Fire and tree recovery on seismic lines

by

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Abstract

The world's forests are highly fragmented by linear disturbances, many of which have failed to recover decades after abandonment. Lack of recovery is common, most notably in xeric and hydric forests. Possible mechanisms for this lack of recovery are: life history traits of local species, lack of recent wildfires that encourage tree regeneration, soil compaction, and simplification of microtopography that leads to a loss of microsites for tree establishment. The persistence of these disturbances affects biodiversity, but of particular concern in Canada's boreal forest are the detrimental effects on threatened woodland caribou. Although natural regeneration of trees on linear disturbances occurs in some places (passive restoration), it is not considered to be an effective recovery strategy for restoring disturbed habitat of woodland caribou. This has led to active restoration efforts of silviculture and tree planting where costs can exceed $12,500 (CAD) per km of seismic line. Current restoration models do not, however, consider wildfires that although destroy planted trees, can also initiate early seral conditions that favor natural regeneration. Here, I examine patterns in passive restoration, with and without recent wildfires, possible mechanisms for places that lack recovery, and the effectiveness of active restoration treatments of seismic lines in northern Alberta, Canada. Life history traits, such as fire serotinous-cones, suckering, and shade tolerance, best explain patterns of recovery for many sites. Overall, regeneration density and tree heights on most lines met suggested restoration guidelines (1000 stems/ha and 5-m height) within a 20-year period. Seismic lines in uplands sites may experience moderate levels of compaction, but it did not appear to affect regeneration rates. Except for fens, wildfires promoted increases in tree regeneration density and height on seismic lines, but this requires waiting for places to burn. Because fens burn less frequently and typically experience lower fire severity, as well as losing microtopography during line clearing, tree recovery here is slower than elsewhere, but may still be suitable considering tree density and heights here are naturally lower. Active restoration treatments of seismic lines, and in particular in peatlands with mounding, promoted natural tree regeneration and tree growth over the short-term (< 5-yrs) thus overcoming site limitations (most notably the loss of microtopography), but longer-term studies are needed to assess their long-term success and cost-benefit of passive restoration strategies that depend on natural regeneration and in many cases wildfires.

Preface

This thesis is an original work from Angelo T. Filicetti.

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Table of contents

List of tables

Table 7.A7: Final models for tree height (m) in 9 common ecosites on seismic lines in north eastern Alberta by using the tree age (Age), tree regeneration density (Regen), the quadratic of tree regeneration density (Regen^2), presence of fire (Fire), stand height (Height), the quadratic of stand height (Height^2), the interaction of Age × Fire (A × F), and the interaction of Width × Height (W × H).

List of figures

Chapter 1: Introduction

1.1 A roadmap to the introduction

The introduction starts with a broad and concise overview of the world's forests and their relationship to disturbances. The focus narrows to the topics of disturbances in boreal forests and finally to the main research topic of my thesis on understanding patterns in recovery of trees on seismic line disturbances in boreal forests of Alberta. I end with an outline of my thesis chapters and how they relate to one another.

1.2 World's forests

Throughout history, much of the world's forests have been overlooked and taken for granted resulting in a dramatic decrease in overall forest cover. A third of the Earth's terrestrial ecosystems are currently covered by forests (Keenan et al. 2015) (see Figure 1.1 and Table 1.1). Despite variations in tree cover over different regions and time, there has been a net overall decrease of ~700-1100 million ha of forest cover over the past 300 years (Foley et al. 2005), and notably ~130 million ha in the last 25 years, particularly in the tropics (see Table 1.1). Land use changes in forests are primarily anthropogenic, mostly due to agriculture, and to a lesser extent urbanization and resource extraction (Foley et al. 2005). Changes in forests result in the loss of ecosystem services, including availability of wood products, food, and fresh water; regulation of climate, biodiversity, disturbance regimes, and water cycles; cultural values; and supporting processes, such as nutrient cycling, primary production, and soil formation (Brandt et al. 2013). Depletion of these services likely contributed to the collapse of human societies, such as the Mayan (Oglesby et al. 2010), Easter Island (Rolett and Diamond 2004), and the onset of the Dark Ages at the end of the bronze age (Chew and Sarabia 2016). Today, reforestation is occurring on former agricultural lands, often in the form of plantations, but these novel forest systems do not provide the same services of natural forests (Chazdon 2008).

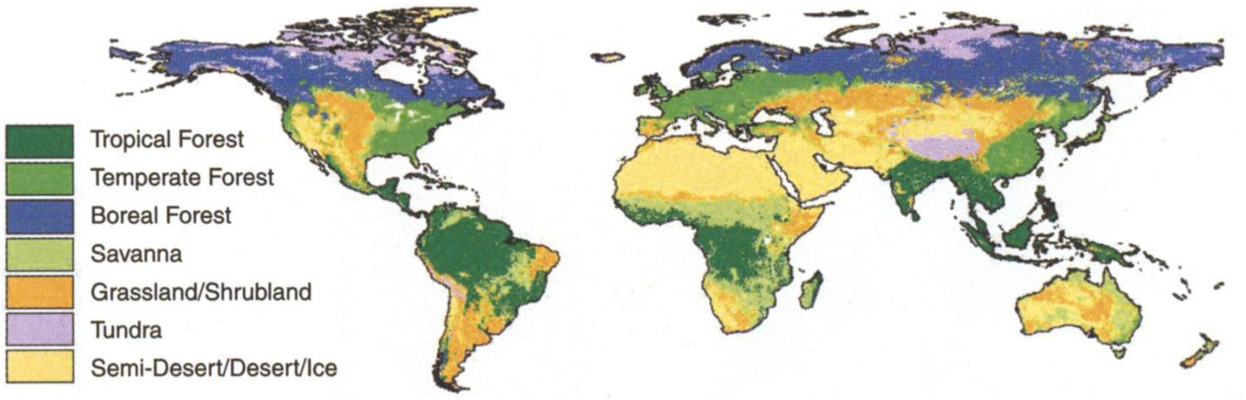


Figure 1.1: Worldwide extent of land-cover. From Foley et al. (2005).

Table 1.1: Distribution of the world’s forested area. From Keenan et al. (2015).

Forest area (10^6 ha).					
Biome	1990	2000	2005	2010	2015
Boreal (inc. polar)	1,219	1,220	1,219	1,225	1,224
Temperate	618	641	659	673	684
Sub tropical	325	325	324	320	320
Tropical	1,966	1,870	1,831	1,798	1,770
Total	4,128	4,056	4,033	4,016	3,999

1.3 Overview of the boreal forest

Boreal forests account for 31% of the Earth’s forests (Keenan et al. 2015). The boreal biome is the most northerly forest, circumpolar in distribution, and bounded by the tree line in the north at different latitudes depending on elevation and distance from the Arctic ocean and at ~50° of latitude in the south (see Figure 1.1). Climate, particularly summer temperatures, limit the northern and southern edges of the boreal biome (Bonan and Shugart 1989). Within the boreal forest, coniferous forests are typical of the more northern latitudes, while deciduous forests are more typical at lower latitudes (Larsen 1980). Similarly, permafrost occurs in the most northern regions and transitioning to discontinuous permafrost to the south until eventually being non-existent in the most southern parts of the region. More favourable conditions for tree establishment and growth are typically found in more southern latitudes reflecting the density of stand conditions going from more closed to open forests as you reach the northern tree line. Boreal forests also occur at high altitudes lying at elevations just below the tree line.

Most broadly, the boreal biome is subdivided in two regions: (1) the Eurasian boreal forest (two-thirds of the biome and primarily within Siberia); and (2) the North American boreal forest (one third of the biome and primarily within Canada) (Taggart and Cross 2009). In the boreal biome, cold and dry winters last longer than 5 months, whereas cool to warm summers last between 1 and 4 months (Larsen 1980). Snow that accumulates over the winter melts in late spring, with little evapotranspiration throughout the summer. Belowground temperatures can remain frozen (permafrost) or cool throughout the summer resulting in poor drainage and growing conditions. The high latitude of boreal forests can lead to daylight hours at, or close to, zero in the winter and up to 24 hours in the summer. The boreal forest is the largest sink of atmospheric carbon among forests, with only half of the carbon in the aboveground plant biomass compared to tropical forests, but 3-times as much carbon sequestered in its soils (Taggart and Cross 2009) (see Table 1.2). Carbon accumulates due to slow decomposition rates in long, cold winters and cool waterlogged summers characterized by anoxic soils.

Table 1.2: Amount of carbon (Pg) stored in different components (aboveground, soil, total) and forest biomes across the globe. From Taggart and Cross (2009).

Forest biome	Aboveground	Soil	Total
Boreal	78	625	703
Temperate	21	100	121
Tropical	159	216	375
Total	258	941	1,199

Diversity of tree species is low in comparison to other forest biomes (de Groot et al. 2013), limited to a few genera of evergreen needle-leaved trees (*Abies* [fir]; *Picea* [spruce]; *Pinus* [pine]), one genera of deciduous needleleaf (*Larix* [larch]), and a number of deciduous broadleaved trees (*Alnus* [alder]; *Betula* [birch]; *Populus* [aspen]). In North America, the most common species are balsam fir (*Abies balsamea*), white spruce (*Picea glauca*), black spruce (*Picea mariana*), tamarack (*Larix laricina*), jack pine (*Pinus banksiana*), lodgepole pine (*Pinus contorta*), balsam poplar (*Populus balsamifera*), and aspen (*Populus tremuloides*). In Eurasia the most common species are: Siberian fir (*Abies sibirica*), Dahurian larch (*Larix gmelinii*), Siberian larch (*Larix sibirica*), Norway spruce (*Picea abies*), Siberian spruce (*Picea obovata*), Siberian pine (*Pinus sibirica*), and Scots Pine (*Pinus sylvestris*). Although floristically simple in trees and vascular plants, boreal forest systems are complex systems due to several interacting environmental factors (Bonan and Shugart 1989), resulting in the evolution of adaptations and life-history strategies to cope with different stages of forest succession (Bergeron 2000).

1.4 Succession in boreal forests

Although climate determines the distribution of boreal tree species at broad scales, edaphic factors (nutrients, moisture content, etc.) filter their occurrence at local scales. Boreal forests follow distinct stages of succession as observed in other forests: stand initiation, stem exclusion, canopy transition, and gap dynamics (Chen and Popadiouk 2002). Species establishment and successional pathways are conditioned by sunlight, soil temperature (including permafrost), cryptograms/seedbed, hydrology, nutrients, and parental seed availability/distance (Bonan and Shugart 1989; Lieffers et al. 1996; Greene et al. 1999) (see Figure 1.2).

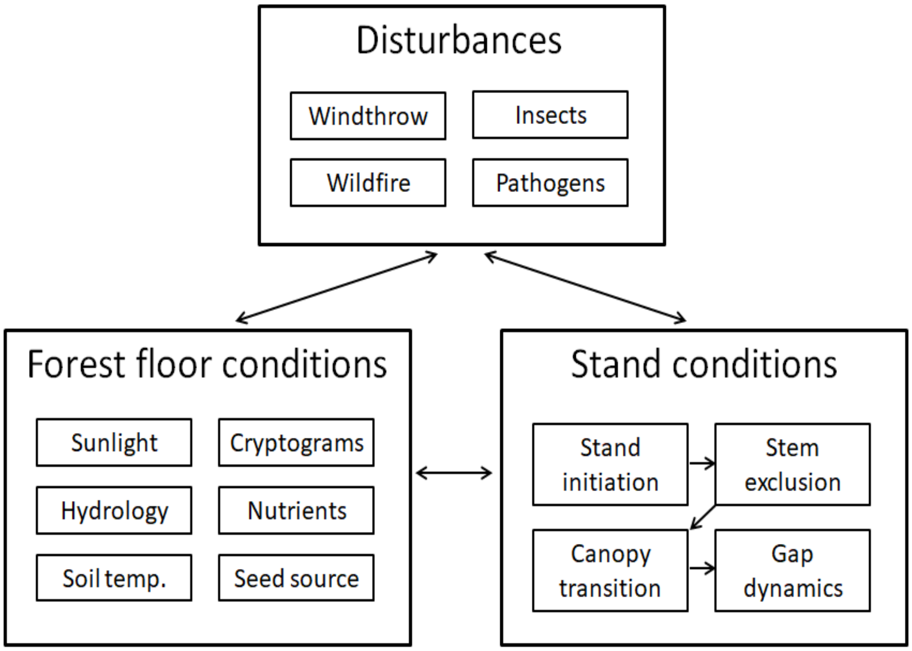


Figure 1.2: Conceptual diagram of the inter-relationships between factors affecting boreal forest succession.

Natural disturbance regimes (wildfires, insect infestations, wind throw) initiate succession dynamics, preventing the formation of old-growth, ‘climax’ forests and maintain a heterogeneous landscape mosaic of different successional phases. Boreal forests that do not experience a disturbance, most notably wildfire, for long periods of time will have trees that are more fire adapted, quicker growing, and shorter-lived replaced by less fire adapted, slower growing, and longer-lived species (Messier et al. 1999; de Groot et al. 2013; Rogers et al. 2015; Cortini et al. 2017). This may result in permanent replacement if return interval is long enough (Desponts and Payette 1992; Lecomte et al. 2006; Senici et al. 2013). The final stage is gap dynamics, where gaps in mature stands due to local disturbances (e.g., wind, insects, disease) increase positively with stand age (Cumming et al. 2000).

1.5 Wildfires in the boreal forests

Wildfire is arguably the most important natural disturbance regime in the boreal forest (Flannigan et al. 2009a): by killing trees and removing biomass on the ground, fire promotes seed beds for germination and growth (Jayen et al. 2006). Yet, wildfire regimes are quite different in the two continents: high-intensity, stand replacing, crown fires are typical of North America, while Eurasian wildfires tend to be at lower intensity (surface fires) and thus lower tree mortality (Rogers et al. 2015). De Groot et al. (2013) found Canadian crown fires accounted for 57.1% of all fires with an average intensity of 6047 kW m^{-1}, while Russian crown fires accounted for 6.5% of all fires (~77% were surface fires) with an average intensity of 4858 kW m^{-1}.

Discrepancies of wildfire regimes in the two continents are a result of the dominant plant species and their life histories, rather than climatic differences. In Canada, species have co-evolved with frequent high-intensity wildfires, developing resilience rather than resistance. For instance, black spruce, the dominant species throughout North America's boreal forest, has highly flammable bark and needle foliage, with low-lying branches that promote surface fires to ladder into the canopy, resulting in more intense wildfires (de Groot et al. 2013). Regeneration does not typically occur through forest floor seed banks as tree seed dormancy in the soil is less than 9 months and the heat from the wildfire will either consume or render the seeds inviable (Greene et al. 1999). Conifers that have aerial seed banks in serotinous and semi-serotinous cones (jack pine and black spruce, respectively) are well adapted to these more intense wildfires releasing seeds *en masse* post-fire and accounting for the majority of the surface area burned (76%) (Rogers et al. 2015). Aspen also regenerates at high rates post-fire, yet does not rely on seed rain but rather on suckering (Greene and Johnson 1999; Frey et al. 2003). Balsam fir and white spruce fill a different niche by avoiding fires yet are able to establish seedlings post-fire with aerial seeds banks that survived the wildfire as shade tolerant species (de Groot et al. 2013).

Eurasia is dominated by species that are adapted to embracing low-intensity wildfires while avoiding high-intensity wildfires, focusing on resistance (Scots pine and larch) and, to lesser extent, outright avoidance of all wildfires (Norway spruce, Siberian spruce, Siberian fir and Siberian pine) (Rogers et al. 2015). Resistance in Eurasian species (Scots pine, Dahurian larch, Siberian larch and to a lesser degree, Siberian pine), is characterized by thick bark to protect stem cambium from heat injury by surface fires (de Groot et al. 2013). Larch, the dominant genera throughout Eurasia's boreal forest, is not easily combustible as it not only possesses thick bark, but is also high in moisture content, particularly in its deciduous needles (de Groot et al. 2013). Differences in wildfire regimes between the two continents has resulted in disparities in tree lifespan, with a maximum of 150–250 years in North America versus > 400 years in Eurasia (de Groot et al. 2013).

1.6 Effects of insect herbivory on boreal forests

Another important source of forest disturbance is insect outbreaks. Insects preferentially seek tree hosts under stress, as stressed plants reallocate energy and resources away from costly defence mechanisms to other metabolic pathways, although continual attacks from insects can increase stress in a healthy tree increasing mortality rates (Bouget and Duelli 2004). Tree exfoliation and death from insect herbivory results in more snags, woody debris, and litter, as well as development of forest gaps. These gaps receive more sunlight and wind, resulting in decreased moisture along forest edges. Insect activity can mediate the occurrence and intensity of wildfires by changing forest structure and microclimate, and the accumulation of dry fuel loads (McCullough et al. 1998). Common defoliators in the coniferous boreal forests are spruce budworm (*Choristoneura fumiferana*) and jack pine budworm (*Choristoneura pinus pinus*), while forest tent caterpillar (*Malacosoma disstria*) and large aspen tortrix (*Choristoneura conflictana*) are typical of deciduous stands (Brandt et al. 2013). Insect herbivory can influence stand dynamics by selective preying on a number of species, progressing or regressing stand development into a later or earlier phase. In eastern Canada, spruce budworm can defoliate coniferous stands interrupting succession towards a more coniferous-dominated forest (McCullough et al. 1998). Climate change can negatively affect trees, as increased temperatures can stress potential host plants, as well as result in greater numbers or migrations of insects

(Logan et al. 2003). Furthermore, as global temperatures increase wildfires frequency, trees that survive wildfires are under higher levels of stress leaving them vulnerable to insect herbivory, particularly from phloem-boring bark beetles or wood-borers (McCullough et al. 1998).

1.7 Wind throw, woody debris, and microsites

Wind throw is dependent on wind speed, which is mostly influenced by local topography, acting against the structural integrity of the tree root anchoring system, which is dependent on soil and root characteristics, and to a lesser extent stand factors (Ruel 1995). Wind throw creates forest gap and habitat heterogeneity, initiating succession and promoting biodiversity (Bouget and Duelli 2004). In turn, forest gaps increase wind speeds and sunlight, heating and drying the forest floor (Bouget and Duelli 2004). The higher wind speeds in forest gaps can increase wind throw; Burton (2002) found that wind throw increased by 46% on inner edges and can be detected > 50 m into a forest. Wind also breaks branches and downs trees either at their roots or along the trunk, typically effecting older stands or stands that have been damaged often by wildfire, insect herbivory, disease, and fungi. Fallen woody debris creates microsites, a food source and habitat for wildlife, and fuel for wildfires. Uprooted trees provide pit-and-mound microtopography and expose belowground soils and biomass (Bouget and Duelli 2004). Ulanova (2000) found 6-25% of the forest surface covered by pit-and-mound microtopography, tree distribution being associated with pit-and-mound microtopography for all forest types with spruce benefitting on mounds and fallen trees. Kuuluvainen and Juntunen (1998) found that seedlings within a forest were more abundant in disturbed microsites created by tree falls, in particular uprooted pits and mounds. Wind throw supplied woody debris and pit-and-mound microtopography was found to provide structural support and suitable habitat for a higher diversity of bryophytes, lichen, and fungi (Jonsson and Esseen 1990; Crites and Dale 1998; Tedersoo et al. 2008). In very wet systems the creation of microsites by bryophytes, particularly *Sphagnum*, in the form of hummocks aid tree establishment and survival (Caners and Lieffers 2014) by overcoming the anoxic saturated conditions near the water table (Lieffers and Rothwell 1987; Lieffers et al. 2017).

1.8 Influences of sunlight in the boreal forest

Sunlight, or more specifically solar radiation within the 400–700 nm, is vital for plants to initiate photosynthesis to store energy into glucose. Plants can perceive sunlight and continually adjust their growth in response to optimize sunlight capture (Franklin 2008). As sunlight arrives in a forest, much of the incoming light is intercepted, reflected, refracted, or transmitted by the canopy, resulting in diffuse light below the canopy. Although the light in the lower canopy is often less in quantity, it can often be of better quality for photosynthetic purposes (Gu et al. 2002). Mature trees compensate these differences by producing lower amounts of leaf area and biomass at these lower layers, relying on fewer, but larger thin leaves. Some species (shade-tolerant) have adapted to take advantage of lower and more diffuse light conditions, being more malleable with allocating resources/growth and ceasing height growth when under shaded canopies (Messier et al. 1999). Light interception is of such importance that trees in shade or in high density stands will regularly allocate resources to growth of stems in such an attempt to utilize sunlight capture (Poorter et al. 2012). Stand density and the ability to intercept sunlight are considered the main factors responsible to stand development, establishment of saplings, and regeneration post-disturbance (Lieffers et al. 1999). Since disturbances are an integral part of the boreal forest, stand development and succession is closely related to competition for sunlight. Stand development usually starts with shade-intolerant early successional species (e.g., aspen, jack pine, birch), see Figure 1.3. These pioneer species eventually develop a closed canopy followed by natural thinning where openings are created for the next successional stage of more shade-tolerant, slower growing, and longer lived species (spruce, fir, etc.). As a forest matures the amount and size of gaps increase, these gaps receive more sunlight where recruitment of new trees develop and succession progresses (Lieffers et al. 1999).

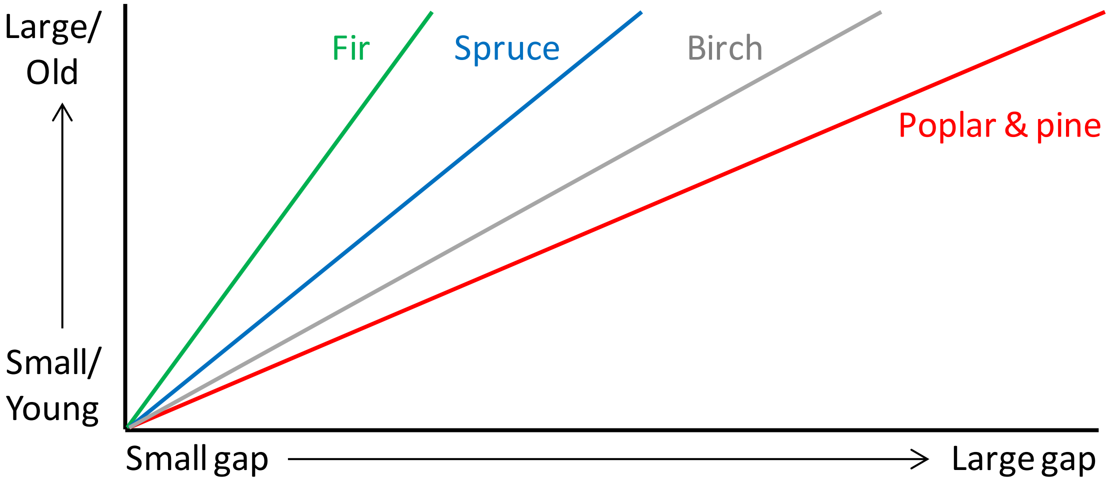


Figure 1.3: Hypothetical relationship of forest gap size to maximum tree height/age of several boreal forest genera. Adapted from Messier et al. (1999).

1.9 Effects of soil and floor conditions (or properties)

Permafrost, low soil temperatures, and high soil moisture typical of the boreal biome has major implications on nutrient cycles and tree growth. These three factors are often interrelated: permafrost is associated with low soil temperatures, it can freeze and lock access to limited nutrients, and inhibit water uptake by plants. Furthermore, permafrost and low soil temperatures impede infiltration, leading to higher soil moisture throughout the growing season. Together, cold and moist conditions reduce decomposition rates and delay nutrient access; permafrost and high water table reduce rooting zones and access to possible nutrients (Bonan and Shugart 1989).

Low nutrient availability is another characteristic of the boreal biome, which often results in slow growth rates for trees. The limited access to rooting depth and surface area of roots/mycorrhizas in many boreal zones exacerbates slow growth, as nutrient poor soils require more rooting depth and surface area to compensate for the poor nutrient status. Furthermore, with limited nutrients (e.g., N and P), fine root biomass decreases (Yuan and Chen 2010). It has been suggested that clear-cutting in sites where nutrients are limited, may further reduce nutrient availability (the stores of nutrients within the trees) and tree growth (Paquin et al. 1998).

Soil nutrient content also influences the vegetation that establishes and thrives in a given location. Evergreens, particularly black spruce, are more successful in nutrient poor sites where the cost of growing annual leaves becomes too costly even with the advantage of a higher photosynthetic rate during the growing season (Givnish 2002). Similarly, white spruce prefers warm, mesic, permafrost-free locations (south slopes and lower latitudes), compared to black spruce which occupies lower productive sites (colder and wetter), due to its lower nutrient requirements and growth potential (Bonan and Shugart 1989). Black spruce has much lower nutrient requirements and can extend its foliage longevity (25–30 years), where even the oldest needles are cost-effective (Bonan and Shugart 1989).

Understory communities can also affect nutrient cycling and overstory succession (Hart and Chen 2006a). Cryptograms, mainly mosses and lichen, are the most common understory community in the boreal forest, and affect the access of nutrients for overstory trees. Cryptograms, especially when in thick mats, can: intercept precipitation and the nutrients therein; lower soil temperatures and decomposition rates; be nitrogen-fixers; absorb nutrients and contain the largest pool of nutrients in the forest (Bonan and Shugart 1989). A thick mat can discourage tree regeneration from seeds and lead to tree regeneration by layering (Paquin et al. 1998). Trees have difficulty in establishing on thick organic soils in boreal forests where there is a decline in survival with organic soils greater than 2.5 cm (Johnstone and Chapin 2006; Greene et al. 2007). Species with larger seed sizes (pine > spruce > deciduous) tend to be more successful in thicker organic soils likely due to larger reserves for root growth and therefore access to stable nutrients and moisture (Johnstone and Chapin 2006). Thick organic mats also inhibit growth. In a study where moss surfaces were disturbed using gardening tools, disturbances significantly improved tree growth on both surfaces (Lafleur et al. 2011). Sites that have more favourable growing conditions for mosses could result in the failure of tree germination and survival by repeated overtopping of the moss surface (Camill et al. 2010).

Trees cannot establish or survive beyond seedlings in very wet conditions due to anoxic saturated conditions near the water table (Lieffers and Rothwell 1987; Lieffers et al. 2017) , therefore bryophytes, particularly *Sphagnum*, are required to create microsites in the form of hummocks (Caners and Lieffers 2014). Although in other conditions, it seems the rhizome matrix created by vascular plants facilitates *Sphagnum* colonization and growth (Malmer et al. 1994). Mosses also seem to fare worse with fewer vascular plants around, which provide shade and higher moisture (Murray et al. 1989; Malmer et al. 2003), therefore there is some uncertainty and debate of which/when mosses are beneficial or detrimental to tree establishment.

Other understory plants can have detrimental effects on tree regeneration, especially when they form a dense layer usually via competition and allelopathy (Royo and Carson 2006).

Lorente et al. (2012) found that ericaceous shrubs compete for soil nutrients and influence soil properties with their phenolic-rich litter, resulting in acidified soils with less available cations and nitrogen. Graminoids can have similar effects on tree regeneration. The grass, *Calamagrostis canadensis*, can compete and inhibit tree regeneration and growth in several ways. *Calamagrostis canadensis* competes for sunlight and nutrients, while its thick growth and litter reduces soil temperatures resulting in reduced access to nutrients and water due to a shorter thaw period and growing season (Hogg and Lieffers 1991). Presence of *C. canadensis* can inhibit aspen sucker emergence by 30% and the suckers that do emerge have 40% less leaf area and are smaller resulting in reduced aspen regeneration and growth (Landhäusser and Lieffers 1998).

1.10 Local anthropogenic disturbances and specifically linear disturbances

In much of the western boreal forest of Canada, the leading source of anthropogenic disturbances is linear in nature, often associated with roads, transmission lines, pipelines, and mineral exploration. Even if some of these disturbances are "soft", or temporary (i.e., for mineral exploration without surface disturbance/loss), expanded development, consistent human use, and slow growth patterns can lead to unforested conditions on the lines decades after they are abandoned (van Rensen et al. 2015). Anthropogenic disturbances, such as these, are a leading cause of forest dissection and fragmentation with the majority (70%) of the world's forests being within 1 km of a forest edge (Haddad et al. 2015).

The most common anthropogenic disturbances in many regions of the western boreal forest, and primarily in Alberta, are seismic lines. Seismic lines are cleared openings (2–14 m), often running for many kilometers and in a grid pattern, being as dense as 40 km/km^2 (i.e., 50 m grid spacing). These lines are created to map underground petroleum reserves through the use of seismic waves. The high density and breadth of seismic lines make them the leading anthropogenic contributor to boreal forest disturbance and fragmentation (dissection) in Alberta (Arienti et al. 2009; Schneider et al. 2010). Many seismic lines have not become reforested decades after their creation, with some lines projected to recover in a century or more (Lee and Boutin 2006). Seismic lines that have been characterized as being in a state of arrested succession are primarily in xeric sandy jack pine or treed peatland sites (van Rensen et al. 2015).

Seismic lines can act as corridors, enhancing movement and porosity within the forest, altering patterns of biodiversity (Riva et al. 2018a; Roberts et al. 2018), (see Figure 1.4). The ecological implication of seismic lines that has gained the most attention is their detrimental effect on woodland caribou (*Rangifer tarandus caribou*), one of the most recognizable species-at-risk in Canada's boreal forest (Dickie et al. 2017a). Seismic lines function as open 'highways' for moose (*Alces alces*), white-tailed deer (*Odocoileus virginianus*), and wolves (*Canis lupus*) leading to increased predation rates on woodland caribou via apparent competition (Latham et al. 2011; Latham et al. 2011; James and Stuart-Smith, 2000). The lack of seismic line recovery, particularly in treed peatlands (woodland caribou habitat), and the grim projections for woodland caribou populations (Dickie et al. 2017a) have led to significant efforts to actively restore seismic lines (Filicetti et al. 2019 [Chapter 4]). In general, restoration efforts have been hindered due to the large costs associated with restoring seismic lines. In northeast Alberta, restoration treatments can exceed $12,500 (CAD) per km of seismic line (Filicetti et al. 2019 [Chapter 4]), which is similar to costs in northeast British Columbia (Johnson et al. 2019). The hundreds of thousands of km of seismic lines that require restoration is believed to be a billion-dollar conservation issue (Hebblewhite 2017). However, wildfires may promote natural tree recovery on seismic lines (passive restoration) over the long-term. On the one hand, wildfires provide the ideal leave-for-natural passive form of restoration for seismic lines by promoting the creation of microtopography (Benscoter et al. 2015), exposing preferential seedbeds (Sirois 1993), and increasing seed rain from fire serotinous and semi-serotinous species (Jayen et al. 2006). On the other hand, wildfires remove preferred winter forage (ground lichens) for woodland caribou for up to 40 years (Skatter et al. 2017; Silva et al. 2019) and the loss of millions of dollars in restoration investments spent on planting trees (Pyper et al. 2014). It may, therefore, be more economically feasible to first understand where active treatments are most needed, where a no cost, leave-for-natural reforestation (passive restoration) strategy could be used, and how natural disturbances like fire can alter conditions that may benefit tree recovery. This is the primary question addressed in this thesis.

1.11 Seismic lines as a disturbance

The exact reason for delayed recovery of seismic lines is unknown, but it is believed to be related to the mechanized creation of seismic lines that simplify microtopography in peatlands (microsites, hummock and hollows); depress its surface leading to a lower depth to water table (flooding); damage/removal of soil, organic matter, and roots; and the life histories of trees present (shade-intolerant, fire serotinous cones, layering, etc.) (see Figure 1.4).

