Subarctic ecosystem resilience under changing disturbance regimes

By

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Abstract

Disturbance regimes are changing across the subarctic as a result of continued climate change. At the northern range edge of the boreal forest, changes to disturbance regimes are predicted to result in a shift in successional trajectory of the current plant community, altering the structure and function of the current ecosystem. As these boreal tree and shrub species are already climatically primed for range expansion, changes to disturbance regimes may facilitate increased establishment of boreal tree and shrub species beyond their current range edge. An investigation of how different disturbances influence biotic and abiotic conditions for early life-stages of boreal tree and shrub species was conducted at the Canadian boreal-tundra treeline ecotone to determine whether disturbances disrupt the ecological inertia of the current ecosystem, creating suitable conditions for successional change and northward boreal tree range expansion. Impacts to microsite conditions by wildfire, insect granivory on spruce cones, and anthropogenic wood harvesting were examined. These disturbance regimes were selected because they are anticipated to change in frequency and extent across the subarctic with continued climate change. Results from each investigation indicated that while disturbances did create conditions that could support increased establishment of boreal tree species, disturbance severities were low, often creating additional challenges for seed germination and establishment. Thus, disturbance induced changes to ecosystem structure and function are not anticipated at these research locations. Future research is required to examine disturbances of different severity at the range edge in order to determine whether disturbances of higher severity are likely to occur and whether they can break the ecological inertia of the current ecosystem.

Keywords: boreal, climate change, disturbance ecology, ecological inertia, insect granivory, *Picea mariana, Picea glauca*, resilience, subarctic, treeline ecotone, wildfire, wood harvesting

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Chapter 1: Introduction and thesis overview

1.0 Introduction

Disturbances are a fundamental component of natural ecosystems, shaping plant communities across temporal and spatial scales (Cairns & Moen, 2004; Holtmeier & Broll, 2018; Johnstone et al., 2016; Vanderwel & Purves, 2014; Weed, Ayres, & Hicke, 2013). A **disturbance** is defined as any discrete event that alters resource availability or the physical environment in a population, community, or ecosystem (White & Pickett, 1985). Controls on disturbances, either directly or indirectly, are dictated by climate and weather, geographic location, and human influence (Dale et al., 2001; White, Wulder, Hermosilla, Coops, & Hobart, 2017). Any disturbance that continues through time in a cyclical pattern can be described by a **disturbance regime**, which includes information on their frequency (i.e., how often they occur), return interval (i.e., time between disturbances), severity (i.e., the effect on the ecosystem), and size (Turner, 2010). Disturbances are a key part of biodiversity and while disturbance events are often considered a destructive force when they occur in areas of high human value or within the built environment (e.g., communities, transportation routes, conservation areas), many are vital for maintaining ecosystem structure and function (Dale et al., 2001). For example, localized disturbances (e.g., herbivory, windthrow) may occur more frequently within a forest stand, allowing shade-intolerant species to rapidly establish within the canopy (Rich, Frelich, & Reich, 2007). Conversely, large-scale disturbances that occur less frequently (e.g., wildfire, logging) may restructure an ecosystem to an earlier successional state and allow plant species to take advantage of new environmental conditions (Flannigan, Stocks, & Weber, 2003; Turner, Romme, & Gardner, 1999). In summary, at any given time an ecosystem consists of a mosaic of post-disturbance plant communities at different successional stages.

Many disturbance regimes exist within the boreal forest. As a result, plant species have evolved numerous survival and reproductive strategies to allow individuals the ability to absorb and adapt to the negative impacts of a disturbance event (Folke et al., 2004; Walker & Meyers, 2004). This ability to successfully reorganize and return to a pre-disturbance ecosystem state (i.e., similar in structure and function) was first described by Holling (1973) as the **resilience** of an ecosystem. As an umbrella term, resilience includes information on an ecosystems elasticity and malleability with disturbances (Westman, 1978); however, for the purpose of my thesis, I chose to focus on the **ecological inertia**, which refers to the conditions and characteristics of the ecosystem state that dictates its ability to resist a change in succession (i.e., resistance or change in ecosystem structure and function; Orians, 1975). Boreal peatlands are an excellent example of an ecosystem with high ecological inertia, as the plant community structure mitigates exposure to drought events and successional shifts through fire from the sufficient retention of soil moisture (Stralberg et al., 2020). Included within the inertia concept is that of **biological legacies**, which refer to the biologically derived information (i.e., adaptations developed from living within a disturbance regime) and materials (i.e., survivors or reproductive potential after a disturbance event) that allow a species to succeed post-disturbance (Johnstone et al., 2016); thus, resisting successional change. In the boreal forest, black spruce (*Picea mariana* (Mill) B.S.P.) represents a dominant tree species and is often used as an example to describe biological legacies. In response to living with wildfire, black spruce has evolved semi-serotinous cones (i.e., information legacy) that slowly release seeds post-wildfire (i.e., material legacy) onto the ground where conditions are often more ideal for germination (e.g., dark, warm, closer to mineral soils; Alexander et al., 2018; Greene et al., 2007; Turner et al., 1999). Ultimately, information regarding species' biological legacies and ecological inertia supports a better understanding of resilience (Reyer et al., 2015; Swanson et al., 2011).

Climate change is acting as a chronic pressure on the resilience of northern ecosystems (Buma, Brown, Donato, Fontaine, & Johnstone, 2013; Stevens-Rumann et al., 2018). This pressure is being experienced most dramatically across the subarctic where temperature increases are occurring at a rate of three times the global average (Bush & Lemmen, 2019). In the boreal forests of north-western North America, increased moisture deficits from longer growing seasons have resulted in significant dieback of forest stands (Stevens-Rumann et al., 2018), while subarctic tundra ecosystems are experiencing a "greening" trend, largely controlled by increased dominance of shrub cover (Martin, Jeffers, Petrokofsky, Myers-Smith, & Macias-Fauria, 2017; Myers-Smith et al., 2020). At the northern edge of the boreal forest, a range expansion of tree species into the tundra biome has also occurred, as climate has become more suitable for tree recruitment (Danby & Hik, 2007; Körner, 1998; Mamet, Brown, Trant, & Laroque, 2019). Nevertheless, this rate has been non-uniform across the subarctic and has been slower than climate-based model predictions (Feuillet et al., 2020; Harsch, Hulme, McGlone, & Duncan, 2009). This may suggest that tundra plant communities at the treeline ecotone may exhibit high ecological inertia and be resistant to change from the singular impact of warming temperatures (Buma, Brown, Donato, Fontaine, & Johnstone, 2013).

Yet, changes to the frequency, severity, and extent of disturbances across northern ecosystems are also occurring from continued climate change (Dale et al., 2001; Buma, Brown, Donato, Fontaine, & Johnstone, 2013; Stevens-Rumann et al., 2018). In recent decades, climate warming has increased the number of extreme wildfires (Hanes et al., 2019; Soja et al., 2007) and insect outbreaks (Navarro, Morin, Bergeron, & Girona, 2018; Pureswaran, Roques, &

Battisti, 2018). Under continued pressures from climate change, these novel disturbance regimes may act as a tipping point for successional change, as the ecological inertia is supressed, resulting in a shift towards a new ecosystem structure and function (Figure 1.1; Bölter & Müller, 2016; Brown & Johnstone, 2012; Johnstone et al., 2016; Reyer et al., 2015). As humans adapt to changing disturbance regimes, so too does their land-use (Gauthier & Vaillancourt, 2009; Seidl et al., 2017), further compounding climate change-driven pressures on ecosystem resilience (Bölter & Müller, 2016; Leverkus et al., 2018). Ultimately, if resilience is reduced through a loss of ecological inertia, changes to the successional trajectory of northern plant communities may occur. A shift in these plant communities would have notable consequences for global carbon pools (Mack et al., 2011), permafrost dynamics (Jones et al., 2015), and the surface energy budget (Chambers, Beringer, Randerson, & Chapin III, 2005), all of which may support positive feedback systems for continued warming (Chapin III et al., 2000).

Despite the concerted effort to understand how climate change will influence northern ecosystems, the effect of changing disturbance regimes on plant communities has generally been underrepresented within the literature (Bölter & Müller, 2016; Turner, 2010). Therefore, in this thesis I aimed to comtribute to the growing body of literature by reducing the knowledge gap related to how disturbances may influence the ecological inertia at the northern range edge of the boreal forest. Specifically, I chose to study how the biotic and abiotic conditions change with disturbance, and how these changes may influence the establishment of early-life stage boreal tree and shrubs species. A better understanding of wildfire, insect granivory, and anthropogenic wood harvesting is required, as the frequency, severity, and extent are anticipated to change under continued climate warming and will likely have notable impacts on plant communities (Lantz, Gergel, & Henry, 2010; Leverkus et al., 2018; Pureswaran et al., 2018). While my research focused on how disturbances change microsite conditions for early-life stages, each study was conducted at different spatial scales and took place in different locations across the Canadian subarctic. My research is summarized in three separate manuscript chapters that are the focus of the next three sections (1.1–1.3). Within these introductory sections, I briefly describe each disturbance and its predicted impact on successional dynamics.

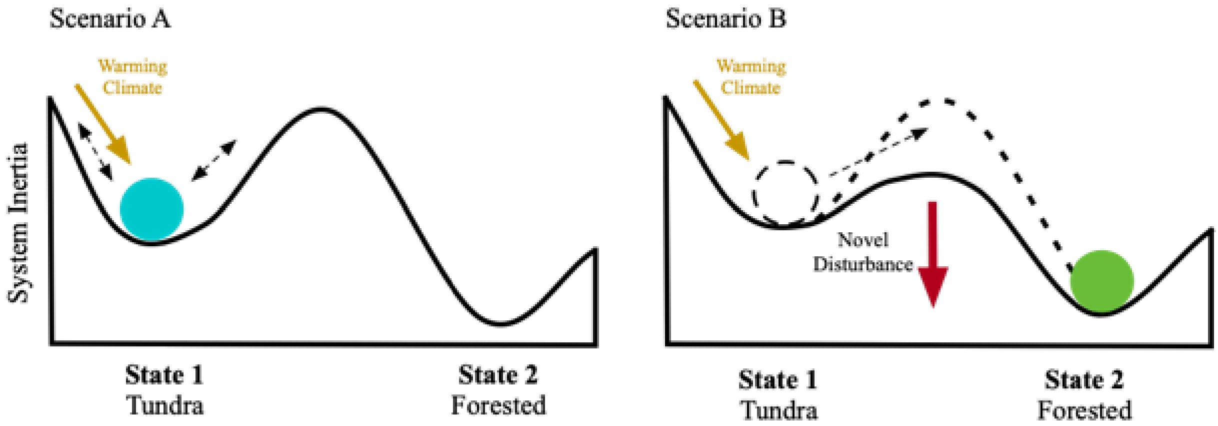

Figure 1.1 Conceptual ball-and-trough model, simulating a loss of inertia and the subsequent shift in successional trajectory. This model is an adapted version of resilience loss presented in Folke et al. (2004) and more recently in Johnstone et al. (2016). Scenario A shows climate change as a chronic pressure on the resilience of the tundra ecosystem (e.g., longer growing season, increased shrub cover). Yet, inertia of the system is high, therefore some changes to the ecosystem may occur but the structure and function of the current state remains intact. Scenario B shows the chronic pressure of climate change coupled with a novel disturbance (e.g., wildfire in tundra). The novel disturbance decreases the inertia of the system through a change in biotic or abiotic conditions, facilitating a transition to a different successional state. A similar scenario can be applied to the range edge forest stands of the eastern subarctic. While climate change may be acting as a chronic pressure on forest stands, a disturbance is needed to suppress the ecological inertia and allow for a shift towards a landscape dominated by shrubs.

1.1 A novel regime change: Wildfires at the boreal-tundra treeline

Wildfires represent the largest natural disturbance governing ecological processes within the boreal forest (Johnson, 1992; Soja et al., 2007; Weber & Flannigan, 1997). Wildfires are primarily controlled by climate, seasonal weather, and the amount of fuel available for consumption (Hanes et al., 2019; Johnston & Flannigan, 2018; Lecomte, Simard, Fenton, & Bergeron, 2006; Seidl et al., 2020). Return intervals in North America range from 50-100 years in Alaska (Kasischke et al., 2010) to 400-500 years in northern regions of Quebec (Laberge & Payette, 1995). Similarly, latitudinal variation in the wildfire regime exists, with a general decreasing frequency as latitude increases (Johnson, 1992). Thus, wildfires have historically been an infrequent disturbance at the boreal forest's northern range edge (Soja et al., 2007) and have been considered rare within the tundra biome (Hu et al., 2015). In the eastern subarctic of northern Labrador, a cold wet climate has also historically reduced the frequency of large-scale wildfires (Steijlen, Nilsson, & Zackrisson, 1995).

Successional dynamics following wildfire have been well documented in the boreal forest of North America (e.g., see Hanes et al., 2019; Johnstone et al., 2020; Turner et al., 1999). In a mature stand, seedling establishment is often low, as deep organic layers limit seed access to soil nutrients and soil moisture (Johnstone & Chapin III, 2006; Shenoy, Kielland, & Johnstone, 2013). Interspecific light resource competition (Tingstad, Olsen, Klanderud, Vandvik, & Ohlson, 2015) and herbivory of young seedlings (Munier, Hermanutz, Jacobs, & Lewis, 2010) are some challenges, among many, that further limit seedling establishment success. However, a wildfire can offer a reprieve from these limitations: aboveground vegetation is removed, and the organic layer is combusted, exposing mineral soil that is high in soil moisture and nutrients (Certini, 2005). As previously described, many plant species have evolved life history strategies in response to living with a historical wildfire regime that allows them to take advantage of these favourable conditions. Serotinous cones in aerial seed banks (*Picea mariana*, *Pinus* spp.), as well as light, wind-dispersed seeds (*Betula* spp. *Picea glauca* (Moench) Voss, *Alnus* spp.), and vegetation re-sprouting from roots (*Betula* spp., *Alnus* spp., *Populus* spp.) allow rapid regrowth of aboveground vegetation after wildfire events (Gordon & Shugart, 1989).

As continued climate warming increases growing season length and the moisture deficit for plant communities, the frequency and extent of wildfire across the northern boreal range edge has changed (Boucher et al., 2020; Coops, Hermosilla, Wulder, White, & Bolton, 2018; Holtmeier & Broll, 2018; Wang et al., 2017). In recent decades, there has been an increased number wildfire events being recorded within the tundra biome (Higuera, Chipman, Barnes, Urban, & Hu, 2011; Hu et al., 2015), as well as the eastern subarctic (Erni, Arseneault, Parisien, & Bégin, 2017; Hanes et al., 2019). As a result, changes to plant communities have been observed (Lantz et al., 2010; Racine, Jandt, Meyers, & Dennis, 2004). In the western subarctic of North America, changes to the successional trajectory of the tundra plant community are anticipated to have numerous bioclimatic repercussions (Chapin III et al., 2000); however, the response to wildfire has not been consistent across the tundra biome (Zhou, Liu, Jiang, Feng, & Samsonov, 2019). This variability in response prompts the question of whether certain tundra plant communities exhibit a high inertia that reduces the possibility of successional change post-wildfire (detailed in Chapter Two).

1.2 Establishing a baseline on a changing disturbance: Insect granivory at treeline

Boreal forest insects have highly specialized life cycles closely linked to climate and their vegetative host species (Dixon, 2003; Worrall et al., 2013). Following the definition of disturbance by White & Pickett (1985), some native and non-native insect species can be classified as biotic disturbances due to their ability to cause landscape-scale damage or mortality to vegetation within a brief period (Pureswaran et al., 2018). While chronic pressures limit host trees' growth and reproductive potential, the most pronounced impact on a forest stand are large episodic outbreaks (Haynes, Allstadt, & Klimetzek, 2014). Nevertheless, boreal forests have historically been resilient to these biotic disturbances and have evolved reproductive adaptations to limit insects' adverse effects on individuals for continued boreal tree recruitment. Seed masting (i.e., the production of many seeds; Linhart, Moreira, Snyder, & Mooney, 2014) and the interannual production of seed crops (Crawley & Long, 1995) are two ways in which trees can effectively satiate insect populations or limit reproduction overlap with high insect population years.

The most common insects reported as biotic disturbances within the boreal forest are defoliators (e.g., eastern spruce budworm [*Choristoneura fumiferana*]), and bark beetles and wood borers (e.g., mountain pine beetle [*Dendroctonus ponderosae*]). These insect types significantly damage or increase their host tree species' mortality and represent both punctuated and chronic biotic disturbances (Shen, Zhang, Liu, & Luo, 2014). Despite cone boring insects (e.g., spruce cone fly [*Strobilomyia* spp. Diptera: *Anthomyiidae*]) being widespread across the boreal forest and causing significant damage to their host trees, they have received comparatively much less attention within the biotic disturbance literature (Gärtner, Lleffers, & Macdonald, 2011; Lewis & Gripenberg, 2008). Cone boring insect granivores represent a unique set of insects, as they do not damage the host tree's physical structure but consume the reproductive units, significantly reducing the plant's resources for propagation (Hedlin et al., 1981; Prévost, 2002; Sweeney & Turgeon, 1994). Moreover, all damage to the reproductive units occurs prior to seed dispersal (Kolb, Ehrlén, & Eriksson, 2007).

Under continued climate change, insect populations are predicted to move northward and upslope as the climate becomes more suitable for sustaining larger populations (Pureswaran et al., 2018; Robinet & Roques, 2010). Larger and more frequent outbreaks are therefore anticipated, which may overcome the resilience of the current plant communities, resulting in a successional trajectory shift (Landry et al., 2016). Yet, at the northern boreal range edge, little is known on their impact to tree species and the biotic and abiotic conditions that support their population (Gärtner et al., 2011; except see Jameson, Trant, & Hermanutz, 2015; Kambo & Danby, 2018). A more detailed understanding of granivorous insects at treeline is of particular interest, as the availability of viable seed represents one of the most critical components to boreal range expansion (Cairns & Moen, 2004; Frei et al., 2018). While treeline is expected to expand northward and upslope under continued climate change (Körner, 1998; Kueppers et al., 2017; Timoney et al., 2019), insect granivory may represent a biotic disturbance that acts as a negative feedback, limiting range expansion by reinforcing the ecological inertia of the system (detailed in Chapter Three).

1.3 Compounding disturbances in coastal forests: Wildfire and fuelwood harvesting

Many people live within the boreal forest and contribute to the structure and functioning of the ecosystem state. After a large-scale disturbance event within a forest stand, the felling and removal of affected trees, known as salvage logging or post-disturbance harvesting, is often used to reduce the disturbance's negative economic impacts on a community (Boucher, Gauthier, Noël, Greene, & Bergeron, 2014). While insect outbreaks and large windstorms can result in rapid wood decay, some post-disturbance wood products are preferred. Wood that is pre-dried by the heat of a wildfire for example, can be easily used for home heating (Mansuy et al., 2015). The scale and intensity at which post-disturbance harvesting occurs depends on population size, accessibility, and geographic location (Leverkus et al., 2018).

Post-wildfire harvesting represented a compounding anthropogenic disturbance increasing pressure on plant species recovering from an initial natural disturbance (Leverkus et al., 2018). While wildfire and logging can separately create suitable microsite conditions that promote seedling establishment and tree recruitment (Greene et al., 2007; Macdonald, 2007; Turner et al., 1999), wildfire followed by wood harvesting can significantly reduce the ecological inertia of the forest stand. For example, the physical removal of the aerial seed bank can decrease the amount of viable seed that is available for dispersal (Donato et al., 2006). Additionally, large machinery can compress the forest floor, altering soil moisture conditions, and damage newly established seedlings (Purdon, Brais, & Bergeron, 2004). A shift in ecosystem structure and function can be anticipated when post-disturbance harvesting occurs and is not properly managed (Bergeron et al., 2017; Kurulok & Macdonald, 2007).

While the relationship between boreal forest resilience and post-wildfire wood harvesting has been examined extensively, our understanding of this relationship is broadly based on central and western boreal forest stands surrounding highly populated areas (see Leverkus et al., 2018). In the eastern Canadian subarctic of northern Labrador, wildfire frequency and severity has been historically low as a result of a cool, wet, maritime climate (Steijlen, Nilsson, & Zackrisson, 1995); therefore, post-wildfire wood harvesting by small communities has been limited. Yet, changes to the wildfire regime and human land-use of these post-wildfire landscapes are anticipated to occur under continued climate change (Erni et al., 2017; Hanes et al., 2019; Siegwart Collier & Mallik, 2010). Thus, a concerted effort linking natural and anthropogenic disturbances to forest resilience in an understudied region of the Canadian subarctic is required to establish a broader understanding of successional dynamics with changing disturbance regimes (detailed in Chapter Four).

1.4 Thesis Objective

The overall goal of my research is to determine whether disturbances disrupt floral composition and reproductive potential of boreal and tundra plant communities across the subarctic, and if so, whether these changes prime the landscape for successional change. Results from my research will support a broader understanding of disturbance regimes under continued climate change, as well as highlight areas where continued disturbance research is required (Lett & Dorrepall, 2018). Specifically, my research supports [1] a better understanding of how a novel wildfire regime will impact tree germination at their range edge, as well as how wildfires alter the treeline tundra plant community structure (detailed in Chapter Two); [2] an increase in the baseline understanding of insect granivory at the boreal-tundra treeline ecotone through an examination of the environmental characteristics across northern Canada that drive insect granivory presence and magnitude (detailed in Chapter Three); and [3] increase forest resilience research in an understudied region of the subarctic (i.e., Nunatsiavut), supporting research efforts on how compounding natural and anthropogenic disturbances influence range edge forest succession (detailed in Chapter Four). Within each Chapter, I asked the following research questions:

Chapter Two

- How does wildfire change the environmental characteristics of hillside boreal forest-tundra treeline ecotones?
- Do wildfires disrupt the treeline ecotone’s ecological inertia, thus favouring boreal range expansion in Yukon?

Chapter Three

- Are there any general abiotic and biotic conditions associated with the presence of insect granivory at the boreal-tundra treeline ecotone?
- Where evidence of granivory occurs, which conditions are associated with its magnitude?
- Is insect granivory at treeline associated with seed viability, and if so, how?

Chapter Four

- What do post-wildfire coastal forest landscapes in the eastern subarctic look like using forest age structure and tree species richness?
- Do the compounding effects of fire and fuelwood harvesting drive boreal seedling regeneration in Nunatsiavut's coastal forests?

1.5 Study Locations

Much like the spatial distribution of disturbances across Canada, my research was conducted across the latitudinal and longitudinal distribution of the Canadian subarctic (Figure 1.2). Permission to conduct research in northern Yukon (described in Chapter Two) was provided by the Vuntut Gwitchin First Nations, as this research takes place on their Traditional Territories. Specifically, my research was located at treeline ecotones near Eagle Plains (Site EPN: 65.78N, -137.76W; Site EPS: 66.46N -136.59W) and Dawson (Site TOW: 64.12N, -140.96W). Data collection at these sites occurred during the summers of 2017 – 2019. Study sites in Yukon was selected because treelines were accessible by vehicle and because northwestern Canada is experiencing the highest degree of warming as a result of climate change (Bush & Lemmen, 2019).

Research locations for Chapter Three were situated at the boreal-tundra treeline ecotone across northern Canada. I collaborated with researchers across six Canadian institutions to carry out coordinated data collection at treelines in Yukon (n = 4), Northwest Territories (n = 2), Manitoba (n = 1), Quebec (n = 1), and Newfoundland and Labrador (n = 2) on the traditional lands of the Vuntut Gwitchin, Tr'ondëk Hwëch'in, Inuvialuit, Tłıchǫ, Sayisi Dene, Inuit of Nunatsiavut, Mi'kmaq, and Beothuk peoples. All data collection occurred during the summers of 2018 (n=8) and 2019 (n=2). Research sites were located based on pre-existing data collection activities.

Data collection in Chapter Four was carried out on the land of the Labrador Inuit in the land claim settlement region of Nunatsiavut. Based on the knowledge of local community members, we selected three separate coastal boreal forests that experienced wildfire in the past three decades and had also been used as winter chainsaw harvesting locations by residences of Nain and Postville for fuelwood. Two sites were north of the community of Nain (Site 1: Tikkoatokak Bay; 56.42N and -62.12W; Site 2: Webb Bay; 56.45N and -61.52W) and one site was west of the community of Postville (Site 3: Beaver River; 54.46N -59.48W). Data collection occurred during the summer of 2018 and was a part of a POLAR Knowledge interdisciplinary research program lead by Dr. Carissa Brown.

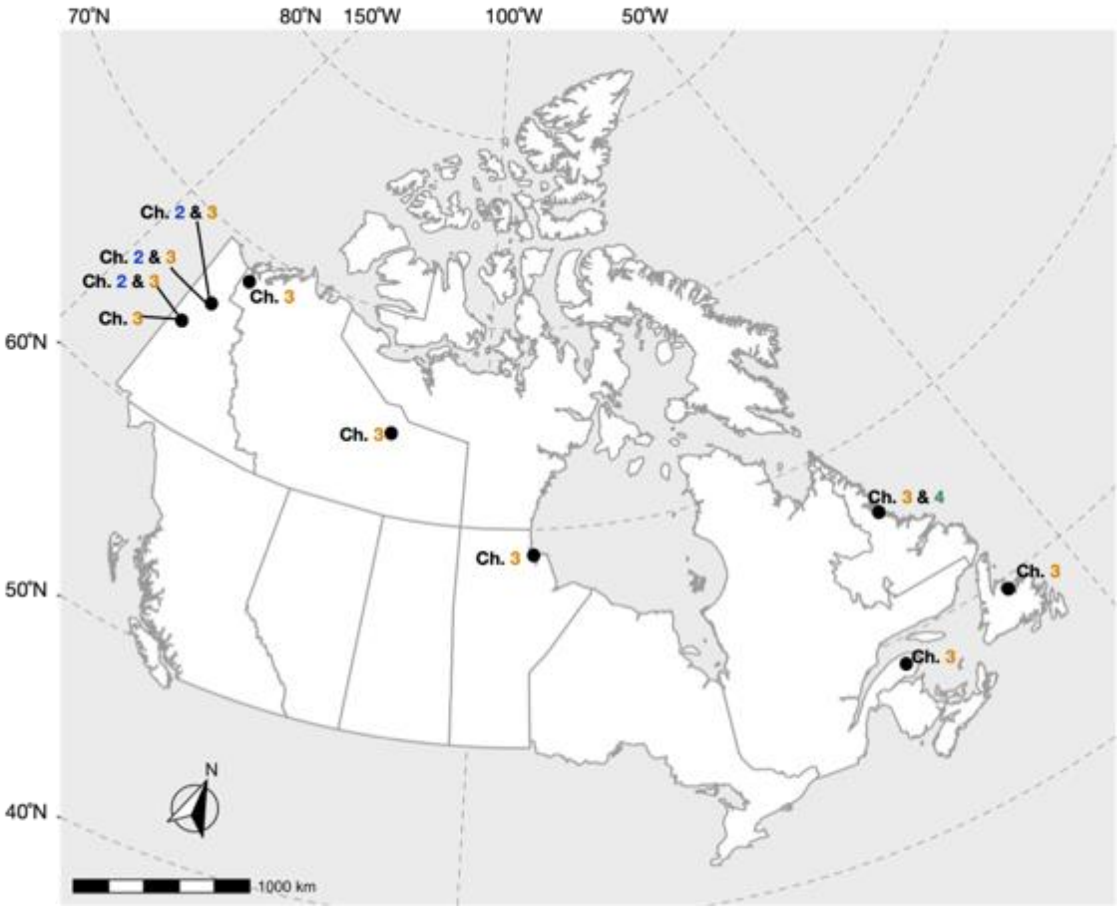

Figure 1.2 Location of all study sites by data chapter. Chapter Two (blue) occurred in Northern Yukon; Chapter Three (orange) occurred at treeline sites from Yukon to Newfoundland and Labrador; Chapter Four (green) occurred in Nain and Postville, Nunatsiavut.

1.6. Study Species

Black spruce is the central study species in each research Chapter. I chose this species for several reasons: black spruce are ubiquitous across the North American boreal forest and represents a dominant tree species in each study region. They are also considered a long-lived species, but tree age largely depends on wildfire return intervals (Greene et al., 1999). Black spruce is a semi-serotinous species that will disperse seeds from their aerial seed bank under extreme heat, after a fire, or with age if fire return intervals are long (Greene et al., 1999). Black spruce is also considered a good indicator of environmental change (Johnstone et al., 2020).

Recruitment failure after a disturbance will likely indicate successional trajectory change (Jayen, Leduc, & Bergeron, 2007; Johnstone, Hollingsworth, & Chapin III, 2008). Finally, spruce is a species of economic importance and is considered a suitable softwood species to harvest for energy purposes across North America (Greene et al., 1999).

White spruce (*Picea glauca*), balsam fir (*Abies balsamea* (L.) Mill.), and eastern larch (*Larix laricina* (Du Roi) K. Koch) are three additional tree species that are included in my research. These species are also long-lived and found throughout the boreal forests of North America. Unlike black spruce, these species are not serotinous and release their seeds from mature cones each year at the end of the growing season (Zasada & Gregory, 1969). While these species often prefer drier conditions, they can be found in mixed-stands with black spruce, depending on geographic location and topography (Greene et al., 1999; Purdy, Macdonald, & Dale, 2002). White spruce was included in the manipulative seeding experiment in Chapter Two. Balsam fir and larch were included in the dendroecological analyses in Chapter Four.

I chose to examine the understory vegetation using a fine-scale functional group framework based on plant morphological and physiological traits (e.g., shrubs, grasses, forbes). While I recognize that having understory vegetation data to the species level would provide a more robust understanding of plant community responses to changing disturbance regimes, functional group data reduces excessive variability within datasets that are already anticipated to have a high degree of variability. Functional group data interpretation is also easier to incorporate in future management operations across ecosystems (Laughlin et al., 2017). Furthermore, the breadth and intensity of data collection in Chapter Two, the collaborative nature of data collection in Chapter Three, and the time limitations discussed in Chapter Four all warranted a more general approach to collecting information on understory vegetation.

