Assessing ecological barriers to black spruce regeneration and forest management in Terra Nova National Park, NL

by © Ellise Lauren Proctor

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Abstract

Terra Nova National Park (TNNP) is dominated by black spruce, which relies on fire to release its seeds and reduce soil organic matter (SOM) thickness for successful regeneration; however, active fire suppression in TNNP has greatly reduced black spruce regeneration over the last century. As a result, TNNP has few young stands and a significant representation of over-mature stands. Additionally, *Kalmia angustifolia* establishes without fire and actively excludes black spruce via various competitive mechanisms, which has caused several areas in TNNP to convert from black spruce stands to *Kalmia* heaths. TNNP has attempted to introduce prescribed fire as one of their management strategies to resolve these issues; however, there are limitations to this management. TNNP is highly interested in alternative management considerations to promote black spruce regeneration; however, to make informed management decisions, TNNP must determine the spatial distribution of two key ecological factors, black spruce seed viability and seedbed quality. We investigated 28 sites and evaluated tree age, seed viability, seedbed quality (*i.e.,* SOM and seedbed type), natural black spruce regeneration, and *Kalmia* presence. Our results identified a strong age-reproduction relationship, an influence of seedbed quality on black spruce regeneration, and the potential for *Kalmia* to interfere with black spruce establishment. By assessing these relationships, we geographically mapped the reproductive potential of black spruce in TNNP. The information collected and analyzed in this project provides a more in-depth understanding of TNNP's black spruce regeneration, directly contributing to TNNP's boreal forest management.

Keywords: forest ecology, population dynamics, conservation management, seed production, seedbed, *Picea mariana*, *Kalmia angustifolia*, Newfoundland

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Land acknowledgement

I respectfully acknowledge that this research took place on Ktaqmkuk, the island of Newfoundland, as the ancestral, unceded homelands of the Beothuk and Mi'kmaq.

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List of Acronyms

CNF	Central Newfoundland Forest
ECM	Ectomycorrhizal
NSF	North Shore Forest
RAD	Resist-Accept-Direct
SOM	Soil organic matter
TNNP	Terra Nova National Park

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Co-Authorship Statement

Dr. Carissa Brown is a co-author of all chapters of this thesis. As the primary author, I have been the primary researcher for the literature review, research proposal design, logistical project planning, field and laboratory work, data analysis, and manuscript preparation. This project was completed in collaboration with Dr. Carissa Brown, who contributed to project design and conceptualization, data analysis, and manuscript preparations.

Chapter 1: Introduction and thesis overview

1.1 Introduction

1.1.1 Boreal forest and fire

The boreal forest covers approximately 30% of the Earth's forested areas (Gauthier et al., 2015). The majority is found across Canada, Russia, Nordic countries (i.e., Finland, Sweden, and Norway), and the northern regions of the United States (i.e., Alaska; Figure 1.1; Burton et al., 2010). In Canada, the boreal forest covers approximately 56% of the land area, thus making this landscape the largest biome in Canada (Burton et al., 2010). The boreal forest is characterized by relatively few tree species, predominantly conifers, including pines (*Pinus* L. spp.), spruces (*Picea* Mill. spp.), firs (*Abies* Mill. spp.), and larches (*Larix* Mill. spp.), with deciduous species including poplars (*Populus* L. spp.), birches (*Betula* L. spp.), willows (*Salix* L. spp.), and alders (*Alnus* Mill. spp.; Burton et al., 2010).

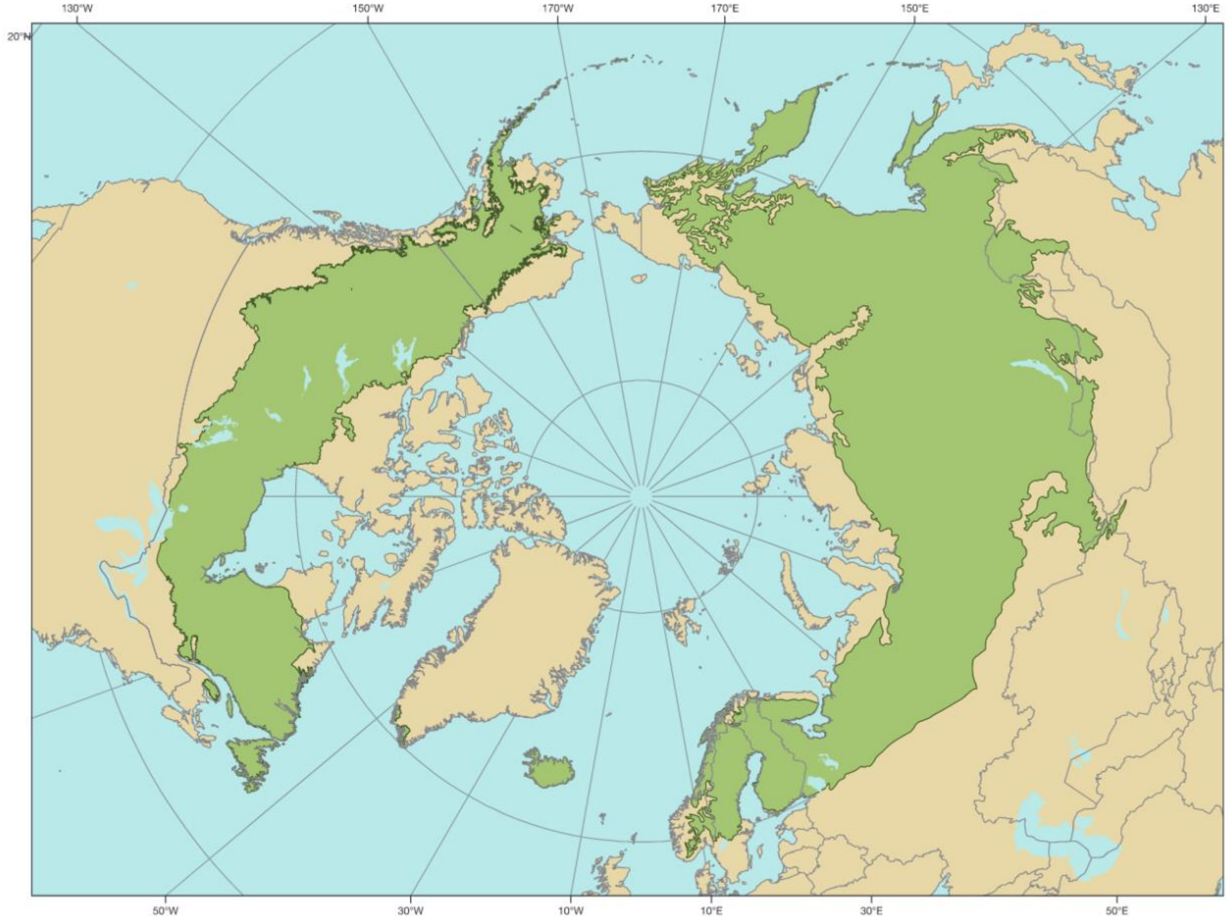

Figure 1.1 Global distribution of the boreal forest (source from Brandt et al., 2013).

The boreal forest is ecologically, economically and culturally significant. It is important in the global carbon cycle, storing more than one-third of the Earth's terrestrial carbon in the organic soil and above-ground biomass (Kasischke et al., 2000). Additionally, the boreal forest plays a massive role in the economic sector (Hart and Chen, 2008). Nearly two-thirds of the Earth's boreal forests are considered to be managed primarily for timber harvesting, and specifically in Canada, around 35 to 40% of the boreal forest is managed (Gauthier et al., 2015). Various harvesting approaches (e.g., shelterwood cutting) can create a stand age heterogeneity across the landscape and promote biological diversity (Hart and Chen, 2006; Savilaakso et al., 2021); however, traditional harvesting management (e.g., clear-cutting) can cause stand homogenization and decreased stand age, resulting in less biological and structural diversity (Venier et al., 2014; Savilaakso et al., 2021). Resource exploration and extraction (e.g., mining, oil, gas and hydroelectricity) have also occurred in the boreal forest. These activities have negatively impacted forest health, such as air, water and soil pollution (Brandt et al., 2013). In Canada, more than 4 million people reside within the boreal forest region, including many Indigenous communities (Uprety et al., 2012). The boreal forest provides critical ecosystem services to those communities, such as fishing, hunting and spiritual activities (Gauthier et al. 2015).

Various types of ecological disturbances, such as fire, insects, and wind, have been an essential part of the dynamics of the boreal forest landscape but have changed significantly with climate change (Flannigan et al., 2009; Shorohova et al., 2011). Fire is arguably the most important ecological disturbance (Bowman et al., 2009) and plays a key role in several ecological processes, including regeneration (Charron and Greene, 2002), plant community structure (Bergeron et al., 2002), and nutrient cycling (Simard et al., 2007); however, insect outbreaks can reduce the carbon sequestering ability of the boreal forest by half (Pan et al., 2011). In North America, the boreal forest has long been adapted to fire as a natural disturbance (Coogan et al., 2021), and those fire regimes vary spatially in size, frequency, timing, and intensity due to climate and vegetation (Flannigan et al., 2009; Coogan, 2021). Western North American boreal regions experience shorter fire return intervals (i.e., fire occurring in the same area) of around 80-150 years (Viereck, 1983; Larsen, 1997), whereas eastern boreal regions experience longer fire return intervals of 270-500 years (Bouchard et al., 2008). Specifically, the island of Newfoundland (hereafter referred to as Newfoundland) is estimated to experience stand-replacing fires every 769 years (Arsenault et al., 2016); however, more recent estimates suggest broader landscapes on the island experience fire every 150 years (e.g., a fire occurred within the boundary of Terra Nova National Park every 150 years; Walker, 2021). Although there are little data available on the island's historic fire regime (Simpson, 2007), anthropogenic fires are prevalent. From 1961 to 2017, park management recorded 31 fires within and adjacent to Park boundaries, with 15 being caused by human activities within the Park (Simpson, 2007; Walker, 2021).

Dominant tree species within the boreal forest, such as jack pine (*Pinus banksiana* Lamb.) and black spruce (*Picea mariana* (Mill.) B. S. P.), have evolved with fire and have developed fire-specific adaptations to survive and thrive following a fire disturbance (Zasada et al., 1992; Greene et al., 1999). These adaptations include serotinous cones, aerial seed banks, and resprouting from roots (Greene et al., 1999; Bouchard et al., 2008).

1.1.2 Black spruce

Black spruce is one of the most dominant tree species in the Canadian boreal forest (Viereck and Johnston, 1990). This long-lived species is found across North America, ranging from northern areas of the United States to northern Labrador on the east coast and across Canada to the west coast of Alaska (Figure 1.2; Viereck and Johnston, 1990). Due to its extensive geographic range, black spruce can tolerate a broad range of environmental conditions (Viereck and Johnston, 1990). Black spruce can tolerate extreme temperature ranges from -62°C to -34°C and from 27°C to 41°C, annual precipitation ranges from 1520 mm in the Maritimes to 150 mm in Alaska, and growing seasons with continuous light near the Arctic Circle to 16 hours of summer daylight near its southern limits (Viereck and Johnston, 1990). Black spruce usually grows on wet organic soils and prefers acidic soils; however, productive stands can be found on various soil types and pH levels (Viereck and Johnston, 1990; Fryer, 2014). One of the most noticeable aspects of many black spruce stands is the almost continuous growth of feathermosses (i.e., *Hylocomium* Schimp. spp.) and sphagnum mosses (*Sphagnum* L. spp.) as the seedbed type (Viereck and Johnston, 1990). Black spruce is economically essential for timber harvesting (Lee et al., 2017) and ecologically for carbon sequestration (Dunn et al., 2007; Walker et al., 2020). Additionally, this species is vital for many wildlife species at different successional stages. For example, newly burned black spruce stands provide foraging opportunities for birds and snags for cavity nesters. Furthermore, moose (*Alces alces* L.), snowshoe hares (*Lepus americanus* Erxleben), wolves (*Canis lupus* L.), and woodpeckers (*Picidae* Leach spp.) use early black spruce successional stands post insect and fire disturbances (Labadie et al., 2021). In contrast, American martens (*Martes americana* Turton), woodland caribou (*Rangifer tarandus caribou* Gmelin), and red squirrels (*Tamaiaciurus hudsonicus* Erxeben) use late postfire stages for food and habitat (Fryer, 2014; Viereck and Johnston, 1990).

Figure 1.2 Black spruce population distribution in North America (source from Fryer, 2014).

Fire plays a critical role in black spruce regeneration and, as a result, black spruce has evolved fire-specific adaptations, such as a semi-serotinous regeneration strategy, to facilitate successful regeneration following a disturbance. Black spruce accumulates semi-serotinous cones in an aerial seed bank, which allows for a large number of seeds to be stored in resin-sealed cones on the tree for multiple years. When a fire occurs, the heat melts the sealing resin, which triggers the cones to open (Greene et al., 1999). Black spruce releases the majority of its seeds within two years following a fire disturbance with a seed dispersal range of ~ 80 m

(Prévost, 1997), and seedling establishment begins immediately after seed release (Moss and Hermanutz, 2009). Although black spruce heavily relies on fire to open its cones, it is not completely necessary, hence their classification as semi-serotinous. In the absence of fire, the resin slowly breaks down, and the cones open, which releases small amounts of seeds over time (Zasada et al., 1992; Brown and Johnstone, 2012). However, the number of seeds released after fire is far more significant than those released over time, resulting in higher regeneration rates (Viereck, 1979). Furthermore, more viable black spruce seeds are required for successful regeneration on thick SOM seedbeds than on thin SOM seedbeds with exposed mineral soil (Johnstone and Chapin, 2006).

Fire return intervals vary across Canada (80 to 300+ years; Viereck, 1983; Larsen, 1997; Bouchard et al., 2008; Arsenault et al., 2016). Black spruce is slow growing and often occurs in nutrient-poor sites, meaning they require long periods to produce enough cones and seeds to self-replace after fire (Viglas, 2011). Individual black spruce age dramatically affects the production of cones and seeds. Black spruce can begin producing cones and viable seeds as young as 20 years old (Viglas et al., 2013); however, climatic factors and resource availability can impact the production age. In the northwest boreal forest of North America, 90-95% of mature black spruce stands (> 100 years old) produced cones and viable seeds, compared to only about 60% of younger black spruce stands (~ 50 years old; Viglas et al., 2013). Where cones were produced in younger stands, seed production was too low to ensure post-fire regeneration (Viglas et al., 2013). Thus, black spruce stands are prone to immaturity risk, where a stand fails to regenerate when it experiences fire prior to producing enough viable seed for self-replacement (Brown and Johnstone, 2012).

Although mature stands have higher seed viability and more seeds in the aerial seed bank, as black spruce ages, the production of viable seeds starts to decline due to lower productivity levels (~ > 200 years old; Greene et al., 1999; Greene and Johnson, 1999). In some areas, asexual vegetative reproduction (i.e., layering) becomes the primary regeneration mode (Morneau and Payette, 1988; Greene et al., 1999). Layering is a natural asexual mode of black spruce regeneration and occurs when the lower branches touch the forest floor and establish roots to create new, genetically identical stems (Viereck and Johnston, 1990; Greene, 1999). This reproduction method is significant in old-growth stands, areas where rapidly growing mosses cover the lower branches, poor nutrient stands, tree line, and areas with long fire-free periods (Morneau and Payette, 1988; Viereck and Johnston, 1990). Layering can play a significant role in black spruce regeneration by maintaining the population when environmental conditions are unsuitable for seed regeneration (Greene et al., 1999; Viktora et al., 2011).

Fire not only triggers black spruce seed dispersal; it also creates a suitable seedbed for black spruce germination and emergence. An undisturbed forest floor is a poor-quality seedbed for regeneration due to the thick, porous layer of soil organic matter (SOM) that desiccates quickly (Charron and Greene, 2002; Johnstone et al., 2008). Feathermosses and sphagnum mosses are the most common seedbed types in mature black spruce stands. However, these seedbed types can hinder black spruce seed germination. Feathermosses may provide a suitable seedbed during wet years, but they are unreliable and usually dry out before penetration by the seed root (Viereck and Johnston, 1990). Sphagnum mosses provide a continuously moist seedbed, but the growth of seedlings may be slow due to a poor supply of nutrients (Viereck and Johnston, 1990). Fire substantially reduces SOM thickness and burns seedbed, which significantly improves the quality of the seedbed by exposing mineral soil (Johnstone and

Chapin, 2006; Greene et al., 2007). The optimal seedbed for black spruce regeneration is exposed mineral soil and less than a few centimetres of SOM (i.e., 2 to 10 cm) on the forest floor (Greene et al., 1999; Greene et al., 2004; Johnstone and Chapin, 2006). This preferred seedbed is rich in necessary nutrients and maintains more consistent moisture levels, which prevents black spruce seeds from desiccating (Prévost, 1997; Johnstone et al., 2008). Ultimately, this improvement in seedbed quality is a critical factor for black spruce regeneration (Mallik and Kayes, 2018).

Black spruce experiences both insect damage and diseases. The eastern spruce budworm (*Choristoneura fumiferana* Clemens) is one of the most damaging insects to black spruce (Viereck and Johnston, 1990). Historically, the spruce budworm was not as harmful to black spruce as to balsam fir (*Abies balsamea* (L.) Mill) since black spruce budbursts occur later in the season; however, black spruce does appear to offer better overwintering habitat than balsam fir (Moise et al., 2023). Rising temperatures due to climate change are also expected to push the budworm range limit further north and cause black spruce to budburst earlier, which will phenologically synchronize with the budworm emergence, causing an increase in black spruce defoliation during outbreaks (Bellemin-Noël et al., 2021). Moreover, the eastern dwarf mistletoe (*Arceuthobium pusillum* Peck) is a destructive disease of black spruce near the Great Lakes and eastern Canada. It can result in reduced vigour, clumped trees, deformed trees and sometimes death (Viereck and Johnston, 1990). Other diseases that are not as damaging include rusts of the genus *Chrysomyxa* Unger, such as cone rust (*Chrysomyxa pirolate* Wint.), and needle cast fungus (*Lophodermium* Chevall. spp.; Viereck and Johnston, 1990).

Black spruce is susceptible to climate change, specifically in central, western and northern Canada, since fire regimes are increasing in intensity, severity, size and frequency due to rising temperatures (Wang et al., 2022b). Climate-induced increases in fire activity can lead to post-fire regeneration failure, as discussed above, when fire-free intervals allow insufficient time for regenerating individuals to produce sufficient cones and seeds (Baltzer et al., 2021; Hart et al., 2019). On the other hand, black spruce also experiences fire suppression via forest management, leading to black spruce regeneration failure due to poor seedbed quality (Simard et al., 2007) and reduced viable seed rain from the aerial seed bank (Viereck, 1979; Zasada et al., 1992).

1.1.3 Fire management in Canada

Fire suppression has been, and still is, an active management practice across Canada (Ryan et al., 2013; Coogan et al., 2021). Historically, Indigenous People have long used Traditional Knowledge of fire as a beneficial tool for landscape modification to support their subsistence lifestyle (Christianson, 2015; Normand et al., 2017). However, European colonization and the development of protected areas (e.g., national parks) limited the ability of Indigenous People to access their ancestral Lands and therefore prohibited Indigenous burning (Wang et al., 2022a). Additionally, extensive fire suppression was implemented in the 20th century as fire was perceived as a destructive force (Ryan et al., 2013), and it was primarily implemented to protect humans, infrastructure, and commercially valuable forests (Cumming, 2005; Hope et al., 2016). As a result, areas that would have historically burned were no longer experiencing fire (Cumming, 2005). Ultimately, this led to altered fire regimes resulting in negative ecological consequences, such as less diverse stand age, structure, and species (Wang et al., 2022a), and a lack of regeneration of fire-adapted species (Simard et al., 2007). Additionally, when fire is absent from a system for too long, a build-up of flammable biomass (e.g., leaf litter, grasses, and trees) can occur, which can lead to more extensive and intensive fires, posing a fire risk to communities, property and ecosystems (Ryan et al., 2013; Parisien et al., 2020).

