent cover variables combined across ecozones. Bold numbers indicate the cut-off at which we assumed an important correlation (≥0.35). Lichen=live and scorched crustose lichens; litter=loose organic material; organic=organic matter; sphagnum=live and scorched *Sphagnum* spp. moss; wood=downed woody debris thicker than a pencil; moss=live and scorched feathermoss; bryophyte=*Ceratadon* spp. and *Marchantia* spp.; rocks=rocks and/or gravel; mineral=exposed mineral soil; charcoal=burnt wood that remained as charcoal (black); water=standing water; ash=deposits of ash.

	lichen	**litter**	**organic**	**sphagnum**	**wood**	**moss**	**brypophyte**	**rocks**	**mineral**	**charcoal**	**water**	**ash**
lichen	1											
litter	-0.15	1										
organic	0.04	0.12	1									
sphagnum	0.06	-0.09	0.06	1								
wood	-0.07	-0.01	-0.13	-0.06	1							
moss	0.04	-0.08	0.08	0.00	0.03	1						
brypophyte	-0.04	-0.13	0.01	-0.03	0.13	-0.04	1					
rocks	0.03	-0.13	**-0.65**	-0.04	-0.01	-0.05	-0.04	1				
mineral	-0.07	-0.02	**-0.61**	-0.04	0.13	-0.06	0.02	0.04	1			
charcoal	-0.12	0.10	-0.09	-0.08	0.10	-0.11	0.03	0.02	0.21	1		
water	-0.01	-0.01	-0.04	0.00	0.00	-0.01	0.00	-0.02	0.02	-0.03	1	
ash	-0.04	-0.04	-0.14	-0.02	0.17	-0.03	0.10	-0.05	0.12	0.06	-0.01	1