Nevertheless, a few understory species were of particular interest and were recorded in greater detail. Specifically, green alder (*Alnus viridis* (Chaiz) D.C. spp. *crispa*) was selected as a species to be used in the manipulative seeding study, as it represents an early colonizer of post-disturbance subarctic landscapes (Lantz et al., 2010; Travers-Smith & Lantz, 2020). I also collected species composition data on *Ceratadon* and *Polytrichum* mosses, as these species often represent early post-fire colonizers that compete with black spruce seedlings for resources (Charron and Greene, 2002, Tsuyuzaki, Narita, Sawada, & Kushida, 2014).

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Co-Authorship Statement

Chapter Two was co-authored with Dr. Carissa Brown. I was the principal contributor in the project proposal, experimental design, implementation of field methods, data analysis and the preparation of the manuscript. Dr. Brown contributed extensively to the experimental design and preparation of the manuscript. Abstract and referencing style in Chapter Two are formatted for specific journal submission requests (in preparation for submission to Ecosystems).

Chapter Three was co-authored with Katie Goodwin, Kirsten Reid, Anna Crofts, Dr. Ryan Danby, Dr. Steven Mamet, and Dr. Carissa Brown. I was the principal contributor in the project proposal, experimental design, implementation of field methods, data analysis, and the preparation of the manuscript. Co-authors contributed with experimental design and field protocol development, data collection, laboratory work, and manuscript review. Abstract and referencing style in Chapter Three are formatted to specific journal submission requests (in preparation for submission to Journal of Biogeography).

Chapter Four was co-authored with Dr. Carissa Brown. I was the principal contributor in the project proposal, experimental design, implementation of field methods, data analysis and the preparation of the manuscript. Dr. Brown contributed extensively through experimental design, data collection, and preparation of the manuscript. Chapter Four has been published in the peer-reviewed academic journal Arctic Science (2020); thus, formatting reflects the journal submission requirements.

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Chapter 2: Wildfires do not ignite boreal forest range expansion into tundra ecosystems in Yukon, Canada

Abstract

The resilience of northern ecosystems is being tested as the temporal and spatial distribution of wildfires continue to change. Wildfires at treeline may facilitate a northward advance of boreal tree species, as the tundra is in close proximity to fire-adapted species climatically primed for range expansion. To study the effects of wildfire on the resilience of the tundra plant community at treeline, we asked (1) how wildfire changes the environmental characteristics of the treeline, and (2) in the absence of viable seed limitation, do wildfires increase the likelihood of tree or shrub seedling emergence? To answer these questions, we measured a suite of biotic and abiotic factors at three paired burned and unburned treelines in Yukon, Canada. Our observational study was paired with a manipulative seeding experiment (1000 seeds • m^{-2}) of black spruce (*Picea mariana* (Mill) B.S.P.), white spruce (*Picea glauca* (Moench) Voss), and green alder (*Alnus viridis* (Chaiz) D.C. spp. *crispa*) to determine seedling emergence potential. Despite significant changes that we would expect to promote seedling emergence (i.e., reduced organic layer depth and vegetation ground cover, increases in growing degree days), all species emergence did not increase at burned treelines, but were limited to moist substrates that were found at both burned and unburned treelines. We speculate that, from the perspective of a seed, wildfire induced changes to the seedbed (forest floor) may have benefited seedling emergence, but more extreme surface temperatures made survival more challenging. Our study indicated no relationship between wildfire and seedling emergence at treeline; however, greater consideration of winter conditions, treeline characteristics (e.g., density of trees) and tundra plant community type (e.g., wet versus mesic) should allow us to better predict the conditions under which wildfire can facilitate tree or shrub range expansion.

Keywords: disturbance, winter climate, snow depth, growing degree days, frost, range expansion, treeline, wildfire, subarctic

2.1 Introduction

Impacts of continued climate change on natural disturbance events are predicted to affect ecosystem resilience and plant successional dynamics (Turner, 2010; Johnstone and others, 2016). Across the boreal biome, climate change has resulted in longer growing seasons, increasing the frequency of soil moisture deficits (Trugman and others, 2018; Hansen and Turner, 2019; Pastick and others, 2020). Longer growing seasons and drier conditions indirectly affect wildfire occurrence, as ignition events are controlled by climate, seasonal weather, people, and the amount of dry fuel available for consumption (Lecomte and others, 2006; Kasischke and Turetsky, 2006; Johnston and Flannigan, 2018; Hanes and others, 2019; Seidl and others, 2020). While responses to the fire-climate relationship vary with geographic location, models consistently predict a change in wildfire regimes across North America (Xi and others, 2019; Parisien and others, 2020). Observed increases in the frequency, severity, and extent of wildfires in northwestern North America support those model predictions (Johnstone and others, 2004; Soja and others, 2007; Hanes and others, 2019). Increased research on ecosystem recovery under novel wildfire regimes is therefore warranted (e.g., Turner, 2010; Buma and others, 2013; Zhou and others, 2019; Brehaut and Brown, 2020).

Adjacent to the boreal forest, the tundra biome has also experienced a change in the frequency of wildfires in recent decades (Soja and others, 2007; Higuera and others, 2011; Hu and others, 2015). While fires have generated biological legacies within many boreal vegetative species (Johnstone and others, 2016), the tundra has historically seen few wildfires due to its extreme cold climate and lack of fine fuels (Hu and others, 2015). Unlike boreal forests then, tundra ecosystems may not have adapted to wildfire as a regular disturbance and thus, may result in a shift in plant succession (Higuera and others, 2008; Johnstone and others, 2016). North of the Arctic Circle, wildfire induced shifts in the tundra plant community have been observed with greater graminoid (Barrett and others, 2012) and shrub dominance post-wildfire (Racine and others, 2004; Lantz and others, 2010; Rocha and others, 2012). Yet, this change in the successional trajectory has not been consistent across the tundra (Bret-Harte and others, 2013; Zhou and others, 2019), suggesting there are underlying patterns and processes that may make certain pre-disturbance tundra plant communities susceptible to a shift in succession under continued climate change.

The boreal forest-tundra treeline ecotone represents a unique opportunity to examine the effects of wildfire on tundra plant communities. At the treeline ecotone, tundra ecosystems meet the leading edge of boreal forest ecosystems, which are fire-adapted and climatically primed for northward range expansion (Korner, 1998; Kueppers and others, 2017; Feuillet and others, 2020). While temperature-based models have predicted an upslope and northward advance of boreal tree species into the tundra (Parmesan and Yohe, 2003; Settele and others, 2014), the observed response has been variable (Harsch and others, 2009; Rees and others, 2020). The lag between the fundamental and realized niche of boreal species suggests that temperature alone cannot predict range expansion (Harsch and others, 2009; Brown and others, 2019). While viable seed production is low across the ecotone and can successfully limit range expansion (Viglas and others, 2013) at the population or hillside-scale (i.e., a treeline ecotone that occurs within a relatively short elevational distance; Bader and others, 2020), the ecological inertia, or resistivity, of the tundra at treeline may be high, as a result of their biotic and environmental characteristics (e.g., structure of tundra vegetation, limited soil moisture). This high ecological inertia may provide a buffer against any shift in plant community composition (Johnstone and others, 2016; Stralberg and others, 2016). Nevertheless, the inertia may be broken when continued climate warming increases viable seed production and is paired with wildfire, and the tundra vegetation community is within the natural dispersal distance of fire-adapted tree and shrub species (Buma and others, 2013). Therefore, our research aims to fill the knowledge gap of understanding how wildfire affects the structure of the treeline ecotone, as a shift in the successional trajectory may have numerous functional and bioclimatic repercussions (Chambers and others, 2005; Mack and others, 2011; Jones and others, 2015).

We set out sampling transects across three wildfires that had burned within the last two decades on the boreal-tundra treeline ecotone to explore two objectives, [i] to determine how wildfires change environmental characteristics of the treeline ecotone throughout the course of the year; and [ii] to examine whether wildfires can disrupt the ecological inertia of the treeline ecotone, thus favouring boreal range expansion. For objective one, we hypothesized that the presence of wildfire would substantially change biotic and abiotic conditions at each site, between burned and unburned treelines. Specifically, we predicted that similar to an interior boreal forest experiencing a wildfire, organic layer depth, vegetation cover, and available soil moisture at treeline would be reduced, as a result of material combustion (Greene and others, 2007; Hesketh and others, 2009). In addition, because all study sites had burned in different years within the past two decades, we predicted that if a site had experienced a wildfire more recently, then environmental conditions would be more uniform (i.e., have low variance). Conversely, we predicted that burned treelines that experienced a wildfire more than ten years ago would be more similar to the unburned treeline, indicating high ecosystem resilience

(Holling, 1973). These predictions were based on our understanding of wildfire impacts to biotic and abiotic conditions within boreal forests (Certini, 2005), the short regeneration window that occurs in western North America post-wildfire (Johnstone and Kasischke, 2005), and the wildfire characteristics common in the study region (Brown and Johnstone, 2012). We tested our predictions using an intensive natural field experiment where numerous abiotic and biotic factors were measured across three separate pairs of burned and unburned treeline ecotones in Yukon, Canada.

For our second objective, we hypothesized that when the natural seed availability constraint is removed, boreal tree and shrub emergence across the treeline ecotone would increase as a result of wildfire. We predicted that if a wildfire occurred, post-fire conditions would be similar to those created by a wildfire in interior boreal forests (see aforementioned changes in the first objection), priming the landscape for seedling establishment. We tested this hypothesis at two of the tree study sites using a manipulative seeding experiment for black spruce (*Picea mariana* (Mill.) B.S.P.), white spruce (*Picea glauca* (Moench) Voss), and green alder (*Alnus viridis* (Chaiz) D.C. spp. *crispa*). In this study, a successful break in the ecological inertia across a treeline for early life stages was defined as any significant increase in the seedling emergence or interannual survival when compared to the unburned treelines.

2.2 Methods

2.2.1 Study area

Research took place in northern Yukon, Canada on traditional territories with permission from the Vuntut Gwitchin First Nation. This region is characterized by a cool continental climate with an annual mean temperature of -6.2˚C, an average maximum of 14˚C in July and an average minimum of -27˚C in January (Environment and Climate Change Canada, 2020). Mean annual precipitation is approximately 400 mm, the majority of which falls as rain during the summer months. Black spruce is the dominant tree species in the region; however, white spruce and larch (*Larix larincina* (Du Roi) K. Koch) are found throughout the landscape. While treeline form and tundra vegetation at the upper edge of the treeline ecotone is variable across the region, we limited our study to diffuse treeline ecotones (i.e., gradual reduction of tree density when moving upslope; Bader and others, *in review*) with mesic tundra that was dominated by low height shrubs and lichen vegetation.

We selected three burned treeline ecotones that experienced wildfire in the past two decades for this intensive natural field experiment. Two of the sites were located near Eagle Plains and burned in 2017 (Eagle Plains South: EPS; 65.78N, -137.76W) and 2007 (Eagle Plains North: EPN; 66.46N -136.59W), with an area burned of approximately 86,127 ha and 6,369 ha, respectively. The third site was located west of Dawson and burned in 2005 over approximately 27,000 ha (Top of the World: TOW; 64.12N, -140.96W). Each wildfire was heterogeneous in its consumptive path across the treeline ecotone, facilitating a natural comparison between burned and unburned elevational treelines occurring along hillslopes in close proximity (i.e., less than 10 km apart between treatments). While it is likely that the unburned treatment at each site experienced a fire in the past, we selected locations using the Yukon fire history map records that indicated no wildfire occurrence since at least 1940, the earliest government records of fires in northern Yukon available (Government of Yukon, 2020). In addition, when we arrived on site, we ensured no evidence of recent fires was visible (e.g., burn scars, charred material in organic layer).

We recognize that drawing conclusions from a limited number of study sites at various stages of post-wildfire recovery reduces the predictive power of our analyses and impacts our ability to speak to regional patterns. Yet, conditions that facilitate increased germination success occur at a microsite scale (Graae and others, 2012); therefore, our approach (fewer sites with heavy instrumentation) provides a more detailed understanding of wildfire impact on potential germination and establishment of seedlings when compared to a study with more sites examined at broader scales.

2.2.2 Field measurements

To determine whether burned treelines would be different in biotic and abiotic conditions when compared to unburned treelines (Objective 1), we collected data on stand characteristics, soil properties (both environmental and abiotic), as well as ground vegetation percent cover (listed in detail in Table 2.1). These data were also used to inform our predictions that conditions at the burned treeline would be more suitable for seed germination throughout the year and conditions would be less uniform as time-since-wildfire increased.

At each of our sites we established four 100 m transects that ran parallel with the changing stand density of the hillslope treeline ecotone within the burned and unburned treeline pair (i.e., transects moved upslope from forested to tundra vegetation). We located the initial transect by first positioning ourselves within an area that was visually representative of the larger ecotone, then located the highest upslope reproductive (i.e., cone bearing) tree, as a means to denote the upper range limit of the local population. This reproductive tree represented the middle or “0 m” marker of the transect (Figure 2.1). We established each subsequent transect by walking at least 20 m away from the 0 m marker of the previous transect and locating the closest upper most reproductive tree. Transects ran + 40 m upslope from the 0 m marker towards the more continuous tundra and – 50 m downslope into the more forested part of the treeline ecotone. Despite experiencing a wildfire, we were still able to locate the 0 m marker for each transect at each burned treeline due to the post-fire reproductive strategy of black spruce. Burnt cones that remained on trees were frequent enough to support transect establishment.

Table 2.1 Summary table of all biotic and abiotic data recorded at the plot, transect, and treatment (i.e., burned and unburned) level of each site. A total of 160 plot level data points were recorded at each burned and unburned treeline (total of 40 data points per transect or 320 per site); but data points were averaged to 10 datapoints per transect because four points were taken every 10 m. This resulted in 10 data points per transect (40 data points per treatment). A total of 10 data points were collected at the transect level and up to 10 data points were collected at the site level. Site level data collection depended on access and availability of nutrient capsules and data loggers.

Plot level (40 data points/transect)			
abiotic	units	biotic	units
Soil temperature point measure	˚C	Tall multistemmed shrubs (shrubs>0.4 m)	%
Soil moisture point measure	mm • 10 cm soil depth^{-1}	Erect dwarf shrubs (shrubs 0.1 - 0.4 m)	%
Soil pH	pH	Prostrate dwarf shrubs (shrubs < 0.1 m)	%
Organic layer depth	cm	Vascular non-wood herbaceous plants	%
Rock depth	cm	Graminoids	%
		Acrocarpous moss	%
		Pleurocarpous moss	%
		Ceratadon	%
		Politrichum	%
		Fruticose lichen	%
		Foliose lichen	%
		Crustose lichen	%
		Leaf litter	%
Transect level (10 data points/transect)			
abiotic	units	biotic	units
Daily soil temperature (ibutton)	˚C	Natural seed rain	seeds • m^{-2}
		Natural seedlings	seedings • m^{-2}
		Stand density	stems • m^{-2}
Treatment level (5 -10 data points/transect)			
abiotic	units		
Total nitrogen (2018 growing season)	ppm		
NH_4^+ (2018 growing season)	ppm		
Phosphorus (2018 Growing Season)	ppm		
Daily soil temperature (Em50 sensor)	˚C		
Daily soil moisture (Em50 sensor)	mm • 10 cm soil depth^{-1}		
Daily snow depth	cm		
Daily surface air temperature	˚C		

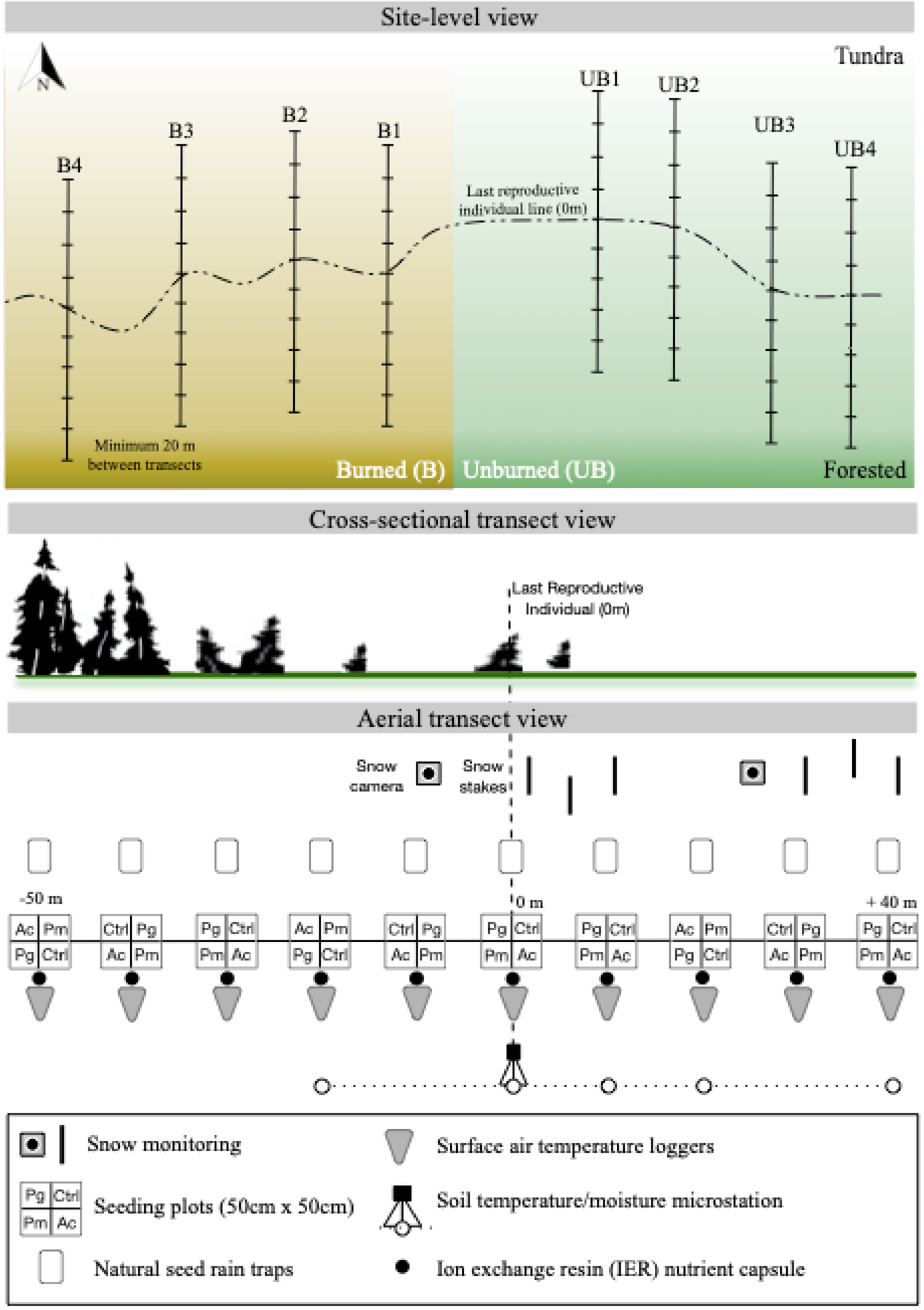

Figure 2.1 Site- and transect-level (cross-sectional and aerial) view of study sites. Four transects of 100 m in length were positioned in both burned and unburned treelines. Direction of transects is parallel with the decreasing density of trees from forested to tundra vegetation. Aerial view of transect shows two snow cameras with at least six snow stakes (black lines), as well as 10 seed rain traps every 10 m. Seeded plots for black spruce (Pm – *Picea mariana*), white spruce (Pg – *Picea glauca*), green alder (Ac – *Alnus viridis* spp. *crispa*), and a control (Ctrl) were 50 cm x 50 cm and were positioned every 10 m along each transect.

We divided each transect into ten 10 m blocks and established four 50 cm x 50 cm plots every 10 m for the manipulative seeding experiment described later (i.e., plots < blocks < transects; Figure 2.1). We measured a suite of abiotic and biotic characteristics within each block that has been found to be important for tree seed germination; however, the number of replicates for each factor varied based on feasibility (i.e., accessibility of data loggers, cameras, etc.; Table 2.1). At the seeding plot level, we collected data on percent cover of functional group ground vegetation, but also took note of the percent cover of select moss species (i.e., *Polytrichum* sp. and *Ceratadon* sp.) that are important indicators of spruce seedling establishment (Charron and Greene, 2002). We also recorded organic layer depth and took several point measurements of soil temperature (Hanna Instruments HI 98331 Soil Test meter) and volumetric soil moisture (Procheck, Decagon Devices, Pullman, WA, USA). These point measurements were collected within the same day for each site, and within a week between sites.

At the block level, we measured stand density within a 10 m x 10 m area for a total area of 0.4 ha per treeline. Stand density was quantified as the number of stems • m^{-2}. We collected data on natural seed rain using 40 seed traps distributed every 10 m along each transect at sites EPS and EPN. Only ten seed traps in the burned and unburned treelines were used at site TOW due to resource and time constraints. Seed traps were constructed of 50 cm x 25 cm x 5.7 cm deep plastic greenhouse trays lined with artificial grass that protected trap contents from wind (following Johnstone and others, 2009). Seed traps were emptied twice during the growing season, in June and August, to collect as much natural seed rain as possible, as well as limit any early germination occurring in the trays prior to collection. Annual seed trap data were quantified as number of seeds • m^{-2}. We also measured natural seedling establishment in each block by quantifying the number of seedlings less than 50 cm in height along a 10 m x 1 m belt transect (seedlings • m^{-2}).

To show how burned and unburned treelines differ throughout the year, volumetric soil moisture and soil temperature were monitored continuously at a depth of 5 – 10 cm using five 5TE probes connected to Em5 dataloggers (Decagon Devices, Inc., Pullman, Washington) across the burned and unburned treeline ecotone at each site. At each burned and unburned treeline, probes were located at the -20 m, -10 m, 0 m, +10 m, and +40 m markers along the third (middle) transect. For site EPS, five additional loggers were positioned along the first transect to derive a better picture of soil moisture and temperature variability one-year post-fire. All volumetric water content (m^3 • m^{-3}) data were converted to mm of water per 10 cm depth of soil for subsequent analyses. We measured inorganic soil nitrogen (total nitrogen and NH_4^+) and phosphorus availability for the 2018 growing season using 20 ion exchange resin (IER) devices along transect one and three (Unibest Company, Bozeman, Mont). IER devices were inserted into the soil at a depth of 5-10 cm as early as possible during the 2018 growing season and removed the first week of August prior to the first frost event. Note that because we do not have specific bulk density measurements to accompany each resin capsule, these nutrient data refer to nutrients available to plants within the immediate area rather than a reflection of what quantity is specifically in the soil. Finally, snow depth and duration were monitored daily using time lapse cameras directed at six to ten 80-cm-tall measuring sticks. These sticks had markers every 10 cm; thus, data resolution is reduced to 10 cm intervals.

All of these field measurements were conducted at each burned and unburned treeline at each site; however, due to fieldwork time constraints, data collection at the site TOW was reduced. While there were still four 100 m transects in each treatment at TOW, plot level data collection was reduced to one plot per block. In addition, we were unable to collect 2018 growing season nutrient data.

2.2.3 Seeding experiment

To assess whether wildfires at treeline would facilitate the range expansion of boreal tree and shrub species in the absence of seed limitation (Objective 2), we added 100 seeds of black spruce, white spruce, and green alder in the separate 50 cm x 50 cm plots that had been established in 2017 (site EPN) and 2018 (site EPS) along each transect with the burned and unburned treelines. We added additional seed (100 seeds per plot) during the summers of 2018 and 2019 to each plot for each site. Seeded plots were accompanied with a control plot with no seed addition to measure natural emergence. Seed addition occurred as early in the field season as possible (i.e., early June), as seeds had already been cold stratified in storage. Each plot was examined visually for potential seedling emergence in mid-June and early August of each year. Seed was not added to site TOW due to limited seed availability.

The majority of the seed was obtained from the National Tree Seed Centre at the Atlantic Forestry Research Centre in Fredericton, NB where they are stored at -20˚C (Table 2.S1). We did not want to deplete the few northern seed stocks of the NTSC, so additional white spruce seed were ordered from the Forestry Management Branch of Yukon Energy, Mines, and Resources. All ordered seed collections are from locations in close proximity to experimental sites (i.e., northern Yukon) expect for green alder, which were collected from northern Quebec. While it is not in close proximity to the Yukon, this collection represented the most northern collection available for green alder.

2.2.4 Statistical analyses

To answer our first research question of the difference between biotic and abiotic conditions between burned and unburned treelines, we averaged plot-level data (i.e., four plots per block) at sites EPS and EPN to a single plot level data point for every block within a transect. We averaged plot data to match data collection design at TOW where ground cover data were only recorded at one plot per block. We also removed any clear outliers from each site-level dataset. We defined outliers as data points that did not make biological sense (e.g., soil temperatures above 40˚C). Plot-level data of burned and unburned treeline ecotones were compared at the site-level using one-way ANOVAs. This analysis allowed us to determine which factors at each site exhibited a significant change after wildfire, as well as the directionality of the change. We also performed a Bartlett test of homogeneity of variance on each factor within each site to determine whether the distribution of the data points changed between burned and unburned treelines (Blauw and others, 2015). While the Bartlett test is commonly used to indicate whether the variance of two groups is similar, we were more interested in significant differences between groups, which would support our hypothesis that environmental conditions across a treeline ecotone become more similar post-wildfire. Due to the many number of tests, we used a *p*-value of 0.01 to be conservative with our findings. Model assumptions were checked by assessing the level of overdispersion and plotting residuals versus fit.

We combined all site data and used nonmetric multidimensional scaling (NMDS) ordination to visually assess the difference between burned and unburned treelines and time-since-wildfire. This analysis was conducted using the ‘metaMDS’ function in the package ‘vegan’ (Oksanen and others, 2017) in R (R Development Core Team, 2018**)**, with plot-level data converted into a Bray-Curtis dissimilarity matrix, three dimensions, and 100 independent runs. While the Bray-Curtis is considered an appropriate distance measure for plant community data, we used the 'rankindex' function in the 'vegan' package prior to multidimensional analyses to ensure it represented the best dissimilarity index for our dataset, which included both environmental and plant community data.

Environmental data collected at the treatment level were used to calculate daily mean, minimum, and maximum soil temperature, as well as daily mean soil moisture. We then used these data to quantify growing degree days (GDD) by using the sum of degree days in each month when mean temperature was greater than or equal to 5˚C (Sirois, 2000), and freezing degree days (FDD) when temperatures were less than 0˚C (Beer and others, 2007). To determine whether burned treeline ecotone experienced a lengthening of the growing season, we quantified the number of days and summed temperatures during the fall (Sept 01 – Nov 01) and spring (March 15 – June 01) when the maximum temperature was greater than 5˚C. Finally, number of extreme freeze-thaw events were calculated for the fall and spring by summing the number of days in which soil temperature maximum was greater than 0˚C and the minimum was below 0˚C (Guiden and others, 2019).

To answer our second research question on seedling emergence across the treeline ecotone, we planned to incorporate biotic and abiotic variables that exhibited significant change post-wildfire into linear mixed models using annual emergence of tree and shrub species as the response variable; however, emergence was extremely low across all sites and treatments (see Table 2.S2). Moreover, early green alder seedlings were indistinguishable from other early shrub species and were nearly impossible to find in an unburned plot. We could not justify the use of linear mixed models with so few occurrences; therefore, we used Pearson's correlation to make bivariate comparisons of seedling emergence and plot-level variables. We considered any correlation greater than 0.3 to be indicative of an important association (Raynolds and others, 2004).

2.3 Results

2.3.1 Plot-level data

Stand density was similar across burned and unburned treatments for sites EPN and TOW, while the unburned treeline ecotone at EPS was denser than the burned treeline (burned in 2017; F-value = 7.051, *p* = 0.001; Table 2.2). All sites exhibited low mean natural seed rain, but sites did not respond in the same direction. Significantly greater seed rain occurred in 2019 (F-value = 6.168, *p* = 0.005) at the burned treeline at site EPS when compared to the unburned treeline (Table 2.3). Conversely, significantly lower seed rain occurred in 2018 (F-value = 20.37, *p* = 0.005) at the burned treeline at site EPN (burned in 2007) when compared to the unburned treeline. Natural seedling emergence was low across sites (both burned and unburned treelines); however, mean seedling density was significantly greater at the burned treeline ecotone at site EPN when compared to the unburned treeline (F-value = 12.76, *p* = 0.005).

Within each site, most vegetation functional groups showed a reduction in mean percent cover after wildfire (Figure 2.2). Soil characteristics for sites EPS and TOW indicated a significant decrease in mean organic layer depth at each burned treeline ecotone when compared to their unburned pair (Table 2.2; Table 2.3); however, few plots exhibited a complete loss of organic layer (see standard deviation of Table 2.3). No significant difference in mean growing season nutrient availability was evident, except for phosphorus at site EPS, which showed a significant increase at the burned treeline when compared to the unburned pair.

Table 2.2 Summary data for burned and unburned treelines at each site. All data are reported as averages (± standard deviation). For stand density, data are from the forty 10 m^2 blocks. For natural regeneration, data are from the forty 1 m x 10 m transects. For seed rain, data are from the forty 50 cm x 25 cm x 5.7 cm deep seed traps (except for site TOW, which only had ten seed traps for each burned and unburned treeline). For organic layer depth, data are from the 160 measurements taken at each burned and unburned treeline at each site.