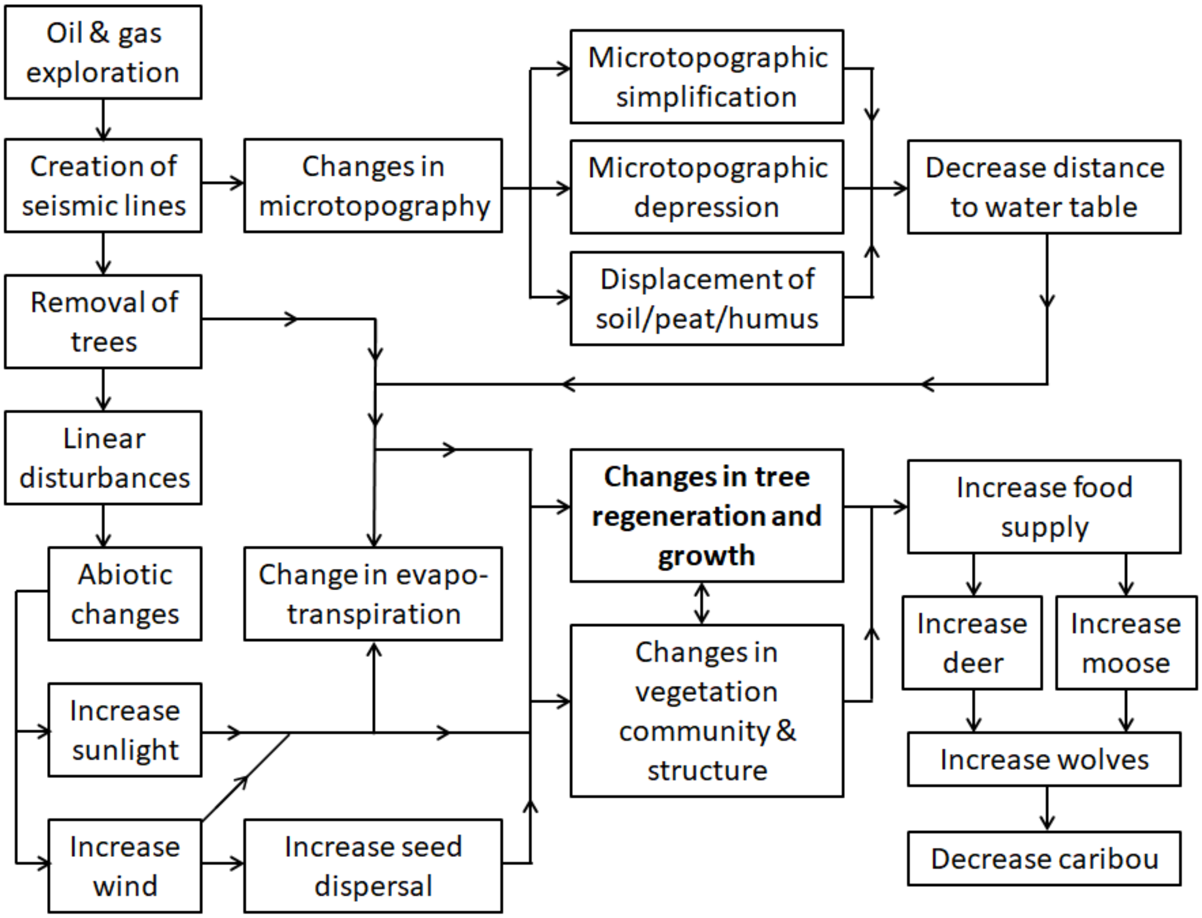


Figure 1.4: Conceptual diagram illustrating the effect of seismic line disturbances on other ecological factors.

Unlike wildfires, seismic line disturbances provide little benefit to tree regeneration (see Table 1.3). Wildfires increase, while seismic lines decrease, microtopography, depth to water table, and coarse woody debris. Wildfires increase seed rain, while seismic lines have an unknown effect, but can increase seed dispersal (of multiple species) by increased wind speeds (Roberts et al. 2018; Stern et al. 2018). Wildfires reduce organic layer depth, while seismic lines, depending on the machinery and operator used, can maintain or reduce organic layer depth. If organic layer depth is reduced, it can become waterlogged, while fine mulching can increase organic layer and cryptogram colonization (Crites and Dale 1998). Root damage, depression, and compression can lead to difficulties in layering/suckering, layering is more common in sites not experiencing wildfires and usually occurs where seed germination and seedling growth is impaired (Greene et al. 1999). Layering/suckering is common for aspen, balsam poplar, black spruce, and cedar, while being less common for balsam fir, tamarack, and white spruce and rare for pines (Greene et al. 1999). Aspen and balsam poplar can have suckers spreading 6–10 m from the parent, but black spruce is much more limited to a few meters (Greene et al. 1999). It may therefore be that this new form of disturbance arrests tree succession by alterations to the ground surface, which the boreal forest is not adapted to.

Table 1.3: How differrent disturbances affect common factors of tree establishment and growth. The black upwards arrow, red downward arrow, and blue sideways arrows signify an approximate increase, decrease, and neutral change respectively.

Factor	Wildfire	Insect	Windthrow	Seismic line
Sunlight	↑	↑	↑	↑
Seed rain	↑	↔	↔	↔
Nutrients	↑	↑	↑	↔
Coarse woody debris	↑	↑	↑	↓
Microsites	↑	↑	↑	↓
Seedbed quality	↑	↑	↑	↓
Moisture	↓	↓	↓	↑
Depth to water table	↑	↔	↔	↓

1.12 General methods & study design

Sampling of seismic lines was dependent on seismic line type, forest type, ecosite, fire history, and access. A number of strategies and stratifications were used to emphasize sampling across different forest and ecosites within recently (< 23-years) burned or unburned stands. Below is a description of site selection by each of the key study variables.

1.12.1 Seismic line type

There are two main categories of seismic lines: (i) continually human disturbed, this includes highways; paved, gravelled, and dirt roads; continual/regular and recent ATV usage from recreational users or industry; continual/regular and recent re-cleared seismic lines; and (ii) minimal human disturbed, this includes seismic lines that have had an opportunity to regenerate trees and that are not continually and/or severely disturbed by human use. Only minimal human disturbed seismic lines were sampled in this thesis. Seismic line type could only be verified in the field. All seismic line access routes, or other features, feeding into a site required having minimal to no recent disturbances (with the exception of wildfire and wildlife trails).

A second classification of seismic lines relates to their size and to some degree history. This classification is: (i) 2D lines, also called legacy lines, which tend to be older (created prior to 1995) and importantly are wider (4–12 m wide) with grid spacing often being ≥ 300 m; and (ii) 3D lines, also called low impact seismic lines, which tend to be created after 1995 and are narrower (2.5–4 m wide) and more dense (grid spacing being ≤ 300 m and in some places grid spacing as dense as every 50 m in both east-west and north-south directions). Throughout this study both 2D and 3D lines were sampled, although the more accessible sites in this study tended to have more 2D lines. 2D lines also had a longer fire history which was a focus of this work. Rather than categorically classify lines into an either-or class (2D vs. 3D), I instead used line width as an explanatory variable for tree regeneration throughout the thesis. Although we would expect age of line to be an important factor, width of line was consistently more important than age for tree density, but not tree heights.

1.12.2 Forest type and ecosite

Forests were stratified into different stand types using the Ducks Unlimited Enhanced Wetland Classification map (Ducks Unlimited Canada 2011) and field sites further classified by ecosites (individual chapters generally focus on closely related ecosites) based on nutrient and moisture regimes. Specifically, a total of nine ecosite combinations were studied (i.e., poor-xeric, poor-mesic, poor-hydric, medium-xeric, medium-mesic, medium-hygric, medium-hydric, rich-hygric, and rich-hydric) using field interpretations of the Alberta Biodiversity Monitoring Institute ecosite classification guidelines (Alberta Biodiversity Monitoring Institute 2018) (Table 1.4). Google Earth and Bing Maps were also used to guide site locations prior to field visits. Sampling effort reflects the approximate area of each ecosite within the study area, with less sampling effort to rarer ecosites. If for any reason a decision needed to be made between two sites, the ecosite that was rarer was sampled to obtain enough replicates for uncommon ecosites.

Table 1.4: Defintion of forest types (ecosite) using common overstory and understory species and mature stand heights.

Ecosite	Common overstory species	Common understory species	Mature height (m)
Poor xeric	Jack pine	Bearberry, lichen	15 (0.48)

Poor mesic	Black spruce	Bog cranberry, feather moss	12 (0.80)
Poor hydric	Black spruce	Bog cranberry, cloud berry, peat moss	7 (0.55)
Medium xeric	Aspen & Jack pine	Bearberry, hairy wildrye, buffaloberry	18 (1.63)
Medium mesic	Aspen & White spruce	Squashberry, bunchberry, buffaloberry	20 (0.65)
Medium hygric	Balsam poplar & White spruce	Horsetail, willows, currants	21 (2.31)
Medium hydric	Black spruce & Tamarack	Bog cranberry, graminoids, peat moss	8 (0.40)
Rich hygric	Balsam fir & White spruce	Red osier dogwood, thick feather moss	21 (1.94)
Rich hydric	Black spruce & Tamarack	Graminoid dominance, peat moss	8 (0.79)

1.12.3 Wildfire history

Sampling sites were stratified across several burn years (exceptions being chapter 2 where only one wildfire was sampled, and chapter 4 where no wildfires were sampled). Specifically, I separated sites into two categories: (i) recent wildfires ≤ 23 years old (I define hereafter as 'burnt'); and (ii) sites that did not experience a wildfire in over 65 years and thus are considered mature forests (I define this group as 'unburnt' although certainly these sites have burned at some point in their history). Six wildfires were selected due to their large size (> 40 km^2) that allowed at least 12 sample sites, age distribution (1–23 years old prior to sample collection), as well as accessibility. The age distribution of wildfires, ≤ 23 years old, was chosen for three reasons: (1) much older wildfires have little evidence of fire severity; (2) wildfires needed to occur after seismic line creation since my question was about the effects of wildfires after line creation; and (3) the study area had no large wildfires between 23 and 30 years old.

Fire severity, time since last wildfire, and simply the presence-absence of recent (≤ 23 yrs.) wildfire was obtained using provincial spatial wildfire databases (Alberta Agriculture and Forestry 2017). This layer was not always accurate in quantifying fire severity and in some cases fire presence at local scales, therefore, fire severity was collected in field in the adjacent stand. Specifically, fire severity was defined using percent overstory tree mortality with sites used only when fire severity was similar for the seismic line and adjacent forests on both sides of the line. If possible, a distribution of fire severity was a secondary goal, but some wildfires where seismic lines occurred did not vary much in fire severity. Therefore, if for any reason a decision needed to be made between sampling two sites, the site with a rarer fire severity was sampled.

1.12.4 Locating final field sites and sampling

Locations were selected from a random set of available possible locations (see requirements listed above and below), with each site requiring consistent forest stand conditions (i.e., height, density, age) across an area large enough to be sampled (≥ 30 m radius around the paired plots). Sites were at least 400 m apart, to reduce spatial autocorrelation and avoid pseudo-replication, with a preference to have sites on separate seismic lines and only on the same line and/or within 400 m unless in different wildfire severities (> 30% difference), forest types (ecosites), stand heights (40% difference with a minimum of +/- 4 m), orientation of lines (> 45° difference), and > 60 m distance from any other site on the seismic line. Sites were selected with the aim of maximizing the above requirements, but certain regions (i.e., a wildfire) had limited possibilities so maximizing sites became a higher priority. Regardless, many sites were much greater than 400 m apart and the overall region studied with plots spanned over an area > 30,000 km^2. The starting locations of plots on seismic lines, once sites were located, were based the requirements above and/or a random number generated, indicating steps to be taken, and/or on a random toss of a metal stake. Each plot represented a 30-m belt transect with the seismic line transect located along the center of the seismic line, while the adjacent forest paired control transect was located 25 m into the adjacent forest running parallel to the seismic line. A coin toss was used to randomly assign which side of the seismic line the adjacent forest control plot was located. All regenerating trees were counted in 1-m wide belt quadrat along the transect line and 2-m wide belt quadrat for large trees (see individual chapters for thresholds). Orientation (bearing) and width of each seismic line was recorded for each site. Additional stand information was collected for the adjacent forest control plot, including fire severity (defined as percent overstory tree mortality), stand basal area by species using a 2-factor metric prism (m^2/ha) at the midpoint of the adjacent forest transect (15 m line distance), stand age of representative mature trees in the same plot using dendrochronological aging via tree cores at DBH (diameter at breast height), and representative tree height using a Haglof Vertex IV (Sweden) hypsometer.

1.12 Thesis outline

The objective of this thesis is to discover why certain seismic lines are not recovering and if wildfire or mechanical site preparations can remedy this issue. The thesis is organized in chronological order as the studies were completed (see Figure 1.5): Chapter 2 investigates tree regeneration density on seismic lines in xeric sandy jack pine forests and how regeneration on these lines is almost completely dependent on aerial seedbanks of serotinous jack pine; Chapter 3 describes the simplification and depression in microtopography from the mechanical creation of seismic lines; Chapter 4 examines the effectiveness of restoration treatments (mechanical site preparation and tree plantings) of seismic lines in treed peatlands; Chapter 5 investigates treed peatlands regeneration density on seismic lines and the effects of altered microtopography and wildfire; Chapter 6 investigates soil compaction in mesic upland forest seismic lines, as well as regeneration density and the effects of compaction and wildfire; Chapter 7 is an amalgamation of Chapters 1, 5, and 6 describing occurrence, abundance, and new to the other chapters growth trajectories across all ecosites in northeast Alberta based on seismic line (orientation, width, etc.) and stand characteristics (height, basal area, etc.) with a major focus on geospatial predictors (annual temperature and precipitation, compound topographic index, etc.) to allow regional predictions at local scales.

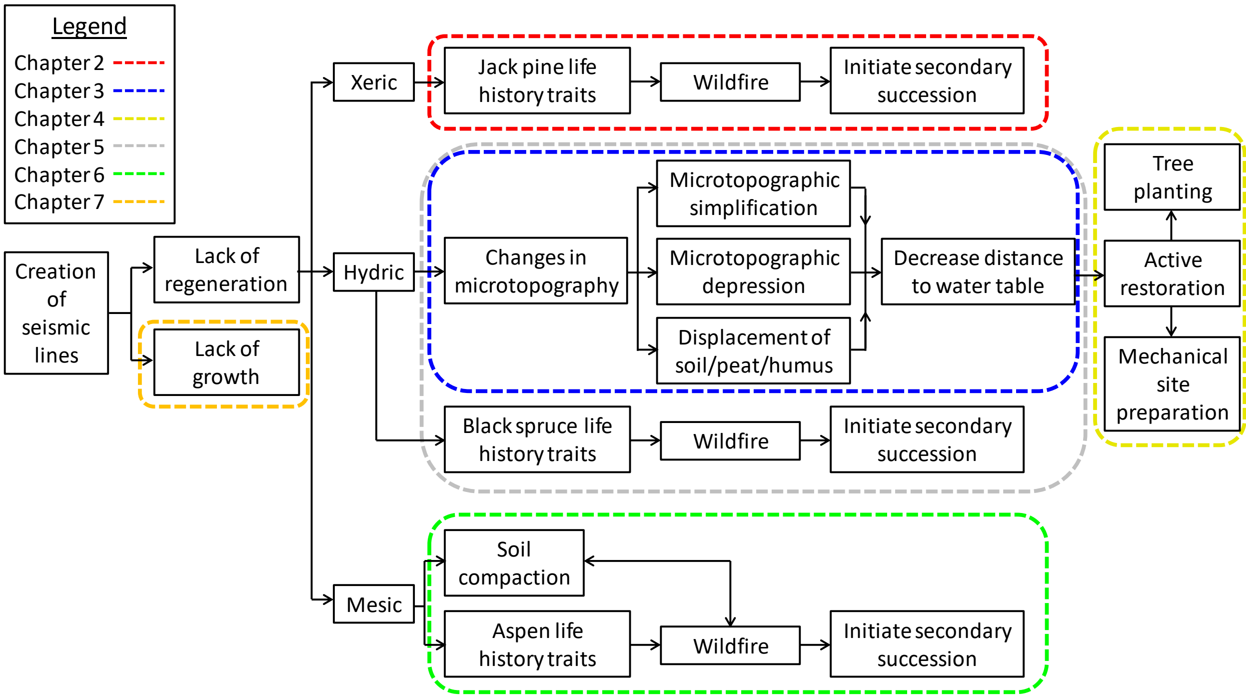


Figure 1.5: Overview of thesis chapters based on ecosite, factors limiting tree regeneration, disturbances, abiotic factors, life history traits, and restoration.

Chapter 2: Fire and forest recovery on seismic lines in sandy upland jack pine (*Pinus banksiana*) forests

2.1 Abstract

Networks of narrow linear (~3–12 m wide) forest disturbances used for petroleum exploration (seismic lines) are common throughout Alberta's boreal forest. These 'seismic' lines have often failed to recover trees decades after their initial disturbance, especially within treed peatland and jack pine (*Pinus banksiana*) forests. This has led to regional increases in forest fragmentation contributing to declines in threatened woodland caribou. Restoration of seismic lines to forests is now a top priority for conservation and recovery of woodland caribou, but is expensive and often ignores the occurrence of wildfires that may destroy restoration investments (planted trees), yet also recruit trees. This is especially relevant to jack pine forests that burn more frequently than other forests and depend on moderate to high intensity fires to release seeds *en masse* from their serotinous cones. Although much is known about jack pine tree recruitment following fire, little is known about patterns of tree recovery on seismic lines and how this varies with fire severity, line width (forest gap size), and line orientation. Here, we examine natural tree recovery across a gradient in fire severity (defined as percent overstory tree mortality) with different seismic line characteristics (forest gap width and orientation), as compared to adjacent forest stands, in jack pine forests 5-years post-fire in northeast Alberta, Canada. Overall, jack pine regeneration was consistently 2-fold higher on seismic lines compared to adjacent burned forests with stem density increasing with fire severity in both sites, especially when fire severity was greater than 40%. We suggest that the observed increases in tree regeneration on seismic lines may be due to (1) removal of biomass and exposure of mineral soils on seismic lines creating more favorable conditions for jack pine seeds and seedlings; and/or (2) increases in available light resulting in better growing conditions and survival for this shade-intolerant species. Finally, we suggest that natural recovery (passive restoration) of seismic lines should be expected post-fire in jack pine stands and thus active restoration of these sites through silviculture and tree planting may not be the wisest use of limited restoration dollars if fires are locally common.

2.2 Introduction

Oil sands exploration and extraction in northern Alberta, Canada have affected the boreal forest in a number of ways, particularly through fragmenting forests with roads, pipelines, transmission lines, and drilling well pads. However, the largest anthropogenic contributor of forest fragmentation is seismic lines (Arienti et al. 2009; Schneider et al. 2010) often reaching densities of 40 km/km^2 (i.e., 50 m grid spacing). Seismic lines are narrow (3–12 m) linear corridors (Figure 2.1) designed in a network of repeating corridors where trees are removed for the purpose of petroleum exploration (seismic assessments). These disturbances can simplify microtopography and compact the soil surface leading to failures in tree regeneration (Lee and Boutin 2006; Caners and Lieffers 2014; van Rensen et al. 2015; Lieffers et al. 2017). This has contributed to changes in wildlife populations and more broadly, biodiversity (Timoney and Lee 2001; Hooper et al. 2005; Lee and Boutin 2006; Kemper and Macdonald 2009a, 2009b; Caners and Lieffers 2014). The most high-profile species-at-risk in Canada's boreal forest are woodland caribou (Environment Canada 2012). Although seismic lines are generally avoided by caribou (James and Stuart-Smith 2000; Dyer et al. 2001, 2002), they are favored by wolves increasing their movement efficiency in caribou habitat (James and Stuart-Smith 2000; Latham et al. 2011a). This can reduce survival rates of caribou and as a consequence contribute to caribou population declines (James and Stuart-Smith 2000; Dyer et al. 2001, 2002; Latham et al. 2011a). Mitigation efforts are now extensively being used to address this issue by restoring tree growth on seismic lines or, over shorter periods, reducing wolf use of lines by adding structural barriers to movement. Long-term restoration goals hinge, however, on recovery of trees on seismic lines.

Costs of these active restoration treatments are high averaging \$12,500 (CAD) or more per km of seismic line with treatments involving site preparation (mounding, ripping) and tree planting. Conversely, passive restoration strategies for seismic lines that rely on natural rates of reforestation (i.e., leave-for-natural) have no direct costs, but depend on extended timeframes of recovery (Lee and Boutin 2006; van Rensen et al. 2015). Understanding where reforestation is occurring is therefore a priority in planning and prioritizing the location of restoration activities. Wildfires, the largest contributor to boreal forest disturbance, are one possible leave-for-natural passive form of restoration, but also represent a risk to investments in active restoration treatments where tree planting occurs. Much less is known, however, on how wildfires affect recovery rates of seismic lines despite being a major driver of successional changes in the boreal forest and a risk or opportunity for restoration.

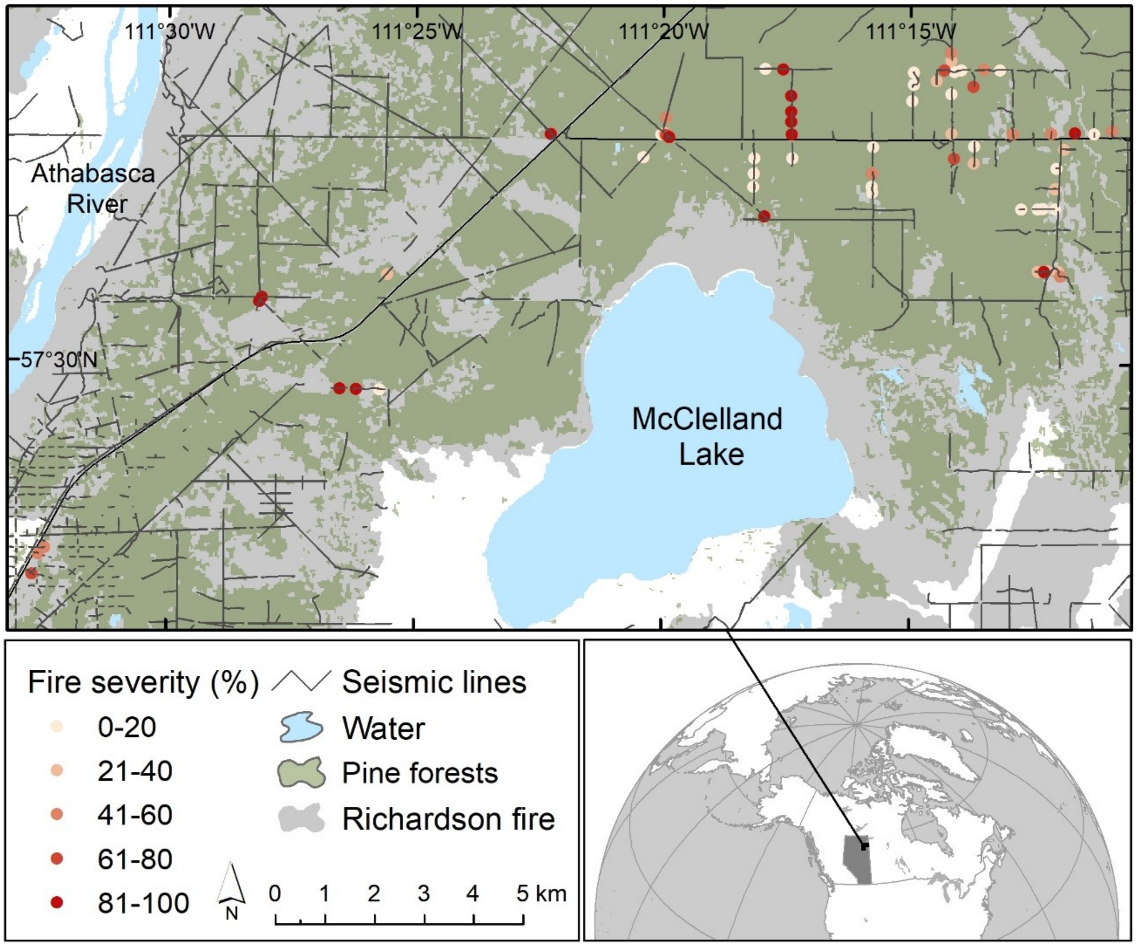


Figure 2.1: Location of study area in northeast Alberta, Canada (inset map), the location of study sample sites relative to fire severity as measured by overstory tree mortality (light red to red square symbols representing the fire severity gradient), location of seismic lines, location of 2011 Richardson fire in gray, and pine forests in dark green for where it burned (most places) or in very few location light green where unburned. Each site represents a pair of plots with one being on the seismic line and the other in the adjacent forest stand. Note that some sites were within 200 to 400 m of each other when fire severity levels differed, stands varied, or there were gaps in the seismic line disturbance.

Seismic line disturbances in xeric sandy jack pine (*Pinus banksiana* Lamb.) forests are one of the two forest-types in northeast Alberta characterized by being in a state of arrested succession (van Rensen et al. 2015). Yet this may be an overgeneralization that is dependent on the time scale examined since jack pine cones are serotinous and typically release their seeds *en* *masse* only after moderate to high intensity fires (Ahlgren and Ahlgren 1960; Cayford and McRae 1983; Lamont et al. 1991) with fire return intervals for jack pine forests in northeast Alberta typically being 28-54 years (Carroll and Bliss 1982; Larsen 1997; Larsen and MacDonald 1998). A more informed test of whether these seismic lines will naturally regenerate is to therefore examine patterns of post-fire recovery. If fires promote recovery of seismic lines in conditions similar to adjacent stands (a form of passive restoration), it would have major implications for planning restoration activities in the boreal forest even if fires are not directly used as active restoration treatments.

In this study, we examined recovery dynamics on seismic lines and adjacent paired forest controls in jack pine forests by fire severity (percent overstory tree mortality), forest stand conditions (age, height, and basal area), and seismic line characteristics (forest gap width and orientation). Specifically, we tested whether fire naturally recovers seismic lines or whether other factors (small gap widths, simplified microtopography, etc.) restrict regeneration compared to adjacent paired forest controls. On the one hand, seismic lines post-fire may provide more exposed mineral soil, sunlight, and wind (seed dispersal), as well as less competition thus favoring tree regeneration for shade-intolerant species like jack pine. On the other hand, micro-terrain on seismic lines may be simplified during construction of seismic lines offering fewer microsites for conditions that would favor tree recruitment following fire, especially under drier post-seed dispersal conditions. We address these questions by examining jack pine and other tree regeneration 5-years post fire on seismic lines compared to adjacent forests in northeast Alberta, Canada.

2.3 Methods

2.3.1 Study area

The study area consists of 100 km^2 of boreal forests within the Regional Municipality of Wood Buffalo and the Athabasca Oil Sands of northeast Alberta. It is approximately 115 km north of Fort McMurray and within a 15-km radius of the west and north ends of McClelland Lake (57º 31′ 56″ N, 111° 21′ 40″ W, Figure 2.1). The area lies on the south end of the Athabasca Plain where the dominant soil is dystric brunisols with surface topography characterized by plains and sandy dunes deposited by eolian forces (Natural Regions Committee 2006; Smith et al. 2011). In most areas, including the focus of this study, the former glacial dunes and sand plains are stabilized with vegetation. Jack pine is by far the dominant tree species with other trees and tall shrubs including trembling aspen (*Populus tremuloides* Michx.), saskatoon (*Amelanchier alnifolia* (Nutt.) Nutt. ex M. Roem.), green alder (*Alnus crispa* (Ait.) Pursh), and pin cherry (*Prunus pensylvanica* L. f.).

The majority of the study area was burned in 2011 by the Richardson Fire (Figure 2.1), which was one of the largest fires documented in western Canada burning an area of 576,000 ha.

Understory species were described for the area 4-years post fire by Pinno and Errington (2016) with species richness highest in low severity burns and plant cover lowest in high severity burns. Pinno et al. (2013) also examined jack pine recruitment in the Richardson fire 1-year post fire finding it to be highly variable depending on fire severity and stand age, but did not assess linear disturbances associated with seismic lines, which is the objective of this study. Seismic lines varied in width from 3.5 to 9.5 m and were created between 2005 and 2008 (3 to 6 years prior to the fire).

2.3.2 Site selection and field methods

Sampling locations were selected across the full gradient of fire severity, measured by overstory tree mortality, with stratification to five categorical fire severity classes used to help allocate sampling effort across the area (Figure 2.1): 0-20% (n = 27 sites), 21-40% (n = 11 sites), 41-60% (n = 10 sites), 61-80% (n = 5 sites), and 81-100% (n = 17 sites). Effort was also made to capture the range of forest stand conditions (height, density, age, etc., see Table 2.1). All sites were at least 90 m from any road or trail with a random toss of a metal stake on the seismic line used to designate the starting location of plots. As a single seismic line can stretch for kilometers, a single site per seismic line was used in most cases unless forest stand conditions and/or fire severity varied in which case additional sites at least 200 m apart were sometimes added.

In total, 70 sites were sampled in the summer of 2016 with each site consisting of a pair of plots for a total of 140 plots (see Figure 2.2 for example site photograph). The paired plots were each represented by: (1) a plot on the seismic line; and (2) a plot in the adjacent forest. Each site (paired plots – seismic line and adjacent forest control) was selected based on the requirement of having uniform forest stand conditions (i.e., height, density, age) and fire severity for the pair of plots and each plot consisting of a 30 m transect. Seismic line transects were located in the center of the seismic line, while the adjacent paired control plots were located 25 m into the adjacent forest running parallel to the seismic line. A coin toss was used to randomize

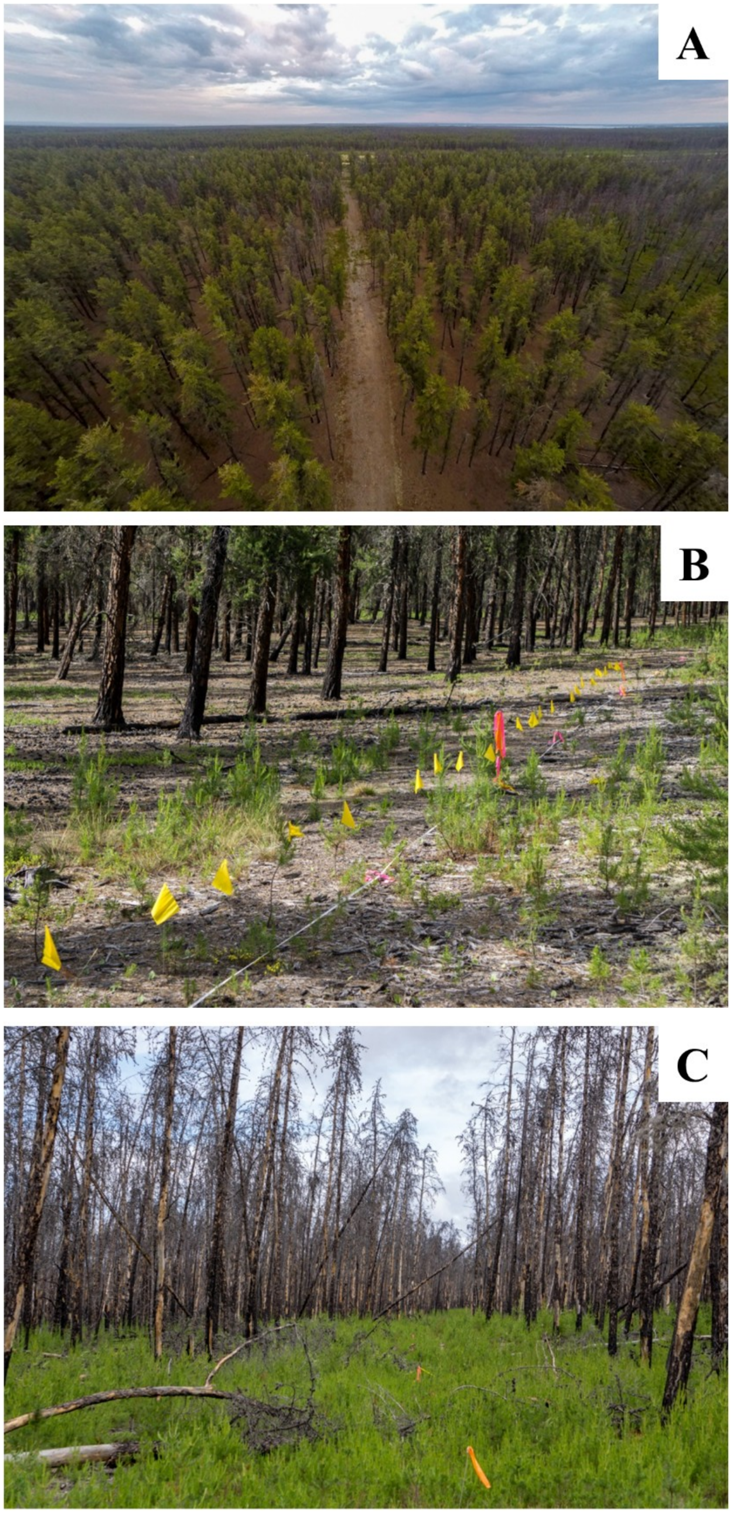


Figure 2.2: Oblique aerial photograph (July 12, 2017) of a seismic line disturbance within a jack pine (*Pinus banksiana*) forest in northeast Alberta, Canada (A) and ground photographs

depicting tree regeneration 5-years post-fire under low severity (B) and high severity (C) conditions (June 16, 2016). Photographs by S.E. Nielsen.

which side of the seismic line the adjacent forest control plot was located. Tree regeneration and forest stand conditions on seismic lines and adjacent forest stands were measured along 30 m transects with regenerating trees and shrubs counted in 1 m x 30 m 'belt' quadrats and trees (≥1 cm DBH) counted in 2 m x 30 m belt quadrats. Additional information was collected in the adjacent forest stand including stand basal area by species using a 2-factor metric prism at the midpoint of the forest transect (15 m), stand age of representative mature trees in the plot using dendrochronology via tree cores, and representative tree height using a Haglof Vertex IV (Sweden).

