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Effects of wildfires on tree establishment in conifer-
dominated boreal forests in southern Northwest Territories

by

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(BSc. Biology, University of Ottawa, 2015)

THESIS

Submitted to the Department of Biology
Faculty of Science
In partial fulfilment of the requirement for the
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Abstract

Black spruce (*Picea mariana*) and jack pine (*Pinus banksiana*) both release a large majority of their seeds after fire and thus experience large pulses of recruitment during these punctuated events. Global warming is driving intensification of the wildfire regime in the boreal forest, which is resulting in shifts from coniferous to deciduous dominated forests in some parts of the boreal forest of North America. This shift can present consequences for forest structure, ecosystem dynamics, carbon cycling, and wildlife habitat.

During 2014, the Northwest Territories experienced a historically unprecedented fire year with 3.4 million hectares of forest burning. For two summers post-fire, I measured 1) black spruce seed rain at 25 black spruce dominated locations, and 2) seedling establishment at 224 conifer-dominated locations across the Northwest Territories. Using generalized linear mixed models with candidate model-based hypotheses, I sought to estimate 1) whether fire characteristics or ecological legacies better predict total and viable black spruce seed rain; 2a) the drivers of species-specific seedling establishment post-fire, and 2b) whether there is evidence of a change in species dominance following this extreme fire season.

Models with variables linked to fire characteristics provided the best fit to observed variations in both total and viable seed rain. Canopy consumption by fire was a significant predictor of viable seed rain; stands that experienced a less severe burn had more viable seeds. After two years of data collection on the Taiga Plains, both pre-fire black spruce-dominated and pre-fire mixed stands showed a significant decrease in black spruce relative abundance and an increase in the proportion of jack pine. On the Taiga

Shield (where there was only one year of data collected), deciduous seedlings were more abundant.

This research has demonstrated key findings about post-fire successional dynamics and patterns of dominance in the Northwest Territories. Increased canopy combustion is likely to result in decreased availability of viable black spruce seed rain, with implications for regeneration processes such as reduced recruitment rates. Differences in post-fire establishment patterns were seen across the Taiga Plains and Taiga Shield, suggesting that the two areas are responding differently to altered disturbances as a result of climate change. These results can be used in ongoing modeling efforts to determine how future changes to this landscape will modify forest composition, wildlife habitat, and forest processes.

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Thank you to all the PIs and post-docs who have contributed to the larger NWT fire research program that I have been a part of - I have learnt a lot from you all and have really enjoyed my time working with everybody: Nicola Day, Jill Johnstone, Steve Cumming, Michelle Mack, Merritt Turetsky, Xanthe Walker, and Jennifer Baltzer.

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Table S18. Correlation matrix for all continuous predictor variables on the Taiga Shield (n=114). Bolded values indicate correlations that were >0.3 . Residual organic soil depth has been log-transformed. Depth of Burn and Fire Weather Index (FWI) were eliminated from further analyses since they were highly correlated with other variables.

Table S19. Correlation matrix for all continuous predictor variables on the Taiga Plains (n=110). Bolded values indicate correlations that were >0.3 . Residual organic soil depth has been log-transformed. Depth of Burn and Fire Weather Index (FWI) were eliminated from further analyses since they were highly correlated with other variables. Both Date of Burn (DOB) and residual organic soil depth were left in further analyses since visual inspection of this correlation showed it to be weak.

Chapter 1: General Introduction

1.1 The role of boreal forests on the global scale

Globally, the boreal forest accounts for 30% of forests, covers more than 12×10^6 km² of land, and spans more than 10 degrees of latitude in some areas (Baumgartner 1979, Payette 1992, Brandt et al. 2013). It is the northernmost forested biome and includes a range of vegetation communities, geologic histories, soil types, and climates (Brandt et al. 2013). Boreal forests are located in high latitude environments (Burton et al. 2010), and grow under the constraints of short growing seasons and severe winters (Burton et al. 2010, Kneeshaw et al. 2011). Services provided include carbon sequestration, water purification, wildlife habitat for many species, and provision of raw materials and human food (Brandt 2009). Due to its many renewable resources, it is a large contributor to the economy of many countries including Canada, Russia, Norway, and Finland (Brandt 2009). The boreal forest is the largest store of terrestrial carbon on earth, a majority of which is stored in the soils of the forest floor (Kasischke et al. 1995). Further, it sequesters approximately 20% of the carbon sink generated by forests worldwide (Pan et al. 2011). The boreal zone regulates global climate through exchanges of energy and water (Steffen et al. 2015), and can influence global albedo as a result of its large, dark surfaces which absorb much of the incident radiation (Juday 2005).

1.2 Boreal forests and climate change

In recent decades, the planet has become progressively warmer; between 1951 and 2012, the global average surface temperature increased by 0.12°C per decade (IPCC, 2013). Global warming causes reductions in high-albedo surfaces such as snow and ice, largely through reduced snow or ice-covered periods. This results in longer periods during the year during which dark, low-albedo surfaces that represent the snow or ice-free periods are abundant, resulting in

increased absorption of energy. As a consequence of this and other factors, high latitude environments are experiencing amplified global warming (Johannessen et al. 2016). By the end of the century, mean annual air temperatures are expected to increase globally by 3.3–5.4°C; in the Taiga Plains and Boreal Shield West ecozones, temperatures are predicted to increase by as much as 7°C (IPCC 2007, Price et al. 2013). Global warming has a range of impacts on forest ecosystems including extreme weather patterns (Allen et al. 2010), insects and diseases (Dukes et al. 2009, Sturrock et al. 2011), and, importantly, the intensification of wildfire.

With a changing climate, we expect to see the number of spread days (i.e. days of extreme weather that account for a substantial proportion of the area burned) to increase by at least 50%. Additionally, we expect fire seasons with large numbers of spread days to occur more frequently (Wang et al. 2017). Throughout the 21st century, the boreal forest is predicted to experience an increased frequency of both large and crown fires (Wotton et al. 2017), as well as increased area of burning (Abatzoglou and Williams 2016). The National Forestry Database has records for area burned by forest fires in Canada since 1970. Nationwide, 7 out of the 10 largest fire years (in terms of area of forest burned), occurred between 1990 and 2015 (Canadian Forest Service, 2017) with 2017 poised to be a record-breaking year in terms of area burned.

1.3 Boreal forest successional dynamics

Forest harvesting and the development of associated silvicultural methods (Daniel et al. 1979; Matthews 1989) have contributed to a deep understanding of patterns of succession and regeneration in boreal forests (reviewed in Youngblood and Titus 1996). With regard to succession and fire, previous work has been carried out throughout the boreal forest, including in the Northwest Territories (see Johnson 1981; Johnson and Rowe 1975; Day et al. 2017; deGroot et al. 2004; Thomas and Kiliaan 1998), and successional literature has provided the framework

for studies of forest resilience to disturbance. In the boreal forest, wildfire is the primary disturbance agent, and it plays a dominant role in forest dynamics, structure, and function (Flannigan et al. 2005; Beck et al. 2011). The mean fire return interval in the western Canadian boreal forest is 180 years (De Groot et al. 2013). This cycle is short enough that many of the original tree colonizers of a forest stand are often present when the stand reburns (Johnstone and Chapin 2006a). Given the importance and regularity of fire in the boreal forest, it is imperative that tree species are adapted to disperse their seed after fire. Jack pine (*Pinus banksiana*) and black spruce (*Picea mariana*) are two of the most dominant and widespread conifers in the North American boreal forest and both rely heavily on fire for seed dispersal. The cones are stored in aerial seed banks in the canopy or on branches. Heat from the fire removes the waxy coating on these cones, resulting in release of the seeds that are stored within, and a rapid increase in seedling establishment in the subsequent years (Lamont et al. 1991). After fire, birch and aspen can colonize an area via long distance wind dispersal of seeds from unburned neighbouring stands or vegetative regeneration in which they resprout from roots and stumps (Zasada et al. 1992).

After a low severity burn, much of the organic layer is still intact. As this layer is relatively porous (Keeley 2009), surficial soil layers (where seedlings root) dry quickly and seedling establishment is limited (Johnstone and Chapin 2006b). Coniferous seedlings are best able to establish on organic layers that are thinner than the hypocotyl length of the seedling; optimal seedbed thickness is anything less than 3cm (Hesketh et al. 2009). Birch and aspen produce much smaller seeds than do larger seeded conifers and therefore establishment on thick organic substrates is much less successful (Johnstone and Chapin 2006b). Instead, deciduous species must be present at the site pre-fire and rely on asexual regeneration from belowground

(Viereck 1973). As a result of these regeneration strategies, patterns of self-replacement have dominated in the boreal forests in western North America (Bourgeau-Chavez et al. 2000).

Given the changes in disturbances that we expect to see as a result of climate change, it is important to know how ecosystems will recover. The resilience of an ecological system is a “measure of the persistence of systems and of their ability to absorb change and disturbance and still maintain the same relationships between populations or state variables” (Holling 1973). The associated feedbacks of a system either result in recovery to the original state or reorganization into a new state, depending on the system’s resilience (Holling 1973, Gunderson and Holling 2002). Systems that have multiple stable states can be ‘tipped’ from one state to another after the first state loses its resilience (Scheffer et al. 2001). To shift into an alternative stable state, there must first be a disturbance which is large enough to kill a substantial proportion of the dominant species. Following this, there is a stage of recruitment of an alternative species which begins the formation of the alternative stable state (Petraitis and Latham 1999). Large and severe fires, such as those expected under continued climate warming have the potential to drive such state changes.

If the resilience threshold of the system is exceeded, abrupt changes in community composition can occur (Scheffer et al. 2001). Fire regimes that differ from the usual cycle can weaken the maintenance function that forest fires play in the boreal forest by changing what types of forests grow back after fires. (Johnstone et al. 2010a). Severe fires burn more deeply into the organic layer which can result in the exposure of the underlying mineral soil. There is then increased seedling recruitment of both coniferous and deciduous seedlings due to the greater ability of mineral soil to retain water and greater access to nutrients in mineral soil substrates, providing superior establishment conditions for all species (Bonan 1992, Johnstone and Chapin

2006b). Severe fire years have recently occurred in Alaska (summarized in Kasischke et al. 2010). This results in changes in community structure, as large portions of the organic layer have been consumed, exposing mineral soil seedbeds on which deciduous species become dominant (Johnstone and Chapin 2006a, Johnstone et al. 2010b). Burning of organic soil results in nutrient mineralization and post-fire soils experience increased levels of microbial activity and nutrient release (Bourgeau-Chavez et al. 2000). Fire can impact soil moisture in several ways. First, any deposition of ash at the surface will produce a hydrophobic environment that is not good for seedling establishment or water retention (Verma and Jayakumar, 2012). Second, thick residual organic layers are often porous and also have low water retention (Certini 2005). Consequently, there is an optimum depth of residual organic layer on which coniferous seedlings are best able to establish on (Hesketh et al. 2009).

Since regeneration of fire adapted conifers relies on local seed rain for the germination of seedlings, it is necessary for the seeds to be viable when they are dispersed. It takes approximately 50 years for the seedbank in black spruce trees to fully develop (Viglas et al. 2013). Thus, when stands are burned in intervals of less than 50 years, the density of black spruce seedlings post-fire will be low, regardless of the composition of the seedbed simply because the seeds in the cone bank are not mature enough to germinate. In these cases, following fire, the aerial seedbanks have low availability of viable seeds and as a result, recruitment rates are reduced (Johnstone and Chapin 2006a, Viglas et al. 2013). Intense and severe fires in black spruce systems have been shown to be able to heat the seeds in the aerial seedbank enough to either kill them and result in decreased germination or consume the seedbank entirely and remove the regeneration potential of that species (Zasada et al. 1979, Arseneault 2001, Johnstone et al. 2009).

Recent studies in Alaska and the Yukon have examined the impact of severe fires on regeneration processes in the boreal forest and have characterized an increase in the dominance of deciduous species (Johnstone and Chapin 2006a, Johnstone et al. 2010a). Jack pine is not present in these forests as its range only includes areas that were glaciated during the Pleistocene epoch. In northwestern North America, this range includes in the NWT, but not Alaska or the Yukon (Flint 1957, Critchfield 1985). After the Pleistocene, jack pine migrated northwest from the Lake States and towards the Mackenzie Valley, while lodgepole pine (*P. contorta*) moved eastward from its refugia. The two species overlap in their distribution in south-central Alberta, east of the Rocky Mountains (Critchfield 1985; Strong and Hills 2005). The presence of jack pine in the boreal forest of the NWT results in a unique species pool in northwestern North America which due to its life history, can impact successional outcomes following fire.

Differences in the resource use and life histories underlie forest successional processes, with faster growing species typically acting as early colonizers and being replaced by slower growing species that have more conservative resource use strategies. This is not the case in boreal systems where self-replacement dominates but may be increasingly important as climate warming induced changes in the fire regime alter the post-fire establishment conditions. For example, growth rate differentials between black spruce and aspen are such that aspen is much faster growing and therefore when it establishes in high densities, it is able to completely dominate stands (Yarie and Billings 2002). Similarly, black spruce is much slower growing than jack pine (Ilisson and Chen 2009, Héon et al. 2014, Bartels et al. 2016). Indeed, it is often characterized by its slow growth (Viereck and Little 1972) and tolerance of resource-poor conditions (Viereck 1983; Fryer et al. 2014). Jack pine grows faster, and tends to be prominent upslope and on ridgetops, areas that typically have higher resource availability (Rudolf and

Laidly 1990). Changing patterns of disturbance in Alaska have seen an increase in dominance of ‘faster’ growing species (i.e., aspen) relative to the previously dominant ‘slower’ growing species (i.e., black spruce). In these systems, the germination potential of aspen is limited to sites which have thin residual organic layer (Johnstone and Chapin 2006b). Establishment of jack pine is not limited by the residual organic layer thickness to the same degree as aspen is. In fact, as a result of its larger seed and longer hypocotyl, it can establish on thicker substrates than can black spruce (Hesketh et al. 2009). In addition to its greater growth potential, jack pine has some key reproductive advantages that may make it better suited to extreme fire conditions. Maturation of the aerial seedbank in jack pine occurs earlier than that of black spruce (Crayford and McRae 1983; Viglas et al. 2013), suggesting that they may be better adapted to a shorter fire return interval. Further, jack pine cones have thicker scales than black spruce cones, making them more resistant to high heat (Beaufait 1960, Zasada et al. 1979, Arseneault 2001, Arseneault and Sirois 2004). These aspects of jack pine’s life history may thus serve to perpetuate its ecological legacy as disturbance patterns in the boreal forest change (see Lavoie and Sirois 1998, Pellerin and Lavoie 2003, Le Goff and Sirois 2004, Boiffin and Munson 2013). In short, such biogeographical differences can alter expectations surrounding the response of otherwise similar systems to severe disturbance.

1.4 Rationale behind this research

The fire season of 2014 was the largest and most intense on record for the Northwest Territories (NWT) with 3.4 million hectares of forest burning and fires occurring later in the season than usual, implying more severe fires (Environment and Natural Resources 2014). This was also the largest area burned in any one province or territory in one year. Other large fire years occurred in the NWT in 1994 and 1995 (3.01 million hectares and 2.83 million hectares,

respectively), Quebec in 2013 (1.87 million hectares), Yukon in 2013 (1.79 million hectares), and Saskatchewan in 2015 (1.78 million hectares) (Canadian Forest Service 2015).

It is currently unknown how the boreal forest of the NWT will respond to climate change induced alterations in disturbance. The large fire year in 2014 provides an opportunity to assess the resilience of the NWT boreal forest to these changes and to evaluate post-fire patterns of dominance. The study presented here is unique in several ways. First, the NWT has been relatively understudied. Thus far, a majority of research documenting changes in patterns of dominance as a result of altered patterns of disturbance have occurred in Alaska (see Johnstone and Chapin 2006a, Johnstone et al. 2010a), and Quebec (see Boiffin and Munson 2013). Second, the boreal forest of the NWT is a high latitude boreal forest which results in unique soil properties, such as the presence of permafrost. If regeneration failure occurs at high latitudes, the potential exists for a shift towards a tundra or grassland dominated system (Brown and Johnstone 2012). Third, this study was undertaken at a large spatial scale. Our sites cover 400km of latitude, are established in seven distinct burn complexes, and are located across two different ecozones (the Taiga Plains and the Taiga Shield). Finally, as described above, jack pine is a dominant species in the NWT, unlike Alaska or the Yukon, resulting in a unique species composition in northwestern North America (Flint 1957, Critchfield 1985) with implications for post-fire successional processes (see Lavoie and Sirois 1998, Pellerin and Lavoie 2003, Le Goff and Sirois 2004, Boiffin and Munson 2013).

1.5 Study Species

1.5.1 Black spruce

Black spruce is a small to medium sized tree; mature individuals range from 9-15m tall (Fryer 2014). It is found in areas with long, cold winters and short, warm summers and is

abundant on nutrient poor and poorly drained soils (Viereck 1983). In high latitude forests, black spruce is most commonly found on soils that are underlain by permafrost (Fryer 2014). Black spruce is slow-growing (Viereck and Little 1972) and shade-tolerant, but grows fastest in full sun (Vincent 1965). It has a conservative life history, which allows it to tolerate low resource conditions (Viereck 1970, Van Cleve and Viereck 1981). Trees can live up to 250-300 years in the absence of disturbance (Bergeron and Dubuc 1989). Seed production begins after ten years and maximum seed production occurs at 50-150 years (Viereck 1983). In Alaska, Viglas et al. (2013) found that after 30 years, black spruce had a 50% chance of having cones; at 100 years, they had a 90% chance. Further, cone and seed production rates increased with age up to 150 years. Seeds in new cones are approximately 88% viable (Safford 1974) while seeds that have been stored in cones for 15 years have close to zero viability (Greene et al. 2004). Once seeds have been released, viability quickly decreases. In the Northwest Territories, up to six years post fire, viability ranged between 0-19%; 20 years post-fire, it dropped to $\leq 1\%$ (Wein 1975). Seeds are released from semiserotinous cones in response to fire (Beaufait 1960, Zasada et al. 1992b, Arseneault 2001), or gradually over time, in the absence of fire (Viereck 1983). Dispersal can happen at any time of year but is maximal in winter and spring (Horton and Lees 1961, Viereck and Johnson 1990). Seeds are winged and lightweight, and disperse within 80m of the parent tree (Greene et al. 2004).

1.5.2 Jack pine

Jack pine is a dominant, shade-intolerant, small to medium sized conifer (Rudolph and Laidly 1990). It is found on level to gently rolling sand dunes, rock outcrops and lake shores as well as in soil over peat, bedrock and permafrost, and is one of the fastest growing conifers in its native range during its first 20 years (Rudolph and Laidly 1990). A large majority of jack pine

have serotinous cones but a few individual trees are non-serotinous or have a combination of cone types (Critchfield 1985). Serotinous cones only open under high temperatures, usually as a result of fire, but high air temperatures ($>27^{\circ}\text{C}$) can also melt the resin bonds and open cones (Rudolph and Laidly 1990). Jack pine seeds are winged and can be dispersed 30-40m, or twice the height of the parent tree. They are the smallest seeds of all North American pines (Eyre and LeBarron 1944). Seed viability in closed cones decreases with time. Prior to six years old, seeds showed 78-89% viability; this dropped to 62% in cones older than six years (Eyre and LeBarron 1944). Experimental burns in the Northwest Territories produced viable seed rain estimates of 26.4 – 431.3 seeds/m²; these estimates accounted for 94% of the variation in seedling establishment in the same plots (de Groot et al. 2004). Seedlings establish best on exposed mineral soil or thin organic layers ($<0.5\text{cm}$) (Chrosiewicz 1974), and develop a tap root that is maintained through to maturity (Rudolph and Laidly 1990). Seed development in cones begins at age ten (Crayford and McRae 1983). Jack pine canopies begin to senesce at ~75 years (Crayford and McRae 1983) and after 200 years, jack pine tend to completely die off (Bergeron and Dubuc 1989). They are replaced by longer lived or more shade-tolerant species such as black spruce. Black spruce is slower growing and longer lived than jack pine; if both species seed into a site at the same time, it is likely that black spruce will become codominant after 90 years and eventually succeed jack pine (Johnson 1992). However, shade tolerance alone is not enough to ensure replacement, particularly in the western Canadian boreal forest where fire return intervals are such that sites are likely to burn before the shade tolerant species are able to become the (co)-dominant species (Johnson et al. 1994).

1.5.3 Trembling aspen

The distribution of trembling aspen stretches from Newfoundland to Alaska to Mexico, making it the most widely distributed tree in North America (Little 1971). Mature individuals range in height from 16m (British Columbia; Chen et al.1998), to 28m (Quebec; Bose et al. 2014). After 10-20 years, aspen can begin producing large seed crops with maximum production occurring at 50 years (Howard 1996). It is found on most soil types but does best on moist, well-drained or sandy soils (Hosie 1979). Seed dispersal (via wind) occurs in early summer within a few days of ripening (Fowells 1965, Howard 1996), lasts two to three weeks (Perala 1990), and distributes seeds up to several kilometres from the parent tree (Howard 1996). Up to 88% of fresh seed is viable (Morgan 1969) and under favourable conditions, will remain viable on the forest floor for two to four weeks (Perala 1990). Since there are very specific conditions for optimum germination to occur (moist, mineral seedbeds, adequate drainage and temperature, and little competition (McDonough 1979)), asexual re-sprouting from roots is the most common method of regeneration (Schier 1973; Frey et al. 2003). Although not required for regeneration, aspen has adapted to resprout vigorously immediately following fire. Sprouts are very fast growing and can outcompete other species that are establishing. Consequently, within a decade post-fire, even aged aspen stands are common (DeByle 1985) potentially as result of their higher stem density than either black spruce or jack pine (Greene and Johnson 1999).

1.5.4 Alaska paper birch

Alaska paper birch (*Betula neolaskana*) is a medium-sized (20-24m), single or multi stemmed tree that ranges from Newfoundland to Alaska and tends to form almost pure stands on recently disturbed sites (Haeussler and Coates 1986, Uchytel 1991). It is found in bogs and other areas with poorly drained soils (Hosie 1979). Birch is a shade intolerant, pioneer species and as

such is rarely found in late successional forests. It is favoured in the 50-125 year fire cycle that occurs across the Canadian boreal forest (Safford 1983, Uchytíl 1991). Birch is short-lived, with a maximum age of approximately 140 years, reaching maximum height after 60-70 years (Haeussler and Coates 1986). Seed production begins after 15 years and peak production occurs at 40-70 years, with heavy seed crops produced every other year (Safford et al. 1990, Uchytíl 1991, Gustine et al. 2014). Seeds are small, double-winged, and most fall within 30-60m of the parent tree (Safford 1983). 90-95% of seed is shed from September to November and seeds dispersed later in this period have the highest germination rates (Perala and Alm 1990). Best germination occurs on mineral soil seedbeds, under shaded conditions (Safford 1983).

1.6 Objectives and Hypotheses

My overarching research goal was to determine if extreme fire conditions result in changes in patterns of dominance and forest composition in the boreal forest of the NWT. To achieve this, I had three specific objectives:

1) My first objective was to estimate the drivers of black spruce seed availability and viability post-fire. Two potential mechanisms drive post-fire seed rain: fire characteristics and ecological legacies. I predict that ecological legacies (the species traits and propagules that persist after a disturbance and allow an ecosystem to recover to a similar state as it was pre-disturbance (Franklin et al. 2000, Johnstone et al. 2016)), will be a greater controlling factor for total seed rain as this provides an estimation of seed availability. Successful propagation of ecological legacies is required to ensure forest regeneration. Therefore, I predict that in stands where higher quantities of ecological legacies persist (i.e., close to unburned edge, high proportion of black spruce basal area, and shallow residual organic layer), there will be higher levels of total black

spruce seed rain. I predict that fire characteristics will be the primary controls on seed viability and that stands that experience less severe burns will have high levels of viable seed rain.