	EPS		EPN		TOW	
	unburned	burned	unburned	burned	unburned	burned
mean stand density (stems • m^{-2})	0.052 (± 0.03)	0.030 (± 0.04)	0.050 (± 0.08)	0.073 (± 0.13)	0.024 (± 0.03)	0.026 (± 0.04)
mean natural regeneration (seedlings • m^{-2})	0.048 (± 0.08)	0 (±0.00)	0.045 (± 0.103)	0.658 (± 1.08)	0.063 (±0.11)	0.050 (±0.12)
mean seed rain 2018 (seeds • m^{-2})	0.009 (±0.02)	0.021 (± 0.03)	0.570 (± 0.05)	0.018 (± 0.03)	NA	NA
mean seed rain 2019 (seeds • m^{-2})	0.014 (± 0.03)	0.035 (± 0.05)	0.220 (± 0.03)	0.007 (± 0.02)	0.100 (± 0.12)	0.05 (± 0.11)
mean organic layer depth (cm)	20.68 (± 5.65)	8.78 (± 7.08)	9.68 (± 9.01)	6.46 (± 5.73)	15.73 (± 6.10)	5.8 (± 3.29)

NA refers to no data collected

When all plot data from each site were visualized within the three-dimensional NMDS space, we found a clear divide between burned and unburned ordination scores, except for TOW, which exhibited increased overlap between burned (burned in 2005) and unburned treelines (Figure 2.3). The largest difference between burned and unburned characteristics was captured by Axis 1 and was mostly explained by soil temperature, and percent cover of tall multi-stemmed shrubs and *Ceratadon* moss.

Table 2.3 One-way ANOVA and Bartlett's Test comparing all biotic and abiotic factors of each burned and unburned treeline within each site. Significance of $p \leq 0.01$ shown by '*'. Direction in ANOVA indicates whether there was a positive (+) or negative (-) change in direction of the mean value from the unburned treeline. Direction for the Bartlett's test indicates whether there was an increase (+) or decrease (-) in variance around the mean. Only significant changes are shown.

	EPS (1 year post-burn)				EPN (10-year post-burn)				TOW (13-year post-burn)			
	ANOVA		Bartlett's Test		ANOVA		Bartlett's Test		ANOVA		Bartlett's Test	
Covariate	F-value	Direction	K^2	Direction	F-value	Direction	K^2	Direction	F-value	Direction	K^2	Direction
Stand characteristics												
natural seed rain 2018	5.99		3.54		20.37*	(-)	4.34		na		na	
natural seed rain 2019	6.17	(+)	12.66*	(+)	4.03		9.15*	(-)	1.00		0.38	
natural regeneration density	16.02*	(-)	INF*	(-)	12.76*	(+)	128.2*	(+)	0.25		0.29	
Soil characteristics												
organic layer depth	110.2*	(-)	13.95*	(+)	6.62	(-)	10.926*	(-)	82.07*	(-)	13.8*	(-)
Total Nitrogen	0.81		1.76		0.41		0.06		Na		Na	
Inorganic NH4	0.63		1.79		0.37		0.05		Na		Na	
Phosphorus	36.54*	(+)	43.95*	(+)	1.87		6.48		Na		Na	
Ground cover												
tall multi-stemmed shrubs (TMS)	9.99*	(-)	165.7*	(-)	22.38*	(-)	21.49*	(-)	4.69		52.30*	(+)
erect dwarf shrubs (EDS)	50.20*	(-)	32.20*	(-)	1.03		3.13		0.37		5.23	
prostrate dwarf shrubs (PDS)	251.60		8.06*	(-)	100.2*	(-)	19.55*	(-)	1.53		8.44*	(+)
vascular non-woody herbs	40.45*	(-)	12.66*	(+)	4.84		0.27		0.58		15.10*	(+)
graminoids	22.70*	(-)	8.70*	(-)	2.31		14.29*	(+)	31.51*	(-)	20.77*	(-)
acrocarpous moss	4.70		1.92		7.38		291.51*	(-)	12.31*	(-)	INF*	(-)
pleurocarpus moss	135.1*	(-)	184.3*	(-)	24.35*	(-)	INF*	(-)	76.98*	(-)	40.61*	(-)
ceratodon purpureus	4.98		58.05*	(+)	47.1*	(+)	87.29*	(+)	3.27		63.14*	(+)
politrichum moss	5.09		8.12*	(-)	52.39*	(+)	98.60*	(+)	0.24		13.79*	(+)
fruticose lichen	14.42*	(-)	21.80*	(-)	86.67*	(-)	229.8*		2.37		6.14	

leaf litter	1.01		23.59		1.07		2.44		1.77		16.90**	(+)
Environmental characteristics												
soil moisture (Aug 2018)	28.01*	(+)	10.93*	(+)	0.35		0.09		0.83		2.91	
soil moisture (Jun 2019)	13.79*	(+)	6.37*	(+)	3.31		1.07		0.47		2.73	
soil moisture (Jul 2019)	5.45		0.72		3.42		2.06		0.74		0.23	
soil moisture (Aug 2019)	4.11		60.16*	(-)	0.08		0.21		0.74		0.11	
soil temperature (Aug 18)	0.04		4.76		49.4*	(+)	6.80		85.89*	(+)	3.55	
soil temperature (Jun 19)	79.68*	(-)	5.23		421.3*	(+)	42.72*	(+)	9.74*	(+)	6.18	
soil temperature (Jul 19)	2.51		14.13*	(+)	81.83*	(+)	26.92*	(+)	62.8*	(+)	0.85	
soil temperature (Aug 19)	16.24*	(+)	20.13*	(+)	15.91*	(-)	1.27		61.15*	(+)	7.98*	(-)

* $p \leq 0.01$

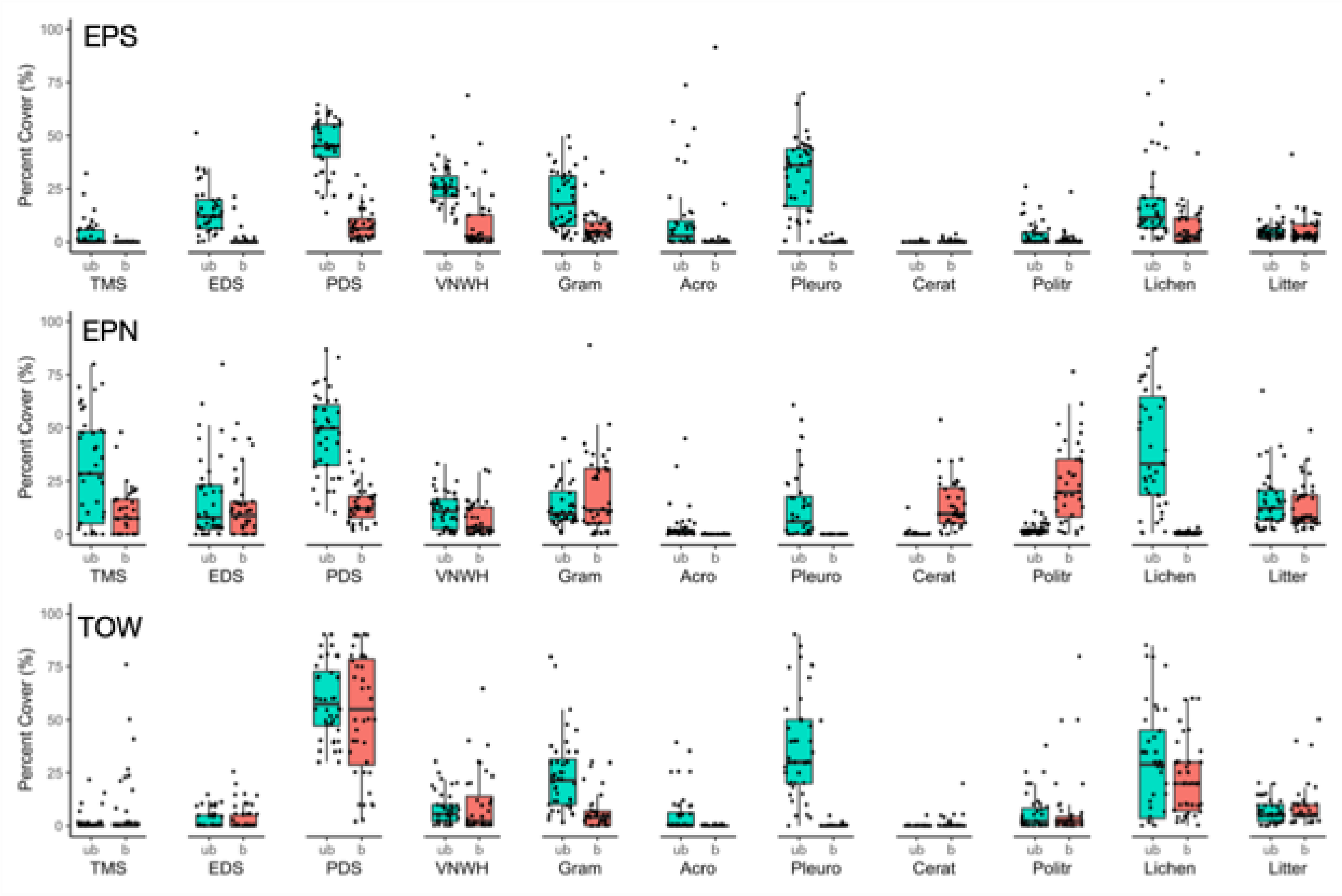

Figure 2.2 Percent cover of the plot-level vegetation for the burned (red) and unburned (blue) treelines for each site. Acronyms for the categories are as follows: tall multi-stemmed shrubs (TMS), erect dwarf shrubs (EDS), prostrate dwarf shrubs (PDS), vascular non-wood herbaceous plants (VNWH), graminoids (Gram), acrocarpous mosses (Acro), Pleurocarpous mosses (Pleuro), *Ceratadon* spp. (Cerat), *Polytrichum* spp. (Politr), fruiticose lichen (Lichen), and leaf litter (Litter).

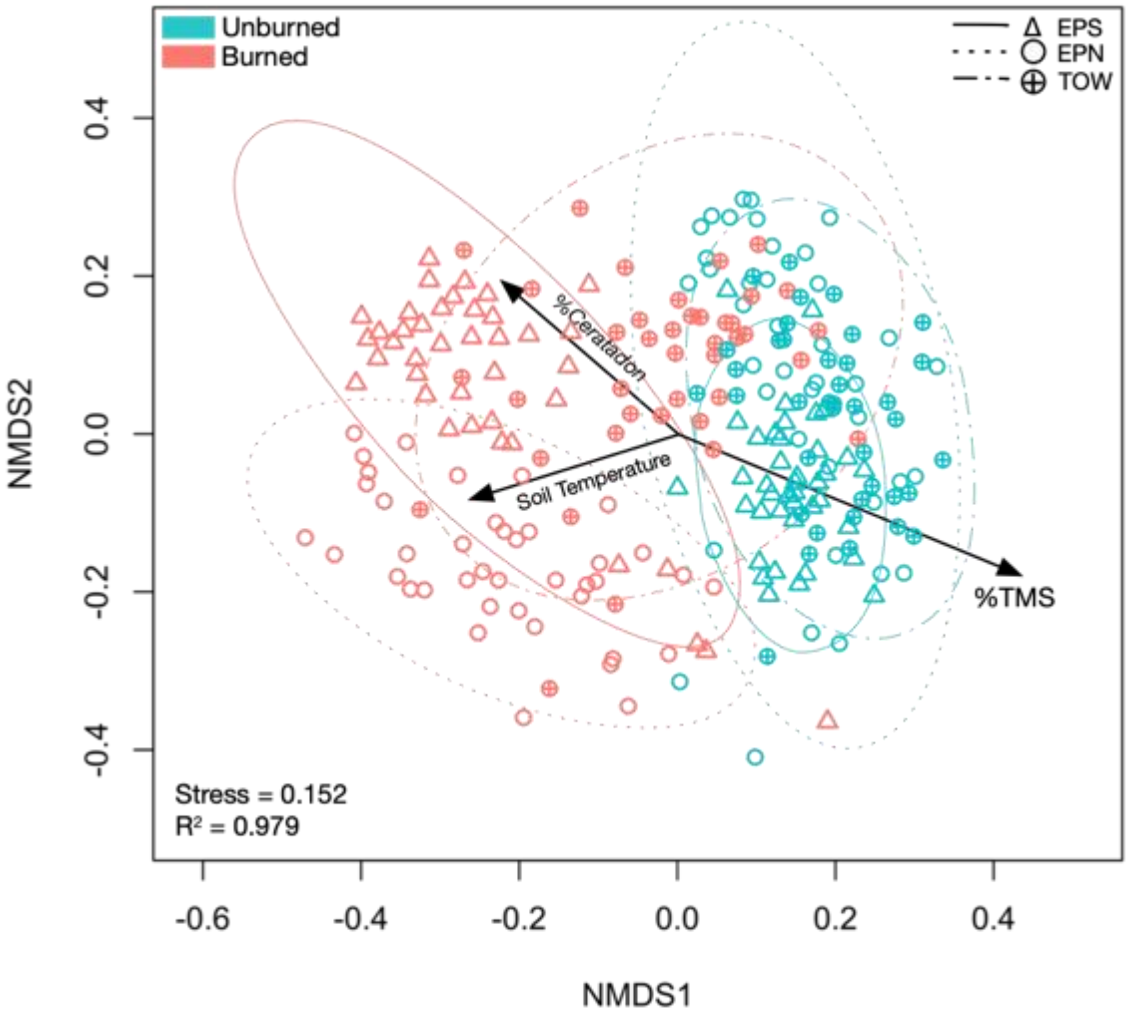

Figure 2.3 Non-metric multidimensional scaling (NMDS) ordination (k=3, stress = 0.152) of treeline site plant community functional groups and environmental conditions grouped by burned (red) and unburned (blue) locations. Sites are coded by point shape: triangle (EPS), circle (EPN), and filled circle (TOW). Each point represents a 50 cm x 50 cm plot. Points closer together are more similar than those farther apart.

2.3.2 Site-level environmental data

Daily mean temperatures were consistently greater during the growing season and lower during the winter across all burned treeline ecotones of each site (Figure 2.4). At site EPS, daily mean soil moisture was also greater at the burned treeline ecotone during the growing season;

however, differences in soil moisture between burned and unburned treelines at site EPN and TOW were marginal (Figure 2.4). The aforementioned soil moisture and temperature point measure data presented in the ANOVA table support these results (Table 2.3). Across all sites, the greatest difference in temperature between burned and unburned treelines occurred during the growing season; however, temperature differences were often more consistent throughout the winter (Figure 2.5). As a result of these annual temperature differences between burned and unburned treelines we found that each site had greater GDD at burned treelines (Figure 2.6). Similarly, burned treelines experienced greater FDD at each site. Snow depth was also consistently lower in the burned treeline ecotone for sites EPS and EPN throughout the winter (Figure 2.S2).

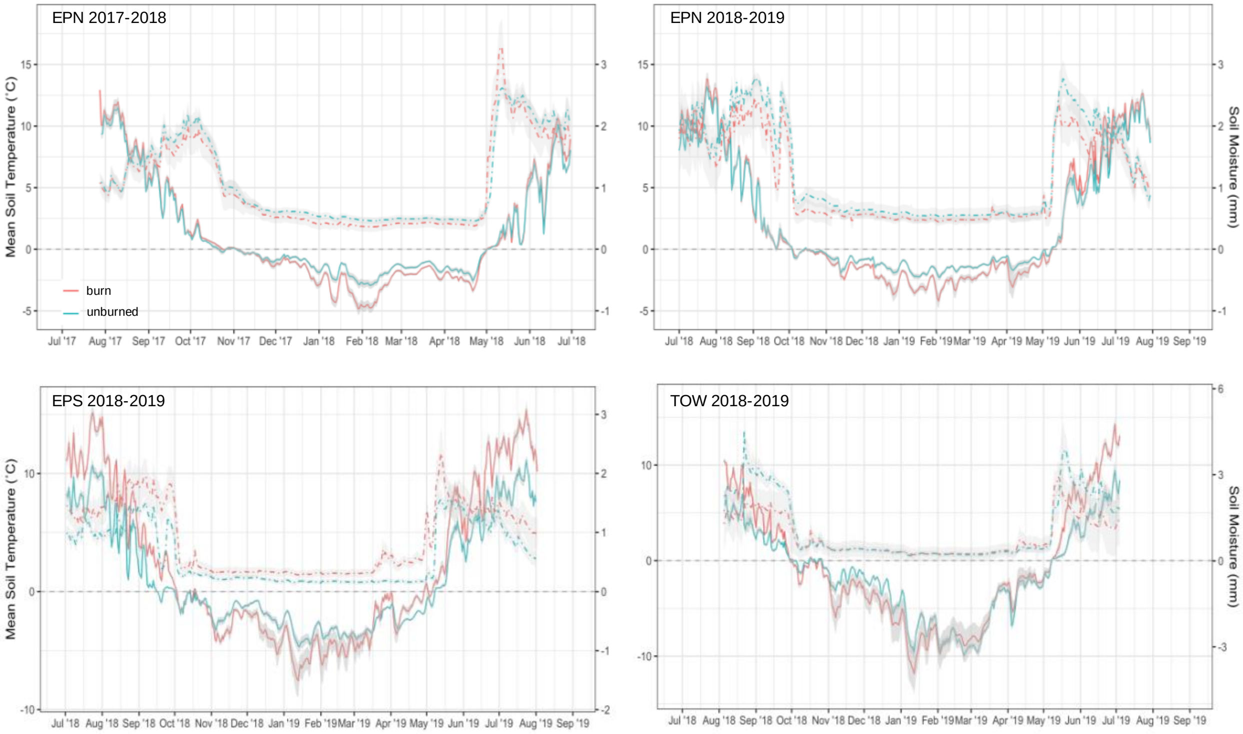

Figure 2.4 Daily mean soil temperature (solid line) and soil moisture (dashed line) data from the Em5 dataloggers (Decagon Devices, Inc., Pullman, Washington). Each site includes data on burned (red) and unburned (blue) treelines. Grey filled area surrounding lines represents standard error (SE) for daily data points. Multi-year data from site EPN are divided into the top left (2017-2018) and top right (2018-2019) panels.

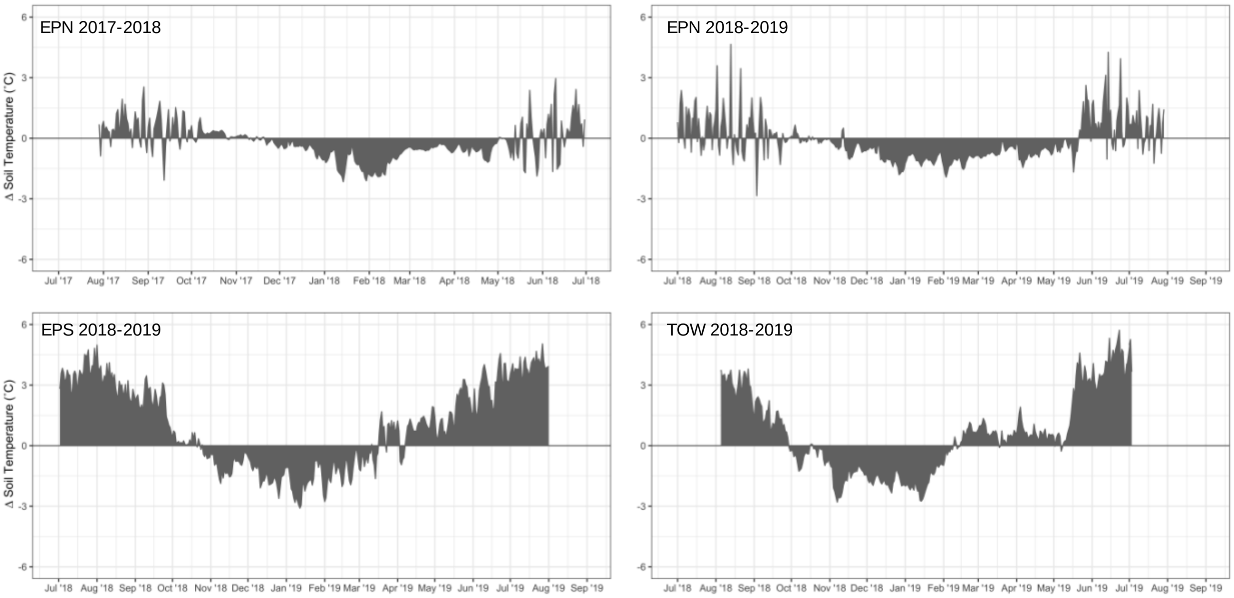

Figure 2.5 The difference in daily mean soil temperature (˚C) between the burned and unburned treatments for each site (burned subtract unburened data). Data derived from the Em5 dataloggers (Decagon Devices, Inc., Pullman, Washington). Multi-year data from site EPN are divided into the top left (2017-2018) and top right (2018-2019) panels.

Daily environmental data during the fall and spring seasons at each site showed burned treelines experienced more days where the maximum soil temperature reaches above 5˚C when compared to the unburned treeline (Table 2.4). While this finding was not consistent at site EPN (see data of Fall 2018, Spring 2019), the sum of temperatures at the burned treeline ecotone at site EPN was approaching those of the unburned pair. While there were more freeze-thaw events at site EPS during the spring at the burned treeline ecotone when compared to the unburned treeline, we detected no consistent relationship between freeze-thaw events and treatments across all sites (Figure 2.S3).

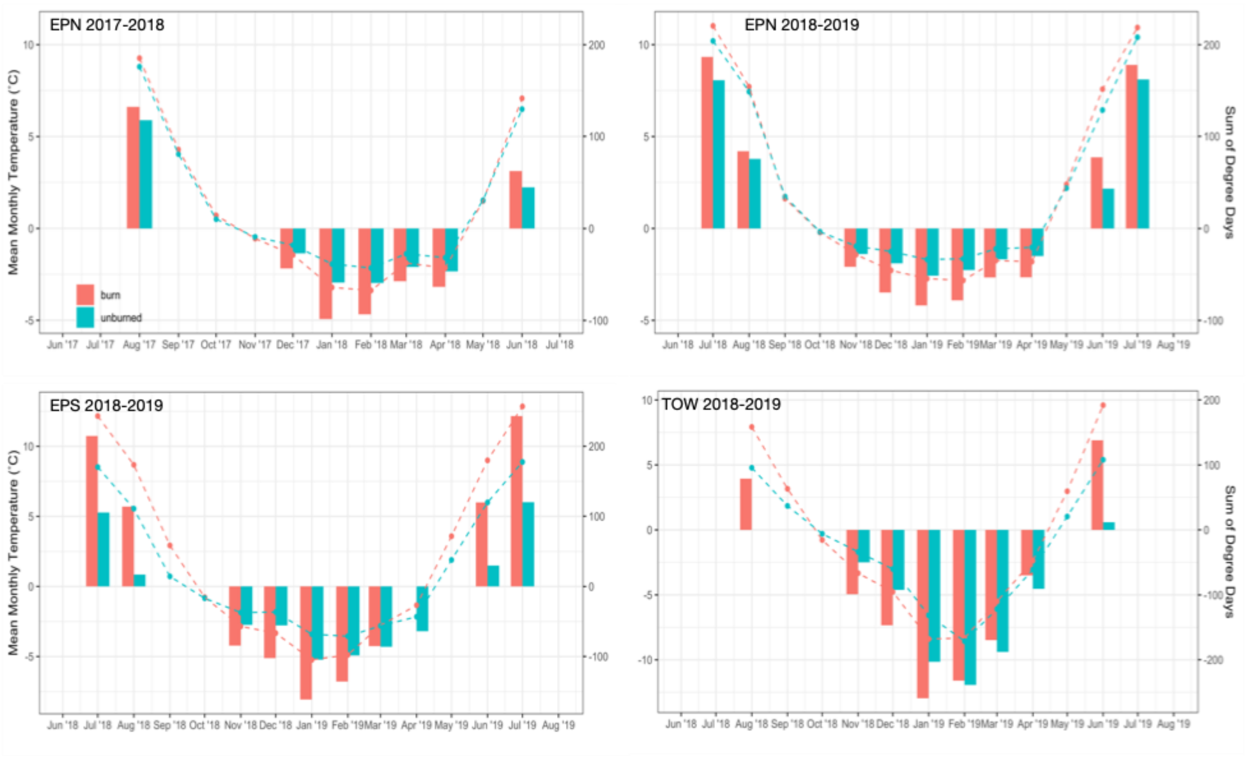

Figure 2.6 Site level data showing monthly mean soil temperatures (dashed line) and sum of degree days (bar graph) for both burned (red) and unburned (blue) treelines. Growing degree days (GDD) are indicated by positive (above zero) values, while freezing degree days (FDD) are shown to be in the negative. Data derived from the Em5 dataloggers (Decagon Devices, Inc., Pullman, Washington). Multi-year data from site EPN are divided into the top left (2017-2018) and top right (2018-2019) panels.

2.3.3 Seeding experiment

Despite the relatively high *ex-situ* germination success of seeds used in the manipulative seeding experiment (~60-97%; Table 2.S1), the number of plots with successful emergence from seed addition was low across all sites (Table 2.S2). Of the plots where emergence was recorded (typically much less than 50% of the forty plots within the burned and unburned treelines), the total number was commonly less than 10 seedlings within a plot, even after two years of seed addition (total of 300 seeds per plot from 2017-2019). The unburned treatment at site EPS had a greater number of plots with black and white spruce emergence (In 2019, Pm: unburned = 12, burned = 8; Pg: unburned = 20, burned = 12); conversely, the burned treatment at EPN exhibited greater emergence for both species (in 2019, Pm: unburned = 1, burned = 22; Pg: unburned = 8, burned = 23). Therefore, greater seedling emergence was not consistently found in the burned treelines. Interannual correlation between 2017-2019 seedling emergence of black and white spruce data was high (i.e., $r \geq 0.3$); therefore, only correlations between August 2019 seedling emergence data and environmental conditions are reported. At site EPN, black and white spruce emergence were positively correlated to June 2019 soil temperature (Pm: $r = 0.41$; Pg: $r = 0.34$) and percent cover of *Polytrichum* sp. moss (Pm: $r = 0.60$; Pg: $r = 0.43$). At site EPS, black spruce emergence was positively correlated to June 2019 soil temperature ($r = 0.32$) and percent cover of acrocarpous mosses ($r = 0.59$), while white spruce emergence was positively correlated to organic layer depth ($r = 0.34$) and percent cover of acrocarpous mosses ($r = 0.56$).

Table 2.4 Fall (September 01 – Nov 01) and Spring (March 15 – June 01) soil temperature data for each burned and unburned treeline of each site. Data derived from the Em5 dataloggers (Decagon Devices, Inc., Pullman, Washington). Max temp ≥ 5˚C refers to the number of days in which the maximum soil temperature reached above 5˚C with the sum of temperatures above the 5˚C threshold for those days in brackets. Freeze-thaw events refer to the number of days during the fall and spring in which the difference between the maximum and minimum crossed over 0˚C.

		EPS		EPN		TOW	
		unburned	burned	unburned	burned	unburned	burned
Fall 2017	max temp. ≥ 5˚C	na	na	18 (133.71)	20 (146.83)	na	na
	freeze-thaw events	na	na	2	3	na	na
Spring 2018	max temp. ≥ 5˚C	na	na	10 (69.21)	8 (59.83)	na	na
	freeze-thaw events	na	na	1	1	na	na
Fall 2018	max temp. ≥ 5˚C	3 (16.53)	14 (87.22)	4 (25.34)	3 (21.58)	0 (0)	19 (122.2)
	freeze-thaw events	10	7	8	4	11	12
Spring 2019	max temp. ≥ 5˚C	12 (90.08)	15 (153.26)	15 (119.02)	14 (126.56)	8 (46.64)	16 (151.7)
	freeze-thaw events	1	13	1	1	1	1

2.4 Discussion

Our results highlight the transformative effects wildfire can have across a treeline ecotone but indicate they do not promote boreal forest range expansion. For example, vegetative ground cover and depth of the organic layer was significantly reduced at each site's burned treeline when compared to their unburned pair. Wildfire also changed environmental conditions throughout the year. Soil temperature during the growing season was warmer at each burned treeline and was much colder throughout the winter, which we speculate is associated with a decrease in snow depth at burned treelines. In summary, while some environmental conditions changed to promote the emergence of black and white spruce seedlings, others shifted to make interannual survival more challenging. These results are supported by the low level of seedling emergence from our manipulative seeding experiment. Moreover, seedlings that were present were not correlated with specific post-wildfire site conditions (e.g., reduced organic layer depth and vegetation ground cover), but rather warm, moist conditions that occurred at unburned treelines and burned treelines that experienced a low-severity wildfire. Here, we connect our empirical findings to boreal tree species life history requirements to explain why post-wildfire conditions at the treeline ecotone did not align to promote boreal tree range expansion.

At a microsite-scale, there are several wildfire induced changes to the treeline ecotone that are presumed to increase the emergence and establishment success of spruce seedlings. First, consistent with our prediction, each burned treeline exhibited a significant reduction in organic layer depth when compared to their unburned pair. Experimental evidence suggests the combustion of the organic layer is associated with increased seedling establishment within the boreal forest, as germinating seeds are closer to mineral soils that have a more stable moisture supply (Hesketh and others, 2009; Brown and others, 2015). Organic layer combustion also increases access to essential plant nutrients, such as inorganic phosphorus and nitrogen, within the mineral soils (Butler and others, 2017). While we did not find any significant change to nitrogen availability, we did find phosphorus to be significantly greater at the burned treeline at site EPS, which had burned most recently in 2017, but not at the other two sites that had burned in 2005 (TOW) and 2007 (EPN). This seemingly ephemeral increase in phosphorus availability shortly after wildfire is consistent with the literature (Certini, 2005) and could provide further evidence of an advantageous surface nutrient pulse for seedlings after wildfire. Second, many vegetative functional groups exhibited a significant reduction in percent cover when compared to their respective unburned treeline ecotone. *Ceratadon* sp. and *Polytrichum* sp. mosses only showed a significant increase in percent cover at the burned treeline at site EPN; however, this increase was expected, as these moss species are early colonizers post-wildfire (Charron and Greene, 2002). This overall decrease in vegetative ground cover reduces interspecies competition for light, essential nutrients, and physical space required by germinating spruce seeds, thus facilitating a greater probability of seedling establishment during the first two decades after wildfire (Johnstone and others, 2004).