Table 2.1: Stand characteristics and tree regeneration rates for 70 burned jack pine stands studied in northeast Alberta, Canada. Regeneration density is reported for both forest stands (*n* = 70) and adjacent disturbed seismic line corridors (*n* = 70).

Stand variable	Minimum	Median	Maximum	Mean (S.E.)
Tree mortality (%)	0	40	100	46.5 (4.3)
Stand age	33	77	135	77 (2.9)
Height (m)	3.6	15.4	23.2	14.8 (0.5)
Tree diameter (DBH)	3.3	15.2	29.5	14.8 (0.8)
Basal area (m^2/ha)	2	18	34	17.3 (0.9)
Trees/ha (belt plots)	167	1,917	13,667	3,124 (382)
Jack pine regeneration (stems/ha)				
Seismic line	0	18,500	535,333	62,419 (11,890)
Adjacent stand	0	3,167	296,000	29,419 (6,284)
Non-jack pine regeneration (stems/ha)				
Seismic line	0	1	137	14.2 (3.0)
Adjacent stand	0	0	92	12.0 (2.6)

2.3.3 Analysis of seismic lines, fire severity, and stand characteristics on regeneration density

First, to visualize the main experimental effects, we plotted the mean and standard errors of regeneration density (per m^2) for both jack pine and all other tall woody species (aspen, saskatoon, green alder, and pin cherry) against the two main experimental variables of fire severity (5 ordinal categories) and plot location (seismic line versus adjacent forest) for all 140 plots (70 pairs). We then used paired t-tests (*ttest* command in STATA 13.1/SE; StataCorp,

2013) to evaluate whether regeneration densities (log-transformed) were higher on seismic lines than adjacent plots by each fire severity class. Non-parametric Wilcoxon sign-rank tests on raw densities were also examined, but they did not differ with t-tests using log-transformed densities and were therefore not further reported.

Second, we used generalized linear mixed effects models (*xtreg* command in STATA 13.1/SE; StataCorp, 2013) to relate linear changes in jack pine regeneration and regeneration of other species (both log transformed with a constant of 1 added) to location treatment (seismic line versus adjacent control forest), fire severity measured on a continuous scale (% overstory tree mortality), and forest stand measures including tree height, stand basal area, and stand age. Models were fit separately for jack pine and all other species grouped together. Site was used as a random effect to account for the paired nature of the seismic line and adjacent control forest plots. The location variable was dummy (binary) coded as 1 for seismic lines and 0 for adjacent control forests. Responses on seismic lines were therefore relative to reference conditions (changes) in the adjacent forest stand.

Model selection was as follows: (1) all main treatment variables (fire severity [continuous scale] and the binary seismic line location variable) were included regardless of their significance; (2) non-linear effects of fire severity and an interaction between fire severity and seismic line location were tested and added only if significant; and (3) variables for stand characteristics (including quadratic terms for non-linear responses and interaction terms with main treatment variables) were tested and included only if significant. Significance in linear terms was considered at $\alpha = 0.05$ or $\alpha = 0.10$ if it related to a quadratic non-linear response. Collinearity among continuous variables were assessed using Pearson correlations with no variables considered colinear when $|r| = > 0.7$ (highest correlation was between height and age at $r = 0.64$). For the final model, we report model parameters for treatment variables and other significant variables, as well as model goodness of fit using the ‘overall’ R^2 value that is based on the combination of ‘between’ R^2 (representing variance between sites such as fire severity and stand conditions) and ‘within’ R^2 (representing variance within sites or in this case the binary seismic line variable) components. Model assumptions were examined for independence, normality of response variables and presence of outliers, and correlations ($r > |0.7|$) among independent variables. Variables were removed and/or modified (transformed) to meet model assumptions.

2.3.4 Analysis of line (forest gap) width, orientation, and stand conditions on regeneration density

Here, we isolated the responses of tree regeneration (jack pine and other species) on seismic lines to line (forest gap) width and line orientation. In doing so, we removed all adjacent paired forest plots since they did not represent discrete forest gaps. This resulted in a total sample size of 70 plots. Because plots were no longer paired with the forest controls, we used simple linear regression (*reg* command in STATA 13.1/SE; StataCorp, 2013). Model selection was similar to that of the prior models using linear mixed effects regression with the exception of the exclusion of the location treatment variable since it was no longer relevant and the inclusion of line width (forest gap size) and line orientation as fixed variables since we were specifically interested in whether these line characteristics affected regeneration responses on seismic lines. Line width varied between 3.5 m and 9.5 m (mean of 6.1 and SE = 0.1), while line orientation represented the compass bearing of seismic lines transformed to an index between 0 (east-west orientation) and 1 (north-south orientation) following the methods of van Rensen et al. (2015). Most lines in the area were on north-south and east-west axes. As in the prior section, forest stand measures of tree height, stand basal area, and stand age were considered including their interaction with other factors such as seismic line (forest gap) width.

2.4 Results

2.4.1. Stand characteristics

Total basal area (m^2/ha) in adjacent forest stands, including recent dead snags from the fire, varied from 2 to 34 (mean of 17.3, SE = 0.9), stand age varied from 33 to 135 years (mean of 77, SE = 2.9), and tree heights varied from 3.6 to 23.2 m (mean of 14.8, SE = 0.5). Table 2.1 provides a more complete overview of basic stand characteristics of burned forests adjacent to seismic lines. Other species of trees and tall shrubs (e.g., aspen, saskatoon, green alder, and pin cherry) were found in approximately half of all plots (38 out of 70 seismic line plots, 34 out of 70 adjacent forest control plots, and thus 72 out of all 140 plots), but at a significantly lower density than jack pine. Overall, the composition of trees and shrubs across all plots were as follows: 92% jack pine, 2.2% saskatoon, 1.7% aspen, 1.5% green alder, and 1.1% pin cherry.

Understory vegetation was dominated by bearberry (*Arctostaphylos uva-ursi*), blueberry (*Vaccinium myrtilloides*), and reindeer lichens (e.g., *Cladina rangiferina, C. mitis, C. stellaris.*).

2.4.2 Seismic lines versus adjacent forest by fire severity class

Wildfires within jack pine forests promoted tree regeneration on seismic lines with 92% of regenerating stems being jack pine and the remaining 8% from aspen and three species of tall shrubs (saskatoon, green alder, and pin cherry). For jack pine itself, regeneration densities were positively related to fire severity, particularly when fire severity was > 40%, where densities were consistently 2-fold higher in seismic lines compared with adjacent forest stands (Figure 2.3A). In fact, the highest rates of jack pine regeneration occurred at the highest fire severity (81-100%) with densities reaching 14.8 (SE = 3.7) trees/m^2 on seismic lines and 7.3 (SE = 1.8) trees/m^2 in adjacent forest stands (Figure 2.3A). In contrast, at the lowest fire severity (0–20%) jack pine regeneration averaged only 1.0 (SE = 0.2) trees/m^2 in seismic lines and 0.08 (SE = 0.03) trees/m^2 in adjacent forests (Figure 2.3A). Comparison tests by fire severity class supported significant differences ($p < 0.05$) in regeneration density of jack pine between seismic lines and adjacent forest for all fire severity classes, except for 61-80% severity where it was only marginally significant ($p < 0.078$), although it should be noted that this class also had the lowest statistical power with the fewest number of plots ($n = 5$ pairs).

In comparison to jack pine, regeneration for all other trees (and tall shrubs) was much lower in number and non-linearly related to fire severity (Figure 2.3B). For this group, regeneration peaked at moderate levels of fire severity (41–60%) with 1.0 (SE = 0.5) trees/m^2 in seismic lines and 0.7 (SE = 0.4) trees/m^2 in adjacent forests (Figure2.3B). When comparing directly to jack pine, peak regeneration levels for non-jack pine species were at least 10-fold lower than that of jack pine. Comparison tests between seismic lines and adjacent forests for non-jack pine regeneration did not support differences among any fire severity class ($p > 0.226$) illustrating no obvious changes in regeneration within forest gaps from seismic lines.

2.4.3 Seismic lines (vs. forest), fire severity, and stand characteristics on regeneration density

The final generalized linear mixed effects model for jack pine included positive effects for seismic line treatment ($\beta = 0.573$, $p < 0.001$) and fire severity ($\beta = 0.021$, $p < 0.001$), and a non-linear relationship with forest stand height ($\beta_{height} = 0.314$, $p < 0.001$; $\beta_{height^2} = -0.010$, $p <$

0.001) (Table 2.2). Stand basal area and stand age were not significantly related to patterns in jack pine regeneration, nor were there further interactions between variables. Model predictions and observed data demonstrated that jack pine regeneration peaked when stand height was ~16 m and at 100% fire severity. Interestingly, there was no correlation in observed values between stand height and fire severity ($r = -0.099$, $p = 0.246$), nor interactions between these variables. Model fit was high with an 'overall' R^2 of 0.62, a 'within' R^2 of 0.36 for the seismic line treatment, and a 'between' R^2 of 0.69 that reflected site differences due to fire severity and stand characteristics.

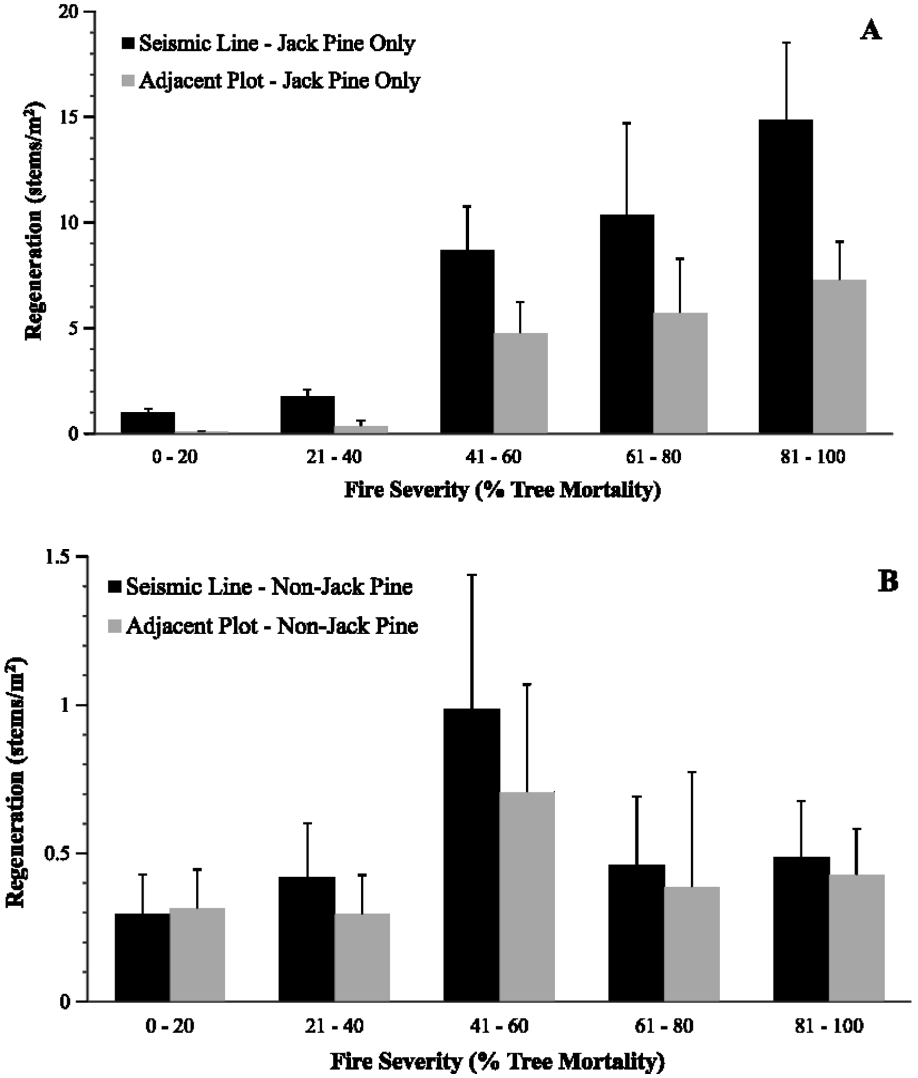


Figure 2.3: Regeneration as a response to fire severity (overstory tree mortality): (A) jack pine regeneration increased with fire severity with a marked increase in sites where fire severity was > 40%; (B) regeneration densities of other tree and shrub species demonstrated increases until ~50% fire severity and thereafter declines. Note regeneration scale in (A) is ~12-times greater than that in (B).

Table 2.2: Generalized linear mixed effect model parameters relating regeneration density of jack pine and other woody species to treatment variables of seismic lines (vs. adjacent control forests) and fire severity, as well as stand characteristics (forest stand height and stand age). No interaction terms were supported, while treatment variables were included regardless of significance.

	jack pine			*other species*		
Variable	β	S.E.	*p*	β	S.E.	*p*
Seismic line (binary)	0.573	0.092	< 0.001	0.036	0.041	0.387
Fire severity (overstory tree mortality)	0.021	0.002	< 0.001	0.002	0.001	0.034
Forest stand height	0.314	0.079	< 0.001	0.084	0.011	< 0.001
Forest stand height^2	-0.010	0.003	< 0.001			
Stand age (yrs.)				-0.037	0.010	< 0.001
Stand age^2				0.0002	0.00005	0.001
Constant (intercept)	-2.510	0.561	< 0.001	0.637	0.326	0.050
Model fit (R^2)		0.62			0.41	

In contrast to jack pine regeneration, the final model for other regenerating trees and tall shrubs was not affected by the seismic line treatment ($\beta = 0.036$, $p = 0.387$) and was positively and linearly related to forest stand height ($\beta = 0.084$, $p < 0.001$) (Table 2.2). Regeneration of these species was still positively related to fire severity, but much weaker in strength ($\beta = 0.002$, $p = 0.034$) and did not support non-linear effects as suggested in Figure 2.3B once other factors were considered. This included a strong non-linear effect of stand age ($\beta_{age} = -0.037$, $p < 0.001$; $\beta_{age^\wedge 2} = 0.0002$, $p = 0.001$; Table 2.2) whereby regeneration density that is initially highest in young, taller stands thereafter decreased with stand age until stabilizing around 80-105 years and then again increasing slightly in stands >105 years old prior to the fire. However, this may reflect the fact that the two highest regeneration densities observed were for a 39-year old stand burned at a 60% severity having 4.6 stems/m^2 on seismic lines (much less in adjacent forest) and a 135-year old burned stand (oldest sampled) at a 20% fire severity with 2.8 stems/m^2 on both the seismic line and adjacent plot. The other plots generally had regeneration densities of < 2 stems/m^2 and a general trend towards peak regeneration densities in 60–80-year old burned stands. Model fit was moderate with an ‘overall’ R^2 of 0.41, a ‘within’ R^2 of 0.01 for the seismic line treatment demonstrating the lack of relationship for seismic line effects, and a ‘between’ R^2 of 0.50 that reflected site differences due to fire severity and stand characteristics that largely affected non-jack pine regeneration patterns.

2.4.4 Line (forest gap) width, orientation, and adjacent stand conditions on regeneration density

The final regression model for regeneration within only seismic lines was related to seismic line characteristics (width and orientation), fire severity, and adjacent stand conditions of stand height (see Table 2.3). For jack pine, this included a positive relationship with fire severity ($\beta = 0.022$, $p < 0.001$) and a non-linear response to forest stand height ($\beta_{height} = 0.371$, $p < 0.001$; $\beta_{height\text{^}2} = -0.013$, $p < 0.001$). Both responses were similar to the prior model considering both seismic lines and adjacent forests, but with jack pine regeneration further related to line characteristics of line orientation and width. Specifically, jack pine regeneration decreased on north-south orientated lines ($\beta = -1.346$, $p = 0.038$), while not being significantly related to line width alone ($\beta = -0.035$, $p = 0.641$), but was significant when line width interacted with stand height ($\beta_{heightXwidth} = 0.102$, $p = 0.025$) (Table 2.3). Here, jack pine regeneration increased in wider lines when adjacent stand heights were higher. Overall model fit was high with an adjusted-R^2 of 0.64 (Table 2.3).

Table 2.3: Linear regression model parameters relating regeneration density of jack pine and other woody species to fire severity, seismic line characteristics (width and orientation), and stand conditions (forest stand height) only on seismic lines. Note that seismic line width and orientation were included regardless of significance.

	jack pine			*other species*		
Variable	β	S.E.	*p*	β	S.E.	*p*
Fire severity (overstory tree mortality)	0.022	0.002	< 0.001	0.012	0.005	0.009
Fire severity^2				-0.0001	0.00004	0.021
Forest stand height	0.371	0.092	< 0.001	-0.132	0.057	0.023
Forest stand height ^2	-0.013	0.003	< 0.001			
Line (forest gap) width	-0.035	0.074	0.641	-0.306	0.148	0.043
Line orientation (north index)	-1.346	0.635	0.038	-0.202	0.093	0.034
Line width × Stand height	0.102	0.040	0.014	0.027	0.009	0.004
Constant (intercept)	-1.883	0.820	0.025	1.482	0.879	0.097
Model fit (R^2)		0.64			0.46	

In comparison to jack pine, the regeneration of other trees and tall shrubs was non-linearly related to fire severity ($\beta_{severity} = 0.012$, $p = 0.009$; $\beta_{severity\text{^}2} = -0.0001$, $p = 0.021$) peaking in density around 60% fire severity and negatively related to forest stand height ($\beta = -0.132$, $p = 0.023$) (Table 2.3). Additional responses to line characteristics included negative relationships in regeneration with line width (β = -0.306, *p* = 0.043) and north-south orientated lines (β = -0.202, *p* = 0.034) with again a positive interaction supported between stand height and line width (β = 0.027, *p* = 0.004) (Table 2.3). Thus, although regeneration on seismic lines for non-jack pine species declined in wider, north-south lines, it was much higher when in wider lines adjacent to taller forest stands.

2.5 Discussion

2.5.1 Regeneration post-fire on seismic lines versus adjacent forest stands

Wildfires within jack pine forests of northeast Alberta promoted jack pine regeneration (92% of stems) over regeneration of trembling aspen and three species of shrubs. Fire severity was positively related to total regeneration density, particularly for jack pine. Linear open corridors associated with seismic line exploration also resulted in higher jack pine regeneration, especially for moderate and higher severity (> 40% tree mortality) fires where stocking density was twice as high in the most severe fires on seismic lines (14.8 trees/m^2) than in adjacent stands (7.3 trees/m^2). These results are somewhat contrary to Pinno et al. (2013) who found the highest seedling densities in moderate severity burns with the highest severity fires in young stands averaging only 1164 seedlings per ha (0.12 trees/m^2). This compares to an average of 73,000 survived seedlings per ha 5-years post fire in the highest severity burned forests in our study. We did not, however, sample very young (< 30 years of age) stands as did Pinno et al. (2013) where they found low post-fire recruitment. Although cones can be present in young jack pine stands, their cone density may be lower and less serotinous (Gauthier et al. 1993a) and perhaps most problematic for recruitment are seed loss from direct burning of cones in shorter trees (de Groot et al. 2004). Indeed, when considering jack pine recruitment, the two most important factors are the number of viable seeds and the favorability of the seedbed (Sirois 1993).

In our case, the number of viable seeds should not affect regeneration differences between seismic lines and adjacent forests since both plots were receiving approximately the same source and amount of seeds (25 m from each other) with stands all > 30 years of age (threshold from Pinno et al. 2013). In contrast, the seedbed between seismic lines and adjacent forests varied substantially with the mechanized creation of seismic lines resulting in removal of woody biomass, including stumps, 3-6 years prior to the fire and in many cases exposure of mineral soils that should favor jack pine regeneration (Ahlgren and Ahlgren 1960; Chrosciewicz

1974; Cayford and McRae 1983). Although microtopography is often simplified on seismic lines reducing tree recruitment (Lieffers et al. 2017), this was not to the detriment of jack pine regeneration in our study. Therefore, the process which originally removed jack pine forests as small linear openings for oil sands exploration was benefiting jack pine regeneration post-fire potentially due to increases in available mineral soil, but also potentially by increases in light on seismic lines. Although we did not directly measure light levels, jack pine is known to be shade intolerant (Ahlgren and Ahlgren 1960; Cayford and McRae 1983; Rudolph and Laidly 1990; Weber and Stocks 1998; Arseneault 2001) and lines create forest openings that should increase light levels, especially for wider lines (see Section 2.5.2 for more discussion).

Jack pine regeneration was also affected by forest stand heights with peak regeneration occurring at sites where stand heights were approximately 16 m. In our study, ~16 m high forests ranged in age from 62-year-old stands to the oldest stands sampled of 135 years. Interestingly, stand height was not correlated with fire severity suggesting that the effects of stand height had more to do with cone density and seed viability, although cones positioned in lower parts of the canopy can be directly consumed by the fire thus reducing post-fire seed rain (de Groot et al. 2004).

In contrast to jack pine, other regenerating trees (trembling aspen) and tall shrubs (saskatoon, green alder, and pin cherry) were not affected by the presence of open linear corridors associated with seismic line disturbances, but were positively affected by fire severity and stand height, and non-linearly related to stand age (generally negative effect). Patterns of recruitment in these species therefore had more to do with characteristics of the stand conditions and fire and may reflect past distribution of plants since all four of species can root sucker following disturbance, particularly for aspen (Frey et al. 2003). Regardless, regeneration density of these other species was quite small representing only 8% of total stems with jack pine being the dominant species in both seedlings and alive or dead overstory trees. This is typical for these sandy plain jack pine forests. In fact, in the 56 jack pine stands studied in the same area by Pinno et al. (2013), no other tree species were present.

2.5.2 Effect of seismic line width and orientation on post-fire regeneration

Forest gap size in boreal forests is known to affect regeneration patterns in trees (Kneeshaw and Bergeron 1998), including jack pine (Gauthier et al. 1993b; Frelich and Reich

1995), as it affects among other things competition for available light (Lieffers et al. 1999) and soil properties (Kuuluvainen 1994). In our study, width of forest gaps associated with seismic lines varied between 3.5 and 9.5 m and was positively related to regeneration density in non-jack pine species and for jack pine when adjacent to taller forest stands. This suggests that resources, particularly for light, were limiting recruitment. This is further supported by lower jack pine recruitment in adjacent stands where snags and alive trees reduced light and availability of other resources. Although the seedbed may have been different between seismic lines and forests, the fact that line width affected recruitment suggests light is a limiting factor. However, competition for other resources (nutrients and moisture) may also play a role with width of seismic line likely relating to different intensities of initial soil disturbance. Further study is needed to assess resource competition among forest gaps that are much smaller than typically studied and for differences in soil disturbances and microsites.

A second factor that affects light levels and potentially seed dispersal on seismic lines is line orientation. East-west orientated lines are expected to have greater available light in the groundlayer compared with that of north-south lines (van Rensen et al. 2015), while wind conditions are dominantly from the west providing possible dispersal corridors for seed (Roberts et al. 2018). In support of the light limitation and perhaps seed dispersal hypothesis, we found increases in recruitment of trees on east-west orientated lines over that of north-south lines. These results are similar to that of van Rensen et al. (2015) who found significantly higher probability of forest recovery on seismic lines orientated east-west than north-south in a region of treed peatlands south of our study area. Although one may expect a multiplicative effect on tree regeneration based on line orientation and width if light were limiting, there was no support for their interaction in our tests suggesting that conditions for regeneration were more suitable if in either wider lines or east-west orientated lines, as well as wider lines when adjacent stand height was taller.

2.6 Conclusions and management implications

Overall, our results support the suggestion that the inferred lack of tree regeneration on seismic lines in xeric jack pine forests is due to the timing of its measurement as it relates to stand replacing fires since jack pine cones are serotinous releasing their seeds *en masse* only after fires (Ahlgren and Ahlgren 1960; Cayford and McRae 1983; Lamont et al. 1991). Given that fire frequency in these areas range from 28-54 years (Carroll and Bliss 1982; Larsen 1997; Larsen and MacDonald 1998), cost-benefits of active restoration projects of tree planting and site preparation to those of passive forms of restoration relying on natural regeneration following wildfire should be considered. Here, we found no evidence for the need of site preparation for burned seismic lines in jack pine stands, while investments in tree planting in these sites may be short-lived if wildfires do occur. Indeed, jack pine regeneration following moderate to high severity fires on seismic lines were 2-fold higher than in adjacent forests, although these differences may lessen over time as the natural process of stand thinning progresses (Yarranton and Yarranton 1974; Carroll and Bliss 1982; Arseneault 2001). The passive form of restoration of these sites through fire has the potential to save significant amounts of restoration dollars and still contribute to the long-term conservation objectives, including caribou recovery. Future research should examine whether these patterns hold within other recently burned forest types including those with trees having semi-serotinous cones such as black spruce.

Chapter 3: High precision altimeter demonstrates simplification and depression of microtopography on seismic lines in treed peatlands

3.1 Abstract

Seismic lines are linear forest clearings used for oil and gas exploration. The mechanical opening of forests for these narrow (3–10 meter) lines is believed to simplify microtopographic complexity and depress local topographic elevation. In treed peatlands, simplified microtopography limits tree regeneration by removing favourable microsites (hummocks) for tree recruitment and increasing the occurrence of flooding that reduces survival of tree seedlings. Little, however, has been done to quantify the microtopography of seismic lines and specifically the degree of alteration. Here, we measured microtopography at 102 treed peatland sites in northeast Alberta, Canada using a high precision hydrostatic altimeter (ZIPLEVEL PRO-2000) that measured variation in local topography of seismic lines and adjacent paired undisturbed forests. Sites were separated into four peatland ecosite types and the presence or absence of recent (< 22 years) wildfires. Paired t-tests were used to compare microtopographic complexity and depression depth of seismic lines compared with adjacent forests. Microtopographic complexity on seismic lines was simplified by 20% compared to adjacent stands with no significant change between recently burned and unburned sites, nor between ecosites. Not only were seismic lines simplified, but they were also depressed in elevation by an average of 8 cm compared to adjacent forests with some minor variation between ecosites observed, but again not with recent wildfires. Thus, simplification of microtopographic complexity and the creation of depressions can persist decades after initial disturbance with some differences between peatland ecosites, implying the need for ecosite-specific restoration of topographic complexity. The importance of microtopography for tree regeneration on seismic lines remains an important question for reforestation of these disturbances and thus long-term recovery of habitat for species dependent on undisturbed peatlands, including woodland caribou.

3.2 Introduction

With major increases in the global population over the last two centuries (Alexandratos 2005), there is an increasing demand for natural resources. However, exploration and extraction of these resources alters the environment and thus affects ecological processes, function, and biodiversity. In Canada's boreal forest, one major source of disturbance is from energy exploration and extraction, particularly in the oil sands region of northeast Alberta. Boreal forests become fragmented during exploration and extraction due to roads, pipelines, transmission lines, well pads, seismic lines, and other associated infrastructure (Schneider 2002). However, the most common disturbances are seismic lines (Schneider 2002; Lee and Boutin 2006). These relatively narrow (3–10 m) linear disturbances are created by machinery to remove trees via mulching and/or bulldozing, thus allowing access to remote areas for mapping bitumen depth and volume. Not only do seismic lines persist, they are also quite abundant with densities as high as 40 km/km² (i.e., 50 m spacing in a grid of lines), with conservative estimates over larger areas of the region averaging 1.5 km/km² (Schneider 2002). Although these disturbances are not permanent features, representing instead narrow forest clearings where aboveground woody vegetation is removed, they still alter the physical characteristics of the landscape, as well as ecosystem processes, including fire (Lefort et al. 2003; Arienti et al. 2009; van Rensen et al. 2015; Veblen et al. 2016).

When seismic lines were created, the assumption was that due to their relatively narrow nature, they would recover naturally and quickly, but this has not been the case (Lee and Boutin 2006; van Rensen et al. 2015). Forest regeneration and recovery rates in these disturbed areas are often poor, with only 8.2% of seismic lines recovering to woody vegetation after 35 years, and greater than 60% persisting in a cleared state (Lee and Boutin 2006). Lee and Boutin (2006) suggest recovery time for seismic lines would be ~112 years based on current median recovery rates. As this number is based on seismic lines that have not been transitioned to transportation corridors (roads, pipelines, power lines, etc.), the harsh reality is that many will persist, in one form or another, much longer. The "pulse of growth" in industrial development that accompanied the initial establishment of seismic lines is further exacerbated by the increasing use of seismic lines as transportation corridors, promoting seismic line persistence and leaving little chance for recovery (Schneider 2002). Northeast Alberta is located in the physiographic region of the northern Alberta lowlands (Natural Regions Committee 2006) that are dominated by peatlands composed of poor fens, rich fens, and bogs (Natural Regions Committee 2006), which overlap with prime locations for oil and gas exploration.