In 1968, the Canadian Forest Fire Danger Rating System was developed and was a significant accomplishment of early wildland fire research (Coogan et al., 2021). Two subsystems, the Fire Behaviour Prediction System and the Fire Weather Index system, are used today in operational fire management and constitute an essential part of the fundamental knowledge of fire in Canada (Coogan et al., 2021). However, it wasn't until 1979 that fire was officially recognized as an ecological process in several park ecosystems in Canada (Hawkes, 1990). The first large-scale prescribed fire was the 1988 Minnewanka I fire in Canada's oldest national park, Banff National Park, Alberta (i.e., 1885; Hawkes, 1990). Recently, 29% of Parks Canada's Conservation and Restoration projects use prescribed fires to restore species and ecosystems (Parks Canada Agency, 2018).

Although fire has been recognized as a critical component of the Canadian boreal forest, fire management is inherently difficult since protecting human lives and communities is of priority, and the negative impacts of fires on society, culture, and economy are always the most significant concern (Wang et al., 2022a). For example, Land managers may want to maximize fire's ecological benefits for fire-dependent systems; however, effective control and suppression of fires are always critical to prevent extreme fire disasters that threaten human life and property (Wang et al., 2022a). In some boreal forest areas, wildfires are monitored and left to burn where they are less of a natural hazard (i.e., less risk to human life and infrastructure).

As a result of these challenges, fire suppression remains a critical management practice in the Canadian boreal forest; however, other disturbances such as logging, insect outbreaks, and wind-throw are still present. These disturbances can vary in severity; however, they are rarely as severe as stand-replacing fire since there is little disturbance to the understory, which can lead to altered understory community composition, diversity and abundance (Roberts, 2004; Hart and Chen, 2008). For example, in eastern Canada, the lack of fire coupled with other low-severity disturbances can lead to the overabundance of ericaceous shrubs, which can result in the conversion of boreal stands to heaths (Lebel et al., 2008; Lorente et al., 2013).

1.1.4 Kalmia angustifolia

Kalmia angustifolia L. (hereafter referred to as *Kalmia*), commonly known as goowiddy in Newfoundland and sheep laurel elsewhere, is a common, native ericaceous understory shrub distributed throughout Ontario, Quebec, and Atlantic Canada (Yamasaki et al. 1998; Inderjit and Mallik 1999). *Kalmia* has a broad ecological range, extending from wet to dry and organic to sandy loam soils, and can grow under various disturbance regimes (e.g., fire, wind throw and logging; Mallik, 1994; Inderjit and Mallik, 1999; Mallik, 2003). *Kalmia* tends to form a thick and vigorous forest understory vegetation in open canopy black spruce forests, particularly in central Newfoundland’s medium and poor nutrient site types (Mallik, 1994; Mallik et al., 2012). Light is an important abiotic factor for *Kalmia* establishment and growth (Inderjit and Mallik, 2002). Although *Kalmia* can adapt to various light conditions (Mallik et al. 2012), it is more vigorous in open canopy black spruce forests with partial shade as it allows sufficient light while providing shelter from wind and high sun exposure (Mallik, 1994; Mallik, 1995).

Kalmia can reproduce through seeds and vegetatively; however, vegetative regeneration is more common (Mallik, 1993). *Kalmia* has three methods of vegetative regeneration: (i) layering, (ii) stem-base sprouting and (iii) rhizome growth. Stem base and rhizomes are more common and efficient than layering since layering is limited to old, undisturbed vegetation.

Kalmia's extensive rhizomatous growth and vigorous stem base sprouting ability make this plant very effective in vegetative regeneration (Mallik, 1993). These rapid and aggressive vegetative regeneration methods outcompete and suppress other plants in post-disturbance habitats (Mallik, 1993; Inderjit and Mallik, 1999, Siegwart Collier and Mallik, 2010).

In Newfoundland, *Kalmia* is often a natural component of black spruce ecosystems (Meades and Moore, 1989), where it is scattered beneath spruce stands, mainly where canopy gaps are located (Yamasaki et al., 1998). Historically, it is assumed that natural fire controlled the *Kalmia* population; however, fire suppression and low-level disturbances may promote *Kalmia* proliferation, which has extensively invaded many black spruce stands (Power, 2000).

Low-level disturbances, such as low-severity fires, clear-cutting, wind-throw and insect herbivores, can cause a shift from productive conifer stands to *Kalmia*-dominated heaths (Yamasaki et al., 1998; Mallik, 2001; Mallik, 2003). Specifically, *Kalmia* can survive non-severe fires (i.e., low temperatures) by having underground rhizomes and stem base underneath the humus layer. Fire may consume the above-ground part of the plant, but the below-ground part survives, which allows *Kalmia* to regenerate following a disturbance (Mallik, 1993). After a disturbance that opens the forest canopy, the increase in light makes forest ecosystems vulnerable to extensive increases in *Kalmia* abundance (Bloom and Mallik, 2004). Several studies have suggested that prolonged occupancy of *Kalmia* leads to vegetation change and can cause habitat degradation for black spruce (Damman, 1971; Inderjit and Mallik, 1999; Mallik and Inderjit, 2001; Bloom and Mallik, 2006; Mallik, 2022).

Kalmia proliferation and black spruce regeneration failure may occur via indirect and direct competition through allelopathy (Mallik, 1987; Zhu and Mallik, 1994), soil nutrient stress/imbalance (Inderjit and Mallik, 1999; Yamasaki et al., 2002), inhibition of SOM decomposition (Mallik, 2001; Joanisse et al., 2007; Mallik, 2022), and limitation of ectomycorrhizal association on conifer roots (Mallik 1987; Yamasaki et al., 1998) and mycorrhizal capacity with *Kalmia* (Figure 1.3; Wallstedt et al., 2002).

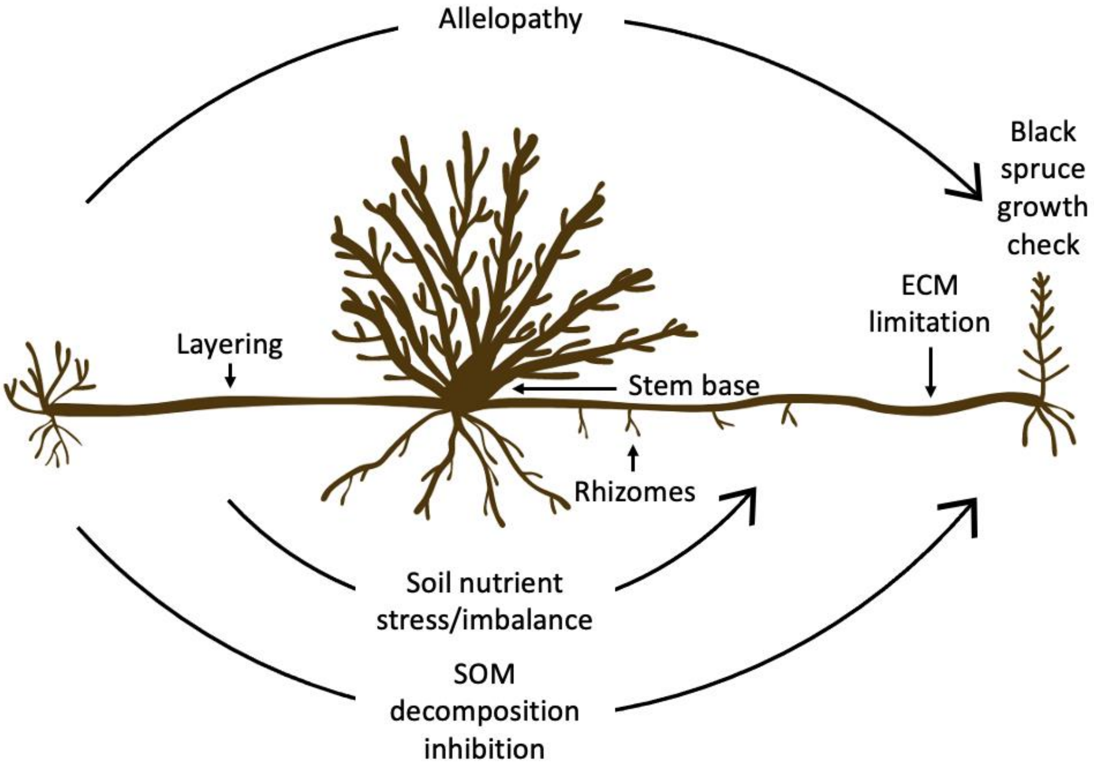

Figure 1.3 Black spruce growth check resulting from effective vegetative regeneration strategies (i.e., layering, stem base and rhizomes) and direct and indirect competitive abilities, including allelopathy, soil nutrient stress/imbalance, soil organic matter (SOM) decomposition inhibition, and ectomycorrhizal (ECM) limitation on black spruce roots (modified from Mallik, 2003).

Allelopathy is a competitive advantage when a plant produces chemicals that inhibit neighbouring species (Inderjit and Mallik, 2002). Some studies have shown the possibility of *Kalmia* being allelopathic and impacting black spruce (Mallik, 1987; Zhu and Mallik, 1994); however, there are barriers to determining if *Kalmia* has allelopathic properties. Many of the phenolic acids reported from *Kalmia* are common in the plant kingdom, and none are specific to *Kalmia*. This makes it difficult to believe that these common acids, which are widely present in plants, could explain the high competitive ability of *Kalmia* (Inderjit and Mallik, 2002).

Additionally, it is not possible to confirm or deny allelopathy by showing the presence of phenolics and secondary compounds in *Kalmia*, as they may undergo chemical, physical, and biological degradation after entering the soil. Experiments in laboratory and greenhouse settings have shown the potential of allelopathy in *Kalmia*, but this is due to specific conditions. In the field, nature is complex, and it isn't easy to simulate exact field conditions in labs and greenhouses (Mallik and Inderjit, 2001; Inderjit and Mallik, 2002).

While *Kalmia* is a natural component of the black spruce landscape, an overabundance of *Kalmia* can have implications on black spruce health, with the potential to cause cascading effects on the boreal forest system. While it is challenging to determine the specific competitive mechanisms of *Kalmia* since more than one competitive pathway could interfere with black spruce, the literature provides substantial evidence that *Kalmia* inhibits black spruce regeneration and growth. Therefore, management must consider *Kalmia* for black spruce regeneration when *Kalmia* is present. Several studies have shown the success of various management options, such as scarification (Thiffault et al., 2017) and herbicide usage (Moroni et al., 2009), that control of *Kalmia*.

1.1.5 Terra Nova National Park, NL

Terra Nova National Park (TNNP), NL, is a model system for investigating the effects of fire suppression on black spruce forest regeneration potential in the presence of *Kalmia*. Located on Ktaqmkuk (i.e., Newfoundland), this Park was established in 1957 from provincial Crown land and protects 402 km^2 of the Eastern Newfoundland Atlantic Region, characterized by boreal forest and rocky coastline (Figure 1.4; Parks Canada, 2009).

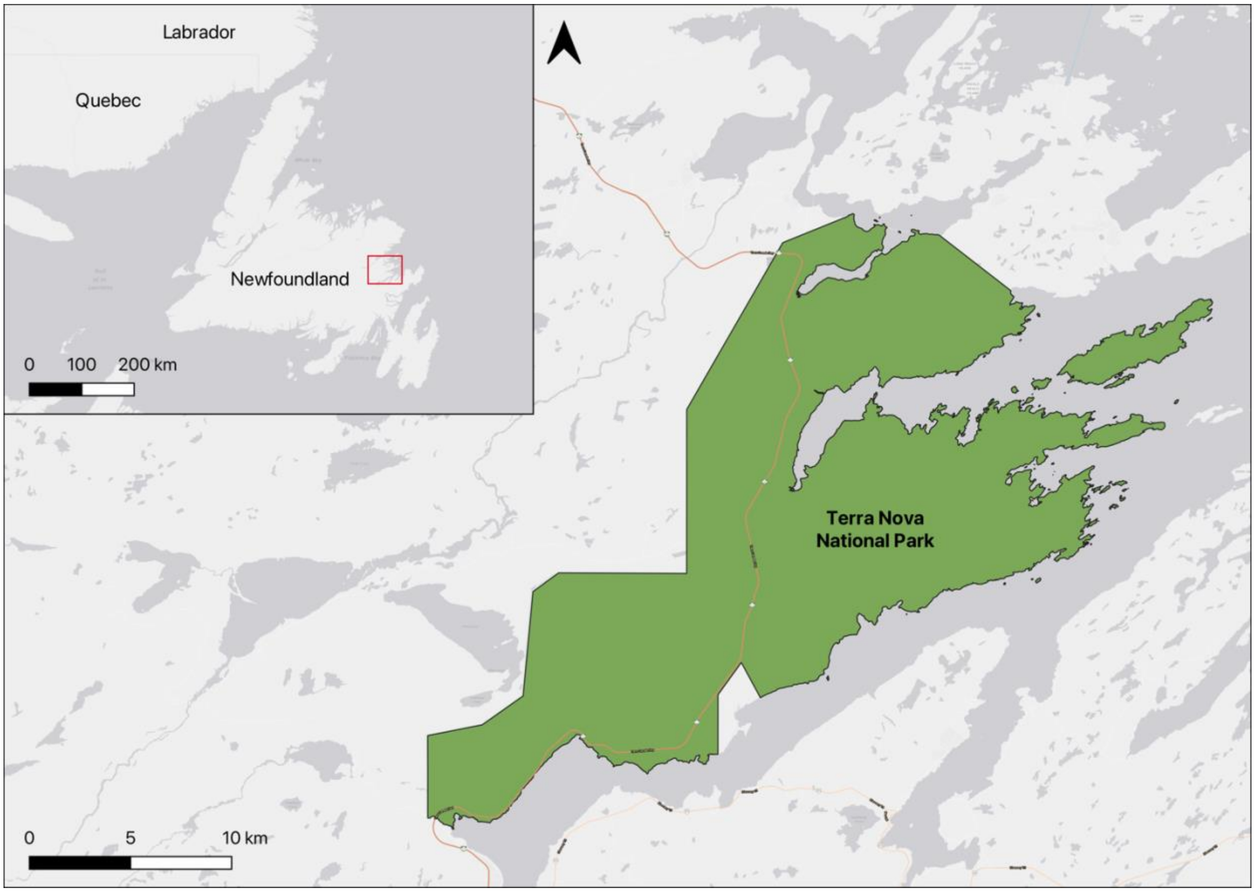

Figure 1.4 Map of Terra Nova National Park, Newfoundland, Canada.

TNNP has a maritime influenced climate due to the Labrador Current, with brief cool summers and moderate winters (Parks Canada, 2009). Approximately 70% of the Park is forested, black spruce being the dominant species and smaller areas composed of balsam fir and hardwoods such as paper birch (*Betula papyrifera* Marsh.), red maple (*Acer rubrum* L.), and trembling aspen (*Populus tremuloides* Michx.; Parks Canada, 2009). Black spruce covers approximately 74% of the Park's forest area, with 60.5% as a primary species, 8.5% as a secondary species (e.g., fir-spruce stands), 3% in *Kalmia* heaths, and >2% scattered throughout bogs, fens, and other barrens (Simpson, 2007).

The Park has several introduced animal species that directly and indirectly impact black spruce establishment and regeneration and *Kalmia* proliferation. The non-native American red squirrel was introduced to the island in the mid-1960s and is abundant within TNNP. This species directly predates on black spruce cones and seeds, which could limit the establishment of black spruce forests (Power, 2005). Moreover, non-native moose can indirectly impact black spruce by selectively browsing other species, such as balsam fir. While this may be beneficial for black spruce in terms of herbivory, moose browsing on balsam fir can impede black spruce seedling growth by increasing canopy openness, thus allowing *Kalmia* to establish and grow (Thompson and Mallik, 1989; Thompson et al., 1992).

TNNP has two distinct ecoregions, the Central Newfoundland Forest (CNF) inland and the North Shore Forest (NSF) on the coast (Figure 1.5; Damman, 1983). The CNF ecoregion is heavily forested with black spruce, and *Kalmia*-black spruce forests are very common (Damman, 1983; Walker, 2021). This ecoregion is also drier, and forest fire plays a vital role in the landscape dynamics (Damman, 1983). The NSF ecoregion is mostly forested with balsam fir and other deciduous species, and the quality of forests deteriorates toward the coast with increased wind exposure (Damman, 1983; Walker, 2021).

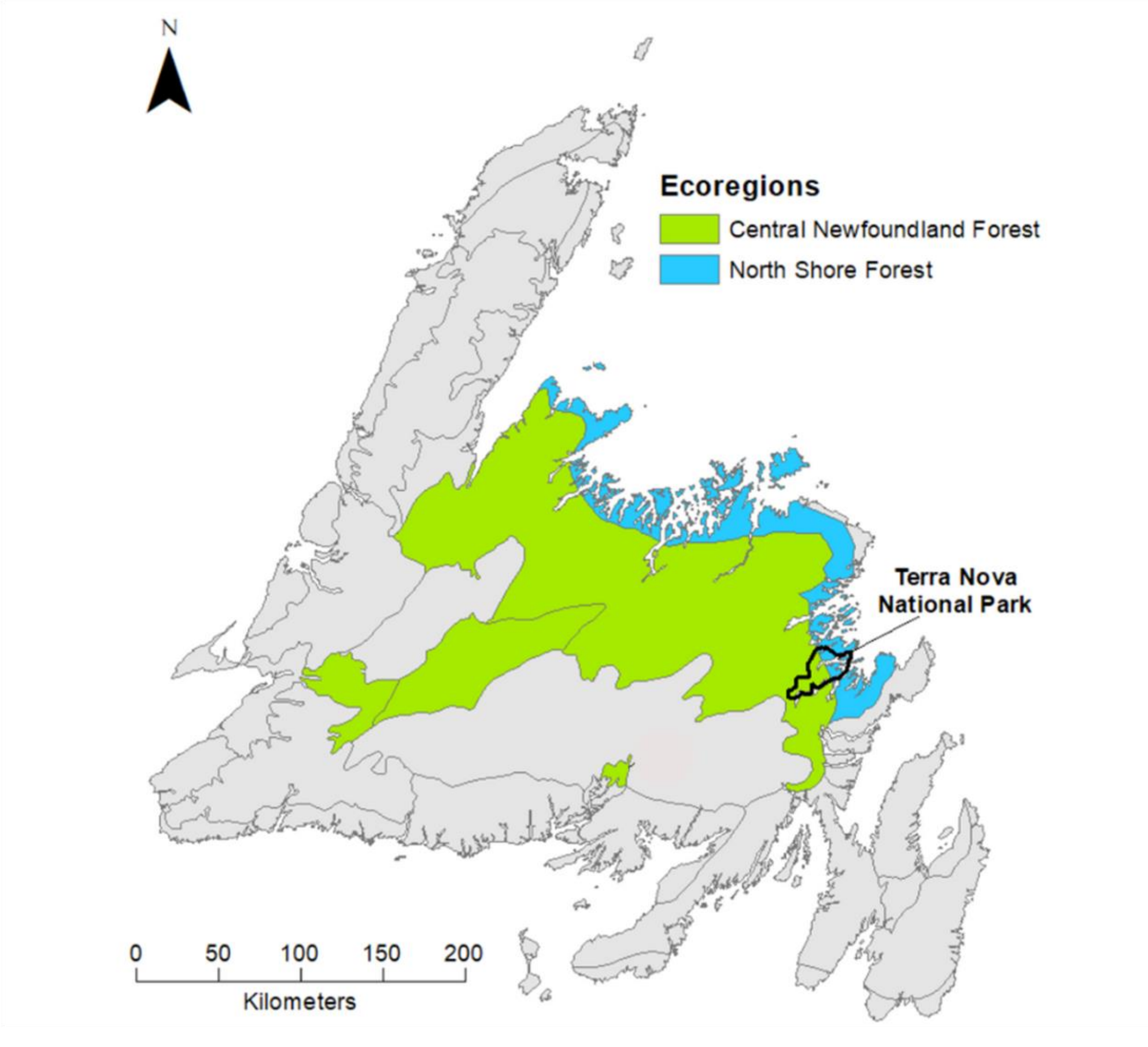

Figure 1.5 Map of Central Newfoundland Forest ecoregion (green) and the North Shore Forest ecoregion (blue) with Terra Nova National Park, NL, outlined in black. As defined by Damman (1983) and Meades and Moores (1989). Data from the Government of Newfoundland (2017; source from Walker, 2021).