The most notable change between burned and unburned treeline ecotones for emergent success within the studied post-wildfire landscapes was an increase in GDD. While climate continues to represent a significant limiting factor for spruce recruitment at its northern range edge (Hobbie and Chapin III, 1998; Holtmier and Broll, 2005; Messaoud and others, 2019), experimental research in boreal forests and treelines across northern Canada suggests a significant increase in GDD is associated with greater density and increased biomass of seedlings due to greater thermal energy availability (Sirois, 2000; Danby and Hik, 2007; Munier and others, 2010; Miller and others, 2017). From our results, we predict that wildfires may further lift this climatic temperature constraint through a reduction in surface albedo, driven by the presence of charred organic material (Certini, 2005; Viglas and others, 2013). In addition to the change in GDD, our results indicate wildfire can create longer growing seasons, as the number of days where the maximum was above 5˚C was comparable to or greater than those in the unburned treeline ecotone. The lengthening of the growing season has also been linked to increased seedling establishment, as seedlings have a longer period of active photosynthesis, prompting greater carbon uptake and increased growth (Kupfer and Cairns, 1996; Holtmeier and Broll, 2005). Nevertheless, we are hesitant to state whether these changes prime a hillslope for boreal tree range expansion, as recent evidence suggests higher GDD and longer growing seasons may also subject seedlings to greater moisture stress (Lett and Dorrepaal, 2018; Hansen and Turner, 2019; Boucher and others, 2020). While our results show daily moisture availability to be lower at the burned treeline at sites EPN and TOW, they do not exhibit a significant difference from the unburned treelines; therefore, a longer temporal analysis of more sites are needed to support this hypothesis.

Despite there being wildfire induced changes that would promote greater seedling emergence at treeline, others shifted to make survival more challenging. While we predicted organic layer and vegetation cover would be reduced post-wildfire, based on our understanding of previous wildfires within the study region (Brown and Johnstone, 2012; Viglas and others, 2013), we anticipated these changes to be more extensive and result in a more uniform post-wildfire treeline ecotone (i.e., more uniform and greater combustion of organic layer). Although we did not measure burn severity directly, there is significant evidence to suggest each treeline ecotone experienced a low to moderate severity wildfire. For example, mean organic layer depth was greater than five cm for each burned treeline, which is consistent with other low-severity wildfires in Alaska (Johnstone and Kasischke, 2005) and Siberia (Alexander and others, 2018). Additionally, the persistence of vascular non-woody herbaceous plants at the burned treeline at site EPS and the dominance of rhizomatous graminoids and ericaceous shrubs at the burned treelines at site EPN and TOW suggest vegetative root structures were not significantly damaged leading to rapid above-ground growth post-wildfire (Johnstone and Kasischke, 2005). The variability in surface charring and plant cover from these wildfires explains why, contrary to our hypotheses, the burned treeline at site EPS did not exhibit the highest convergence in ordination space, even though it had burned most recently. In fact, environmental factors at each burned treeline had a wide range of variance when compared to their unburned treeline pair (see Bartlett's test results in Table 2.3.). Interestingly, site TOW did show greater overlap in environmental conditions within ordination space between the burned and unburned treelines when compared to the other two sites. This increased overlap of environmental conditions between burned and unburned treelines as time-since-wildfire increased is consistent with our prediction. From these results we speculate a return to a pre-fire plant community is likely, as the ecological inertia within the tundra plant community was not reduced enough by the low-severity wildfires.

Our study also shows that within a period of ten years after wildfire, seedlings may be subjected to more extreme environmental conditions. Specifically, a persistent change in winter conditions occurred where mean soil temperature was much lower in the burned treeline, resulting in a greater sum of degree days (FDD) below 0˚C. These results are likely associated with the reduced snow depth and surface insolation caused by a reduction in vegetative ground cover that provides surface complexity to hold snow (Frey, 1983; Domisch and others, 2018). While TOW did not exhibit a consistently lower snow depth throughout the winter at the burned treeline ecotone, later inspection of measuring sticks showed they were positioned within a hollow that would have locally increased snow depth values. Lower snow depth and increased FDD during the winter can expose spruce seedlings to persistent frost and xylem embolism (Mayr and others, 2007; Mamet and Kershaw, 2013), which may be a significant reason why interannual seedling survival from our manipulative seeding experiment was so low.

While each burned and unburned treeline showed a large deviation in temperature during the winter and growing season, we were surprised to see few differences in the timing of snow-melt, as well as the number of freeze-thaw days, apart from site EPS, which experienced far more freeze-thaw days in the spring of 2019. While our study design does not lend itself to speak to the climate-snow relationship, earlier snow melt is predicted as a result of climate change (Guiden and others, 2019). This change in date of snowmelt is likely to increase seedling exposure to extreme temperature fluctuations (Rixen and others, 2012) and frost damage (Liu and others, 2018). Experimental snow removal and temperature manipulations have supported these predictions (Shen and others, 2014; Renard and others, 2016; Domisch and others, 2018). As the burned treeline at site EPS was the only treeline that showed a difference in freeze-thaw days, our results allow us to speculate that the effect of wildfire on snowmelt and freeze-thaw events is either negligible or only occurs shortly after wildfire. We suspect that recovering vegetation within the first few years after wildfire would increase surface complexity and therefore increase snow depth to moderate soil temperature (Renard and others, 2016; Maher and others, 2019). Nevertheless, our results are limited to few study sites, which warrants further investigation of the broader landscape relationship between wildfire, seedling survival and winter conditions (Domisch and others, 2018; Maher and others, 2020).

From the perspective of a seed, the combined effect of low severity fires (i.e., patchy and partial combustion of the vegetation and ground surface), and the change in seasonal temperatures and winter conditions leads us to conclude that the post-wildfire microsite does not promote greater seedling emergence and survival when compared to the unburned treeline. Studies have shown that ideal conditions for successful spruce germination consist of low interspecies competition, and substrates that are warm, moist, and high in nutrients (e.g., Johnstone and others, 2004; Johnstone and Chapin III, 2006; Shenoy and others, 2011; Brown and others, 2015). Our study showed that while wildfire increased GDD and growing season length, the low severity of the wildfire resulted in a higher probability of viable seeds landing on charred organic matter. Even though soil moisture showed no significant difference between burned and unburned treelines at a depth of 5 – 10 cm, the remaining organic material would limit access to this moisture, increasing hydric stress of the seed via rapid surface evaporation and drainage (Kemball and others, 2006; Johnstone and Chapin III, 2006; Veilleux-Nolin and Payette, 2012). We can also predict that if a seed did land on a suitable microsite, (e.g., unburned wet moss substrate or completely combusted organic layer), germination may have been successful, but the seedling would be subjected to persistent cooler temperatures and lower snow depth over the winter, increasing the potential for frost damage and xylem embolism (Mayr and others, 2007; Liu and others, 2018). Finally, all of these challenges accumulate on top of the first overwhelming hurdle for range expansion of woody boreal forest species: the extremely limited natural seed dispersal at all studied treelines, which has been shown to represent a significant bottleneck for expansion (Viglas and others, 2013; Anadon-Rosell and others, 2020).

In conclusion, there are a series of barriers that must be overcome in order for successful seedling establishment, a key step in range expansion, to occur. The prediction that wildfire at treeline will create ideal environmental conditions and promote range expansion of fire-adapted species may therefore be overly reductive and does not take into account the interaction between wildfire and natural site characteristics. Further investigations in a range of tundra plant communities (e.g., wet-sedge meadow) and treeline types (e.g., denser treeline may result in a more severe wildfire) are warranted. The study design of this research also lends itself to a future examination of trends across treeline (i.e., a change in tree density), as transects were positioned parallel with stand density (i.e., moving upslope from the more forested to tundra dominated parts of the ecotone). We also urge for the inclusion of winter climate and snow dynamics within these analyses, as our results show key changes to environmental characteristics during the growing season and throughout the remainder of the year, all of which are likely to influence seedling survival and thus the potential for boreal forest range expansion into tundra ecosystems.

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2.7 Supplementary Materials

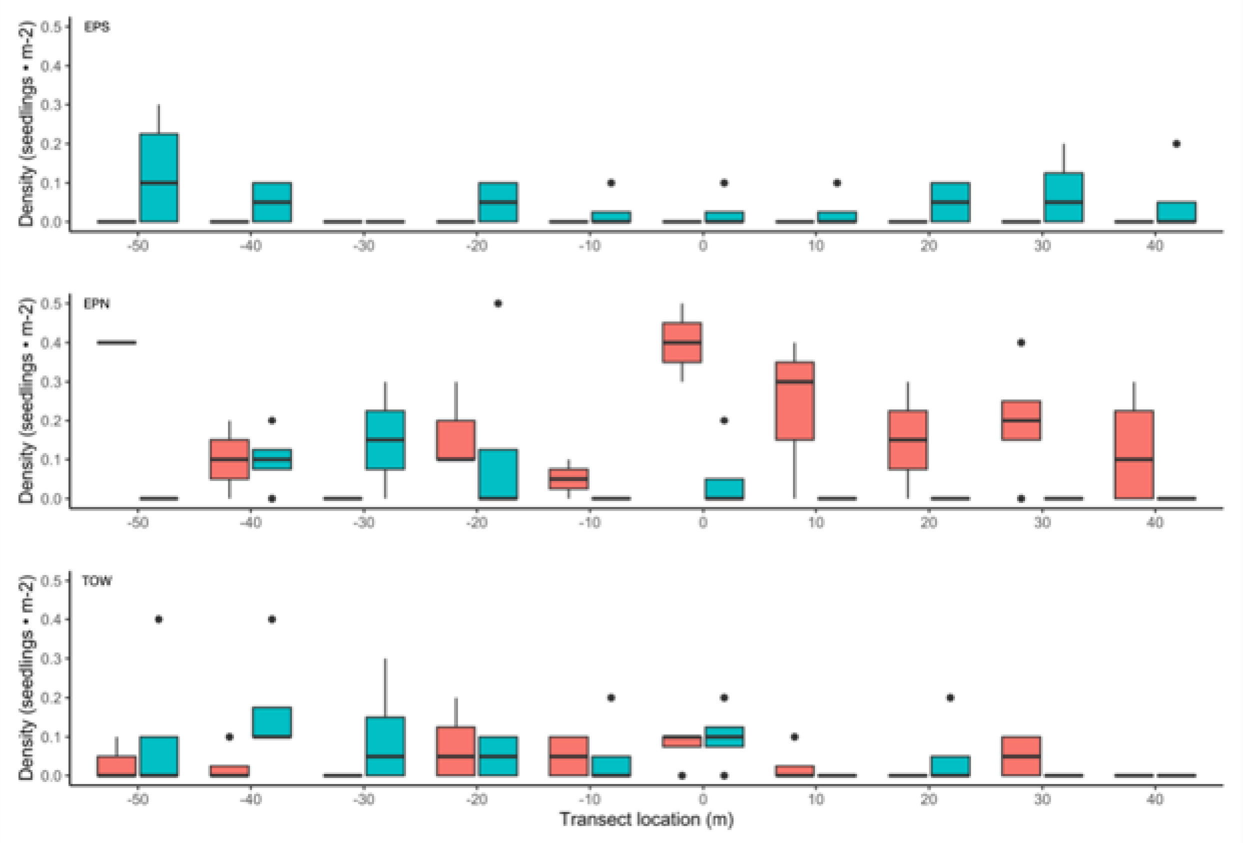

Figure 2.S1 Seedling density (number of seedlings • m^{-2}) along the 100 m transects of each burned and unburned treelines for each site. Mean seedling density was calculated by averaging the number the seedlings within a 10 m x 10 m block along the four transects within the burned or unburned treelines.

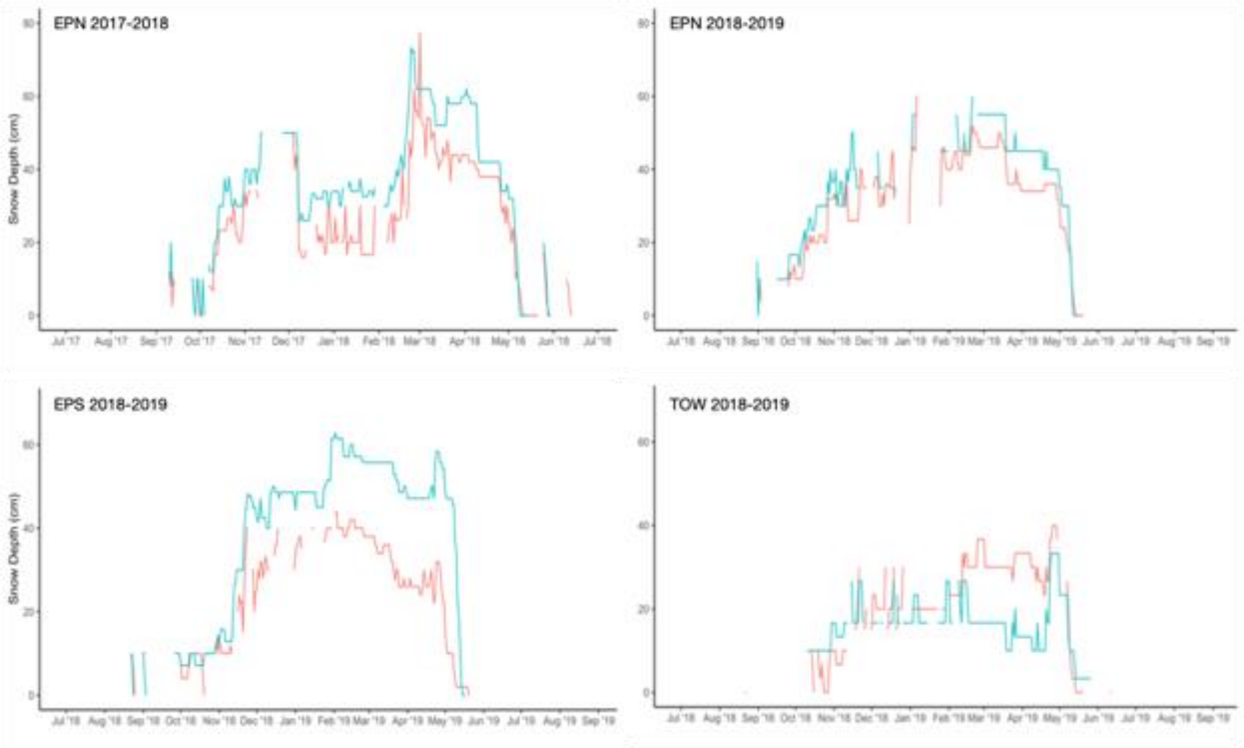

Figure 2.S2 Mean snow depth for the burned and unburned treelines at each site. Mean snow depth data were calculated by averaging the daily snow depth indicated on three (or more) snow stakes at each treeline. Multi-year data from site EPN are divided into the top left (2017-2018) and top right (2018-2019) panels. Broken segments of the line indicate either no snow or no data, due to unclear imagery.

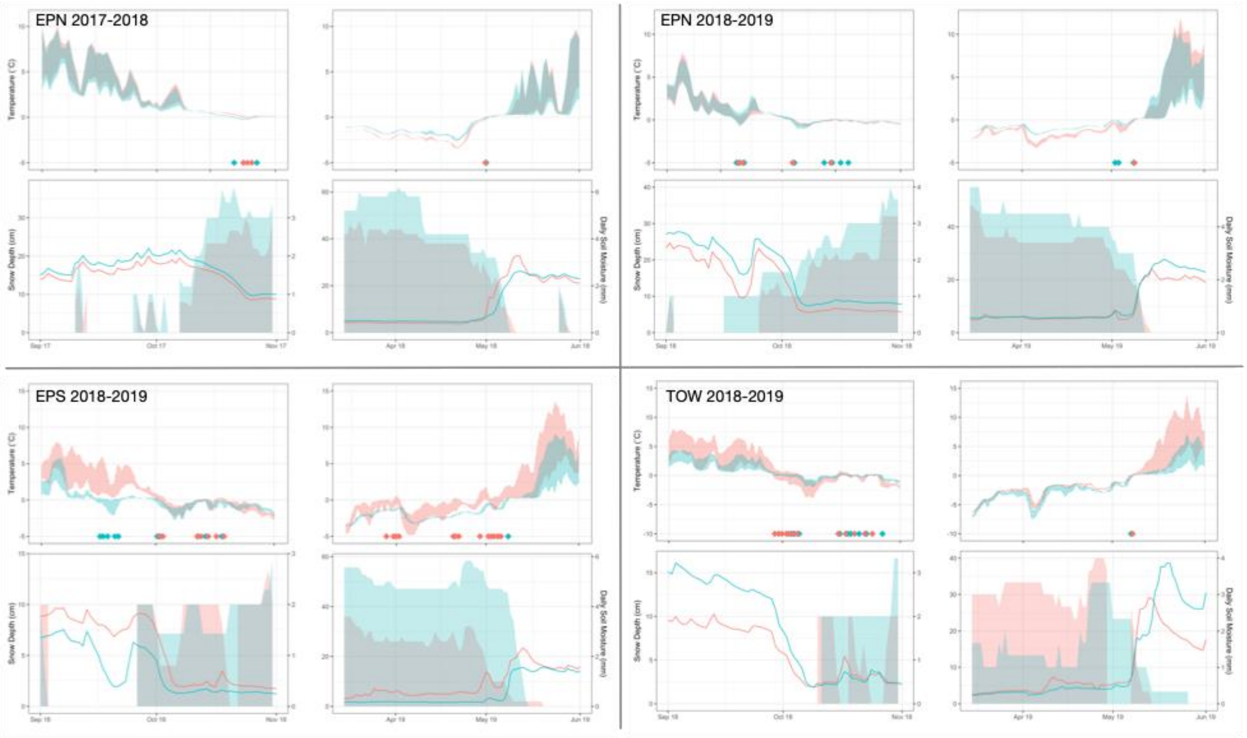

Figure 2.S3 Detailed environmental data for each burned and unburned treeline of each site for the fall (Sept 01 – Nov 01) and spring (March 15 – June 01). Data derived from the Em5 dataloggers (Decagon Devices, Inc., Pullman, Washington). Multi-year data from site EPN are divided into the top left (2017-2018) and top right (2018-2019) panels. For each site, there are four graphics, the top left (fall) and top right (spring) show the daily range in temperature values between the minimum and maximum temperature (line graph). Days in which the temperature range passes over 0˚C (i.e., day of frost) is indicated by a coloured diamond (positioned at the bottom of the graphic). The bottom left (fall) and bottom right graph at each site shows the relationship between daily snow depth (bar graph) and soil moisture (line graph).

Table 2.S1 Results of germination trials for seeds used in seeding experiment. A total of 400 seeds for each species were used, divided into 16 separate petri dishes for a total of 16 replicates of 25 seeds. Prior to the field season, some seeds were cold stratified for a period of 5 days. A two-sample t-test between cold stratified (CS) and no treatment (NT) seeds was performed to determine whether there was any significant effect on total seed germination. Results from the t-test indicated no significant difference between germination means of white spruce from Watson Lake, YT (t=1.7779, df=28.684, p=0.08603) and green alder from Manic, QC (t = 0.47844, df = 29.913, p=0.6358).

Species	Treatment	Seed Source			Germination Success		
		Location	lat	long	Mean (%)	sd	ste
P. glauca	NT	Watson Lake, YT	60	-128.83	82	10.22	2.55
P. glauca	CS	Watson Lake, YT	60	-128.83	74.75	12.7	3.18
P. glauca	NT	Dawson, YT	64.03	-138.58	83.75	8.45	2.11
A. viridis spp. crispa	NT	Manic, QC	49.86	-68.73	61.5	10.62	2.65
A. viridis spp. crispa	CS	Manic, QC	49.86	-68.73	59.75	10.06	2.52
P. mariana	NT	Clear Creek, YT	63.7	-137.67	96.5	3.54	0.88

Table 2.S2 Sum of plot-level seedling emergence data for burned and unburned treelines of each site. Green alder was not included as they were indistinguishable from other early shrub species and were nearly impossible to find in an unburned plot. Seeding data is not available for TOW as seeding did not occur at that site.

	EPS			
	P. mariana		*P. glauca*	
	burn	unburned	burn	unburned
2017	na	na	na	na
2018	1	14	1	13
2019	8	12	12	20

	EPN			
	P. mariana		*P. glauca*	
	burn	unburned	burn	unburned
2017	4	0	4	0
2018	13	4	10	9
2019	22	1	23	8

Chapter 3: Seed and cone predation reduces reproductive potential of treeline conifers across northern Canada

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Abstract

Aim: Across altitudinal and latitudinal treeline ecotones, continued climate warming is predicted to facilitate boreal tree range expansion into tundra environments. Yet, where evidence of a range shift has been detected, the rate is much slower than temperature-based model projections, suggesting that non-climatic mechanisms are also mediating subarctic treeline range dynamics. Our research assessed how biotic interactions, specifically insect cone granivory, may govern viable seed availability of spruce-dominated treelines across northern Canada.

Location: Ten boreal-tundra treelines from Yukon to Newfoundland and Labrador, Canada

Taxon: White spruce (*Picea glauca* (Moench) Voss), Black spruce (*Picea mariana* (Mill.) B.S.P.), *Strobilomyia* spp., *Megastigmus* spp.

Methods: Treeline sites were assessed for presence and magnitude of pre-seed dispersal granivory by insects. We quantified stand density metrics, organic layer depth, and understory vegetation composition at each location. We incorporated those variables into generalized linear mixed models to establish predictors of granivory magnitude and viability of available seed.

Results: Our findings reveal widespread presence of insect granivory and site-specific patterns of granivory driven by increased moss cover and decreased shrub cover and stand density. While all black spruce dominated sites exhibited *ex-situ* seed viability rates greater than 50%, the number of seeds produced per cone varied, suggesting within site abiotic conditions and biotic interaction pressures limit successful colonization of novel environments in advance of seed dispersal.

Main Conclusions: Results from the modelled relationship between cone granivory and seed viability represent an essential step toward understanding how biotic interactions across subarctic treelines influence boreal tree range dynamics before seed dispersal. Connections between granivory magnitude and site-level stand density will help establish how treeline form (i.e., discrete or diffuse) may drive patterns of future insect outbreaks under continued climate warming.

3.1 Introduction

The geographic distribution of treeline ecotones, where continuous forest transitions to treeless plant communities, are closely linked to the climatic tolerance of boreal tree species (Körner, 1998; Körner and Paulsen, 2004). Treelines are anticipated to shift poleward and upslope under continued climate warming (Feuillet et al., 2019; Körner, 1998; Kueppers et al., 2017; Timoney et al., 2019), though range expansion of treelines has been non-uniform in speed and direction (Harsch, Hulme, McGlone, & Duncan, 2009; Mamet, Brown, Trant, & Laroque, 2019; Rees et al., 2020). This inconsistent response suggests the importance of other processes driving treeline range dynamics. Recent evidence of non-climatic drivers, such as competition, herbivory, and parasitism, provides a better understanding of additional factors (e.g., seed availability, dispersal) limiting successful recruitment of boreal tree species beyond their range edge (Brown et al., 2019; Holtmeier, 2012; Munier, Hermanutz, Jacobs, & Lewis, 2010; Hewitt et al., 2016).

Viable seed production and subsequent dispersal are required for landscape-scale treeline advance (Cairns & Moen, 2004; Johnstone et al., 2016), yet these processes are subject to many complex negative biotic disturbances from wildlife and insects (see Brown & Vellend, 2014; Holtmeier, 2012; Wisz et al., 2013). For example, granivory by cone fly species such as *Strobilomyia* spp. (Diptera: Anthomyiidae), represents a biotic disturbance that has the potential to damage up to 100% of seeds within a cone (Hedlin et al., 1981; Turgeon, Roques, & De Groot, 1994). Even when viable seeds are not consumed, the consumption of cone and bract tissue can limit the successful dispersal of seeds through reducing cone flexing (Brockerhoff et al., 1999). The interaction between seed production and the biotic disturbance of granivory by insects has been examined at length within the boreal forest (e.g., Fidgen, Sweeney, & Quiring, 1999; Prévost, 2002; Simard & Payette, 2005). While climate warming is predicted to increase insect populations and their ranges across the boreal forest (Robinet & Roques 2010), granivory has received little attention at its edge, across northern treeline (Gärtner, Lleffers, & Macdonald, 2011; except see Jameson, Trant, & Hermanutz, 2015; Kambo & Danby, 2017). The few studies that have examined granivory by insects at treeline have focused on their effects on seed viability (Jameson, Trant, & Hermanutz, 2015; Calama, Fortin, Pardos, & Manso, 2017), showing widespread insect granivory at each site resulting in a significant loss of reproductive potential. These insect granivores have highly specialized life cycles and are distributed broadly across the

North American boreal forest, aligning with the distribution of their coniferous hosts (Fidgen, Sweeney, & Quiring, 1999; Hedlin et al., 1981; Sweeney & Turgeon, 1994; Turgeon, De Groot, & Sweeney, 1992). Together, evidence from existing site-level studies combined with granivore-host species distribution patterns lead to the prediction that insect granivory is present across all boreal treelines and may limit viable seed availability across the northern edge of the boreal biome. Nevertheless, testing this prediction requires a broader spatial context of whether there are any general site conditions that drive the magnitude of insect granivory and which treelines may be more susceptible, as treelines vary in biotic and abiotic characteristics across northern environments.

We conducted a broad spatial assessment of treeline granivory by insects and asked the following questions: [1] Are there any general abiotic and biotic conditions that are associated with the presence of insect granivory at treeline; [2] where evidence of granivory occurs, which conditions are associated with its magnitude; and [3] is insect granivory at treeline associated with seed viability, and if so how? We hypothesized that the presence of insect granivory would be widespread, but the magnitude would vary based on tree density, as a higher density treeline with more cones may support greater insect populations. We also hypothesized this relationship between tree density and granivory magnitude would result in a negative relationship with viable seed availability, as seeds within cones would be consumed by more insects. To address these questions, we conducted an observational study at black spruce (*Picea mariana* [Mill.] BSP) and white spruce (*P. glauca* [Moench] Voss) dominated hillside treeline ecotones across North America (> 49˚ latitude). We selected *Picea* as the focal tree genus due to its wide geographical distribution and dominant structural and functional role in the boreal forest (Viereck & Johnston, 1990). We focused specifically on cone damage from small, specialized insects rather than other granivores, such as birds and squirrels, which have been previously studied across the boreal forest (e.g., Barringer, Tomback, Wunder, & McKinney, 2012; Boutin et al., 2006; Holtmeier, 2012). We recognize that interannual variability in cone production and insect populations play a critical role in disturbance dynamics. While we are providing a snapshot in time of these dynamics, our extensive spatial analysis represents the first steps in linking environmental conditions to granivory at treeline. Moreover, studies linking environmental condition to reproductive potential are rare and needed to explain future range dynamics (Brown et al., 2019). Our results will therefore help guide future multi-year comparative analyses of treeline disturbances under different biotic and abiotic conditions.

3.2 Materials and Methods

3.2.1 Study sites

We assessed insect granivory and seed viability at 10 boreal-tundra hillside treeline ecotones dominated by black and white spruce across northern Canada (Figure 3.1). Coordinated data collection with a pre-established field protocol occurred at treelines in the Yukon (n = 4), Northwest Territories (n = 2), Manitoba (n = 1), Quebec (n = 1), and Newfoundland and Labrador (n = 2) on the traditional lands of the Vuntut Gwitchin, Tr’ondëk Hwëch’in, Inuvialuit, Tłı̨chǫ, Sayisi Dene, Nunatsiavut, Mi’kmaq, and Beothuk peoples. We completed most data collection during the summer of 2018 (n = 8), with two additional sites sampled in summer 2019 (Table 3.S1). As this was a collaborative effort by several research teams, fieldwork time constraints and remote access limited our ability to collect all necessary data from each site; therefore, two sites (DAN and GSP) are not included in our statistical models (see modelling procedure below) and discussion of results. We still present summary data of cone damage and seed viability from these sites as the scarcity of data from these remotely accessed sites warrants their inclusion and can be used to inform future treeline research. Sites varied in treeline form and were characterized following the definitions presented in Bader et al., (*in review*). We classified sites as diffuse (i.e., tree density decreasing with increasing altitude or latitude), discrete (i.e., continuous tree canopy with no decline in density until abrupt change when reaching tundra vegetation), or tree islands (i.e., groups or linear strips of upright or krummholz trees located beyond latitudinal or altitudinal treeline; Figure 3.2; Table 3.1; Harsch and Bader, 2011; Bader et al., *in review*). Because treelines were classified visually by multiple collaborators, treeline form was not included in subsequent statistical analyses. Instead, we chose to focus on the stand density (number of trees per plot), which is a quantitative measurement that contributes to our understanding of treeline form. It also ensures measurement would be consistent across sites as it was included in the field protocol.