2) My second objective was to a) estimate the drivers of species-specific seedling establishment post-fire, and b) assess whether they differed between ecozones. Three potential mechanisms drive post-fire seedling establishment: seed rain processes, fire characteristics, and seed bed conditions. Both seed rain processes and seedbed conditions are dictated by fire severity. Greater canopy consumption would be expected to result in decreased levels of coniferous seedling establishment (see objective 1), and greater surface consumption would be expected to result in improved seedbed conditions for establishment of all species. For the fire characteristics mechanism, it is predicted that stands burning at later age, later dates of burn and having lower canopy consumption will result in increased seedling establishment. For the seed rain mechanism, stands with higher levels of seed rain (i.e., older stands, lower levels of consumption, and basal area) are predicted to have increased levels of seedling establishment. Stands with shallow residual organic layer, and high ground covers of mineral soil, bryophytes, and charcoal are predicted to have increased seedling establishment.

3) My third objective was to determine if changes in proportional dominance of tree species occurred in the forests of the NWT as has been observed elsewhere. Successional shifts are hypothesized to occur as a result of high depth of burn, severe canopy consumption, shortened fire return interval or a combination of these mechanisms. If there is severe canopy consumption, I predict a shift towards deciduous dominance as these seeds are introduced from outside sources. If there is deep burning or a short fire return interval, I predict a shift away from black spruce dominance and towards either jack pine or deciduous dominance. In the case of deep burning, both deciduous species and jack pine can establish in high densities on exposed mineral

soil. When there is a short fire return interval, deciduous species will be introduced from outside sources and as a result of their earlier reproductive maturation, jack pine are likely to have viable seeds.

1.7 Thesis Overview

The first chapter of this thesis is a general introduction to the fire cycle of the boreal forest and how this is affected by climate change. I will discuss the drivers of succession in the boreal forest and what can happen when altered succession occurs.

The second chapter has been formatted in preparation for submission as a manuscript to the Canadian Journal of Forest Research. My role in the research project included field work, data collection, analysis of the data, and development and revision of the manuscript. This manuscript outlines the drivers of seed rain in the boreal forest after fire. A large fire year in 2014 provided an exceptional opportunity to understand the implications of changing patterns of disturbance for forest recruitment processes in the NWT. Fire characteristics models were the best predictors of both total and viable seed rain and stands that experienced a less severe burn had more viable seeds. Our findings suggest that increasing severity of fire is likely to result in decreased availability of viable black spruce seed in the Northwest Territories' boreal forest with implications for regeneration processes such as reduced recruitment.

In the third chapter, my role included field work, data collection, analysis of the data, and development and revision of the manuscript. This study assesses landscape level resilience of the boreal forest of the NWT. To date, a majority of post-fire successional studies and information about the resilience of the boreal forest have come from Alaska and Quebec, making this one of the first studies to assess the resilience of the NWT, where jack pine plays an important ecological role. Our results show patterns of changing dominance, with shifts occurring from

mixed and black spruce dominated stands to jack pine dominated stands. The presence of jack pine in the NWT appears to be driving different patterns of stand dominance than have been seen in Alaska, implying differences between regions across the boreal forests.

The fourth chapter of this thesis is a general discussion, focussing on how this work contributes to the field of fire ecology, future areas of research, and how the work is integrative.

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Chapter 2: Burn severity predicts black spruce seed availability post-fire in sub-arctic boreal forests

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Abstract: Black spruce (*Picea mariana*) releases a majority of its seeds following fire when its semi-serotinous cones have opened in response to the heat of the fire. Frequency and severity of wildfire are determinants of the number of total and viable seeds available for germination post-fire. During 2014, the Northwest Territories experienced an unprecedented fire year with a total of 3.4 million hectares of forest burning. We measured seed rain for two summers post-fire (2015 and 2016) in 25 black spruce dominated sites that burned in 2014 to assess drivers of black spruce seed rain. Generalized linear mixed models using candidate model based hypotheses were used to test whether fire characteristics or stand structural attributes better predicted total and viable black spruce seed rain. Fire characteristic models were the best predictors of both total and viable seed rain. Canopy consumption was a significant predictor of viable seed rain; stands that experienced a less severe burn had more viable seeds. Our findings suggest that increasing severity of fire is likely to result in decreased availability of viable black spruce seed in the Northwest Territories boreal forest with implications for regeneration processes.

Keywords: Wildfire; Climate Change; Seed Rain; Forest Regeneration; Northwestern Canada

2.1 Introduction

The primary disturbance agent in the boreal forest is wildfire which serves to perpetuate ecology legacies (Paine et al. 1998) and plays a crucial role in forest regeneration. With a changing climate and amplified global warming at high latitudes (Johannessen et al. 2016), we expect a greater number of extreme fire weather days, and fire weather years (Wang et al. 2017). Additionally, area burned and frequency of crown fires are also predicted to increase (Balshi et al. 2009; Wotton et al. 2017). The National Forestry database which maintains records of Canadian wildfires since 1970, indicates that 7 out of 10 largest fire years have occurred between 1990 and 2015 (Canadian Forest Service, 2017). Black spruce (*Picea mariana*) is one of the most widespread conifers in North America's boreal forest and is adapted to release seeds from its serotinous cones in response to fire (Beaufait 1960, Zasada et al. 1992, Arseneault 2001). In the absence of fire, black spruce cones will gradually release their seeds over time (Viereck 1983). Post-fire seed dispersal from black spruce is brief, with a large majority of seed rain occurring in the first two growing seasons post-fire (Charron and Greene 2002) resulting in a large recruitment pulse on the post-fire seed bed (Keeley 2009). This mechanism has allowed black spruce stands to follow a trajectory of self-replacement for several thousand years (Kelly et al. 2013). Understanding drivers of seed rain following severe fire years is therefore essential for predicting the potential outcomes of an altered fire regime on black spruce regeneration and self-replacement. There are two potential large-scale mechanisms that can influence post-fire seed rain; fire characteristics and ecological legacies.

Fire characteristics are comprised of the fire return interval, the area burned, and the fire severity, each of which may affect seed rain processes. It takes approximately 50 years for the aerial seedbank in black spruce to fully develop meaning that stands that burn in intervals of less

than 50 years will have a lower availability of viable seeds and experience reduced recruitment rates (Johnstone and Chapin 2006a, Viglas et al. 2013). Severe fires have been shown to heat the seeds in the aerial seedbank enough to kill them and result in either decreased seed viability or consumption of the seedbank thereby removing the local regeneration potential of that species (Zasada et al. 1979, Arseneault 2001, Johnstone et al. 2009). Further, both canopy and ground fuels dry progressively throughout the season (Viereck 1983, Kane et al. 2007), potentially resulting in more severe fires at the end of the season (Kasischke and Johnstone 2005). Late season fires may thus have a greater impact on regeneration processes and longer and later fire seasons are expected with climate warming. Fire intensity (the energy released along a fire front; Christensen 1995), has been negatively linked to the post-fire regeneration potential of coniferous species (de Groot et al. 2004). Distance to the nearest unburned edge has been shown to be an important factor for the distribution of seeds as the amount of seed dispersed into the burn is proportional to the distance from an unburned edge (Greene and Johnson 2000) meaning that as the area of the burn complex increases, seed rain processes may be more severely impacted, a factor that becomes important for (semi) serotinous species when combined with consumption of cones and loss of seed viability due to severe fire.

Ecological legacies that may be particularly important in the prediction of seed rain include the total basal area (BA) of the species of interest and the site moisture conditions. For species with an aerial seed bank, total BA is positively related to the size of the aerial seed bank (Greene and Johnson 1999, Turner et al. 2007). Thus, species-specific BA is often a good predictor of the amount of available seed and the reproductive potential of a site. Site moisture may be expected to limit seed production in both very wet and very dry sites (Johnstone and Chapin 2006b, Johnstone et al. 2008). Depth of the residual organic layer predicts site soil

moisture (Figure S3) with very wet sites accumulating a thick layer of organic soil (Johnstone et al. 2008).

Extreme fire years present unique opportunities to assess the resilience of species and systems to anticipated future changes in this disturbance regime. In 2014, 3.4 million hectares of forest in the Northwest Territories (NWT) burned making it the largest fire season on record for the NWT. Furthermore, fires burned much later in the season than would normally be the case, implying more severe fires as well (ENR, 2014). This event provided an exceptional opportunity to understand the implications of such an event for forest recruitment processes in the NWT where post-fire regeneration has received relatively little attention (but see Black and Bliss 1978, Johnson 1981).

While depth of the organic layer and the presence of high quality seedbeds are known to drive recruitment and initiate patterns of stand dominance (Charron and Greene 2002, Johnstone and Chapin 2006b), low recruitment and subsequent decreases in the size of the seedbank (Johnstone and Chapin 2006a) as well as low seed production at the edge of species' ranges (Brown and Johnstone 2012), suggest that variations in post-fire seed rain can influence conifer recruitment. In this study, we measure post-fire seed rain to investigate the drivers of black spruce seed availability and viability following fire and explore how these change as a function of fire characteristics and ecological legacies.

2.2 Methods

2.2.1 Study Region

The Taiga Plains is a level II ecozone that traverses the Mackenzie River Valley. 45% of this ecozone is forested, 32% is comprised of wetlands and waterbodies, and 23% by barren lands and grasslands (Environment and Natural Resources 2015). The Taiga Plains spans the

zone of discontinuous permafrost (Heginbottom et al. 1995). Forests are composed of closed to open canopies of mixed and pure stands of black spruce, jack pine (*Pinus banksiana*), white spruce (*Picea glauca*), trembling aspen (*Populus tremuloides*), and Alaska paper birch (*Betula neolaskana*). The Taiga Plains Ecozone is mainly flat with extensive peatland coverage and level to undulating uplands, underlain by glacial till (Ecosystem Classification Group 2007). Study sites were located in the south-western part of the Taiga Plains between Behchokò and Hay River, NT. Mean annual air temperature (1981-2010) for the Yellowknife and Hay River weather stations are -4.3°C and -2.5°C, respectively. The January and July average air temperatures are -25.6°C and 17.0°C for Yellowknife and -21.8°C and 16.1°C for Hay River. Total annual precipitation is 288.6mm for Yellowknife and 336.4 mm for Hay River (Environment Canada 2017).

2.2.2 Site Selection and Study Design

Road accessible sites were selected in three large fire complexes. Each burn was separated into available strata based on date of burn (DOB), pre-fire vegetation and fire history. DOB estimation followed Loboda and Csiszar (2007) and was determined using MODIS satellite imagery (DOB estimation provided by L. Bourgeau-Chavez and N. French; see Supplementary Information for more detailed methods). Using 2005 Land Cover Classification data (LCC05; Canada Centre for Remote Sensing, 2008) all strata were selected in three conifer-dominated land cover classes; 7 – medium crown density with lichen-shrub understory, 9 – low crown density, lichen-rock understory, and 20 – sparse conifers with herbaceous vegetation and grasslands. These land cover classes are common across the Taiga Plains and are frequently used by woodland caribou in the region (GNWT ENR, unpublished data). Based on fire history maps of the area (Canadian Forest Service 2016), strata were classified as being ‘new’ burns (no

recorded fire history since 1960) or re-burns (the site burned between 1960 and 2014) to ensure a wide range of time since last fire. Random points were generated in the different strata in each burn and were constrained so that sites were within 1km of the highway for reasons of access.

During the first site visit (early-mid June, 2015), site moisture category was assessed on a six-point scale (xeric to subhygric) following Johnstone et al. (2008), and described in Table 1. Two additional points were then located within 500m of the random location such that site-level sampling encompassed the range of local moisture conditions. In total, 44 sites and 110 plots were established (Figure 2.1). Each plot consisted of two 30m parallel transects (running south to north); see Figure S1 for the complete transect design. Seed rain was assessed at a subset of 25 black spruce-dominated plots from this broader study design to facilitate a regional comparison between this study and Johnstone et al. (2009) who conducted a similar study after the severe 2004 fires in Alaska. Based on preliminary data including site moisture, canopy consumption, organic soil consumption, and residual organic layer depth, two to three plots were selected per stratum and burn, to ensure that the selected plots encompassed the full range of variation available.

2.2.3 Response Variable

Seed traps were installed at each plot to provide an area-based estimate of seed rain. These consisted of rectangular garden flats (52cm x 22.5cm) with drainage holes and were lined with synthetic grass turf to help trap the seeds. At each plot, 10 traps were positioned between the two 30m transects, were spaced at 3m intervals (Figure S1), and were secured with a large nail in each corner. Traps were left out from June 2015 – August 2016 and collections represented three periods: first summer after fire (late June to late August 2015), second winter after fire (late August 2015 to mid-May 2016), and second summer after fire (mid-May 2016 to

late August 2016). During collection, bags were uniquely labelled and sealed with as little air in them as possible. Samples were stored at -2°C until sorting to prevent germination. In the lab, seeds were separated from organic debris and the total number of seeds per species per trap recorded, providing an estimate of total seed rain on an area basis. Sorted seeds were stored at -2°C until germination trials.

To determine viable seed rain, germination trials were conducted; the protocol for the germination trials follows Leadem et al. (1997). Seeds were surface sterilized, stratified, and then placed on moist filter paper in Petri dishes to germinate in a greenhouse for 21 days with a 16/8h photoperiod and $23/19^{\circ}\text{C}$ day/night temperatures. Samples from each trap were tested separately unless there were more than 100 seeds in a sample in which case the sample was separated into subsamples. Dishes were checked daily to ensure sufficient moisture. After 21 days, a subsample of ungerminated seeds were assessed for viability using sectioning and tetrazolium chloride staining (following Leadem, 1984; see supplemental materials for additional detail).

2.2.4 Measured Predictor Variables

To assess the drivers of seed availability, we measured the following predictor variables along each plot: stand age, proportion of black spruce basal area, canopy consumption, residual organic layer thickness, distance to the nearest unburned edge, depth of burn, DOB, and Fire Weather Index (FWI). Details of each of these measurements follow and measurements are summarized in Table 2. Average stand age was determined at each plot by taking either a cross sectional sample or an increment core at the base of five trees representative of stand-level size and species. Boreal forests stands are relatively even aged because of punctuated periods of regeneration following stand-replacing disturbance and thus only a few samples are needed for stand age determination, particularly in western Canada where fire return intervals are relatively

short (Arseneault 2001, Gutsell and Johnson 2002). Samples were sanded with a progressively finer grit (60-800) until all rings were visible. Samples were then scanned and ring counts were performed twice (WINDENDRO, Version 2009b). Tree ages within a plot were inspected for clustering, since it would be expected that tree age would cluster around the date of post-fire recruitment. When a majority of trees (>50%) fell within a cluster of 10-20 years of a central date, then the plot was assumed to arise from one fire and the age of the oldest tree in the cluster was used to represent stand age.

Date of Burn estimation was determined using MODIS satellite imagery as described above and FWI was obtained from the Global Fire WEather Database (GFWED) (NASA 2017). Fire Weather Index represents the intensity of the spreading fire (Turetsky et al. 2004) and is considered a general index of fire danger throughout Canadian forests (Natural Resources Canada 2008). See Supplementary Information for detailed information about estimations of DOB and FWI. Trees in a 2 x 30m belt transect (grey box in Figure S1) were identified to species and the degree of consumption of the cones was assessed categorically on a five-point scale: 0-no consumption; 1-low consumption, 0 to 33% charred; 2- moderate consumption, 34-66% charred; 3- high consumption, 67-100% charred, none-no cones. Adventitious root height (ARH) was measured as a proxy for the depth of organic soil consumed during the fire following Boby et al., (2010). ARH measurements were calibrated by measuring from the top of the duff layer to the adventitious roots in unburned stands (Boby et al. 2010; Walker et al. in prep). Every tree located within the belt transect was measured for diameter at breast height (1.3m; DBH). Basal area (BA) of each tree in the belt transect was calculated as $BA = \pi (DBH/2)^2$ and the proportion of black spruce basal area was calculated for each site. Since sites were in black spruce-dominated stands, a large majority of seeds caught were black spruce and thus this was

the only species that we modelled. Distance from the centre of each plot to the nearest unburned edge was measured for each plot aurally, via helicopter using GPS coordinates. Depth of the residual organic layer was measured as the depth from the current top of the organic soil layer to either the mineral soil, rock, or seasonal ice below.

2.2.5 Statistical Analysis

All analyses were performed with the R statistical software, version 3.3.1 (R Core Development Team 2016). We tested for collinearity between all pairs of predictors. Based on the presence of a small number of correlated variables (Table S1, Figure S2), the predictor variables were reduced to canopy consumption, stand age, DOB, distance to nearest unburned edge, black spruce BA, and depth of residual organic layer. Depth of residual organic layer was measured 10 times at each plot and the mean value per plot was used for analysis. Canopy consumption, was categorically assessed for all trees in a 60m² area and the mode value per plot was used since the mean value would not represent a category. All other measurements were made once per plot, so the measured value was used. All continuous predictors were standardized thereby producing comparable coefficient values. Seed rain was converted to an area based metric (seeds·m⁻²) based on the size of the seed trap (0.16m² per trap) and is presented on a seed rain per week basis to correct for differences in sampling effort among sampling periods.

To determine how total and viable seed rain differed with time of collection, we used analysis of variance (ANOVA) and Tukey honest significant difference (HSD) post-hoc analysis to test for differences in the mean total and viable seed rain for each sample period. To determine which hypothesis was more influential as a driver of total and viable seed rain, we formed candidate models based on *a priori* hypotheses. The fire characteristics model tests the influence

that fire characteristics have on seed rain processes and includes the predictor variables of canopy consumption, stand age (i.e., fire return interval) and DOB (Table 3, M1). The ecological legacies model focuses on attributes of the plots themselves and includes the predictor variables of distance to nearest unburned edge, black spruce BA, and depth of residual organic layer (Table 3, M2). A global model including all predictor variables and a null model consisting of only the random term were also included.

Cone consumption was recorded on a five-point scale but sites only had three modal levels of cone consumption; low consumption (0-33% charred), moderate consumption (34-66% charred) and no cones. We specified pre-planned contrasts in our models to assess responses from different levels of cone consumption. Contrasts are designed to test whether there are significant differences in total or viable seed rain based on the condition of the cones and were used rather than a Tukey HSD post-hoc analysis since contrasts are developed *a priori* and can test planned comparisons. Contrasts were designed so that all levels of cone consumption were compared to the extreme state (no cones). Contrast 1 compared low consumption to no cones; contrast 2 compared moderate consumption to no cones.

To test the effect of different predictors on the response variables (total seeds·m⁻² and viable seeds·m⁻²), we ran candidate generalized linear mixed effect models. Models were run using the ‘glmmadmb’ function in the ‘glmmADMB’ package (Skaug et al. 2016); this package gives the flexibility to run a generalized linear mixed model (and thus incorporate a random term) while accounting for a zero-inflated data set. The response variables were zero-inflated (Total seed rain: 178 out of 750 observations were 0; Number of viable seeds: 474 out of 750 observations were 0 (Figure S4)), requiring the use of zero-inflated models (Zuur et al., 2009).

Zero-inflated data is count data with a higher proportion of zeros than is expected based on either a Poisson or negative binomial distribution. Zero-inflation needs to be acknowledged in modelling efforts, as ignoring it can result in overdispersion and inflated estimate parameters and standard errors. Zeros are assumed to arise by one of two processes: sampling zeros (or false zeros), and structural zeros (or true zeros). Sampling zeros are a result of study design, or observer or survey error; structural zeros occur as a result of the count data allowing for some results to be zero. Zero-inflated data can be modelled in two different ways. Zero-altered, or hurdle models, model the data in two parts: a binomial part, modeling the presence and absence of the response variable, and a zero-truncated part, which models the count data with a Poisson or negative binomial distribution but does not include zeros in the count data (even structural, or true, zeros). In zero-altered models, there is no distinction between structural and sampling zeros. Zero-altered models can be run in specialized zero-altered programs or packages which model the two processes separately, or can be modelled manually as two processes. Either way, model outputs are obtained for both the binomial model, and the zero-truncated count model. Zero-inflated, or mixture models, also model data in two parts; a binomial process and count process. However, in the count process, the data is not zero-truncated (i.e., zeros are included and are treated as a mixture of both structural and sampling zeros). Zero-inflated models are used when zeros can have arisen as a result of certain covariate conditions and these structural zeros are something that is of interest to the researcher. Specialized zero-inflated models or packages must be used. In zero-inflated models, only one set of model outputs is obtained and this represents both the binomial and count processes (Zuur et al. 2009).

The glmmADMB package allows models to have either a Poisson or a negative-binomial distribution. Since the variance of the data was greater than the mean, it did not fit a Poisson

distribution and a negative-binomial distribution was used. Additionally, while both distributions allow for overdispersion in the response variable to account for the excess zeros, the negative binomial distribution allows for extra overdispersion (i.e., overdispersion in the non-zero responses as well as the zero responses; Zuur et al. 2009). Each model had a random effect of trap nested within plot within burn (1|Burn/Plot/Trap) to account for the temporally and spatially nested design of this experiment (10 traps measured during 3 time periods at each plot and multiple plots within distinct burn complexes). To determine which model represented the best fit of the data, qAICc was calculated for each model. This is the Akaike Information Criterion (AIC) corrected for both small size (c) and overdispersion (q). qAICc values were computed using the 'ICtab' function in the 'bbmle' package (Bolker and R Core Development Team 2016). Models were ranked by their IC weights and the model with the lowest qAICc score where $\Delta qAICc > 2$ was considered the best model (Burnham and Anderson 2002).

R^2 values were calculated for all models using methods from Nakagawa and Schielzeth (2013) who have provided a way to calculate R^2 values for GLMMs and LMMs. Traditional R^2 calculations cannot be applied to mixed models as they cannot deal with the hierarchical nested structure of the random term. Two different R^2 values can be calculated: R^2_C (conditional) and R^2_M (marginal), where the former represents the variation explained by both the fixed and random effects and the latter explains the variation from only the fixed effects. For null models (i.e., modelling only the random term), only the R^2_C is calculated. The method developed by Nakagawa and Schielzeth (2013) is modified for different R packages as well as distributions of data. At the time of publication of this thesis, only R^2_C had been developed for the glmmADMB package.

2.3 Results

Over the three time periods, all seed traps collected a total of 5,705 black spruce seeds (range 0 - 171 per trap), 138 trembling aspen seeds (range 0 - 44 per trap), 33 jack pine seeds (range 0 - 2 per trap), and 6 Alaska paper birch seeds (range 0 - 4 per trap). After standardizing for length of collection time, Summer 2015 had the highest total seed rain ($n=1,436$ seeds). Analysis of variance (ANOVA) on these counts yielded significant variation among collection times ($F_{1, 718} = 14.38$, $P < 0.001$). A post-hoc Tukey test showed that Summer 2015 seed rain was significantly higher than Winter 2016 or Summer 2016 seed rain ($P < 0.001$; Figure 2.2a); mean seed rain in Summer 2015 was 72% higher than Winter 2016 and 59% higher than Summer 2016. The number of viable seeds ranged from 0 to 163 per m^2 (mean 4.67) and was highest in Winter 2016; however, ANOVA results indicated that there was no significant difference among periods ($F_{1, 718} = 2.268$, $P > 0.1$, Figure 2.2b).