Inadequate forest regeneration of seismic lines has implications for abiotic and biotic components of boreal ecosystems. In addition to altering forest structure by creating edge effects (Laurance et al. 2007; Braithwaite and Mallik 2012), vegetative loss on lines alters successional processes that have been shown to promote more seral shrub species (Filicetti et al. 2019 [Chapter 4]). Vegetation removal also alters forest hydrology by reducing water uptake and modifying soil structure and development (Vitt 1994; Chen et al. 2017). Although peatlands are slow growing, they are carbon dense and thus important for carbon sequestration and understanding the effects of disturbance on greenhouse gas emissions (Lovitt et al. 2018). Seismic lines also influence the abundance and behaviour of wildlife species, including, among others, black bears (*Ursus americanus*) (Tigner et al. 2014), grizzly bears (*Ursus arctos*) (Linke et al. 2005), pine marten (*Martes americana*) (Tigner et al. 2015), ovenbirds (*Seiurus aurocapilla*) (Bayne et al. 2005), and butterflies (Riva et al. 2018a). The most contentious wildlife issue is that of woodland caribou (*Rangifer tarandus caribou*), a species at risk (Environment Canada 2012). Studies of woodland caribou movement show that caribou avoid seismic lines during certain parts of the year (Dyer et al. 2001), potentially resulting in smaller range sizes or limited resources. Seismic lines also act as corridors for wolves, which lead to increases in encounters with woodland caribou, ultimately resulting in lower survival of woodland caribou (James and Stuart-Smith 2000; Latham et al. 2011a). Changes in habitat and warmer winters have also increased white-tailed deer populations, further supporting wolf populations, and thus predation on woodland caribou (Latham et al. 2011b). Forest fragmentation associated with seismic lines has been listed as a threat to endangered woodland caribou (Government of Canada 2012), and thus rapid recovery of forest structure on these disturbances is a conservation priority. There are currently no regulatory requirements for restoration, but public pressure is mounting with guidelines now being developed to create standards for restoration and monitoring of recovery.

The areas commonly associated with persistent seismic lines in Alberta are the peatland forests. The wetter, slower growing ecosites (fens and bogs) are organic wetlands whose slower rate of succession is affected by high water tables (Kuhry 1994). Bogs are acidic, mostly rainwater fed, with little to no groundwater flow and at least 40 cm of peat as organic soil (Natural Regions Committee 2006). These sites are associated with acidic-tolerating vegetation (i.e., Ericaceae) and black spruce trees (*Picea mariana* (Mill.) B.S.P.) (Natural Regions Committee 2006). Fens are also defined as having organic soils with at least a 40 cm layer of peat, but with more water-adapted vegetation due to greater water flow, generally from sub-surface water (Natural Regions Committee 2006). Both bogs and fens are high in carbon and therefore important in terms of carbon sequestration.

One aspect that is thought to affect tree recovery on seismic lines is changes in microtopography, yet microtopography is seldom measured, leaving restoration efforts of these sites based largely on anecdotal assessments. Microtopography can be represented by the elevational hummock–hollow patterns typical in peatlands. A reduction of microtopographic complexity on seismic lines reduces tree regeneration by eliminating microsites for seedling establishment (Lee and Boutin 2006; Caners and Lieffers 2014; Lieffers et al. 2017; Filicetti et al. 2019 [Chapter 4]). Patterns of tree recovery on seismic lines are related to the overall moisture regime, with mainly xeric or hydric locations having reduced or even arrested succession (van Rensen et al. 2015). Microtopographic complexity is positively related to forest regeneration in fens in northern Alberta (Schneider 2002), as well as sites with artificial mounding (Schneider 2002; Filicetti et al. 2019 [Chapter 4]). Microtopographic complexity reduces the severity of flooding, which negatively affects tree seedling establishment and survival, thus increasing recovery time post-disturbance (Caners and Lieffers 2014).

Wildfires are thought to affect microtopography in treed peatlands, but most studies have focused on bogs (Benscoter et al. 2015), with limited information on fens. Post-fire microtopography in bogs can increase over longer periods due to greater depth of burns in hollows and faster rates of growth on hummocks (Benscoter et al. 2015) , although more severe wildfires can reduce hummock structure (Benscoter et al. 2005). Wildfires may also reduce available moisture in seismic lines in wetter ecosites such as fens where already stagnant water is likely exacerbated by the compaction or removal of soils (depression) during seismic line construction. A reduction in moisture post-fire might return seismic lines to a drier state, allowing for less water-adapted tree seedlings to re-vegetate. Quantifying the effects of fire and type of treed peatland (ecosite) on microtopographic complexity and depression levels may help us better understand the factors associated with seismic line re-forestation (restoration) thereby guiding predictions of recovery rates and informing restoration treatments, including use of artificial mounding in sites where it would be most beneficial (Filicetti et al. 2019 [Chapter 4]).

Quantifying microtopography poses many challenges. Some studies focus on comparing the height differences between a few hollows to their neighboring hummocks, while others extract large monoliths of peat or use depth to water table as a reference (Weltzin et al. 2001). However, this can be complicated, costly, and temporally variable since water table fluctuates seasonally and yearly (Triisberg et al. 2014; Benscoter et al. 2015). Newer studies have relied on laser leveling (Benscoter et al. 2015; Lieffers et al. 2017), but this can be impractical in a larger forested setting. Here, we tested a relatively new technology that measures minute (sub-centimeter) elevational changes from a reference starting point. Hydrostatic altimeters measure the displacement of liquid within a tube that is connected to two devices designed to quantify changes in elevation when one part of the device is raised or lowered. Hydrostatic altimeters thus use gravity to measure fine scale changes in elevation, and are now sometimes used in construction as a replacement for levelers. This technique previously has had limited application elsewhere, but the newest technology offers highly accurate measures. Here, we used a high-precision hydrostatic altimeter (accuracy of 0.127 cm), the ZIPLEVEL PRO-2000, as a near-remote sensing technique to evaluate the usefulness of this type of technology in quantifying fine-scale changes in microtopography.

The objective of this study is to quantify microtopography on seismic lines and adjacent control forest settings in treed peatlands of northeast Alberta, where these linear disturbances are common and considered a conservation concern. Specifically, we hypothesized that, (1) seismic lines will be depressed in elevation compared to adjacent forest edges due to initial and residual compaction/removal of peat, soils, and hummocks by equipment; (2) seismic lines will have a simplified microtopography compared to adjacent natural stands due to mechanical disturbance and reduction of hummocks during clearing; (3) microtopography of seismic lines will differ by ecosite (rich fens, poor fens, bogs, and poor mesic) considering diverse moisture and nutrient regimes; and (4) recent fires will increase microtopography as it has been previously shown for bogs.

3.3 Materials and Methods

3.3.1 Study area

The study area is located in northeast Alberta, Canada centered around the municipality of Fort McMurray (Figure 3.1) where treed peatlands are common. Elevation ranges from 279 to 741 m. Sites consisted of treed peatlands across four ecosite types (poor mesic, poor fens, rich fens, and bogs; Figure 3.2) with ecosite classification defined by the Alberta Biodiversity Monitoring Institute Terrestrial Field Data Collection Protocols using dominant vegetative community (or that of pre-disturbance), soil characteristics, soil nutrients, and moisture (Alberta Biodiversity Monitoring Institute 2018). Dominant tree species depended on ecosite type and conditions, but typically black spruce was the dominant species in poor mesic, bog, poor fens, and occasionally in rich fens; while tamarack (*Larix laricina* (Du Roi) K. Koch) was usually the dominant species in rich fens and co-dominant in poor fens. In some circumstances, aspen (*Populus tremuloides* Michx.) and/or jack pine (*Pinus banksiana* Lamb.) were present in poor mesic sites, but normally were not dominant. Sample sites included mature peatland forests, as well as areas of five separate recent wildfires occurring within the region including the Mariana Lake Fire (1995), a fire in 1999 and in 2009, the Richardson Fire of 2011, and the Horse River (Fort McMurray) Fire of 2016 (Figure 3.1).

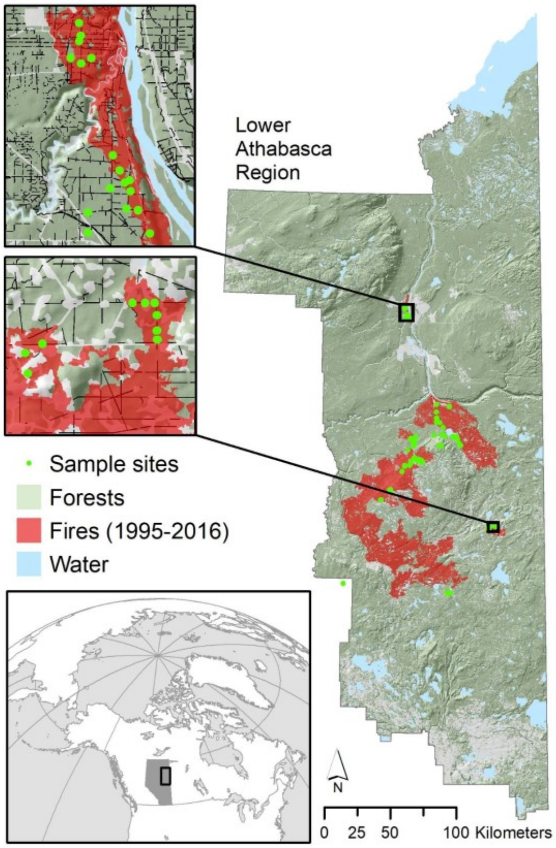


Figure 3.1: Location of 102 study sites in northeast Alberta, Canada (inset map). Green shaded areas in the main map represent forested areas of the Lower Athabasca region, while the light gray color represents open disturbed habitats. Each sample site represents a paired plot with one plot on the seismic line and the other plot 25 m into the adjacent forest in either unburned or burned sites from five different burn years (1995–2016). Sites were restricted to areas not influenced by recent all-terrain vehicle use or recent re-clearing.

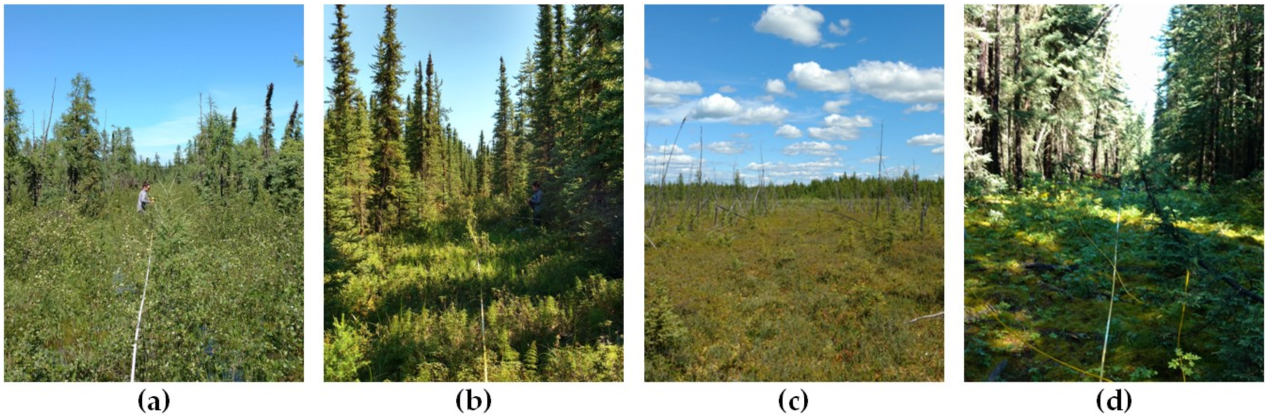


Figure 3.2: Examples of seismic line disturbances for four different peatland forest ecosites in northeast Alberta, Canada: (a) rich fen; (b) poor fen; (c) bog; and (d) poor mesic. All photographs by Angelo T. Filicetti.

3.3.2 Site selection

Field data were collected between May 18 and July 25, 2017. Sample sites (102 sites; 204 paired plots) were selected (stratified) across a range of five fire burn years (1995, 1999, 2009, 2011, and 2016) (Figure 3.1) and from low to high fire severity. Of the 102 sites and 204 plots sampled, 42 sites (84 plots) were unburned sites, 12 sites were sampled from the 1995 fire, 10 from the 1999 fire, 14 from the 2009 fire, 12 from the 2011 fire, and 12 from the 2016 fire (Table 3.1). Fire severity was defined using percent overstory tree mortality with sites used only when fire severity was similar for the seismic line and adjacent forest. We also examined ecosite characteristics as they may create differences in microtopography. Ecosite types included: 15 bogs (6 unburned and 9 burned), 46 poor fens (19 unburned and 27 burned), 18 rich fens (8 unburned and 10 burned), and 23 poor mesic sites (9 unburned and 14 burned) (Table 3.1). This composition of ecosites reflects the distribution found in northeastern Alberta with, for instance, bogs being less common. All plots were at least 60 meters from other forest types, forest edges, or other seismic lines. Sites were at least 400 m apart, to avoid pseudo-replication, with a preference to have sites on separate seismic lines and only on the same line if in a different ecosite. Transects were 20 m in length down the center of the seismic line with an adjacent stand transect running parallel, 25 meters into the forest (randomized for the left or right side of the seismic line).

Table 3.1: Ecological site type and presence or absence of fire for 102 paired sampling sites in northeast Alberta, Canada across five burn years (1995, 1999, 2009, 2011, and 2016). Sites were sampled between 18 May 2017 and 25 July 2017.

Total	Bog	Poor Fen	Rich Fen	Poor Mesic	Total
	15	46	18	23	102
Unburnt	6	19	8	9	42
Burnt	9	27	10	14	60
Fire Year					
1995	3	7	2	0	12
1999	3	1	1	5	10
2009	3	5	0	6	14
2011	0	8	2	2	12
2016	0	6	5	1	12

3.3.3 Field measures of microtopography

Microtopographic complexity and depression depth were measured using a ZIPLEVEL PRO-2000 (Technidea® Corporation, Escondido, CA, USA) High Precision Hydrostatic Altimeter (0.127 cm accuracy). Seismic line depression was assessed via perpendicular measures across the seismic line obtained at 0, 10, and 20 m points of the transect (Figure 3.3). Eleven points were taken at each distance with the adjacent measurements being 0.25, 0.5, and 0.75 m from the outer edge of the seismic line into both left and right sides of the adjacent forests (edges), with five points measured in the middle of the seismic line (seismic line width varied from 3 to 14 m) at increments of 0.25 m (Figure 3.3). Depression depth was calculated as the average difference between the central points to the forest edges. Microtopographic complexity was measured along the center 20 m of each seismic line and its paired adjacent forest control (25 m from seismic line) at intervals of 0.25 m (*n* = 81 observations per transect). Points were measured as elevations or depressions relative to an initially tared zero value at each transects starting point. To account for natural slopes of the terrain along the seismic lines, a best fit regression line was first fit using all measures at each distance (0–20 m in 0.25 m increments) and the absolute difference between each measurement at each distance from the best fit line calculated. Finally, all measures were averaged to estimate the mean absolute residual deviation. This gave me one value for each seismic lines microtopographic complexity as a measure of variation (higher values meaning more complexity and vice versa). Zero microtopographic complexity means that the microtopography was flat and had no discernible hummock/hollow pattern, while a value of zero for depression means that no change/difference in the line's elevation (e.g. no depression in the line).

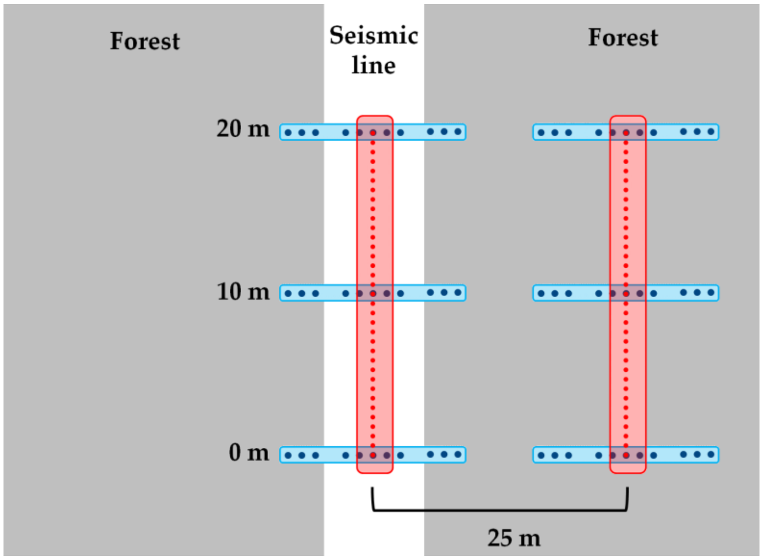


Figure 3.3: Schematic of plot design used for measuring microtopography on seismic lines (white) and in adjacent forests (gray). A 20 m transect, in red, was used to measure complexity with 0.25 m spacing. Perpendicular transects, in blue, measured depression depth with three transects spaced at 0, 10, and 20 m along the main transect at, again, 0.25 m increments.

3.3.4 Data analysis

Depression depth of seismic lines were assessed as the average difference between points on the seismic line and those at forest edges. Differences in microtopographic complexity were calculated using the mean absolute residual deviation of microtopography. Differences in microtopography were graphed by ecosite and presence of fire with paired t-tests used to assess significance in differences between the depth of seismic line depression and microtopographic complexity from that of seismic lines and adjacent forest stands. All analyses were performed in STATA/SE version 15.1 (StataCorp. 2017). Model assumptions were examined for independence, normality of response variables and presence of outliers, and correlations ($r > |0.7|$) among independent variables. Variables were removed and/or modified (transformed) to meet model assumptions.

3.4 Results

3.4.1 Seismic line depression

Seismic lines were depressed in elevation by 8.42 cm when compared to adjacent forests when all ecosite types were assessed together ($t = 9.093$, *df* [degrees of freedom] = 202, $p < 0.001$, Table 3.2). When assessed by ecosite type, seismic lines of all bogs ($t = 3.838$, $df =$

28, $p < 0.001$,), poor fens ($t = 5.730$, $df = 90$, $p < 0.001$), rich fens ($t = 7.050$, $df = 34$, $p < 0.001$), and poor mesic ($t = 3.174$, $df = 44$, $p = 0.001$) ecosite types were significantly depressed compared to forest edges (Figure 3.4). By further separating data by the presence of fire, it was apparent that the presence of fire alone had no effect on changes in microtopography (Figure 3.4).

Table 3.2: The t-test results for microtopographic depression and complexity between seismic lines and adjacent forests using all sites ($n = 102$) regardless of ecosite and fire presence.

Statistic	Depression depth (cm)		Microtopographic complexity (cm)	
	Seismic line	Adjacent forest	Seismic line	Adjacent forest
Mean	−8.42	−0.54	4.85	6.08
Standard error	0.66	0.57	0.22	0.21
t	9.093		4.824	
df	202		202	
p-value	< 0.001		< 0.001	

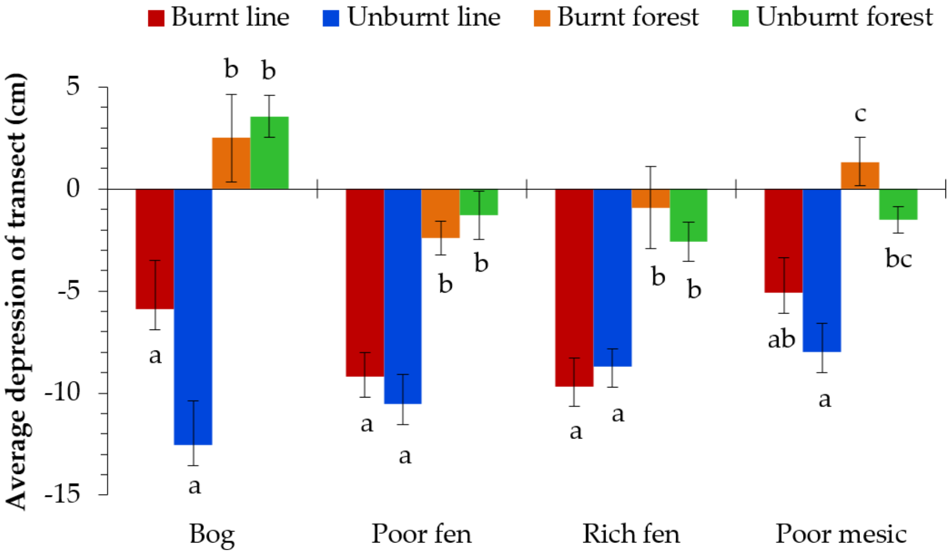


Figure 3.4: Mean and standard error (error bars) of average depression (cm) across four ecosites (bog, poor fen, rich fen, and poor mesic) and four treatments (burnt line, unburnt line, burnt forest, and unburnt forest). Significance of treatments tested with a pairwise comparison (Bonferroni adjustment). Different letters indicate significant ($p < 0.0125$) differences within an ecosite.

3.4.2 Seismic line simplification

Seismic lines were significantly simplified (4.85 cm average mean absolute residual deviation), with a 20% reduction in microtopographic complexity compared to natural adjacent stands (6.08 cm average mean absolute residual deviation) for all 102 paired sites (all unburned and burned sites together; $t = 4.824$, $df = 202$, $p < 0.001$, see Table 3.2). When assessing ecosite types separately, seismic line microtopographic complexity was reduced in bogs ($t = 2.859$, $df = 28$, $p = 0.004$), poor fens ($t = 3.258$, $df = 90$, $p = 0.001$), and rich fens ($t = 3.418$, $df = 34$, $p = 0.001$) compared to that of adjacent forest stands. Seismic lines on poor mesic sites showed no significant difference in microtopographic complexity. The presence of fire did not affect microtopographic complexity for any ecosite (Figure 3.5), nor did the other fire-related variables of severity and time since fire (not shown).

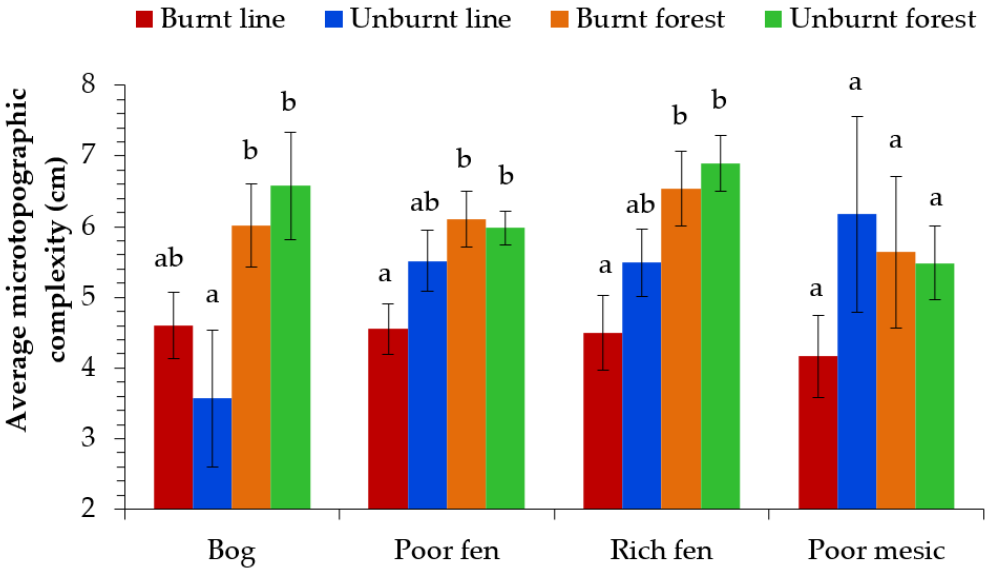


Figure 3.5: Mean and standard error (error bars) of microtopographic complexity across four ecosites (bog, poor fen, rich fen, and poor mesic) and four treatments (burnt line, unburnt line, burnt forest, and unburnt forest). Significance of treatments was tested with a pairwise comparison (Bonferroni adjustment). Different letters indicate significant ($p < 0.0125$) differences within an ecosite.

3.5 Discussion

Seismic lines were depressed in elevation by ~8 cm and their microtopographic complexity simplified by 20% compared to adjacent forest stands. These patterns occurred across all ecosites. In contrast to ecosite differences, wildfires did not reverse or exacerbate this trend, with only minor differences between ecosites. Anecdotal evidence and applications of restoration techniques (Filicetti et al. 2019 [Chapter 4]) indicate that microtopography plays an important role in providing the variety of microsite conditions that aid in re-establishment of seedlings in peatlands. The consistent observation of a depression on lines helps explain the difficulty that treed peatlands have in regenerating trees. This is then exacerbated by the simplification of topography that occurs on these lines.

Results here suggest that seismic lines remain simplified and depressed decades after seismic line construction and that this arrests regeneration of trees (Lee and Boutin 2006; van Rensen et al. 2015). Persistence of seismic line depressions may in part be due to the lack of vegetation regrowth and exacerbated by heightened levels of flooding due to their lower elevation (depression). This suggests a positive feedback that further delays microtopographic recovery of seismic lines. Loss of vegetation due to clearing is known to substantially change hydrological components of forests through both the reduction of water uptake by lost vegetation and alteration of soil structure (Chen et al. 2017). Anecdotal observations during data collection at our sites suggested vegetation on seismic lines was often strikingly different than vegetation on adjacent stands, in part due to water level and differences in microtopography. Vegetation of bogs is usually dominated by black spruce, with various sphagnum species, reindeer lichen (*Cladonia rangiferina*), bog cranberry (*Vaccinium oxycoccus*), and other ericaceous species (Natural Regions Committee 2006), but we noticed many of the seismic lines on bogs contained species that are usually more prominent in wetter areas, such as willow (*Salix* spp.), dwarf birch (*Betula pumila*), or leatherleaf (*Chamaedaphne calyculata*). Seismic lines in poor fens, which are usually associated with black spruce, larch, willow, dwarf birch, leather leaf (Natural Regions Committee 2006), seemed to support species more associated with rich fens, such as water sedges (*Carex aquatilis*), buckbean (*Menyanthes trifoliata*), or march cinquefoil (*Comarum palustre*). Large amounts of nutrients can be lost (changing peak nutrient loss) post-disturbance due to reductions in nutrient acquisition by plants with remnant nutrients transported out of the system prior to uptake by other vegetation (Silins et al. 2014). This supports previous evidence that delays in recovery are a result, at least in part, of the adverse effects caused by flooding on reductions in the establishment of mosses, such as Sphagnum (Caners and Lieffers 2014), and subsequent reductions in autogenic creation of heightened variation of microtopography (Benscoter et al. 2015).

Most of the literature to date focuses on microtopographic changes due to wildfires in bogs, yet other peatland forest types have been less commonly sampled. Previous studies have suggested that fire increases microtopography of bogs (Benscoter et al. 2015), while favoring the creation of hollows over hummocks (Benscoter et al. 2005), and that fires are typically more severe in hollows (Benscoter et al. 2015). However, we saw no effect of fire on seismic line microtopographic complexity or depression depth. Conditions in bogs are not only acidic, but bogs are rainwater fed, resulting in slow vegetation growth and therefore slow nutrient accumulation. It is possible that measured sites have not reached the stage of later succession, where fire was seen to increase microtopographic complexity, because the time since fire of the samples in this study were all within the last 30 years. Previous studies have shown that post-fire microtopography should recover within decades (Benscoter et al. 2005, 2015; Pouliot et al. 2012), mostly due to bryophytes that gradually spread laterally into surrounding hollows (Benscoter et al. 2005), but we suggest here that this may take much longer in the case of seismic lines given the initial depression and simplification is more severe than the effects of fire alone. Poor mesic sites show less depression than poor fens (burned and unburned), which characteristically seems consistent with distinct differences in nutrient and moisture regimes in relation to water presence and depression persistence. Poor mesic sites are located higher in elevation than the other ecosites and thus further above the water table. As a result, poor mesic sites may not be as affected by persistence of flooding or the reliance on greater microtopographic complexity for tree regeneration. Similar studies suggest that these depressions can be severe enough to shift local ecosite type due to higher water tables (Triisberg et al. 2014). This leads to different vegetation in depressions that can persist for many decades (Pouliot et al. 2012; Triisberg et al. 2014) in an early succession state with slower growth rates of vegetation than on hummocks (Benscoter et al. 2005).

Although the apparent lack of influence of fire and the limited influence of ecosite type were inconsistent with expectations and previous literature, this may be due to sample sites being in a variety of treed peatlands, whereas other studies assessing microtopography have focused on open bogs (Kuhry et al. 1993; Benscoter et al. 2005, 2015). Larger sample sizes and/or higher resolution measurements (< 0.25 m increments) may uncover situations where fire affects microtopography or with more pronounced effects between ecosite types. Overall, however, results in this study point to the persistence of lost microtopographic complexity and perpetual depression of seismic lines, which can affect seedling regeneration on seismic lines. It has recently been found that restoration treatments that increase microtopographic variation through artificial mounding, increase woody tree species recruitment in peatland forests (Filicetti et al. 2019 [Chapter 4]). Considering the implications of seismic line persistence on both abiotic and biotic components, these findings advocate for the further understanding of factors affecting microtopography, and how changes in microtopography affect vegetative composition and growth and habitat for biotic species, including long-term recovery of habitat for endangered woodland caribou. Results also suggest that the use of newer technologies, such as the high precision hydrostatic altimeter, can adequately characterize microtopography in the field. With tools such as this, it becomes possible to characterize hummock–hollow composition across a treed landscape and thus assess the possible effects to vegetation establishment, growth, and distribution.

The ZIPLEVEL PRO-2000 high-precision hydrostatic altimeter not only is accurate for construction, but its lightweight design also allows for ease of transport to remote field locations. Other studies measuring microtopography have used levels (Caners and Lieffers 2014) or other time-consuming or expensive methods including light detection and ranging (LiDAR) (Brubaker et al. 2013), unmanned aerial vehicles (UAVs) (Feduck et al. 2018; Franklin 2018; Lovitt et al. 2018), or real-time kinematic (RTK) global positioning system (GPS) (McDonald et al. 2008). The ZIPLEVEL PRO-2000 allowed for a quick setup and provided fast and accurate measurements of micro-elevational changes (~40 minutes per site). The use of hydrostatic altimeters in measuring microtopography is potentially a much simpler and more accurate solution. This novel tool may be useful for other fields of research that require measures of micro-elevational change, with ease of transport, ease of use, and high accuracy. However, comparisons with other methods are still needed to assess cost-benefits of these different technologies.

3.6 Conclusions

Seismic lines are depressed compared to the adjacent forest stands across all ecosite types. Surprisingly, we found no effect of fire on microtopographic complexity or depression depth, while microtopography complexity was simplified across all ecosites except poor mesic stands. The lack of effects of fire on microtopography complexity and depression was surprising, considering prior literature. Differences in microtopography may not be as associated with fire as previously thought or may recover quickly following fire. Deciphering effects of microtopography remains important with seismic lines being a persistent disturbance in boreal landscapes that alter vegetation regrowth. Persistence of microtopographic depression and simplification on seismic lines has implications for reduced tree regeneration (Filicetti et al. 2019 [Chapter 4]). High precision hydrostatic altimeters show promise in quantifying microtopography and should be applied elsewhere to investigate the role of microtopography on ecological and biological responses.

Chapter 4: Caribou conservation: Restoring trees on seismic lines in Alberta, Canada

4.1 Abstract

Seismic lines are narrow linear (~3–8 m wide) forest clearings that are used for petroleum exploration in Alberta's boreal forest. Many seismic lines have experienced poor tree regeneration since initial disturbance, with most failures occurring in treed peatlands that are used by the threatened woodland caribou (Rangifer tarandus caribou). Extensive networks of seismic lines, which often reach densities of 40 km/km2, are thought to have contributed to declines in caribou. The reforestation of seismic lines is therefore a focus of conservation. Methods to reforest seismic lines are expensive (averaging $12,500 per km) with uncertainty of which seismic lines need which treatments, if any, resulting in inefficiencies in restoration actions. Here, we monitored the effectiveness of treatments on seismic lines as compared to untreated seismic lines and adjacent undisturbed reference stands for treed peatlands in northeast Alberta, Canada. Mechanical site preparation (mounding and ripping) increased tree density when compared to untreated lines, despite averaging 3.8-years since treatment (vs. 22 years since disturbance for untreated). Specifically, treated lines had, on average, 12,290 regenerating tree stems/ha, which is 1.6-times more than untreated lines (7,680 stems/ha) and 1.5-times more than the adjacent undisturbed forest (8,240 stems/ha). Using only mechanical site preparation, treated seismic lines consistently have more regenerating trees across all four ecosites (bog, poor fen, rich fen, and poor mesic), although the higher amounts of stems that were observed on treated poor fens are not significantly different from untreated or adjacent undisturbed reference stands.