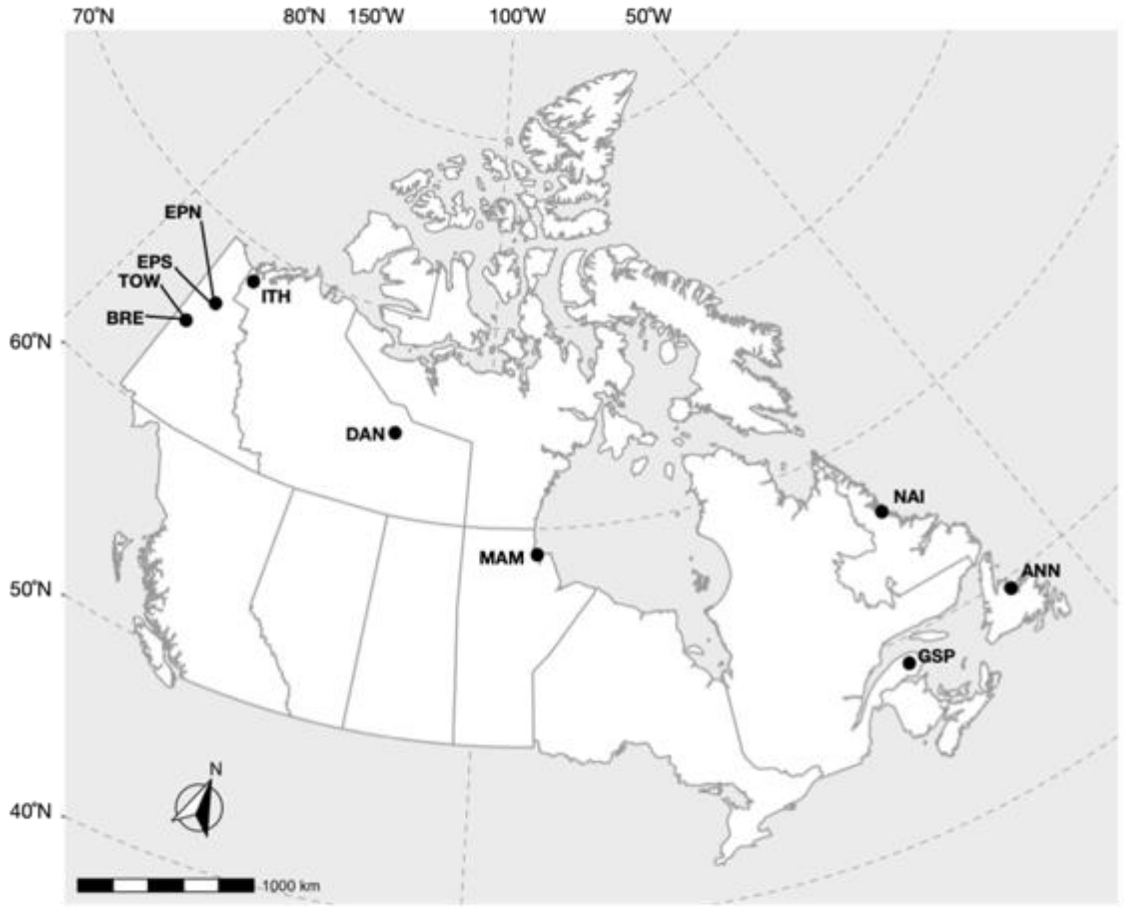

Figure 3.1 Location of study sites across Canada, located on the traditional territories of (from west to east): Vuntut Gwitchin, Tr’ondëk Hwëch’in, Inuvialuit, Tłı̨chǫ, Sayisi Dene, Nunatsiavut, Mi’kmaq, and Beothuk peoples. Site specific data, including information on which collaborators carried out field sampling, are included in Supplementary Table 3.1.

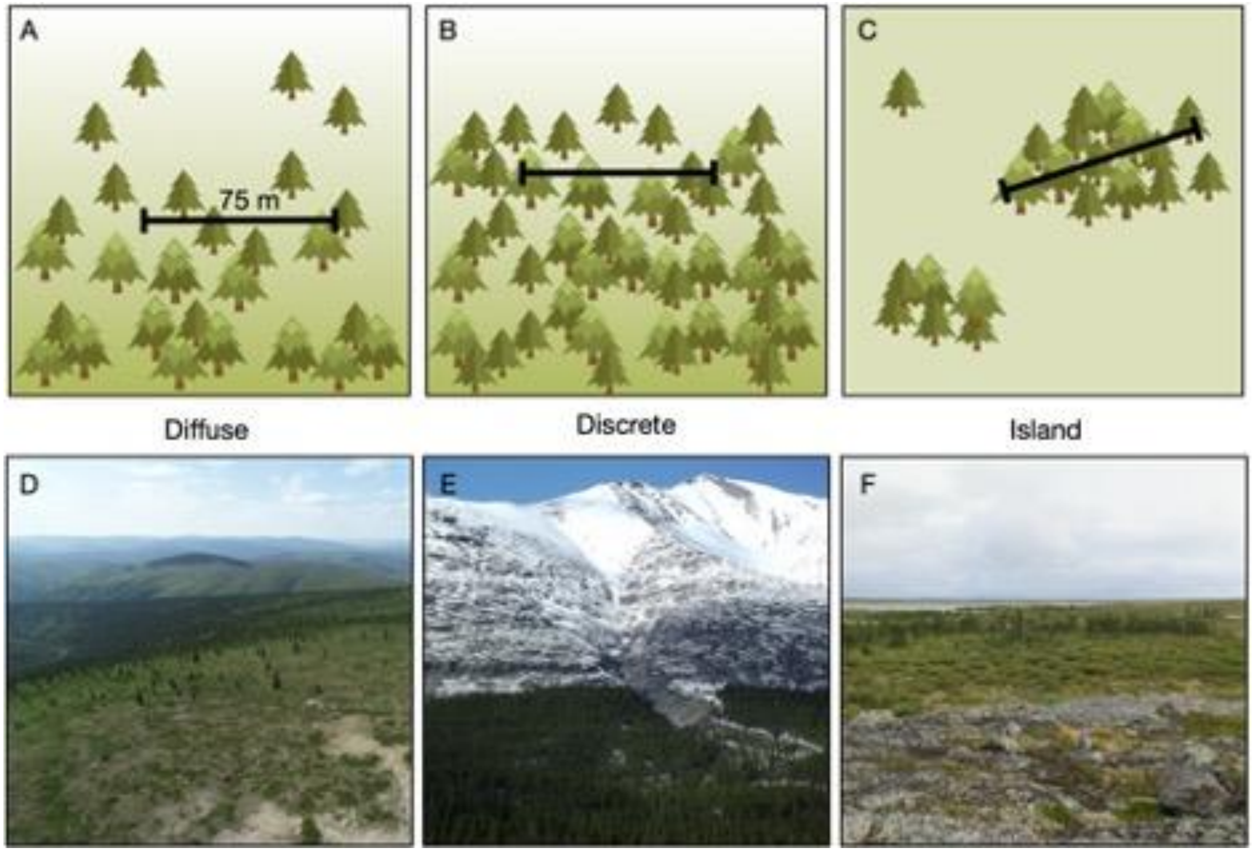

Figure 3.2 Infographic of the three treeline forms that were sampled in this study. Diffuse treelines have a gradual reduction in stand density when moving toward the tundra (in this case, toward the upper edge of the image in A). Discrete exhibits no change in stand density until there is an abrupt stop and tree islands are linear strips or dense clusters of trees well beyond latitudinal treeline. The diffuse and island photographs are actual study sites (TOW and DAN, respectively). The other is an image taken by Lucas Brehaut in northern British Colombia.

Table 3.1 Treeline characterization and summary data on sampling for each study site. Treeline form was determined visually by data collectors, following protocols and definitions outlined in Bader et al. (in review). Dominant species refers to whether the treeline was dominated by black spruce (bs) or white spruce (ws). Total number of cones harvested, proportion cone granivory, and total number of seeds extracted from cones are included. Seeds • cone^{-1} was calculated by taking numbers of seeds extracted per tree • number of cones harvested $^{-1}$. Proportion of viable seed was calculated from germination trials of up to a maximum of 100 seeds • tree $^{-1}$. Cone length, % cone herbivory, seeds•cone $^{-1}$, seeds with embryo, and % viable seed are presented as averages with some showing standard deviation in brackets.

Site	Lat	Long	treeline form	dominant species	trees sampled	cones harvested	cone length (±SD)	% cone herbivory	seeds extracted	seeds • cone^{-1} (±SD)	seeds with embryo (±SD)	% viable seed
GSP	49.00	-65.94	island	ws	16	299	32.6 (5.6)	16.1	10698	37.3 (8.1)	129 (12.6)	1.3
ANN	49.59	-56.23	discrete	bs	17	141	16.5 (5.2)	35.5	3127	17.0 (9.5)	1676 (146.5)	86.6
NAI	56.54	-61.72	diffuse	ws	16	294	27.9 (4.6)	2.7	19	0.1 (0.1)	1 (0.3)	0.0
MAM	58.62	-93.81	diffuse	bs	22	457	18.6 (3.0)	2.2	17467	38.1 (7.6)	12158 (246.3)	65.6
DAN	63.77	-111.23	island	bs	29	591	17.8 (3.3)	15.2	18377	32.0 (8.5)	8218 (177.1)	81.1
BRE	64.22	-140.18	diffuse	ws	11	197	27.7 (10.0)	20.3	3088	14.5 (9.4)	219 (29.3)	0.0
TOW	64.11	-140.96	discrete	bs	28	576	15.4 (2.7)	3.5	5471	9.2 (5.7)	803 (36.3)	61.4
EPS	65.83	-137.77	diffuse	bs	23	500	19.9 (4.0)	23.8	19656	39.2 (9.7)	9484 (306.6)	82.3
EPN	66.50	-136.56	discrete	bs	30	975	21.9 (7.1)	27.3	28390	29.9 (10.2)	12932 (330.5)	57.5
ITH	68.70	-133.56	diffuse	ws	18	222	27.9 (8.2)	33.3	696	2.9 (2.3)	8 (1.3)	0.5

3.2.2 Field measurements

At each site, a 75 m belt transect was established along the ecotone, perpendicular to the tree density gradient in an area that was representative of the larger treeline ecotone. Collaborators ensured the transect was representative by provided photographic evidence of both the site and the landscape. Belt transects were then subdivided into 15 plots (10 m x 5 m) in which sampling occurred (i.e., plot < site). With the exception of two sites (GSP and DAN), all sites were included in the statistical models. Treeline form determined the location of the belt transect within the ecotone (Figure 3.2). For diffuse treelines, the transect was positioned in an area where tree density was visually estimated to be within a range of 10-50 trees • ha^{-1}, while remaining within 100 m of the last reproductive tree before continuous tundra (the approximate dispersal distance of black spruce seeds; Greene et al., 1999). For discrete treelines, transects were established within approximately 100 m of the treeline ecotone edge before continuous tundra. Finally, transects located within a tree island ecotone were positioned across the broadest part of the island to ensure sufficient cone sampling.

Data on abiotic and biotic characteristics were collected based on their biological relevance to insect life history and spruce cone development (Table 3.2). Within each plot at each site, we first recorded tree density data (i.e., trees • $plot^{-1}$ and tree height) of trees ≥ 2 m tall. Tree height was measured using a measuring tape or a clinometer depending on feasibility. Second, ground vegetation was quantified using functional group percent cover in a 1 m x 1 m quadrat that was positioned in an area where the ground cover was visually estimated to be representative of the plot. Functional group categories examined included: shrub cover, herbaceous non-woody plants, graminoids, lichen, moss, leaf litter, and bare organic soil. The shrub cover category was subdivided by height (*sensu* Myers-Smith et al., 2011) into tall multi-stemmed shrubs (TMS; ≥ 0.4 m), erect dwarf shrubs (EDS; 0.1 m – 0.4 m), and prostrate dwarf shrubs (PDS; < 0.1 m), as these height classes are functionally distinct. Because multiple strata were included in the estimate, vegetation percent cover could sum to > 100%. Functional groups at the lowest cover value (i.e., estimates less than 5%) were assigned a percent cover of 2% to ensure consistency between collaborators collecting data. Functional group percent cover was not completed at the site DAN due to time constraints; therefore, this site was not included in the statistical models. The depth of the soil organic layer (cm) was also recorded at each quadrat, quantified by creating a small vertical incision into the ground and measuring the depth to the surface of the mineral soil.

Table 3.2 List of covariates that we hypothesized based on previous research were significant for insect granivory and included in our generalized linear mixed models.

Predictor variables	Units	Rationale for final model inclusion	Reference
organic layer depth	cm	Deeper organic layer may facilitate increased numbers of predators of insect pupae, thus reducing the number of affected cones	*Figden et al., 1999*
tall multi-stemmed shrubs (TMS); erect dwarf shrubs (EDS); prostrate dwarf shrubs (PDS)	% cover	Proportion of shrub vegetation characterizes the treeline vegetation community at a local scale. We hypothesize that increased presence of shrubs of all size classes may decrease food and space resources for insect populations.	
moss	% cover	Increased moss cover indicative of more moist conditions, suitable for insect larvae overwintering	*Hedlin et al., 1981*
leaf litter	% cover	An additional proxy of shrub cover related to overwintering conditions for insect larvae. We hypothesize that increased leaf litter would decrease evidence of cone herbivory as a result of fewer larvae making it to adulthood (i.e., drier than moss cover)	
seeds per cone	seeds • cone^{-1}	Increased food resources for cone insects during oviposition	*McClure et al. 1996*
cone length	cm	Some insect species (e.g., *Strobilomyia* spp) prefer to oviposit on longer cones	*Fidgen et al., 1998*
tree density	trees • m^{-2}	Increased space resources for cone insects during oviposition	*McClure et al., 1998*
tree height	cm	Higher aerial seedbank may reduce insect extent on cones	*McClure et al., 1998*

Cones were harvested from a maximum of 30 trees per site (Table 3.1). We aimed to harvest cones from two trees within each plot; however, when individual plots had no trees, cones were harvested from additional individuals occurring in alternate plots to reach the 30-tree sample size per site. We sampled approximately 20 cones per tree; if fewer than 20 cones were available, we sampled all cones present. We preferentially selected cones that were fully sealed to ensure minimal seeds had been dispersed. For black spruce, harvested cones were approximately 1 – 3 years old, while white spruce cones were sampled at the end of the growing season before seed release (Greene et al., 1999). To ensure sampling was representative of the tree's reproductive capacity, we distributed sampling throughout the tree’s canopy by collecting cones from at least five different branches. Cones from each tree were placed in separate paper bags, labelled with tree and plot ID, and stored in a dry location for more than 60 days before seed extraction. Due to logistical constraints and opportunistic sampling of these remote locations, two of the 10 sites (NAI and ITH) were sampled under less-than-ideal conditions (i.e., sampling immature cones or after seed release for white spruce), resulting in less accurate estimates of total seed per cone. However, granivory could still be accurately assessed at these sites through visual detection of cone damage (described below); hence, they were not removed from analyses.

3.2.3 Laboratory methods

The length of each cone was measured, and cones were inspected for signs of insect granivory, including any evidence of frass (i.e., powdery wood debris generated by wood boring) or exit holes that are common from conophages insect types, such as *Strobilomyia* spp. (Diptera: Anthomyiidae), *Megastigmus* spp., and *Dioryctria* spp. (Hedlin et al., 1981; Sweeney & Turgeon, 1994). Because of the geographic scope of our study, the time at which cones were harvested (mid-late growing season), and the age of cones (~1-3 years), it is likely that our cone damage estimates encompass multiple species. Nevertheless, all species listed above create similar damage to spruce reproductive units (Kegley, 2018; Seifert, Wermelinger, & Schneider, 2000; Skrzypczyńska & Roques, 1987).

To remove seeds from cones, we followed a process outlined in Leadem et al. (1997). Briefly, black spruce cones were soaked in distilled water for 24 hours at room temperature, strained, and air-dried at 20˚C for 24 hours, followed by oven drying at 60˚C for 16 hours. Once completely dry, we shook cones for 10 minutes using an agitation table. We repeated this procedure three times, or until the total seed yield from agitation was ≤ 10. Any seeds that remained in the cone would be assumed not to be released under natural conditions. White spruce cones were simply dried and shaken three times using an agitation table. We counted the number of seeds extracted per tree and normalized the data per cone for any tree that had less than 20 cones.

We inspected a subsample of 100 seeds per tree (or all seeds if <100) for physical damage (i.e., cracks) and damage associated with insect granivory (i.e., boreholes) under a compound microscope. Both physical and insect-related seed damage was minimal across all sites (averaging 0.38 ± 1.19 damaged seeds per 100) and was therefore not included in any further statistical modelling. We manually removed seed wings then separated seeds with embryos from unfilled seeds using the 95% ethanol float test (Leadem et al., 1997). To ensure the test was appropriate, a proportion of seeds that floated (n = 40 maximum) were further inspected for fully developed embryos (Jameson et al., 2015; Sirois, 2000). To quantify the viability of the available seed, we conducted a germination trial where seeds with full embryos (i.e., seeds that sank) were placed on wet filter paper in a 100 x 15 mm Petri dish and allowed to germinate for 28 days at room temperature (20˚C) with 18 hours of light per day. For each tree, we used a maximum of 100 seeds spread across four Petri dishes (i.e., 25 seeds per 100 x 15 mm Petri dish). Seeds were inspected approximately every two days and watered with deionized water, as needed. Prior to the germination trial, white spruce seeds were cold wet stratified at 4˚C for 28 days to break seed dormancy (Bonner and Karrfalt, 2008; Leadem et al., 1997). Black spruce cones experienced stratification during their maturation on parent trees and required no further preparation (Safford, 1974). We considered seeds successfully germinated once the radicle had grown four times the seed coat's length (Leadem et al., 1997). We assumed seeds that did not germinate under laboratory conditions would not be viable under natural conditions (Brown et al., 2019).

3.2.4 Statistical analyses

We modelled the presence and magnitude of insect cone granivory (Q1 and Q2) and reproductive potential of available seed (Q3) using the proportion of cones with granivory and proportion of available seeds that were viable as response variables, respectively. It is important to note that our proportional response data are derived from a subset of cones on trees within each site (i.e., only harvested trees) and thus, are a representation of each site. All data collected, including our response variables, were pooled to a plot level to avoid pseudo replication in our analyses (Table 3.S2).

To answer each of our research questions, we followed the mixed-effects modelling procedure described by Zuur et al. (2009). For each research question, we inspected all predictor variable data for any outliers and tested each for between-site collinearity. All variables were required to have a Pearson's correlation value ≥ 0.70 with a variance inflation factor less than 3.0 (Roland, Schmidt, & Nicklen, 2013). All of the variables listed in Table 3.2 were included in subsequent models. For all models described below, plot within transect was included as a random factor. Marginal and conditional R^2 values were calculated using the r.squarredGLMM() function to determine the degree of inter-site variability. All statistical analyses were conducted in R.3.5.1. (R Core Team) using the package glmmTMB ver. 1.0.2.1 (Magnusson et al., 2020).

We used the hurdle model approach (Zuur, 2009) to assess which variables were associated with insect granivory presence at treeline (Q1) and subsequently, where evidence of cone granivory had occurred, which variables were responsible for the magnitude of insect granivory (Q2). For this modelling approach, we first employed a general linear mixed model (GLMM; family = binomial; link = logit) using presence-absence data of cone granivory across all plots. We then ran a secondary GLMM (family = Poisson; link = log) examining the abundance of cone granivory in plots where granivory was present.

To determine the effect of insect cone granivory on the availability of viable seeds (Q3), we ran a separate GLMM (family = binomial, link = logit) with seed viability as the response variable. In this model, the proportion of cone granivory was included as a predictor variable. Because of the large variation in cone length, the number of seeds per cone, and the number of seeds with embryos between black and white spruce (Table 3.1.), we first ran a model using both species (sites = 8), followed by a model using only black spruce data (sites = 7). We checked all model assumptions by assessing the level of overdispersion and plotting residuals versus fit.

3.3 Results

Evidence of cone granivory was found at every treeline site. The conditional R^2 (Delta R^2 = 0.878) for the cone granivory model was much greater than the marginal R^2 (Delta R^2 = 0.164), suggesting large inter-site variability. High degree of variability between sites is reflected in the magnitude of granivory that showed a mean percentage of granivory of 1-36%; however, trees within plots had a wide range (i.e., 1-100%) of cones that exhibited granivory (Table 3.1.). Results from our presence-absence granivory model (Q1) indicated no association between treeline stand metrics (i.e., seeds per cone, cone length, tree density, and tree height) and the occurrence of granivory (Table 3.3). However, cone granivory presence was negatively associated with increased cover of PDS (prostrate dwarf shrubs; estimate = -0.015, $p < 0.05$), and exhibited a positive association with moss cover (estimate = + 0.008, p = 0.055). The proportion of moss and PDS cover varied with site (r = -0.15) and showed little evidence of one functional group excluding the other (Figure 3.3a). Where granivory was observed, the magnitude (Q2) was negatively associated with tree density (estimate = - 4.474, p = 0.015) and cover of PDS (estimate = - 0.008, p = 0.08) and positively with moss cover (estimate = + 0.005, p = 0.08).

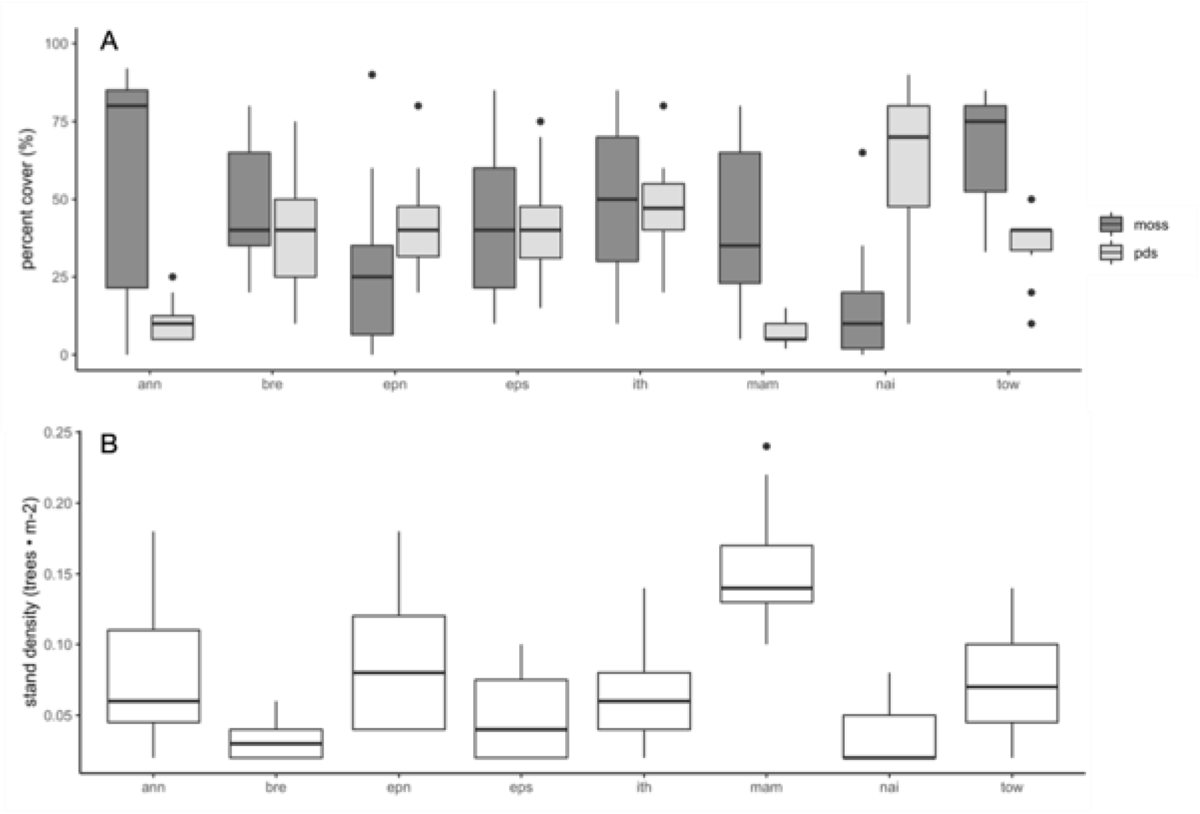

Figure 3.3 Summary data of (A) percent cover of moss (dark grey) and prostrate dwarf shrub (light grey) and (B) stand density (trees • m^{-2}) for each site. Note that DAN and GSP are not included in these boxplots, as we were unable to complete all sampling.

Similar to the variation we observed in the number of cones affected by granivory, the number of viable seed from our sampled cones varied within plots and between sites (Table 3.1; Table 3.S2). The proportion of seeds with embryos to total seeds extracted was less than 50% for all sites except ANN and MAM. Viability of available seed (i.e., germination of sampled seeds with a full embryo) was greater than 50% for all sites dominated by black spruce, while those dominated by white spruce were at or approaching zero viability.

Table 3.3 Parameter estimates with standard errors (SE) for generalized linear mixed models of cone granivory. Both models treated plot within site as a random effect. Conditional and marginal R^2 values were calculated for the binomial model (Delta R^2_c= 0.278; Delta R^2_m=0.029) and the Poisson model (Delta R^2_c = 0.878; Delta R^2_m = 0.164). Significant (α = 0.05) covariate estimates are bolded.

	Binomial (link=logit)				Poisson (link = log)			
	Parameter Estimate	SE	z-value	p value	Parameter Estimate	SE	z-value	p value
Intercept	**- 2.465**	**1.006**	**-2.451**	**0.014**	**+2.653**	**0.648**	**4.096**	**0.000**
organic layer depth	+0.008	0.016	0.477	0.634	+0.009	0.012	0.723	0.469
TMS	- 0.007	0.007	-0.971	0.331	- 0.006	0.005	-1.195	0.232
EDS	- 0.005	0.006	-0.923	0.356	- 0.002	0.004	-0.466	0.641
PDS	**- 0.015**	**0.007**	**-2.081**	**0.037**	- 0.008	0.005	-1.725	0.085
moss	+0.009	0.004	1.917	0.055	+0.005	0.003	1.720	0.085
leaf litter	- 0.006	0.020	-0.280	0.780	- 0.197	0.012	-1.581	0.114
Seeds per cone	+0.002	0.013	0.169	0.866	+ 0.004	0.009	-0.436	0.663
Mean cone length	+0.032	0.027	1.213	0.225	+ 0.019	0.018	1.016	0.309
Tree density	- 3.133	2.557	-1.226	0.220	**- 4.474**	**1.832**	**-2.443**	**0.015**
Tree height	+0.001	0.001	0.614	0.539	0.001	0.001	0.832	0.405

Our pooled black and white spruce binomial model of viability of available seed (Q3) indicated a positive relationship with seeds per cone (estimate = 0.026, *p* = 0.045) and a negative relationship with cone length (estimate = - 0.163, *p* = 0.003; Figure 3.4; Table 3.S3). However, we attribute these results to our time of sampling and the physiology of white spruce cones and will thus not be included in our discussion. Results from our binomial site-level model using only black spruce data indicated no significant relationship between cone granivory and availability of viable seed or any other predictor variable; however, the parameter estimate for the proportion of cone granivory was negative.

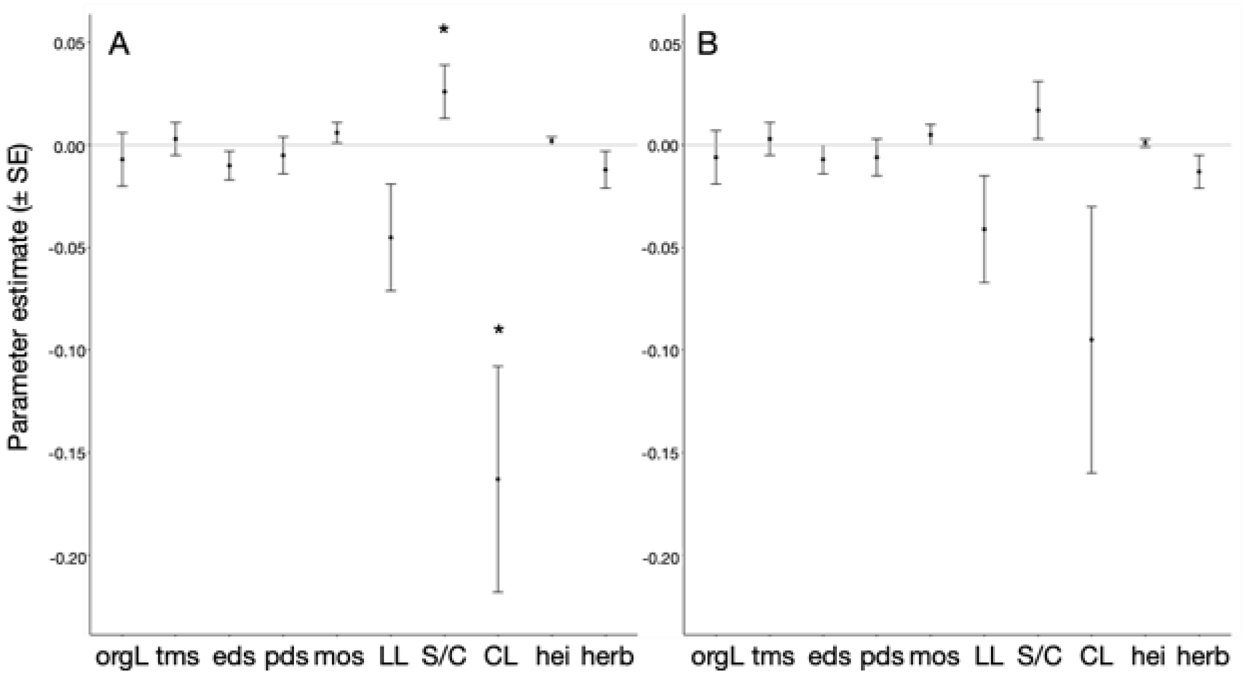

Figure 3.4 Parameter estimates with standard errors (SE) for general linear mixed model output of the availability of viable seed analyses using all sites (A) and sites that were dominated by black spruce only (B). Both models treated plot within site as a random effect. Asterix above covariates indicate significance to $\alpha = 0.05$. Covariate names as follows: organic layer (orgL); tall multi-stemmed shrubs (tms); erect dwarf shrubs (eds); prostrate dwarf shrubs (pds); leaf litter (LL); seeds • cone $^{-1}$ (S/C); cone length (CL), height of tree (hei); proportion of cone granivory (herb).