Several distinct cultural groups have occupied the surrounding areas and Bonavista Bay. The earliest peoples, Maritime Archaic, Dorset and Beothuk, were coastal dwellers. Five prehistoric Indigenous sites have been identified in the Park, and archaeological evidence supports the occupation of Maritime Archaic and Dorset. The presence of Beothuk occupation within the Park has yet to be confirmed, but there is substantial evidence of the Beothuk presence in nearby areas (Parks Canada, 2009). Additionally, there are two Indigenous Mi'kmaq Bands in Newfoundland; Miawpukek First Nation and the Qalipu First Nation (Parks Canada, 2019).

Colonizing of the island by European settlers changed the historic dynamics of the boreal forest. During the early years of colonization, fishing and logging were extremely common. There was little consideration of forest conservation as many uncontrolled forest fires destroyed extensive forested areas (Carroll, 1990). Fire suppression was implemented over the past century, yet many large fires escaped control, impacting stand ages across Newfoundland (Simpson, 2007). Furthermore, logging activities were intense and widespread throughout the 1900s, outside and within future TNNP boundaries (Simpson, 2007). Even after the Park's establishment, cutting activities continued to a limited extent for ten years (Simpson, 2007).

Fire has always been a crucial boreal ecosystem process and helped shape TNNP's landscape (Simpson, 2007; Walker, 2021). Many plant and animal species found in the region are fire-dependent and have co-evolved with this natural process, such as black spruce, white pine (*Pinus strobus* L.), paper birch and pin cherry (*Prunus pensylvanica* L.f.), and animals such as beavers, red crossbills (*Loxia curvirostra* L.), and woodpeckers (Parks Canada, 2009). The present distribution of fire-adapted black spruce in TNNP and central Newfoundland results from past forest fires (Simpson, 2007). Natural fire also plays a key role in controlling the *Kalmia* population (Viereck and Johnston, 1990; Siegwart Collier and Mallik, 2010).

Fire has been relatively absent in many national parks, including TNNP (Simpson, 2007; Parks Canada, 2009), resulting in unexpected negative consequences within the Park. There has been little natural black spruce regeneration in TNNP, which has resulted in a skewed forest age class with older classes (>100 years old) dominating the landscape (Simpson, 2007; Parks Canada, 2009). The mean tree age is 110 years old, and the range is approximately 60 – 240 years old, with as much as 85% of TNNP's forests being >80 years old (Simpson, 2007). This demographic results from the current fire cycle, as it is likely much longer than the historic fire regime of the region prior to European colonization (Simpson, 2007). Older stands tend to produce fewer cones and viable seeds and are more susceptible to disease (Power, 1996). Additionally, the lack of high-severity fire can result in the loss of forested areas through the propagation of *Kalmia* shrub rhizomes that would otherwise have been destroyed by fire (Power, 2000). Several regions of TNNP have converted from productive black spruce stands to *Kalmia* heaths (Parks Canada, 2009).

Due to the prolonged absence of stand-replacing fire and subsequent forest loss, TNNP has recently (i.e., since 2002) attempted to reintroduce fire to the landscape through prescribed fires as one management strategy for forest restoration. One of the primary goals of prescribed fire is to help lower black spruce stand age distributions, improve black spruce regeneration, and control the *Kalmia* population to allow other species to establish (Simpson, 2007; Parks Canada, 2023). The Park has conducted four prescribed fires in 2002, 2008, 2015, and 2016 and has burned a total area of ~425 ha (Table 1.1).

Table 1.1 Summary of prescribed fires within Terra Nova National Parks, NL, boundaries. Data is adapted from Simpson (2007) and Walker (2021).

Location	Date	Total area (ha)
Mill Pond	August 2016	~200.0
Spruce Pond	August 28, 2015	93.5
Field Harbour Pond	July 16, 2008	34.2
Big Brook (escaped prescribed fire)	June 13, 2002	98.0

The Park is divided into three fire management zones, which include intensive (71.1%), intermediate (21.8%), and extensive (7.1%; Parks Canada, 2023). The majority of the Park's area is located within the intensive management zone, which contains the two front country campgrounds, most operational infrastructure, backcountry sites, and visitors in the summer season. Additionally, this zone experiences significant year-round vehicular traffic due to the Trans-Canada Highway (Simpson, 2007). Currently, this zone is managed via complete suppression of wildfires due to the high volume of traffic (i.e., visitors and vehicles) and infrastructure (Simpson, 2007). Prescribed fire is mainly implemented in the intermediate and extensive zones due to their remoteness, limited presence of infrastructure and few visitors (Simpson, 2007).

Several issues are associated with implementing prescribed fire as a management tool in TNNP. The majority of the intensive fire zone is located within the CNF ecoregion. As previously mentioned, this ecoregion is characterized by black spruce and has historically relied on fire as a natural disturbance. However, since this zone currently has complete fire suppression, prescribed fire is not implemented where the black spruce composition is highest. Instead, prescribed fire is used in areas within the NSF ecoregion. Although this ecoregion has black spruce stands, it is mainly forested by balsam fir and other deciduous species that do not depend on fire for successful regeneration (Walker, 2021).

The 2007-2017 fire management plan, which prohibits prescribed fire in the intensive zone, was a local policy choice rather than a logistical choice. The main reason for this choice was the 2002 Big Brook prescribed fire that escaped, instilling fear and loss of trust in many community members living near the Park. However, in the 2023-2023 fire management plan, prescribed fire may be planned and conducted in all Park zones using tactics to meet risk management objectives and ecological goals (Parks Canada, 2023).

There are also ecological and logistical challenges when implementing prescribed fire. Prescribed fire cannot emulate the ecological effects of natural fire (Ryan et al., 2013). In TNNP, to create suitable seedbeds for successful black spruce regeneration and eradicate *Kalmia*, prescribed fires need to be severe (i.e., burned deep into SOM layer). If not severe, fire fails to reduce SOM thickness. *Kalmia* stems and rhizomes can survive below-ground under the SOM layer and effectively regenerate following the disturbance, thus out-competing black spruce seeds and seedlings (Siegwart Collier and Mallik, 2010; Mallik, 2022). However, severe prescribed fires are often resource and time costly and dangerous to neighbouring communities and infrastructure (Mallik and Kravchenko, 2016). Although TNNP wants to potentially implement prescribed fire into the black spruce-dominated intensive fire zone, it is unclear whether these fires will be severe enough to achieve successful black spruce regeneration.

Due to the limitations associated with prescribed fire as stand-alone management, TNNP has continued interest in implementing alternative management options.

1.1.6 Resist-Accept-Direct (RAD) framework

The Resist-Accept-Direct (RAD) framework was developed by and for managers to assist in the decision-making of management for ecosystems going through transformations (i.e., a system that diverges considerably and irreversibly from prior ecosystem structure, composition and structure; Lynch et al., 2021). Historically, ecosystem transformations were resisted by employing management to maintain current or historical ecosystem structure and function (Thompson et al., 2021). However, these ecosystem transformations will be challenging to resist under ongoing and intensifying environmental changes, such as climate change (Lynch et al., 2021). The RAD framework goes beyond traditional resist management by either accepting the ecosystem transformation by not intervening or directing the ecosystem transformation toward a specific alternative outcome (Lynch et al., 2021). Although these are three distinct management choices (i.e., resist, accept, and direct), other management pathways lie between exclusively resisting, accepting or directing (Schuurman et al., 2022). For example, managers may accept the infeasibility of maintaining a specific species where it has occurred historically but attempt to direct that species elsewhere in a location where climatic conditions are more appropriate. Additionally, managers can change the management approach based on how the system transforms over time.

As mentioned, TNNP is undergoing ecosystem transformations. Examples include the conversion of black spruce forest stands to *Kalmia* heaths and balsam fir forest transformations due to insect disturbance and moose herbivory. Current management is either resisting (e.g., prescribed fire) or directing (e.g., moose management and multi-species tree planting) these changes. Prescribed fire has historically been implemented to resist these transformations by adhering to Parks Canada's mandate, which requires that "managers take an integrated approach to ensure the protection of national park’s ecological integrity….” (Parks Canada, 2009). The Canada National Parks Act (2000) defines ecological integrity as “a condition that is determined to be characteristic of its natural region….”. With this in mind, one of the Park's key priorities is to improve ecological integrity (Parks Canada, 2019); however, attempting to resist these ecosystem transformations might not be possible, cost more, require more intensive efforts, and involve trade-offs regarding other management efforts (Lynch et al., 2021; Schuurman et al., 2022).

Alternative management considerations may be more cost and resource effective than prescribed fire to resist these transformations, may help direct these transformations into an alternative preferred state or help accept these ecosystem transformations. Alternative management considerations vary from intense seedbed disturbance through scarification, increasing seed viability through seeding and planting seedlings, and a ‘do nothing’ option which allows natural succession to occur without interference. Additionally, alternative management can be used with prescribed fire to capitalize on the ecological benefits (e.g., prescribed fire and seed). Recently, TNNP has incorporated the RAD framework into their management via the Forest Management and Restoration Plan, which includes black spruce stands and *Kalmia* heaths (L. Siegwart Collier, personal communication, July 27, 2023); however, for Park managers to decide what ecological trajectory to follow and what management to implement for the transformation of black spruce stands to *Kalmia* heaths requires understanding the site's characteristics for specific ecological goals.

1.2 Thesis rationale

While maintaining ecological integrity is of high priority for all national parks in Canada, including TNNP, current Park management plans and forest monitoring data indicate that the ecological integrity condition of TNNP's forest ecosystem is fair and expected to decline (Parks Canada, 2009, 2019; Environmental and Climate Change Canada, 2022). Ecological integrity that is fair or declining indicates that the ecosystem is vulnerable, and management actions may be required.

Black spruce is a key component of TNNP, and the regeneration of this species is critical for maintaining the Park's ecological integrity (Parks Canada, 2023). Black spruce provides necessary resources to several species-at-risk within the Park. Endangered red crossbills rely on mature cone-producing trees, such as black spruce and balsam fir, as a food source; threatened Newfoundland pine marten (*Martes americana atrata* Bangs) depend on black spruce habitat; and endangered boreal felt lichen (*Erioderma pedicellatum* (Hue) P.M.Jørg), and the special concern blue felt lichen (*Degelia plumbea* (Lightf) P.M.Jørg & P.James) both depend on black spruce for their habitat (Parks Canada Agency, 2017).

Park managers attribute the decline of black spruce forest health and lack of regeneration to the absence of stand-replacing fires (Power, 1996; Parks Canada, 2023). TNNP began reintroducing fire into the landscape through prescribed fires in 2002 as a management action towards regenerating black spruce forest stands within the Park (Simpson, 2007; Parks Canada, 2023); however, there are ecological and logistical challenges associated with this management. Although fire was once a critical part of TNNP's black spruce landscape, prescribed fire alone may not be the most appropriate tool for forest restoration. This is due to the barriers associated with prescribed fires, such as the location (Simpson, 2007), the possibility of a *Kalmia* heath rather than a forest stand following fire (Siegwart Collier and Mallik, 2010; Mallik, 2022), and the risks to communities and infrastructure (Mallik and Kravchenko, 2016). Many have cautioned against using prescribed fire only for the sake of using prescribed fire; e.g., resources and time could be heavily invested in prescribed fire without guaranteeing success, and there is a risk that regeneration will not occur as planned (Arsenault et al., 2016). Both young and mature black spruce stands are crucial to TNNP's forest ecosystem, and burning these stands may not be necessary or beneficial (Walker, 2021). Lastly, historically fire-dependent ecosystems are now changing under current climate changes. This makes it challenging for Park managers to determine the fire management baseline as the historical natural fire regime may not be suitable or sufficient to achieve a diverse landscape (Wang et al., 2022). Therefore, management should focus on specific ecological goals and assess each site's characteristics to implement effective management, possibly through alternative management considerations.

The broad aim of this thesis research was to provide the science-based information needed to implement effective alternative management to improve black spruce regeneration in TNNP. By understanding two key ecological filters that control black spruce regeneration, seed viability and seedbed quality, targeted restoration efforts can be implemented to achieve ecological integrity goals (Parks Canada, 2023). Our study will help inform future management plans in TNNP by determining the appropriate type of management needed on individual sites, ultimately improving management effectiveness and conserving time and resource costs (Chazdon, 2017). In summary, this research will directly contribute to the management and understanding of Newfoundland's boreal forest.

1.3 Thesis overview and objectives

In this chapter, we provided an extensive introduction and context for this research. We discussed the ecological role of fire in the boreal forest, specifically for black spruce regeneration and fire management in Canada. We also discussed how TNNP is an ideal model system to understand the effects of fire suppression in relation to black spruce regeneration failure and *Kalmia* over-abundance and how alternative management may be more effective than current prescribed fire management. What follows in Chapter 2 is a description of our study design and findings, including the black spruce age-reproductive relationship, seedbed characteristics on regeneration and the presence of *Kalmia* in black spruce stands. Specifically, this research addressed the following objectives and predictions:

1. **Determine the geographical distribution of black spruce reproductive potential in TNNP.**

   P1: The majority of viable black spruce seeds would be present in mature black spruce stands with thick SOM depth.

2. **Identify the type of seedbeds that promote natural black spruce regeneration.**

   P2: Natural black spruce regeneration would occur where SOM depth is thinnest with little seedbed type present.

3. **Assess the presence of *Kalmia* in black spruce stands.**

   P3: Light availability would influence *Kalmia* establishment, and in areas where *Kalmia* was present, we would observe less black spruce regeneration.

Lastly, in Chapter 3, we outline alternative management considerations for black spruce regeneration in TNNP, which include management description, benefits and possible issues.

Additionally, we discuss the implications of our research and future research suggestions. This research provides a more in-depth spatial understanding of TNNP's black spruce regeneration. Determining specific site characteristics, seed viability and seedbed quality, are necessary to implement the most effective and feasible management for the ecological goal of increasing black spruce regeneration. The findings from this research go beyond TNNP management and advance knowledge in our understanding of black spruce regeneration across the boreal forest.

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Chapter 2: Assessing ecological barriers to black spruce regeneration and forest management in Terra Nova National Park, NL

2.1 Introduction

The boreal forest has long been adapted to fire disturbances (Coogan et al., 2021). Fire regimes vary across North America, with western regions experiencing shorter fire return intervals of around 80-150 years (Viereck, 1983; Larsen, 1997) and eastern regions experiencing longer fire return intervals of 270-500 years (Bouchard et al., 2008). Dominant species within the boreal forest have adapted and evolved with fire and have developed mechanisms to survive and thrive following a fire disturbance (Zasada et al., 1992). These adaptations include serotinous cones, aerial seed banks, and resprouting from roots (Greene et al., 1999; Bouchard et al., 2008).

Black spruce is a long-lived fire-adapted conifer species that is widespread and abundant in the boreal forest (Viereck and Johnston, 1990; Greene et al., 1999). This species is found across North America, ranging from northern areas of the United States to northern Labrador on the east coast and across Canada to the west coast of Alaska (Viereck and Johnston, 1990). Black spruce contains semi-serotinous cones that disperse seeds from their aerial seed banks following a fire disturbance (Greene et al., 1999). Additionally, black spruce seeds require exposed mineral soil for successful regeneration (Greene et al., 1999; Greene et al., 2004; Greene et al., 2007; Johnstone and Chapin, 2006; Johnstone et al., 2008).

However, due to European colonization, fire suppression policies across the boreal forest have been implemented (Grenier et al., 2005; Dupuis et al., 2020). This management was implemented to protect communities, infrastructure, and commercially valuable forests (i.e., logging; Cumming, 2005; Hope et al., 2016). As a result, areas that would have historically burned were no longer experiencing fire (Cumming, 2005), causing stands to increase in age

(Wang et al., 2022) and build-up of flammable biomass (Parisien et al., 2020) and creating unfavourable regeneration conditions for fire-adapted species (Simard et al., 2007).

Terra Nova National Park (TNNP), NL, is a model system for understanding the outcomes of fire suppression and assessing alternative management practices for regenerating fire-adapted species, such as black spruce, in the absence of fire. Fire has been a crucial ecosystem process in TNNP and helped shape the Park’s landscape (Simpson, 2007; Walker, 2021). As a result, black spruce is the most dominant tree species, covering approximately 74% of the Park’s forest area (Simpson, 2007). This species provides ecological services to several species-at-risk within the Park (Parks Canada Agency, 2017); however, fire suppression in TNNP has been an active management practice since the Park's establishment in 1957 (Power, 1996; Simpson, 2007). This management was extremely common in all Canadian National Parks due to fire suppression mandates from Parks Canada (Cumming, 2005; Ryan et al., 2013; Coogan et al., 2021; Wang et al., 2022).

Specifically, the absence of high-severity wildfire has resulted in a spatial mismatch between black spruce seed viability and seedbed quality in TNNP. This mismatch has resulted in little to no natural black spruce regeneration, causing a skewed forest age class with mature stands (> 100 years old) dominating the landscape (Power, 1996; Simpson, 2007; Parks Canada, 2009). Moreover, it is assumed that the lack of stand-replacing fires in the landscape led to the proliferation of *Kalmia* (Simpson, 2007). *Kalmia* is a native understory, ericaceous shrub found throughout TNNP and is often a natural component of black spruce stands (Meades and Moore, 1989; Inderjit and Mallik, 1999; Simpson, 2007; Parks Canada, 2009). However, in the absence of fire, *Kalmia* often outcompetes black spruce due to its competitive abilities and effective vegetative regeneration (Mallik, 2003). This has caused areas of TNNP to convert from black spruce stands to *Kalmia* heaths (Siegwart Collier and Mallik, 2010).

Due to the absence of high-severity wildfire, the ecological integrity condition of TNNP's forest ecosystem is fair and expected to decline (Simpson, 2007; Parks Canada, 2009, 2019; Environmental and Climate Change Canada, 2022). Ecological integrity that is fair or declining indicates that the ecosystem is vulnerable, and management actions may be required. Therefore, managers have reintroduced fire into the landscape through prescribed fires as one management strategy to improve ecological integrity (Simpson, 2007; Parks Canada, 2023). However, there are ecological and logistical challenges associated with prescribed fire.