The model that best explained total seed rain and viable seed rain was the fire characteristics model (Tables 4 and 6). There were no significant individual predictors of total seed rain, although date of burn was marginally insignificant ($P = 0.073$; Table 5). Viable seed rain was significantly related to cone consumption; there were more viable seeds in sites where cones experienced low consumption (0-33% charred) than those where trees had no cones ($P < 0.001$; Table 7, Figure 2.3). Date of burn was also marginally insignificant for this model ($P = 0.079$). Our cross sectioning and staining of ungerminated seeds revealed no viable, ungerminated seeds indicating that our viable seed rain estimates are accurate.

2.4 Discussion

Our results show that in the sub-arctic, boreal forest of the Northwest Territories, cone consumption is the main driver of viable seed rain following fire. Specifically, sites that had no

cones either due to complete consumption or short fire return interval had low seed rain with implications for regeneration processes. Cones experiencing the lowest level of consumption (0-33% charred) had the highest levels of viable seed rain, suggesting that future intensification of the fire regime could serve to negatively influence the regeneration potential of these boreal forest stands.

Drivers of total and viable seed rain

Both total and viable seed rain were higher at earlier dates of burn (Tables 2.5 and 2.7, Figure 2.4). As a result of drying fuels, later season burns are expected to be more severe which could account for lower levels of both total and viable seed rain at later dates of burn. Our AIC-selected model for total seed rain was the fire characteristics model, which explained 87% of variation in seed rain (Table 4) but there were no significant individual predictors from this model. Since no variables pull out as being significant, a combination of all three variables (stand age, cone consumption, and DOB) influences total seed rain.

Cone consumption was a significant predictor of viable seed rain. There were more viable seeds at sites where cones experienced low consumption (0-33% charred) than those where trees had no cones. At 10 out of the 25 plots, trees with no cones also experienced the highest level of above ground consumption (most of the aboveground canopy, except the central trunk and branch stubs, was consumed). This suggests that trees with no cones resulted from a combination of both severe burning and short fire return interval (however, cone consumption and stand age were not highly correlated; $r = -0.2$). In cases of extreme burning, it is expected that the seeds will not be viable due to heat damage (Zasada et al. 1979). Johnstone et al. (2009), found that cone consumption correlated negatively with viable seed rain, which is comparable to the present

findings suggesting that this may be a more generalizable finding in western North American boreal forests.

For total black spruce seed rain, the null model was the second ‘best’ model ($\Delta qAICc = 2.4$) and it explained 80% of the variance (Table 2.4). The R^2_C value calculated represents the variance explained by both the fixed and random effects. In the null model, the R^2_C explains the variance in the random effects alone as there are no fixed effects in this model. Therefore, the nested random effect (trap nested within plot nested within burn) is explaining a majority of the variation encountered with only an additional 7% being explained by the fixed effects in the best selected model. This suggests that there is a large amount of variation between sites and burn complexes. The three burn complexes used in this study were very distinct, ranging from lowland, black spruce peatlands to upland, sandy ridges and differences between burn complexes likely contributes substantially to the variation encountered. A large amount of variation in total seed rain can therefore be attributed to burn complex. Further analyses regarding how these differences influence seed rain is required. Conversely, for viable black spruce seed rain, the null model only explained 14% of the variation (Table 2.6), suggesting that viability is not as variable across the different burn complexes.

Over the course of the three collection periods, we caught only 138 aspen seeds and 33 jack pine seeds (compared to 5,705 black spruce seeds). Aspen seed dispersal occurs in late spring (Lee 2004) and yearly seed crops can produce up to 1.6 million seeds (Schopmeyer 1974, McDonough 1979). While our limited aspen seed collection suggests that these seeds are not reaching our sites, this finding is likely more a function of the timing of our seed trap deployment. During 2015, there was exceptionally heavy aspen seed rain that occurred mid-June (Johnstone, personal observation); unfortunately, our seed traps were deployed about a week

after this event. Jack pine was present in 44% of stands and showed significantly higher seedling establishment rates post-fire in these sites than did black spruce (Reid et al., in prep). Jack pine seed rain has been shown to be completed from as early as 3-4 days post-fire (Eyre and LeBarron 1944, Beaufait 1960); this information in combination with our seedling establishment data suggest we also missed the majority of jack pine seed rain.

We did not find a correlation between distance to the nearest unburned edge and either total or viable seed rain. Our expectation was that distance to the unburned edge would have a negative relationship with total and viable seed rain (Greene and Johnson 2000, Johnstone et al. 2009). Seed dispersal from an unburned edge likely only becomes an important source of seeds when a non-serotinous species is under consideration or when the (semi) serotinous cones within a site are excessively heated or completely combusted. There were significant differences between cone consumption levels and distance to the unburned edge (ANOVA; $F_{2, 747} = 34.42$, $P = 5 \times 10^{-15}$) and a post-hoc Tukey test showed that sites with no cones were significantly farther from the unburned edge than sites with low and moderate cone consumption ($P < 0.001$). Sites with no cones were located from 23 to 710m from the unburned edge. The maximum estimated distance for black spruce seed dispersal is 80m (Johnston 1971); half of the sites without cones were greater than this distance. Fires are less intense closer to the burn edge (Pyne 1997) and it is therefore not surprising that these severely burned sites are farther from the unburned edge than low or moderately burned sites. At sites with no cones, there was a weak, negative relationship between total seed rain and distance to unburned edge ($R^2 = 0.007$; $P = 0.0354$), but not for viable seed rain ($R^2 = 0.002$; $P = 0.303$). As burn size and severity increase, dispersal from adjacent unburned stands becomes less likely as increasing proportions of the burn are spatially isolated from these unburned sources of seed (Tautenhahn et al. 2016); our results support this

idea. As changing fire regime results in more frequent large burns, smaller proportions of the burned landscape will receive contributions of adjacent seed source. For serotinous and semi-serotinous species, where large fires combine with severe burning, there is the potential for regeneration failure and a resulting shift from boreal forests to tundra communities (Hustich 1951, Lutz 1956, Brown and Johnstone 2012).

Regional comparisons of seed rain

We can compare our estimates of total and viable black spruce seed rain to other studies investigating post-fire black spruce seed rain in the western boreal forest. Comparisons are summarized in Table 8. Our study found higher total and viable seed rain than either Johnstone et al., (2009) or Zasada et al., (1979), although total seed rain found by both studies overlapped with the lower end of our range. Stand age between our study and Johnstone et al. (2009) overlap and have similar mean values, suggesting that average stand age does not account for differences in seed rain. If we assume that black spruce forests in the NWT experience the same reproductive dynamics as in Alaska (cone production steadily increases after 50 years; Viglas et al. 2013), then it is likely that a majority of our stands had cones (minimum age of 71 years), whereas not all trees in Johnstone et al. (2009) would have had cones (minimum age of 29 years). Differences in black spruce basal area may explain differences in seed rain. Our study sites had higher values than both other studies, which should lead to greater post-fire seed rain providing some additional level of regeneration resilience. Based on the quantity of organic soil consumed during fires, Walker et al. (*in prep*), concluded that the 2014 NWT fire year was not as severe as severe fire years have been in Alaska. Differences in total and viable seed rain between our study and Johnstone et al. (2009) may also suggest that the 2014 NWT fire season was not as severe as the 2004 fire season in Alaska.

This analysis was performed with an outlier included since running the models with and without the outlier did not affect the model outcome. However, the outlier was the result of a seed trap being placed almost directly under the cone ball of a black spruce tree. Other studies (see Johnstone et al. 2009) have removed such outliers. To be consistent with this study and for more accurate estimations of seed rain, this data should be re-analyzed without the outlier. It is likely that this one data point is causing the total seed rain from this study to be much larger than that of Johnstone et al. (2009) and Zasada et al. (1979).

The results of this study provide insight into the mechanisms that determine post-fire seed availability in black spruce forests. Knowledge of stand regeneration potential provides insight into how stands will recover post-fire. Similar to Alaskan studies, lower levels of cone consumption resulted in more viable seed rain (Johnstone et al. 2009). Distance to the unburned edge, which has shown to be a significant driver of seed rain in severe wildfire events in Alaska, does not appear to be significant in the NWT, suggesting that these fires were not severe enough to require seed input from local sources. Additionally, NWT stands had higher stand BA than stands in Alaska, resulting in higher local seed rain. These findings suggest that severe fires in the NWT may not impact post-fire regeneration in the same way as has been demonstrated in Alaska, and that fire characteristics that affect individual trees (i.e. cone consumption), rather than the stand (i.e. distance to unburned edge), are influencing the regeneration potential.

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Tables and Figures

Table 2.1. Key of the six potential moisture classes used to classify sites (Johnstone et al., 2008).

Moisture Class	Description
Subhygric	Very considerable surface moisture; saturated with less than 5% standing water
Mesic to Subhygric	Considerable surface moisture; depressions or concave toe-slopes
Mesic	Moderate surface moisture; flat or shallow depressions including toe-slopes
Subxeric to Mesic	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

Table 2.2: Summary of continuous predictor variables measured at all 25 study plots.

	Mean \pm SD	Range
Distance to unburned edge (m)	153 \pm 107.0	17.0 – 710
Stand Age (years)	103 \pm 41.0	71.0 – 232
Black spruce BA (m ² •ha ⁻¹)	0.800 \pm 0.22	0.350 – 1.00
Residual Organic Layer Depth (cm)	18.0 \pm 14.0	1.25 – 65.5
Date of Burn (Day of year)	202 \pm 12.0	183 – 225

Table 2.3: List of candidate models used to assess relative influence of variables on total seed rain and number of viable seeds. All models specified the negative binomial family and had a random term of (1|Burn/Plot/Trap) to account for the spatially and temporally nested design of the study.

Model Name	Predictor Variables Included
M1: Fire Characteristics	Stand Age + Canopy consumption + DOB + random term
M2: Ecological Legacies	Distance to unburned edge + Pima BA + residual organic layer depth + random term
M3: Global Model	Stand Age + Canopy consumption + DOB + Distance to unburned edge + Pima BA + residual organic layer depth + random term
M4: Null Model	Random term

Table 2.4. Results of AIC based model selection. Response variable for all models is total seed rain (per m²). For each model, Log-likelihood (Log(L)), Akaike information criterion (corrected for sample size and over dispersed data; qAICc), degrees of freedom (df), model weight, and conditional R² value (R²_c: variance explained by fixed and random factors), are given. Model with $\Delta qAICc > 2$ is considered to be the best fit (Burnham and Anderson 2002). Model structure is described in Table 2.3.

Model	Log(L)	qAICc	$\Delta qAICc$	df	Weight	R ² _c
Fire Characteristics	-2715.7	5453.8	0.0	10	0.689	0.87
Null Model	-2721.0	5456.2	2.4	6	0.210	0.80
Global Model	-2715.2	5458.9	5.1	13	0.054	0.88
Ecological Legacies	-2719.5	5459.2	5.4	9	0.046	0.79

Table 2.5. AIC-selected linear mixed effects model describing total seed rain. The model represents fire characteristics and incorporates stand age, canopy consumption, and date of burn. Pre-planned contrasts were used to compare seed rain at different levels of cone consumption. Contrast 1 compares seed rain from low consumed cones vs. trees with no cones. Contrast 2 compares seed rain from moderately consumed cones vs. trees with no cones. Model details are provided in Table 2.3.

	Estimate	Std. Error	z-value	Pr(> z)
Intercept	3.060	0.373	8.20	2.3x10 ⁻¹⁶
Stand Age	-0.156	0.121	-1.29	0.197
Canopy consumption (Contrast 1: Low consumption vs. No cones)	0.312	0.303	1.03	0.303
Canopy consumption (Contrast 2: Moderate consumption vs. No cones)	0.186	0.325	0.57	0.568
Date of Burn	-0.365	0.204	-1.79	0.073

Table 2.6. Results of AIC-based model selection. Response variable for all models is number of viable seeds (per m²). For each model, Log-likelihood (Log(L)), Akaike information criterion corrected for sample size and over dispersed data (qAICc), degrees of freedom (df), model weight and conditional R² value (R²_C: variance explained by fixed and random factors), are given. Model with $\Delta qAICc > 2$ is considered to be the best fit (Burnham and Anderson 2002). Details of candidate models are provided in Table 3.

Model	Log(L)	qAICc	$\Delta qAICc$	df	Weight	R ² _C
Fire Characteristics	-1353.3	2728.9	0.0	10	0.763	0.11
Global	-1351.4	2731.3	2.4	13	0.228	0.13
Null	-1361.8	2737.8	8.9	6	0.009	0.14
Ecological Legacies	-2719.5	5459.2	2730.4	9	< 0.001	0.57

Table 2.7. AIC-selected linear mixed effects describing number of viable seeds (per m²). The model represents fire characteristics and incorporates stand age, canopy consumption, and date of burn. Pre-planned contrasts were used to compare seed rain at different levels of cone consumption. Contrast 1 compares seed rain from low consumed cones vs. trees with no cones. Contrast 2 compares seed rain from moderately consumed cones vs. trees with no cones.

	Estimate	Std. Error	z-value	Pr(> z)
Intercept	2.7705	0.0645	42.94	< 2x10 ⁻¹⁶
Stand Age	-0.0881	0.0638	-1.38	0.1677
Canopy consumption (Contrast 1: Low consumption vs. No cones)	0.3408	0.0979	3.48	0.0005
Canopy consumption (Contrast 2: Moderate consumption vs. No cones)	0.0252	0.1006	0.25	0.8023
Date of Burn	-0.1128	0.0642	-1.76	0.0790

Table 2.8. Comparison between black spruce seed rain from this study as well as Johnstone et al. (2009) and Zasada et al. (1979), both from the Alaskan boreal forest.

	Present Study	Johnstone et al. (2009)	Zasada et al. (1979)
Location	Southern Taiga Plains, NWT	Interior Alaska	Wickersham Dome Fire, Fairbanks, AK
Time of study	Years 1 and 2 post-fire	Years 1 and 2 post-fire	Years 1 – 3 post-fire
Total Seed Rain (seeds·m ⁻² ·year ⁻¹)	0 – 855 ^a	0 – 193	289 – 386 (Year 1) 41 – 77 (Years 2 – 3)
Viable Seed Rain	0 – 163 seeds·m ⁻² ·year ⁻¹ 0 – 100% (Mean 12% ± 0.86)	0 - 90 seeds·m ⁻² ·year ⁻¹	28 – 47 seeds·m ⁻² ·year ⁻¹ (Years 2 – 3)
Basal Area (m ² ·ha ⁻¹)	1.4 – 37.1	0.1 – 28	1.8 – 6.9
Seed traps (per collection period)	250	624	NA
Stand age (range and mean ± SE)	71 – 232 103 ± 22	29 – 240 104 ± 4.55	50 – 125

^a Seed counts *not* adjusted for length of collection period to facilitate comparison since other studies have not accounted for the different lengths of sampling period

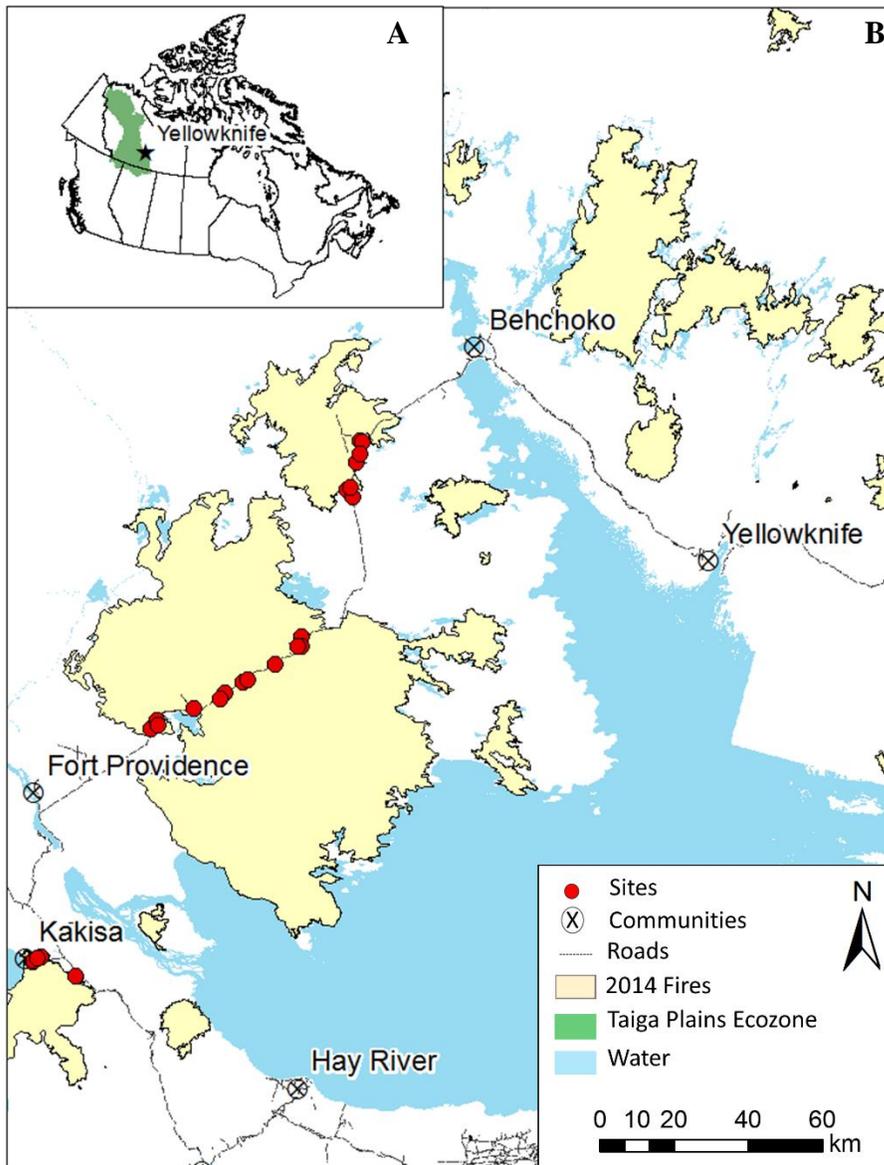


Figure 2.1. Map of study sites. **A** Sites are located close to Yellowknife, NT and are within the Taiga Plains Ecozone (shaded area). **B** All sites burned in 2014 and are located in three burn complexes. Sites are within 1km of Highway 1 (SS33 Burn) or Highway 3 (ZF20 and ZF46 burns).

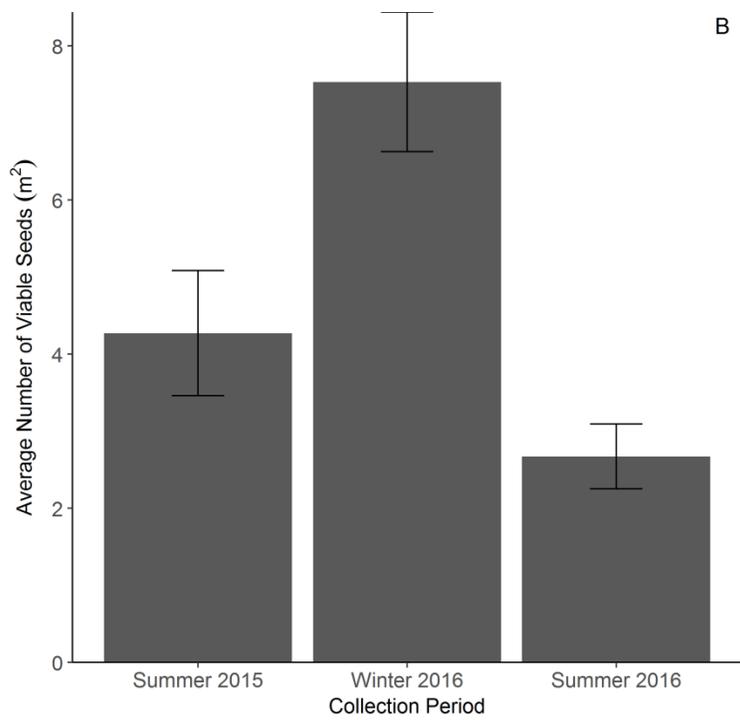
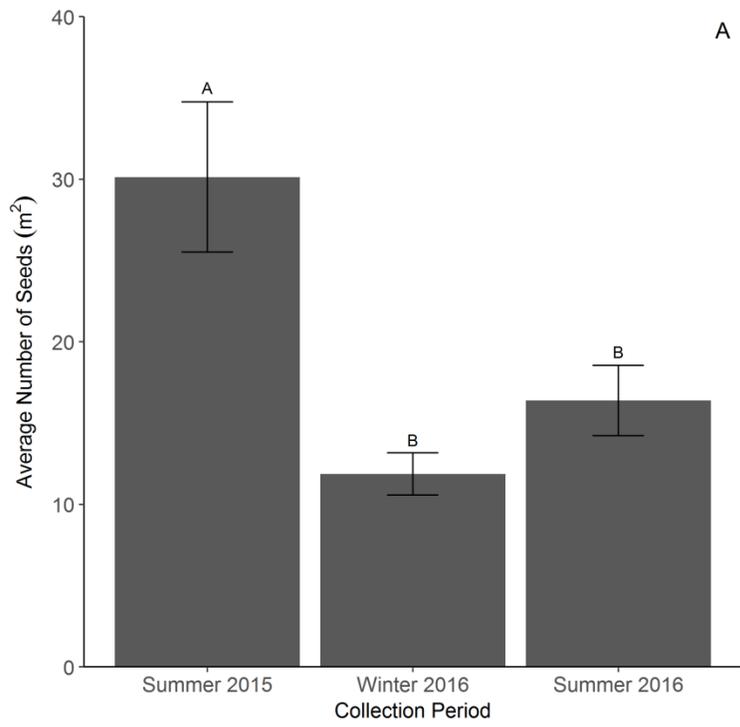


Figure 2.2. Mean values (\pm SE) of **A)** total black spruce seed rain (per m²), and **B)** viable black spruce seed rain (per m²) during the different collection periods. **A)** ANOVA results showed significant variation among collection periods ($F_{1, 718} = 14.38$, $P < 0.001$); a post-hoc Tukey test showed that black spruce seed rain during Summer 2015 (first year post-fire) was significantly higher than the two subsequent periods ($P < 0.001$). **B)** There are no significant differences between viable black spruce seed rain at the different collection periods (ANOVA; $F_{1, 718} = 2.268$, $P > 0.1$).