3.4 Discussion

Insect granivory was present at all treelines, supporting the initial hypothesis that the distribution of cone insects is widespread. The mean magnitude of insect granivory at each site (1-36% of sampled cones with evidence of granivory) was within the range observed in other treeline or high elevation forests studied across the boreal biome (Jameson et al., 2015; Kolb, Ehrlén, & Eriksson, 2007; Prévost, 2002; Seifert et al., 2000). Of greater interest was the variability we detected in granivory between plots within a site, as the magnitude ranged from 1 to 100% of all cones sampled. This wide range of granivory pressure within our data indicates that within a short linear distance (< 75 m), some trees may experience little to no granivory, while others can experience substantial damage to their reproductive units. Therefore, based on our model results, we predict that all treelines would experience insect granivory, while treelines with a lower density of trees and a moss understory may increase the potential for greater insect granivory under non-masting conditions.

The observed association between lower tree density and increased magnitude of granivory demonstrates a potential density-dependent relationship between insect populations and cone production at treeline. Despite the consistent presence of insect granivory at the boreal-tundra treeline ecotone, cone and viable seed production remains limited due to environmental conditions (Viglas, Brown, & Johnstone, 2013; Brown et al., 2019). Our findings suggest that at treelines where there are fewer trees with cones (i.e., low density, and under non-masting conditions), supporting the insect population which maintain high reproductive potential may be difficult. Our findings are supported by a recent study that examined the relationship between interannual white spruce cone production and pre-dispersal insect cone damage (Leeper & LaMontagne, 2021). Results indicated that insect damage was highest when annual cone production was low, suggesting the predator satiation hypothesis is satisfied through masting events, where large increases in cone production reduce the overall impact of insect damage on reproduction potential. While we were unable to examine interannual variability of cone production, the inverse relationship between stand density and cone granivory reflects similar conclusions.

The relationship between lower tree density and increased magnitude of granivory is further supported by our model results which indicated no within-conifer granivory relationship with cone morphology predictor variables (i.e., cone length and number of seeds per cone). Previous studies have shown the relationship between cone morphology and ovipositing to be inconsistent within insect species (positive: Fidgen, Quiring, & Sweeney, 1998; Mosseler &

Tricco, 1991; Leeper & LaMontagne, 2021; negative: McClure et al., 1998), suggesting the relationship may be a product of either resource quality or availability (DeSoto, Tutor, Torices, Rodríguez-Echeverría, & Nabais, 2016). We speculate that at low density treelines, insects may choose ovipositing on an unoccupied cone rather than searching for a cone of a given size, increasing the importance of resource availability. Adult female spruce cone flies oviposit one to five eggs per developing cone, depending on annual cone production (McClure, Quiring, & Turgeon, 1998). Moreover, these cone flies and other conophyte species tend to avoid ovipositing on cones that are already occupied (Fidgen, Sweeney, & Quiring, 1999). Thus, while a greater number of trees in close proximity may support an increased success of rapidly ovipositing on an unoccupied cone (Fogal & Larocque, 1992; Boivin, Doublet, & Candau, 2019), we hypothesize that the effect of granivory is magnified on individual trees when tree density is lower.

Nevertheless, the association we detected between lower tree density and magnitude of granivory runs counter to the preference/performance hypothesis (Thompson, 1988), where females should favour ovipositing conditions that result in the greatest survival of offspring (i.e., denser treelines with greater number of cones). It has also been suggested that emissions (i.e., volatiles and pheromones) produced at various phenological phases of cone production can initiate a signal for adult cone flies to oviposite (Turgeon, Roques, & De Groot, 1994). We expect this to occur at higher levels when tree density is greater. We therefore suggest that our findings are context-dependent to treeline populations, where higher density tree populations may not be within dispersal distance of granivores. In addition, because all data collection occurred within a 75 m transect, further research is required to determine whether the spatial patterning of insect granivory is consistent across landscapes and the larger boreal-tundra treeline ecotone.

The positive association between increasing moss cover and magnitude of granivory is likely associated with moisture conditions at treeline, as moss is indicative of microsites that hold greater soil moisture and are shaded by trees (Dearborn & Danby, 2017; Fenton & Bergeron, 2006; Goodwin & Brown, 2019). Moss can also be associated with a deeper organic layer (Fenton & Bergeron, 2006; Turetsky, Wieder, Halsey, & Vitt, 2002); however, there is evidence to suggest that a deeper organic layer could expose overwintering larvae to an increased number of predators (Fidgen, Sweeney, & Quiring, 1999). Nevertheless, moist surface conditions are favourable to cone insects, especially cone flies, as larvae drop from cones mid-summer to overwinter in the organic layer (Fidgen, Sweeney, & Quiring, 1999). Field and lab studies have shown that if surface conditions are dry, a greater proportion of larvae will desiccate and not reach adulthood (Sweeney & Turgeon, 1994). Furthermore, preference towards a substrate with increased moisture retention would also explain the negative relationship between shrub cover, specifically PDS, and the presence of granivory at treeline, as PDS reflects dry and rocky areas with a shallow organic layer (Goodwin & Brown, 2019).

It is important to reiterate that our methods did not allow us to quantify total seed loss from insect granivory, as cone and seed damage by insects had already taken place before laboratory seed extraction. We did not compare average seed loss from insect granivory and cannot explicitly state whether insect seed loss is greater at high- or low-density treelines. Visual estimates of total number of cones showed a greater number of cones at sites with higher tree density (see Table 3.S2), which may indicate why the magnitude of seed loss from insect granivory is less at more dense treelines, as trees produce enough cones to support the insect population while still maintaining their reproductive fitness (Linhart, Moreira, Snyder, & Mooney, 2014). Nevertheless, many studies have shown the significant negative pressure insect granivory has on the total number of seed available within a forest stand (DeSoto et al., 2016; Kolb et al., 2007; Mosseler & Tricco, 1991; Rosenberg, Nordlander, & Weslien, 2015). While we did not quantify the influence of mammalian herbivory on pre-dispersal seed availability, despite their known influence (Holtmeier, 2012), our study highlights specific treeline characteristics that support greater insect populations, which also reduces available seed before seed dispersal.

The majority of seeds being produced at each site did not have a fully developed embryo. This is typical of cone producing trees at treeline, as environmental conditions at the range edge are less-suitable for seed maturation (Anadon-Rosell, Talavera, Ninot, Carrillo, & Batllori, 2019; Mamet et al., 2019; Sirois, 2000; Viglas, Brown, & Johnstone, 2013). As previously stated, essential resources for seed development are also limited at treeline, resulting in decreased pollination success and increased seed abortion (Brown et al., 2019; Wilcock & Neiland, 2002). Nevertheless, we hypothesized that the availability of viable seed would reflect predictor variables, which did not occur (Figure 3.4). As previously stated, our pooled black and white spruce seed viability model indicated cone size and number of seeds per cone were significant in our model, yet we are confident these results are skewed by the white spruce treeline sites. We suspect that viability of available seed did not reflect any predictor variable because of low sample size in our model. However, we did find evidence of a negative association between cone granivory and the viability of available seed, supported by the parameter estimate of cone granivory with standard error not overlapping with zero (Figure 3.3). This result is similar to findings from lower elevation forest stands (DeSoto et al., 2016; Kolb et al., 2007; Mosseler &

Tricco, 1991; Rosenberg, Nordlander, & Weslien, 2015); thus, while we speculate that pre-dispersal insect granivory has a similar effect on availability of viable seed at treeline populations across northern Canada, a greater number of sites should be examined to determine whether these model results are robust.

In conclusion, our study shows that however complex cone development or insect population dynamics are, the biotic disturbance of insect granivory at the boreal-tundra treeline is present across Canada within a short period of time (i.e., a single growing season). Yet, the magnitude of granivory increases when tree density is lower and when understory cover is dominated by moss. We acknowledge the low number of sample sites included in our models. A low site number does influence our predictive power, but we believe this is an essential step in examining an understudied biotic disturbance at treeline. This is especially true under the context of climate change, as continued climate warming is predicted to increase and change the geographic distribution of many biotic and abiotic disturbances (Robinet & Roques, 2010; Turner, 2010; Wolf, Kozlov, & Callaghan, 2008). Moreover, disturbances that influence viable seed availability do not happen in a vacuum and are likely to interact with others that affect substrate conditions (e.g., wildfire, pathogens), further influencing boreal tree species' ability to carry out seed-mediated reproduction at their range edge. Our identified relationships between cone granivory and environmental characteristics provide an important contribution toward understanding the abiotic drivers of biotic interactions, thus informing future treeline predictive models. Our findings do need to be tested at other geographic locations, which can be done quickly, as a data collection protocol has been established that takes into account the time-sensitive nature of remote access fieldwork. Our spatial analysis should also complement future studies on the temporal component of insect cone granivory as cone production and insect populations vary with year.

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3.7 Supplementary Material

Table 3.S1 Summary information for sampling sites

Site	Traditional Territory	Region	Latitude	Longitude	Field Sampling Carried out by	Sampling Period
GSP	Mi'kmaq	Quebec	49.00	-65.94	Anna Crofts	Fall 2019
ANN	Beothuk	Newfoundland	49.59	-56.23	Lucas Brehaut, Anna Crofts	Fall 2018
NAI	Nunatsiavut	Nunatsiavut	56.54	-61.72	Lucas Brehaut	Summer 2018
MAM	Sayisi Dene	Manitoba	58.62	-93.81	Steven Mamet	Fall 2018
DAN	Tłı̨chǫ	Northwest Territories	63.77	-111.23	Ryan Danby	Summer 2018
BRE	Tr'ondëk Hwëch'in	Yukon	64.22	-140.18	Lucas Brehaut	Summer 2018
TOW	Tr'ondëk Hwëch'in	Yukon	64.11	-140.96	Lucas Brehaut	Summer 2018
EPS	Vuntut Gwitchin	Yukon	65.83	-137.77	Lucas Brehaut, Katie Goodwin, Kirsten Reid	Summer 2018
EPN	Vuntut Gwitchin	Yukon	66.50	-136.56	Lucas Brehaut, Katie Goodwin, Kirsten Reid, Carissa Brown	Summer 2018
ITH	Inuvialuit	Northwest Territories	68.70	-133.56	Lucas Brehaut, Kirsten Reid	Summer 2019

Table 3.S2 Plot level summary data for each site.

site	plot	trees • m^{-2}	tree height (cm)	total visual cone est.	no. cones sampled	cone herbivory (%)	seeds • cone^{-1}	total seeds	seeds with embryo	seeds in germ trial	seeds germinated (%)
ann	1	0.08	250.75	18	11	18	10.40	103	31	31	77
ann	2	0.06	266.33	13	11	36	14.36	158	93	93	99
ann	3	0.06	423.67	140	27	37	22.54	625	198	142	92
ann	4	0.04	385.00	9	9	33	10.13	101	66	66	97
ann	5	0.06	239.67	4	1	1.00	12.00	12	1	1	0
ann	6	0.02	221.00	1	1	1.00	4.00	4	2	2	1.00
ann	7	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
ann	8	0.02	200.00	NA	NA	NA	NA	NA	NA	NA	NA
ann	9	0.04	291.00	NA	NA	NA	NA	NA	NA	NA	NA
ann	10	0.12	327.17	24	16	13	24.63	394	268	100	93
ann	11	0.06	247.00	NA	NA	NA	NA	NA	NA	NA	NA
ann	12	0.08	260.50	11	11	55	36.82	405	197	100	48
ann	13	0.12	409.17	72	12	58	11.66	118	55	55	95
ann	14	0.14	323.71	48	20	45	14.77	263	183	147	97
ann	15	0.18	295.33	22	22	23	26.71	944	582	103	96
bre	1	0.06	441.67	981	61	18	16.78	1029	133	0	0
bre	2	0.04	392.50	155	32	16	3.33	82	0	0	0
bre	3	0.02	266.00	NA	NA	NA	NA	NA	NA	NA	NA
bre	4	0.02	220.00	NA	NA	NA	NA	NA	NA	NA	NA
bre	5	0.04	474.00	58	20	10	16.50	330	9	9	0
bre	6	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
bre	7	0.04	376.50	40	24	42	9.94	221	10	10	0
bre	8	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
bre	9	0.02	400.00	140	20	35	9.75	195	59	0	0
bre	10	0.02	317.00	*3*	NA	NA	NA	NA	NA	NA	NA

bre	11	0.04	256.50	60	40	13	30.78	1231	8	0	0
bre	12	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*
bre	13	0.02	800.00	1	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*
bre	14	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*
bre	15	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*
dan	1	0.66	282.18	1143	40	13	29.93	1197	342	184	64
dan	2	0.78	269.82	1539	39	3	36.94	1442	1015	200	77
dan	3	0.82	278.80	1466	41	15	27.91	1152	475	200	86
dan	4	0.48	293.17	1887	40	15	41.15	1646	1247	200	88
dan	5	0.70	345.20	1855	40	13	36.78	1471	397	200	83
dan	6	0.20	339.40	1645	40	15	24.38	975	395	200	74
dan	7	0.42	320.10	783	40	23	26.48	1059	574	200	90
dan	8	0.14	232.86	718	40	5	23.23	929	598	200	85
dan	9	0.32	321.69	1008	40	20	31.93	1277	435	195	91
dan	10	0.08	369.25	511	40	20	38.28	1531	71	71	79
dan	11	0.12	261.50	384	40	8	41.45	1658	489	200	83
dan	12	0.24	274.33	531	44	16	18.00	838	276	100	75
dan	13	0.28	339.79	1200	44	20	25.01	1118	749	200	78
dan	14	0.22	339.18	1122	50	26	28.73	1435	230	177	72
dan	15	0.02	243.00	45	13	15	49.92	649	312	100	93
epn	1	0.08	347.85	557	59	31	40.42	2393	977	200	63
epn	2	0.12	399.77	1591	59	12	25.56	1507	641	200	57
epn	3	0.04	393.05	142	60	23	22.97	1378	251	141	73
epn	4	0.10	440.50	1157	61	31	42.63	2583	1832	200	71
epn	5	0.04	450.30	1088	58	31	39.31	2280	1098	200	73
epn	6	0.06	376.40	810	60	17	45.63	2738	1282	200	81
epn	7	0.18	329.63	1969	93	35	25.71	2421	533	272	62
epn	8	0.04	298.00	392	71	27	27.56	1973	929	200	46
epn	9	0.18	342.59	2004	115	10	36.29	3926	2146	300	51
epn	10	0.16	453.20	1634	101	23	32.02	3230	1587	235	41
epn	11	0.10	423.96	1650	108	44	15.83	1660	772	200	43
epn	12	0.06	402.80	633	64	48	17.89	1145	447	200	50
epn	13	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*
epn	14	0.04	638.99	1023	66	21	17.35	1156	437	300	0
epn	15	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*
eps	1	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*
eps	2	0.06	298.67	420	63	17	32.02	1993	1240	241	84
eps	3	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*
eps	4	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*
eps	5	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*
eps	6	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*
eps	7	0.10	269.60	705	87	31	43.01	3709	1843	400	65
eps	8	0.02	330.00	220	22	9	49.68	1093	843	100	88
eps	9	0.02	432.90	417	23	57	40.17	924	397	100	91
eps	10	0.02	290.00	110	21	10	19.00	399	155	100	79
eps	11	0.08	375.50	789	109	18	37.16	4274	2306	432	85
eps	12	0.04	293.00	480	23	26	37.70	867	140	100	90
eps	13	0.08	290.25	420	87	11	40.82	3590	1291	400	82
eps	14	0.04	301.50	150	45	24	37.19	1708	822	177	93

eps	15	0.02	342.00	160	20	85	54.95	1099	447	100	66
gsp	1	0.06	112.30	350	40	23	55.23	2209	11	11	0
gsp	2	0.04	106.50	200	20	15	35.45	709	1	1	0
gsp	3	0.06	152.30	1200	40	5	22.54	881	13	13	0
gsp	4	0.04	90.00	50	40	30	34.40	1376	6	6	0
gsp	5	0.04	195.50	450	20	25	28.55	571	6	6	0
gsp	6	0.04	107.50	26	21	14	43.58	451	4	4	0
gsp	7	0.02	219.00	75	20	15	41.55	831	9	9	0
gsp	8	0.02	539.00	1000	19	16	34.95	664	13	13	15
gsp	9	0.02	467.00	500	19	0	35.89	682	53	53	0
gsp	10	0.02	328.00	500	20	10	36.10	722	7	7	0
gsp	11	0.04	152.50	50	20	5	42.15	843	2	2	0
gsp	12	0.04	147.00	50	20	25	37.95	759	4	4	0
gsp	13	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
gsp	14	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
gsp	15	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
ith	1	0.06	446.33	40	17	35	6.24	79	0	0	0
ith	2	0.14	499.14	109	37	59	7.35	285	0	0	0
ith	3	0.02	686.00	10	6	67	3.67	22	0	0	0
ith	4	0.04	447.00	15	14	50	1.93	27	0	0	0
ith	5	0.08	311.75	20	20	20	0.70	14	0	0	0
ith	6	0.10	450.20	21	20	10	0.87	33	0	0	0
ith	7	0.08	392.25	33	19	37	3.00	74	0	0	0
ith	8	0.04	409.00	6	6	0	0.33	2	0	0	0
ith	9	0.04	566.50	6	3	67	4.33	13	0	0	0
ith	10	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
ith	11	0.04	528.00	21	20	15	1.80	36	0	0	0
ith	12	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
ith	13	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
ith	14	0.06	333.33	110	60	28	1.85	111	8	8	50
ith	15	0.06	383.00	NA	NA	NA	NA	NA	NA	NA	NA
mam	1	0.16	471.25	400	34	9	43.88	1492	986	200	79
mam	2	0.14	448.57	125	38	5	33.55	1265	559	200	68
mam	3	0.14	390.00	180	46	4	42.55	1977	1126	200	68
mam	4	0.24	419.17	210	49	0	37.70	1807	979	200	68
mam	5	0.12	430.00	195	39	3	39.21	1528	621	200	67
mam	6	0.10	430.00	40	44	0	36.59	1534	731	200	73
mam	7	0.12	421.67	5	NA	NA	NA	NA	NA	NA	NA
mam	8	0.14	481.43	70	29	0	24.70	698	226	132	65
mam	9	0.22	466.36	232	77	3	29.86	2353	1183	200	58
mam	10	0.20	457.00	150	16	0	21.25	340	152	100	73
mam	11	NA	NA	NA	8	0	33.75	270	131	200	45
mam	12	0.14	540.00	320	65	0	46.77	3282	1068	200	58
mam	13	0.14	518.57	10	NA	NA	NA	NA	NA	NA	NA
mam	14	0.12	483.33	240	28	0	50.59	1261	621	178	69
mam	15	0.18	516.67	70	NA	NA	NA	NA	NA	NA	NA
nai	1	0.02	612.00	46	19	0	0.00	0	0	0	0
nai	2	0.06	329.67	3	2	0	0.00	0	0	0	0
nai	3	0.04	302.50	97	41	0	0.00	0	0	0	0

nai	4	0.02	509.00	84	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*
nai	5	0.02	285.00	13	9	0	0.00	0	0	0	0
nai	6	0.02	509.00	42	20	0	0.30	6	1	1	0
nai	7	0.04	361.00	68	22	5	0.32	7	0	0	0
nai	8	0.02	298.00	27	24	4	0.00	0	0	0	0
nai	9	0.04	475.00	24	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*
nai	10	0.02	537.00	118	25	4	0.16	4	0	0	0
nai	11	0.08	392.25	54	48	8	0.03	2	0	0	0
nai	12	0.06	481.00	259	42	0	0.00	0	0	0	0
nai	13	0.02	413.00	185	21	0	0.00	0	0	0	0
nai	14	0.02	464.00	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*
nai	15	0.06	555.67	31	20	5	0.00	0	0	0	0
tow	1	0.14	323.86	1137	110	5	3.40	368	81	81	69
tow	2	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*
tow	3	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*
tow	4	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*
tow	5	0.06	278.67	319	44	7	9.77	447	90	90	62
tow	6	0.08	292.75	335	40	5	14.18	567	175	175	85
tow	7	0.04	307.50	128	20	0	3.35	67	11	11	27
tow	8	0.10	306.00	439	83	1	15.05	1247	186	155	81
tow	9	0.04	300.00	250	41	7	3.48	146	8	8	75
tow	10	0.06	227.33	250	60	3	7.40	444	7	7	29
tow	11	0.10	263.40	622	78	5	19.00	1496	208	217	81
tow	12	0.12	348.33	289	100	0	6.89	689	37	37	78
tow	13	0.02	410.00	320	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*
tow	14	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*
tow	15	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*

Table 3.S3 Parameter estimates and standard error (SE) of generalized linear mixed models of viability of available seed for all species (black and white spruce) and black spruce only. Both models treated plot within site as a random effect. Significant (α = 0.05) covariate estimates are bolded.

	All Species (Binomial [link = logit])				Black spruce (Binomial [link = logit])			
	Parameter Estimate	SE	z-value	p value	Parameter Estimate	SE	z-value	p value
intercept	**3.431**	**1.436**	**2.389**	**0.017**	**2.782**	**1.398**	**1.990**	**0.047**
organic layer	-0.007	0.013	-0.509	0.610	-0.006	0.013	-0.446	0.656
tms	0.003	0.008	0.377	0.706	0.003	0.008	0.328	0.743
eds	-0.010	0.007	-1.580	0.114	-0.007	0.007	-0.987	0.324
pds	-0.005	0.009	-0.530	0.596	-0.006	0.009	-0.620	0.536
moss	0.006	0.005	1.407	0.160	0.005	0.005	1.200	0.230
leaf litter	-0.045	0.026	-1.702	0.089	-0.041	0.026	-1.535	0.125
seeds per cone	**0.026**	**0.013**	**2.003**	**0.045**	0.017	0.014	1.232	0.218
cone length	**-0.163**	**0.055**	**-2.966**	**0.003**	-0.095	0.065	-1.464	0.143
tree density	-0.222	2.570	-0.086	0.931	-1.259	2.562	-0.491	0.623
tree height	0.002	0.002	0.906	0.365	0.001	0.002	0.744	0.457
cone herbivory	-0.012	0.009	-1.351	0.177	-0.013	0.008	-1.546	0.122

Chapter 4: Boreal tree regeneration after fire and fuelwood harvesting in coastal Nunatsiavut

Abstract

Consecutive landscape-scale disturbances are known to influence boreal forest regeneration, yet few published data exist on the compounding effects of natural and anthropogenic disturbance on regeneration in subarctic forests. We conducted a dendroecological study of eastern coastal boreal forest regeneration two decades after fire at three subarctic forest stands that are important sources of fuelwood for the people of Nunatsiavut (Labrador, Canada). We quantified spruce (*Picea* spp.) and balsam fir (*Abies balsamea* (L.) Mill.) seedling regeneration, standing dead tree density, trees harvested within burned forests, and aged proximal unburned stands. Age of unburned forest varied with site; however, each exhibited continuous regeneration over several decades. Despite low seedling regeneration at each site (stems • m^{-2}; less than 35% of pre-fire stem density), model results indicated harvesting post-fire did not impact seedling regeneration. Our results indicate that tall mutli-stemmed shrubs may establish a negative pressure on seedling abundance, possibly related to resource availability. Nevertheless, because unburned forest stands exhibit a range in tree age we argue shrubs may simply be a set of early successional species rather than indicate a change in successional trajectory. Examination of a larger chronosequence within coastal forest stands of Nunatsiavut is warranted to further understand forest regeneration in the eastern subarctic under changing disturbance regimes.

Keywords: Labrador, fire, disturbance, seedlings, salvage logging, subarctic, *Picea mariana, Picea glauca, Abies balsamea*

4.1 Introduction

Large-scale natural disturbance and human land use drive boreal forest ecosystem structure and function (White and Pickett 1985; Gauthier et al. 2009). Across northern latitudes, forest age and regeneration dynamics are closely linked to fire frequency and severity, as boreal tree species have evolved regeneration strategies increasing fitness in post-fire conditions (Johnson 1992; Weber and Flannigan 1997; Soja et al. 2007). Serotinous cones in aerial seed banks (*Picea mariana* [Mill.] B.S.P., *Pinus* spp.), and light, wind dispersed seeds (*Betula* spp., *Picea glauca* [Moench] Voss) allow for quick post-fire germination and establishment on combusted organic layers that are warmer and higher in nutrient availability than pre-fire (Certini 2005; Splawinski et al. 2018). In addition to post-fire seed dispersal strategies, other species carry out vegetation resprouting from roots (*Betula* spp., *Populus* spp.) for post-fire regeneration facilitating rapid colonization post-disturbance.

While fire continues to be the largest natural disturbance across boreal North America (single events of 200 hectares or more; Hanes et al. 2019) forest management practices and intensive logging activities also affect forest regeneration dynamics (Boucher et al. 2017; Greene et al. 2007; Leverkus et al. 2018). Under the context of continued climate change, having a better understanding of how these disturbances affect patterns of forest succession is warranted, as fire frequency is likely to increase and land-use requirements are anticipated to change (Gauthier et al. 2009; Seidl et al. 2017). Furthermore, natural and anthropogenic disturbances do not occur in isolation; therefore, a concerted effort is required to understand the compounding impacts of disturbances on forest regeneration (Brown and Johnstone 2012; Buma et al. 2013; Turner 2010).

Across northern latitudes, changes in the successional trajectory of boreal forests have been observed after experiencing a large-scale fire followed by intensive post-fire commercial timber logging (Boucher et al. 2014; Kishchuk et al. 2015). Post-disturbance forests are often dominated by shade-intolerant deciduous tree and shrub species rather than a return to the expected pre-disturbance coniferous stand (Kurulok and Macdonald 2007). A shift towards an increase in ericaceous shrub dominance is also evident with understory vegetation composition (Jean et al. 2019). This abrupt shift in forest structure is hypothesized to be a result of a loss in resilience (Johnstone et al. 2010). Consecutive disturbances exceed some acceptable threshold of the dominant tree species, facilitating the establishment of an alternative species (Boiffin and Munson 2013; Buma et al. 2013). Thus, while fire often provides suitable seedbed for black spruce (Gordon and Shugart 1989), for example, an intensive logging activity post-fire may result in an inhospitable seedbed for spruce, but not for tree species like trembling aspen (*Populus tremuloides* Michx.; Hessl et al. 2002; Boucher et al. 2014). Evidence of boreal forest resilience loss has already been established in both central (Boiffin and Munson 2013) and western North America (Whitman et al. 2018).

Yet, similar patterns of forest regeneration or resilience loss following disturbance are not uniform across all boreal forests (Greene et al. 2006; Bouchard and Pothier 2011) and should not assume to be the case for understudied coastal forests of the eastern subarctic. These forests are defined by maritime climates and are heavily influenced by seasonal atmospheric-oceanic dynamics (Roberts et al. 2006). A cooler and wetter climate lowers the frequency and severity of forest fire events, allowing forests to remain in late successional stages for longer time periods (Steijlen et al. 1995). Because of the low fire frequency, few published studies exist on the fire return intervals for the eastern subarctic region (Foster 1982). Additionally, published research of stand age from dendrochronological studies is limited to interior Labrador (Trindade et al. 2011; Nishimura and Laroque 2011), historical settlements (Lemus-Lauzon et al. 2018; Roy et al.

2017), or areas in close proximity to present day communities (Lemus-Lauzon et al. 2016), further reducing our ability to understand regeneration and disturbance dynamics.

While there is a history of wood harvesting across eastern coastal forests of Nunatsiavut (Figure 4.1) and in southern interior Labrador (Lemus-Lauzon et al. 2016), harvesting rates are less than those of central and western forests of North America. Much of the current literature across the boreal forest examines the effects of harvesting when more than 70% of a stand is removed (Leverkus et al. 2018). These percentages are comparable to commercial wood harvesting rates in southern Labrador (Roberts et al. 2006); however, harvesting pressure decreases with increasing latitude and distance from community in Nunatsiavut due to the small human population centers. In this region, wood harvested in the winter by chainsaw after a forest fire remains an important fuel source for heating, as it is of much higher quality when compared to unburned wood; therefore, having a clear understanding of post-fire successional trajectories after consecutive disturbances is important in this region, as disturbances are of different severity (i.e., lower severity fire, fewer trees harvested) but still may have implications for the accessibility of quality fuelwoods. Despite the largely held expectation that consecutive disturbances impact boreal forest regeneration (Turner 2010), few published data exist on how post-fire fuelwood harvesting affects seedling generation and future forest composition in the eastern Canadian subarctic, notwithstanding known differences in the aforementioned disturbance regimes. An examination of the burned forests used by the Inuit of Nunatsiavut (Nunatsiavummiut) as a fuel source provides a unique opportunity to examine forest dynamics not only as consecutive disturbances of lesser intensity (i.e., less severe fire and lower harvesting pressure), but also within an understudied region of the North American boreal forest (Leverkus et al. 2018).