4.2 Introduction

The leading anthropogenic contributor of forest disturbances in Alberta is seismic lines (Arienti et al. 2009; Schneider et al. 2010), which reach densities of up to 40 km/km^2. Seismic lines are narrow (3–8 m) linear clear-cut disturbances (Figure 4.1), which are often in a grid-like network that is created for underground petroleum exploration. These features are called seismic lines due to the use of seismic vibrations that map underground petroleum resources.

Research has demonstrated the effects of seismic lines on biodiversity (Riva et al. 2018a; Roberts et al. 2018), and of particular interest in the decline of woodland caribou (*Rangifer tarandus caribou*) (Dyer et al. 2001, 2002), a species-at-risk in Alberta (Government of Alberta: Alberta Environment and Parks 2017). These effects are often most pronounced in treed peatlands where forest recovery from disturbance is slow (Lee and Boutin 2006; van Rensen et al. 2015) and of high conservation value given the local use of these habitats by woodland caribou (Rettie and Messier 2000). Approximately 35% of the world's peatlands are within Canada, covering about 12% (or 1.24×10^6 km^2) of the country and up to 50% of northern Alberta (Vitt 1994; Lieffers et al. 2017). In the portions that are treed, slow growing black spruce (*Picea mariana* (Mill.) B.S.P.), and tamarack (*Larix laricina* (Du Roi) K. Koch) tend to dominate, where most other tree species cannot establish. These treed peatlands are the preferred habitat of woodland caribou, allowing them to separate themselves from predators and other prey, since predation is the limiting factor on woodland caribou survival (Rettie and Messier 2000). Seismic lines in treed peatlands alter vegetation composition by promoting early seral shrubs and increasing access into woodland caribou

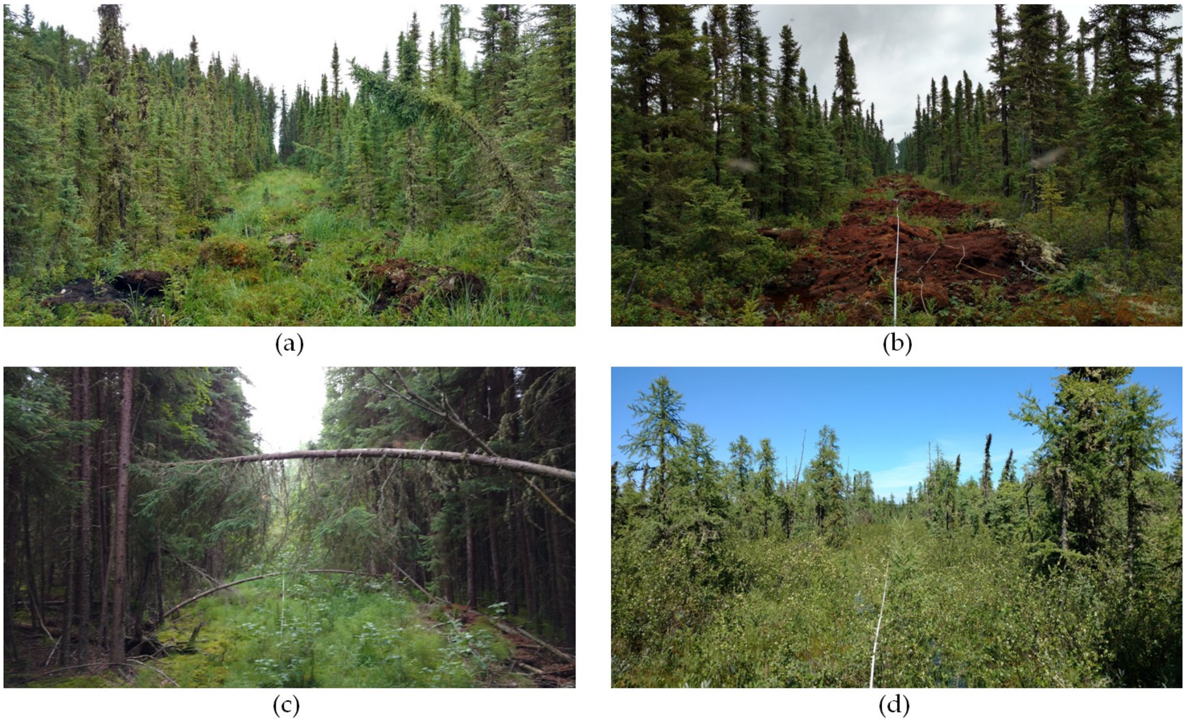

(a) (b) (c) (d)

Figure 4.1: Examples of seismic lines in northern Alberta, Canada: (a) treated (mounding and planting) poor fen; (b) treated (mounding and planting) bog; (c) untreated poor mesic forest; and, (d) untreated rich fen. All photographs by Angelo T. Filicetti.

habitat (treed peatlands) that benefit white-tailed deer (*Odocoileus virginianus*) and moose (*Alces alces*) (Latham et al. 2011b). Increases in deer and moose numbers result in increases in their primary predator, wolves, which, together with greater access into treed peatlands from seismic lines, are thought to lead to greater predation rates on caribou, thus representing a case of apparent competition (James and Stuart-Smith 2000; Latham et al. 2011a).

The mechanized creation of seismic lines can simplify microtopography (Stevenson et al. 2019 [Chapter 3]), remove peat and soil, and create a depressed surface, all of which lead to failures in tree recruitment (Lee and Boutin 2006; Caners and Lieffers 2014; van Rensen et al. 2015; Lieffers et al. 2017). The failure to recruit trees in treed peatlands has resulted in open seismic lines that lack trees for in excess of 50 years. Typically, trees in peatlands grow on hummocks versus hollows as areas with higher depth to water improve the survivability and growth of trees, which is likely due to a larger rooting depth, a warmer microclimate, and better aeration (Lieffers and Rothwell 1987; Lieffers and Macdonald 1989; Roy et al. 1999; Lieffers et al. 2017). Thus, restoring microtopography and/or creating elevated sites may be required for future tree recruitment on seismic lines within treed peatlands.

Restoration treatments of seismic lines in northeast Alberta average $12,500 (CAD) per km. The high costs for treatments on seismic lines are due to their narrow linear shape (kilometers long but only 3–8 m widths) and their remoteness (exceedingly difficult to access). The treatments often involve site preparation (mounding, ripping) and tree planting. Mounding involves the excavation and inversion of organic and mineral soil, resulting in a raised mound of material and an adjacent depression, essentially creating an artificial hummock and hollow (Sutton 1993). These mounds create an elevated growing site (hummock) for potential seedlings with favourable conditions, thus increasing the potential rooting depth and providing warmer microclimate and better aeration (von der Gönna 1992; Pyper et al. 2014). Ripping is applied to drier sites (in this paper, referred to as poor mesic, which typically occurs on small inclines in elevation due to the nature of the undulating plains in this area) and it consists of a plow or ripping teeth that are used to de-compact the soil and create microsites that improve moisture availability and aeration (von der Gönna 1992; Pyper et al. 2014). Leave-for-natural passive restoration that waits for natural recovery has no additional costs, but, due to the limited information available on where natural recovery is successful, how long it takes, and the poor rate of recovery that seismic lines in treed peatlands have exhibited, it is uncertain where this type of strategy can be used (Lee and Boutin 2006; van Rensen et al. 2015).

Delayed recovery of seismic lines, especially in the woodland caribou range, has led to significant efforts to actively restore them. These restoration treatments are currently voluntary, with the possibility of being regulatory in the future. Restoration projects, such as those by Cenovus Energy, Canadian Natural Resources limited (CNRL), and the Regional Industry Caribou Collaboration (RICC), aim to restore seismic lines in woodland caribou habitat by using mechanical site preparation (MSP) to stimulate the survival and growth of seedlings. Since there is limited published literature evaluating the success of these practices in treed peatlands, we evaluated the response of trees (planted and natural ingress) to different restoration treatments that are related to site preparation and tree planting in treed peatlands to better understand how treatments interact with site factors to promote the survival and growth rates of seedlings. Specifically, we hypothesize that the MSPs of lines will increase regeneration rates relative to that of untreated lines and that untreated lines will have lower regeneration rates than the adjacent forest controls, illustrating the conservation issue of a general lack of natural regeneration on seismic lines. Although treatments alone are predicted to facilitate natural regeneration, we measured a number of site factors (stand height, basal area, water availability, line orientation, etc.) to assess and control for their effect on local regeneration patterns.

4.3 Materials and Methods

4.3.1 Study area

We examined seismic line tree regeneration for three restoration projects, which include the Cenovus Energy LiDea 1 and LiDea 2 projects and the CNRL Kirby project, both within the Athabasca Oil Sands of northeast Alberta between the communities of Conklin and Cold Lake (Figure 4.2). Restoration for each project occurred at different times and locations. The seismic lines in these areas were initially cleared in the mid-1980s to the late-1990s, with MSPs being applied to these lines between 2012 and 2015. On average, the untreated seismic lines were last disturbed (cleared) ~22 years prior to field measures, while treated seismic lines had MSP applied ~3.8 years prior to field measurements. Widths of seismic lines ranged from just under 3 m to just over 8 m (see Figure 4.1 for examples).

Plantings on treated lines reflected tree species that were present in the adjacent control forest that is typical of the respective ecosite (tamarack in fens, jack pine (*Pinus banksiana* Lamb) in poor mesic, black spruce across all of the ecosites). Tree planting for treated seismic lines was at a rate of ~1,300 stems per hectare. This density was chosen due to uncertainty regarding the amount of natural ingress and the number of viable microsites that would be created by the large mounds, but allowed for a minimum of one planting per mound. Planting was carried out during the last week of July and the first week of August, with summer stock being grown from the Mostoos Hills Central Mixedwood Uplands (CM 3.1) Seedzone following the Alberta Forest Genetic Resource Management and Conservation Standards (Alberta Agriculture and Forestry: Forestry Division 2016). All of the seedlings were grown in standard 410A styroblocks; pine seedlings were grown in blocks with copper coating to prune roots.

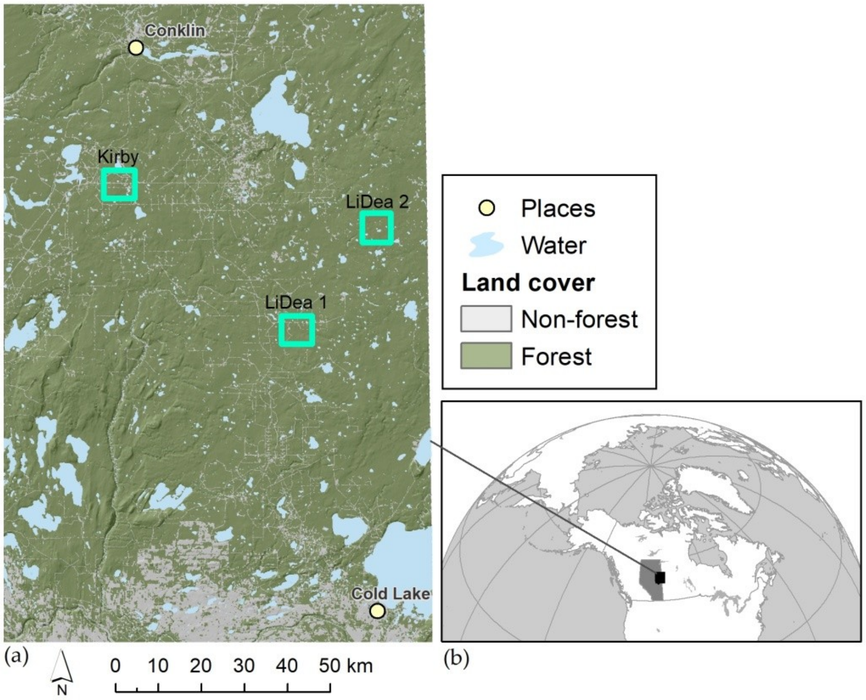


Figure 4.2: Location of the study areas: (a) notable population centers and the location of the three restoration projects (Kirby, LiDea 1, and LiDea 2) within this study; and, (b) outline of the province of Alberta, Canada within North America, and location of study.

Mounding was accomplished using a 20 tonne construction excavator with a bucket attachment (sizes were 0.75 to 0.90 m^3). Site preparation was completed by excavating and inverting material, forming a mound of mineral and/or organic soil and an adjacent depression.

Equipment operators were instructed to make mounds that were 0.75 m in width, 1 m in length, and 0.80 m in peak height, allowing for settling, which was expected to occur with mounded organics. Three mounds were placed across the width of the seismic line, in a diamond or checkered pattern, regardless of the seismic line width. A mound was placed in the middle of the seismic line width every 6 m. Similarly, every 6 m, an additional two mounds were placed along the seismic line length, between the center mounds, at the opposite edges of the seismic line width, creating a 1-2-1-2-1 checkered pattern.

This area lies within the boreal forest zone and it is characterized by a gently undulating plain, where even small changes in microtopography (0.5 m) can result in different moisture regimes and vegetation (Natural Regions Committee 2006). The focus of this study is on treed peatlands, which are classified as treed bog, poor fen, rich fen, and poor mesic ecosites using the Alberta Biodiversity Monitoring Institute (ABMI) ecosite classification. Dominant tree species are black spruce, tamarack, and to a lesser extent, jack pine. Wildfires have affected both the LiDea 1 and LiDea 2 sites with fires occurring in 1980 and 1993, respectively, although only affecting a minority of the overall treatment area. In both project areas, the wildfires occurred several years before the seismic lines were created and therefore many years before MSPs.

4.3.2 Site selection and field methods

To avoid pseudo replication, the criteria for selecting sample sites on untreated seismic lines were: (1) minimum distance between plots of 400 m; and, (2) distance may be less between plots only if on a separate seismic line with a different orientation (more than a 45° difference) and/or if ecosite altered within a 400 m radius. Sampling of treated seismic lines was limited to where MSPs were applied, but with use of similar criteria to the untreated lines. The starting locations of plots on seismic lines, once sites were located, were based on a random toss of a metal stake.

Overall, 127 sites with paired plots, with one plot on the seismic line and one plot in the adjacent forest control were sampled in the summer of 2017 for a total of 254 plots. The sampling distribution by ecosite included eight bogs (16 plots), 51 poor fens (102 plots), 33 rich fens (66 plots), and 35 poor mesic sites (70 plots). This distribution of samples reflects the abundance of different ecosites in the area with, for instance, bogs being increasingly uncommon in the project areas.

Each site (paired plots—seismic line and adjacent forest control) was selected based on the requirement of having uniform forest stand conditions (i.e., height, density, age) for the pair of plots, with each plot consisting of a 30 m transect. The seismic line transects were located in the center of the seismic line, while the adjacent paired control plots were located 25 m into the adjacent forest running parallel to the seismic line. A coin toss was used to randomize which side of the seismic line the adjacent forest control plot was located. The tree regeneration and forest stand conditions on the seismic lines and adjacent forest stands were measured along 30 m transects with regenerating trees and shrubs being counted in 1 m x 30 m 'belt' quadrats and trees (≥ 1 cm diameter at breast height (DBH)) counted in 2 m x 30 m belt quadrats. Additional information was collected in the adjacent forest stand, including stand basal area by species using a two-factor metric prism at the midpoint of the forest transect (15 m), stand age of representative mature trees in the plot using dendrochronology via tree cores, and representative tree height using a hypsometer (Haglof Vertex IV, Langsele, Sweden).

4.3.3. Regeneration density by restoration area, restoration treatment, plot location, and stand characteristics

Since the creation of the seismic line and the initial application of MSPs destroy/kill all mature trees and well over 90% of regenerating trees, all of the trees on the seismic line can be considered to be regenerating trees. We wanted to have most, if not all, trees on the seismic line being considered to be regenerating trees, as we are interested in how well seismic lines are restoring, but this becomes problematic when comparing to the adjacent forest. We therefore used a "cut-off DBH" to classify regenerating trees for both seismic lines and adjacent forests. Accordingly, a regenerating tree is defined as any tree in the seismic line or adjacent forest less than 1 cm DBH, which accounted for > 97% of all trees on seismic lines (see Table 4.1).

Table 4.1: Stand characteristics and tree regeneration rates for 127 sites (254 plots) sampled in northeast Alberta, Canada. S.E. is standard error.

Stand variable	Minimum	Median	Maximum	Mean (S.E.)
Age	5	52	165	56.6 (1.8)
Height	2	9.5	25.2	10.3 (0.3)
Basal area (m^2/ha)	0	12	44	13.7 (0.5)
Tree stems per ha (DBH < 1 cm)				
Seismic line	0	9,000	39,333	10,186 (719)
Adjacent stand	0	6,000	48,333	8,236 (631)
Tree stems per ha (DBH ≥ 1 cm)				
Seismic line	0	0	2,500	85 (30)
Adjacent stand	667	7,167	22,500	7,294 (371)

First, to visualize the main experimental effects, we plotted the mean and standard errors of regeneration density (stems per ha) for all tree species (see Figure 4.A1 and Table 4.A1 and A2 in Appendix A) against the restoration area (LiDea 1, LiDea 2, and Kirby), ecosite, restoration treatment (untreated, mounding/planting, ripping/planting), and plot location (seismic line versus adjacent forest) for all 127 sites (254 plots). Preliminary analyses found that the ecosite was highly influential in the patterns of regeneration density (particularly for certain species) with multiple interactions being required to account for ecosite level complexity. To minimize the complexity of models and to better understand ecosite-specific responses, we analyzed separately regeneration by each ecosite.

Responses were assessed using generalized linear mixed effects models (xtreg command in STATA 15.1/SE; StataCorp, 2017, College Station, TX, USA) (Züur et al. 2009), where we related linear changes (gaussian distribution, identity link with exchangeable correlation structure) in regeneration density ($\log_{10}$ transformed with a constant of 1 added) to the restoration area (LiDea 1, LiDea 2, or Kirby), restoration treatment (untreated, mounding/planting, or ripping/planting), plot location (seismic line versus adjacent forest), and stand variables (basal area, stand height, and stand age). Site was used as a random effect to account for the paired nature of the seismic line and the adjacent control forest plots. Separate binary dummy variables were used to represent the presence in a project restoration area (0 if site was not in project area and 1 when site was in project area), restoration treatment (0 for untreated as reference category and 1 for treated), and plot location (0 for adjacent forest reference category and 1 for seismic line). The responses on restoration area, therefore, reflect the possible regional differences between areas, while the responses on seismic lines reflect changes from the adjacent forest stand.

Model selection was as follows: (1) main treatment variables (restoration treatments and binary seismic line location variable) were included, regardless of their significance given the purpose of the study; and, (2) variables for site location and stand characteristics were tested and only included if significant (at $\alpha = 0.05$). Collinearity was assessed using Pearson correlations with no variables being considered colinear ($|r| \geq 0.7$, the highest correlation was between stand height and basal area at $r = 0.67$). For the final model, we report model parameters for treatment variables and other significant variables, as well as model goodness of fit using the ‘overall’ R^2, the ‘between’ R^2 (representing variance between sites such as fire severity and stand conditions), and the ‘within’ R^2 (representing variance within sites or in this case the binary seismic line variable) components. Note that these are pseudo-R^2 values and thus they represent relative measures of fit. Model assumptions were examined for independence, normality of response variables and presence of outliers, and correlations ($r > |0.7|$) among independent variables. Variables were removed and/or modified (transformed) to meet model assumptions.

4.3.4 Regeneration patterns based on seismic line characteristics

For this analysis, regeneration density was defined as any tree in the seismic line, regardless of its DBH with analyses being restricted only to seismic lines (adjacent forests plots removed resulting in 127 plots), allowing for seismic line characteristics to also be tested. Here, we assessed the effectiveness of restoration treatments and that of line orientation, line width (forest gap), stand conditions, and ground cover (visual estimates of percent ground cover were assessed along 2 m x 30 m belt quadrats). As the removal of all adjacent plots eliminates the paired design, we used simple linear regression (reg command in STATA 15.1/SE; StataCorp, 2017, College Station, TX, USA), again using the $\log_{10}$ transformed regeneration density as the response variable. A similar model selection process was used as that in Section 4.3.3, but without the random effect for plot location, since the pair of plots was not used and here the inclusion of seismic line variables of line orientation, line width (forest gap), and ground cover variables. The line width varied between 2.5 m and 8.5 m (mean of 4.9 and SE [standard error] = 0.1), while line orientation represented the compass bearing of seismic lines that were transformed to an index between 0 (east-west orientation) and 1 (north-south orientation) following the methods of (van Rensen et al. 2015). Most lines in the area were on north-south and east-west axes. Forest stand measures of tree height, stand basal area, and stand age were considered, including their interaction with other factors, such as seismic line (forest gap) width and orientation.

4.3.5 Tree regeneration height on seismic lines and time since disturbance

For each seismic line, we also measured the height of regenerating trees within the 1 m x 30 m belt quadrat to identify which factors promote the growth of trees. Analysis and model selection is identical to Section 4.3.4 and no significant responses were observed. Similarly, time since disturbance (creation of the seismic line and application of MSP) was never significant in any of the models.

4.4 Results

4.4.1 Overall characteristics

The age of stands ranged from 5 to 165 years (mean of 56.6, SE = 1.8), stand height varied from 2 to 25.2 m (mean of 10.3, SE = 0.3), basal area (using a 2x factor prism) in adjacent stands varied from 0 to 44 m^2/ha (mean of 13.7, SE = 0.5), while trees per hectare ranged from 1,333 to 45,000 (mean of 14,587, SE = 742.8). See Table 4.1 for a list of stand conditions across the plots. The most common tree species, in order of most to least common, were: black spruce, tamarack, jack pine, aspen (*Populus tremuloides* Michx.), Alaska birch (*Betula neoalaskana* Sarg.), and balsam poplar (*Populus balsamifera* L.); similarly, the most common shrubs were: willow (*Salix* spp.), bog birch (*Betula pumila* L.), and prickly rose (*Rosa acicularis* Lindl.).

On average, the treated lines had 12,290 (SE = 890) regenerating stems/ha, untreated lines had 7,680 (SE = 1085) regenerating stems/ha, and the adjacent undisturbed forests had 8,240 (SE = 631) regenerating stems/ha. Treated lines, therefore, had 1.6-times more regenerating stems per hectare than the untreated lines and 1.5-times more stems per hectare than adjacent undisturbed forests (Figure 4.3). There are more regenerating stems on treated seismic lines, when compared to untreated lines and adjacent undisturbed forests across each ecosite (Figure 4.3). For bogs, poor fens, rich fens, and poor mesic sites effect size suggest that the treated seismic lines are, respectively, 85%, 56%, 81%, and 82% more likely to have higher regeneration rates than the average untreated seismic line and that adjacent forests are likely to have 81%, 45%, 60%, and 57% higher regeneration rates than the average untreated seismic line. Note the lack of larger trees (DBH ≥ 1 cm) on seismic lines as compared to adjacent stands, illustrating low tree growth and survival on seismic lines in treed peatlands.

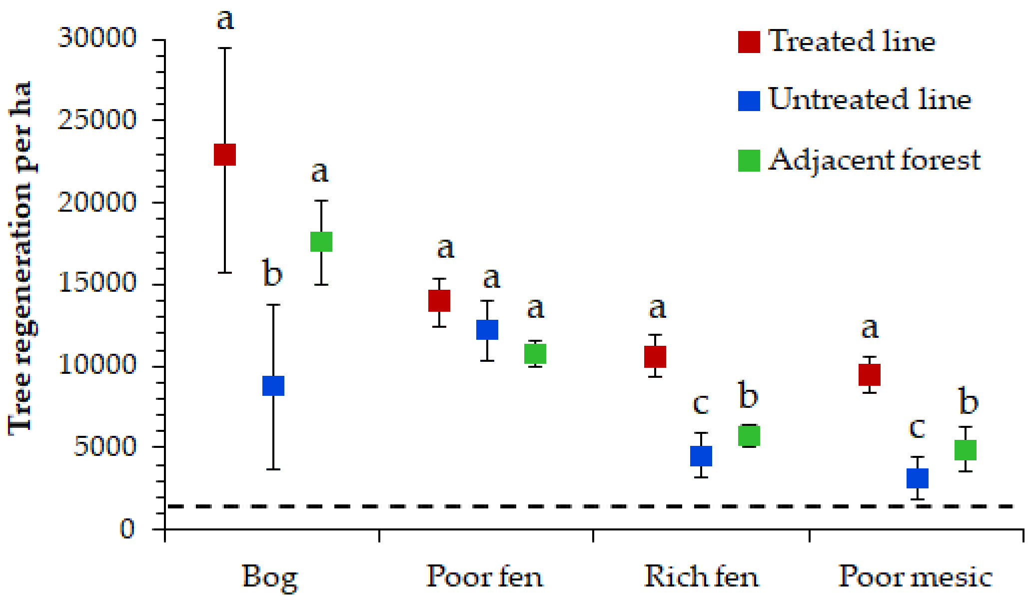


Figure 4.3: Mean and standard error (error bars) of tree regeneration (diameter at breast height (DBH) < 1 cm), across four ecosites and three treatments. Significance of treatments within each ecosite was tested with a pairwise comparison (Bonferroni adjustment) with different letters indicating significant ($p < 0.017$) differences within an ecosite. Note, dashed line represents the amount of planted stems per hectare in treated lines (1300 stems/ha).

4.4.2 Restoration effectiveness on seismic lines versus adjacent forest

Untreated seismic lines consistently had lower tree stem density for bog, rich fen, and poor mesic ecosites when compared to adjacent reference forests (see Figure 4.3 and Table 4.2), but not for poor fens. Similarly, restoration treatments consistently increased the numbers of tree stems in bogs, rich fens, and poor mesic ecosites, but once again, not for poor fens. Restoration sites also affect tree density with the LiDea 1 site having higher average stem densities in poor fens than the other two restoration areas. Nevertheless, the LiDea 2 site had a lower average stem density in rich fens (Table 4.2). Note, the time since treatment and time since the creation of the line were never individually significant. Overall model fit was low for poor fens ($R^2 = 0.08$, $p = 0.04$) and moderately high for all other ecosites ($R^2 > 0.30$, $p < 0.01$). Within model fit reflected the strength of the difference between the seismic line and adjacent forest plot, with R^2 being low in both types of fens ($R^2 = 0.04$ for poor fens and $R^2 = 0.17$ for rich fens) and high ($R^2 > 0.50$) for both bogs and poor mesic forests (Table 4.2).

Table 4.2: Random effect linear model (xtreg) parameters (coefficient, β; and standard error, SE) relating regeneration density (DBH < 1 cm) ($\log_{10}$ transformed) of all tree species to all three restoration areas, restoration treatment (mounding and planting or ripping and planting), and seismic line location (vs. adjacent forest control). Both restoration treatment and seismic line location were included regardless of significance. *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$.

Tree density (stems/ha)	Bog β (SE)	Poor fen β (SE)	Rich fen β (SE)	Poor mesic β (SE)
Constant (intercept)	16,450 (30)***	7,743 (14)***	6,454 (20)***	2,710 (20)***
Site (restoration area)				
LiDea 1		41 (17)*		
Kirby				
LiDea 2			−44 (24)**	
Restoration treatment				
Mounding & Planting	300 (67)**	34 (24)	271 (37)***	N/A
Ripping & Planting	N/A	N/A	N/A	731 (38)***
Seismic line location				
Seismic line plot	−70 (52)**	−16 (20)	−55 (32)**	−63 (30)***
Model statistics				
n	16	102	66	70
R^2 (within)	0.52	0.04	0.17	0.51
R^2 (between)	0.29	0.12	0.44	0.21
R^2 (overall)	0.41	0.08	0.31	0.32
Wald χ^2	9.82	8.30	27.53	43.72
p-value	0.007	0.040	< 0.001	< 0.001

4.4.3 Seismic line regeneration density

When excluding the adjacent forest and including line characteristics and ground cover, the differences in stem density between ecosites were more apparent. Even with the addition of these other factors, the most influential variables were still that of the restoration treatments (see Table 4.3). The best model describing tree regeneration density on seismic lines in bogs consisted of only the bearing of the seismic line. Here, poor fens, contrary to Section 4.4.2, significantly benefitted from the restoration treatment, but only when accounting for the abundance of lichen and graminoids, which were detrimental to regeneration. Tree regeneration in rich fens was positively affected by the restoration treatment and stand height, with the mounding and planting treatment being the most effective here when compared to other wet ecosites (bogs and fens). Finally, poor mesic sites benefitted the most of all of the ecosites from their restoration treatment, here being ripping and planting, with no other variable affecting tree regeneration patterns.

Table 4.3: Linear regression model parameters (coefficient, β; and standard error, SE) relating regeneration density ($\log_{10}$ transformed) of all tree species found on seismic lines to restoration treatment, line characteristics, stand variables, and percent ground cover. *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$. RMSE is root mean squared error.

Tree density (stems/ha) on seismic line only	Bog β (SE)	Poor fen β (SE)	Rich fen β (SE)	Poor mesic β (SE)
Constant (intercept)	5,024 (45)***	13,012 (22)***	534 (80)***	1,224 (32)***
Restoration treatment				
Mounding & Planting		70 (26)*	206 (49)**	N/A
Ripping & Planting	N/A	N/A	N/A	540 (44)***
Line characteristics				
Bearing	477 (84)*			
Stand variables				
Stand height (m)			19 (8)*	
Ground Cover (%)				
Lichen		−5 (3)*		
Graminoid		−5 (1)***		
Model statistics				
n	8	51	33	35
R^2	0.58	0.30	0.39	0.44
Prob > F	0.028	< 0.001	< 0.001	< 0.001
RMSE	0.36	0.35	0.48	0.46

4.5 Discussion

4.5.1 Restoration effectiveness on seismic lines versus adjacent forest

Overall, the results indicate that the presence of a seismic line lowers tree regeneration rates and that the application of restoration treatments increases the tree regeneration rates across all ecosites (see Table 4.2). Therefore, early indications suggest that these MSPs are beneficial in initializing the restoration of caribou habitat, thus supporting our initial hypothesis. Except for poor fens, adjacent forests are more likely to have higher regeneration rates than untreated seismic lines, supporting our hypothesis, but the effect sizes suggest only bogs are notable. An untreated seismic line, a clear-cut area (low competition) with a small gap size (easily available seed source), would be expected to have higher regeneration rates than the adjacent forest but this is not being observed in this study or others (Lee and Boutin 2006; van Rensen et al. 2015). The lack of tall trees in the untreated seismic lines observed here is similar to other studies (Lee and Boutin 2006; van Rensen et al. 2015), suggesting that untreated seismic lines in treed peatlands have poor tree growth and survival.

The creation of a seismic line can eliminate microtopography and depress the overall topographic elevation (Stevenson et al. 2019 [Chapter 3]), resulting in shallower water tables and thus changes in ground cover and tree abundance. This includes a general trend towards more tamarack and less black spruce in the untreated poor and rich fens (see Figure 4.A1 and Table 4.A1 in Appendix A). The untreated seismic lines have consistently lower tree densities than adjacent forest controls with poor fens being the exception due to these changes in microtopography and the slow recovery rate and rate of growth in trees in these ecosites. The decades of poor tree density that are experienced on these lines act as pathways of low resistance to wolves and are detrimental in effect to the caribou population. On the other hand, treated seismic lines have consistently greater tree densities than both the untreated seismic lines and adjacent forest controls, with poor fens again being the exception. Furthermore, the treated seismic lines averaged 3.8 years since treatment, while untreated seismic lines were last disturbed (cleared) ~22 years prior. Adjacent forest controls have not been anthropogenically disturbed, although a small number of sampled areas within the restoration projects experienced wildfires in 1980 or 1993. The higher tree densities that were experienced in the relatively short-term (3.8 years) on treated lines can function as obstacles to wolf movement and should benefit caribou populations if the densities stay consistent into the future.