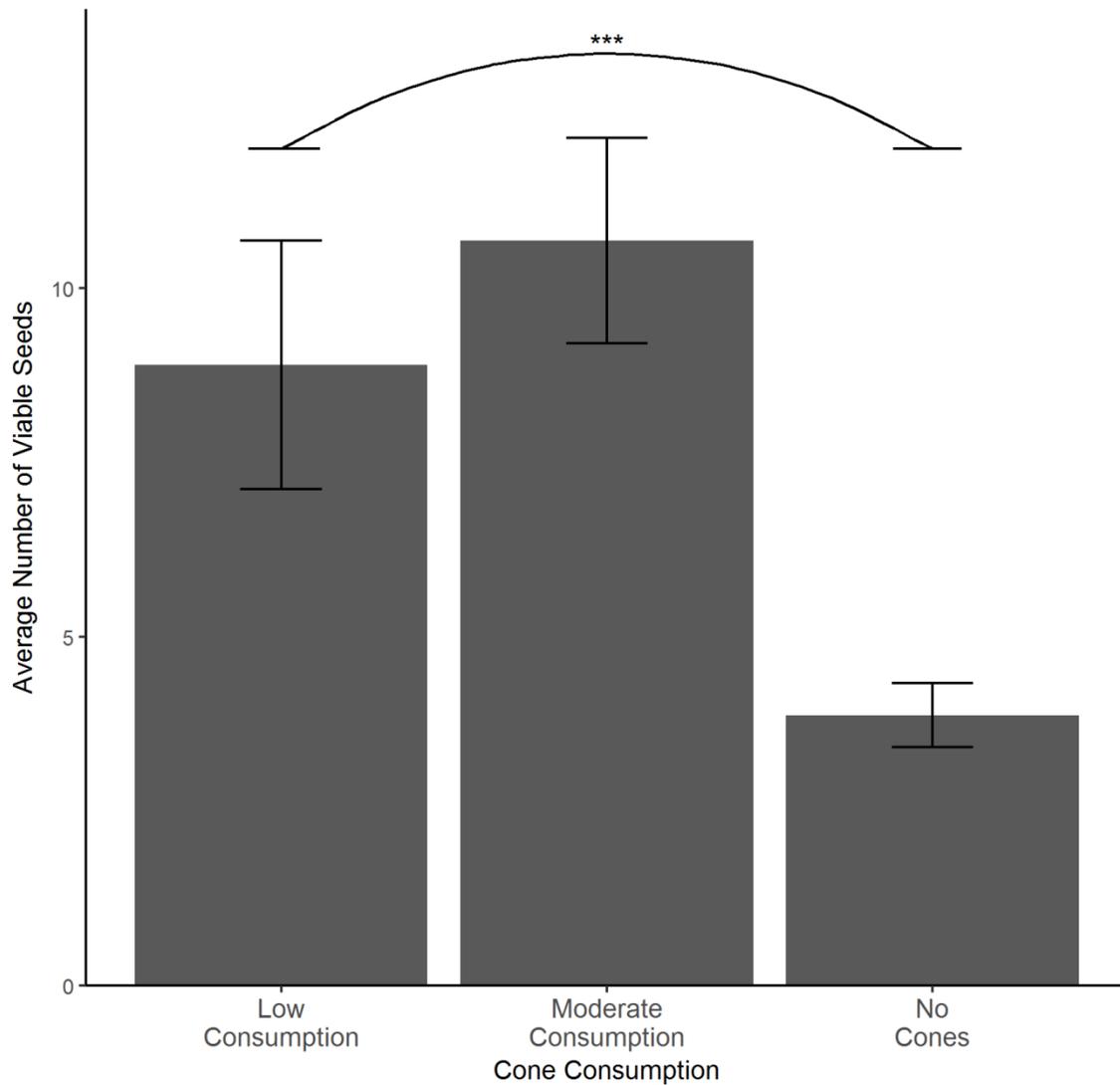


Figure 2.3. Average number of viable seeds (per m²) at different levels of canopy consumption. Low consumption represents cones that were 0-33% charred during fire and moderate consumption represents cones that were 34-66% charred. Trees with no cones experienced a severe fire and there was total combustion. Statistically significant pre-planned contrasts are shown by asterisks (***) ($P < 0.001$).

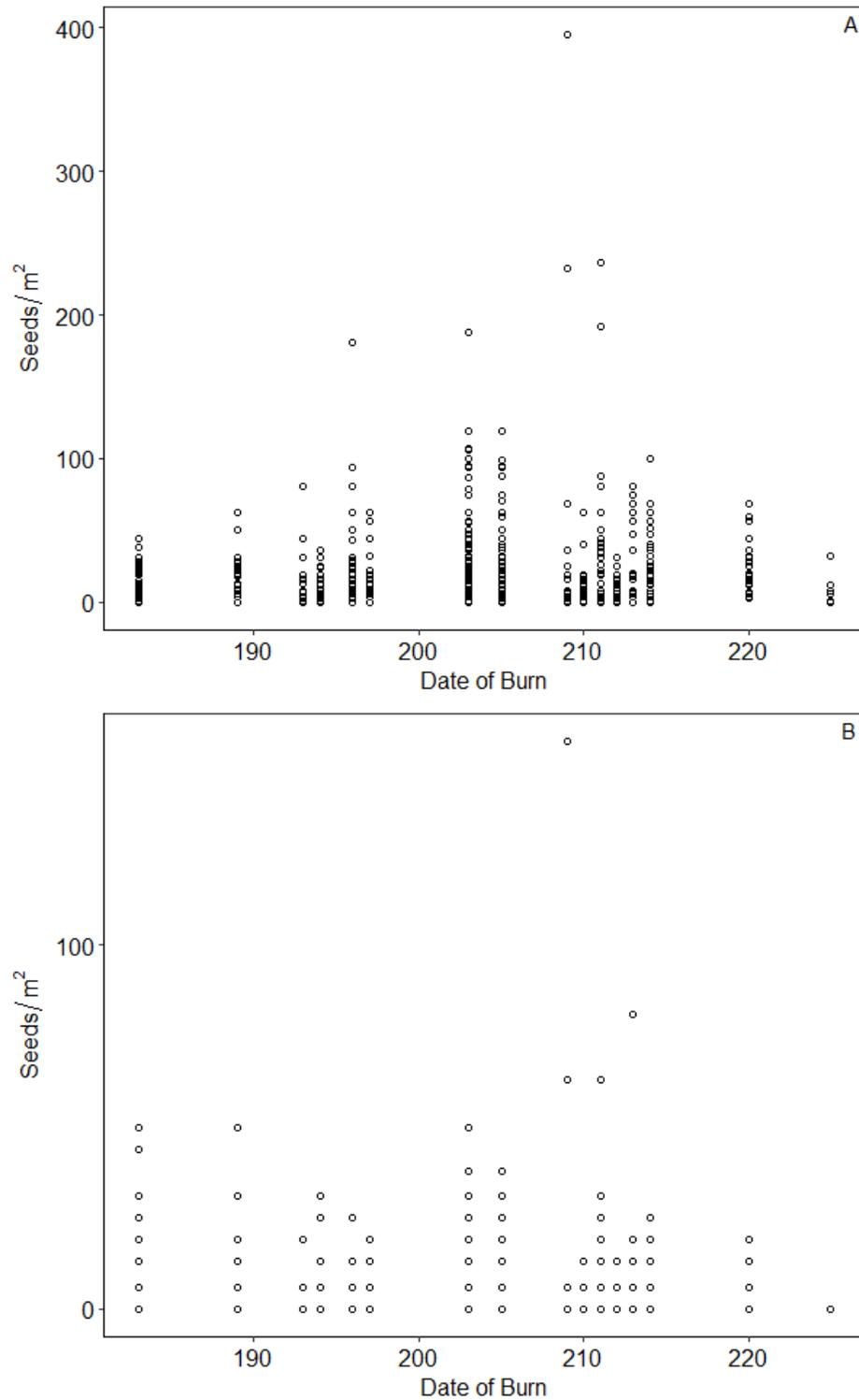


Figure 2.4. Relationship between date of burn and **A)** total seed rain, and **B)** viable seed rain. Both relationships show higher levels of seed rain at earlier dates of burn. Relationships are marginally non-significant (**A** $P = 0.73$; **B** $P = 0.79$).

Chapter 3: Jack pine dominance increases following a severe fire year in the southern Northwest Territories

In preparation

Abstract: Black spruce (*Picea mariana*) and jack pine (*Pinus banksiana*) both experience large pulses of recruitment following fire since this is when they release a majority of their seeds. Changes in fire patterns associated with global warming have initiated alternate successional trajectories in parts of the boreal forest and shifts from conifer- to deciduous- dominated forests have been characterized. During 2014, the Northwest Territories experienced an unprecedented fire year with a total of 3.4 million hectares of forest burning. We measured seedling establishment for two summers post-fire (2015 and 2016) at 224 transects across the NWT that burned in 2014. Using generalized linear mixed models and candidate model based hypotheses we sought to determine *a*) the drivers of species-specific seedling establishment post-fire, and *b*) how biogeographical legacies can influence ecological memory with a changing disturbance cycle. Bryophyte cover (*Marchantia* sp. and *Ceratodon* sp.) was a positive driver of establishment of all species. In year one post-fire, there was a shift from coniferous to deciduous dominance but where two years of establishment data are available, the same shift is not seen in the second year suggesting high mortality in deciduous species immediately post-fire. Pre-fire black spruce-dominated and mixed stands decreased significantly in black spruce dominance, which was driven by an increase in the proportion of jack pine. Biogeographical legacies play an important role in determining successional trajectories post-fire. In the Northwest Territories, the presence of jack pine presents a competitive fast-growing conifer that can establish quickly post-fire. Subsequently, alternative successional trajectories that have not been demonstrated after severe fire years in other parts of the boreal are occurring suggesting that generalizations of successional patterns based on location may not be applicable.

3.1 Introduction

Wildfire is the main cause of disturbance in the boreal forest and as such, forest regeneration depends on and is adapted to it (Heinselman 1981, Payette 1992). Changes in global temperatures are amplified at northern latitudes (IPCC 2013, Johannessen et al. 2016), which is predicted to increase the number of extreme fire events that occur (Wang et al. 2017). The frequency of large, crown fires is expected to increase as is the area of burned annually (Balshi et al. 2009; Wotton et al. 2017). In Canada, 7 out of the 10 largest fire years on record have occurred between 1990 and 2015 (based on records beginning in 1970; Canadian Forest Service 2017). Climate warming induced changes to the fire regime can affect post-fire regeneration potential in two main ways: 1) through a shortening of the fire return interval with implications for on-site seed availability; and 2) through increases in the severity of canopy or soil combustion, or both. If the fire return interval is less than the time it takes for seedbanks to become fully developed, post-fire seedling recruitment is likely to be dampened (Crayford and McRae 1983, Johnstone and Chapin 2006a, Viglas et al. 2013). Increasing fire severity and intensity has the potential to heat cones sufficiently to either kill the seed and result in decreased germination, or to completely consume the aerial seedbank, leaving no seeds for regeneration (Zasada et al. 1979, Arseneault 2001, Johnstone et al. 2009). Since fires usually result in near total removal of the duff layer, sites experiencing a long fire return interval are more likely to experience severe burns as a result of organic matter build up and greater fuel availability (Mann et al. 2012). Shallow organic layers are likely to result in areas of high density seedling establishment, since thin substrates or exposed mineral soil provide better seedbeds, particularly for small seeded deciduous species that cannot establish easily on thick organic substrates (Schopmeyer 1974, Johnstone and Chapin 2006b).

Resilience is the ability of a system to persist through a disturbance and retain the same structures, functions, and feedbacks, post-disturbance (Holling 1973). Resilience is a consequence of biologically-derived legacies which serve to preserve ecological memory and help to shape the recovering ecosystem (Franklin et al. 2000, Johnstone et al. 2016). Biological legacies can take two forms: information or material legacies. Information legacies are the species traits that are present as a result of historical disturbance cycles and biogeography. These traits arise as adaptations to disturbance regimes and allow post-disturbance ecosystems to recover to a similar state as they were pre-disturbance (Johnstone et al. 2016). Material legacies consist of the individuals or propagules that persist in an ecosystem after a disturbance. These are determined by the characteristics of the disturbance as well as the state of the ecosystem at the time of the disturbance. Legacies serve as a way for ecological memory to be transferred from the pre-disturbance system to the post-disturbance system (Johnstone et al. 2016). When disturbances fall within the historical disturbance regime, the ecological memory carried by legacies will help to maintain the dominance of the species that dominated pre-fire. A cycle of self-replacement and ecological resilience ensues (Johnstone et al. 2016).

In the boreal forest, biological legacies have developed as species have adapted to the historical fire regime. Serotiny is an example of an information legacy and seeds are a material legacy. As a result of their legacies, black spruce and jack pine have experienced patterns of self-replacement post-fire (Frelich and Reich 1999, Chapin et al. 2004, Kurkowski et al. 2008). With a changing disturbance regime, current legacies are under threat (Keeley et al. 2011). The loss of resilience can cause a system to shift to an alternative stable state which differs in its dominant life forms and relationships (Scheffer et al. 2001). Recent shifts to alternative stable states have occurred in Alaska and the Yukon where severe fire years have led to shifts from black spruce to

trembling aspen dominated forests (Johnstone and Chapin 2006a, Johnstone et al. 2010).

Vegetation shifts as a result of a changing climate and disturbance have been seen at the paleoecological scale as well. Fire frequency in interior Alaska peaked 3,000 to 6,000 years ago, as a result of increased site flammability when black spruce invaded forests previously dominated by white spruce and deciduous species (Kelly et al. 2013). There was a rise in fire severity and area burned and subsequently the less flammable deciduous vegetation was favoured over the typical black spruce self-replacement patterns (Kelly et al. 2013).

The nature of such shifts will be dictated in part through the available species pool. Species establishment is determined by historical filters that dictate which species will reach the site (Lambers et al. 2008). Therefore, from a vegetation perspective, the outcome of a disturbance will be a result of the combination of the historical biogeography and the disturbance characteristics. Floristically, the boreal forest of North America is relatively homogenous with only nine dominant species (Ritchie 1987, Payette 1992). Since these species do not co-occur everywhere, it is to be expected that there will be some regional differences in post-disturbance recovery. For example, as a result of glacial history, jack pine is present and dominant in the Northwest Territories, but not in the Yukon or Alaska (Flint 1957, Critchfield 1985). Post-fire successional trajectories may be expected to differ in regions with and without jack pine due to its ecological role as a fast-growing, competitive conifer that regenerates vigorously following fire.

In 2014, the Northwest Territories (NWT) experienced its largest and most intense fire season on record. In total, 3.4 million hectares of forest burned and fires occurred later in the season than usual, implying greater fire severity (ENR, 2014). This large fire year provided an opportunity for a novel assessment of the resilience of the boreal forests of the NWT following a

severe fire event and contributes to an improved understanding of drivers of post-fire succession. To date, a majority of post-fire successional studies and information about the resilience of the boreal forest have come from Alaska (Johnstone and Chapin 2006a, Johnstone et al. 2010) and more southerly forests in Quebec (Boiffin and Munson 2013). The NWT thus far has been relatively understudied and we anticipate that responses in this system may differ as a result of its historical biogeography. In other regions of the boreal forest, shifts to deciduous dominance have occurred with favourable site conditions such as exposed mineral soil, surficial soil moisture, and thin residual organic layers (Johnstone and Chapin 2006b). The optimal recruitment conditions for different species in the NWT are unknown as is the response of a system where the competitive coniferous species, jack pine, is present. Both jack pine and black spruce are present in the NWT and we can therefore determine how the biological legacies of both species play a role in post-fire successional trajectories.

In this study, we measure post-fire seedling establishment across southern NWT to investigate drivers of post-fire tree recruitment and successional pathways after an extreme fire event. Our research goals were to determine 1) the drivers of species-specific seedling establishment post-fire and if they differ across ecozones; and 2) whether there is evidence of a shift towards deciduous dominance when a competitive conifer is present.

3.2 Methods

3.2.1 Study Region

The Taiga Plains (hereafter the Plains) and Taiga Shield (hereafter the Shield) are level II ecozones located in the Northwest Territories. Forests in both ecozones are composed of a mix of open and closed canopies of black spruce, jack pine, trembling aspen (*Populus tremuloides*), Alaska paper birch (*Betula neolaskana*), and white spruce (*Picea glauca*) (Ecosystem

Classification Group 2007, 2008). The Shield has extensive glacial till deposits and spans the zones of continuous and discontinuous permafrost, where ground that is at or below 0°C for at least two years is found under all or some land surfaces, respectively (Harris et al. 1988, Ecosystem Classification Group 2008). The Plains span the zone of discontinuous permafrost, and are largely flat, with extensive peatland coverage (Ecosystem Classification Group 2007).

The nearest long-term, Environment Canada weather stations are located in Hay River, NT (the southernmost edge of our sites and on the Plains) and Yellowknife, NT (the southernmost edge of our Shield sites). Mean annual air temperature (1981-2010) for the Yellowknife and Hay River weather stations are -4.3°C and -2.5°C, respectively. The January and July average air temperatures are -25.6°C and 17.0°C for Yellowknife and -21.8°C and 16.1°C for Hay River. Total annual precipitation is 288.6mm for Yellowknife and 336.4 mm for Hay River (Environment Canada 2017).

3.2.2 Site Selection and Study Design

Sites were selected in seven large fire complexes (four on the Plains, three on the Shield) in the NWT that burned in 2014 (Figure 3.1). Burns were separated into different strata as follows. Using MODIS satellite imagery, date of burn (DOB) was estimated based on protocol from Loboda & Csiszar (2007) (DOB estimation provided by L. Bourgeau-Chavez and N. French). Strata were selected in conifer-dominated landcover classes from 2005 Land Cover Classification data (LCC05; Canada Centre for Remote Sensing, 2008). Selected landcover classes are all commonly used by woodland caribou in the region (GNWT ENR, unpublished data). Within each of these strata, we further differentiated into areas that had no recorded fire history or those that fire history records indicate had burned since 1960 (Canadian Forest Service

2016). Random points were generated in each stratum of each burn and were constrained so they were within 1km of a highway, water, or helicopter drop-off location.

Soil moisture category was assessed on a six-point scale (xeric to subhygric) based on Johnstone et al. (2008). Within 500m of this first plot, two additional plots were established so that the three plots spanned the available moisture conditions. In total, 86 sites and 224 plots were established. Each sampled plot was composed of two 30m parallel transects (running south to north). See Figure S5 for the complete transect design.

3.2.3 Response Variable

Along each transect, germinated seedlings in five 1m² quadrats were counted and identified to species. In 2015, seedlings were too immature to distinguish between black spruce and jack pine, so conifers were identified to the family level (*Pinaceae*). We were not confident that we captured the entirety of first year establishment on the Plains due to early season sampling in year 1 (June 2015); we therefore re-visited these sites in May 2016, to re-assess seedling establishment for the whole of the first year. The Shield sites were sampled later in the summer (late July and August 2015) and we are therefore confident we captured the entirety of first year establishment on the Shield. In late summer 2016, we re-visited the Plains sites again to get estimates of recruitment two years post-fire. The Shield sites were remote and thus it was not logistically possible to revisit them. In total, we have two years of establishment data for the Plains sites (year 1: *Pinaceae*, trembling aspen; year 2: black spruce, jack pine, trembling aspen) and one year for the Shield sites (*Pinaceae*, trembling aspen, Alaska paper birch).

3.2.4 Measured Predictor Variables

To assess the drivers of seedling establishment, or variables which act as a catalyst to produce the response variable, we measured the following predictor variables at each plot: stand

age, stand basal area, canopy consumption, date of burn (DOB), Fire Weather Index (FWI), percent ground cover of mineral soil, bryophytes and charcoal, burn depth, and depth of residual organic layer. Details of each of these measurements follow and are summarized in Table 3.2.

To assess stand age, five trees representative of stand-level size and species were sampled via stem cross section or increment core. Only a few samples are required to accurately assess stand age as a result of post-fire recruitment pulses and subsequently relatively even aged stands (Arseneault 2001, Gutsell and Johnson 2002). Samples were sanded with progressively finer grit sandpaper until all rings were visible, then scanned and aged (WINDENDRO, Version 2009b, Regent Instruments Inc., Quebec, Canada). It is expected that tree ages within a stand will cluster around a central date of post-fire recruitment; when a majority of trees in a plot clustered within 10-20 years, the plot was presumed to arise from one fire and the age of the oldest tree in the cluster was used to represent stand age.

DOB estimation was determined using MODIS satellite imagery and Fire Weather Index (FWI) was obtained from the Global Fire WEather Database (GFWED) (NASA 2017). FWI represents fire danger throughout Canadian forests (Natural Resources Canada 2008) and indicates the intensity of the spreading fire (Turetsky et al. 2004). See Supplementary Information for detailed information about estimations of DOB and FWI. Stand structural attributes were assessed in a 2 x 30m belt transect (grey box in Figure S5). Trees were identified to species. The degree of consumption of the cones was assessed categorically on a five-point scale: 0-no consumption; 1- low consumption, 0 to 33% charred; 2 - moderate consumption, 34-66% charred; 3 - high consumption, 67-100% charred; none - no cones. The degree of consumption of the canopy fuels (needles, branches etc.) was also assessed categorically; 0 - alive and no consumption; 1 - low consumption, only needles consumed; 2 - moderate

consumption, with few needles and small twigs remaining but many branches; 3 - high consumption, most of the aboveground canopy except the central trunk consumed. All trees were measured for diameter at breast height (1.3m; DBH), and basal area (BA) of each belt transect was calculated ($BA = \pi [(DBH/2)]^2$). As a proxy for depth of burn, we followed protocol from *Boby et al.*, (2010), to measure adventitious root height (ARH). As a result of green moss accumulation in unburned stands, there is likely to be an underestimation of depth of the soil organic layer. To account for this offset, ARH measurements were calibrated in unburned stands by measuring from the top of the duff layer to the adventitious roots (*Walker et al. in prep*). In the same quadrats where seedlings were counted, percent ground cover of seedbeds was recorded. Ground cover of mineral soil, early colonizing bryophytes (*Marchantia* sp. and *Ceratodon* sp.), and charcoal were used in analyses since these are all considered important determinants of postfire seedbed quality.

3.2.5 Statistical Analysis

All analyses were performed with the R statistical language, version 3.3.1 (R Core Development Team 2016). We tested for collinearity between all pairs of predictors using a correlation of 0.3 as our threshold. Based on the presence of a small number of correlated variables (Tables S18, S19), predictor variables were reduced to canopy consumption, stand age, DOB, total stand basal area, depth of residual organic layer and ground covers (mineral soil, bryophytes, and charcoal). Canopy consumption was categorically assessed for all trees in a 60m² area and the mode value per plot was used since the mean value would not represent a category. For all other variables, the measured values were used. All continuous predictors were standardized thereby allowing coefficient values to be comparable.

To test the importance of different potential drivers of seedling establishment, we formed candidate models based on *a priori* hypotheses. The seed rain model tests the influence that post-fire seed rain has on seedling establishment; it includes the predictor variables of stand age, cone consumption and stand basal area (Table 3.3, M1). The fire characteristics model tests the influence of canopy consumption, stand age (fire return interval) and date of burn (DOB) (Table 3.3, M2) on seedling establishment. The seed bed conditions model focuses on the attributes of potential microhabitats on which seedlings can establish and includes the predictor variables of depth of residual organic layer and ground cover of mineral soil, bryophytes, and charcoal (Table 3.3, M3). A global model including all predictor variables and a null model consisting of only the random term were also included (Table 3.3, M4 & M5).

We specified pre-planned, user-defined contrasts to assess responses from distinct levels of categorical predictor variables (cone and tree consumption); each contrast is designed to test whether there are significant differences in established seedlings based on the condition of the cones or other canopy fuels. Contrasts were used rather than a Tukey HSD post-hoc analysis since they allow one to test planned comparisons that are considered *a priori* to be more important. For cone consumption, each contrast compares a level of cone consumption to trees with no cones. For tree consumption, each contrast compares levels of consumption to no consumption (live trees). No cones and no consumption are the extreme states of each variable and are thus the baseline for comparison.