The geographical location of prescribed fire is critical for black spruce regeneration. Currently, TNNP only implements prescribed fire in remote areas of the Park (Simpson, 2007), where black spruce stands are less continuous and have greater heterogeneity. Instead, prescribed fire should be used in areas dominated by black spruce; however, these areas are currently under a fire suppression regime since it is mainly located near Park infrastructure, communities and the Trans-Canada Highway (Simpson, 2007). Furthermore, prescribed fire is rarely a high-severity fire (i.e., high temperatures), which is needed to create suitable conditions for black spruce regeneration (Siegwart Collier and Mallik, 2010; Mallik, 2022). This is primarily due to the narrow boundaries placed on prescribed fire management to mitigate risk (e.g., escape fires and excessive smoke in communities). Achieving stand-replacing fires through prescribed fire is possible but difficult, as they are expensive, logistically challenging, and potentially dangerous to neighbouring communities and infrastructure (Mallik and Inderjit, 2001; Mallik and Kravchenko, 2016). Lastly, historically fire-dependent ecosystems are now changing under current climate changes, making it challenging to implement fire as the historical natural fire regime may not be suitable or sufficient to achieve a diverse landscape (Wang et al., 2022).

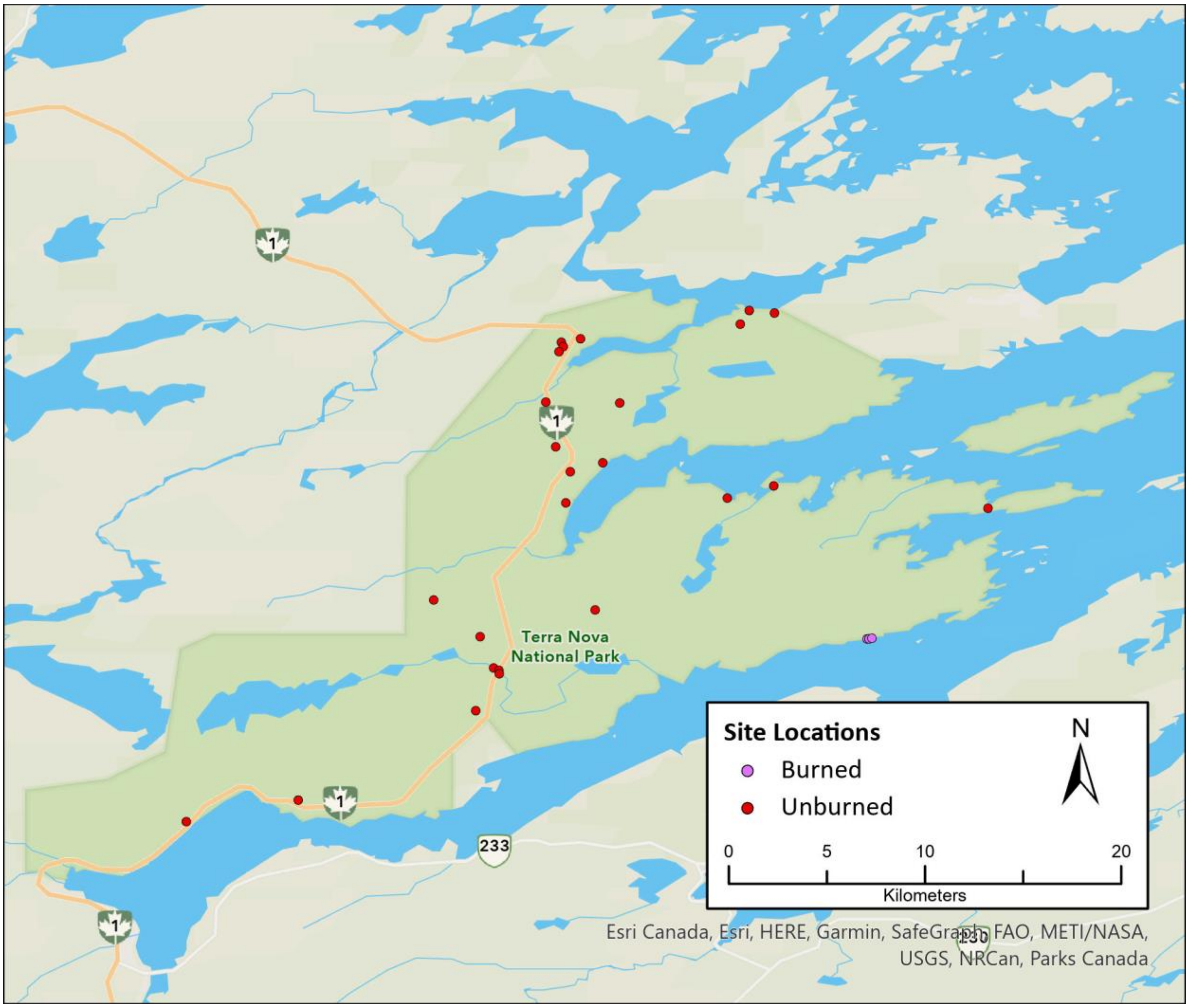
Due to the barriers associated with prescribed fire, forest management alternatives may be more effective for black spruce regeneration in TNNP. However, before management can be implemented, two key ecological filters, seedbed quality and seed viability, that control black spruce regeneration need to be investigated. By spatially assessing these two filters, management for black spruce regeneration can be specific to a site's characteristics, improving management effectiveness and reducing time and resource costs.

The objectives of our research were to: (i) determine the geographical distribution of black spruce reproductive potential in TNNP; (ii) identify the type of seedbeds that promote natural black spruce regeneration; and (iii) assess the presence of *Kalmia* in black spruce stands. We predicted that: (i) the majority of viable black spruce seeds would be present in mature black spruce stands with thick soil organic matter (SOM) depth; (ii) natural black spruce regeneration would occur where SOM depth is thinnest with little seedbed type present; and (iii) Light availability would influence *Kalmia* establishment, and in areas where *Kalmia* was present, we would observe less black spruce regeneration. Through our research, we aimed to provide a more in-depth spatial understanding of TNNP's black spruce regeneration to help inform boreal forest management within the Park.

2.2 Methods

2.2.1 Study area

Field research was conducted in June 2022 in Terra Nova National Park, Newfoundland and Labrador. The Park is located in central eastern Newfoundland (48° 31' 42.3372" N, 53° 52' 56.8056" W) and is approximately 402 km^2 (Parks Canada, 2009; Figure 2.1). TNNP represents the Eastern Newfoundland Atlantic Region, characterized by irregular coastlines, rocky terrain, drumlinoid hills, boreal forest, and bogs (Parks Canada, 2009). The Park is mainly composed of forested terrain (79%), with black spruce being the most dominant forest cover species. Black spruce occupies 60.5% of the Park as the primary tree species, 8.5% as a secondary species (e.g., fir-spruce), 3% on *Kalmia* barrens, and > 2% scattered throughout bogs and other barrens (Simpson, 2007). Balsam fir is the second most dominant tree species, occupying 11.3% as the primary species and 10.5% as the secondary species (Simpson, 2007). Non-forested communities encompass 21% of the Park, such as fens (8%), bogs (7.1%), and barrens (1.2%; Simpson, 2007).



Esri Canada, Esri, HERE, Garmin, SafeGraph, FAO, METI/NASA, USGS, NRCan, Parks Canada

Figure 2.1 Map of Terra Nova National Park, Newfoundland, Canada. The map indicates the location of the study sites in June 2022. There are 25 unburned (red dots) and three burned (purple dots) sites (n = 27; map credit: Armando Gonzales, 2022).

From 1981 to 2010, the TNNP area had an annual daily average temperature of 4.8°C (Government of Canada, 2023). The mean monthly temperatures ranged from -6.3°C in January to 16.5°C in August, and temperature extremes ranged from -31°C in February to 34°C in July (Government of Canada, 2023). From 1981 to 2010, annual precipitation averaged 1217.7 mm

(Government of Canada, 2023). The mean monthly rainfalls ranged from 87.3 mm in August to 117.8 mm in October, with precipitation mostly rain from Spring to Fall and snow in the Winter (Government of Canada, 2023).

The Park's temperature and precipitation may differ spatially due to two distinct ecoregions: Central Newfoundland Forest (CNF) on the west and the North Shore Forest (NSF) on the east (Damman, 1983). The CNF ecoregion has the most continental climate of any ecoregion of Newfoundland. It has the highest summer temperatures and lowest winter temperatures, with a growing season of 140-160 days, and precipitation is average for the island (Damman, 1983). Within the CNF ecoregion, the subregion TNNP is located in has the lowest rainfall compared to the other subregions and occasionally experiences prolonged dry spells. This ecoregion is considered one of the driest parts of the island due to high evapotranspiration losses in the summer. Forest fire plays a critical role in the landscape dynamics in this ecoregion. As a result, the CNF ecoregion is heavily forested with black spruce and is the most distinctly boreal part of the island, with many southern boreal zone species absent (e.g., *Betula alleghaniensis* Britt.; Damman, 1983). The area within TNNP is dominated by black spruce, and *Kalmia*-black spruce stands and balsam fir stands are widespread (Damman, 1983).

The NSF ecoregion comprises the coastal zone on the Island's north side and has some of the warmest summers of any coastal area on the island (Damman, 1983). The growing season is approximately 150 days, which is shorter and cooler than the CNF ecoregion (Damman, 1983). The ecoregion is primarily forested but includes some barrens, especially in coastal sites (Damman, 1983). While vegetation is similar to the CNF, it mainly comprises balsam fir and deciduous species (Walker, 2021). Additionally, the quality and height of the forest decline towards the coast and with increased wind exposure (Damman, 1983).

2.2.2 Field methodology

To assess the spatial mismatch between black spruce seed viability and seedbed quality, 25 forested sites were chosen from the Park's pre-existing network of long-term sampling plots in consultation with TNNP ecologists (Figure 2.1). The selected sites met the following criteria: i) dominated by a black spruce canopy (> 75%); ii) not burned for at least 30 years; and iii) accessible for sampling within the time constraints of our field season. To assess differences in SOM depth and black spruce seedling regeneration between site types, we also randomly selected three burned sites within the perimeter of a prescribed fire that was implemented in August 2016. Each site was sampled using an 11.4 m radius circular plot (408 m^2) following the Canada-wide Ecological Monitoring and Assessment Network protocol (Roberts-Pichette and Gillespie, 1999; Figure 2.2). Three parallel 10 m transect lines were strategically placed 5 m apart within each site to capture within-site variation. Along each transect, we sampled quadrats every 1 m where we assessed seedbed quality, natural black spruce regeneration, and *Kalmia* stem density within a 0.25 m radius circular plot around the quadrat as described below in section 2.2.2.2. Lastly, the same person completed all observations and measurements throughout fieldwork to decrease observer bias and ensure uniformity in the data.

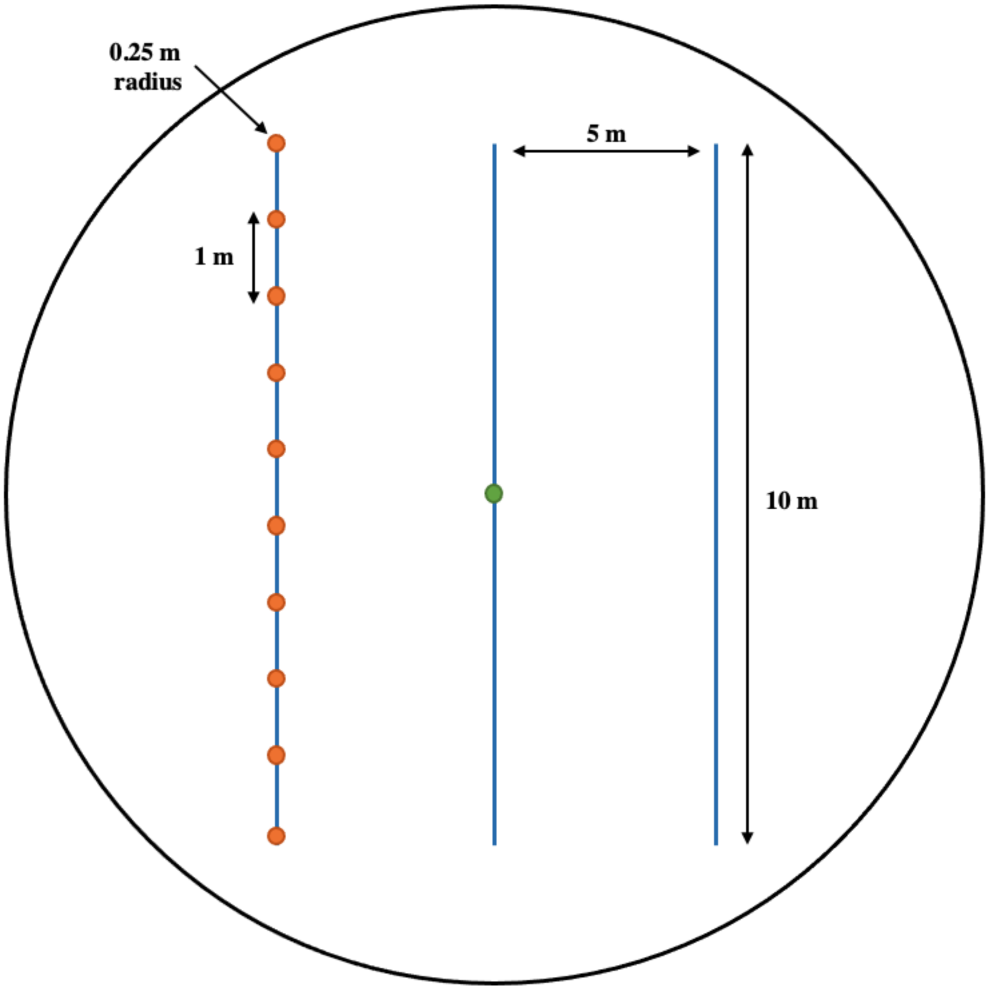


Figure 2.2 Study design of the 25 unburned and three burned sites (408 m^2) in June 2022 in Terra Nova National Park, NL. Light availability (i.e., canopy openness) was measured in the center of the plot (green dot), and seedbed quality (i.e., soil organic matter depth and seedbed type), natural black spruce regeneration, and Kalmia stem density were assessed at quadrat measurements (0.2 m^2; orange dots). Seed viability and tree age were determined by collecting approximately 30 cones and coring four black spruce trees within the site parameter (black circle).

2.2.2.1 Site level measurements

To evaluate the geographical distribution of black spruce seed viability, we aimed to collect a minimum of 30 black spruce cones per site for future seed viability testing in the lab. Individual black spruce cones and cone-bearing clippings were harvested from the ground of each site in June 2022. Cones were collected within a 50 m radius from the center of the site (408 m^2) since this is within the dispersal distance of black spruce seeds (~80 m; Prévost, 1997). Cones were collected in a paper bag and stored at room temperature until seed extraction in the laboratory. Burned sites were excluded from this assessment because the post-fire regenerating black spruce trees were immature.

To assess the age-reproductive relationship of each unburned site, we sampled four tree cores per site using an increment borer for a total of 100 black spruce tree cores from 25 unburned sites; however, upon further laboratory inspection, one core was rotten, thus making it uncountable and removed from this study. Cores were sampled from black spruce trees that were representative of the dominant size class of each site. The borer was placed approximately 30 cm from the ground at a 90-degree angle (Speer, 2010). The borer was rotated clockwise until approximately halfway through the tree (i.e., the pith; Speer, 2010). Tree cores were carefully extracted from the tree and placed in a straw to protect the integrity of the core. Burned sites were excluded from this assessment as we were not determining the age-reproductive relationship in those sites.

Lastly, to test our prediction that light availability influences *Kalmia* establishment, we measured canopy openness using a convex forest densiometer in the centre of each site (408 m^2).

2.2.2.2 Quadrat level measurements

To determine seedbed preference for black spruce regeneration, we evaluated SOM depth, seedbed type and natural black spruce regeneration at quadrats (0.2 m^2) along the three transects within each site. SOM depth was measured using a serrated knife to create a small opening in the forest floor, and a ruler was used to measure the depth of the SOM layer. A distinct difference in soil texture between SOM (i.e., soft) and mineral soil (i.e., rocky) helped us accurately determine the bottom of the SOM. This method was preferred over the pit method as it causes less soil disturbance and is much more time efficient.

Seedbed type (e.g., feathermoss, sphagnum moss; see Table 2.3 for all categories) was assessed using a binary scoring system of present (1) or absent (0) at each quadrat. To evaluate whether natural regeneration occurred, we counted all black spruce seedlings (≤ 2 m height) at each quadrat. To determine if *Kalmia* interferes with natural black spruce regeneration, *Kalmia* stem density was counted at each quadrat.

2.2.3 Laboratory methodology

2.2.3.1 Seed viability

To assess the potential for natural regeneration within each site, we conducted laboratory germination trials of black spruce seeds. Black spruce seeds were extracted in the laboratory following an established standardized protocol outlined in Leadem et al. (1997) and Sirois (2000). Briefly, the cones were soaked in water for 24 hours, left to dry at room temperature for 24 hours, and then dried in an oven at 60°C for 16 hours. Afterwards, cones were tumbled in a sieve shaker for 10 minutes to separate the seeds from the cone material. The extraction procedure was repeated three times, and any seeds that remained in the cone were assumed not to be released under natural conditions.

Extracted seeds were hand-counted, and cone-level seed production was calculated per site as the total number of seeds extracted divided by the total number of cones collected. To determine seed viability, we conducted a 28-day germination trial where a random 100 seeds subsample from each site was placed on a moist filter paper in a 9 cm Petri dish and watered with deionized water when needed (Figure 2.6). If fewer than 100 seeds were extracted from the site, all extracted seeds were used. Seeds experienced 16 hours of light daily using a growth lamp (6400 K full-spectrum, T5 lamp with omni-max reflector; Jump Start, Hydrofarm, Petaluma, CA, USA), which mimics natural sunlight during peak growing season at room temperature (20°C). Seeds were considered germinated if the radicle was four times the length of the seed coat (Leadem et al. 1997; Figure 2.7). We assumed seeds that did not germinate under laboratory conditions would not be viable under natural conditions (Brown et al., 2019). We calculated viable seed availability per site as the number of viable seeds divided by the germination seed subsample. Then we multiplied by the total number of seeds extracted for a site.

2.2.3.2 Age determination

To estimate tree age to assess age-reproductive relationships, we counted tree rings of each core. Cores were air-dried for at least 24 hours before mounting on wooden core mounts to prevent cracks (Speer, 2010). Cores were sanded using a belt sander with progressively finer grit from 80, 120, 180, 220, 400, to 600 grit. Once the cores were sanded, the rings of each core were counted using a magnification lens. Only the latewood (i.e., dark rings) was counted, and each ring counted represents one year (Figure 2.8). Each site's mean tree age was calculated to assess site level relationships.