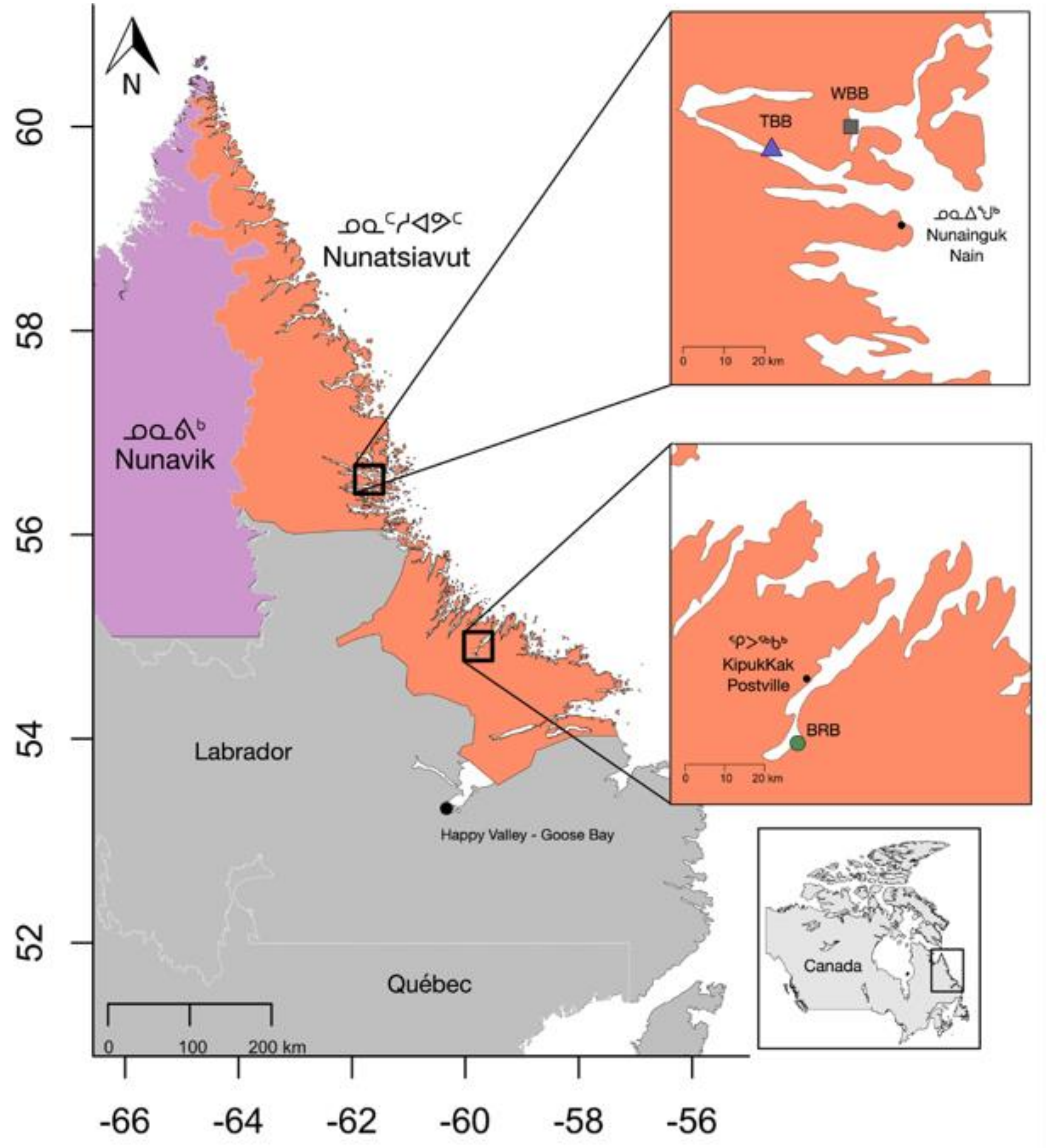

Figure 4.1 Location of our study region and the three sampling sites near Nain and Postville (insets). Sites were located within the land claim settlement region of Nunatsiavut in close proximity to the coast (< 1km). Sites are identified by shape and colour within the insets (BRB – green circle; TBB – blue triangle; WBB – grey square).

The objectives of our research were twofold: [i] to describe post-fire coastal forest landscapes in the eastern subarctic based on forest age structure and tree species richness; and [ii] determine how the compounding effects of fire and fuelwood harvesting drive boreal tree seedling regeneration in the coastal forests of Nunatsiavut. We expected that harvesting within the two decades after fire would have a negative effect on seedling regeneration due to the physical damage of seedlings (i.e., trampling; Royo et al. 2016), potential removal of tree seed during harvesting, as well as resource competition with rapidly establishing large shrub species (e.g., *Betula glandulosa* Michx.; Cranston and Hermanutz 2013), even under winter harvesting conditions. We tested this prediction using a dendroecological approach at three different "burned woods" (local term used to define post-fire stands) in Nunatsiavut, estimating the approximate age of each surrounding unburned forest, post-fire harvesting intensity, and total natural seedling regeneration (stems • m^{-2}) occurring within the burned forests. Results from this study help inform the current Nunatsiavut Energy Security Plan (Nunatsiavut Government 2016), add to a limited body of research on the interactive effects of disturbances under continued climate change (Turner 2010), and address the spatial knowledge gap of forest regeneration post-disturbance in coastal boreal forests of the eastern subarctic (Leverkus et al. 2018).

4.2 Materials and Methods

4.2.1 Study area

Our study took place in the easternmost part of northern continental Canada, the homeland of the Labrador Inuit in the land claim settlement region of Nunatsiavut (Figure 4.1). Regional landscapes are characterized by post-glacial features; broad plains pocketed by lakes and peatlands cover much of the interior, while bedrock-controlled hills and deep rivers dominate the eastern seaboard (Richerol et al. 2012). Shallow organic layers and sandy till soils underlay these coastal boreal forests over bedrock. Black spruce is the dominant tree species, although white spruce (*Picea glauca* [Moench] Voss), eastern larch (*Larix laricina* [Du Roi] K. Koch), and balsam fir (*Abies balsamea* [L.] Mill.) increase in density in areas of higher elevation or where soils are more productive (Engstrom and Hansen 1985). Ground vegetation is characterized by continuous hair-cap moss cover (*Polytrichum spp.*) and the presence of several multi-stemmed woody shrub species that vary from 0.1 m to 2 m in height (e.g., Grey-leaf willow: *Salix glauca* L., Labrador tea: *Rhododendron groenlandicum* [Oeder] Kron and Judd*;* Engstrom and Hansen 1985).

Nunatsiavut experiences a subarctic climate and local temperatures and precipitation patterns are strongly influenced by their proximity to the Labrador Current (Hare and Hay 1974). Recorded climate normal data from Nain, Nunatsiavut indicate a mean annual temperature of -2.5˚C, with a mean monthly temperature of +11˚C in August and -18˚C in January (Environment and Climate Change Canada 2018). Mean annual precipitation of 925 mm is divided equally between winter snow and summer rain (Environment and Climate Change Canada 2018).

We selected three burned forest stands for analysis in the region. Each site has been, and continues to be, chainsaw harvested by Nunatsiavummiut (people of Nunatsiavut) for fuelwood. Two sites were located approximately 20 km north from the community of Nain and burned in 2001 (Tikkoatokak Bay Burn-TBB; Burn size approximately 279 ha; N 56˚ 42.275’ W 062˚ 12.555’) and 2004 (Webb Bay Burn-WBB; Burn size approximately 67 ha; N 56˚ 45.379’ W 061˚ 52.178’), respectively (Figure 4.1). The third site is located 20 km west of the community of Postville (Beaver River Burn – BRB; Burn size greater than 10,000 ha; N 54˚ 46.828’ W 59˚ 48.489’) and burned in 1996. Based on the number of standing dead trees, remaining cone structures, and depth of organic layer two decades after fire, we can assume that all sites experienced a low intensity fire or light surface burn (as defined by Turner et al. 1994) and varied only slightly in total area harvested (see Results).

4.2.2 Data collection

During the summer of 2018, we established five belt transects (5 m x 50 m) at each of the three burned stands. We positioned four transects within each burn, at least 20 m apart from each other. The fifth transect was located in the proximal unburned forest at each site. The unburned transect was located at least 100 m from the closest transect in the burn and at least 50 m into the continuous forest. All transects ran parallel with site slope; thus, covering a gradient of edaphic conditions. Although transects in the burn were close to the unburned forest edge, we attempted to place transects within an area representative of the larger burn complex at a broader landscape-scale by visually inspecting drone imagery. All transects were divided into five plots for data collection that each measured 5 m x 10 m. It is important to note that we assumed the unburned forest to be representative of the entire landscape pre-fire due to their locale immediately adjacent to burned stands and their similar topography and forest structure. We realize that there may be an unknown ecological reason as to why the forest did not burn, which would make it an unsuitable comparison for our study. However, the density of trees in burned (i.e., standing dead • m^{-2}) and unburned forests were similar (see Results), further suggesting the stands were comparable.

To describe species richness and age structure of each unburned forest, we first counted individual trees greater than two metres tall by species within the belt transect to estimate stand density. We then selected 10 - 12 trees per site representative of the surrounding forest (i.e., similar in species, dbh, and height) for dendrochronological analysis (following Speer 2010). We collected two perpendicular cores from as close to the base of the tree as possible to retrieve the approximate age of the individual. For each cored tree we recorded basal diameter, diameter at breast height (DBH; diameter at height of 1.37 m), and height at which the core was taken. These data also allowed us to determine whether a strong positive relationship existed between older trees and larger growth measurements, which has been found across northern latitudes (Fritts 1976). At the BRB site, we sampled five black spruce and five eastern larch trees, as they are dominant overstory tree species in the forest. Upon returning to the lab, cores were mounted and sanded to a high polish. Tree rings were counted using a Velmex sliding stage micrometer with digital encoder (Velmex Inc., Bloomfield, NY).

In each burn, we collected data on seven variables that, based on previous research, we hypothesized would explain natural seedling regeneration density at each site (Table 4.1). We define seedling as all individuals recruiting post-fire (i.e., less than 30 years old, shorter than 2 m in height). We performed a species count to quantify seedling regeneration per square metre for all individuals taller than 50 cm along each transect. We did not record data on seedlings shorter than 50 cm because few were identified across all sampling areas. Additionally, there was an extremely low probability of finding all seedling of that size class within the complex shrub and graminoid understory. Data on seedling species richness was compared to species richness within the adjacent unburned forest. We recognize that the unburned forest may not be representative of the burned forest; however, we were unable to confidently identify standing dead to a species level due to the weathering of definable features and the age of the burn. Within each plot, we quantified pre-fire stand density by counting stems (stems • m^{-2}), and plot-level basal area (m^2 • ha^{-1}), which was calculated from basal diameter of each standing dead and felled tree. Only felled trees visibly connected to a root system were included in the basal area calculation. Note that while basal area is typically determined using DBH (Speer 2010), we opted to use basal diameter as our measure of stand density so that we could get a more accurate depiction of total number of trees within a plot, as well as have a consistent measurement between non-harvested and harvested trees that were cut below DBH height (or 1.37 m).

Table 4.1 List of covariates based on previous research that we hypothesized would have an effect on seedling regeneration numbers (response variable).

Covariate	Abbreviation	Units	Rationale	Reference
Basal area of harvested trees	HA	$m^2 \cdot ha^{-1}$	The more trees that are harvested the fewer tree regeneration occurs due to seedling trampling and seedbed damage.	*Morissette et al. 2002* *Kishchuk et al. 2015*
Pre-fire stand density	PreFSD	$m^2 \cdot ha^{-1}$	A more dense forest would have increased reproductive structures, which would allow for higher probability.	*Rossi et al. 2012*
Organic layer depth	OL	cm	Residual organic layer from a low-severity burn may become compacted, limiting successful seedling establishment.	*Purdon et al. 2004* *Brown and Johnstone 2012*
Shrub cover	TMS, EDS, PDS	% cover	Rapidly establishing large shrub species will out-compete low growing boreal tree seedlings for space and resources.	*Cranston and Hermanutz 2013* *Jäderlund et al. 1998* *DeLuca et al. 2002*
Haircap moss (*Polytrichum spp.)*	*Polytrichum*	% cover	Presence of haircap moss has been established to be a good indicator of regeneration success for both black spruce and jack pine seedlings	*Greene et al. 2004* *Jayen et al. 2006*

In order to better understand the growing conditions for natural seedling regeneration, we measured organic layer by creating a small vertical incision into the ground and measuring the depth (cm) and estimated percent cover of hair-cap moss using a 0.5 m x 0.5 m quadrat in the centre of each plot. Hair-cap moss was selected for analysis as it is a preferred germination bed for black spruce (Greene et al. 2004; Jayen et al. 2007). We also estimated percent cover (rounded to the nearest 5%) of shrubs at the center of each plot using a 1 m x 1 m quadrat within each plot, as shrubs have been found to both facilitate (Perkins 2015) and compete with (Cranston and Hermanutz 2013) tree seedling establishment. Because shrubs have an important height component and overlapping species should be considered within the estimate (i.e., volume), total percent cover could sum to above 100% per quadrat. We used the following shrub categories, previously defined by Myers-Smith et al. (2011), in which the same species can be found in multiple categories based on their height structure: (1) Tall multi-stemmed shrubs (TMS; height 0.4 – 4.0 m); (2) Erect dwarf shrubs (EDS; height 0.1 - 0.4 m); and (3) Prostrate dwarf shrubs (PDS; height < 0.1 m; often forming in mats).

The above measurements on growing conditions were not completed in the unburned forest due to weather-induced time constraints during our boat-access data collection. While we are aware that not having data in the unburned forest limits our ability to provide a direct comparison to the burned forest stand, this question was not within the scope of our research, which was focused specifically on the compounding effects of consecutive disturbances. We argue the measurements that were collected in each burned forest were suitable for answering the question of stand density regeneration.

4.2.3 Statistical analyses

Our first means of describing the unburned forest stands was to determine whether these mature coastal boreal forest stands were initiated via episodic (i.e., occurring within a small time frame post-disturbance *sensu* Johnstone et al. [2010]) or continuous regeneration (i.e., gradual establishment over decades post disturbance [Steijlen et al. 1995]). We developed chronologies within each unburned forest site that were cross-dated to an interseries correlation value of r > 0.20. While a correlation value of 0.2 is not necessarily strong, high correlation values do not ensure that samples were cross-dated accurately (Douglass 1941); therefore, we inspected each sample multiple times under the microscope to ensure that all tree rings were accounted for. After cross-dating, and when possible, an adjustment was performed to reach a more accurate tree age approximation when coring missed the sample pith (following Conway and Danby 2014). The number of missing rings was estimated by dividing the mean ring-width of the 10 innermost rings by the radius of a concentric circle generated from the final tree ring visible on the core (Hessl and Graumlich 2002). We plotted DBH of each tree against the newly approximated age of cored trees to assess whether the relationship between forest age and tree size of coastal populations matched allometric relationships observed in continental forest stands (i.e., were bigger trees older?).

Our approach to modeling seedling regeneration density post-fire and fuelwood harvest followed the mixed effects modeling procedure outlined by Zuur (2009) as follows. We first tested for collinearity at the plot level to ensure each predictor variable had a variance inflation factor < 3.0 and correlations between each had r ≤ 0.70 (Roland et al. 2013; See Table 4.1. for complete list of predictor variables used in each model). We then applied a hurdle model, which is a two-part model that allowed us to account for zero-inflation in the response variable. The first model was a general linear mixed model (GLMM; family = binomial; link=logit) of presence/absence data of seedlings in transects within site (Zuur 2009). We followed this model by running an additional GLMM (family = negative binomial; link=logit), looking only at data in plots where seedlings were present. In each model, number of seedlings were used as the response variable, and transects within sites were included as random effects. An interaction term between pre-fire stand density and all shrub cover categories (i.e., TMS, EDS, and PDS) was also included to determine whether any resource and space competition was evident. Model assumptions were tested by viewing level of over dispersion and plotting residuals versus fit. All statistical analyses were conducted in R.3.5.1. (R Core Team) using the package ‘dplR’ (Bunn 2010) and the package ‘lme4’ ver. 1.1-19 (Bates et al. 2015).

4.3 Results

4.3.1 Mature subarctic forests

Forest density along the unburned transect differed between sites; within the 200 m^2 area surveyed within each site, BRB had the greatest number of individuals (2.48 stems • m^{-2}) and WBB had the fewest trees (0.86 stems • m^{-2}; Table 4.2). When examining tree species richness, black spruce was the dominant tree species across all sites; however, balsam fir and eastern larch were subdominant species at all sites, contributing between 16 and 34% of the forest composition.

Table 4.2 Characterization of the unburned forest composition across a belt transect (5 m x 50 m) for each site, including relevant information for the cored trees. Mean DBH and Basal values are listed, as well as the average height at which the core was taken (HOC) and series intercorrelation derived from 'dplR' (Bunn 2010). Species acronyms are as follows: Pm (*Picea mariana*), Ab (*Abies balsamea*), Ll (*Larix laricina*).

Site	Species (count)	Species (sample no.) for Dendrochronology	DBH ± SD (cm)	Basal diameter ± SD (cm)	Average HOC (cm)	Series intercorrelation
BRB	*Pm* (217) *Ab* (75)	*Pm* (10)	20.17 ± 3.25	25.46 ± 4.59	45.5	0.398
TBB	*Pm* (85) *Ab* (22) *Ll* (21)	*Pm* (5) *Ll* (5)	11.80 ± 2.32 11.92 ± 1.54	15.78 ± 3.85 16.46 ± 2.10	40.0 46.8	0.215 0.278
WBB	*Pm* (28) *Ll* (15)	*Pm* (12)	33.93 ± 7.00	40.00 ± 7.62	40.08	0.582

Dendroecological data from the unburned forests indicate a large range in ages within sites (TBB – 112 year range; BRB – 91 year range; WBB – 186 year range). Despite these large range values, tree ages within sites were more similar than among sites. TBB was the youngest forest (mean age of 112 years ± 27 standard deviation [SD]), followed by BRB (170 years ± 43 SD), and WBB (227 years ± 53 SD). We found a positive association between tree size and age across sites (linear regression estimate = 4.7309, SE = 0.6991, t-value = 6.767, $p < 0.05$), but not within site (BRB p = 0.07; TBB p = 0.62; WBB p = 0.29; Figure 4.2).

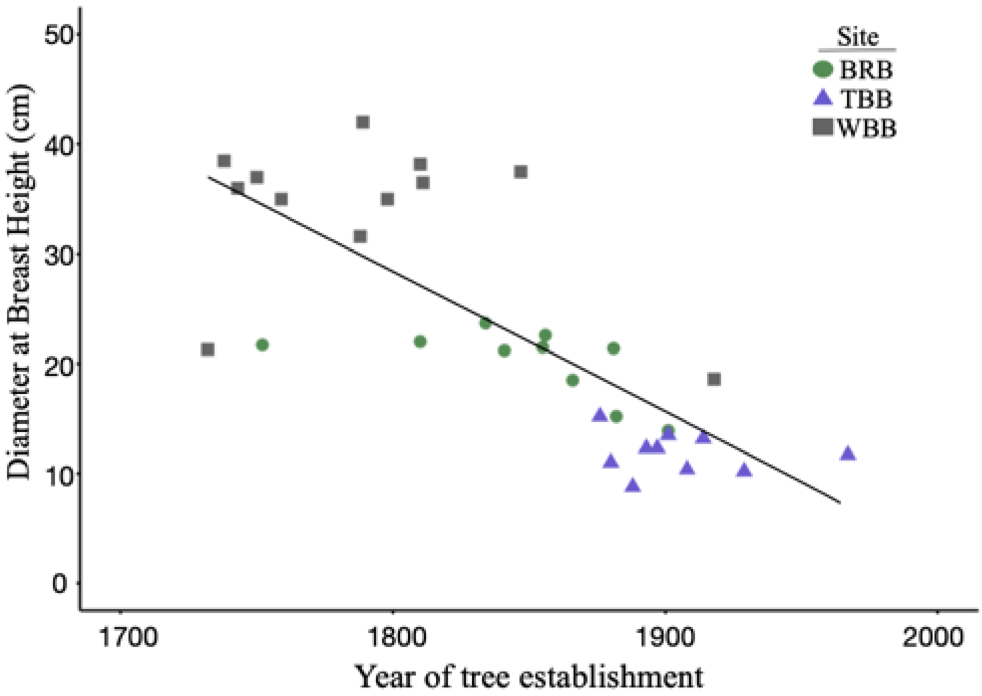

Figure 4.2 Relationship between year of establishment (oldest on the left, youngest to the right) and DBH of all sampled trees. Sites are identified by shape and colour (BRB – green circle; TBB – blue triangle; WBB – grey square).

4.3.2 Post-fire and harvest stand characteristics

Within the burned woods, the number of standing dead trees (including felled trees) was similar to that of the adjacent unburned forest, except for at BRB, which had less than half as many burned stems as the unburned forest. Limited harvesting occurred at each site within the sampling area (Table 4.3). Proportional to the number of standing dead trees within all transects, WBB experienced the highest proportion of wood harvested (34%) followed by TBB (14%) and BRB (8%). Trees at both TBB and WBB were harvested at a similar height (65 cm), which was half the mean harvesting height at BRB (102 cm). Despite differences in harvesting height, mean comparison of harvested tree DBH was not significantly different (p = 0.498).

Table 4.3 Site level information for each burned forest, including mean data on harvesting and seedling regeneration. Organic layer (OL) measured in centimetres. Species acronyms are as follows: Pm (*Picea mariana*), Pg (*Picea glauca*), Ab (*Abies balsamea*), Ll (*Larix laricina*), Bp (*Betula papyrifera*).

	Burned Forest and Harvest					Forest Regeneration			
Site	OL depth (cm)	stems • m^{-2}	harvested trees • m^{-2}	harvesting height (cm)	harvested tree diameter ± SD (cm)	site regen • m^{-2}	prop. regen	species (count)	regeneration height (cm)
BRB	15.80	2.48	0.21	102	12.15 ± 5.37	0.28	0.11	*Pm* (55) *Ab* (1)	86.65
TBB	16.75	2.38	0.34	65	11.41 ± 4.44	0.64	0.27	*Pm* (62) *Pg* (41) *Ll* (13) *Ab* (10) *Bp* (1)	128.78
WBB	16.50	0.86	0.30	65	12.87 ± 19.68	0.09	0.10	*Pg* (16) *Ll* (1)	82.18

Natural seedling regeneration greater than 50 cm height per square metre was low at each site (Table 4.3). Seedling density was less than 30% of the pre-fire stand density (number of stems) across all sites (BRB: 11%, TBB: 27%, WBB: 10%). While we cannot be certain that the unburned species composition was directly comparable to that of the standing dead, tree species richness, as indicated by seedling regeneration (i.e., stems • m^{-2}), did not change at BRB, but increased at TBB when compared to the unburned forest (see number of species in Table 4.2 and 3). In addition, despite the uneven sampling design between burned and unburned forests, no black spruce seedlings were found at WBB post-fire and a greater number of white spruce seedlings were found at TBB and WBB than were present in the unburned forest stand. Fewer larch seedlings had established across all sties when compared to the count data of the unburned forest.

4.3.3 Regeneration

Our binomial GLMM indicated that neither harvesting, stand density, organic layer depth, shrub cover, or moss cover were associated with seedling occurrence (i.e., presence/absence). While our sampling design prevents us from assessing the stand-alone effects of harvesting without fire, our model indicated that the compounding effects of post-fire harvesting does not have a significant effect on the occurrence (presence or absence) of boreal tree species seedlings > 50 cm across all sites, despite regeneration rates being low (Table 4.4, Figure 4.3). Our negative binomial model, which predicted seedling abundance in plots where seedlings were present, indicated that the number of seedlings was positively associated with the percent cover of tall multi-stemmed shrubs (TMS), except in plots with high pre-fire basal area (Table 4.4; Figure 4.4). The interactive effects of TMS and pre-fire basal area had a negative relationship with seedling regeneration density ($p = 0.053$). While this relationship does not fall below an alpha-value of 0.05, it is worth noting, especially since other interaction terms explained very little variation with regards to seedling per square metre.

4.4 Discussion

Here, we describe the structure and disturbance dynamics of coastal boreal subarctic forests, an understudied region of the North American boreal forest ecosystem. Prior to the most recent fires (i.e., unburned forest stands), initial establishment of the coastal boreal forest stands varied by site, with an estimate of stand establishment beginning around 1700 for WBB, post-1750 for BRB, and after 1850 for TBB. Initial forest stand establishment may have been a result of a novel disturbance (e.g., newly harvested; Roy et al. 2017; Lemus-Lauzon et al. 2018) or a change in climate and microsite conditions (Trant and Hermanutz 2014). While our study approach does not lend itself to answering the question of how these forest stands established, our data suggest that continuous, rather than episodic regeneration, occurred across all unburned sites after the year 1700. These findings are comparable to previous dendroecological studies completed in coastal Nunatsiavut (Payette 2007; Roy et al. 2017) and Nunavik (northern Quebec; Payette and Gagnon 1985).

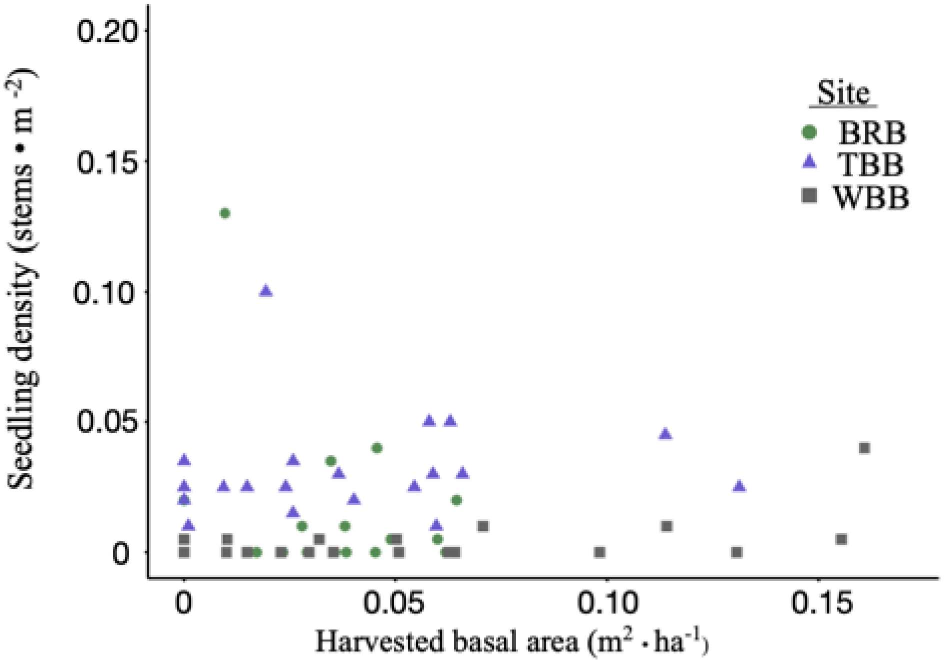

Figure 4.3 No clear relationship indicated between harvested basal area (m^2 • ha^{-1}) and number of seedlings. Site is indicated by shape and colour (BRB – green circle; TBB – blue triangle; WBB – grey square).

Table 4.4 Parameter estimates with standard errors (SE) for generalized linear mixed models of seedlings (number of seedlings per transect; Negative Binomial distribution). Both models treated transect within site as a random effect. Significant (α = 0.05) covariate estimates are bolded.

	Binomial				Negative Binomial			
Model Term	Parameter Estimate	SE	z-value	p value	Parameter Estimate	SE	z-value	p value
Intercept	32.66	79.23	0.412	0.680	0.43	1.16	0.374	0.709
Harvest area	-33.39	125.61	-0.266	0.790	4.19	4.54	0.922	0.357
Organic layer depth	1.79	1.38	1.296	0.195	-0.02	0.02	-1.137	0.256
pre-fire basal area	206.04	585.09	-0.352	0.725	4.75	7.53	0.630	0.529
TMS	-0.20	0.51	-0.39	0.697	0.04	0.02	**2.316**	**0.021**
EDS	-0.15	0.20	-0.766	0.444	0.01	0.02	0.380	0.704
PDS	-1.09	1.72	-0.635	0.525	0.02	0.03	0.624	0.532
Polytricum	1.51	1.76	0.859	0.390	-0.03	0.02	-1.497	0.134
PreFSD • TMS	-1.69	2.97	-0.569	0.569	-0.19	0.10	**-1.929**	**0.054**
PreFSD • EDS	4.90	4.06	1.207	0.228	-0.04	0.09	-0.407	0.684
PreFSD • PDS	5.16	11.92	0.433	0.665	-0.07	0.16	-0.415	0.678
PreFSD• Polytrichum	-5.32	8.14	-0.654	0.513	0.22	0.14	1.550	0.121

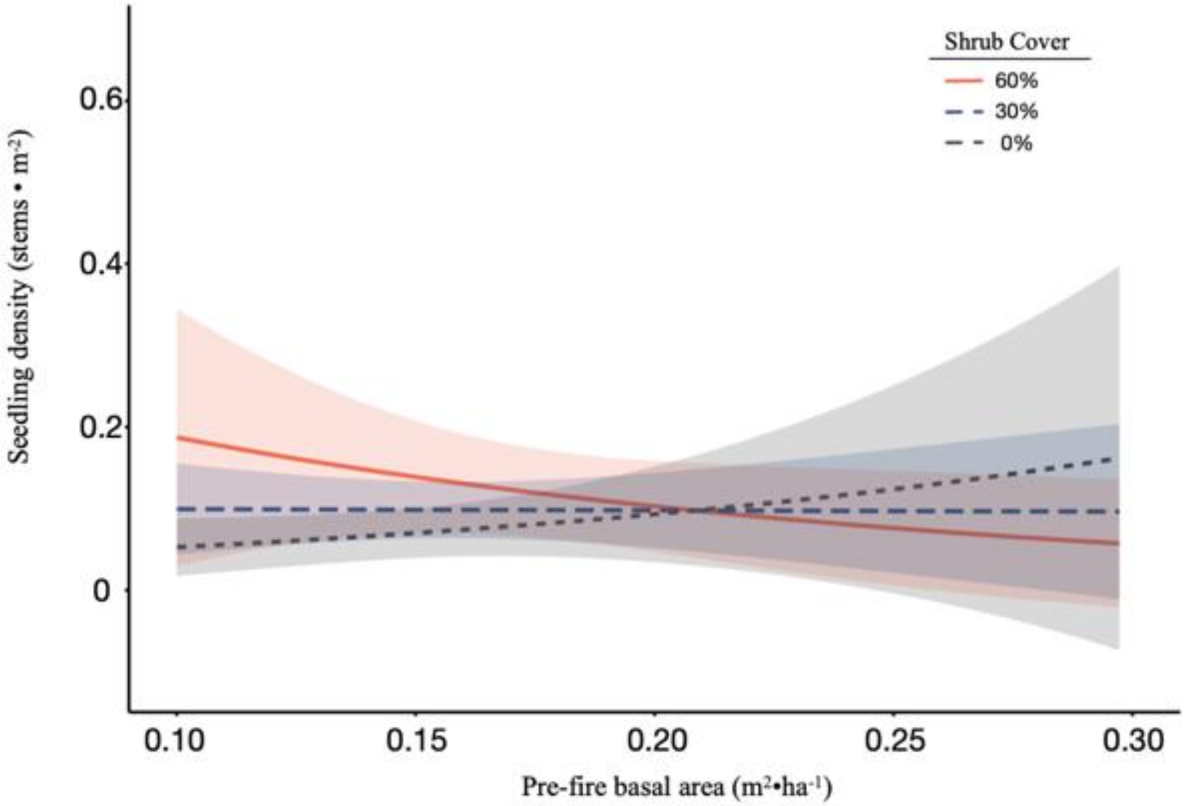

Figure 4.4 Generalized linear mixed model predicted values of seedlings as a function of the interaction between pre-fire basal area (m^2 • ha^{-1}) and percent cover of tall multi-stemmed shrub species. All lines represent the model fit to the covariates, with shading representing the 95% confidence intervals. Narrow shaded areas indicate higher model confidence. Percent shrub cover categories were selected based on the mean, as well as the first and third quartile of shrub cover values.