To assess the drivers of species-specific seedling establishment (objective 1), the modeled response variable was binomial, representing the presence or absence of seedlings of each species in each quadrat. We used a proportional change response variable to determine a) if a shift in species dominance occurred, and b) if there was a shift, what predictor variables were

driving it (objectives 2 and 3). A proportional response variable allows us to observe changes in the stand composition between pre- and post-fire conditions. The response variable is the change in proportional dominance between pre-fire vs. the post-fire stand. A positive value represents a proportional increase in dominance of that species in the post-fire stand. Proportional change provides an estimate of stand-level resilience to fires as seedling densities tend to be very high immediately post-fire compared to mature stands which have experienced self-thinning (Johnson and Fryer, 1989). We ran a mixed model for each of the following five sets of data using the proportional response variable: 1) changes in conifer dominance on the Plains in year one post-fire; 2) changes in conifer dominance on the Shield in year one; 3) changes in black spruce and jack pine dominance in pre-fire black spruce-dominated sites in year two on the Plains; 4) changes in black spruce and jack pine dominance in pre-fire jack pine-dominated sites in year two on the Plains and; 5) changes in black spruce and jack pine dominance in pre-fire mixed sites in year two on the Plains. A black spruce or jack pine dominated stand was composed of $\geq 80\%$ of that species pre-fire. A mixed stand was dominated by $\leq 80\%$ of both black spruce and jack pine.

Using the candidate generalized linear mixed models, we tested the effect of different predictor variables on the response variables with each model representing one of the three *a priori* hypotheses. Models were run using the ‘glmer’ function in the ‘lme4’ package (Bates et al. 2015). Binomial models for objective 1 specified a binomial distribution; proportional models in objective 2 had a Gaussian distribution. Each model had a random effect of plot nested within site (1|Site/Plot) to account for the spatially nested design of this experiment (two or three transects per site). AICc was calculated for each model to determine which model best represented the data. This is the Akaike Information Criterion corrected for small sample size.

AICc values were computed using the ‘ICtab’ function in the ‘bbmle’ package (Bolker and R Core Development Team 2016). Models were ranked by their IC weights and the model with the lowest AICc score where $\Delta\text{AICc} > 2$ was considered the best model (Burnham and Anderson 2002).

R^2 values were calculated for all models using methods from Nakagawa and Schielzeth (2013) who have provided a way to calculate R^2 values for GLMMs and LMMs. Traditional R^2 calculations cannot be applied to mixed models as they cannot deal with the hierarchical nested structure of the random term. Two different R^2 values can be calculated: R^2_C (conditional) and R^2_M (marginal), where the former represents the variation explained by both the fixed and random effects and the latter explains the variation from only the fixed effects. R^2_C and R^2_M values were calculated for each model using the MuMIn package (Barton 2016). Since R^2_M represents the variation explain by the fixed effects only, it will have a value of 0 for null models.

3.3 Results

In year one on the Shield, there were a total of 50 aspen seedlings counted in 16 quadrats. In year one on the Plains, there were no birch seedlings counted and in year two, there were a total of four birch seedlings in two quadrats. Due to these small sample sizes and the low predictive power, we did not model aspen on the Shield, or birch on the Plains.

3.3.1 *Species-specific drivers of seedling establishment*

Results of AIC-based model selection can be found in Supplementary Information (Tables S3.1a- S3.1g). Drivers of seedling establishment in year one are as follows. For the Shield, significant positive drivers of birch establishment were bryophyte cover, and plot basal area; plot age was a negative driver (Figure 3.2, Table S3). Significant positive drivers of conifer

establishment were bryophyte cover and charcoal cover (Figure 3.2, Table S4). For the Plains, aspen responded positively to bryophyte cover and negatively to residual organic layer depth (Figure 3.3, Table S5); conifer establishment was positively influenced by bryophyte cover and negatively by residual organic layer depth (Figure 3.3, Table S6). For seedling establishment in year two on the Plains, black spruce showed a positive relationship with bryophyte cover and canopy fuel consumption (needles, branches etc.), a negative relationship with date of burn and cone consumption (Figure 3.4, Table S7). Jack pine showed a positive relationship with bryophytes and date of burn (Figure 3.4, Table S8). Aspen establishment was solely predicted by a positive relationship with bryophyte cover (Figure 3.4, Table S9).

3.3.2 Impacts of ecozone on seedling establishment drivers

Across the two ecozones, conifer seedling establishment was positively related to bryophyte cover (Tables S4, S6). Conifer establishment responded negatively to residual organic layer on the Plains and positively to charcoal cover on the Shield. Deciduous seedling establishment was positively associated with bryophyte cover on both the Plains and Shield (Tables S3, S5). On the Plains, aspen establishment was negatively associated with depth of residual organic layer. On the Shield, birch establishment was negatively associated with stand age and positively associated with stand basal area.

3.3.3 Evidence of a successional shift

In year 1 on the Plains, there was a shift towards aspen dominance, driven by a positive relationship with bryophyte presence ($P < 0.001$; Table 4). For all other successional shift models, the null model was selected (based on AIC-based model selection; Tables S10- S17). Figures 3.5 and 3.6 show boxplots of the proportional change variable (difference between pre-fire proportion and post-fire proportion) and graphically represents the changes in stand

composition. On the Plains, in year one, there is a shift from coniferous to aspen dominance ($t = -2.9695$, $P = 0.003$) but in year two this compositional shift has disappeared ($t = -1.555$, $P = 0.12$), suggesting high deciduous mortality. In year one on the Shield, there is a significant shift from coniferous to birch dominance ($t = -7.4043$, $P < 0.001$). In year two on the Plains, in pre-fire jack pine dominated stands, there is no change in dominance for either black spruce ($t = 0.97909$, $P = 0.72$) or jack pine ($t = -0.71785$, $P = 0.72$). In pre-fire black spruce dominated and mixed stands, there is a shift away from black spruce dominance ($t = -19.489$, $P < 0.001$ and $t = -20.518$, $P < 0.001$ respectively) and a corresponding shift towards jack pine dominance ($t = 16.489$, $P < 0.001$ and $t = 16.32$, $P < 0.001$ respectively).

3.4 Discussion

Our results show that in the sub-arctic boreal forest of the Northwest Territories, seedling establishment is driven by moist microhabitats which are often found in association with early colonizing bryophytes. In both ecozones, one-year post-fire, a proportional shift from conifer to deciduous dominance is apparent, but in year two, there is no longer evidence of this shift on the Taiga Plains. This suggests high mortality in deciduous species during these early periods of recruitment. In pre-fire black spruce-dominated stands or mixed jack pine-black spruce stands, there is a significant increase in the proportion of jack pine post-fire. These results suggest that jack pine can establish in much higher densities than black spruce, at least following such a widespread and severe fire year. Future changes to the fire regime will determine how the successional trajectories of these forests play out and whether jack pine becomes an ever more prominent species in these boreal forests.

Under current predictions, more frequent fires are expected in the boreal forest (Beck et al. 2011) which could serve to favour jack pine over black spruce as they become reproductively

mature at an earlier age (Desponts and Payette 1992, Le Goff and Sirois 2004). Seedbank development occurs after 10 years in jack pine and 50 years in black spruce (Crayford and McRae 1983, Viglas et al. 2013). However, fires occurring too frequently will serve to be detrimental to jack pine. At very young ages, cones will not be as serotinous as in older trees and therefore will not contribute to the seed bank (Gauthier et al. 1993). In extended fire-free periods, jack pine is likely to be replaced by longer lived species. Build-up of the soil organic layer will decrease the vigour of jack pine and aerial seedbanks will begin to decrease in size and trees will begin to senesce (Desponts and Payette 1992, Arseneault 2001). If jack pine can maintain at least a few trees in a mature stand, it has the ability to conserve dominance because it has higher germination and survival rates than black spruce on charred seed beds (Thomas and Wein 1985, Sirois 1993). Shifts from black spruce to jack pine dominated stands have been documented in other parts of the boreal forest. In Quebec, Boiffin and Munson (2013) observed a change in proportional dominance; pre-fire, 90% of plots were black spruce dominated whereas post-fire, 60% were jack pine dominated. Shifts from black spruce to jack pine have been seen in well drained sites (Lavoie and Sirois 1998, Le Goff and Sirois 2004), and increased fire frequency and drier climates have resulted in the expansion of jack pine into bog environments in southern Quebec (Pellerin and Lavoie 2003). Weather during both the fire-season and the first summer after fire can play a role in regeneration patterns by contributing to higher intensity fires and post-fire water stress (Black and Bliss 1980; Bessie and Johnson 1995; Lavoie and Sirois 1998).

Date of Burn (DOB) influences which species of conifer established; black spruce is more likely to establish after an early season burn and jack pine after a late season burn (Figure 3.4). DOB is negatively correlated to depth of the residual organic layer ($r = -0.33$), indicating that sites with a later date of burn have less residual organic layer. Thinner residual organic

layers result in higher rates of seedling establishment as seedlings are less likely to dry out (de Groot et al. 2004). As a result of quicker and longer radicle extension (Thomas and Wein 1985), jack pine can access moisture supplies faster and deeper than black spruce can. Jack pine seeds do not require stratification and can germinate within 15- 60 days of being released (Galloway 1986, Bell 1991). Black spruce seeds require time to break their dormancy and this occurs under moist conditions (Zasada et al. 1992). If seeds are released early in the summer, black spruce can stratify throughout the summer and germinate by the end of the season; if they are released at the end of the summer, they will stratify over winter and emerge as seedlings in the spring. Further, at higher air temperatures, jack pine germinate quicker than black spruce (Wang and Lechowicz 1998). These higher temperatures may be reflective of later season temperatures and help to explain the higher probability of jack pine establishment at later DOB.

A surficial bryophyte layer keeps soil temperatures cool and moist by insulating the ground (Bonan 1991; Gornall et al. 2007; Blok et al. 2011). As a result, bryophytes are known to establish in moist-microhabitats and are considered early post-fire colonizers (Foster 1985; Rambo 2001; Ryömä & Laaka-Lindberg 2005). The presence of bryophytes is therefore indicative of surficial soil moisture and mineral soil exposure, making these areas preferential for establishment of all species.

In year one on both the Plains and the Shield, there were significant shifts towards deciduous dominance (Figure 3.5). In year two on the Plains, this shift is no longer present (Table S11). Declines in aspen density during the first two growing seasons are to be expected (Zasada et al. 1992). Further, misidentification of deciduous species in year one was common. Seedlings are very small and immature *Salix spp.* and *Epilobum angustifolium* can often be confused for small aspen seedlings, for example. In year two, these seedlings are more readily

discernible and more accurate estimations of seedling establishment can be made. Sites on the Shield were not re-assessed in year two due to logistical constraints. Due to the pattern that has emerged on the Plains, sites on the Shield will be re-assessed in year three to provide a more thorough understanding of successional patterns in both ecozones.

Biogeographical legacies appear to play important roles in boreal forest successional trajectories. Where jack pine is absent, aspen serves as a post-fire competitor to black spruce and as a result of exposed mineral soil and/or complete combustion of black spruce cones, is able to establish in high densities and dominate the canopy (Johnstone and Chapin 2006b). Where jack pine is present, it appears to play the role of the post-fire competitor. It is a fast-growing species with rapid, deep tap root extension (Rudolph and Laidly 1990) and if it can seed into a site, it is able to do so more quickly and at much higher rates than black spruce (Weber et al. 1987, de Groot et al. 2003) resulting in a change in dominance. In post-fire succession studies in Alaska, lodgepole pine seedlings showed higher rates of growth than either spruce or aspen (Johnstone and Chapin 2006b); given the similarities between jack and lodgepole pine, it is not unreasonable to expect that jack pine seedlings would also experience a height advantage over both spruce and aspen.

Shifting to jack pine dominated forests will serve to change how the forests function. In Alaska where shifts to deciduous dominated forests have been characterized, there have been increases in forest albedo (Beck et al. 2011). However, a shift from black spruce to jack pine would likely not result in such dramatic changes in albedo (Betts and Ball 1997, Lukeš et al. 2013). Forest flammability would likely change as fuel loads in jack pine and black spruce differ. The fuel structure of black spruce makes fires more likely to reach the crown than in jack pine stands. In black spruce forests, the ground has a highly flammable shrub layer which carries the

flames above the surface and promotes ignition of low, lichen covered dead branches (i.e. ladder fuels) that move the flames to the crown (Viereck 1983). A lack of ladder fuels in jack pine stands and a gap between the crown and the base of the tree make sustained crown fires rare (Stocks and Alexander 1980). Forest floor depth and fuel loads are higher in black spruce forests than jack pine (Letang and de Groot 2012). In black spruce forests, *Cladonia* spp lichens, an important food source of caribou (*Rangifer tarandus granti*), are abundant (Joly et al. 2007). Shifts from black spruce to deciduous forests result in changes to wildlife habitat as these lichens are largely absent in deciduous dominated forests. *Cladonia* spp lichens are present in jack pine forests (Carroll and Bliss 1982) suggesting that a shift to jack pine dominance would not present such an extreme change in wildlife habitat. However, these lichens are largely absent in recently burned forests (Collins et al. 2011). The threat of a more frequent and wide-spread fire regime could serve to decrease the preferred winter range for caribou as more forests become recently burned and do not have the *Cladonia* lichens for caribou to subsist on (Rupp et al. 2006). This may alter the landscape-scale distribution of caribou as well as their population dynamics (Joly et al. 2007).

The results of this study provide insight into the response of the boreal forest of the Northwest Territories to a changing pattern of disturbance. Our results show patterns of changing dominance. It is important to note that these changes are not necessarily indicative of an alternative successional trajectory. For a shift to occur, these new patterns would have to dominate for multiple fire cycles and cohorts. If, after this initial dominance of jack pine, the fire cycle lengthens, then it is likely that black spruce will succeed into these sites. However, if the cycle shortens, as predicted by global change models, jack pine will likely increase in dominance in these forests and this will be indicative of a shift. The presence of jack pine in the forests of

the NWT appear to be driving different patterns of stand dominance than have been seen in Alaska and the Yukon, implying differences between regions across the Northwestern boreal forests as a result of biogeographical legacies.

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Tables and Figures

Table 3.1. Key of the six potential moisture classes used to classify sites (Johnstone et al., 2008).

Moisture Class	Description
Subhygric	Very considerable surface moisture; saturated with less than 5% standing water
Mesic to Subhygric	Considerable surface moisture; depressions or concave toe-slopes
Mesic	Moderate surface moisture; flat or shallow depressions including toe-slopes
Subxeric to Mesic	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

Table 3.2. Summary of continuous predictor variables measured at all plots.

	Taiga Plains		Taiga Shield	
	Mean \pm SE	Range	Mean \pm SE	Range
Bryophyte Cover (%)	4.000 \pm 0.70	0.0 – 100.0	3.000 \pm 0.40	0.0 – 100.0
Mineral Soil Cover (%)	7.000 \pm 0.90	0.0 – 100.0	6.000 \pm 0.90	0.0 – 100.0
Charcoal Cover (%)	1.000 \pm 0.01	0.0 – 20.00	1.000 \pm 0.10	0.0 – 5.000
Stand BA (m ² •ha ⁻¹)	19.00 \pm 0.48	0.03 – 45.35	8.700 \pm 0.30	0.30 – 30.70
Stand Age (years)	100.0 \pm 2.0	33.0 – 232.0	101.0 \pm 3.0	19.0 – 215.0
Date of Burn (Day of year)	200.0 \pm 0.6	183 – 225.0	197.0 \pm 0.40	185 – 217.0
Fire Weather Index	33.22 \pm 0.54	9.81 – 52.39	30.85 \pm 0.66	8.40 – 53.46
Residual Organic Depth (cm)	13.00 \pm 0.69	0.0 – 64.00	13.00 \pm 0.73	0.0 – 56.00
Burn Depth (cm)	9.4 \pm 0.2	0.0 – 19.6	10.7 \pm 0.2	3.9 – 17.80

Table 3.3: List of candidate models used to assess relative influence of variables on seedling establishment. All models had a random term of (1|Site/ Plot) to account for the spatially nested design of the study.

Model Name	Predictor Variables Included
M1: Seed Rain Processes	Stand Age + Canopy consumption + Stand basal area + random term
M2: Fire Characteristics	Canopy consumption + Stand Age + Date of Burn (DOB) + random term
M3: Seed Bed Conditions	Depth of residual organic layer + mineral soil ground cover + bryophyte ground cover + charcoal ground cover + random term
M4: Global Model	Stand Age + Canopy consumption + Stand basal area + DOB + residual organic layer + mineral soil ground cover + bryophyte ground cover + charcoal ground cover + random term
M5: Null Model	Random term

Table 3.4. A: Results of AIC based model selection for proportional change happening 1-year post-fire on the Taiga Plains. Response variable for all models is the proportional change in conifer dominance between pre- and post-fire conditions. For each model, Log-likelihood (Log(L)), Akaike information criterion (corrected for small sample size AICc), degrees of freedom (df), model weight, and model R² values (R²_C: variance explained by the fixed and random factors; R²_M: variance explained by the fixed factors) are given. Model with $\Delta\text{AICc} > 2$ is considered to be the best fit (Burnham and Anderson 2002). Model structure is described in Table 3. **B.** Best model selected for proportional change happening 1-year post-fire on the Taiga Plains. Modeled response variable is the proportional change in conifers between pre- and post-fire conditions. AIC-selected linear mixed effects model describing proportional change happening 1-year post-fire on the Taiga Plains. The model represents the elements of the seed bed and incorporates ground cover of mineral soil, bryophyte, and charcoal, and depth of the residual organic layer.

A	Model	Log(L)	AICc	ΔAICc	df	Weight	R ² _M	R ² _C
	Seed Bed Conditions	-157.1	330.6	0	8	0.74	0.06	0.62
	Null Model	-162.3	332.8	2.1	4	0.26	0.00	0.58
	Fire Severity	-167.1	352.7	22.1	9	<0.001	0.06	0.60
	Seed Rain Processes	-170.4	361.3	30.7	10	<0.001	0.04	0.60
	Full Model	-169.1	376	45.3	18	<0.001	0.13	0.66
B		Estimate	Std. Error	df	t value	Pr(> t)		
	Intercept	-0.0702	0.04211	22.1	-1.667	0.11		
	Mineral Cover (%)	-0.0137	0.0214	361.5	-0.642	0.522		
	Bryophyte Cover (%)	-0.1091	0.01903	354.4	-5.732	2.12 x10⁻⁰⁸		
	Charcoal Cover (%)	-0.0134	0.0175	316.2	-0.765	0.445		
	Residual Organic Layer (cm)	0.00855	0.02664	320.8	0.321	0.748		

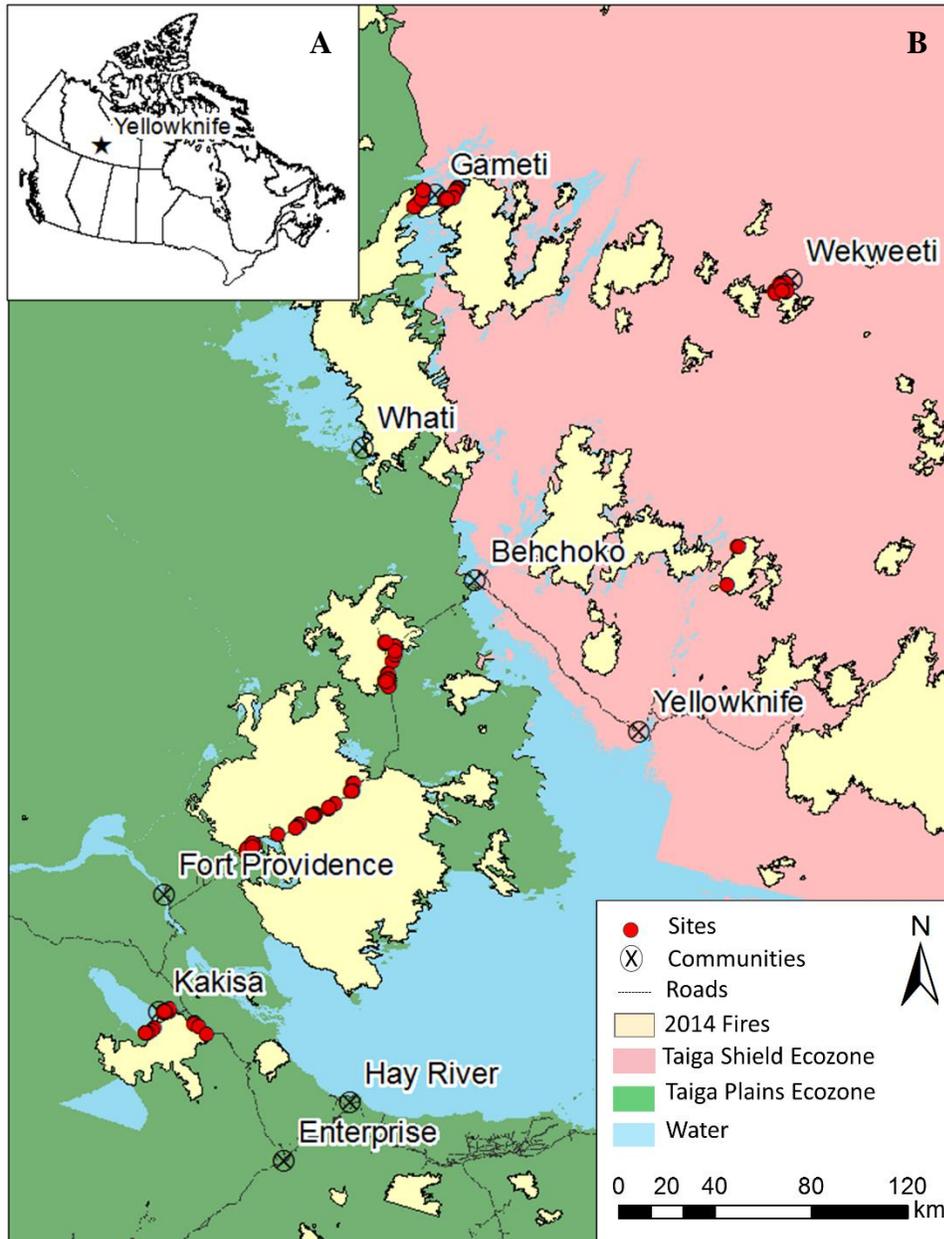


Figure 3.1. Map of study sites. **A** Sites are located in the southern Northwest Territories. **B** Four burns are in the Taiga Plains Ecozone and three are in the Taiga Shield Ecozone. All sites burned in 2014 and within 1km of highway, water or helicopter drop off.