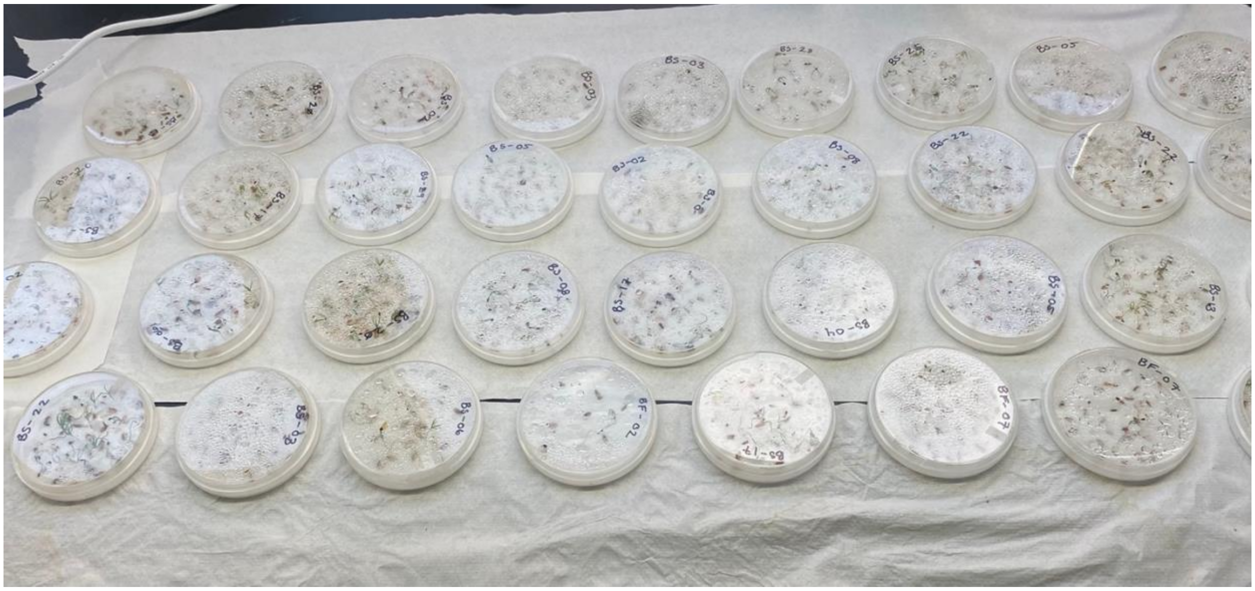


Figure 2.3 Black spruce germination trial in August 2022. Each petri dish contained approximately 30 seeds on moistened filter paper. Petri dishes were kept under appropriate growing conditions (16 hour light and 20°C) for 28 days.

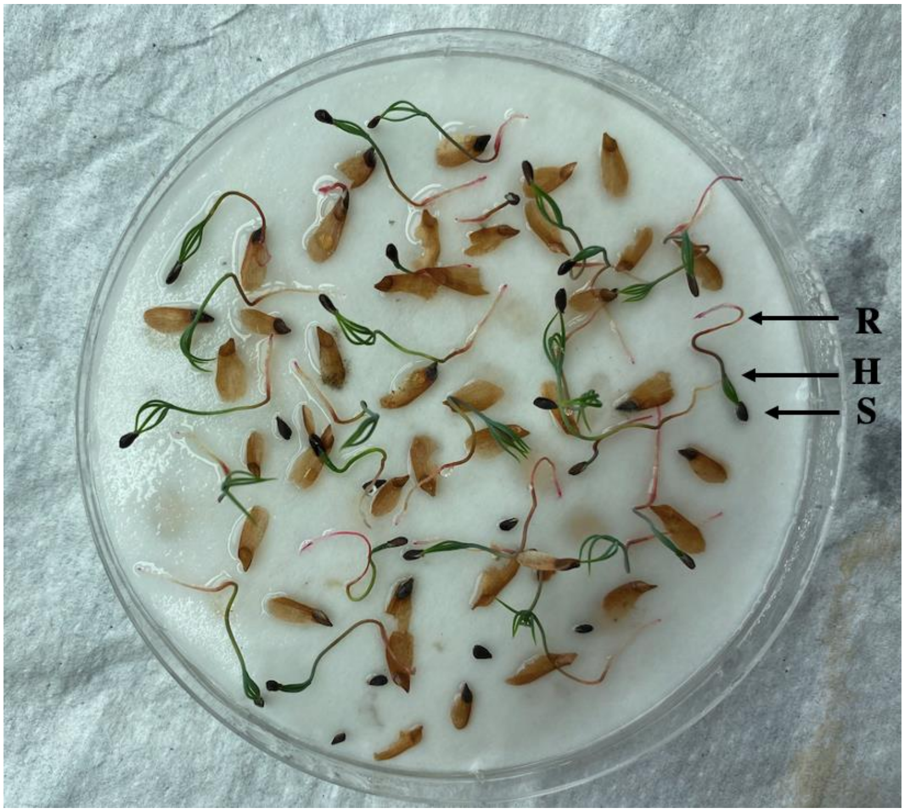


Figure 2.4 Black spruce germination trial in August 2022. The radicle (R) is the first vegetative part to emerge out of the black spruce seed (S), which is then followed by the hypocotyl (H). A seed is considered viable if the radicle is four times the length of the seed.

Figure 2.5 Mounted and sanded black spruce tree cores. Cores were sanded using a belt sander with progressively finer grit from 80, 120, 180, 220, 400, and 600 grit. The latewood (i.e., dark rings) was counted to estimate age.

2.2.4 Statistical analyses

To determine the reproductive potential of black spruce in TNNP, we used a generalized linear model to analyze seed viability (response variable) to tree age and SOM depth (explanatory variables). Mean SOM depth (cm) was included in this analysis since older stands generally have thicker SOM depth which can affect regeneration success (Greene et al., 1999; Charron and Greene, 2002). We used a binomial distribution since the response variable is proportional data (e.g., number of seeds germinated and not germinated; Zuur et al., 2009).

To assess seedbed preference for black spruce regeneration, SOM depth and site type (i.e., burned or unburned) were analyzed. Initially, this model was analyzed with a generalized linear model using raw black spruce seedling count data. However, the number of black spruce seedlings (response variable) had a large number of zeros observed, which is common in ecological data. We used a zero-altered or hurdle model to deal with the excess number of zeros (i.e., zero inflation; Zuur et al., 2009). Zero-altered models consist of two parts. First, the data is modelled as presence/absence of black spruce seedlings in a binomial model. Non-zero observations (i.e., black spruce seedling counts > 0) are then modelled with a truncated Poisson model (i.e., count model) with a log link function (Zuur et al., 2009). We first constructed a model using zero-altered models with Poisson distributions (ZAPs), incorporating the natural logarithm as the link function (Zuur et al., 2009). We then ran a zero-altered model with negative binomial error distributions (ZANBs). A likelihood ratio test was conducted to determine whether ZAPs or ZANBs fit our data better. We selected ZAPs over ZANBs since the overdispersion is explained by the excessive number of zeros (ZAPs) and not in the non-zero count data (ZANBs; Zuur et al., 2009). Our ZAPs model included the number of black spruce seedlings as our response variable and SOM depth and site type (i.e., burned or unburned) as our predictor variables, with the addition of an interaction term. The binomial model included the same predictor variables. Our burned site data sample size was small, as sampling was opportunistic; therefore, the unbalanced design meant we were limited in comparisons between burned and unburned stands. Thus, we conducted the same hurdle model analysis described above, but with only our unburned sites, as these site types compose the majority of our data.

To determine black spruce seedbed type preference, we performed a Chi-Square Test to determine differences between the frequency of a specific seedbed type observed (i.e., observed data) and the frequency of a specific seedbed type observed with black spruce seedling(s) present (i.e., expected data). Our null hypothesis was that black spruce seedling presence was the same in our observed and expected data. Using the presence of black spruce seedling(s) rather than black spruce count data gave a more accurate representation of the data since several data points contained two or more seedbed types. If we were to count black spruce seedlings for each seedbed type, we would get an over-representation of the number of black spruce seedlings.

To determine if canopy openness affected *Kalmia* growth, we used a generalized linear model to assess *Kalmia* stem density (response variable) to light availability (explanatory variable). This model assumed a Poisson distribution since the response variable was count data (Zuur et al., 2009).

Lastly, to evaluate the relationship between *Kalmia* on black spruce regeneration, we initially used a generalized linear model to assess the number of black spruce seedlings (response variable) to *Kalmia* stem density (explanatory variable). However, as previously mentioned, our black spruce seedling count data has a large number of zeros, which led us to use a zero-altered or hurdle model to deal with the excess number of zeros (i.e., zero inflation; Zuur et al., 2009). A likelihood ratio was conducted to determine whether ZAPs or ZANBs fit our data better. We selected ZAPs over ZANBs since the overdispersion is explained by the excessive number of zeros (ZAPs) and not in the non-zero count data (ZANBs; Zuur et al., 2009). Our ZAPs model included the number of black spruce seedlings as our response variable, and *Kalmia* stem density as our predictor variable. The binomial model included the same predictor variable.

For all models, we assessed model fit using residual diagnostics (Zuur et al., 2009). All statistical analyses were performed with R version 4.2.1 via RStudio version 2022.12.0+353 (R Core Team, 2022) using the “pscl” package for zero-altered models (Zeileis et al., 2008; Jackman, 2020) and the “lmtest” package for likelihood ratios tests (Zeileis and Hothorn, 2002).

2.3 Results

2.3.1 Black spruce reproductive potential

In total, 818 cones were collected, and the number of viable seeds in the aerial seed bank ranged from 0 to 1609 seeds. Seven sites yielded less than 30 cones, and one site yielded zero cones due to the lack of ground cones. The site with no cones had young black spruce individuals with the mean tree age being 32 years old and was not yet producing cones and viable seeds. In total, 99 tree cores were assessed. Tree ring counts provided us with the minimum age of an individual, and the mean tree age was used to determine site-level relationships. Sampled trees ranged in age from 18 to 143 years old.

The number of viable black spruce seeds was positively correlated with mean tree age (p-value = 0.046; Table 2.1; Figure 2.6) and mean SOM depth (p-value = 0.03; Figure 2.7). Moreover, there was an interaction effect between mean tree age and mean SOM depth on seed viability (p-value = 0.01; Table 2.1), indicating that older stands with thicker SOM had higher seed viability. The ecoregion of each site was identified in Figure (2.6); however, this was not included in our analysis due to the uneven distribution of the ecoregions (i.e., more CNF sites than NSF).

Table 2.1 Summary of results from a generalized linear model on black spruce seed viability to mean tree age and mean soil organic matter depth (cm) (df = 23). The site's mean tree age and mean soil organic matter depth were used as predictor variables, and the intercept represents the unburned site. This model assumes a binomial distribution. Values in bold indicated a significant difference (α ≤ 0.05).

Parameter	Estimate	Std. Error	z-value	p-value
Seed Viability				
Black Spruce				
Intercept	2.7103	2.1700	1.249	0.21
Mean SOM depth	-0.2590	0.1167	-2.220	**0.03**
Mean age	-0.0547	0.0274	-1.997	**0.046**
Mean SOM depth: Mean age	0.0039	0.0015	2.666	**0.01**

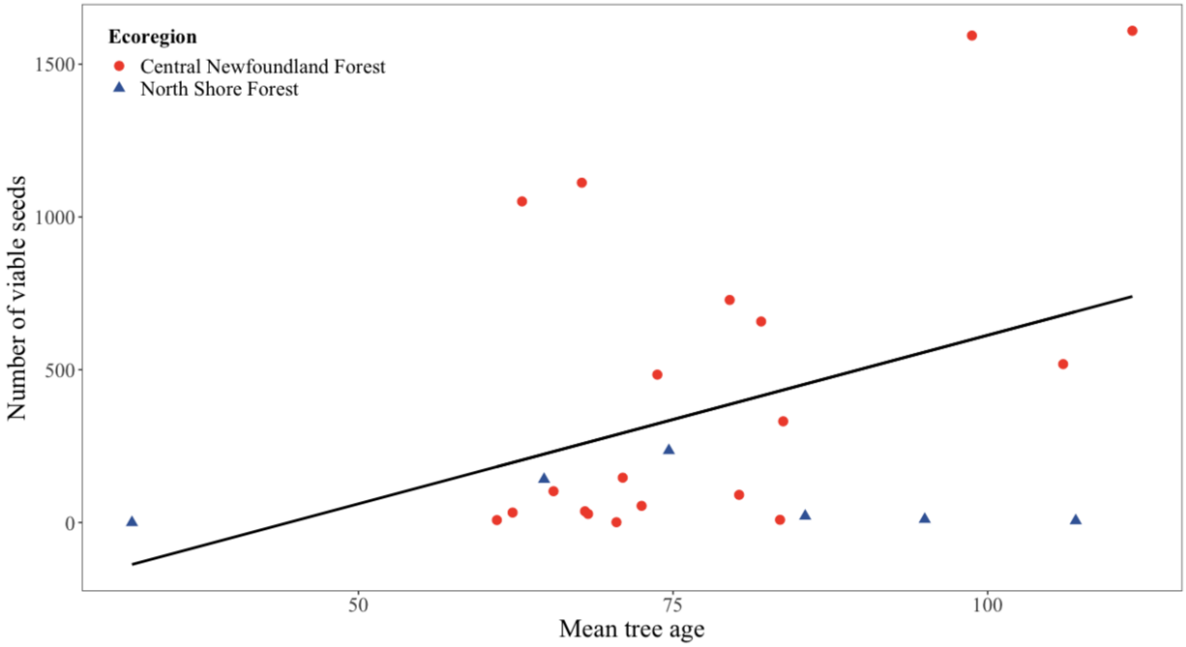


Figure 2.6 Linear regression between black spruce mean tree age and the number of black spruce viable seeds per site. There was a significant relationship (p-value = 0.046). Each dot represents an unburned site (n = 25), and colour and shape differences represent ecoregions.

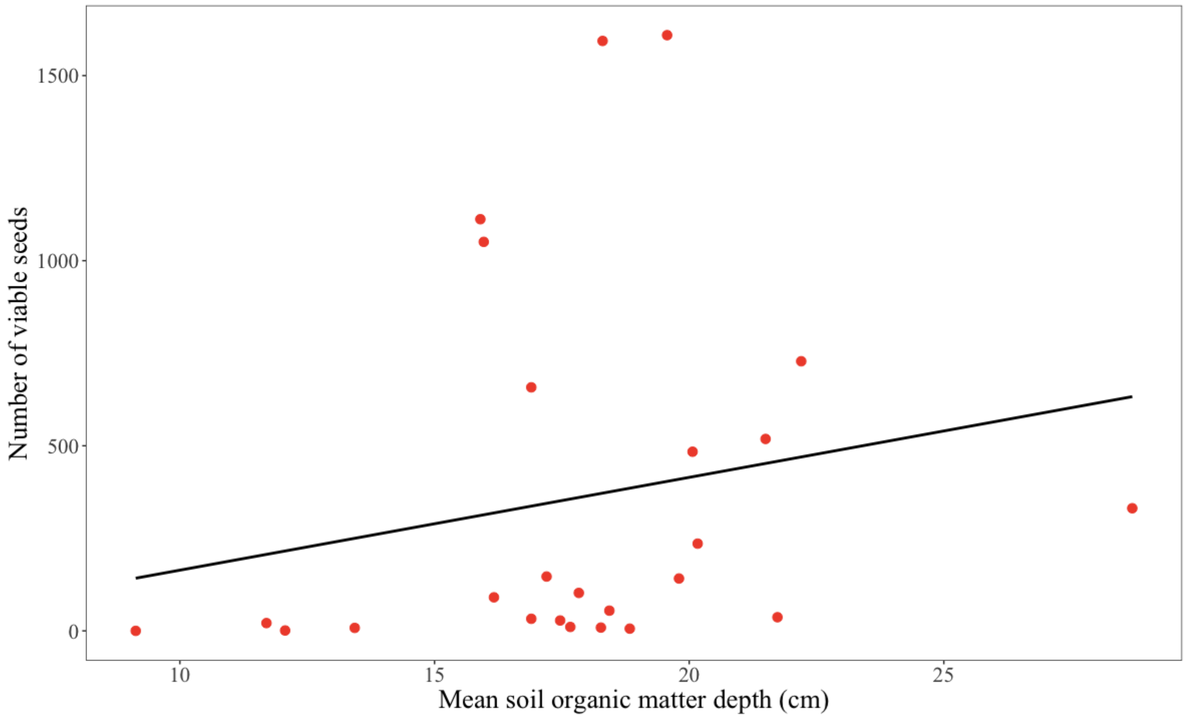


Figure 2.7 Logistic regression between mean soil organic matter depth (cm) and the number of black spruce viable seeds per site. There was a significant relationship (p-value = 0.03). Each dot represents an unburned site (n = 25).

2.3.2 Seedbed suitability

2.3.2.1 Soil organic matter depth and site type

In total, 840 SOM depths were measured at quadrat measurements in 25 unburned and three burned sites. SOM depth ranged from 1 cm to 47 cm, and 105 black spruce seedlings were counted at 55 quadrat measurements. Specifically, 23 black spruce seedlings were counted at 11 of the 90 burned quadrat measurements, and 82 black spruce seedlings were counted at 44 of the 750 unburned quadrat measurements. The first binomial model with both burned and unburned sites, which was built upon presence/absence data, indicated a significant interaction term between SOM depth and site type (i.e., burned or unburned; p-value = 0.03; Table 2.2; Figure 2.8). Black spruce seedling abundance was inversely correlated with SOM depth (p-value = 0.02) and significantly more abundant on burned sites than on unburned sites (p-value = 0.01). There were no significant relationships detected in the count model. When we remove burned sites from our analysis, there is no significant relationship between SOM depth and the number of black spruce seedlings (Table 2.3).

Table 2.2 Summary of results from the zero-altered models, binomial and count, of total black spruce seedlings (df = 8). Both models included soil organic matter depth (cm), site type (i.e., burned or unburned), and their interaction term. The count model assumes a Poisson distribution. Values in bold indicate that a significant difference ($\alpha \leq 0.05$) was detected in the model.

	Binomial model				Count model			
Model term	Estimate	Std. error	z-value	p-value	Estimate	Std. error	z-value	p-value
Intercept	0.4735	0.9861	0.480	0.63	0.7270	0.5850	1.243	0.21
SOM depth	-0.3573	0.1507	-2.372	**0.02**	-0.0333	0.0953	-0.349	0.73
Site type	-2.6561	1.0747	-2.472	**0.01**	-0.3077	0.7038	-0.437	0.66
SOM depth * Site type	0.3228	0.1526	2.115	**0.03**	0.0285	0.0979	0.291	0.77

Table 2.3 Summary of results from the zero-altered models, binomial and count, of total black spruce seedlings in unburned sites (df = 4). Both models included soil organic matter depth (cm). The count model assumes a Poisson distribution. Values in bold indicate that a significant difference (α ≤ 0.05) was detected in the model.