Continuous regeneration was expected, as boreal tree reproductive capacity (i.e., fewer filled seeds and lower germination rates) decreases with latitude (Sirois, 2000). The cold and wet climate of northern coastal Nunatsiavut favour slow cone production by virtue of longer periods of time required to produce heavy cone bearing crowns (Vincent 1965; Steijlen et al. 1995). Specific to black spruce, we would expect low levels of seed dispersal, as there are few hot and dry weather events that would break cone serotiny. Additionally, fire in Nunatsiavut still remains an infrequent large-scale disturbance on the landscape and would therefore have limited influence on seed dispersal (Roy et al. 2017). Similar trends in boreal tree regeneration and seed dispersal have been observed in northern Sweden (Steijlen et al. 1995) and at range-edge, or treeline locations in central Labrador (Trant and Hermanutz 2014). The weak relationship between site level tree size and stand age also points towards continuous rather than episodic regeneration, as continued stand development increases the effect of size hierarchy between seedlings (Mast and Veblen 1999). Yet, this weak age-size relationship may simply be a product of low sampling size and should be investigated further to determine whether our above hypothesis is supported.

Contrary to previous studies, our findings indicate no significant relationship between post-fire harvesting and seedling regeneration (Leverkus et al. 2018). While our study design did not allow us to explicitly test the effects of each disturbance separately on forest regeneration, fires are infrequent and harvesting post-fire is observable and a preferred practice in the region. There are several possible explanations for this result. First, post-fire harvesting was low across all sites (<35%) when compared to other commercial timber logging activities across boreal North America. For example, in Quebec (Boucher et al. 2014), Alberta (Kishchuk et al. 2015), and Saskatchewan (Morissette et al. 2002) over 90% of trees were harvested shortly after the fire to minimize loss of available cuts. Low harvesting rates in Nunatsiavut are likely a product of site accessibility and community size, which has a combined population of less than 2,000 people for Nain and Postville. Wood is harvested for immediate community needs and while boat access to these coastal burns is possible in the summer, chainsaw harvesting during the winter is only feasible when deep snowpack covers the understory shrub vegetation and frozen sea ice, which is defined as critical infrastructure for the Nunatsiavummiut (Bell et al. 2014), allows for wood hauling via snowmachine. In more southern continental study locations, yearround road access allows large machinery to access recently burned forests and remove as much harvest wood as is needed (Greene et al. 2006).

Second, chainsaw harvesting in deep snowpack conditions would limit disturbance to the natural seedbed (Jean et al. 2019). When a site is harvested by large machinery, seedlings are more likely to be damaged through trampling (Donato et al. 2006; Royo et al. 2016). Site conditions may also become drier through soil compression and a reduction in available shade, thus exceeding the resilience capacity of the dominant tree species and favouring the establishment of drought tolerant grass and shrub species (Purdon et al. 2004; Greene et al. 2006). In northern Alberta for example, approximately half of the mid-successional aspen-dominated boreal forest stands that had experienced logging were associated with a greater presence of large shrub species when compared to mid-successional burned stands (Kurulok and Macdonald 2008). In Nunatsiavut, seedlings would not be damaged, as snowpack remains consistent across the site late into the spring and the remaining unharvested trees would ensure ample shade for growing seedlings. While these sites have undergone successive disturbances, compounding effects between fire and harvesting on boreal regeneration may be muted due to the conditions in which harvesting occurs. In the time frame of our study, we may assume that despite burned forest stands in Nunatsiavut being used as a fuel source for the communities, regeneration within the stand is more strongly controlled by a singular disturbance (i.e., fire) rather than the interaction between consecutive disturbances (i.e., fire and harvest). However, even less is known about the role of other ecological disturbances across the eastern subarctic (e.g., insect outbreaks, moose herbivory). It is important to reiterate that our study is limited to an analysis of winter wood harvesting, as it is the only practiced method in the region. While harvesting during other seasons may produce different results, we argue that any future research on the effects on a changing climate in northeastern coastal boreal forests may be interested in focusing research efforts on the effects of a changing fire regime rather than the interactive effects of fire and harvest when winter harvesting rates are low (i.e., < 35%).

Natural seedling regeneration two decades after fire and harvesting was less than 30% of the pre-fire stand density across all sites. While our results might be interpreted as a loss of ecosystem resilience and subsequent regeneration failure, based on previous work in Alaska (Johnstone et al. 2004) and southern Québec (Perrault-Hébert et al. 2017), we argue instead that our sampling occurred too early within a longer continuous regeneration window based on our age-reconstruction of the unburned stands. In western North America, stands that experience frequent fires (every 80-120 years) undergo pulse recruitment and have the majority of trees establish within the first decade after fire (Johnstone et al. 2004; Brown and Johnstone 2012). These trees rapidly grow to reproductive maturity and establish a large seedbank in advance of the next fire. Alternatively, in Scots pine (*Pinus sylvestris* L.) stands of northern Sweden, regeneration continues over several decades after fire, which is speculated to be a result of low fire frequency, where fires occur every 160-400 years (Steijlen et al. 1995). Multi-decadal regeneration has also been found to occur at treeline locations in northern Quebec (Sirois and Payette 1991), and western Labrador (Simon and Schwab 2005).

In addition to different fire frequencies, many of the fires that have been studied in western North America are also higher in severity, consuming much more of the organic layer that limits access to ideal substrate (Johnstone et al. 2004). Germination and successful seedling establishment is often reduced when fire severity is low, as is evident in our study system as well others (Jayen et al. 2007; Crotteau et al. 2013). Drawing parallels between climatic conditions (Hofgaard et al. 1991), fire frequency, and severity data presented in our study provide some evidence that these coastal boreal forests in Nunatsiavut may be more similar to coastal-influenced forests of northern Sweden and Nunavik (northern Quebec) rather than those of western and central North America. While we did not explicitly compare Eurasian and North American boreal forest, our findings may highlight essential differences between forests within boreal North America and illustrate our need to carry out research in under-studied coastal subarctic boreal ecosystems.

Despite seedling regeneration being low, changes in species richness was evident at two out of three sites. We attribute this increase in species richness to a fire induced change in microsite conditions (Kurulok and Macdonald 2008). Although we do not have comprehensive data comparing abiotic and biotic covariates between burned and unburned forests, which we acknowledge in our methods, we can rely on the literature to infer some fire-induced site-level changes in seedbed quality (Certini 2005). For example, soil conditions post-fire are drier as a result of increased runoff (Lukenbach et al. 2016) and evaporation from the black (low albedo) surface (Thompson et al. 2015). White spruce and balsam fir generally prefer drier soil conditions when compared to black spruce, and much like our study, have been found to increase in numbers after a fire (Kurulok and Macdonald 2008). In northern Quebec, low severity fires (mortality < 25%) were also found to have the highest tree species richness when compared to forest stands that experienced more severe fires (Purdon et al. 2004). From our organic layer data and the more northern geographic position of TBB and WBB, when compared to BRB, we could assume that these forests experienced even lower severity fires, which would provide further evidence for a change in tree species richness (Purdon et al. 2004), as well as the slow generation rate for all seedlings (Foster 1985). The spatial extent of both TBB and WBB fires were also much smaller than BRB. While pulses of tree species richness have been linked to anthropogenic and non-anthropogenic disturbance events in Nunatsiavut (Roy et al. 2017), the question of species richness and post-fire succession in Nunatsiavut needs to be explicitly addressed to reach a more definitive conclusion on changes in species richness post-disturbance.

Contrary to our hypothesis, the abundance of tall multi-stemmed shrubs (TMS) had differential effects on seedling abundance, depending on the pre-fire structural characteristics of the forest stand. When TMS were low to mid abundance (TMS < 30%), there was a positive association with seedlings. This association may indicate interspecies facilitation, whereby shrubs provide more suitable microclimates for seedlings through increased shade availability and soil moisture retention (Perkins 2015). These findings are similar to experimental seeded plots in southern Spain, where emergence and survival of Scots pine seedlings were highest under shrub canopy (Castro et al. 2004). In Labrador, interspecific facilitation of black spruce has also been found to occur with the presence of feathermoss (*Pleurozium sp.*; Wheeler et al. 2011). The relationship between TMS and seedling density becomes negative when high percent cover of TMS (TMS > 30%) interacts with dense pre-fire basal area. The interaction term may signify a switch from interspecies facilitation to competition, where higher-density stands would have fewer suitable spots for both shrub and boreal tree seedling regeneration, facilitating a transition towards a landscape dominated by rapidly establishing shrub species (Cranston and Hermanutz 2013). Manipulative shrub field studies in northern Swedish boreal forests have found that increased bilberry (*Vaccinium myrtillus* L.) is associated with lower densities of Norway spruce (*Picea abies* L.), as a result of below-ground resource competition (Jäderlund et al. 1997). Because shrub species are typically rapid colonizers after a disturbance due to their nitrogen fixing and vegetative resprouting structures (Simon and Schwab 2005; Lantz et al. 2010) we can assume that if space (both below and aboveground) and resources, including light, are limited, shrub species would likely outcompete tree seedlings, which may result in a successional trajectory change in the post-fire landscape.

Yet, if we ascribe to our sampling occurring too early in the continuous regeneration window, the relationship between TMS and seedling abundance may not be evidence of interspecies competition, but rather represent a successional stage in eastern subarctic boreal development. In western boreal forests, burned substrate is rapidly colonized by nitrogen fixing alder species (Lantz et al. 2010) and deciduous tree species, such as aspen and birch (Landhausser and Wein 1993). These shade-intolerant species are succeeded by coniferous species once they grow above the shrubs and begin to shade them out. While there is no evidence to suggest an increase in deciduous tree species two decades after fire in Nunatsiavut, TMS shrubs may represent the early successional species. Once again, if we draw comparisons to Swedish boreal forests, we find that dwarf ericaceous shrub cover (including *Empetrum hermaophroditum* Hagerup. and *Calluna vulgaris* L.) represent dominant successional species (cover ≥ 50%) a few decades after fire, followed by slow increase in Scots pine density (DeLuca et al. 2002). In our case, TMS shrub cover (including *Vaccinium* and *Salix* spp.) may represent early successional species followed by a slow increase in black spruce.

In conclusion, our study provides evidence to suggest that despite the low number of natural seedlings two decades after fire, current chainsaw harvesting rates by Nunatsiavummiut after fire do not represent a significant effect on boreal tree regeneration. We acknowledge our sampling scheme is small as a result of weather-related time constraints and boat-only access. The size of our study should be considered when interpreting our results, especially when comparing species richness of burned and unburned forests, as some unknown ecological factor may make the locations incomparable. Nevertheless, our results represent an important first step in providing context to forest regeneration in eastern coastal boreal forests that are commonly used by the Nunatsiavummiut.

While there is an indication that forest resilience has been lost and tall multi-stemmed shrub species are out-competing boreal tree seedlings for space and resources, the question of whether this is in fact the case, needs to be explicitly addressed. Determining whether these forest stands are undergoing a successional trajectory change after fire can be determined in several ways. First, a larger chronosequence of fires that occurred in coastal Nunatsiavut 50-200 years ago could be established to determine whether large shrubs still represent a dominant species in the post-fire landscape. Second, we need to investigate the reproductive potential at these sites. A multi-year latitudinal transect examining inter-annual cone production and seed viability would provide us with a better understanding of the capacity in which these coastal forests are able to regenerate after a large-scale disturbance. And finally, albeit challenging, these sites could be monitored over the next several decades to review decadal seedling growth and presence. If seedling density remains low, perhaps conditions have changed, and these forests may be experiencing a successional change.

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Chapter 5: Conclusion

5.1 Summary

Northern plant communities are experiencing more extreme environmental conditions with continued climate change (Dale et al., 2001; Martin, Jeffers, Petrokofsky, Myers-Smith, & MacIas-Fauria, 2017; Myers-Smith et al., 2020). Longer growing seasons have increased plant moisture stress (Stevens-Rumann et al., 2018), while changes to winter snow cover have exposed plants to more intense weather conditions (Mamet & Kershaw, 2013; Mayr, Cochard, Améglio, & Kikuta, 2007). These changes are more pronounced across the subarctic, where increases to surface air temperatures are occurring at a rate three times the global average (Bush & Lemmen, 2019). Simultaneously, climate change has altered the frequency, severity, and extent of natural and anthropogenic disturbances (Hanes et al., 2019; Navarro, Morin, Bergeron, & Girona, 2018; Seidl et al., 2020). Despite disturbances being an integral part of biodiversity, changes to disturbance regimes have applied further pressure to the resilience of plant communities within subarctic ecosystems (Johnstone et al., 2016). As a result, a warming climate coupled with a change in disturbance regimes have been predicted to result in a rapid successional shift in northern ecosystem structure and function (Bölter & Müller, 2016; Buma, Brown, Donato, Fontaine, & Johnstone, 2013; Reyer et al., 2015).

In some regions of the subarctic, observational and experimental evidence has supported the prediction that changing disturbance regimes driven by climate change are altering the successional trajectory of terrestrial ecosystems (Johnstone et al., 2020; Travers-Smith & Lantz, 2020). A change in wildfire frequency has shifted black spruce forest stands to shrub and grass dominated landscapes in both Alaska (Johnstone et al., 2020) and Yukon (Brown & Johnstone, 2012). Similarly, in northern Quebec, increased post-wildfire wood harvesting has shifted recruitment towards a greater density of deciduous tree species (Bouchard & Pothier, 2011). These shifts in ecosystem states can be attributed to a loss of ecological inertia, either through a change in reproductive potential (i.e., loss of available seed) or microsite conditions for seedling germination and establishment (Buma et al., 2013).

Yet, successional changes to northern plant communities have been non-uniform across the subarctic (Bret-Harte et al., 2013; Zhou, Liu, Jiang, Feng, & Samsonov, 2019). This variable response in succession from climate warming is best illustrated at the boreal-tundra treeline ecotone, where range expansion of boreal tree and shrub species have not matched climate-based model predictions (Harsh et al., 2009). Therefore, it has been speculated that some current plant communities within the subarctic are resistant to change (i.e., high ecological inertia) even when exposed to new or changing disturbance regimes (Folke et al., 2004; Johnstone et al., 2016; Stralberg et al., 2020). However, a recent meta-analysis performed by Lett & Dorrepaal (2018) on the current understanding of global drivers of seedling establishment at alpine treelines indicated that research on the effects of disturbance (e.g., herbivory, fire, wind, and freezing) on seedling establishment is extremely limited (i.e., less than ten out of 366 experimental and observational papers). Thus, the aim of my thesis was to reduce the knowledge gap of how disturbances influence boreal tree succession at their northern range edge of the Canadian subarctic. Specifically, my thesis examined how wildfires (Chapter Two), insect granivory (Chapter Three), and anthropogenic wood harvesting (Chapter Four) influence biotic and abiotic conditions and whether they promote or inhibit seed germination and seedling establishment. At the northern boreal range edge, these disturbance regimes are considered novel or anticipated to change under continued climate warming (Lantz, Gergel, & Henry, 2010; Leverkus et al., 2018; Pureswaran, Roques, & Battisti, 2018). While research discussed in Chapter Four is framed as being conducted within the eastern subarctic coastal boreal forest, study sites were still considered range edge populations as they were located in close proximity (< 2 km) to elevational treeline.

My research helps to fill the significant knowledge gap of how disturbances at the boreal-tundra treeline ecotone influence early-life stage tree recruitment. Specifically, I provide a broad spatial understanding of the many microsite conditions that seeds and seedlings are exposed to at treeline post-disturbance, as my research was conducted in remote and understudied regions across the Canadian subarctic. Although I examined three different disturbances, all data collection followed similar protocols to establish a large database of post-disturbance microsite conditions for subarctic ecosystems. In each study, understory vegetation was recorded to functional group, ensuring that data can be easily incorporated into global models of vegetation change (Neilson et al., 2005; Vanneste et al., 2017). Furthermore, data collection for insect granivory provided a broad spatial understanding of spruce tree fecundity at treeline, which has recently been highlighted as an essential predictor variable when modeling future boreal tree range expansion (Brown et al., 2019; Wang, He, Thompson, Spetich, & Fraser, 2018).

5.2 Key findings and future research directions

Successful tree recruitment consists of several steps, each accompanied by a number of hurdles that need to be overcome in order to advance to the next life stage (Holtmeier, 2009, Evans & Brown, 2017, Crofts & Brown, 2020). At earlier life stages of boreal tree species, resource availability and interspecies competition represent examples of significant hurdles for the production and dispersal of viable seed, as well as the germination and establishment of seedlings (Munier, Hermanutz, Jacobs, & Lewis, 2010; Tingstad, Olsen, Klanderud, Vandvik, &

Ohlson, 2015). Under the context of range expansion, these early-life stages may also experience additional hurdles for potential recruitment, as they are required to overcome the ecological inertia of the uncolonized ecosystem state (Holtmeier, 2009; Buma et al., 2013; Crofts & Brown, 2020). Despite a reduced climatic hurdle from continued climate warming, results from my thesis suggest that within the study years, wildfire, insect granivory, and wood harvesting at the northern boreal range edge are not severe enough disturbances to reduce the ecological inertia of the current plant communities. Thus, I speculate that disturbances of lower severity do not prime the landscape for range expansion of boreal tree species at my study locations.

Within the boreal forest, moderate to high severity wildfires are required to create microsite conditions that are suitable for increased seedling establishment (Turner, Romme, & Gardner, 1999). High severity wildfires increase the combustion of the organic layer, facilitating greater seed access to mineral soils that are high in nutrients and soil moisture (Shenoy, Kielland, & Johnstone, 2013). Suitable microsite conditions for seed germination also need to occur at the treeline ecotone to facilitate range expansion; yet, observational evidence from my research in Yukon and the coastal boreal forest stands of Nunatsiavut show these conditions did not occur, as all wildfires were of low severity. As a result, low seed germination and seedling establishment were observed. This low level of germination and establishment suggests that wildfires did not disrupt the ecological inertia of the current ecosystems enough to support increased boreal tree recruitment. While predictive models have shown how wildfire distribution will change across the subarctic under climate change (Hanes et al., 2019; Soja et al., 2007), much of the literature predicting changes to wildfire severity has occurred in western USA forests (Doerr & Santín, 2016, except see Guindon et al., 2020). Therefore, an important future research direction is to examine changes in wildfire severity across the subarctic. This more robust understanding of wildfire severity would support better predictions of successional dynamics at the northern boreal range edge. Specifically, predicting changes to wildfire severity would support boreal treeline range expansion models by determining where range expansion may occur if subjected to higher severity wildfires. A better understanding of wildfire severity will also help determine whether wildfires in coastal Nunatsiavut will increase in severity and act as a negative feedback for boreal tree regeneration, as tree seed access to suitable microsite conditions may increase.

Despite the known negative impacts on individual trees within a forest stand by insects (Pureswaran et al., 2018) and post-disturbance wood harvesting (Bouchard & Pothier, 2011), model results of both insect granivory and post-wildfire wood harvesting showed no significant relationship with availability of viable seed and seedling establishment, respectively. Similar to my wildfire research findings, I speculate the impact of these disturbances were not severe enough to reduce the ecological inertia of the present ecosystem. Post-wildfire harvesting in more populated areas of the boreal forest has been associated with a shift in successional trajectory, as harvesting efforts remove upwards of 90% of the standing dead trees (Boucher, Gauthier, Noël, Greene, & Bergeron, 2014; Kishchuk et al., 2015). In Nunatsiavut, the process of chainsaw harvesting by snowmobile limits the number of trees that can be removed from a site. Furthermore, winter harvesting reduces microsite damage, as heavy snowpack protects the ground surface during wood harvesting. Similarly, as severe insect outbreaks are often associated with successional change (Landry, Parrott, Price, Ramankutty, & Damon, 2016), chronic pressures at the boreal range edge may not represent a biotic disturbance that significantly reduces the availability of viable seed, even at the treeline ecotone where seed production is limited. Nevertheless, seed viability research conducted within my thesis was carried out on a subset of seeds; therefore, future research is required to determine whether these viability rates are consistent across a much larger area. The effects of both wood harvesting and insect granivory during my years of study were muted and therefore may not play a significant role in changing the resilience of the current ecosystem. A longer temporal analysis of these disturbances is required to determine if their severity changes through time.

In addition to the low-severity of all disturbance regimes, a common thread between wildfires at treeline, insect granivory at treeline, and wood harvesting in Nunatsiavut was the presence and influence of shrub cover on boreal tree recruitment. I speculate that low severity wildfires in forest stands coupled with a shrub dominated understory may lead to a post-disturbance increase in shrub cover, representing either a shift in successional trajectory (discussed in Chapter Two) or a natural early successional stage (discussed in Chapter Four). Shrub cover was also associated with the reduced presence of insect granivory, which could provide spatial information on where this biotic disturbance may be greater in magnitude across the boreal-tundra treeline ecotone. As changes in shrub cover are anticipated across the subarctic (Myers-Smith et al., 2020), their role in ecosystem resilience post-disturbance needs to be further examined (Travers-Smith & Lantz, 2020). Evidence in both boreal and tundra plant communities have already shown a shift towards a shrub dominated landscape post-wildfire (Brown & Johnstone, 2012; Lantz et al., 2010); therefore, it is extremely likely that shrubs will play a dominant role in shaping subarctic landscapes under continued climate change (Myers-Smith et al., 2020). An important future research direction on subarctic ecosystem resilience is an examination of alternate pathways of successional trajectory change. Specifically, resilience research needs to examine whether post-disturbance landscapes will shift towards a shrub dominated landscape rather than return to the previous forested ecosystem structure and function.

My results also revealed how variable microsite conditions can be, as well as highlight their importance for the establishment of early-life stage boreal tree species. While site-level data collection in Chapter Two occurred within an approximate 0.8 ha area (0.4 ha at burned and unburned treelines), observational evidence of biotic and abiotic conditions exhibited a high degree of variability. These results further support the idea that while climate may be suitable for range expansion of boreal tree species, site conditions that increase the success of recruitment are limited even after experiencing a disturbance (Johnstone et al., 2016). Similarly, in Chapter Three, data collection at each site occurred within a short 75 m x 10 m belt transect, but model results indicated stand density and moss cover were positively associated with magnitude of insect granivory. As stand density and moss cover varied greatly within each site, a better spatial knowledge of these site characteristics may broaden our understanding of this biotic disturbance, which could increase our predictive capabilities in locating future insect outbreaks. Ultimately, an increased understanding of microsite conditions across the subarctic will improve our predictive modeling capabilities of ecosystem resilience, especially when incorporated into climate change models (Neilson et al., 2005).

While my research does not include the impacts of herbivory from birds and other mammals on boreal range expansion at the treeline ecotone, these biotic disturbances occur both prior to and after seed dispersal, and are known to play a critical role in boreal tree recruitment (e.g., see Brown & Vellend, 2014; Davis & Gedalof, 2018; Hargreaves et al., 2019; Hulme, 1996; Kolstad, Austrheim, Solberg, Vriendt, & Speed, 2018). Across mountainous areas of Europe and North America, browsing by large ungulates has a strong negative influence on tree growth, which can slow cone production and limit available seed (Angell & Kielland, 2009; Kolstad, Austrheim, Solberg, Vriendt, & Speed, 2018; Speed, Austrheim, Hester, & Mysterud, 2010). Additionally, bird species can further limit seed availability prior to seed dispersal by feeding on seeds of existing cones or hoarding them in seed caches (Tomback, 2005). Across the boreal forest, seedling browsing and post-dispersal seed herbivory is heavily controlled by hares (*Lepus timidus, Lepus, americanus*), squirrels (*Sciurus* spp., *Tamasciurus* spp.), and other small rodents (Holtmeier, 2012). In non-masting years, these species have the ability to remove most viable seed from a forest stand (Boutin et al., 2006; Brown & Vellend, 2014; Frei et al., 2018). All of these biotic disturbances are anticipated to change under continued climate warming (Holtmeier, 2012); yet research on how biotic disturbances like herbivory influence early life-stage development of boreal tree species at treeline remains limited (Lett and Dorrepaal, 2018). Incorporating the effects of bird and mammalian herbivory on tree recruitment therefore represents the next logical step in understanding how disturbances influence the boreal tundra treeline ecotone.

Ultimately, my research findings support initiatives by local and territorial government agencies, as well as conservation groups, to better understand the impacts of climate change on disturbance regimes and subarctic ecosystems. The baseline knowledge I provide on how disturbances impact successional dynamics of the northern boreal range edge will directly support current and future conservation efforts aimed at identifying essential habitat for barren-ground caribou (*Rangifer tarandus*). Caribou represents a species that holds significant ecological and socioeconomic importance within the subarctic (Joly, Duffy, & Rupp, 2012; Mallory & Boyce, 2018). At the boreal-tundra treeline ecotone, large herds exert significant grazing pressures on plant communities and provide a substantial food source for large predators. They also play an important role in Northern recreation (e.g., tourism, hunting) and subsistence harvesting. While wildfire is predicted to influence the short-term seasonal migratory routes of caribou populations (Mallory & Boyce, 2018), results from Chapter Two indicate the ecological inertia of the tundra plant community may be maintained by low-severity fires, limiting the long-term impact on essential caribou habitat. Nevertheless, increased productivity of shrubs (Chapter Four) may improve habitat quality for moose, which may increase resource competition among large ungulate herbivores (Sharma, Couturier, & Côté, 2009)

5.3 Research limitations

While there are several temporal and spatial limitations to my research, most of them were sufficiently addressed. While I was successful in completing an extensive spatial analysis of the many biotic and abiotic mechanisms that can influence early-life stage boreal tree and shrub establishment success post-disturbance, climate at the northern range edge of the boreal forest remains a fundamental control on viable seed production, seedling establishment, and tree growth (Holtmeier, 2009). As a result, any assessment of recruitment potential conducted within a short time period does not sufficiently capture interannual climate variability. The frequency, extent, and severity of natural and anthropogenic disturbances also changes with interannual climate variability (Dale et al., 2001; Stevens-Rumann et al., 2018). Thus, early-life stages will be exposed to different degrees of disturbance pressures and severities over time. Despite not collecting interannual data, my research represents a “snapshot in time” and provides an essential spatial analysis required to further understand the relationship between changing disturbance regimes and subarctic ecosystem resilience. Long-term monitoring is essential to disentangle the effects of interannual climate variability from site conditions on boreal tree and shrub establishment at their range edge (Brown, Liu, Yan, & Johnstone, 2015).

Like most northern ecology field research, my analyses were limited by the remote nature and geographic location of each study. Conducting field-based research in Yukon and Nunatsiavut during a three-year period posed some logistical challenges, yet all established research sites, especially those described in Chapter Two, can be used as long-term monitoring sites and will provide baseline data for future ecological studies. Furthermore, research conducted in Nunatsiavut supported interdisciplinary research on permafrost dynamics (Wang, 2020), and subsistence food resource availability (Dwyer-Samuel, Hermanutz, & Cuerrier, unpublished data), which provided a more robust analysis of environmental change in the understudied coastal forests of eastern subarctic. For Chapter Three, I wanted to reach as many treeline ecotones as possible, which required me to establish a collaborative project. As this research was considered an additional component to my collaborator's field research programs, I reduced the amount of time that was required for data collection, thereby decreasing data resolution. Nevertheless, successful data collection to support model development was completed. I am hopeful that, as a result of a well-defined data collection protocol for Chapter Three, this research will continue into the future and provide a better spatial and temporal understanding of insect cone granivory.

5.4 Conclusion

The effects of climate change-driven disturbance regimes are anticipated to impact the resilience of subarctic ecosystems. My research conducted across the Canadian subarctic, however, indicated that the severity of disturbances at the treeline ecotone was muted, suggesting the ecological inertia of the current plant community is maintained. I therefore speculate that while climate may create conditions suitable for boreal tree range expansion, a disturbance induced shift in the successional trajectory is unlikely to occur at these research locations. My research increased our spatial understanding of the impacts that disturbances can have on life-stage boreal tree regeneration through standardized data collection protocol. Nevertheless, as a result of my research questions and study designs, my ability to address regional patterns is somewhat limited; thus, increased efforts to further understand disturbances of different severities across the subarctic are warranted. Future research should also include the possibility of alternate successional trajectories rather than assume a return to the previous ecosystem state is more probable, as increased in shrub cover will likely play an important role in future post-disturbance landscapes.

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