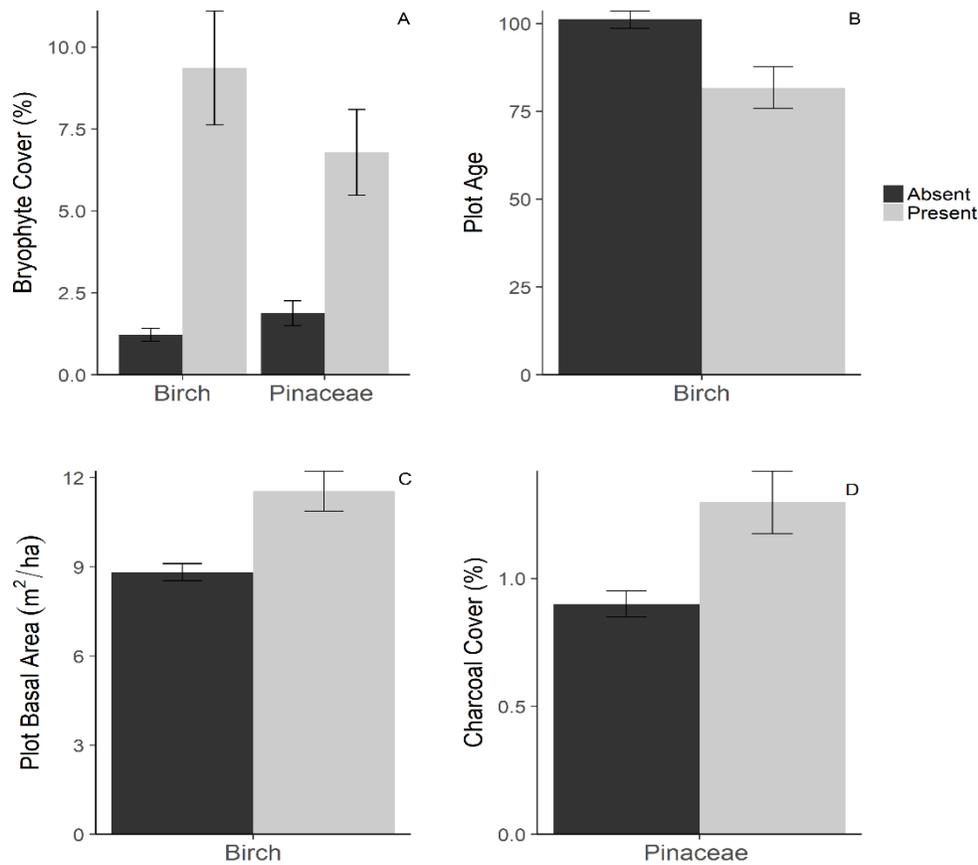


Figure 3.2. Mean value (\pm SE) for presence and absence of species establishment for each significant predictor variable on the Taiga Shield (non-significant drivers are not included). **A** Birch and *Pinaceae* (where differences between black spruce and jack pine were not discernible) are more likely to be present with high bryophyte cover; **B** Birch is more likely to be present in younger stands; **C** Birch is more likely to be present with high plot basal area; **D** *Pinaceae* is more likely to be present with high levels of charcoal cover.

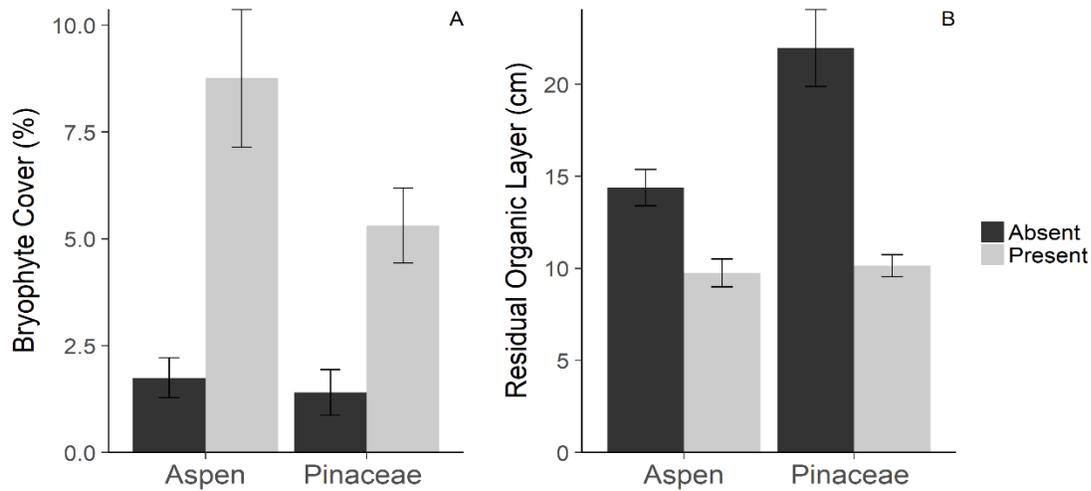


Figure 3.3. Mean value (\pm SE) for presence and absence of species establishment for each significant predictor variable on the Taiga Plains in year one (non-significant drivers are not included). **A** Aspen and *Pinaceae* (where differences between black spruce and jack pine were not discernible) are more likely to be present with high bryophyte cover; **B** Aspen and *Pinaceae* are more likely to be present with low depths of residual organic layer.

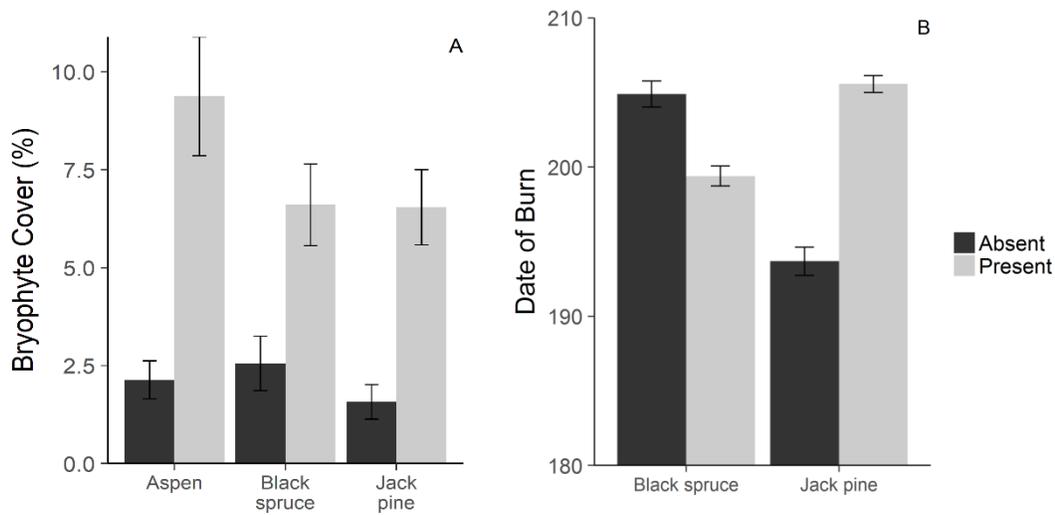


Figure 3.4. Mean value (\pm SE) for presence and absence of species establishment for each significant predictor variable on the Taiga Plains in year two (non-significant drivers are not included). Plots show species that have significant relationships with presented drivers (non-significant drivers are not included). **A** Aspen, black spruce, and jack pine are more likely to occur with bryophyte cover; **B** Black spruce is more likely to be present after early season burns; jack pine is more likely to be present after late season burns. Y-axis is bound by the length of the fire season during 2014 (range: 183-225).

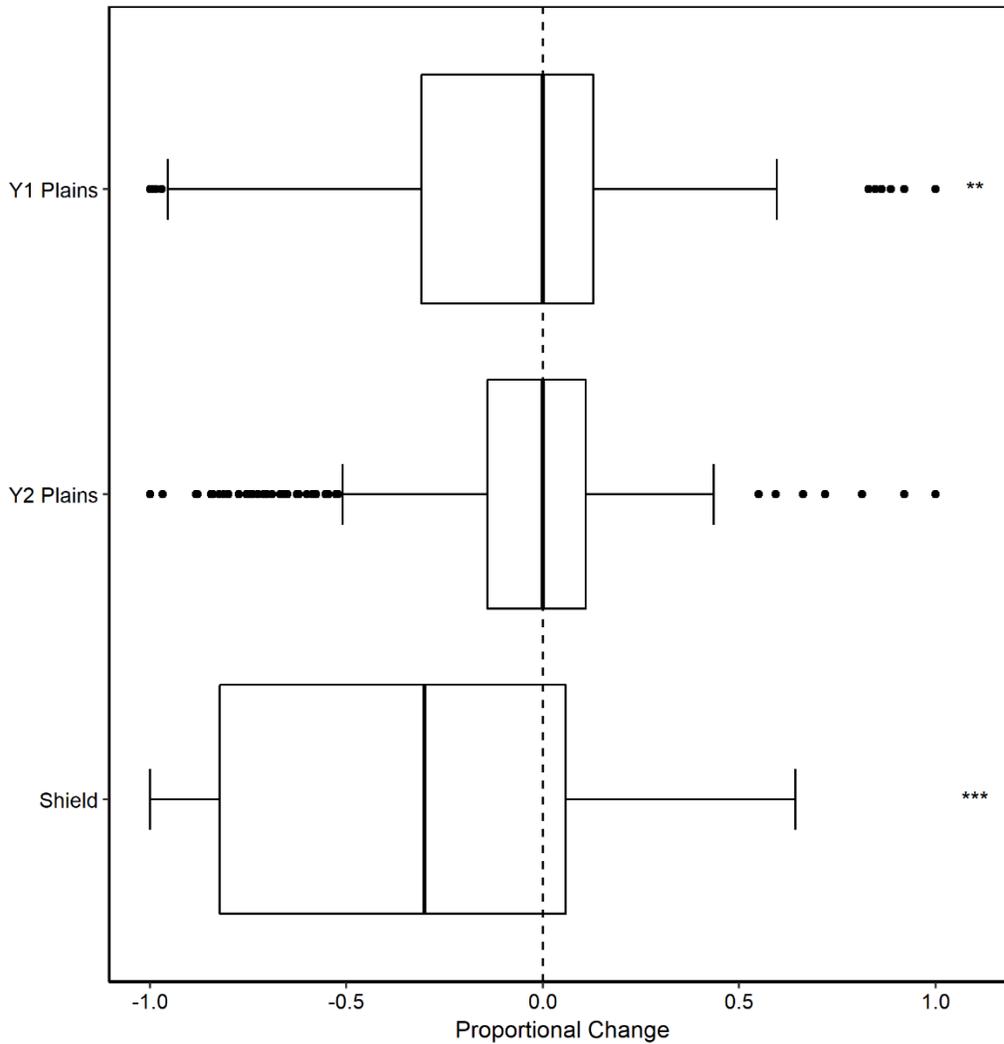


Figure 3.5. Proportional changes of coniferous species between pre- and post-fire periods. Positive responses indicate an increase in conifer dominance post-fire. Negative proportional change values indicate a post-fire decrease in conifer dominance and a corresponding increase in deciduous dominance. To determine if proportional change is significantly different than 0, one sample Student's t-tests were used. For year 1 on the Plains, there is a significant decrease in the proportion of conifers post-fire and a shift towards *Populus tremuloides* dominance ($t = -2.9695$, $P = 0.003$). This same shift is not seen in year 2 on the Plains ($t = -1.55$, $P = 0.12$). On the Shield, there is a significant decrease in the proportion of conifers post-fire and a shift towards *Betula neolaskana* dominance ($t = -7.404$, $P < 0.0001$). Year 2 data are not available for the Taiga Shield sites.

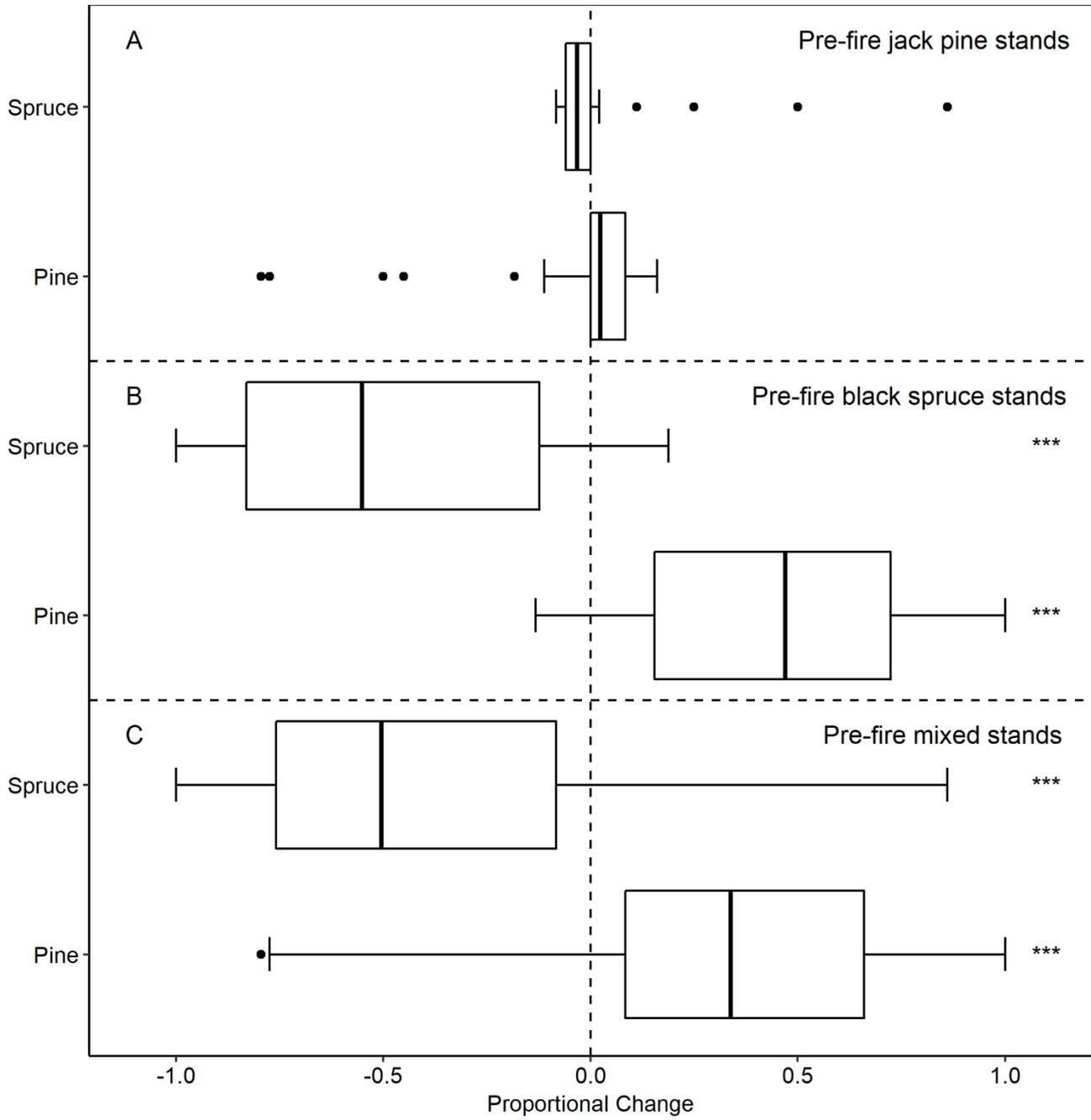


Figure 3.6. Proportional changes of dominant tree species between pre- and post-fire conditions. Positive values on x-axis indicate an increase in dominance of the modelled species (y-axis); black spruce is represented on the y-axis as ‘Spruce’, jack pine is represented as ‘Pine’. Negative proportional change values indicate a decrease in dominance of the modelled species. To determine if proportional change is significantly different than 0, one sample Student’s t-tests were used. **A** Proportional change of black spruce and jack pine in pre-fire jack pine dominated stands. There are no significant changes in dominance between pre- and post-fire stands (black spruce: $t = 0.979$, $P = 0.716$; jack pine: $t = -0.718$, $P = 0.716$); **B** Proportional change of black spruce and jack pine in pre-fire black spruce-dominated stands. There is a significant decrease in the proportion of black spruce ($t = -19.489$, $P < 0.001$) and a significant increase in the proportion of jack pine ($t = 16.489$, $P < 0.001$); **C** Proportional change of black spruce and jack pine in pre-fire mixed stands. There is a significant decrease in the proportion of black spruce ($t = -20.518$, $P < 0.001$) and a significant increase in the proportion of jack pine ($t = 16.32$, $P < 0.001$).

Chapter 4: General Discussion

4.1 Synthesis of results

My overarching research goal in this thesis was to determine if the boreal forest of the Northwest Territories is experiencing a change in patterns of dominance as a result of changing patterns of disturbance. In Chapter 2, I measured post-fire seed rain to investigate the drivers of black spruce seed availability and viability following fire and explored how these change as a function of fire characteristics and ecological legacies. In Chapter 3, I sought to examine the drivers of species-specific seedling establishment post-fire, and how biogeographical legacies affect ecological memory with a changing pattern of disturbance. Seed rain and seedling establishment both play crucial roles in post-fire forest recovery and influence the successional trajectory of the forest. In other regions of the boreal forest, changes to the fire regime have resulted in decreased black spruce seed availability as a result of severe cone combustion (Zasada et al. 1979, Arseneault 2001, Johnstone et al. 2009) or burning of immature cones (Johnstone and Chapin 2006, Viglas et al. 2013) and recruitment failures due to poor seedbed conditions (Johnstone and Chapin 2006b, Veilleux-Nolin and Payette 2012), competition from deciduous species (Johnstone and Chapin 2006a, Johnstone et al. 2010b), or reduced seed availability (Brown and Johnstone 2012).

Results from the two studies presented here suggest that black spruce forests in the NWT may not be resilient to a changing pattern of disturbance. Results from Chapter 2 show that with increasing fire severity, there is decreased availability of viable black spruce seed rain. Under an intensifying fire cycle, black spruce forests will likely experience dampened recruitment due to decreased availability of viable seeds. In Chapter 3, I demonstrated a shift towards jack pine dominance in stands that were mixed (jack pine and black spruce) or black spruce dominated

prior to fire. The shift towards jack pine dominance that I have characterized likely occurred as a result of a) this species' early rates of reproductive maturation (Crayford and McRae 1983), which make it less sensitive to fire return interval, and b) its rapid post-fire seed abscission (Greene et al. 2013), which allows it to rapidly colonize burned sites. As patterns of disturbance continue to change, both of these factors may serve to favour this species' dominance. Another trait that should serve to favour jack pine under future fire scenarios is its cone scales which are thicker than those of black spruce, making them more resistant to severe fires (Beaufait 1960, Zasada et al. 1979, Arseneault 2001, Arseneault and Sirois 2004). Further work assessing the response of jack pine cones to severe fires is required since the role of fire intensity in the regeneration of jack pine forests is unclear; high intensity burns have resulted in both positive (Weber et al. 1987) and negative (Arseneault 2001) influences on regeneration.

In the Quebec boreal forest, where both jack pine and black spruce are present, shifts to jack pine dominance have occurred in both well drained and bog environments, as well as in plots that were dominated by black spruce pre-fire (Lavoie and Sirois 1998, Pellerin and Lavoie 2003, Le Goff and Sirois 2004, Boiffin and Munson 2013). In the NWT, a combination of low levels of viable black spruce seeds and the early regeneration strategies of jack pine may be causing this system to shift toward greater jack pine dominance.

Here, I have investigated post-fire seedling recruitment (Chapter 3) that has been influenced by constraints on seed availability (Chapter 2). A next step is to investigate drivers of seedling establishment without constraints on seed availability. An additional experiment has been established by the larger research team of which I am a part. This is designed to test the role that environment plays in species-specific recruitment, in the absence of dispersal limitation. We have added a known amount of viable seed to each plot so we will be able to determine which

conditions result in optimum recruitment and growth for each species. Results from that study will further tease apart the constraints on seedling establishment.

There is little evidence in the literature about successional patterns of Northwest Territories boreal forests. This stage of high density jack pine may be an ephemeral successional stage that will disappear once black spruce begin grow. As a result of limited long-term monitoring in the NWT, we do not know if high density jack pine establishment is a pattern that regularly occurs in these forests. In our dataset, we have sites that we know were classic black spruce lowland sites pre-fire and these sites have been densely colonized by jack pine. As a result of the site moisture conditions, jack pine may not be able to survive in these sites long term. Sites for this project were established as permanent sampling plots with the intention that they can be revisited in the future and I propose that long-term monitoring is required. Long term studies in the NWT and other boreal forest regions show that a majority of recruitment occurs within the first few years post-fire and that patterns of early establishment are representative of how the canopy will look in subsequent decades (Lavoie and Sirois 1998, Charron and Greene 2002, Gutsell and Johnson 2002, Day et al. 2017). As a result of these patterns, we assume that the patterns of dominance that we currently see will set the trajectory for future dominance.

Due to logistical constraints, sites on the Taiga Shield were not re-assessed in year two post-fire. Due to the high mortality of deciduous seedlings experienced between years one and two on the Taiga Plains, I think that it is important to re-count sites on the Taiga Shield to determine if the shift to deciduous dominance still holds after the initial anticipated mortality of birch seedlings. These re-counts will happen in July 2017 and will be incorporated into the manuscript for chapter 3.

Due to the prevalence of jack pine in the NWT, interactions between jack pine and black spruce and the roles that they play post-fire are important. In the present study, the timing of our seed trap deployment resulted in missing seed rain of the other species of interest, in particular jack pine. Future fire studies in the NWT should seek to obtain information about seed abscission rates of both jack pine and black spruce to determine if patterns are the same as in Quebec (see Greene et al. 2013). To study this, seed traps would need to be deployed almost immediately post-fire in either pre-selected areas or in experimental or control fires; logistically, experimental or control fires would be ideal for this type of study.

4.2 Future modeling efforts

1. For the statistical models in chapter 2, a negative binomial distribution was used as the variance of the response variable was greater than the mean, suggesting overdispersion. It has been questioned how much overdispersion is present in this dataset and how much it will influence the model outcomes. Prior to publication, models will all be re-run using both Poisson and negative binomial distributions, and AICc values will be compared between the two sets of models.
2. Data for the response variable in chapter 2 was transformed to account for the amount of time that each trap was left out for (i.e. number of weeks in each sampling period). As a result of this transformation, the data no longer has a negative binomial (or Poisson) distribution. Instead, the raw count data should be used as the response and additional parameter can be added to the model to account for the different length of sampling periods (offset = $\log(\text{weeks})$).
3. In chapter 2, there is uneven distribution in the canopy combustion variable (cone consumption) and it is heavily skewed towards the ‘no cones’ category. An additional

variable was assessed in the field (tree consumption) and this is a more comparable metric to other fire studies. This metric will thus be used in this analysis as publications are refined.

4. At the time of completing the original data analysis for this thesis, it was only possible to calculate R^2_C for models that used the glmmADMB package. It is now possible to calculate the R^2_M as well and this will be included for the manuscript.
5. In the counts of seed rain, one seed trap at two different time periods had particularly high counts of seeds. Data analysis was performed both with and without this outlier and the results were consistent. However, this seed trap was located close to a black spruce cone ball and to be consistent with other seed rain studies, it should be removed from further analysis.
6. Since the null model was selected so frequently (chapter 2) and explains a lot of variation compared to the deterministic model (chapter 3), the random term is explaining a lot of the variation encountered. As a result of landscape scale variability, burn complex is explaining a lot of the variation. Burn complex was included in the random term in chapter 2 to provide consistency between this study and others in the larger NWT fire project of which this study is a part of and should be included in future analysis for chapter 3. It is important to consider differences of both mean seed rain and patterns of dominance across different burn complexes to see whether differences are significant.

4.3 Summary

The model that best predicted total and viable black spruce seed rain was the fire characteristics model. Canopy consumption was a significant predictor of viable seed rain; stands that experienced a less severe burn had more viable black spruce seed rain. Establishment of all

species was greatest when there was high ground cover of *Marchantia* sp. and *Ceratodon* sp. The presence of bryophytes is indicative of surficial surface moisture (Foster 1985; Rambo 2001; Ryömä & Laaka-Lindberg 2005), and exposed mineral soil, both of which are high quality seedbeds for seedling establishment. Early season burns were more likely to result in black spruce establishment; late season burns were more likely to result in jack pine establishment. This is possibly as a result of cooler soil temperatures in early season burns which allows black spruce to break their dormancy period, as well as thinner residual organic layer in late season burns. Pre-fire black spruce dominated and mixed stands showed a significant decrease in black spruce dominance and an increase in the proportion of jack pine dominance suggesting that an alternative successional trajectory has been initiated.