	Binomial model				Count model			
Model term	Estimate	Std. error	z-value	p-value	Estimate	Std. error	z-value	p-value
Intercept	-2.1826	0.4272	-5.109	<0.0001	0.4193	0.3913	1.072	0.284
SOM depth	-0.0346	0.0241	-1.433	0.152	-0.0048	0.0224	-0.213	0.832

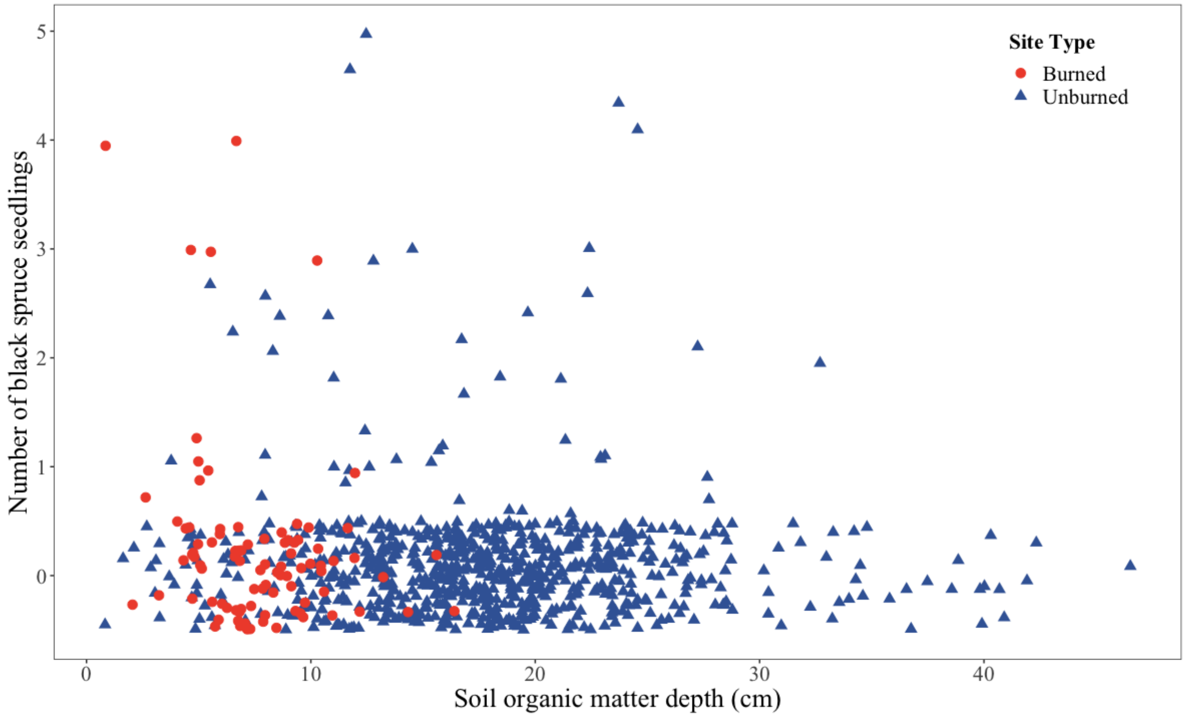


Figure 2.8 The number of black spruce seedlings observed on their respective soil organic matter depth (cm) in burned (n = 25) and unburned (n = 3) sites. There was a negative relationship between natural black spruce regeneration and soil organic matter depth (p-value = 0.02), a difference in natural black spruce regeneration between site types (p-value = 0.01) and an interaction between soil organic matter depth and site type on natural black spruce regeneration (p-value = 0.03). The colour and shape differences represent different site types. A jitter function was applied to see the large number of observations recorded at zero.

2.3.2.2 Seedbed type

Seven different seedbed types were observed: bare, feathermoss, leaf litter, other non-vascular plants, other vascular plants, reindeer lichen (*Cladonia rangiferina* (L.) Weber ex F.H.Wigg), and sphagnum moss. Seedbed types in other non-vascular plants included big shaggy moss (*Rhytidiadelphus triquetrus* (Hedw.) Warnst.), broom moss (*Dicranum scoparium* Hedw.), greater whipwort (*Bazzania trilobata* (L.) Gray), haircap moss (*Polytrichum juniperinum* Hedw.), liverwort (e.g., *Porella* L. spp.), and waxy leaf moss (*Dicranum polysetum* Sw.). Seedbed types in other vascular plants included bunchberry (*Cornus canadensis* L.), creeping snowberry (*Gaultheria hispidula* (L.) Muhl. ex Bigelow), and grass (*Poaceae* spp. Barnhart). These seedbed types were grouped because each had less than 30 observations individually. A total of 1011 seedbed type observations were recorded, and 75 of those observations had black spruce seedlings. There are more seedbed type observations than the total quadrat measurements (n = 840) because finding more than one seedbed type at one quadrat was common. The most common seedbed type was feathermoss, which covered 74.08% of the quadrat areas we sampled, and the least common seedbed types were reindeer lichen (2.47%), other vascular plants (2.67%) and other non-vascular plants (2.87%). However, black spruce seedlings were only observed 6.01% of the time feathermoss was present; whereas, black spruce seedlings were observed 31.03% of the time other non-vascular plants were present. Specifically, haircap moss was the only species in other non-vascular plants where we observed black spruce seedlings (Table 2.3; Figure 2.9).

Feathermoss had the most significant difference between total observations (i.e., observed) and total black spruce presence observed (i.e., expected; Table 2.4; Figure 2.9). Feathermoss was observed 749 times; however, black spruce was only present on 45 of those seedbeds. This difference is significant as shown by a Chi-Square Test (p-value = < 0.0001; Table 2.5). Other non-vascular plants had the smallest difference between total observations (i.e., observed) and total black spruce presence observed (i.e., expected; Table 2.4; Figure 2.9). Other non-vascular plants were observed 29 times, nine of which had black spruce present. This difference is significant as shown by a Chi-Square Test (p-value = 0.001; Table 2.5). Note, other vascular plants were excluded from the Chi-Square Test since they had zero black spruce seedling observations.

Table 2.4 Summary of black spruce seedling presence at each seedbed type recorded in June 2022 in Terra Nova National Park, NL. A total of 1011 seedbed types and 75 black spruce seedling presence observations were recorded. In many cases, there was more than one seedbed type in a single observation. Therefore, black spruce presence was counted for this model rather than the number of observations since there was a high chance of double counting. In 30 of our 75 black spruce seedling presence observations, more than one seedbed type was present. * Other non-vascular plants include big shaggy moss, broom moss, greater whipwort, haircap moss, liverwort, and waxy leaf moss. ** Other vascular plants include bunchberry, creeping snowberry, and grass.

Seedbed type	Number of total observations	Number of black spruce seedling presence	Percentage of total observations	Percentage of black spruce seedling presence
Bare	74	9	7.32%	12.16%
Feathermoss	749	45	74.08%	6.01%
Leaf litter	55	6	5.24%	11.32%
Other non-vascular plants *	29	9	2.87%	31.03%
Other vascular plants **	27	0	2.67%	0.00%
Reindeer lichen	25	3	2.47%	12.00%
Sphagnum moss	55	3	5.34%	5.56%

Table 2.5 Summary of results from the chi-squared tests between total seedbed type observed and black spruce presence observed on the seedbed type. Other vascular plants were excluded as they had no observed black spruce seedlings. Values in bold indicate that a significant difference ($\alpha \leq 0.05$) was detected in the model. * Other non-vascular plants include big shaggy moss, broom moss, greater whipwort, haircap moss, liverwort, and waxy leaf moss. ** Other vascular plants include bunchberry, creeping snowberry, and grass.

	X^2	**df**	**p-value**
Seedbed type			
Bare	50.904	1	**< 0.0001**
Feathermoss	624.20	1	**< 0.0001**
Leaf litter	37.441	1	**< 0.0001**
Other non-vascular plants *	10.526	1	**0.001**
Other vascular plants **	NaN	NaN	NaN
Reindeer lichen	17.286	1	**< 0.0001**
Sphagnum moss	45.632	1	**< 0.0001**

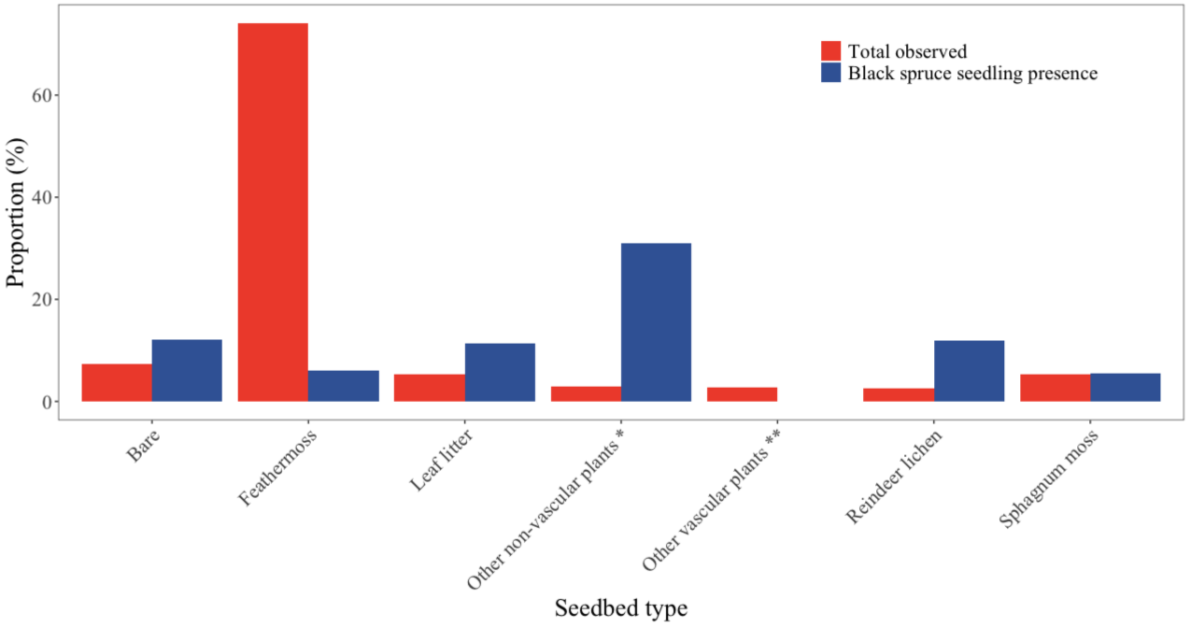


Figure 2.9 Proportion (%) of seven seedbed types observed in total and with black spruce seedling(s) present. A total of 1011 seedbed type observations were observed across 28 sites, and 75 black spruce seedling presence was observed. The most common seedbed type was feathermoss (74.08%), and the least common seedbed types were reindeer lichen (2.47%) and other non-vascular plants (2.87%). However, other non-vascular plants had black spruce present the most (31.03%) compared to the number of times it was observed. * Other non-vascular plants include big shaggy moss, broom moss, greater whipwort, haircap moss, liverwort, and waxy leaf moss. ** Other vascular plants include bunchberry, creeping snowberry, and grass.

2.3.3 The presence of Kalmia angustifolia in black spruce stands

We determined the relationship between *Kalmia* and light availability (i.e., canopy openness) since this abiotic factor can be significantly altered through natural disturbances (i.e., wind-throw) and anthropogenic disturbances (i.e., forest management), which may impact *Kalmia's* growth and establishment. Our analysis revealed that light availability positively affected *Kalmia* stem density (p-value = < 0.0001), meaning more *Kalmia* stems were found when there was higher canopy openness (Table 2.6; Figure 2.10).

Additionally, to evaluate the relationship between *Kalmia* and natural black spruce regeneration, we analyzed the relationship between *Kalmia* stem density and black spruce seedling observations. We observed 735 quadrat measurements with zero black spruce seedlings and 55 quadrat measurements with one or more black spruce seedlings present. The binomial model, which was built upon presence/absence data, and the count data model did not indicate a significant relationship between the number of black spruce seedlings and *Kalmia* stem density (Table 2.7; Figure 2.11. We also wanted to determine if viable seeds are dispersing onto *Kalmia*-dense understories. Visually, viable seeds land on a range of *Kalmia* stem densities, and sites with high seed viability are likely to disperse on a seedbed with a high mean *Kalmia* stem density (Figure 2.12).

Table 2.6 Summary of results from a generalized linear model on *Kalmia angustifolia* stem density to light availability (df = 749). Light availability was used as the predictor variable, and the intercept represents sample quadrats along the transects in unburned sites. This model assumes Poisson distribution. Values in bold indicated a significant difference ($\alpha \leq 0.05$).

Parameter	Estimate	Std. Error	z-value	p-value
Kalmia stem density				
Intercept	1.4257	0.0316	45.16	< 0.0001
Light availability	0.0107	0.0006	18.03	**< 0.0001**

Table 2.7 Summary of results from the zero-altered models, binomial and count, of total black spruce seedlings (df = 4). Both models included *Kalmia angustifolia* stem density. The count model assumes a Poisson distribution. Values in bold indicate that a significant difference (α ≤ 0.05) was detected in the model.

	Binomial model				Count model			
Model term	Estimate	Std. error	z-value	p-value	Estimate	Std. error	z-value	p-value
Intercept	-2.7033	0.1853	-14.585	<0.0001	0.5626	0.1588	3.542	< 0.0001
Kalmia stem density	0.0073	0.0193	0.378	0.71	-0.0334	0.0208	-1.606	0.12

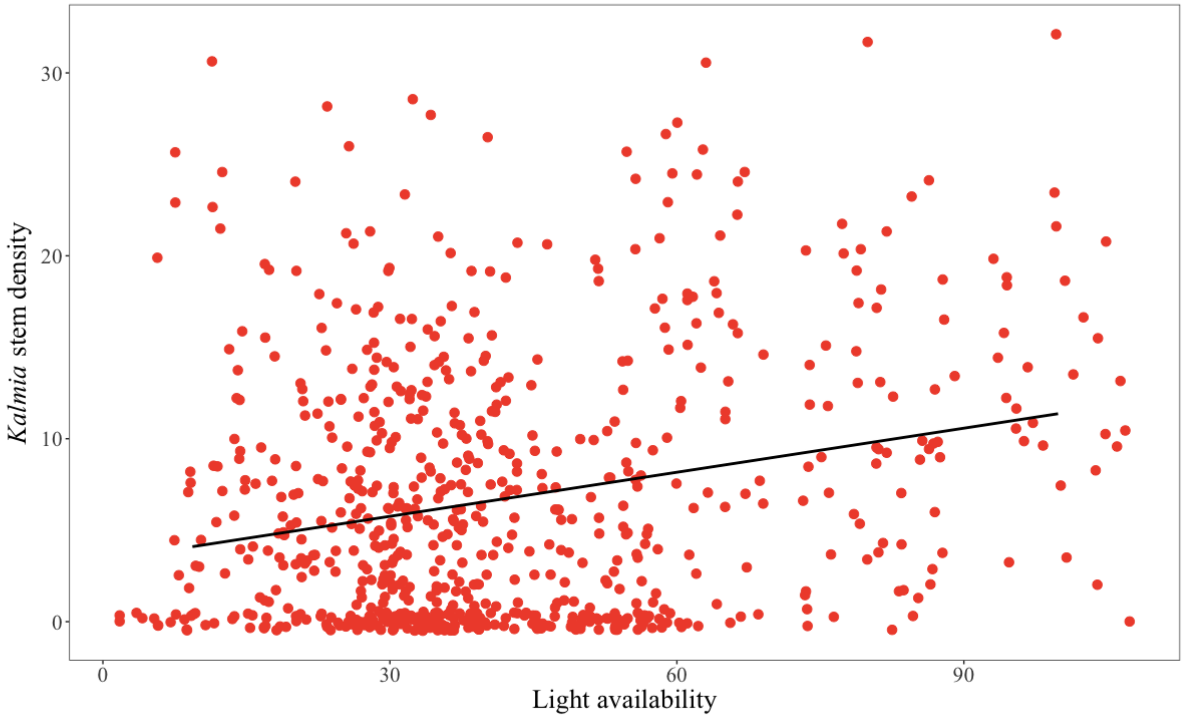


Figure 2.10 Linear regression between light availability (i.e., canopy openness) and *Kalmia angustifolia* stem density. There was a significant relationship (p-value = < 0.0001). Each dot represents a quadrat measurement in unburned sites (n = 750). A jitter function was added to observe overlapping data.

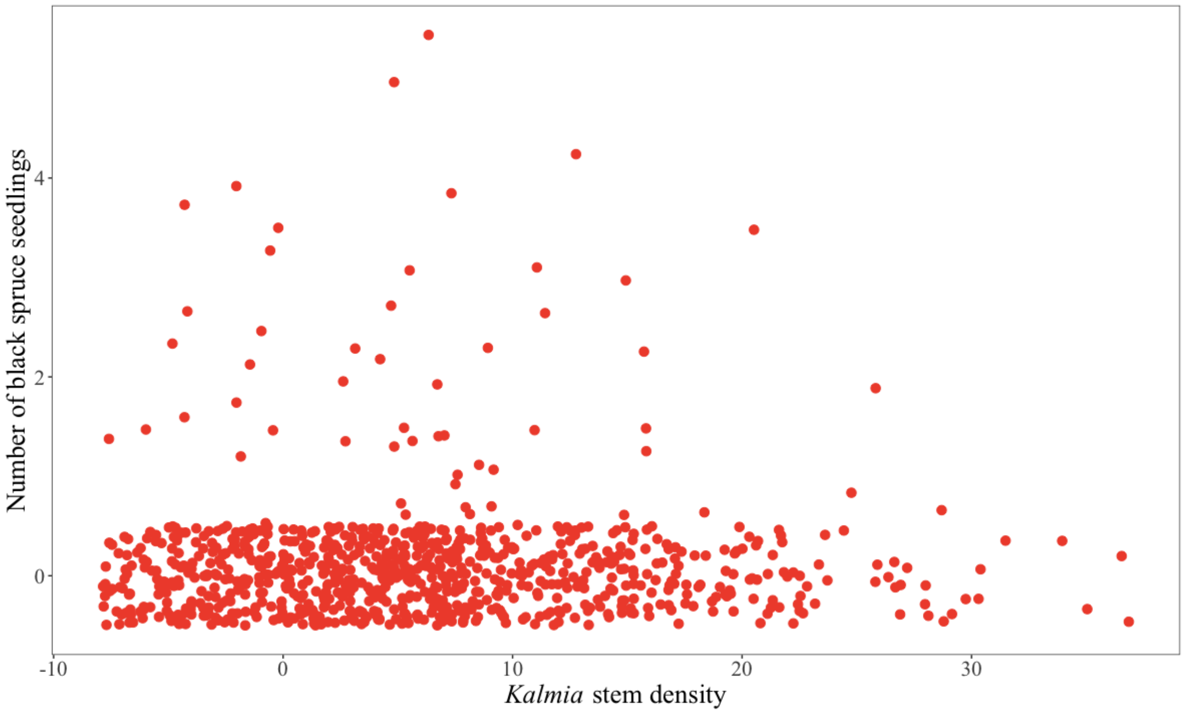


Figure 2.11 Number of black spruce seedlings observed on their respective *Kalmia angustifolia* stem density. Each dot represents a quadrat measurement in burned and unburned sites (n = 840). A jitter function was added to observe overlapping data.