In treated rich fens and, to a lesser degree, poor fens, there is a reversal of the decrease in overall black spruce (see Figure 4.A1 and Table 4.A1 in Appendix A). The lack of black spruce recovery in poor fens seems to account for the deficit in overall tree density experienced post-treatment.

The three restoration areas (LiDea 1, Kirby, and LiDea 2) had minor differences in tree regeneration between them, in fact, there were only two main differences observed. On the one hand, the overall patterns in tree density in LiDea 1 had higher average stem counts in poor fens than when compared to the other two restoration project areas. This suggests that MSP for poor fens in LiDea 1 were perhaps better implemented (differing applications/personnel and/or time since treatment; note, time since treatment and the creation of the line were never significant on their own). Another possibility could be that the LiDea 1 area was, on average, drier or had a higher depth to water than the other two restoration sites. On the other hand, the LiDea 2 site had a lower stem count in rich fens, which may reflect the fact that the restoration area experienced wildfire in 1980, potentially was wetter (trees were shorter and with lower basal area), or had less effective treatments. There were, however, differences when considering individual species (see Figure 4.A1 and Table 4.A1 in Appendix A).

4.5.2 Seismic line regeneration density

With the exception of bogs, the most consistent predictor for higher tree densities on seismic lines was the restoration treatment. The best model for bog consisted of only the bearing of the seismic line, suggesting that sunlight may be the largest factor influencing regeneration in bogs. However, these results may be misleading for two reasons: (1) bogs had the lowest sample size; and, (2) most bog sites were in LiDea 2, which partially burned during a fire in 1980, many years before initial seismic line creation and decades before MSPs.

The patterns of tree regeneration in poor fens were complex, despite poor fens having the largest sample size. A pattern for poor fens only becomes significant when mounding and planting was combined with lichen and graminoid ground cover suggesting that the effectiveness of treatments is site dependent and at least partially affected by lichen and graminoid cover or the factors that promote their growth. This may have to do with the way that we classified poor fens in the field, or due to the fact that poor fens are ecologically in between rich fens and bogs, as typically rich fens evolve into poor fens and then into bogs (Kuhry et al. 1993). Perhaps their use as an indicator of water availability reflects the importance of lichen and graminoid ground cover (Weltzin et al. 2000) and whether the poor fen is more similar to a rich fen or a bog. Although graminoids can be an indicator of wet conditions (rich fen), they also can increase competition with that of seedlings, while lichen mats may produce poor seedbed conditions (Madec et al. 2012; Mallik and Kayes 2018). Many studies demonstrate the effectiveness of herbicides on seedling survival and growth post-MSP, as they eliminate the competing shrubs and graminoids (Sutherland and Foreman 2000; Löf et al. 2012). The application of herbicides on seismic lines would be costly, due to their shape and remoteness, especially if reapplications are necessary. If the current mounding application in poor fens continues to show non-significant effects when compared to untreated lines and adjacent forests, perhaps a different MSP or silvicultural treatment should be considered. Note that there have been reports that MSPs can still have an influence on seedling growth for a period of 10 years (Lafleur et al. 2011).

Restoration treatment and stand height affected tree regeneration in rich fens. Of all the wetter ecosites (bogs/fens), rich fens benefited the most (proportionally) from mounding and planting. Stand height is likely a proxy of depth to water table (Lieffers and Rothwell 1987; Bubier 1991), a proxy for most of the rich fen sites in LiDea 2 (which was discussed in section 4.5.1), and it affects seed dispersal and/or seed abundance (the minimum stand height for rich fens was 3.4 m and the mean was 7.9 m, shorter trees tend to be accompanied with lower basal area and generally less fit trees (Boucher et al. 2006). A large proportion of natural ingress in treated rich fens is, surprisingly, aspen (see Figure 4.A1 and Table 4.A2 in Appendix A). Aspen is typically not a species found in rich fens and they are unlikely to survive long-term, but it does demonstrate the potential for additional species typical of the ecosite to become recruited on exposed mounds.

Poor mesic sites benefitted the most from their restoration treatment of ripping and planting, with no other factor being found to significantly affect tree regeneration patterns. Ripping and planting could have experienced the most benefit here due to improved germination; it is likely that the limiting factor in poor mesic sites is seedbed conditions and seed availability (Sirois 1993).

4.5.3 General responses

The lack of responses in tree height and the effect of time since disturbance or treatment were likely due to: (1) all MSPs were applied within five years of field measurements; (2) all of the MSPs were applied within three years of each other; (3) each project area had their MSPs applied at identical times (+/- a month); and, (4) other studies suggest there is little to no difference in the effect of time since disturbance on untreated lines (Lee and Boutin 2006; van Rensen et al. 2015).

The densities that were observed on treated sites are likely to decrease over time due to competition and self-thinning, yet no evidence of this was observed during field measurements. Competition and self-thinning seems unlikely to occur in the near future, as tree densities and heights are not exceedingly high. A study on seismic lines, five-years post-fire in a jack pine

(*Pinus banksiana*) dominant stand (a shade-intolerant species), had much higher regenerating tree densities and heights, yet showed no signs of competition/self-thinning (Filicetti and Nielsen 2018 [Chapter 2]).

Higher stocking rates, herbicides, and fertilizers could improve survival and growth rates, but at much higher financial and possibly ecological cost. Therefore, if this pilot demonstrates that MSPs are successful at obtaining adjacent forest stand densities and restoring caribou habitat, it would be much more cost effective to apply such treatments elsewhere in the future. Many studies already suggest that mechanical site preparation is the most cost effective treatment to apply for seedling survival and growth (von der Gönna 1992; Lafleur et al. 2011; Löf et al. 2012), but this had not been formally tested for seismic lines.

Logistics is a key challenge for seismic line restoration in northern Alberta due to the remoteness, wetness, narrow linear shape, and the undulating nature of the landscape, which leads to abrupt changes in ecosites along the line. Within a few hundred meters it is not uncommon to have multiple ecosites, ranging from rich fen to poor xeric. This results in restoration challenges, as a seismic line may require several different MSPs. Winter conditions have proved most effective for use of machinery, given the wet nature of the landscape (Pyper et al. 2014). The excavators that were used here were chosen for their adaptability as well as their ability to create larger mounds. Continuous mounders have the capacity to improve the productivity of mounding, but this machinery produces smaller mounds. Smaller mounds have been found to be less effective, as they do not overcome issues in wetter landscapes (distance to the water table, drainage, etc.), winter frost damage common in high latitudes, and decreases in size occurring from settling and erosion experienced by mounds in the first years post-creation (Sutton 1993). Although mounding generally costs more than other MSPs, it is needed to avoid establishment/survival issues with a high-water table and it is typically recommended for such sites (von der Gönna 1992; Löf et al. 2012). Ideally, local variation in water table would be first measured, and then MSP planning would proceed, but water table can experience large fluctuations between years and seasons, with estimates of this variation being complicated and costly (Triisberg et al. 2014). If a suitable estimate for water table could be measured and a cut-off depth found where mounding would be less effective, then other MSPs could be considered. Many of the other MSPs (scalping, trenching, mixing, etc.) are considered to be inappropriate for wet sites that are typical of treed peatlands (von der Gönna 1992).

Often, ripping is used as a standalone or initial treatment to overcome issues of compaction (Löf et al. 2012) and it has worked well in poor mesic sites in this study.

4.6 Conclusions

Seismic lines in treed peatlands are not recovering following disturbance, with some staying unforested for many decades (Lee and Boutin 2006; van Rensen et al. 2015). Trees that do establish on seismic lines often have difficulty in growth and survival due to simplification in microtopography and a lower water table depth. Restoration treatments increased tree density when compared to the untreated lines, despite averaging 3.8-years since treatment application (vs. untreated lines averaging 22 years). On average, the treated lines have 12,290 regenerating stems/ha, which is 1.6-times more than the untreated lines (7,680 stems/ha) and 1.5-times more than the adjacent undisturbed forest (8,240 stems/ha), as well as having consistently more tree stems across all ecosites. MSPs on seismic lines show promise in restoring caribou habitat (treed peatlands), but further studies with a longer time horizon are required. The lack of strong treatment effects between treated and untreated seismic lines in poor fens (the highest sampled ecosite) suggest that the cost-effectiveness of these applied methods are questionable for this one ecosite. Poor and rich fens, though, do experience a shift to higher tamarack density post-seismic line creation and a shift back to more black spruce after receiving mounding treatment. Therefore, mounding can be considered to be an effective restoration treatment for poor and rich fens.

Appendix A

Table 4.A1: Random effect linear model (xtreg) parameters (coefficient, β; and standard error, SE) relating regeneration density (DBH < 1 cm) ($\log_{10}$ transformed) of all tree species to all three restoration areas, restoration treatment (mounding & planting or ripping & planting), and seismic line location (vs. adjacent forest control). Both restoration treatment and seismic line location were included regardless of significance. *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$.

Tree density (stem/ha)	Bog				Poor fen			
	Tamarack β (SE)	Black spruce β (SE)	Jack pine β (SE)	Aspen β (SE)	Tamarack β (SE)	Black spruce β (SE)	Jack pine β (SE)	Aspen β (SE)
Constant (intercept)	0 (40)	16,404 (29)***		0 (29)	169 (31)***	7,937 (12)***	3 (5)	4 (11)
Site (restoration area)								
LiDea 1					175 (40)**			
Kirby								
LiDea 2								
Restoration treatment								
Mounding & Planting	185 (96)	247 (64)*		836 (67)***	−9 (48)	26 (25)	−12 (10)	1515 (22)***
Ripping & Planting	N/A	N/A		N/A	N/A	N/A	N/A	N/A
Seismic line location variable								
Seismic line plot	105 (79)	−71 (51)*		44 (56)	300 (36)***	−51 (21)***	10 (9)	19 (18)
Stand variables								
Stand height (m)					−11 (5)*			
Basal area of target tree								
Basal area of other tree species								
Model statistics								
n	16	16		16	102	102	102	102
R^2 (within)	0.55	0.54		0.80	0.39	0.24	0.01	0.85
R^2 (between)	0.16	0.27		0.59	0.20	0.02	0.04	0.60
R^2 (overall)	0.41	0.41		0.73	0.28	0.13	0.02	0.76
Wald χ^2	9.18	9.98		35.42	43.30	16.16	1.97	347.80
p-value	0.010	0.007		< 0.001	< 0.001	< 0.001	0.373	< 0.001

Table 4.A1. *Cont.*

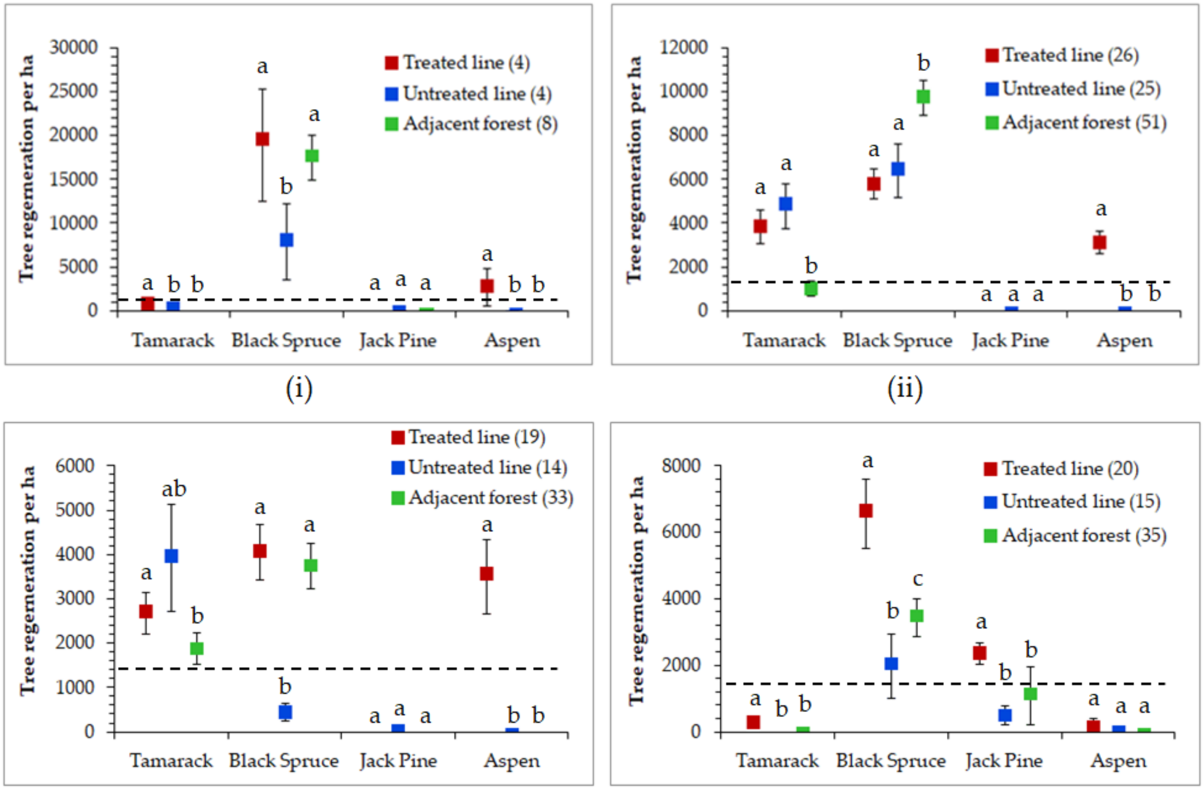
Tree density (stem/ha)	Rich fen				Poor mesic			
	Tamarack	Black spruce	Jack pine	Aspen	Tamarack	Black spruce	Jack pine	Aspen
	β (SE)	β (SE)	β (SE)	β (SE)	β (SE)	β (SE)	β (SE)	β (SE)
Constant (intercept)	1,974 (33)***	1,263 (22)***	0 (5)	49 (20)*	13 (13)	8,588 (82)***	185 (30)***	13 (14)
Site (restoration area)								
LiDea 1	198 (41)**							
Kirby								
LiDea 2				−56 (24)***				
Restoration treatment								
Mounding & Planting	127 (53)	671 (35)***	−16 (11)	1,072 (36)***	N/A	N/A	N/A	N/A
Ripping & Planting	N/A	N/A	N/A	N/A	150 (27)***	438 (43)***	1,837 (35)***	−2 (29)
Seismic line location variable								
Seismic line plot	17 (45)	−87 (30)***	19 (10)	19 (32)	−16 (23)	−60 (35)**	−9 (27)	17 (26)
Stand variables								
Stand height (m)						−8 (4)*		
Basal area of target tree		9 (2)***			44 (16)*			67 (14)***
Basal area of other tree species	−12 (2)***						−5 (2)**	
Model statistics								
n	33	33	33	33	35	35	35	35
R^2 (within)	0.23	0.55	0.07	0.70	0.35	0.23	0.86	0.02
R^2 (between)	0.51	0.76	0.04	0.68	0.22	0.35	0.24	0.33
R^2 (overall)	0.38	0.67	0.06	0.69	0.28	0.30	0.57	0.19
Wald χ^2	36.72	126.82	3.82	140.05	26.07	26.33	198.10	15.48
p-value	< 0.001	< 0.001	0.150	< 0.001	< 0.001	< 0.001	< 0.001	0.001

Table 4.A2: Linear regression model parameters (coefficient, β; and standard error, SE) relating regeneration density ($\log_{10}$ transformed) of all tree species found on seismic lines to restoration treatment, line characteristics, stand variables, and percent ground cover. *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$. RMSE is root mean squared error.

Tree density (stem/ha) on seismic line only	Bog				Poor fen			
	Tamarack β (SE)	Black spruce β (SE)	Jack pine β (SE)	Aspen β (SE)	Tamarack β (SE)	Black spruce β (SE)	Jack pine β (SE)	Aspen β (SE)
Constant (intercept)	34 (30)	4,809 (44)***		44 (71)	1,342 (100)***	5,213 (27)***	-3 (7)	25 (22)
Site (restoration area)								
LiDea 1					540 (45)***			
LiDea 2								
Restoration treatment								
Mounding & Planting				836 (114)*				1,490 (32)***
Ripping & Planting	N/A	N/A		N/A	N/A	N/A	N/A	N/A
Line characteristics								
Bearing	1,152 (53)**	389 (82)*						
Stand variables								
Stand height (m)					−16 (5)**			
Basal area of target tree						4 (2)*		
Basal area of other tree species								
Ground Cover (%)								
Open water						−2 (1)*		
Bryophyte					2 (1)*			
Sphagnum fuscum							2 (1)*	
Graminoid						−3 (1)*		
Model statistics								
n	8	8		8	51	51	51	51
R^2	0.85	0.54		0.59	0.44	0.31	0.10	0.67
Prob > F	> 0.001	0.038		0.026	< 0.001	< 0.001	0.021	< 0.001
RMSE	0.25	0.36		0.47	0.54	0.33	0.19	0.43

Table 4.A2. *Cont.*

Tree density (stem/ha) on seismic line only	Rich fen				Poor mesic			
	Tamarack β (SE)	Black spruce β (SE)	Jack pine β (SE)	Aspen β (SE)	Tamarack β (SE)	Black spruce β (SE)	Jack pine β (SE)	Aspen β (SE)
Constant (intercept)	404 (94)*	163 (30)**	8 (8)	186 (44)**	0 (22)	798 (33)***	256 (29)***	322 (93)**
Site (restoration area)								
LiDea 1								
LiDea 2				−81 (47)***				
Restoration treatment								
Mounding & Planting		1,170 (41)***		933 (48)***	N/A	N/A	N/A	N/A
Ripping & Planting	N/A	N/A	N/A	N/A	152 (30)**	450 (46)***	1265 (36)***	
Line characteristics								
Bearing								−48 (33)*
Stand variables								
Stand height (m)	18 (8)*							
Basal area of target tree								
Basal area of other tree species							−6 (2)***	
Ground Cover (%)								
Open water								
Bryophyte								
Sphagnum fuscum								
Graminoid								
Model statistics								
n	33	33	33	33	35	35	35	35
R^2	0.12	0.64	0.00	0.68	0.27	0.38	0.70	0.14
Prob > F	0.047	< 0.001	0.000	< 0.001	0.001	< 0.001	< 0.001	0.029
RMSE	0.54	0.42	0.18	0.48	0.34	0.48	0.37	0.35



(i) (ii)

(iii) (iv)

Figure 4.A1: Mean and standard error (error bars) of tree regeneration (DBH < 1 cm), across four tree species and three treatments. Where each ecosite is represented by: (i) bog; (ii) poor fen; (iii) rich fen; and (iv) poor mesic. Significance of treatments within each ecosite was tested with a pairwise comparison (Bonferroni adjustment) with different letters indicating significant ($p < 0.017$) differences within a species. Note, dashed line represents the amount of planted stems per hectare in treated lines (1300 stems/ha). Scales vary.

Chapter 5: Tree regeneration on industrial linear disturbances in treed peatlands is hastened by wildfire and delayed by loss of microtopography

5.1 Abstract

The world's forests are highly fragmented by linear disturbances, many of which have failed to recover decades after abandonment. Lack of recovery is common in unproductive forests, such as treed peatlands, due to conditions that limit tree growth including simplification of microtopography (loss of microsites). The persistence of these features affects biodiversity, but of particular concern in Canada is the detrimental effects on threatened woodland caribou. Although natural regeneration of trees in peatlands occurs in some places, it is not an effective recovery strategy for restoring habitat of woodland caribou. This has led to restoration activities with costs exceeding $12,500/km (CAD). However, current restoration does not consider wildfires that can destroy planted trees, but also initiate early seral conditions that favor natural regeneration. Here we compared tree regeneration on seismic lines and adjacent forest controls for burnt (75 sites) and unburnt (68 sites) treed peatlands in northeast Alberta, Canada. Tree regeneration (stems with a DBH<1cm per ha) varied from 28,500 in burnt lines, 11,440 in unburnt lines, 18,210 in burnt forest, and 9,520 in unburnt forest. Wildfires promoted denser regeneration in sites with a greater proportion of serotinous species and water table depth. Microtopography and terrain wetness explained regeneration on burnt lines, but not unburnt lines. In burnt and unburnt lines, sunlight, microtopography, and depth of water table most affected tree regeneration patterns.

5.2 Introduction

The world's forests are being increasingly fragmented from anthropogenic disturbances, including linear disturbances associated with, among other things, roads, transmission lines, pipelines, and oil and gas exploration. Indeed, the majority (70%) of the world's forests are now within 1 km of a forest edge (Haddad et al. 2015). Even when linear disturbances are considered temporary (i.e., for mineral exploration), they can become permanent through consistent human use and expanded development. For instance, many "soft" linear features (such as unpaved roads or skid trails) fail to become reforested even decades after they are abandoned (Mercier et al. 2019). This pattern is most common in unproductive forests, such as treed peatlands, because of their slow growth and the generally harsh environment for tree growth.

One such anthropogenic disturbance common in boreal forests of western Canada is seismic lines. Seismic lines are narrow (3–12 m) linear openings (Figure 5.1) created for mapping underground petroleum reserves through the use of seismic waves/vibrations. These lines can stretch for kilometers, are typically in a grid pattern, and can be as dense as 40 km/km^2 (50 m grid spacing) (Filicetti et al. 2019 [Chapter 4]). Given their high density, seismic lines are the leading anthropogenic contributor to disturbance and fragmentation (dissection) of the boreal forests in Alberta, Canada (Arienti et al. 2009; Schneider et al. 2010).

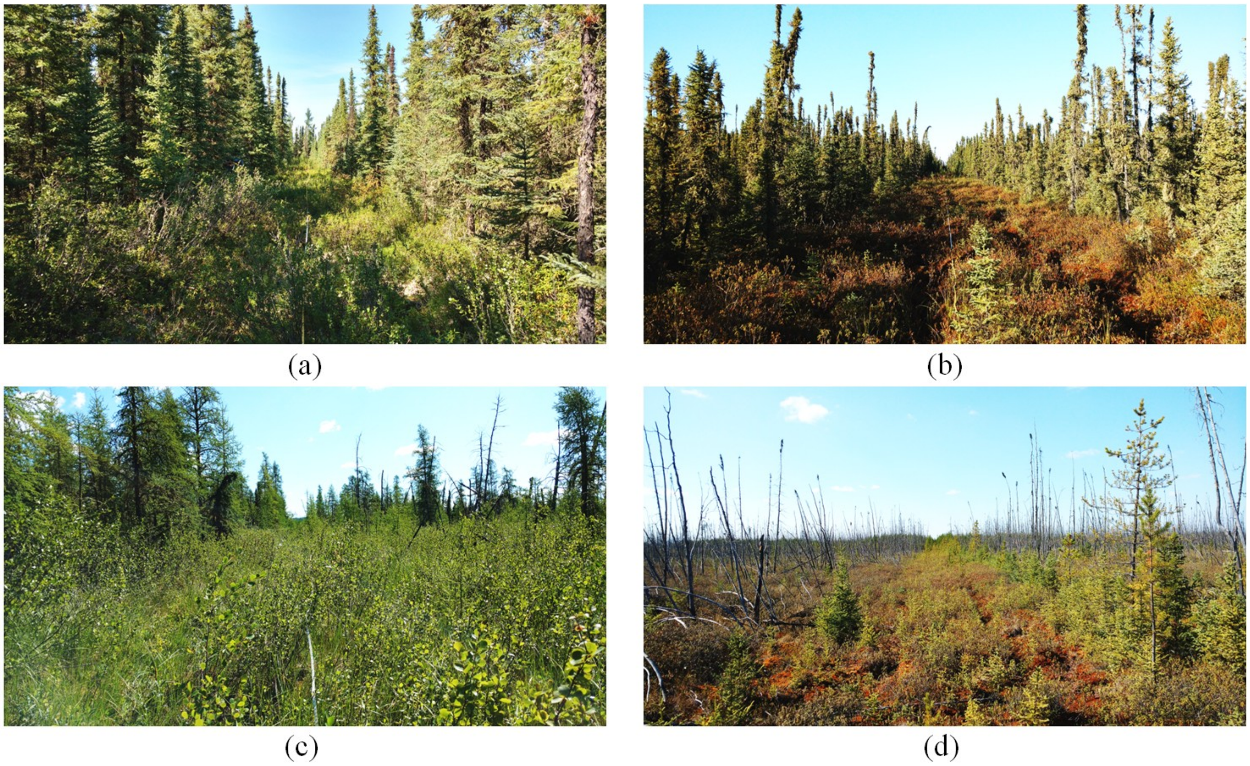

(a)
(b)
(c)
(d)

Figure 5.1: Examples of linear seismic disturbances in northern Alberta, Canada boreal forest peatlands: a) poor fen; b) bog; c) mid-severity burnt rich fen; and (d) high-severity burnt bog. All images courtesy of Angelo T. Filicetti.

Many seismic lines in the boreal forest have not transitioned back to a forested state decades after their disturbance. In particular, treed peatlands have been shown to be the least likely to recover in Alberta (Lee and Boutin 2006; van Rensen et al. 2015; Filicetti et al. 2019 [Chapter 4]). The exact reason for this delayed recovery is complex and not fully understood, but it is believed to be related to the characteristics of the initial disturbance. This includes the mechanized creation of seismic lines that simplifies the microtopography of peatlands (hummocks and hollows) and depresses its surface, resulting in a high water table (flooding) that leads to failures in tree recruitment and establishment (Lieffers et al. 2017). Seismic lines can also act as corridors for the movement of organisms that alter patterns of biodiversity and wildlife dynamics (Riva et al. 2018a; Roberts et al. 2018). Of particular interest is the decline in woodland caribou (*Rangifer tarandus caribou*), one of the most high-profile species-at-risk in Canada's boreal forest (Dickie et al. 2017a). These open corridors can function as 'highways' for white-tailed deer (*Odocoileus virginianus*), moose (*Alces alces*), and wolves (*Canis lupus*) leading to increases in encounters with wolves and predation rates on woodland caribou via apparent competition with white-tailed deer and moose (Latham et al. 2011; Latham et al. 2011; James and Stuart-Smith, 2000). The poor recovery rate of seismic lines in treed peatlands (woodland caribou habitat) and major declines in woodland caribou populations (Dickie et al. 2017a) have led to significant efforts to actively restore seismic lines (Filicetti et al. 2019 [Chapter 4]). However, restoration treatments in northeast Alberta can exceed CAD $12,500/ km of seismic line (Filicetti et al. 2019 [Chapter 4]) with hundreds of thousands of kilometers of seismic lines thought to need treatment, resulting in a billion-dollar conservation issue (Hebblewhite 2017). It may, therefore, be more economically feasible and efficient to first understand where treatments are most needed, where a no cost leave-for-natural reforestation (passive restoration) strategy could be used, and how natural disturbances like wildfire can alter conditions that may benefit long-term tree recovery.

Wildfires are the most common natural disturbance in the boreal forest, having seemingly both positive and negative effects on seismic line tree recovery. On the one hand, wildfires provide the ideal leave-for-natural passive form of restoration for seismic lines by promoting the creation of microtopography (Benscoter et al. 2015), exposing preferential seedbeds (Sirois 1993), and increasing seed rain from fire serotinous and semi-serotinous species (Jayen et al. 2006). On the other hand, wildfires can eliminate gains from active restoration treatments, leading to a loss of restoration investments in tree planting (Pyper et al. 2014) and removal for up to 40 years of preferred winter forage (lichens) for woodland caribou (Skatter et al. 2017).

Here we examine reforestation dynamics on seismic lines in treed peatlands across six separate wildfires spanning a 22-year post-fire history in northeast Alberta. Our objectives were to assess: (i) whether wildfires promote the regeneration density of peatland forests on seismic lines compared with paired adjacent burnt forest and unburnt forests controls; (ii) which stand and line characteristics (stand age, height, basal area; line width and orientation) promote or impede the regeneration density of peatland forests on seismic lines; and (iii) whether changes in seismic line microtopography (complexity and depression), along with local terrain wetness, limit regeneration density in peatlands. Specifically, we hypothesize that: (i) sites will have higher regeneration density post-fire, in particular for sites with higher amounts of semi-serotinous species (e.g., black spruce), as wildfires in the boreal forest initiate early seral conditions favorable for regeneration density; (ii) seismic lines will increase regeneration density at higher rates if; (a) they have experienced a wildfire, for the same reasons as above; and (b) are located on sites that have more productive adjacent stands (taller trees, higher basal area, etc.), because these sites will provide more seeds and microsites for tree establishment and (iii) that variables related to water table depth (lack of microtopographic complexity, line topographic depression, and terrain wetness), will be related to local regeneration failures on seismic lines because microsites available for tree establishment will be limited.

5.3 Methods

5.3.1 Study area

The study area of northeast Alberta, Canada stretches from Wandering River and Conklin in the south, to McClelland Lake in the north encompassing ~30,000 km^2 of the Athabasca Oil Sands (Figure 5.2). Our sample plots were all within the Boreal Plains ecozone (at the Canadian national scale) overlapping with the Boreal Forest Natural Region (at the Alberta provincial scale) where small changes in topography (~0.5 m change in elevation) can result in abrupt changes of ecosite due to differences in the water table (Natural Regions Committee 2006). Widths of seismic line disturbances ranged from just under 3 m to just over 12 m (see Figure 5.1 for examples). None of the seismic lines in this study were replanted or subject to any silvicultural treatment or mechanical site preparation.

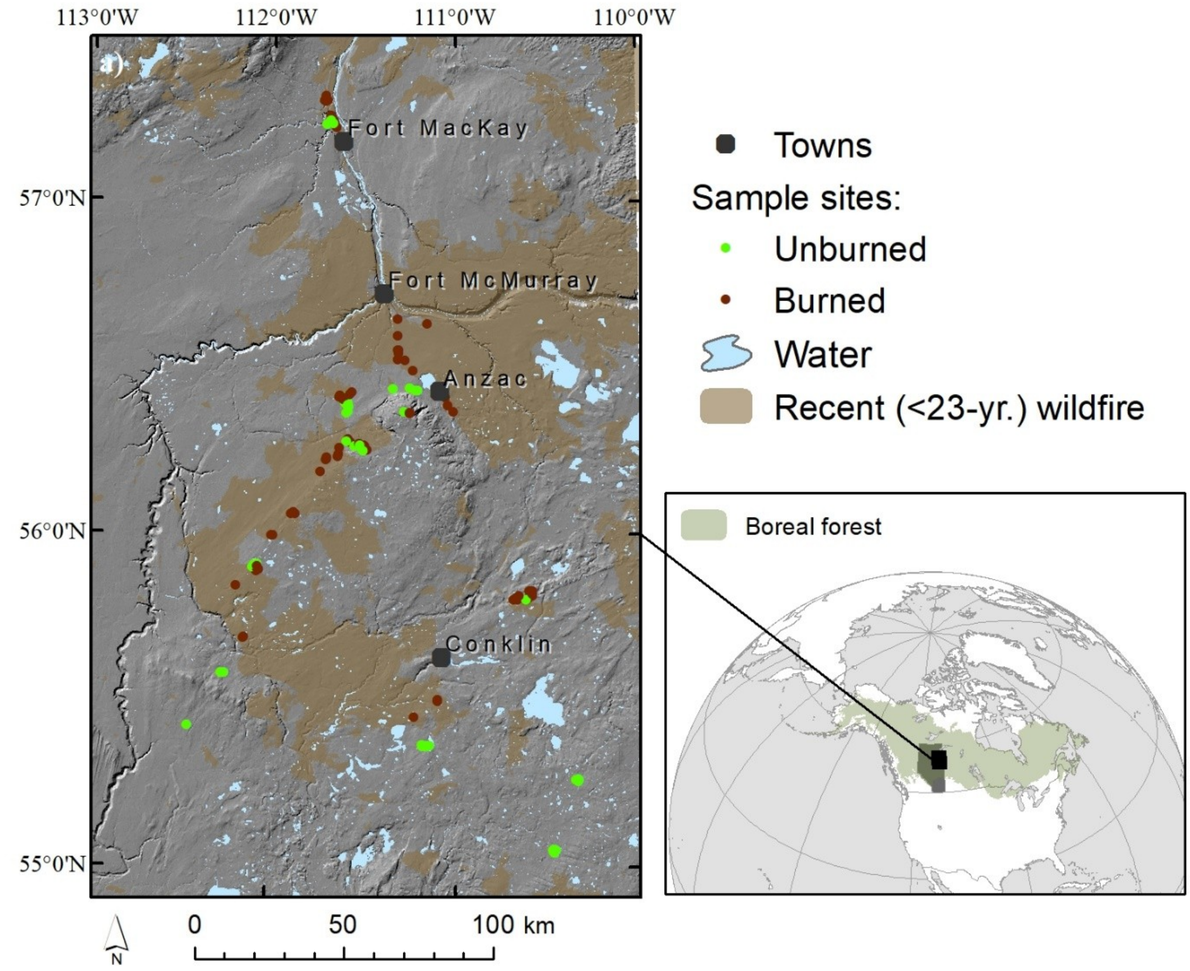


Figure 5.2: Location of study sites (plots) within northeast Alberta, Canada and with respect to recent (1 to 22-year-old) wildfires, major water features, towns, and base terrain. Plots are labeled as either unburnt in recent time or burnt within the past 22-years. Inset map of North America illustrates extent of boreal forest in North America, location of Alberta, Canada (dark grey), and study area extent (black box).