This is the first study to explore post-fire successional dynamics in the boreal forest of the NWT which has a unique composition in Northwestern North America as a result of its biogeographical history and the presence of jack pine (Flint 1957, Critchfield 1985). As global temperatures continue to rise, we expect the fire regime to continue to change (Kasischke and Stocks 2000, Beck et al. 2011) and so it is imperative that we know how forests are responding. Fires that are too frequent or severe serve to reduce the regeneration potential of black spruce forests by reducing quantities of seed rain. Instead, these conditions may promote the dominance of jack pine.

4.4 Contributions

This research provides new information about post-fire forest regeneration and successional trajectories in the Northwest Territories. Many other studies have looked at post-fire responses of boreal forests in Alaska and Quebec to a changing fire regime (Johnstone and Chapin 2006a, Johnstone et al. 2010, Boiffin and Munson 2013), but this is the first study to look

at the boreal forest of the NWT. The boreal forest of the NWT is unique in its composition in western North America's boreal forest. The distribution of jack pine extends into NWT but not into Alaska and the Yukon where other resilience and successional trajectory studies have occurred (Flint 1957, Critchfield 1985). While studies from Quebec have documented shifts towards jack pine dominance, the boreal forest of the NWT is located at much higher latitudes than the Quebec boreal forest; our study sites range from 60.8°N to 64.2°N, while sites in Quebec that have documented shifts to jack pine range from 48°N to 54°N. Further, sites in Quebec are located in areas of continuous boreal forest and in zones of isolated to sporadic permafrost. Our sites range from continuous boreal forest at the southern edge to close to the boreal forest-arctic tundra boundary in north and all sites are located in the zone of discontinuous permafrost. Forests that are limited in their growth by climate have been shown to transition from boreal forest to tundra as a result of fires (Sirois 1992, Brown and Johnstone 2012) making these sites at the northern edge of their distribution of particular interest.

With a changing climate, large and extreme fire years are becoming more likely. The 2014 fire season was the largest on record in the NWT and as a result, provided an exceptional opportunity to examine the resilience of these forests to changing patterns of disturbance. Post-fire seed availability and seedling recruitment are important mechanisms for determining the establishment of patterns of dominance (Greene et al. 1999). Results from this research show that fire severity is a determining factor for both seed availability and seedling establishment. For seed rain processes, fire characteristics factors that affect individual trees (i.e., cone consumption), rather than the stand (i.e., distance to unburned edge), are influencing the regeneration potential. Our research shows evidence for a shift in dominance from black spruce to jack pine dominated stands. Additionally, higher rates of jack pine establishment occurred as a

result of late season fires and a correspondingly thinner residual organic layer. If the fire return interval continues to be short, this will promote the dominance of jack pine.

In summary, this research indicates that the boreal forest of the NWT may not be responding to changing patterns of disturbance in the same direction or magnitude as other boreal forests in Northwestern North America where similar studies have been undertaken as a result of biogeographical legacies.

4.5 Integrative Approach

The Integrative Biology program at Wilfrid Laurier aims to “provide students with a trans-disciplinary approach to biological research that allows them to explore the answers to complex questions from a perspective that bridges the traditional subdisciplines of biology, across diverse taxa, over time scales ranging from short (physiological) to long (evolutionary).”

Work that I have completed for my MSc has been a part of a large, multi-investigator study that involves researchers and methods from many different disciplines. The numerous principle investigators and trainees involved in this project include ecologists, biogeochemists, mycologists, soil scientists, permafrost scientists, and spatial modellers from many different institutions across Canada and the USA. As a result, measurements taken at each site are being used for carbon analysis, combustion estimations, analyses of fire resistant fungi, and models of thawing permafrost among others. Results from my study and other vegetation work from this project will be used to parameterize upscaling efforts required to conduct landscape level assessments of potential changes to caribou habitat with climate change and associated changes to fire disturbance patterns. Being exposed to many disciplines and the objectives and methods associated with these diverse sub-projects has resulted in me becoming more integrative in the questions that I ask and the way that I think about my study system.

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Supplementary Information

Seed Viability

To determine viable seed rain, germination trials were conducted using the sorted seeds from the seed traps. The protocol for the germination trials follows Leadem et al., (1997). Specifically, all seeds were surface sterilized by immersing them in H₂O₂ for five minutes and rinsed three times with de-ionized water. All seeds were then stratified by soaking for 24 hours in 20-25°C de-ionized water, following which the seeds were placed in plastic bags or vials for 21 days at 2-5°C. Seeds were placed on moist filter paper on Petri dishes to germinate in a greenhouse for 21 days where conditions were 23°C for 16 hours of light and 19°C for 8 hours of dark. Dishes were set up in a randomized blocking design with 10 independent blocks and dishes distributed randomly amongst blocks. Samples from each trap were tested separately unless there were more than 100 seeds in a sample in which case the sample was separated into subsamples. Dishes were checked daily to ensure sufficient moisture. At the end of the 21-day germination period, the number of germinated seeds were counted.

Viability tests were then run on a subsample of seeds that did not germinate to determine whether they are viable to germinate (i.e. filled seeds) or not. 10 ungerminated seeds from each site were tested for viability (n=250 seeds). Protocol for the viability test follows Leadem (1984). Seeds were soaked overnight in 20°C water to soften the tissues. A thin layer of the endosperm was sliced off and the cut seeds were placed in Petri dishes and covered with 1% Tetrazolium (TZ) solution (pH= 6.5-7). Seeds were then incubated for 2-8 hours and removed when staining is complete. To determine when staining is complete, an additional dish of seeds was stained and seeds were cut periodically to assess how far the staining has progressed and to ensure that the staining did not get too dark. When staining was complete, the TZ solution was drained and the

seeds were rinsed 2-3 times with water. Seeds were then cut in half to view the embryo. The protocol by Leadem (1984) provides figures which were then used to assess the make-up of inside of the seed. None of the seeds that were tested for viability were viable, indicating that all seeds that were viable germinated during the preceding experiment.

Date of Burn estimation

Methods for estimating date of burn (DOB) follow those of Loboda & Csiszar (2007) and were determined using MODIS satellite imagery. DOB estimation was provided by L. Bourgeau-Chavez and N. French. The algorithm used finds the earliest date of burning in a fire complex (the date of ignition) and finds all active burning pixels (250m²) that occur before a temporal threshold and are within 2.5km of the initial pixel. Once a point is assigned to a fire event, it is excluded from further consideration. The cluster is complete once no new points fall within the time and space thresholds set; a new cluster then begins based on the first unassigned date.

Fire Weather Index metric

Fire Weather Index (FWI) was obtained from the Global Fire WEather Database (GFWED) (NASA, 2016). FWI is a combination of the initial spread index (ISI) and the build-up index (BUI); it represents the intensity of the spreading fire (Turetsky et al., 2004). ISI rates the predicted fire spread, by combining the fine fuel moisture code (FFMC) and the effect of wind. BUI rates the amount of fuel available for combustion by combining the Duff Moisture Code (DMC; a rating of the moisture content in the duff layer which gives an indication of fuel consumption), and the Drought Code (DC; an indicator of seasonal drought effects) (Natural Resources Canada 2008).

Reid – Supplementary Information

Table S1. Correlation matrix for all predictor variables for seed rain analysis. Bolded values indicate correlations that were >0.3. Residual organic soil depth has been log-transformed. Depth of Burn was eliminated from further analyses since it was highly correlated with other variables. Fire Weather Index (FWI) was removed from further analysis because it correlated with Date of Burn (DOB); in the larger study, this variable was also removed because it highly correlated with DOB. Other correlations were visually inspected but we chose to leave them in the analysis since there did not appear to be any visual correlation between the variables. Visual representations of all correlations are in Figure S2.

	Stand age (years)	Distance to unburnt edge (m)	Black spruce BA (m ² ·ha ⁻¹)	Burn depth (cm)	Date of Burn (DOB; day of year)	Fire Weather Index (FWI)	Residual organic soil depth (cm)
Stand age (years)	1						
Distance to unburnt edge (m)	0.246536	1					
Black spruce BA (m ² ·ha ⁻¹)	0.434026	0.100749	1				
Burn depth (cm)	0.613408	0.059433	0.382944	1			
Date of Burn (DOB; day of year)	-0.493430	0.053812	-0.028177	-0.138348	1		
Fire Weather Index (FWI)	0.167072	-0.224715	-0.025633	-0.180712	-0.328443	1	
Residual organic soil depth (cm)	-0.223272	-0.145169	-0.083169	0.009813	-0.183890	0.098785	1

Table S2a. Results of AIC based model selection for birch seedling establishment on the Taiga Shield in 2015 (Year 1 post-fire). Modeled response variable is the presence or absence of seedlings in each quadrat. For each model, Log-likelihood (Log(L)), Akaike information criterion (corrected for small sample size AICc), degrees of freedom (df), model weight, and model R^2 (R^2_C : variance explained by the fixed and random factors; R^2_M : variance explained by the fixed factors), are given. Model with $\Delta AICc > 2$ is considered to be the best fit (Burnham and Anderson 2002).

Model	Log(L)	AICc	$\Delta AICc$	df	Weight	R^2_C	R^2_M
Full Model	-151.4	331.9	0	13	0.966	0.70	0.63
Seed Bed Conditions	-161.1	338.6	6.7	7	0.034	0.56	0.38
Seed Rain Processes	-176	364.2	32.3	5	<0.001	0.42	0.25
Fire Characteristics	-185.8	390	58.1	8	<0.001	0.60	0.39
Null Model	-193.4	395	63.1	3	<0.001	0.40	0.00

Table S2b. Results of AIC based model selection for *Pinaceae* seedling establishment on the Taiga Shield in 2015 (Year 1 post-fire). Modeled response variable is the presence or absence of seedlings in each quadrat. For each model, Log-likelihood (Log(L)), Akaike information criterion (corrected for small sample size AICc), degrees of freedom (df), model weight, and model R² (R²_C: variance explained by the fixed and random factors; R²_M: variance explained by the fixed factors), are given. Model with $\Delta\text{AICc} > 2$ is considered to be the best fit (Burnham and Anderson 2002).

Model	Log(L)	AICc	ΔAICc	df	Weight	R ² _C	R ² _M
Seed Bed Conditions	-181.6	379.5	0	7	0.986	0.48	0.11
Full Model	-175.2	388.1	8.6	17	0.014	0.62	0.44
Fire Characteristics	-188.1	394.6	15.1	8	<0.001	0.58	0.39
Null Model	-194.9	398	18.4	3	<0.001	0.41	0.00
Seed Rain Processes	-191	402.5	23	9	<0.001	0.43	0.05

Table S2c. Results of AIC based model selection for aspen seedling establishment on the Taiga Plains in spring 2016 (Year 1 post-fire). Modeled response variable is the presence or absence of seedlings in each quadrat. For each model, Log-likelihood (Log(L)), Akaike information criterion (corrected for small sample size AICc), degrees of freedom (df), model weight, and model R^2 (R^2_C : variance explained by the fixed and random factors; R^2_M : variance explained by the fixed factors), are given. Model with $\Delta AICc > 2$ is considered to be the best fit (Burnham and Anderson 2002).

Model	Log(L)	AICc	$\Delta AICc$	df	Weight	R^2_C	R^2_M
Seed Bed Conditions	-258.9	534.1	0	7	0.979	0.5	0.15
Full Model	-256.5	541.9	7.7	13	0.021	0.51	0.18
Seed Rain Processes	-273	558.2	24	5	<0.001	0.41	0.03
Null Model	-275.2	558.4	24.3	3	<0.001	0.41	0.00
Fire Characteristics	-272.8	564.1	29.9	8	<0.001	0.43	0.40

Table S2d. Results of AIC based model selection for *Pinaceae* seedling establishment on the Taiga Plains in spring 2016 (Year 1 post-fire). Modeled response variable is the presence or absence of seedlings in each quadrat. For each model, Log-likelihood (Log(L)), Akaike information criterion (corrected for small sample size AICc), degrees of freedom (df), model weight, and model R^2 (R^2_C : variance explained by the fixed and random factors; R^2_M : variance explained by the fixed factors), are given. Model with $\Delta AICc > 2$ is considered to be the best fit (Burnham and Anderson 2002).

Model	Log(L)	AICc	$\Delta AICc$	df	Weight	R^2_C	R^2_M
Seed Bed Conditions	-197.5	411.2	0	7	0.981	0.59	0.19
Full Model	-190.8	419.1	7.9	17	0.019	0.62	0.30
Fire Characteristics	-205.9	430.3	19.1	8	<0.001	0.54	0.13
Null Model	-212.2	432.4	21.2	3	<0.001	0.55	0.00
Seed Rain Processes	-207	434.4	23.2	9	<0.001	0.57	0.12

Table S2e. Results of AIC based model selection for black spruce seedling establishment on the Taiga Plains in late summer 2016 (Year 2 post-fire). Modeled response variable is the presence or absence of seedlings in each quadrat. For each model, Log-likelihood (Log(L)), Akaike information criterion (corrected for small sample size AICc), degrees of freedom (df), model weight, and model R² (R²_C: variance explained by the fixed and random factors; R²_M: variance explained by the fixed factors), are given. Model with $\Delta\text{AICc} > 2$ is considered to be the best fit (Burnham and Anderson 2002).

Model	Log(L)	AICc	ΔAICc	df	Weight	R ² _C	R ² _M
Full Model	-262.8	560.8	0	16	0.9965	0.68	0.28
Seed Bed Conditions	-278.2	572.8	12	7	0.0025	0.67	0.07
Fire Characteristics	-278.3	574.9	14.1	8	<0.001	0.62	0.16
Seed Rain Processes	-280.1	578.5	17.8	8	<0.001	0.61	0.11
Null Model	-287.2	582.5	21.7	3	<0.001	0.61	0.00

Table S2f. Results of AIC based model selection for jack pine seedling establishment on the Taiga Plains in late summer 2016 (Year 2 post-fire). Modeled response variable is the presence or absence of seedlings in each quadrat. For each model, Log-likelihood (Log(L)), Akaike information criterion (corrected for small sample size AICc), degrees of freedom (df), model weight, and model R² (R²_C: variance explained by the fixed and random factors; R²_M: variance explained by the fixed factors), are given. Model with $\Delta\text{AICc} > 2$ is considered to be the best fit (Burnham and Anderson 2002).

Model	Log(L)	AICc	ΔAICc	df	Weight	R ² _C	R ² _M
Full Model	-200.2	437.7	0	17	0.997	0.75	0.45
Seed Bed Conditions	-216.6	449.4	11.7	7	0.0029	0.71	0.14
Fire Characteristics	-218.7	455.7	18	8	<0.001	0.73	0.30
Seed Rain Conditions	-220.1	460.7	23	9	<0.001	0.71	0.17
Null Model	-231.3	470.8	33.1	3	<0.001	0.73	0.00

Table S2g. Results of AIC based model selection for aspen seedling establishment on the Taiga Plains in late summer 2016 (Year 2 post-fire). Modeled response variable is the presence or absence of seedlings in each quadrat. For each model, Log-likelihood (Log(L)), Akaike information criterion (corrected for small sample size AICc), degrees of freedom (df), model weight, and model R² (R²_C: variance explained by the fixed and random factors; R²_M: variance explained by the fixed factors), are given. Model with $\Delta\text{AICc} > 2$ is considered to be the best fit (Burnham and Anderson 2002).

Model	Log(L)	AICc	ΔAICc	df	Weight	R ² _C	R ² _M
Seed Bed Conditions	-295.4	607.1	0	7	0.7029	0.43	0.09
Full Model	-290	608.8	1.7	13	0.295	0.44	0.16
Fire Characteristics	-300.6	619.5	12.4	8	0.0014	0.42	0.08
Null Model	-306.7	621.5	14.4	3	<0.001	0.41	0.00
Seed Rain Processes	-306.3	624.7	17.6	5	<0.001	0.41	0.01

Table S3. Best model selected for birch seedling establishment on the Taiga Shield, one year post-fire. Modeled response variable is the presence or absence of seedlings in each quadrat.

	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	-5.3078	175.615	-0.03	9.76x10 ⁻⁰¹
Mineral Cover	0.09761	0.16242	0.601	0.54786
Bryophyte Cover	1.26924	0.30054	4.223	2.41x10⁻⁰⁵
Charcoal Cover	0.18671	0.16195	1.153	0.24896
Residual Organic Layer	-0.3691	0.20385	-1.811	0.07018
Stand Age	-0.7068	0.25709	-2.749	0.00598
Date of Burn	0.1663	0.22589	0.736	0.46162
Stand BA	0.76881	0.20922	3.675	0.00024
Tree consumption (Contrast: No consumption vs. Low consumption)	-3.4512	175.615	-0.02	0.98432
Tree consumption (Contrast: No consumption vs. Moderate consumption)	-3.2643	175.616	-0.019	0.98517
Tree consumption (Contrast: No consumption vs. High consumption)	-3.2313	175.616	-0.018	0.98532

Table S4. Best model selected for *Pinaceae* seedling establishment on the Taiga Shield, one year post-fire. Modeled response variable is the presence or absence of seedlings in each quadrat.

	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	-1.8007	0.32394	-5.559	2.72x10 ⁻⁰⁸
Mineral Cover	0.3033	0.17809	1.703	0.08855
Bryophyte Cover	0.52206	0.16981	3.074	2.11x10⁻⁰³
Residual Organic Layer	0.01536	0.19831	0.077	0.93825
Charcoal Cover	0.48577	0.16745	2.901	0.00372

Table S5. Best model selected for aspen seedling establishment on the Taiga Plains, one year post-fire. Modeled response variable is the presence or absence of seedlings in each quadrat.

	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	-0.8882	0.22953	-3.87	1.09x10 ⁻⁰⁴
Mineral Cover	-0.1084	0.1591	-0.681	0.49568
Bryophyte Cover	0.7763	0.20623	3.764	1.67x10⁻⁰⁴
Charcoal Cover	-0.0236	0.14939	-0.158	0.8745
Residual Organic Layer	-0.5429	0.21444	-2.532	0.01135

Table S6. Best model selected for *Pinaceae* seedling establishment on the Taiga Plains, one year post-fire. Modeled response variable is the presence or absence of seedlings in each quadrat.

	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	2.11941	0.32448	6.532	6.50x10 ⁻¹¹
Mineral Cover	-0.0211	0.19596	-0.108	0.91408
Bryophyte Cover	0.60593	0.34825	1.74	8.19x10⁻⁰²
Charcoal Cover	0.42311	0.28168	1.502	0.13307
Residual Organic Layer	-0.8959	0.24487	-3.659	0.00025

Table S7. Best model selected for black spruce seedling establishment on the Taiga Plains, two years post-fire. Modeled response variable is the presence or absence of seedlings in each quadrat.

	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	-1.4106	0.73567	-1.917	5.52x10 ⁻⁰²
Cone Consumption (Contrast: Low consumption vs. No cones)	-2.5145	0.99235	-2.534	0.01128
Cone Consumption (Contrast: Moderate consumption vs. No cones)	0.79797	0.93203	0.856	3.92x10 ⁻⁰¹
Cone Consumption (Contrast: High consumption vs. No cones)	2.80507	1.29829	2.161	0.03073
Tree consumption (Contrast: No consumption vs. Low consumption)	-0.1787	0.57873	-0.309	0.75744
Tree consumption (Contrast: No consumption vs. Moderate consumption)	-1.4859	0.63984	-2.322	0.02022
Tree consumption (Contrast: No consumption vs. High consumption)	-1.3064	0.55029	-2.374	0.01759
Mineral Cover	-0.1893	0.17793	-1.064	0.28726
Bryophyte Cover	0.64895	0.22644	2.866	0.00416
Charcoal Cover	0.11992	0.14639	0.819	0.4127
Residual Organic Layer	-0.4334	0.23224	-1.866	0.06201
Stand Age	0.05728	0.29458	0.194	0.84582
Date of Burn	-0.8746	0.3276	-2.67	0.00759
Stand BA	0.22253	0.28822	0.772	0.44006

Table S8. Best model selected for jack pine seedling establishment on the Taiga Plains, two years post-fire. Modeled response variable is the presence or absence of seedlings in each quadrat.

	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	1.8781	0.6158	3.05	2.29x10 ⁻⁰³
Cone Consumption (Contrast: No consumption vs. No cones)	1.1729	0.8609	1.362	0.17307
Cone Consumption (Contrast: Low consumption vs. No cones)	0.2194	0.8189	0.268	7.89 x10 ⁻⁰¹
Cone Consumption (Contrast: Moderate consumption vs. No cones)	-0.5888	0.6519	-0.903	0.36646
Cone Consumption (Contrast: High consumption vs. No cones)	0.9088	1.2324	0.737	0.46088
Tree consumption (Contrast: No consumption vs. Low consumption)	-0.3189	0.5589	-0.571	0.56831
Tree consumption (Contrast: No consumption vs. Moderate consumption)	0.4748	0.6698	0.709	0.47837
Tree consumption (Contrast: No consumption vs. High consumption)	-0.9332	0.5852	-1.595	0.11081
Mineral Cover	0.1433	0.207	0.692	0.48892
Bryophyte Cover	0.6598	0.2949	2.237	0.02528
Charcoal Cover	0.361	0.2393	1.508	0.13143
Residual Organic Layer	-0.427	0.255	-1.675	0.09399
Stand Age	0.1397	0.2904	0.481	0.63046
Date of Burn	1.2644	0.379	3.336	0.00085
Stand BA	0.2212	0.2851	0.776	0.4377

Table S9. Best model selected for aspen seedling establishment on the Taiga Plains, two years post-fire. Modeled response variable is the presence or absence of seedlings in each quadrat.

	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	-0.7961	0.19476	-4.088	4.36x10 ⁻⁰⁵
Mineral Cover	0.02859	0.14771	0.194	0.84652
Bryophyte Cover	0.59308	0.17215	3.445	5.71 x10⁻⁰⁴
Charcoal Cover	0.06631	0.12561	0.528	0.59759
Residual Organic Layer	-0.2952	0.18087	-1.632	0.10268

Table S10. Results of AIC based model selection for proportional change happening 1-year post-fire on the Taiga Shield. Modeled response variable is the proportional change in conifers between pre- and post-fire conditions. For each model, Log-likelihood (Log(L)), Akaike information criterion (corrected for small sample size AICc), degrees of freedom (df), model weight, and model R^2 (R^2_C : variance explained by the fixed and random factors; R^2_M : variance explained by the fixed factors), are given. Model with $\Delta AICc > 2$ is considered to be the best fit (Burnham and Anderson 2002).

Model	Log(L)	AICc	$\Delta AICc$	df	Weight	R^2_M	R^2_C
Null Model	-25.6	59.6	0.0	4	1	0.00	0.89
Seed Rain Processes	-28.1	78.1	18.5	10	<0.001	0.15	0.90
Fire Characteristics	-30.6	78.5	18.9	8	<0.001	0.04	0.89
Seed Bed Conditions	-32.6	82.5	22.9	8	<0.001	0.02	0.90
Global Model	-38.4	116.8	57.2	17	<0.001	0.18	0.90

Table S11. Results of AIC based model selection for proportional change happening 2-years post-fire on the Taiga Plains. Modeled response variable is the proportional change in conifers between pre- and post-fire conditions. For each model, Log-likelihood (Log(L)), Akaike information criterion (corrected for small sample size AICc), degrees of freedom (df), model weight, and model R^2 (R^2_C : variance explained by the fixed and random factors; R^2_M : variance explained by the fixed factors), are given. Model with $\Delta AICc > 2$ is considered to be the best fit (Burnham and Anderson 2002).