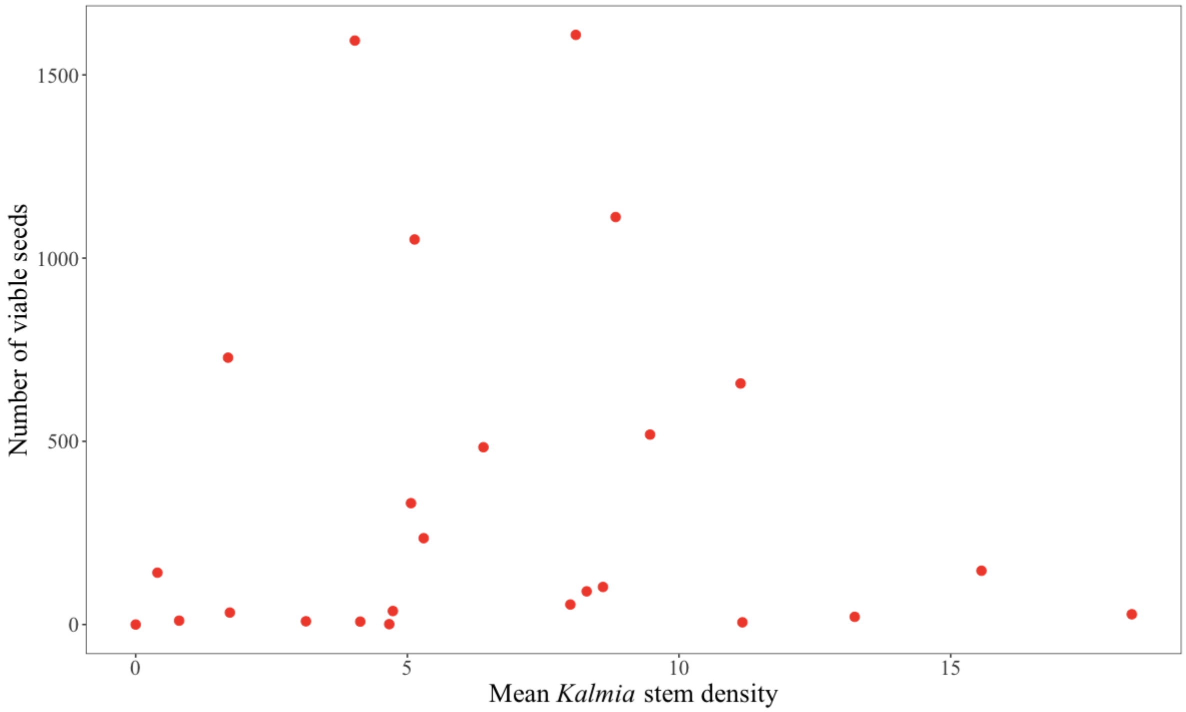


Figure 2.12 The number of black spruce viable seeds per site observed on its respective mean *Kalmia angustifolia* stem density. Each dot represents an unburned site (n = 25).

2.4 Discussion

We identified ecological barriers to black spruce regeneration in Terra Nova National Park, where we found a spatial mismatch between the occurrence of viable black spruce and seedbed suitability for black spruce. Specifically, we found that older black spruce trees in stands with thicker SOM depth generally had more viable seeds. Yet, we found the majority of natural black spruce regeneration was associated with thinner SOM depths observed in burned sites and preferred seedbed types not well represented within the Park. We found a positive relationship between light availability and *Kalmia* stem density. Although we did not find a significant association between *Kalmia* stem density and black spruce regeneration, we found black spruce produce viable seeds across a range of *Kalmia* stem densities, potentially leading to regeneration implications as those seeds disperse onto *Kalmia* seedbeds. Here, we discuss the evidence for these findings and their importance in future forest management within TNNP.

2.4.1 Black spruce reproductive potential

Our observed association between viable seed production, tree age, and SOM depth follows the established cycle of post-fire regeneration, where black spruce individuals increase viable seed production through time, in concert with post-fire thickening of SOM layers. Through time, the stand produces enough viable seeds to self-replace after fire (Viglas et al., 2013), and the fire itself reduces SOM depth and creates a suitable seedbed for black spruce. Yet, a problem emerges when managing for black spruce regeneration in stands not experiencing fire.

As seen in the analysis, mature black spruce with a high number of viable seeds typically have thicker SOM; however, in our analysis with only unburned sites, there was no correlation between SOM depth and the number of black spruce seedlings, which could be explained by layering as it allows black spruce seedlings to establish in thicker SOM depths. Our findings highlight the need for SOM reduction, via fire or other means, for seedling establishment and seedling recruitment.

While there is a potential for the high number of viable seeds in mature stands to overcome the constraints on regeneration created by thick SOM depths, it is more likely that the strong filter created by a poor seedbed creates a spatial mismatch between viable seed production and seedbed quality. As explained, this mismatch is due to a lack of disturbance in the landscape, which allows the SOM layer to accumulate. This accumulation can hinder black spruce regeneration since viable seeds can land on thick SOM, which desiccates quickly, thus significantly reducing natural regeneration (Johnstone et al., 2008; Charron and Greene, 2002). Black spruce can regenerate naturally without fire via layering and occasional seedling establishment; however, it is difficult to regenerate a single cohort stand without fire. Therefore, since seed viability and SOM depth are key ecological filters driving black spruce regeneration, our geographic assessment can help identify site-specific management strategies to increase black spruce regeneration.

The positive, linear relationship we detected between tree age and seed viability also indicates that we did not capture the plateau and decline in reproductive potential with age that we expected (e.g., Greene et al., 1999). We may not have captured over-mature trees (i.e., past reproductive age) in our study because our method of estimating tree age, where the total number of counted rings gave us the minimum age of that individual rather than the actual age. Additionally, there is a possibility we did not core over-mature black spruce individuals, or we sampled clonal individuals of older trees. It is known that TNNP has over-mature trees (Simpson, 2007), and these trees may have lower seed viability, which results in layering (i.e., asexual regeneration) rather than seed regeneration (i.e., sexual regeneration; Morneau and Payette, 1988; Greene et al., 1999). Additionally, several sites had low cone abundance which could be due to squirrel predation, over-mature individuals, or younger individuals in the site, as these are present in TNNP (Power, 2005; Simpson et al., 2007). Future efforts should attempt to capture the full demographic structure of black spruce stands within TNNP.

2.4.2 Seedbed suitability

2.4.2.1 Soil organic matter depth and site type

Despite the presence of viable seeds in stands throughout the Park, we found very few black spruce seedlings. Where black spruce regeneration occurred, SOM depth was the thinnest, as expected. Specifically, we detected a negative relationship between natural black spruce regeneration and SOM depth, more black spruce seedlings on burned sites than unburned sites and an interaction between SOM depth and site type on black spruce seedling abundance. Black spruce is strongly associated with thinner SOM depths with exposed mineral soil for regeneration (Greene et al., 1999; Johnstone and Chapin, 2006), and it is well known that fire (i.e., our burned sites) can create this seedbed (Johnstone and Chapin, 2006; Greene et al., 2007). The burned SOM layer is rich in necessary nutrients and continually stays moist, which prevents black spruce seeds from drying out (Johnstone et al., 2008), which explains why more black spruce seedlings were found on burned sites with thinner SOM depths. However, these seedbeds were largely absent within the Park; therefore, using fire to increase black spruce regeneration might not be beneficial without further management interventions like post-fire seeding or planting.

Moreover, we only assessed three burned sites in relatively close proximity, which could impact our analysis due to our data's lack of sampling and variability compared to unburned sites. We also only sampled sites near the NSF shoreline due to time constraints, and forest quality is known to deteriorate closer to the coast because of increased wind exposure (Damman, 1983). If we sampled closer to the northern perimeter of the fire, which is further inland, we would have seen a higher amount of black spruce stands and potentially more black spruce seedlings (L. Siegwart Collier, personal communication, December 1, 2022).

An important consideration in any assessment of black spruce recruitment is the origin of the seedlings. In unburned sites, it was difficult to determine if the black spruce seedlings we observed originated from seed (i.e., sexual regeneration) or layering (i.e., asexual regeneration). We found several clusters of black spruce seedlings near the base of black spruce trees, and some seedlings were growing from the branches of fallen black spruce trees, which could indicate layering in our sites. As mentioned, layering is more common in over-mature stands with lower seed viability and in stands with long fire-free periods, both of which occur in TNNP (Morneau and Payette, 1988; Viereck and Johnston, 1990; Power, 1996; Simpson, 2007). Layering is not necessarily bad, as it is a natural form of black spruce regeneration (Viereck and Johnston, 1990) and can maintain the population when conditions are unsuitable for sexual reproduction (Viktora et al., 2011). Yet, asexual reproduction, such as layering, removes the opportunity for increasing genetic diversity in a stand undergoing increasing pressures of global change. Regardless of their origin, we still detected little natural black spruce regeneration within TNNP. From our results, black spruce can regenerate under the preferred SOM depths; however, these seedbed types are widely absent across the Park.

2.4.2.2 Seedbed type

We found a spatial mismatch between the dominant seedbed type within the Park and the seedbed type preferred for black spruce regeneration. Feathermoss was the most dominant seedbed type (74%); however, black spruce seedlings were only observed 6% of the time feathermoss was present. There is mixed evidence about whether feathermoss inhibits or facilitates black spruce regeneration. Some have found that feathermoss provides a suitable seedbed for regeneration by maintaining favourable moisture and temperature conditions

(Wheeler et al., 2011; Mallik and Kayes, 2018), whereas others have found that feathermoss inhibits regeneration by drying out too quickly, which can lead to seed desiccation (Prévost 1997; Charron and Greene, 2002; Hébert et al., 2006). A possible explanation for the differences in these findings could be due to climatic factors. Feathermoss may provide a suitable seedbed during wet years but are unreliable and usually dry out before penetration by the seed root (Viereck and Johnston, 1990; Wheeler et al., 2011). Moreover, macroclimate and forest canopy closure can impact seedbed type. For example, canopy openings can favour the growth of sphagnum moss rather than feathermoss (Pacé et al., 2017).

Within TNNP, the majority of the landscape and the sites we sampled were within the CNF ecoregion, which is considered one of the driest parts of the island in terms of soil moisture supply and has the highest black spruce coverage (Damman, 1983). We did find feathermoss dominated the forest floor in our sites; however, it was not associated with high black spruce regeneration. Although feathermoss may facilitate regeneration during wet years, climatic factors are difficult to predict, and most of TNNP is situated in a drier ecoregion. Our results led us to conclude that feathermoss generally inhibits rather than facilitates black spruce regeneration in TNNP.

Other non-vascular plants were only found in 3% of the areas we assessed; however, black spruce seedlings were observed 31% of the time other non-vascular plants were present. Specifically, within the other non-vascular plant seedbed types, black spruce seedlings were exclusively found on haircap moss, which was only observed in our burned sites. Haircap moss is considered an early successional species that can establish following a fire (Fryer, 2008). This bryophyte can penetrate its rhizoids into mineral soil, thus allowing it to colonize sites following a fire disturbance (Kim et al., 2014; Fryer, 2008). Haircap moss is characteristically found on burned mineral soil and in black spruce stands after a fire and can dominate postfire seedbeds one to 15 years after a fire, with feathermoss and sphagnum moss dominating the landscape afterwards (Hawkes, 1983; Fryer, 2008).

Additionally, haircap moss has been found to facilitate black spruce regeneration. Several studies have found that the abundance of black spruce seedlings increased with the presence of haircap moss, aligning with our findings (Charron and Greene, 2002; Greene et al., 2004; Jayden et al., 2006). This association could be due to the ability of haircap moss to retain water and stay moist for longer, reducing the risk of seedling desiccation (Charron and Greene, 2002).

2.4.3 The presence of Kalmia angustifolia in black spruce stands

We did detect that light availability (i.e., canopy openness) was positively associated with *Kalmia* stem density. Light is not only an important abiotic factor for the establishment and growth of *Kalmia* (Mallik, 1993) but also for black spruce (Paquin et al., 1999). However, when an increase in light is achieved through a low-level seedbed disturbance (i.e., logging), the lack of forest floor disturbance can promote the regeneration and growth of *Kalmia* rather than black spruce (Hart and Chen, 2008). An increase in light can also cause an increase in the production of allelochemicals in *Kalmia* (Mallik, 1995), which may, in turn, inhibit black spruce regeneration. Due to *Kalmia*'s regeneration abilities, if present at a site, this could accelerate the growth and establishment of *Kalmia* rather than improving black spruce regeneration since *Kalmia* can establish earlier and more effectively than black spruce (Hébert et al., 2010; Siegwart Collier and Mallik, 2010). This relationship is important to identify since several management options, such as standing-thinning, clear-cutting, and prescribed fire, increase canopy openness but rarely disturb the forest floor in order to create the preferred seedbed quality for black spruce regeneration and fully remove *Kalmia*'s below-ground parts. Therefore, understanding key factors influencing *Kalmia* abundance, such as light availability, is necessary to implement the most appropriate management for black spruce regeneration in TNNP.

However, we did not detect a relationship between *Kalmia* stem density and black spruce seedling occurrence in black spruce stands, which may be explained by the little regeneration we observed. *Kalmia* has various competitive pathways that could interfere and outcompete with black spruce regeneration. By only counting black spruce seedlings and *Kalmia* stem density, our study may not have detected a more complex relationship between the species as *Kalmia* interference on black spruce is likely explained by more than one form of interference (Mallik and Inderjit, 2001). However, the ability of *Kalmia* to interfere with black spruce regeneration has been widely researched (Mallik, 1987; Mallik, 2001; Inderjit and Mallik, 2002; Yamasaki et al., 2002; Mallik, 2022), thus we continued to assess whether viable seeds were dispersing onto *Kalmia* dominated understory communities. We found that viable black spruce seeds are likely to disperse on a range of *Kalmia* stem densities, implying the potential for *Kalmia* interference on black spruce recruitment within the Park. It is essential to include an assessment of *Kalmia* abundance when determining a site's most appropriate management option, as it is well established that *Kalmia* can inhibit black spruce germination, establishment and growth.

2.4.4 Alternative management considerations

In TNNP, fire has been reintroduced to the landscape through prescribed fires in some stands; however, there are challenges related to this management, such as the location of the burns (Simpson, 2007; Walker, 2021), the lack of high-severity fires to create a suitable seedbed for black spruce and control *Kalmia* abundance (Siegwart Collier and Mallik, 2010), resource and time costs (Mallik and Kravchenko, 2016), and implications with using the historical fire regime under current climate changes (Wang et al., 2022). These barriers associated with prescribed fire as stand-alone management may hinder its effectiveness in improving black spruce regeneration while controlling the *Kalmia* population. As a result, TNNP may implement forest management alternatives to improve black spruce regeneration and control *Kalmia* abundance where needed. Our study has provided a more in-depth analysis of the spatial mismatch of two key ecological filters, seedbed quality and seed viability, that control black spruce regeneration and have identified the potential for further *Kalmia* interference on black spruce regeneration in TNNP.

To address and manage this spatial mismatch and *Kalmia* over-abundance in the absence of fire, alternative management considerations can include: (i) physical treatments such as scarification, mulching forest floor, stand-thinning, and seeding and planting seedlings, and (iii) chemical treatments such as spot fertilization and herbicide treatment. These management considerations can be used stand-alone or with other management, including prescribed fire. Specifically, to improve seed viability in sites that have poor viable seed production, management actions should focus on increasing the number of viable seeds on the site, which could be achieved by planting seedlings (Lavoie et al., 2007). To improve seedbed quality in sites that we have identified to have poor seedbeds, management needs to focus on disturbing the thick SOM layer on the forest floor. Management options such as scarification can manually remove the SOM layer and expose the mineral soil for regeneration (Thiffault et al., 2017). However, for many of the sites in our study, seedbed quality and seed viability are insufficient for black spruce regeneration, which may require more than one form of management (e.g., scarification and seeding or planting). Additionally, management that focuses on reducing the

Kalmia abundance in high-cover sites, through actions such as scarification and clipping, may be required (Thiffault et al., 2010; Mallik and Inderjit, 2001).

More broadly, the Resist-Accept-Direct (RAD) framework acknowledges all potential management options when managing an ecosystem undergoing transformations. The RAD framework goes beyond the traditional management approach of resisting ecosystem change and includes either accepting the novel state or directing the transformation to an alternative state (Lynch et al., 2021). Within TNNP, resisting ecosystem changes by implementing prescribed fire is currently being used in some areas; however, resisting these changes might not be possible. TNNP has incorporated the RAD framework into their Forest Management and Restoration Plan, and alternative management considerations can further benefit this plan by being used to resist, accept, or direct the transformations of black spruce stands into *Kalmia* heaths.

Lastly, for any form of management, there should be a focus on specific ecological goals and an assessment of a site's characteristics to implement effective management and prioritize site restoration based on site degradation (Charron and Hermanutz, 2016, 2017). If not, there may be a decrease in management effectiveness and a loss of time and resources. Additionally, Indigenous Knowledge and local community opinions must be considered for all management options at every stage, as doing so will enrich the management's ecological, socio-economic and political outcomes (Uprety et al., 2012; Parks Canada, 2019).

2.5 Conclusions

Our study has provided the geographical distribution of the spatial mismatch between seed viability and seedbed quality, which are essential for the success of black spruce regeneration. We have shown a strong black spruce age-reproductive relationship with older individuals containing more viable seeds and the reliance of black spruce regeneration on thinner SOM depths and seedbed types not well represented within the Park. Moreover, we found a positive interaction between light availability and *Kalmia* and the possibility of *Kalmia* interfering with black spruce regeneration via viable seeds landing on a range of *Kalmia* stem densities. Our findings increase our understanding of key factors influencing black spruce regeneration, which can direct and inform future forest management planning in TNNP.

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Chapter 3: Summary and conclusions

3.1 Summary of findings

In Terra Nova National Park (TNNP), NL, there is little natural black spruce regeneration due to the lack of high-severity wildfires in the landscape (Simpson, 2007). As a result, several areas of the Park are converting from black spruce stands to *Kalmia* heaths (Power, 2000; Parks Canada, 2009). We investigated the effects of fire suppression on black spruce regeneration via two key ecological filters, seed viability and seedbed quality, to help direct forest management within the Park. We assessed 25 unburned black spruce-dominated sites and three burned sites. To analyze the age-reproductive relationship, we collected black spruce cones and cored black spruce trees within each unburned site. At all sites, we measured soil organic matter (SOM) depth, determined seedbed type, and counted black spruce seedlings and *Kalmia* stem density. Our results suggest that mature black spruce stands have more viable seeds than younger stands; however, these stands typically have thicker SOM depths, indicating a spatial mismatch between viable seed production and seedbed quality due to the lack of disturbance in the landscape.

Our findings support evidence that black spruce seedlings prefer seedbeds with thinner SOM depths and other non-vascular seedbed plants (i.e., haircap moss) in burned sites. Yet, these sites are largely absent from the Park, resulting in little natural black spruce regeneration. Lastly, we found that viable black spruce seeds are likely to disperse on a range of *Kalmia* stem densities, highlighting the potential for interference in black spruce recruitment. TNNP can use our findings to implement site-specific management to increase black spruce regeneration.

3.2 Alternative management considerations

Seed viability and seedbed quality of a site must be determined to implement effective and targeted management for black spruce regeneration. With the data collected and analyzed, we created a map showing sites with either high seed viability, high seedbed quality, or neither (Figure 3.1). This map is subjective to what would be considered high seed viability and high seedbed quality, and the thresholds for these filters can change depending on environmental conditions and TNNP's goals. For example, the threshold for seed viability depends on seedbed quality. If a site has a thin SOM depth (2 to 10 cm; Greene et al., 2004; Johnstone and Chapin, 2006), less viable seeds are needed to produce one two-year-old seedling (61 seeds; Johnstone and Chapin, 2006); however, if a site has a thick SOM depth (> 10 cm), more viable seeds are required (383 seeds to produce one two-year-old seedling; Johnstone and Chapin, 2006). For our map, we considered a site to have high seed viability if the site had 383 viable seeds or more and a high seedbed quality if the SOM depth was 10 cm or less (Greene et al., 2004; Johnstone and Chapin, 2006).