Here, treed peatlands, representing as much as 60% of the overall regional landscape, include bogs, poor fens, rich fens, and poor mesic ecosites. Peatlands are wetlands that can accumulate > 40 cm of organic matter (peat) from vegetation, most often from mosses. There are numerous classifications for peatlands, but here we use the definition from the *Terrestrial data collection protocols* (Alberta Biodiversity Monitoring Institute 2018) and the *Encyclopedia of Ecology* (Vitt 2008). There are four types of peatland ecosites, they are: bog, poor fen, rich fen, and poor mesic. Bogs are characterized as ombrotrophic, acidic (pH of 3.5-4.5), dominated by sphagnum mosses with black spruce [*Picea mariana* (Mill.) B.S.P.] often being the exclusive tree present. Poor fens are characterized as minerotrophic, acidic (pH of 3.5-5.5), dominated by sphagnum mosses with black spruce and a minority of tamarack [*Larix laricina* (Du Roi) K. Koch]. Rich fens are characterized as minerotrophic, neutral (pH of 5.5-8.0), dominated by true mosses (or brown mosses) with black spruce and tamarack. Rich fens are often distinguished from poor fens by being wetter and richer in nutrients. Poor mesic sites are not technically a wetland or peatland ecosite because the depth to water table is slightly greater than the other ecosites mentioned, but poor mesic sites occur in the same locations often transitioning into peatlands. Poor mesic sites are dominated by feather mosses with black spruce and a minority of jack pine (*Pinus banksiana* Lamb.), aspen (*Populus tremuloides* Michx.), and white spruce (*Picea glauca* Moench. Voss).

5.3.2 Site selection and field methods

Sample sites on seismic lines were a minimum of 400 m apart unless on a separate seismic line with a different orientation (more than a 45° difference) and/or if ecosite differed. Six wildfires were selected for having multiple ecosites and being large enough to contain at least 12 sites to sample, as well as accessibility and variation in stand age (1, 6, 8, 15, 18, and 22 years prior to sample collection). Locations were selected from a random set of available possible locations within 3.4 km ($\bar{x}$ = 580 m) of roads, with each site requiring consistent forest stand conditions (i.e., height, density, age) across an area large enough to be sampled (> 1 ha). A random toss of a metal stake was used to determine specific starting location of all plots. All of the field work occurred in the summer of 2017, with 143 sites sampled. Each site being represented by a pair of plots with one plot on a seismic line and the other 25 m into the adjacent reference forest (*n* = 286 plots); a coin toss was used to randomly assign which side of the seismic line the adjacent forest plot would be located. Distribution of plots by ecosites was 29 bogs (58 plots), 61 poor fens (122 plots), 23 rich fens (46 plots), and 30 poor mesic forests (60 plots). Of the 143 sites, 68 sites (48%) had not experienced a wildfire in over 65 years (we defined as “unburnt”), while 75 of the sites (52%) had experienced a wildfire in the last 22 years (defined as “burnt”). Sites that had experienced a wildfire in the last 22 years, by ecosite were: bogs at 19 sites (38 plots or 65%); poor fens at 32 sites (64 plots or 52%); rich fens at 10 sites (20 plots or 44%); and poor mesic at 14 sites (28 plots or 47%).

Each plot represented a 30-m belt transect with the seismic line transect located in the center of the seismic line, while the adjacent paired control transect was located 25 m into the adjacent forest running parallel to the seismic line (see Filicetti and Nielsen, 2018 [Chapter 2] for more details). Regeneration density, shrub density, and tree density were measured within belt-plots along each 30 m transect. Regeneration density [< 1 cm diameter at breast height (DBH)] and shrubs were counted in 1 × 30 m belt quadrats (30 m^2), while trees (≥1 cm DBH) were counted in 2 × 30 m belt quadrats (60 m^2). All of the stem densities were calculated to a common scale of 100 m^2 (0.01 ha) for modeling, but in some cases were reported as stems per hectare for ease of comparison with the literature. Additional stand information was collected for the adjacent forest plot including fire severity (defined as percent overstory tree mortality), stand basal area by species using a 2-factor metric prism (m^2/ha) at the midpoint of the adjacent forest transect (15 m), stand age of representative mature trees in the same plot using dendrochronological aging via tree cores, and representative tree height using a Haglof Vertex IV (Sweden) hypsometer.

5.3.3 Effects of fire and seismic line presence on regeneration density

We first visualized the main experimental effects on regeneration density by plotting the mean and standard errors of regeneration density for all tree species against the presence of a recent (22 years) wildfire, ecosite type, and seismic line presence (versus adjacent forest). Initial analyses found no difference between wildfire ages, except for the most recent (1 year old) fire, but this difference was eliminated after considering each ecosite separately. It was apparent that ecosite differences were substantial and thus we analyzed regeneration density for each ecosite to account for these ecosite level complexities. We then used mixed-effects negative binomial models (*xtnbreg* command in STATA 15.1/SE; StataCorp, 2017) to test for significant differences in regeneration density in units of trees per 100 m^2 of wildfire (burnt versus unburnt) and seismic line presence by ecosite. Site ID was used as a random effect to account for the paired nature of the seismic line and adjacent control forest plots within a single site. Separate binary dummy variables were used to represent the presence (1) or absence (0) of a recent wildfire, and seismic line (1) or adjacent forest (0) plots. Control plots and reference conditions for categorical contrasts of variables in models were therefore sites in mature, undisturbed forests. Model selection of predictor variables was limited to the interaction of two main treatment variables [binary fire presence and binary seismic line presence (versus. adjacent forest)], regardless of their significance. Initial collinearity among variables was assessed using Pearson correlations. We found only two variables considered colinear ($|r|$ = > 0.7), stand height and stand age at $r = 0.71$. We therefore did not include stand height and stand age together in the same model. We report coefficients from negative binomial models, but also interpret them as percentage change in regeneration per one unit change in the predictor variable by exponentiating them, subtracting one, and multiplying by 100% {[exp(var) -1]×100%}. Finally, a mixed-effects negative binomial model was used with the combination of presence/absence of wildfire and seismic line presence (burnt line, unburnt line, burnt forest, unburnt forest), to predict regeneration density, and a pairwise test with a Bonferroni adjustment (*pwcompare mcompare(bonferroni)*; STATA 15.1/SE StataCorp, 2017) to test for significance between variables within ecosites. Model assumptions were examined for independence, normality of response variables and presence of outliers, and correlations ($r > |0.7|$) among independent variables. Variables were removed and/or modified (transformed) to meet model assumptions.

5.3.4 Effects of stand, fire severity, and seismic line characteristics on regeneration density

For this analysis, regeneration density was defined as any tree on the seismic line regardless of its DBH with the analysis restricted to only seismic line plots. This allowed us to directly examine the effects of fire severity and seismic line characteristics, such as line orientation and line (forest gap) width. We also considered the effect of the adjacent stand on regeneration within lines including tree height, stand basal area, stand age, and their interaction with seismic line (forest gap) width and orientation. Because we removed the adjacent forest plot from the paired design (random effect) from section 5.3.3, we used standard negative binomial regression count models (*nbreg* command in STATA 15.1/SE; StataCorp. 2017). Model selection of predictor variables was based on the inclusion of variables for seismic line and stand characteristics only if significant (at $\alpha = 0.05$). Line width varied between 3 and 12 m ($\bar{x} = 5.9$ and SE = 0.1), while line orientation represented the compass bearing of seismic lines transformed to an index between 0 (east-west orientation) and 1 (north-south orientation) following the methods of van Rensen et al. (2015). Most lines in the area were on north-south and east-west axes (76 %). In addition to line characteristics, we examined the effects of graminoid, woody debris, lichen, bare ground, bryophyte, *Sphagnum fuscum*, and open water (only woody debris, bryophyte, and open water were found to be significant and thus used in our models) on regeneration density based on their average percent cover within six quadrats (2 × 5 m) along the transect. Again, all analyses of regeneration density were at a scale of 100 m^2. Finally, contour graphs were used to illustrate predictions from our models explaining regeneration density as a function of different seismic line and stand characteristics.

5.3.5 Effects of microtopography and water table on regeneration density

For a subset of sites (*n* = 102) we measured microtopographic patterns along the transect to characterize microtopographic complexity (the measure of how much the hummocks and hollows vary in their peaks and troughs along the central 20 m length of the 30 m transect at 25 cm intervals), and depth of topographic depression (average height difference between the center of the seismic line and the adjacent forest; where positive values mean belowground elevation compared with the adjacent forest) on the seismic line based on data reported in Stevenson et al. (2019) [Chapter 3] and here related to regeneration density within those same plots. Specifically, we used a ZIPLEVEL PRO-2000 (Technidea®Corporation, Escondido, CA, USA) high-precision hydrostatic altimeter. We also considered terrain wetness as measured topographically from the compound topographic wetness index (CTI, Moore et al. 1991) using a 15-m Lidar-derived digital elevation model. Because terrain wetness was measured at a meso-scale, it will not resolve differences within paired plots, but should provide a general gradient of wetness between sites. Standard negative binomial regression models (*xtnbreg* and *nbreg* command in STATA 15.1/SE; StataCorp, 2017) were again used to relate regeneration density (per 100 m^2) to microtopography, terrain wetness, and their interactions with variables retained only if significant ($\alpha = 0.05$). Because of the smaller sample sizes of where microtopography was measured (*n* = 102 sites), all of the ecosites were used in analyses of microtopography. Initial analyses, however, demonstrated clear differentiation between unburnt and burnt seismic lines, so we further divided data into unburnt (*n* = 42) and burnt (*n* = 60) seismic lines groups for the final analyses.

5.4 Results

5.4.1. Stand characteristics and overall regeneration density patterns

The age of the stands ranged from 1 to 158 years ($\bar{x}$ = 34.4, SE = 2.7); stand height varied from 0 to 24.8 m ($\bar{x}$ = 5.9, SE = 0.4); basal area in adjacent stands varied from 0 to 36 m^2/ha ($\bar{x}$ = 5.9, SE = 0.8); and trees per hectare ranged from 0 to 37,333 stems ($\bar{x}$ = 13,196, SE = 672), see Table 5.1. The most common tree species, in order of most to least common, were: black spruce at 83%, tamarack at 10%, jack pine at 4%, Alaska birch at 1.7 % (*Betula neoalaskana* Sarg.), aspen at 1.5%, and balsam poplar at 0.6% (*Populus balsamifera* L.); similarly the most common shrubs were: willow at 45% (*Salix* spp.), bog birch at 40% (*Betula pumila* L.), and prickly rose at 8% (*Rosa acicularis* Lindl.).

Table 5.1: Stand characteristics and tree regeneration densities (per ha) for 143 sites sampled on seismic lines and adjacent forests (286 plots) in northeast Alberta, Canada.

Stand variable	Minimum	Median	Maximum	Mean (S.E.)
Age (years)	1	22	158	34.4 (2.7)
Height (m)	0	5.1	24.8	5.9 (0.4)
Basal area (m^2/ha)	0	8	36	8.9 (0.6)
Tree stems per ha (DBH < 1 cm)				
Seismic line	0	9,667	156,333	20,385 (2,285)
Adjacent stand	0	9,667	115,000	13,887 (1,216)
Tree stems per ha (DBH ≥ 1 cm)				
Seismic line	0	0	19,833	972 (211)
Adjacent stand	0	5,667	18,667	6,598 (336)

On average, the burnt lines had 28,500 (SE = 3,875) regenerating stems/ha, unburnt lines had 11,440 (SE = 1,640) regenerating stems/ha, the adjacent burnt forests had 18,210 (SE = 2,090) regenerating stems/ha, and the adjacent unburnt forest had 9,520 (SE = 990) regenerating stems/ha. The burnt lines, therefore, had 2.5-times more regenerating stems per hectare than the unburnt lines ($p < 0.001$), 1.7-times more regenerating stems per hectare than burnt forest, but not statistically significant ($p = 0.999$), and 3.1-times more regenerating stems per hectare than unburnt forest ($p = 0.048$) (Figure 5.3). The burnt forests had 1.9-times more stems per hectare than unburnt forests ($p = 0.999$) and 1.5-times more stems per hectare than the unburnt lines ($p = 0.024$). There were, therefore, more regenerating tree stems on the burnt seismic lines, compared with the unburnt lines, adjacent burnt forest, and adjacent undisturbed forests illustrating that wildfires, regardless of their severity or timing, can promote natural regeneration density (passive restoration) of most linear disturbances in peatlands.

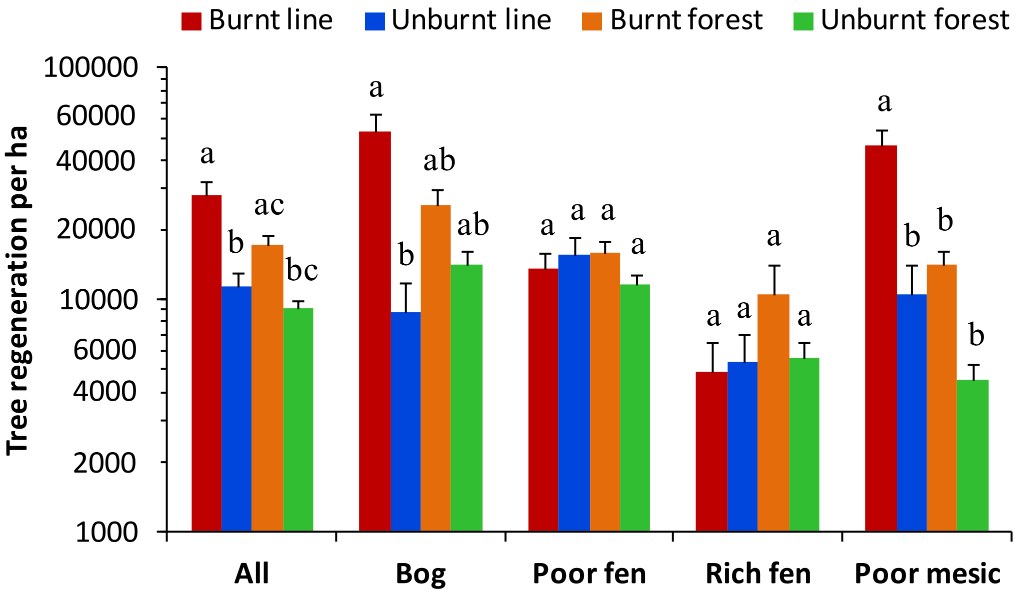


Figure 5.3: Tree regeneration (DBH < 1 cm) across all sites (All) and separately for each of the four peatland ecosites for both burnt and unburnt conditions. Significance of treatments within each ecosite were tested using a mixed-effects negative binomial model with a pairwise comparison (Bonferroni adjustment) with different letters indicating significant differences within an ecosite at $p < 0.0125$ (error bars are standard errors).

5.4.2 Effects of fire and seismic line presence on regeneration density for each ecosite

The interaction between seismic line presence and wildfires within the last 22 years was only significant for bogs and poor mesic sites, demonstrating a positive effect on regeneration density (Figure 5.3 and Table 5.2). Overall, regeneration density in bogs was 4% higher in the burnt versus unburnt sites, 42% less on the seismic lines versus adjacent forest, but 146% higher for the burnt seismic lines (Figure 5.3 and Table 5.2). The regeneration density in poor fens was 2% higher in the burnt versus unburnt sites, 11% less on the seismic lines versus adjacent forest, and 4% less for the burnt seismic lines. The regeneration density in rich fens was 17% lower in the burnt versus unburnt sites, 49% less on the seismic lines versus adjacent forest, and 3% less for the burnt seismic lines. The regeneration density in poor mesic stands was 97% higher for a wildfire in the adjacent forest versus the unburnt adjacent forest, while decreasing by 13% on seismic lines and increasing by 225% in the presence of a wildfire on a seismic line (Figure 5.3 and Table 5.2).

Table 5.2: Mixed-effects negative binomial regression model parameters (coefficient, β; and standard error, SE) relating regeneration density (DBH < 1 cm) of all tree species to presence of fire and presence of seismic line (vs. adjacent forest control). Both fire and seismic line presence were included regardless of significance given that they were study design (treatment) variables. *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$.

Tree density (stems/100 m^2)	Bog β (SE)	Poor fen β (SE)	Rich fen β (SE)	Poor mesic β (SE)
Constant (intercept)	0.40 (0.35)	0.18 (0.19)	-0.22 (0.28)	-0.23 (0.26)
Fire				
Presence of fire	0.04 (0.32)	0.02 (0.21)	-0.19 (0.38)	0.68 (0.29)*
Fire × Seismic line	0.90 (0.40)*	-0.04 (0.29)	-0.03 (0.60)	1.18 (0.38)**
Seismic line presence				
Seismic line plot	-0.54 (0.34)	-0.12 (0.21)	-0.68 (0.37)	-0.14 (0.31)
Model statistics				
n	58	122	46	60
Log likelihood	-380.6	-585.2	-228.7	-348.2
Wald c^2	9.14	0.95	5.62	63.49
Prob > χ^2	0.027	0.813	0.132	< 0.001

5.4.3 Effects of stand, fire severity, and seismic line characteristics on regeneration density

When eliminating the adjacent paired forest plots and only assessing seismic lines based on surrounding stand characteristics (basal area, stand height, stand age), line characteristics of line width (gap) and bearing, fire severity, and ground cover, the differences in regeneration density on seismic lines between ecosites was more apparent. Wildfire age was often non-significant, and both fire severity and fire presence were consistently better predictors; this remained true even when considering interactions between wildfire age and fire severity.

The regeneration density on lines within bogs were moderately influenced by fire severity, with a 2% increase in regeneration density per 1 unit increase in fire severity. The regeneration density increased by 36% per 1 m increase in line width and increased by 101% on north–south lines compared with the east–west lines (Figure 5.4 and Table 5.3). Regeneration density in both fen types was not related to wildfire presence or severity, but the regeneration density in poor fens was positively related to basal area of black spruce and negatively related to the cover of open water within the plot. Specifically, there was a 4% increase in regeneration density per 1 m_2/ha increase of black spruce and a 4% decrease in regeneration density per one unit increase in cover of open water. In contrast, the regeneration density in rich fens was influenced by line bearing, coarse woody debris, and bryophyte cover. Specifically, regeneration density decreased by 390% on north–south lines compared with east–west lines, increased by 213% per one unit increase in woody debris cover, and increased by 8% per one unit increase in bryophyte cover (Figure 5.4 and Table 5.3). Finally, regeneration density in poor mesic ecosites was positively related to fire severity, increasing by 2% per one unit increase in fire severity and negatively related to stand basal area of non-black spruce trees decreasing by 27% per 1 m^2/ha of non-black spruce trees.

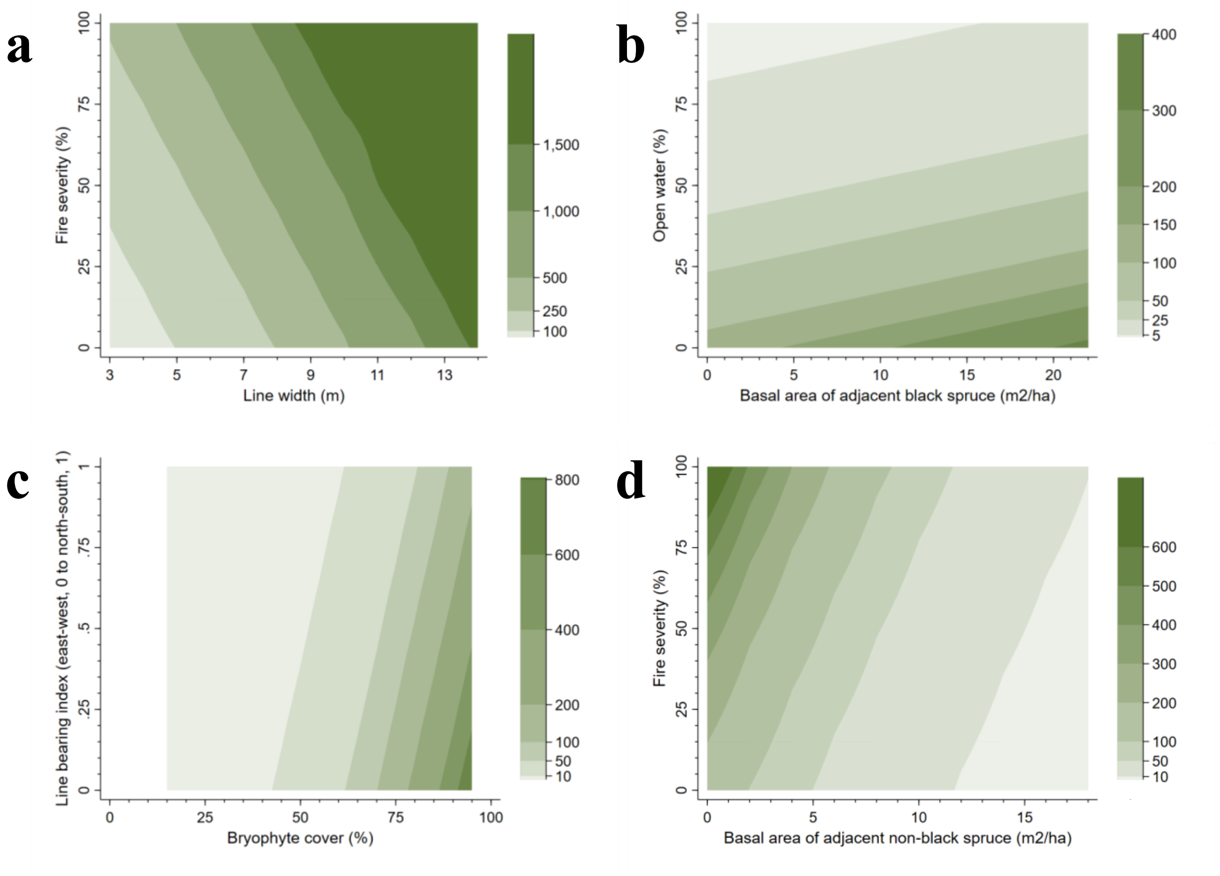


Figure 5.4: Predicted density of all trees regenerating (per 100 m^2) on seismic lines (negative binomial count model) in the four peatland ecosites based on a combination of site factors: (a) bogs, using line width and fire severity with the example here being north-south bearing lines; (b) poor fens, using basal area of adjacent black spruce and ground cover of open water; (c) rich fens using bryophyte ground cover and line bearing; and (d) poor mesic, using basal area of adjacent non-black spruce trees and fire severity. Note that scales of regeneration density (contour colors) differ between ecosites.

Table 5.3: Standard negative binomial regression model parameters (coefficient, β; and standard error, SE) relating regeneration density (per 100 m^2) of all tree species on seismic lines to fire severity (% tree mortality), line characteristics, stand variables, and percent ground cover. *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$.

Tree density (stems/100 m^2)	Bog β (SE)	Poor fen β (SE)	Rich fen β (SE)	Poor mesic β (SE)
Constant (intercept)	2.38 (0.78)**	4.82 (0.23)***	-1.29 (1.65)	5.07 (0.27)***
Fire				
Severity	0.016 (0.004)***			0.016 (0.004)***
Stand				
Bearing (0-1 index)	0.70 (0.34)*		-1.59 (0.69)*	
Width (m)	0.31 (0.13)*			
Black spruce (m^2/ha)		0.04 (0.02)*		
Non- black spruce (m^2/ha)				-0.24 (0.04)***
Ground Cover (%)				
Woody debris			1.14 (0.45)*	
Open water		-0.04 (0.02)*		
Bryophytes			0.08 (0.03)*	
Model statistics				
n	29	61	23	30
LR χ^2	24.60	8.84	12.45	25.76
Prob > χ^2	< 0.001	0.012	0.006	< 0.001

5.4.4 Effects of microtopography and water table on regeneration density

For unburnt seismic lines, microtopographic complexity was the only explanatory variable negatively related to regeneration density (15% decrease in regeneration density per one unit increase in microtopographic complexity), but this was weak overall ($p = 0.062$, Table 5.4) suggesting less support for the hypothesis that a lack of microtopographic complexity limits regeneration density on unburnt seismic lines in peatland forests. In contrast, regeneration density on burnt seismic lines was significantly and negatively related to both the compound topographic wetness index (CTI) and the amount of microtopographic depression on the line (Figure 5.5 and Table 5.4) suggesting stronger limitations in regeneration density post-fire to microtopography. Specifically, terrain wetness and microtopographic depression were both negatively related to regeneration density with a 23% decrease in regeneration density per one unit increase in terrain wetness and a 4% decrease in regeneration density for every centimeter of depression on the seismic line (Figure 5.5 and Table 5.4).

Table 5.4: The best fitting negative binomial model for predicting tree regeneration (per 100 m^2) for (A) unburnt and (B) burnt (excluding fire related variables) seismic lines. The best model for unburnt seismic lines (A) included only microtopographic complexity, while the burnt seismic line model (B) included line depression depth and the compound topographic index (CTI) representing terrain wetness (higher values more wet).

Parameters		β	S.E.	*p*
A.	*Non-Burnt seismic lines only*			
	Intercept	5.543	0.427	< 0.001
	Microtopographic complexity	-0.136	0.073	0.062
B.	*Burnt seismic lines only*			
	Intercept	7.851	0.653	< 0.001
	Terrain wetness (CTI)	-0.207	0.058	< 0.001
	Depression depth	-0.043	0.019	0.026

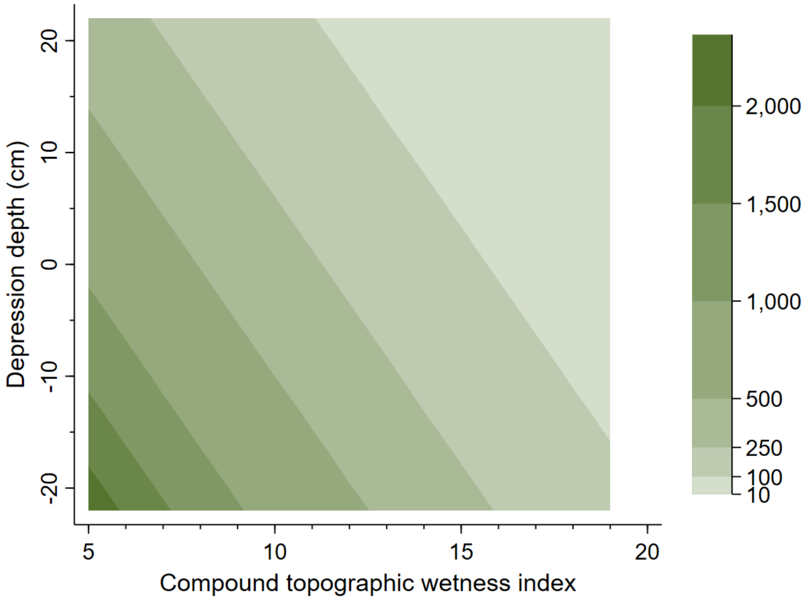


Figure 5.5: Predicted regeneration density (per 100 m^2) (negative binomial count model) in burnt seismic lines as a function of compound topographic wetness index (CTI; higher values representing greater wetness at a meso-scale) and depression depth (cm) at local scales (transect). Note that positive values of depression depth relate to greater belowground depths of the line compared to that of the adjacent forest and thus more likely to be near the water table or wet.

5.5 Discussion

5.5.1 Effects of fire and seismic line presence on regeneration density

Unburnt seismic lines had similar regeneration density rates to adjacent forests, contrary to prior observations of a general lack of tree recruitment on lines (Lee and Boutin 2006; van Rensen et al. 2015; Filicetti et al. 2019 [Chapter 4]). However, we would expect higher regeneration density in forest openings, such as seismic lines, where seed sources are nearby (adjacent to line) and sunlight more available than in the adjacent forest understory (Stern et al. 2018). In contrast to unburnt lines and forest, wildfires consistently increased regeneration density in adjacent forest stands across all ecosites when compared with unburnt forest stands. Likewise, regeneration density increased on burnt seismic lines compared with unburnt seismic lines in bogs and poor mesic sites, but not poor and rich fens. This suggests that seismic lines have a long-term detrimental effect on regeneration in one type of peatland – fens. One possible mechanism by which seismic lines reduce regeneration density in peatlands, and especially within fens, is the elimination of microtopographic complexity (hummocks-hollows; Lieffers et al. 2017) and the depression of the ground on seismic lines due to the mechanical nature of their creation (Stevenson et al. 2019 [Chapter 3]). This results in a shallower water table and thus changes in vegetation even to the extreme of converting lines to sedge-dominated communities with standing water that restricts any tree recruitment (Lieffers et al. 2017). If a tree can establish within certain microsites that are closer to the water table, there is no guarantee that it will eventually thrive because of the abnormally high mortality rates for trees above a certain size (Lieffers et al. 2017). Although microtopographic changes in peatland ecosites are similar (Stevenson et al. 2019 [Chapter 3]), their effect on regeneration density in fens appears to be much more negative, even after wildfires. One study found substantial increases in the natural regeneration density on treated (mounded) seismic lines in fens, even above the rate of regeneration density that were planted as part of the treatments (Filicetti et al. 2019 [Chapter 4]), demonstrating that the main limitation of tree recruitment in fens is the depth of the water table and lack of microtopography. Moreover, measures of regeneration density on these mounded treatments were 4 years post-treatment compared with untreated lines disturbed by the creation of seismic lines ~22 years prior demonstrating how restoration of the microtopography can promote rapid natural regeneration density on the mounds.

5.5.2 Effects of stand, fire severity, and seismic line characteristics on regeneration density

It was surprising to find that time to the last wildfire was often non-significant for regeneration density and that fire severity was consistently the better predictor. It is likely that wildfire age was not particularly useful for regeneration density because of seed abscission patterns post-fire, where black spruce cones release 70% of their seeds within 2 years and 90% within 5 years post-fire, whereas jack pine cones release 90% of their seeds within the first year (Greene et al. 2013). Additionally, the viability of tree seeds stored in the boreal forest floor is generally low (Bonan and Shugart 1989), where black spruce lose their ability to germinate within 10 to 16 months (Fraser 1976). Therefore, with most seed abscission and germination occurring within 5 years, it should not be too surprising that time post-wildfire ages greater than 5 years (only one wildfire sampled in this paper was within 5 years post-fire) has little to no additional recruitment.