Model	Log(L)	AICc	$\Delta AICc$	df	Weight	R^2_M	R^2_C
Null Model	-52.5	113.1	0.0	4	0.9988	0.00	0.58
Seed Bed Conditions	-55.1	126.5	13.4	8	0.0012	0.04	0.58
Seed Rain Processes	-59.9	136.1	23.0	8	<0.001	0.07	0.60
Fire Characteristics	-60.1	138.7	25.6	9	<0.001	0.04	0.60
Full Model	-70.0	173.6	60.5	16	<0.001	0.12	0.63

Table S12. Results of AIC based model selection for proportional change of jack pine in pre-fire mixed stands. Modeled response variable is the proportional change of jack pine between pre- and post-fire conditions. For each model, Log-likelihood (Log(L)), Akaike information criterion (corrected for small sample size AICc), degrees of freedom (df), model weight, and model R² (R²_C: variance explained by the fixed and random factors; R²_M: variance explained by the fixed factors), are given. Model with $\Delta\text{AICc} > 2$ is considered to be the best fit (Burnham and Anderson 2002).

Model	Log(L)	AICc	ΔAICc	df	Weight	R ² _C	R ² _M
Null Model	-42.4	93.1	0.0	4	0.9983	0.53	0.00
Fire Characteristics	-44.7	106	12.9	8	0.0015	0.56	0.14
Seed Bed Conditions	-46.9	110.5	17.4	8	<0.001	0.54	0.06
Seed Rain Processes	-52.3	121.2	28.1	8	<0.001	0.56	0.01
Full Model	-56.1	144.5	51.5	15	<0.001	0.57	0.19

Table S13. Results of AIC based model selection for proportional change of black spruce in pre-fire mixed stands. Modeled response variable is the proportional change of black spruce between pre- and post-fire conditions. For each model, Log-likelihood (Log(L)), Akaike information criterion (corrected for small sample size AICc), degrees of freedom (df), model weight, and model R^2 (R^2_C : variance explained by the fixed and random factors; R^2_M : variance explained by the fixed factors), are given. Model with $\Delta AICc > 2$ is considered to be the best fit (Burnham and Anderson 2002).

Model	Log(L)	AICc	$\Delta AICc$	df	Weight	R^2_C	R^2_M
Null Model	-52.6	113.3	0.0	4	0.96	0.61	0.00
Fire Characteristics	-51.7	119.9	6.6	8	0.04	0.62	0.19
Seed Rain Processes	-60.1	136.8	23.4	8	<0.001	0.63	0.05
Seed Bed Conditions	-63.7	144	30.7	8	<0.001	0.61	0.01
Full Model	-69.4	170.7	57.3	15	<0.001	0.20	0.63

Table S14. Results of AIC based model selection for proportional change of jack pine in pre-fire jack pine stands. Modeled response variable is the proportional change of jack pine between pre- and post-fire conditions. For each model, Log-likelihood (Log(L)), Akaike information criterion (corrected for small sample size AICc), degrees of freedom (df), model weight, and model R^2 (R^2_C : variance explained by the fixed and random factors; R^2_M : variance explained by the fixed factors), are given. Model with $\Delta AICc > 2$ is considered to be the best fit (Burnham and Anderson 2002).

Model	Log(L)	AICc	$\Delta AICc$	df	Weight	R^2_C	R^2_M
Null Model	0.6	8.1	0.0	4	1	0.21	0.00
Fire Characteristics	-3.3	27.9	19.8	8	<0.001	0.26	0.25
Seed Bed Conditions	-3.8	28.9	20.8	8	<0.001	0.44	0.26
Seed Rain Processes	-5.9	33.1	25	8	<0.001	0.37	0.11
Full Model	-11	76.1	68	15	<0.001	0.73	0.21

Table S15. Results of AIC based model selection for proportional change of black spruce in pre-fire jack pine stands. Modeled response variable is the proportional change of black spruce between pre- and post-fire conditions. For each model, Log-likelihood (Log(L)), Akaike information criterion (corrected for small sample size AICc), degrees of freedom (df), model weight, and model R^2 (R^2_C : variance explained by the fixed and random factors; R^2_M : variance explained by the fixed factors), are given. Model with $\Delta AICc > 2$ is considered to be the best fit (Burnham and Anderson 2002).

Model	Log(L)	AICc	$\Delta AICc$	df	Weight	R^2_C	R^2_M
Null Model	3.5	3.9	0.0	4	1	0.78	0.00
Fire Characteristics	2.7	18.7	14.8	7	<0.001	0.82	0.34
Seed Rain Processes	4.7	21.1	17.2	8	<0.001	0.81	0.44
Seed Bed Conditions	-0.6	31.7	27.8	8	<0.001	0.79	0.18
Full Model	0.9	74.2	70.3	12	<0.001	0.84	0.52

Table S16. Results of AIC based model selection for proportional change of jack pine in pre-fire black spruce stands. Modeled response variable is the proportional change of jack pine between pre- and post-fire conditions. For each model, Log-likelihood (Log(L)), Akaike information criterion (corrected for small sample size AICc), degrees of freedom (df), model weight, and model R^2 (R^2_C : variance explained by the fixed and random factors; R^2_M : variance explained by the fixed factors), are given. Model with $\Delta AICc > 2$ is considered to be the best fit (Burnham and Anderson 2002).

Model	Log(L)	AICc	$\Delta AICc$	df	Weight	R^2_C	R^2_M
Null Model	-33.6	75.5	0.0	4	1	0.40	0.00
Fire Characteristics	-36.9	90.9	15.4	8	<0.001	0.44	0.13
Seed Bed Conditions	-39.1	95.2	19.7	8	<0.001	0.42	0.06
Seed Rain Processes	-40.3	97.7	22.2	8	<0.001	0.44	0.08
Full Model	-48	129.6	54.1	15	<0.001	0.48	0.22

Table S17. Results of AIC based model selection for proportional change of black spruce in pre-fire black spruce stands. Modeled response variable is the proportional change of black spruce between pre- and post-fire conditions. For each model, Log-likelihood (Log(L)), Akaike information criterion (corrected for small sample size AICc), degrees of freedom (df), model weight, and model R^2 (R^2_C : variance explained by the fixed and random factors; R^2_M : variance explained by the fixed factors), are given. Model with $\Delta AICc > 2$ is considered to be the best fit (Burnham and Anderson 2002).

Model	Log(L)	AICc	$\Delta AICc$	df	Weight	R^2_C	R^2_M
Null Model	-51.7	111.7	0.0	4	0.84	0.51	0.00
Fire Characteristics	-49.2	115.1	3.4	8	0.16	0.52	0.24
Seed Rain Processes	-55.9	128.5	16.8	8	<0.001	0.52	0.13
Seed Bed Conditions	-61.8	140.4	28.7	8	<0.001	0.49	0.02
Full Model	-66.2	164.9	53.2	15	<0.001	0.52	0.25

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Table S18. Correlation matrix for all continuous predictor variables on the Taiga Shield (n=114). Bolded values indicate correlations that were >0.3. Residual organic soil depth has been log-transformed. Depth of Burn and Fire Weather Index (FWI) were eliminated from further analyses since they were highly correlated with other variables.

	Mineral cover (%)	Bryophyte cover (%)	Charcoal cover (%)	Residual organic soil depth (cm)	Stand age (years)	Depth of burn (cm)	Date of Burn (DOB; Day of year)	Fire Weather Index (FWI)	Total basal area (m ² ·h ⁻¹)
Mineral cover (%)	1								
Bryophyte cover (%)	0.142631	1							
Charcoal cover (%)	0.112791	0.001363	1						
Residual organic soil depth (cm)	-0.211329	-0.130135	-0.154342	1					
Stand age (years)	-0.146921	-0.098707	-0.133433	0.190470	1				
Depth of burn (cm)	-0.067633	0.075029	-0.083916	0.302738	0.463497	1			
Date of Burn (DOB; Day of year)	0.177432	0.237334	0.016578	-0.085552	-0.277856	-0.204612	1		
Fire Weather Index (FWI)	0.204207	0.208918	0.049781	-0.077547	-0.262044	-0.152690	0.598754	1	
Total basal area (m ² ·h ⁻¹)	0.091402	0.132168	0.148239	-0.281227	0.287915	0.260285	-0.076905	0.124081	1

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Table S19. Correlation matrix for all continuous predictor variables on the Taiga Plains (n=110). Bolded values indicate correlations that were >0.3. Residual organic soil depth has been log-transformed. Depth of Burn and Fire Weather Index (FWI) were eliminated from further analyses since they were highly correlated with other variables. Both Date of Burn (DOB) and residual organic soil depth were left in further analyses since visual inspection of this correlation showed it to be weak.

	Mineral cover (%)	Bryophyte cover (%)	Charcoal cover (%)	Residual organic soil depth (cm)	Stand age (years)	Depth of burn (cm)	Date of Burn (DOB; Day of year)	Fire Weather Index (FWI)	Total basal area (m ² ·h ⁻¹)
Mineral cover (%)	1								
Bryophyte cover (%)	-0.019410	1							
Charcoal cover (%)	0.267395	0.036258	1						
Residual organic soil depth (cm)	-0.242112	-0.042744	-0.156074	1					
Stand age (years)	-0.056086	0.052186	-0.078075	0.036783	1				
Depth of burn (cm)	-0.204832	0.150377	-0.103929	0.406130	0.487106	1			
Date of Burn (DOB; Day of year)	0.166000	0.031313	0.065484	-0.343214	-0.228822	-0.334229	1		
Fire Weather Index (FWI)	-0.034466	0.037940	0.006351	0.152919	-0.151681	0.065149	-0.395600	1	
Total basal area (m ² ·h ⁻¹)	-0.028950	0.027590	0.044125	-0.201833	0.110946	-0.017065	-0.159344	-0.021915	1

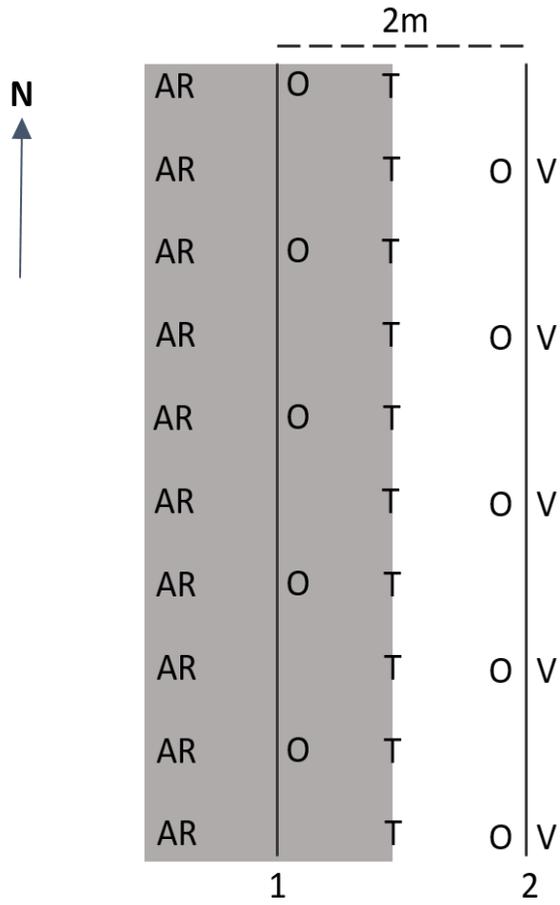


Figure S1. Transect set-up and sampling design. V- vegetation quadrats; O- residual organic soil depth; AR- depth of burn; T- seed traps; grey box- measurements of pre-fire stand structure and canopy consumption.

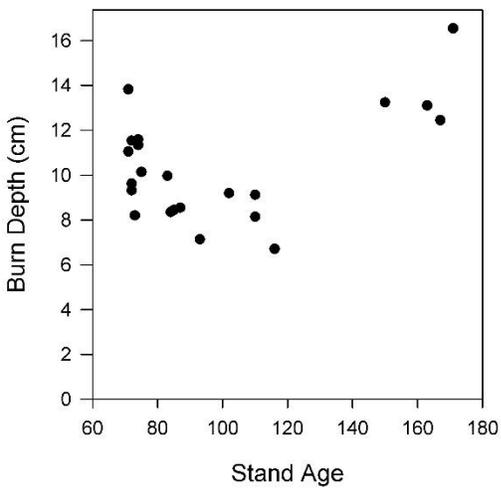
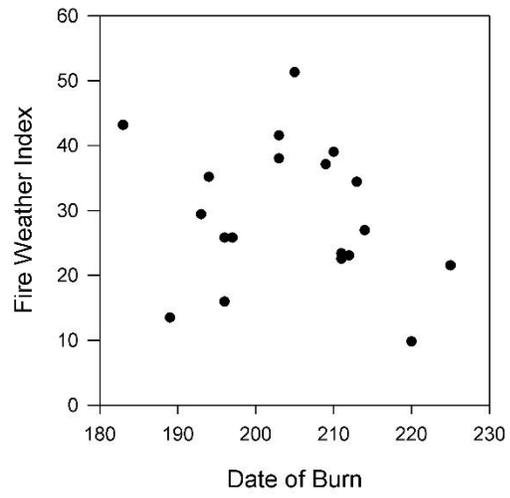
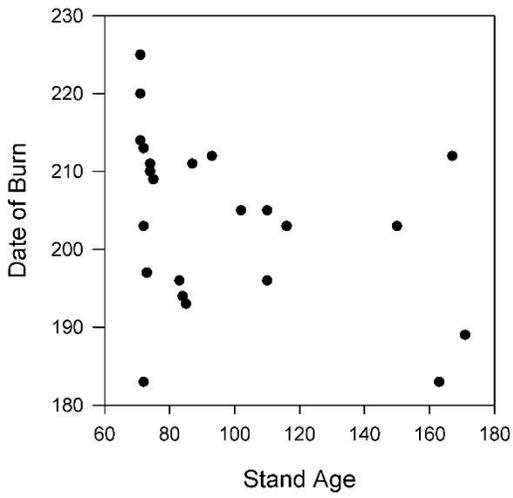
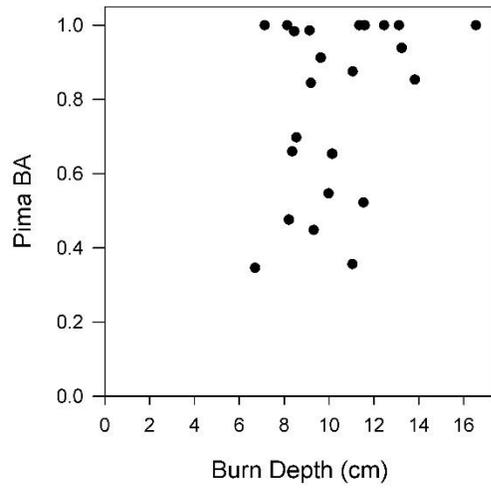
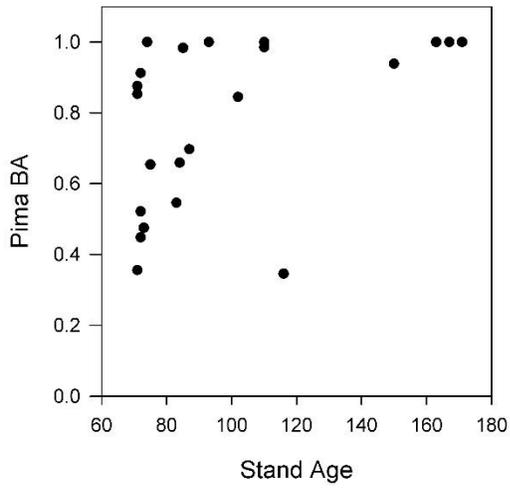


Figure S2. Visual representation of correlations that were >0.3 (Table S1). Pima BA represents the proportion of basal area in each seed trap study plot that was black spruce. Fire Weather Index and burn depth were removed from further analysis because of their high correlations with other variables. After visual inspections, both variables from the other correlations were left in because we determined that the relationships were not strong enough to remove a variable.

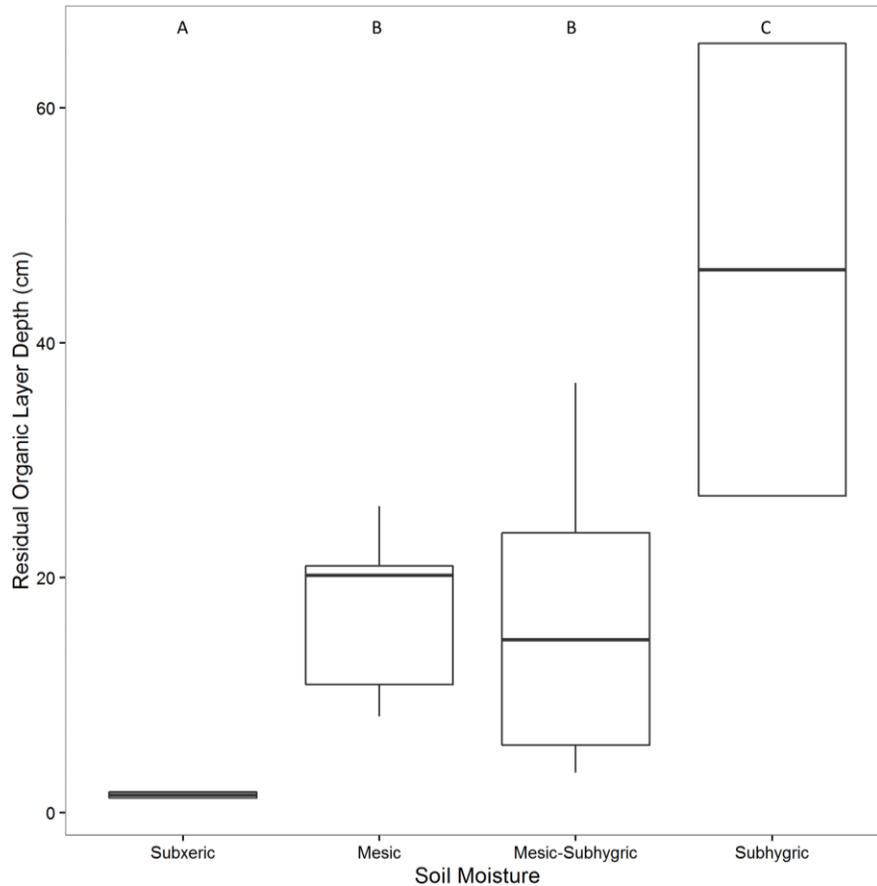


Figure S3. Residual organic layer depth at each of the four moisture categories represented at the 25 sites. Since variables are positively correlated, soil moisture was removed from further analyses. Letters represent significant differences between soil moisture classes. The boxes encompass the middle 50% of the distribution and the horizontal lines in the boxes represent the median values. The whiskers show the maximum and minimum values which are not outliers (the 95% quartiles).

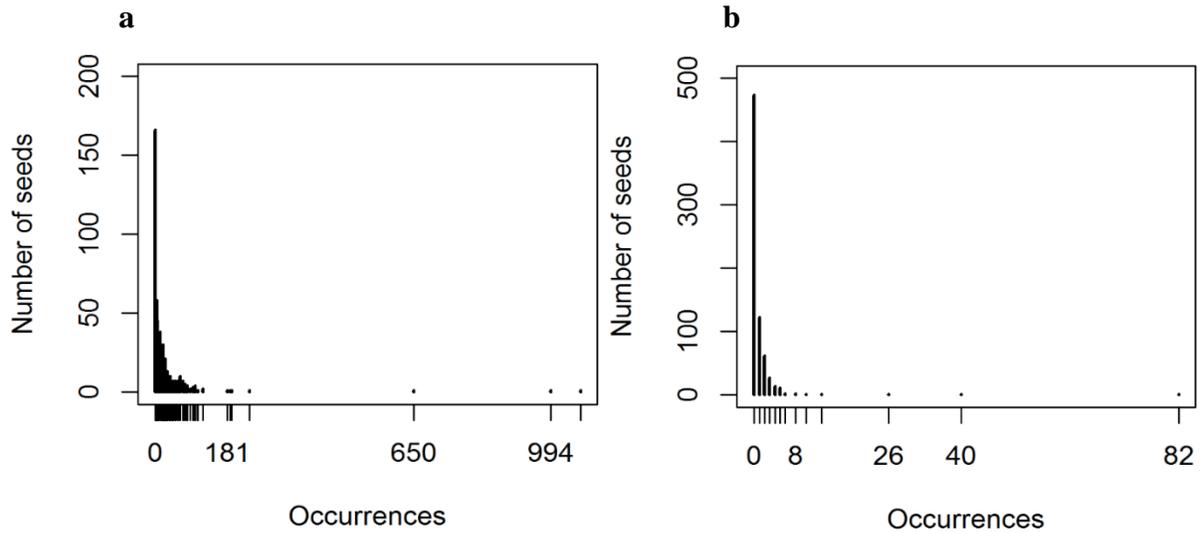


Figure S4. Frequency distributions of raw counts of a) total black spruce seed rain, and b) viable black spruce seed rain. Plots indicate that data was zero-inflated: a) 178 out of 750 observations were 0; b) 474 out of 750 observations were 0). The response variable used for modelling was corrected for both density and sampling effort (due to the three separate collection periods being different lengths).

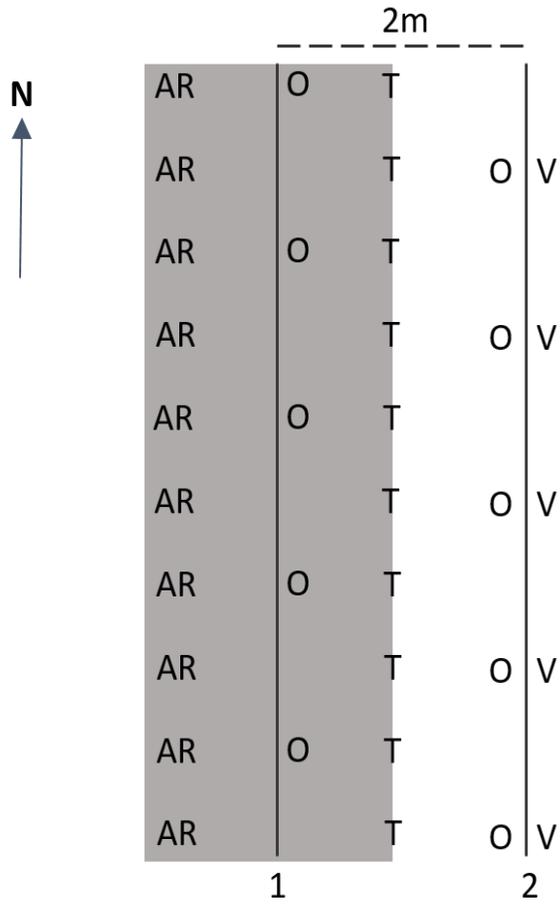


Figure S5. Transect set-up and sampling design. V- vegetation quadrats; O- residual organic soil depth; AR- depth of burn; T- seed traps; grey box- measurements of pre-fire stand structure and canopy consumption.