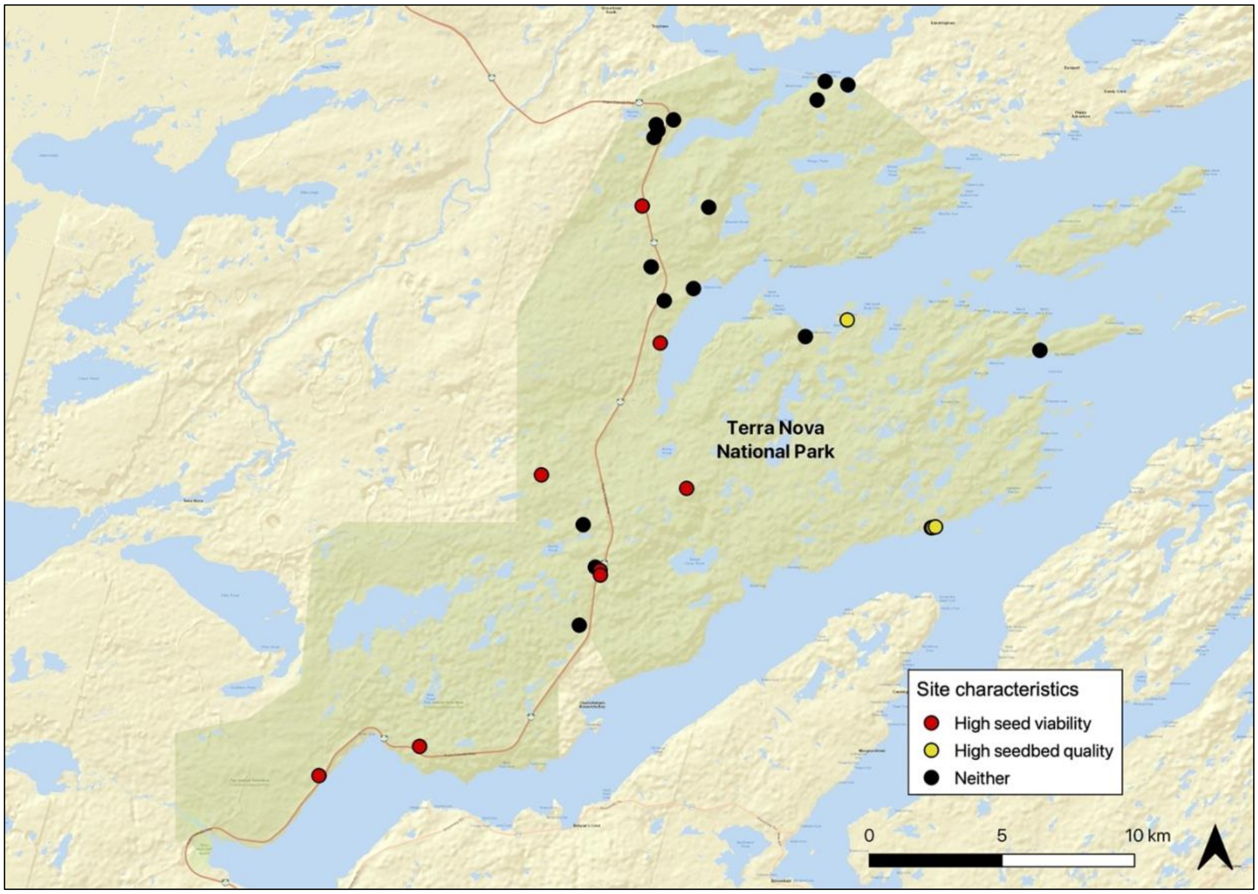

Figure 3.1 Map of Terra Nova National Park, NL, with our 25 unburned and three burned sites. Sites had high seed viability if a site had 383 viable seeds or more (Johnstone and Chapin, 2006), and sites had high seedbed quality if a site had soil organic matter depth of 10 cm or more (Greene et al., 2004; Johnstone and Chapin, 2006).

Within our study, one unburned site and all three burned sites had high seedbed quality; however, the unburned site had low seed viability. Seeding or planting black spruce seedlings would be a management consideration to increase the number of viable seeds at this site. Seeding is when viable seeds are obtained from nearby forestry centers and broadcast across a site by hand or air. Mass seeding helps to overcome several challenges black spruce seeds encounter when germinating and establishing. This management is feasible regarding resource and time costs; however, it does require manual labour as seeding is best implemented by hand. Planting black spruce seedlings requires physically planting seedlings older than six months grown in greenhouses and forestry centers. Planting seedlings does require more manual labour and is more expensive than seeding; however, seedlings have a higher chance of survival and success (Le Goff et al., 2005; Mallik and Kravchenko, 2018). Both seeding and planting seedlings have been effective (Lavoie et al., 2007; Mallik et al., 2010), and these management considerations can be used in remote areas of TNNP with a low commitment since maintenance is generally not required after seeding or planting seedlings is performed on a site.

Eight unburned sites had high seed viability; however, these sites had a poor quality seedbed (i.e., thick SOM depth). Although these sites are ideal for prescribed fire, the location of the sites may hinder the use of this management as they are close to infrastructure, communities and the Trans-Canada Highway. Scarification is a commonly used alternative management option to improve seedbed quality and is a form of manual ground disturbance that reduces SOM and exposes mineral soil (Mallik and Kravchenko, 2016). Furthermore, scarification enhances the quality of the soil, such as improving the temperature, humidity and fertility, which creates a more favourable seedbed for black spruce regeneration (Thiffault et al., 2004). Scarification can be implemented on a small scale using manual equipment (i.e., rotary tiller) or on a large scale using mechanical machinery (i.e., disk- or cone-trenching) at various intensities, such as single- or double-pass over the soil. Several studies suggest disk scarification and double-pass is the most effective method for promoting black spruce regeneration as it is a high enough disturbance to remove the SOM layer and inhibit competing shrubs (Prévost, 1997; Thiffault et al., 2012; Hérbert et al., 2014); however, some have found that single-pass scarification with either disk- or cone-trenching is sufficient to promote regeneration (Prévost and Dumais, 2018). Scarification requires heavy machinery, which may not be possible in remote areas of TNNP, and this management can cause intensive soil disturbance, especially if a double pass method is used, which can lead to soil degradation (Mallik and Kravchenko, 2016). This may not be a desirable management option within TNNP as there are strong public opinions to conserve the natural environment (Mallik and Kravchenko, 2016).

Stand-thinning is another management consideration and can be used stand-alone or in conjunction with scarification. As mentioned, more viable seeds are required for black spruce regeneration when SOM depth is thick; thus, stand-thinning could be used if a site has high seed viability. Stand-thinning can increase canopy openness and resource availability (i.e., light and nutrients) while causing less disturbance than scarification.

The remaining 16 unburned sites had neither high seed viability nor seedbed quality, and intensive management would be needed to improve black spruce regeneration in these sites. One common management consideration is coupling scarification and seeding or planting black spruce seedlings. Several studies have shown the benefits of coupling these management options to support black spruce regeneration (Greene et al., 2002; Hébert et al., 2014; Prévost and Dumais, 2018); however, implementing these two managements can be resource and time costly and can only be executed at accessible sites due to the equipment required (i.e., rotary tiller and skidder).

None of our sites had high seed viability and high seedbed quality, and we are unsure if these site conditions exist within the Park. This finding was expected as the landscape currently does not experience high-level disturbances frequently. If these conditions were found within the Park, a possible management consideration would be an unmanaged “do nothing” approach, as natural black spruce regeneration should occur.

Although we did not find a significant relationship between *Kalmia* and black spruce, *Kalmia* can inhibit and outcompete with black spruce seeds and seedlings (Mallik, 1987; Inderjit and Mallik, 1999; Mallik, 2003). Therefore, if *Kalmia* is found on any site, management must control the abundance for the success of black spruce regeneration. Four unburned sites had a mean *Kalmia* stem density of less than two stems at each quadrat measurement (0.2 m^2); one unburned site and all burned sites had no *Kalmia* present. The remaining 20 unburned sites had a mean *Kalmia* stem density greater than two stems at each quadrat measurement. In these circumstances, management considerations include scarification, seeding and planting seedlings, spot fertilization, and physical *Kalmia* damage (i.e., herbicide, clipping and mulching). Various combinations of these management considerations can be used, and some have shown the benefits of scarification, fertilization and herbicide application for black spruce regeneration in *Kalmia*-dominated sites (Thiffault et al., 2010; Thiffault et al., 2017); however, the use of fertilization is not recommended by some, as *Kalmia*'s extensive root system can uptake these nutrients better than black spruce which further helps their establishment and growth (Thiffault et al., 2004).

Herbicide usage is often problematic from a biocultural perspective in protected areas, and plastic mulch could be an alternative to herbicide usage, effectively controlling *Kalmia* (Krishnapillai, 2009); however, plastic mulch is non-biodegradable and costly, and may also impact key microbiota in the soil. Additionally, scarification may not be desirable due to the high level of soil disturbance; however, micro-site mulching produces less soil disturbance with similar black spruce seedling growth than scarification in the presence of *Kalmia* (Mallik and Kravchenko, 2016). Moreover, any management that increases canopy openness, such as stand-thinning and clear-cutting, is not recommended as stand-alone management since *Kalmia* positively reacts to increases in light availability (Reicis et al., 2020). Most management considerations for controlling *Kalmia* require a high amount of time and resource costs; therefore, determining each site's degradation levels can help prioritize site management (Charron and Hermanutz, 2016).

TNNP should continue to implement the resist-accept-direct (RAD) framework, which encompasses all potential management options. The alternative management considerations described above are to resist the formation of *Kalmia* heaths and promote black spruce stands by improving black spruce regeneration; however, resisting ecosystem transformations may not be possible. For TNNP, resisting these novel changes by implementing prescribed fire in sites undergoing environmental changes may not be advisable, and using alternative management to resist change may require high resource and time costs. Accepting or directing these changes within the Park may be more cost and resource effective (Lynch et al., 2021). Alternative management can be used to accept the transformations of black spruce stands to *Kalmia* heaths via an unmanaged approach or direct changes into a more favourable state.

Whether TNNP resists, accepts or directs these changes highly depends on their management goals. Regardless, the data and results from this study further help with TNNP forest management decisions. While prescribed fire may be constricted to specific areas of the Park (i.e., remote) and may not be the most appropriate management, fire is still important to the landscape; therefore, we recommend following a ‘let it burn’ policy for naturally ignited fires that do not threaten human life or infrastructure to capitalize on the ecological benefits of fire.

Additionally, it is not only important to consider the ecological effects of these management considerations but also the socio-political effects. Local knowledge from surrounding communities greatly benefits forest management by contributing to the success of management and increasing the social acceptability and feasibility of projects (Uprety et al., 2012). Community engagement is key to the success of implementing alternative management considerations.

3.3 Study limitations

One limitation of this study was the accessibility of field sites and time constraints during our fieldwork data collection. As a result, several sites that would have been ideal for this project were not assessed due to their remote location. Additionally, our project compared an uneven number of unburned sites (n = 25) to burned sites (n = 3, visited opportunistically and not part of the original study design). Again, this was primarily due to time and location constraints, and more sites in different locations of the burned area would have provided more variability in the data. Despite the unevenness of burned to unburned sites, our results identified significant SOM depth and black spruce seedling differences in site types.

In addition, our seed viability data would have been more informative if we had a set measurement unit for the number of viable seeds (i.e., collecting cones in a fixed area or counting all cones on trees within a fixed area); instead, we attempted to collect a minimum of 30 cones per site. In the sites we assessed, the number of cones greatly varied and determining seed viability per unit area would have been more time-consuming and would have captured less variability. We consider this a fieldwork trade-off between having a lot of detail for a few sites or less for more sites.

Another limitation of our data collection is the lack of black spruce seedlings we observed which may have impacted our results when analyzing the *Kalmia*-black spruce relationship. Our results did not find a significant relationship between *Kalmia* and black spruce seedlings; however, if we had more black spruce seedling observations, we may have detected a negative relationship between the abundance of *Kalmia* and black spruce seedlings as this relationship is well established in the literature.

3.4 Future study suggestions

Our study assessed various site characteristics necessary for black spruce regeneration, which can be directly applied to management decisions. Park managers can use the data collected to implement targeted, goal-oriented management specific to a site (i.e., increase black spruce regeneration, ‘do nothing,’ etc.). We suggest implementing experimental plots of alternative management considerations at multiple sites with different characteristics to assess the most effective management option. This can be conducted by Park managers or academic institutions (i.e., honour, master, and Ph.D. students) and would further help guide forest management decisions by evaluating each management option's applicability, cost and effectiveness.

Management would further benefit from conducting our field methodology in more sites throughout the Park to capture more spatial variability of seed viability and seedbed quality. This will help implement alternative management considerations and prescribed fire if the Park continues to use this management. Currently, the Park is only using fire in remote areas, which are primarily located in the North Shore Forest (NSF) ecoregion; however, Figure (2.9) from Chapter 2 shows that the NSF ecoregion has lower seed viability regardless of black spruce age, meaning the Park may be implementing prescribed fire in areas that do not have enough viable seeds for stand replacement post-fire; therefore, more seed viability research should be conducted to understand better the spatial distribution of viable seeds within the Park to increase the effectiveness of future prescribed fire. Moreover, further understanding of seedbed quality will be valuable for management efforts, especially for seeding and planting seedlings on favourable seedbeds (Lavoie et al., 2007; Maillk et al., 2010; Maillk and Kravchenko, 2018).

Lastly, *Kalmia* is a natural component of TNNP, and the historical abundance of *Kalmia* is unclear, meaning the transformation from black spruce stands to *Kalmia* heaths may be a natural cycle in the landscape. Therefore, we suggest further studies should focus on obtaining pollen cores to understand *Kalmia*'s historic role in TNNP to manage *Kalmia* in the future.

3.5 Conclusions

Black spruce is essential to TNNP's landscape, and conserving this species is integral to maintaining ecological integrity. Spatially determining the two key ecological filters that control black spruce regeneration, seed viability and seedbed quality, can help direct forest management. Our results indicate that older black spruce stands have higher seed viability; however, due to the lack of disturbance, these stands have thicker SOM depths which can hinder regeneration success. We also found that the preferred seedbed type for black spruce regeneration (i.e., haircap moss) was largely absent from the Park, and feathermoss was the most dominant seedbed type. Lastly, we detected the potential of *Kalmia* interference on black spruce regeneration. Although TNNP wants to resist the transformation of black spruce stands to *Kalmia* heaths through prescribed fire or alternative management considerations, it may no longer be possible under ongoing environmental changes. Several of the sites we assessed are heavily degraded (i.e., high *Kalmia* abundance and low black spruce regeneration), and management to restore black spruce stands may be too costly or ineffective; therefore, our data can be used to accept or direct these changes via the RAD framework. Nevertheless, the data we collected and analyzed can be used for various black spruce management options depending on TNNP management goals.

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Appendix I: Site characteristic data

Table AI.I Characteristics for each site and the corresponding alternative management considerations.

Site	Coordinates	Ecoregion	Mean tree age	Viable seed availability	Mean SOM depth (cm)	Mean *Kalmia* stem density	Alternative management considerations
bS-01	48.6336051 -53.96906438	CNF	65.50	102.48	17.83	8.600	Scarification AND physical *Kalmia* damage WITH seeding/planting seedlings
bS-02	48.63164853 -53.96817574	CNF	62.25	32.63	16.90	1.733	Scarification OR stand-thinning AND seeding/planting seedlings
bS-03	48.62930338 -53.97014201	CNF	83.50	8.84	18.26	3.133	Scarification AND physical *Kalmia* damage WITH seeding/planting seedlings
bS-04	48.63519942 -53.96026614	CNF	72.50	54.60	18.43	8.000	Scarification AND physical *Kalmia* damage WITH seeding/planting seedlings
bS-05	48.46491988 -54.00824352	CNF	80.25	90.56	16.16	8.300	Scarification AND physical *Kalmia* damage WITH seeding/planting seedlings
bS-06	48.5743257 -53.96496499	CNF	68.00	36.80	21.73	4.733	Scarification AND physical *Kalmia* damage WITH seeding/planting seedlings
bS-08	48.64698923 -53.87148239	NSF	64.75	141.44	19.80	0.400	Scarification OR stand-thinning AND seeding/planting seedlings
bS-10	48.64190697 -53.88713889	NSF	74.66	235.62	20.16	5.300	Scarification AND physical *Kalmia* damage WITH seeding/planting seedlings
bS-13	48.58575156 -53.9716419	CNF	71.00	146.74	17.20	15.566	Scarification AND physical *Kalmia* damage WITH seeding/planting seedlings
bS-17	48.49881705 -54.00624762	CNF	68.25	28.00	17.46	18.333	Scarification AND physical *Kalmia* damage WITH seeding/planting seedlings

bS-19	48.42398719 -54.08953143	CNF	82.00	657.85	16.90	11.133	Scarification AND physical *Kalmia* damage WITH seeding/planting seedlings
bS-20	48.57842429 -53.95008535	CNF	83.75	331.20	28.70	5.066	Scarification AND physical *Kalmia* damage WITH seeding/planting seedlings
bS-21	48.51107613 -53.9535779	CNF	106.00	518.40	21.50	9.466	Scarification AND physical *Kalmia* damage WITH seeding/planting seedlings
bS-22	48.51562801 -54.02752167	CNF	73.75	483.93	20.06	6.400	Scarification AND physical *Kalmia* damage WITH seeding/planting seedlings
bS-23	48.60622111 -53.97618136	CNF	79.50	728.32	22.20	1.700	Scarification OR stand-thinning
bS-24	48.4833835 -53.99763448	CNF	111.50	1609.20	19.56	8.100	Scarification AND physical *Kalmia* damage WITH seeding/planting seedlings
bS-25	48.48183101 -53.99747525	CNF	98.75	1593.60	18.30	4.033	Scarification AND physical *Kalmia* damage WITH seeding/planting seedlings
bS-26	48.41411541 -54.14076749	CNF	67.75	1112.03	15.90	8.833	Scarification AND physical *Kalmia* damage WITH seeding/planting seedlings
bS-28	48.55760915 -53.77371026	NSF	107.00	6.00	18.83	11.166	Scarification AND physical *Kalmia* damage WITH seeding/planting seedlings
bS-29	48.56225407 -53.89309108	NSF	85.5	21.00	11.70	13.233	Scarification AND physical *Kalmia* damage WITH seeding/planting seedlings
bF-02	48.6058053 -53.94231963	CNF	70.5	1.00	12.06	4.666	Scarification AND physical *Kalmia* damage WITH seeding/planting seedlings
bF-07	48.6481464 -53.88302795	NSF	95.00	10.56	17.66	0.800	Scarification AND seeding/planting seedlings

bF-16	48.5600746 -53.967005	CNF	63.00	1050.84	15.96	5.133	Scarification AND physical *Kalmia* damage WITH seeding/planting seedlings
bF-18	48.48450227 -54.00006625	CNF	61.00	8.00	13.43	4.133	Scarification AND physical *Kalmia* damage WITH seeding/planting seedlings
bF-11-30	48.5678532 -53.87180058	NSF	32.00	0.00	9.13	0.000	Seeding OR planting seedlings
Fire 1	48.49779 -53.82905	NSF	NA	NA	8.50	0.000	Seeding OR planting seedlings
Fire 2	48.49786 -53.82821	NSF	NA	NA	7.60	0.000	Seeding OR planting seedlings
Fire 3	48.49808 -53.82687	NSF	NA	NA	7.03	0.000	Seeding OR planting seedlings