Regeneration density on seismic lines in bogs was positively related to fire severity, positively related to width of line (forest gap size), and the bearing of lines (north-south lines being more beneficial). These results are similar to responses observed by Filicetti and Nielsen (2018) [Chapter 2] in (xeric) burnt jack pine sites that were dominated by trees with serotinous cones, and in bogs with north-south oriented seismic lines (Filicetti et al. 2019 [Chapter 4]). Because black spruce has semi-serotinous cones that release substantial amounts of seed post-fire and bogs are dominated by black spruce, it is not surprising to observe increased regeneration density post-fire in these communities. Here we found regeneration density in bogs post-fire were more than double that observed on seismic lines treated with mounding and planting (Filicetti et al. 2019 [Chapter 4]), suggesting that in specific scenarios wildfires could result in leave-for-natural regeneration that would be beneficial and cost-effective. Increased regeneration density for wider seismic lines are likely to be associated with increases in sunlight (Filicetti and Nielsen 2018 [Chapter 2]; Stern et al. 2018). They also receive higher wind speeds in northeast Alberta (Roberts et al. 2018; Stern et al. 2018). Higher winds could lead to increased seed dispersal (Roberts et al. 2018) and evapotranspiration. Evapotranspiration plays an important role in regulating the water table, with the removal of trees raising the water table (Jutras et al. 2006). Regardless, the effect of line bearing and width appears to be reduced post-fire, possibly due to increases in sunlight and/or changes in hydrology (higher evaporation rates and increased depth to water table leading to more available microsites) (Thompson et al. 2014).

Patterns of regeneration density on seismic lines in poor fens were best explained by the basal area of black spruce in the adjacent stand and the cover of open water on the seismic line. The positive relationship of regeneration density in poor fens and a higher basal area of black spruce are not related to their cones' semi-serotinous nature, or wildfires. Fens with more black spruce than tamarack are associated with greater overall tree abundance and size. Fens with more black spruce than tamarack are also characterized by a shift away from rich fens, because rich fens evolve into poor fens and then bogs (Kuhry et al. 1993), with a corresponding decrease in tamarack with site decreases in nutrients, a lower water table, and increased competition for sunlight (Lieffers and Rothwell 1987; Frolking et al. 2001). The cover of open water was related to wetter sites with a higher water table, fewer available microsites, lower cover of bryophytes (Pearson correlation, r = -0.47), and greater cover of graminoids (r = 0.37) that increase competition and litter (Hogg and Lieffers 1991). Regeneration density in rich fens was positively related to the east-west bearing of the seismic line and increases in woody debris and bryophyte cover. This may mean that rich fens, which typically have short trees (on average 6.7 m in this study) and fewer trees per unit area than other ecosites, may receive more sunlight on east-west lines, especially on their northern edge. Bryophytes, particularly *Sphagnum*, are required for hummock formation and are therefore crucial to tree establishment (Caners and Lieffers 2014). Likewise, woody debris provides structural support for bryophytes to establish (Crites and Dale 1998). Although cover of woody debris had a large effect on regeneration density compared with bryophytes (regeneration density increase of 213% per one unit increase of woody debris cover versus an increase of 8% per one unit increase of bryophyte cover), bryophyte cover was on average 45-times higher than woody debris overall, suggesting that bryophytes had a larger contribution to regeneration density. In rich fens, bryophyte cover was negatively related to cover of graminoids (r = -0.67) and open water (r = -0.40), both of which appear to limit regeneration density in both poor and rich fens.

And finally, regeneration density in poor mesic sites depended on fire severity and amount (basal area) of trees other than black spruce. The relationship with fire severity in poor mesic sites is expected given that it is dominated by black spruce, and to a lesser extent jack pine, which are semi-serotinous and serotinous, respectively. Here, we found that regeneration density on burnt seismic lines in poor mesic sites was more than 4-times that of observed on seismic lines treated with ripping and planting from another study (Filicetti et al. 2019 [Chapter

4]), suggesting that fire is highly effective in initiating natural regeneration in poor mesic sites like bogs. Similar to bogs, wildfires in poor mesic sites could be a beneficial and cost-effective leave-for-natural solution utilized in specific situations.

The negative effect of the amount (basal area) of trees other than black spruce on regeneration density in poor mesic seismic lines suggests less non-black spruce regeneration as the ecosite shifts to transitional uplands where aspen, birch, and especially jack pine dominate. Basal area of trees other than black spruce may reflect conditions where jack pine fares better on seismic lines post-fire, but tends not to regenerate in the absence of fire (Filicetti and Nielsen 2018 [Chapter 2]). Therefore, the closer a poor mesic site lies to the xeric side of the spectrum (more jack pine), the less regeneration there is in the absence of fire.

5.5.3 Effects of microtopography and water table on regeneration density

Regeneration density on burnt seismic lines were negatively related to terrain wetness and line depression where conditions limit regeneration density because of both a higher water table and fewer available microsites (Filicetti et al. 2019 [Chapter 4]). Yet, in unburnt seismic lines, microtopography and terrain wetness did not fully explain local patterns of regeneration owing to risk of flooding (high water table) and loss of microtopography. We did not, however, expect differences between burnt and unburnt lines as a high-water table and a lack of microtopographic complexity would limit regeneration density regardless of recent fire disturbance history. One possible reason for this unexpected result is that wildfires can exaggerate microtopographic complexity (Benscoter et al. 2015), although differences in microtopographic complexity were not observed between the burnt and unburnt seismic lines in our sites (Stevenson et al. 2019 [Chapter 3]). Seismic lines also act as wildfire barriers or skips (refugia) as observed here (Figure 5.1) and elsewhere (Riva et al. 2020). We therefore think a change in microtopography post-fire is an unlikely explanation. Another possibility is that, although not significant, bogs and poor mesic seismic lines were less depressed post-fire than poor and rich fens (Stevenson et al. 2019 [Chapter 3]), which may affect the regeneration rates observed here. Wildfires can also alter hydrology in peatlands, with burnt peatlands having higher evapotranspiration that can lower water tables (Thompson et al. 2014). This pattern is especially apparent in *Sphagnum*-dominated peatlands (bogs) and is more dramatic under more severe fires (Kettridge et al. 2019) that occur less often in fens.

5.6 Management implications

The mechanized creation of seismic lines alters the establishment and growth trajectories of regenerating forests, in some cases resulting in clearings (open corridors) that last decades or longer. Reforestation of these cleared lines is important for woodland caribou, yet difficult and costly to apply because of to the narrow and long nature of seismic lines and their vast numbers across a large landscape. Distinguishing which locations benefit from active restoration and which can be left-for-natural (passive) restoration, particularly after wildfire, has the potential to save substantial investments in restoration and caribou conservation. Sites with more serotinous and semi-serotinous species do recover at denser rates post-fire. Microtopography and terrain wetness could explain regeneration density on burnt lines, but not unburnt lines. In unburnt and burnt seismic lines sunlight, microtopography, and depth of water table seem to play critical roles in regeneration density, particularly in fens, where restoring trees is the most inhibited of the peatland ecosites, even post-fire. Triage of where to spend limited conservation dollars (including restoration) is an ongoing debate in conservation biology. Here, we are not suggesting to simply wait for wildfire to restore seismic lines. We are instead suggesting that recently burnt sites, and possibly areas likely to experience wildfires in the near future, should be considered lower priority for restoration. With climate change, large parts of the boreal forest, including northeast Alberta, are expected to receive more intense, more frequent, and larger wildfires (Flannigan et al. 2009a, 2009b). Locally, there are large variations in fire frequency within the landscape, owing to natural landscape features (Nielsen et al. 2016), dominant tree species (Larsen 1997), time since last fire (Beverly 2017), and fuel loads (Johnston et al. 2015). Areas with caribou herds, if caribou conservations is an agreed upon objective, should clearly get priority, but otherwise we do not promote widespread use of limited restoration dollars without considering trade-offs associated with natural recovery, especially with that of wildfire.

Chapter 6: Response of mesic upland boreal forests to linear disturbances, ground compaction, and wildfires

6.1 Abstract

Petroleum exploration has fragmented Alberta's boreal forest. Seismic lines, clear-cut linear disturbances (~3–14 m wide), are the largest anthropogenic disturbance in the boreal forests of Alberta. Many seismic lines have failed to recover decades post-creation leading to changes in forest dynamics and biodiversity. These linear features function as both habitat and corridors for many species, while resulting in detrimental effects to others, most notably the threatened woodland caribou (*Rangifer tarandus caribou*). Industry and government have been investigating possible interventions to restore these lines, including the application of intensive silvicultural treatments and tree planting, but these applications are expensive (> $12,500/km) and do not account for wildfires that can destroy restoration investments (planted trees), yet also initiate early seral conditions that favor recovery. Here, I compared bulk density and regeneration density in burnt and unburnt mesic upland seismic lines with adjacent (paired) forest controls in northeast Alberta, Canada. Bulk density on seismic lines increased by 36% compared to undisturbed adjacent forests, while bulk density increased by 12% following recent wildfires in both seismic lines and adjacent forests, but this smaller increase following wildfire was not significant. Regeneration density was 1.7-times higher on burnt seismic lines compared to unburnt lines and lower in undisturbed adjacent forests compared with lines. Specifically, regeneration density averaged 19,622 stems/ha in burnt lines, 11,870 stems/ha in unburnt lines, 16,739 stems/ha in adjacent burnt forest, and 6,934 stems/ha in adjacent unburnt forest. Although bulk density was higher on seismic lines, it did not appear to influence regeneration density, nor regeneration height. We suggest that leave-for-natural recovery (passive restoration) of seismic lines can be expected post-fire in mesic upland forests and therefore active restoration, through intensive silviculture treatments, should be considered only after wildfire frequency has been considered to increase efficacy of restoration efforts. Further, most seismic lines already have regeneration densities well above the Alberta guidelines suggested minimum of 1,000 stems/ha for upland sites, therefore, leave-for-natural recovery relative to stocking densities should be universally applied or guidelines need to change.

6.2 Introduction

Seismic lines, clear-cut linear disturbances (~3–14 m wide), are created for the purpose of generating and measuring seismic waves/vibrations to map underground petroleum reserves. Individually, seismic lines can run for many kilometers and are typically in a grid-like pattern with densities reaching up to 40 km/km^2. After wildfires, seismic lines are the largest disturbance to Alberta's forests (Arienti et al. 2009; Schneider et al. 2010). Many seismic lines have not reforested many decades post-disturbance (MacFarlane 2003; Lee and Boutin 2006; van Rensen et al. 2015). Recent studies demonstrating simplified microtopography and a depression in elevations on seismic lines in treed peatlands have suggested that these factors affect reforestation patterns on lines (Lovitt et al. 2018; Filicetti et al. 2019 [Chapter 4]; Stevenson et al. 2019 [Chapter 3]; Filicetti and Nielsen 2020 [Chapter 5]). Anecdotal evidence from industry, government, and researchers suggest that compaction from the mechanized creation of seismic lines may lead to poor regeneration due to root damage, reduced soil aeration, and poorer root penetration (Revel et al. 1984; MacFarlane 2003; Lee and Boutin 2006), yet this has not been extensively examined and may only reflect a small subset of conditions among seismic lines. The changes in microtopography, depression, and compaction may result in biotic shifts of trees to graminoids and shrubs (Revel et al. 1984; MacFarlane 2003; Lee and Boutin 2006; Filicetti et al. 2019 [Chapter 4]; Stevenson et al. 2019 [Chapter 3]; Filicetti and Nielsen 2020 [Chapter 5]).The effects of soil compaction, primarily from studies in forest clear-cuts, can be complex and depends on the soils and trees present, the degree of compaction, and the timing of compaction (Greene and Johnson 1999; Frey et al. 2003). However, the machinery and protocols that operators use, as well as the size of the forest gap, differ substantially between clear-cuts and seismic lines. In mesic upland forests dominated by aspen (*Populus tremuloides* Michx.) the minimum amount of compaction required to adversely affect tree establishment, growth, and survival is ~1.55-1.65 g/cm^3 (Daddow and Warrington 1983; Sealey and Van Rees 2019).

Due to their affect on biodiversity, seismic lines have been of much interest to conservation in western Canadian boreal forests despite being small in their overall footprint (Riva et al. 2018; Roberts et al. 2018; Shonfield and Bayne 2019; Riva and Nielsen 2020). Perhaps the most notable species of concern are woodland caribou, a high-profile species-at-risk in Canada's boreal forest (Dickie et al. 2017a). Seismic lines function as movement corridors for many animals, allowing movements of species into preferred woodland caribou habitat that were not previously as accessible (Rettie and Messier 2000). These access routes have increased opportunities of predation by wolves and bears resulting in declining caribou populations (James and Stuart-Smith 2000; Latham et al. 2011a).

In most cases, wildfires initiate and accelerate reforestation on seismic lines in both treed peatlands and xeric jack pine forests (Filicetti and Nielsen 2018 [Chapter 2], 2020 [Chapter 5]), but little is known about responses to wildfires on seismic lines in mesic forests that are dominated in this region by aspen. Aspen is known to sucker post-fire (Greene and Johnson 1999; Frey et al. 2003; Jean et al. 2020) and thus predicted to recover on lines like that of other fire-dependent forests if left alone (i.e., restricting recreational use of lines or line reuse by industry). However, wildfires can increase soil compaction (Kozlowski 1999; Snyman 2005), which may further compound compaction on seismic lines from its initial creation and thus further limit tree regeneration.

Efforts to actively restore seismic lines often involve silvicultural treatments (Filicetti et al. 2019 [Chapter 4]), however, restoration treatments in these remote areas can exceed $12,500 (CAD) per km (Filicetti et al. 2019 [Chapter 4]; Johnson et al. 2019). Recently, the Government of Alberta has released guidelines to aid in deactivating seismic lines, suggesting that a minimum regeneration density for upland sites be 1,000 stems/ha (Government of Alberta 2017). Since costs are high, understanding where treatments are most needed and where a no-cost leave-for-natural reforestation (passive restoration) strategy can be used is needed to efficiently plan restoration efforts. Wildfires are the most common disturbance in the boreal forest and pose both a potential benefit and detriment to seismic line recovery. On the one hand, wildfires provide an ideal leave-for-natural passive form of restoration for seismic lines as they promote early seral conditions by exposing preferential seedbed conditions and seed rain from fire serotinous and semi-serotinous species (Filicetti and Nielsen 2018 [Chapter 2]). On the other hand, wildfires can destroy active restoration treatments associated with tree planting that can cost millions of dollars.

Here, I compare tree regeneration density on seismic lines to paired adjacent forest controls for unburnt forests to that of burnt forests in mesic upland stands dominated by aspen for six recent (≤ 23-yrs) wildfires in northeast Alberta, Canada. My objectives were to: (1) compare levels of compaction (bulk densities) for seismic lines to adjacent forest controls for both unburned and burned stands; (2) determine the effect of compaction on regeneration density on seismic lines; (3) examine whether wildfires promote regeneration on seismic lines compared to adjacent burnt and unburnt forests controls; and (4) test whether stand conditions (age, height, and basal area) and line characteristics (width and orientation) promote or impede regeneration. Specifically, I hypothesize that: (1) seismic lines will be compacted compared to adjacent forest controls, as anecdotal evidence suggests, and that fires will further increase this compaction; (2) compaction will reduce regeneration density presumably due to past root damage, less soil aeration, and poorer root penetration; (3) wildfires will promote regeneration on these seismic lines since these mesic upland forests are dominated by aspen which is fire-adapted and commonly regenerates post-fire by suckering and in some cases seed. I predict that these seismic lines will increase regeneration at higher rates if: (a) compaction on seismic lines does not surpass 1.55-1.65 g/cm^3; (b) they have experienced a wildfire, for the same reason as above; (c) are located on more productive sites based on stand characteristics in the adjacent forest (e.g., taller trees and higher growth rates and basal area) as these sites will provide more seeds and underground suckers; and (d) graminoid ground cover, and therefore competition, remains low.

6.3 Methods

6.3.1 Study area and stand characteristics

The study area is centered around Fort McMurray in northeast Alberta, Canada, laying within the boundaries of McClelland Lake in the north, Conklin in the southeast, and Wandering River in the southwest (Figure 6.1). The area encompasses ~25,000 km^2 of boreal forest in both upland and peatland environments and is represented as being in the Athabasca Oil Sands region. The focus of this study is mesic upland forests where the most common tree species, in order of most to least common, are: aspen (63%); white spruce (*Picea glauca* Moench. Voss) (17%); jack pine (*Pinus banksiana* Lamb.) (7%); Alaska birch (*Betula neoalaskana* Sarg.) (5%); balsam poplar (*Populus balsamifera* L.) (5%); and balsam fir (*Abies balsamea* (L.) Mill.) (2%); similarly the most common shrubs were: prickly rose (*Rosa acicularis* Lindl.), squashberry (*Viburnum edule* (Michx.) Raf.), and green alder (*Alnus crispa* (Ait.) Pursh). The mesic upland forests in this region can be divided into four forest types (ecosites) which are: (1) medium xeric with an overstory dominated by jack pine and aspen with occasional white spruce and an understory containing bearberry (*Arctostaphylos uva-ursi* (L.) Spreng.), hairy wildrye (*Leymus innovatus* (Beal) Pilg.), and buffaloberry (*Shepherdia canadensis* (L.) Nutt.); (2) medium mesic with an overstory dominated by aspen and to a lesser extent white spruce and an understory containing squashberry (*Viburnum edule* (Michx.) Raf.), bunchberry (*Cornus canadensis* L.), and buffaloberry); (3) medium hygric with an overstory dominated by aspen, balsam poplar, and white spruce and an understory containing horsetail (*Equisetum* spp.), willows (*Salix* spp.), and currants (*Ribes* spp.); and (4) rich hygric with an overstory dominated by balsam fir and white spruce with occasional aspen and balsam poplar and an understory containing ferns, red osier dogwood (*Cornus sericea* (*stolonifera*) L.), and thick feather mosses using definitions from the Alberta Biodiversity Monitoring Institute ecosite classification (Alberta Biodiversity Monitoring Institute 2018).

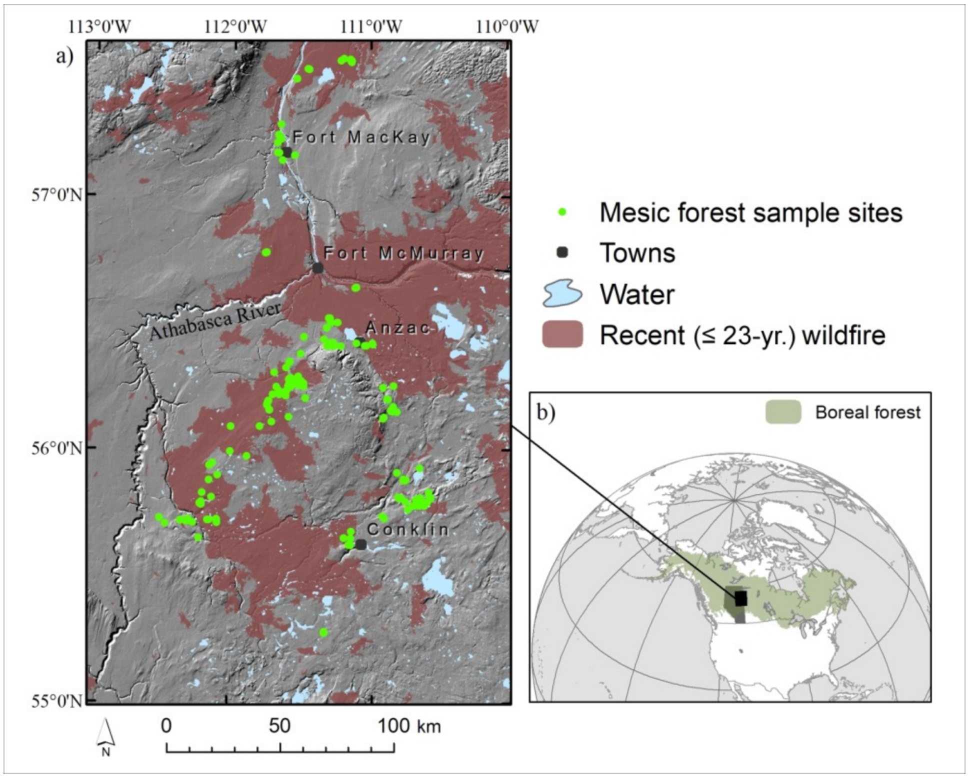


Figure 6.1: Location of the study area: a) location of sampling sites within northeast Alberta, Canada with extent of recent (≤2 3-years) wildfires in red and notable population centers in dark gray ovals; b) outline of the province of Alberta, Canada (grey) within North America and the region of boreal forests in North America.

Age of stands ranged from 2 to 138 years ($\bar{x}$ = 51, SE = 2.9), stand height varied from 0.2 to 36 m ($\bar{x}$ = 16, SE = 0.8), basal area using a 2-factor metric prism in adjacent stands varied from 0 to 68 m^2/ha ($\bar{x}$ = 25, SE = 1.1), while saplings and understory trees (< 5 cm diameter at breast height [DBH]) ranged from 0 to 17,000 ($\bar{x}$ = 5,185, SE = 317) stems per hectare (Table 6.1). Widths of seismic lines ranged from 2.5 to 14.0 m ($\bar{x}$ = 6.5, SE = 0.21) (see Figure 6.2 for examples). None of the seismic lines in this study were replanted or treated with any silvicultural treatment or mechanical site preparation, nor had evidence of extensive or recent all-terrain vehicle (ATV) use. Thus, this study does not represent intensively disturbed and re-used lines, but rather where extensive human activity is not high.

Table 6.1: Stand characteristics and tree regeneration for 146 mesic upland forest sites sampled in northeast Alberta, Canada. This includes both recently burned and mature forests for paired plots in seismic lines and adjacent forests ($n = 292$).

Stand variable	Minimum	Median	Maximum	Mean (S.E.)
Age (years)	2	57	138	51 (2.9)
Height (m)	0.2	17	36	16 (0.8)
Basal area (m^2/ha)	0	24	68	25 (1.1)
Tree stems per ha (DBH < 5 cm)				
Seismic line	0	12,250	69,333	16,197 (1060)
Adjacent stand	0	8,833	56,833	12,400 (858)
Tree stems per ha (DBH ≥ 5 cm)				
Seismic line	0	0	7,500	708 (119)
Adjacent stand	0	1,250	5,500	1,586 (100)

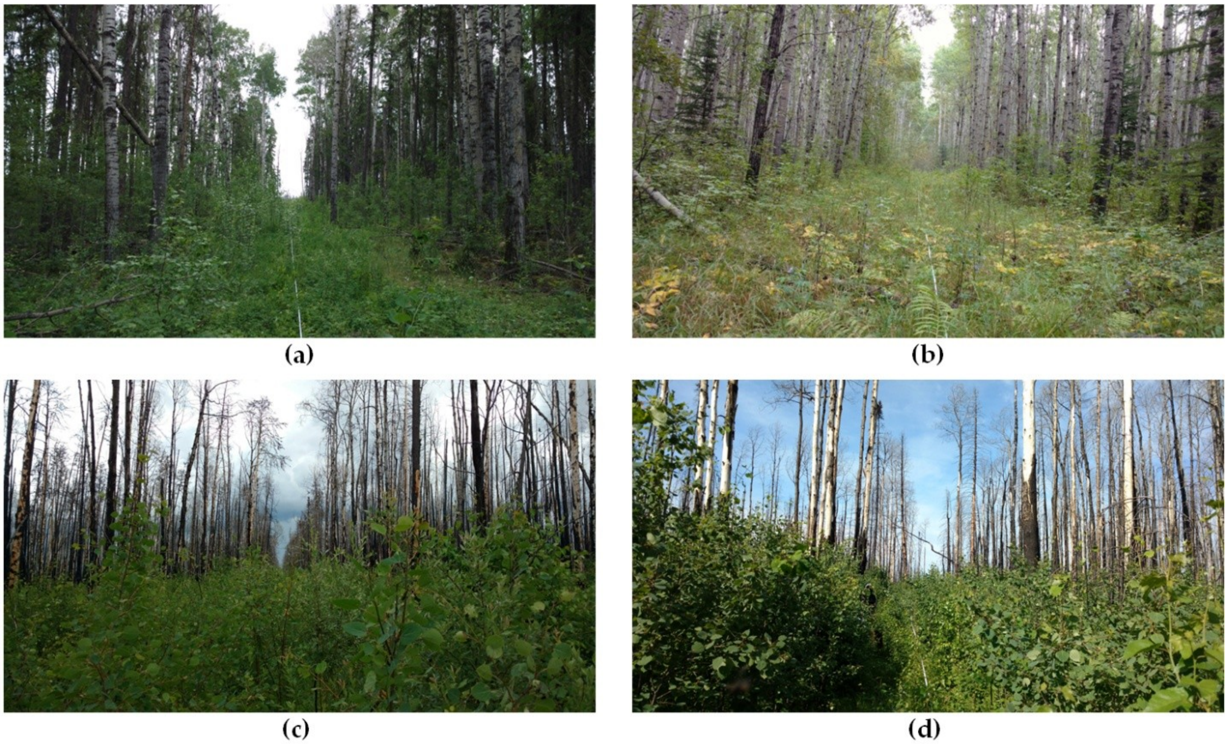


Figure 6.2: Example seismic lines in mesic upland forests of northern Alberta, Canada for: unburnt lines in mature forests (a & b) and burnt lines (c & d) from recent (≤ 23-yr old) high severity fires.

6.3.2 Site selection and field methods

Sample sites on seismic lines were a minimum of 400 m apart unless on a separate seismic line with a different orientation (more than a 45° difference) and/or if ecosite differed. Six wildfires were sampled due to their large size (> 40 km^2) that allowed at least 12 sample sites, presence of ecosites of interest, and age distribution (2, 7, 9, 16, 19, and 23 years prior to sample collection). The age distribution of wildfires, ≤ 23 years old, was chosen for three reasons: (1) much older wildfires have little evidence of fire severity; (2) wildfires needed to occur after seismic line creation; and (3) the study area had no large wildfires between 23 and 30 years old. Locations were selected from a random set of available possible locations within 4 km ($\bar{x}$ = 610 m) of roads with final sites requiring consistent forest stand conditions (i.e., height, density, age) across an area large enough to be sampled. Selection of where to start a plot on a seismic line was determined by a random toss of a metal stake.

All field work occurred in the summer of 2018 with 146 sites sampled with each site being represented by a pair of plots with one plot on a seismic line and the other 25 m into the adjacent reference forest (*n* = 292 plots). A coin toss was used to randomly assign which side of the seismic line the adjacent forest plot was located. Distribution of sample sites by ecosite for mesic forest types included 18 medium-xeric (36 plots), 102 medium-mesic (204 plots), 12 medium-hygric (24 plots), and 14 rich-hygric (28 plots) ecosites. Out of the 146 sites, 68 sites (47%) did not experience a wildfire in the past 65 years (defined as ‘unburnt’), while 78 sites (53%) had a wildfire in the last 23 years (defined as ‘burnt’). Sites that experienced a wildfire in the last 23 years by ecosite were: medium-xeric at 13 (26 plots or 72%), medium-mesic at 53 (106 plots or 52%), medium-hygric at 8 (16 plots or 67%), and rich-hygric at 4 (8 plots or 29%). Sampling effort among ecosites was unequal with one ecosite (medium-mesic) accounting for 70% of sites since it was the most common in the region (sampling effort by ecosite was representative of the area of each ecosite thus rarer ecosites had fewer samples). Preliminary analyses demonstrated similarities among ecosites with only adjacent stand basal area of jack pine, which is uncommon in the ecosite, differing. All ecosites were therefore combined to increase sample sizes and simplicity of reported results, but see Appendix 6.A for the results of individual ecosites.

Each plot represented a 30-m belt transect with the seismic line transect located along the center of the seismic line, while the adjacent paired control transect was located 25 m into the adjacent forest running parallel to the seismic line (see Filicetti and Nielsen 2018 [Chapter 2], 2020 [Chapter 5] for more details). Bulk density measurements were taken at the 10, 15, and 20 m distances of each transect, accounting for 3 samples per plot and 6 per site for a total of 876 samples. The 3 bulk density samples in a plot were averaged for a single plot value. First and foremost I wanted to measure whether seismic lines were compressed compared to the adjacent forests. Soil compression may not be substantial in many sites since most seismic lines have only one pass of machinery and/or were created in winter when soils were frozen and/or were created many years/decades prior to sampling. I therefore focused on shallow depths (< 20.1 cm) for soil cores as deeper soils were unlikely to experience noticeable compression. Furthermore, organic soils are less dense and less compressible; thus, if the soil profile had thick organic layers it was again unlikely to experience noticeable compression. The upper organic layers, L and F, were always removed while the deeper H layers were only fully removed if shallower than 15 cm. A cylinder with 5.1 cm height and 10.8 cm diameter (467 cm^3) was used for bulk density samples. Note, even mineral soil layers can contain 17% organic carbon which typically has a bulk density of 0.30 g/cm^3, which is below the value of most samples (78%) observed in this study. Samples were oven dried at 110° C for 24 hours, then all coarse material (rocks, roots, etc.) greater than 2 mm were sieved with all masses and volumes recorded. Woody shrub and tree densities were measured within belt-plots along each 30 m transect. Tree and shrub regeneration (< 5 cm DBH) densities were counted in 1 × 30 m belt quadrats (30 m^2), while mature trees and shrubs (≥ 5 cm DBH) were counted in 2 × 30 m belt quadrats (60 m^2). The purpose of the two categories (< 5 cm DBH and ≥ 5 cm DBH) was to compare tree/shrub density on seismic lines to adjacent forests at a cut-off size that emphasized recent regeneration, as the adjacent forest, by definition, had many mature trees. Therefore, when examining regeneration for seismic line and adjacent forests, the < 5 cm DBH was used, while analysis of regeneration on only seismic lines used all trees/shrubs, regardless of DBH as all trees on a seismic line were assumed to be regenerating post-disturbance (only 4.2% of all trees/shrubs on seismic lines had a DBH ≥ 5 cm). Since I was interested in large woody trees/shrubs that will reforest seismic lines and slow animal movements through increases in horizontal and vertical structure, I combined green alder, a shrub that grows tall and dense, with trees and defined this as 'regeneration density' for all subsequent analyses. All stem densities were calculated to a common scale of stems per 100 m^2 (0.01 ha) for analysis, but in some cases reported as stems per hectare for ease of comparison with the literature. Average height of regeneration on seismic lines was called 'line regeneration height' and based on height measurements of ten trees, ignoring obvious outliers when tree counts exceeded ten, within the 2 × 30 m seismic line belt. Additional stand information was collected for the adjacent forest plot, including fire severity (defined as percent overstory tree mortality), stand basal area by species using a 2-factor metric prism (m^2/ha) at the midpoint of the adjacent forest transect (15 m line distance), stand age of representative mature trees in the same plot using dendrochronological aging via tree cores at DBH, and representative tree height using a Haglof Vertex IV (Sweden) hypsometer.

6.3.3 Relationship between fire, seismic line, and bulk density on regeneration density and height

Bulk density measures were stratified into six categories and sub-categories: seismic lines (146 plots); adjacent forests (146 plots); burnt lines (78 plots); unburnt lines (68 plots); burnt forests (78 plots); and unburnt forests (68 plots). A paired *t*-test was used to examine whether seismic lines differed from the paired adjacent forests controls, while two-sample *t*-tests were used to test for differences on seismic lines (burnt lines vs unburnt lines) and in forests (burnt forests vs unburnt forests). To examine whether bulk density affected regeneration density or line regeneration height, negative binomial regression models (*nbreg* command in STATA 15.1/SE; StataCorp, 2017) were used to test for differences in tree regeneration density in units of trees per 100 m^2, while regression models (*reg* command in STATA 15.1/SE; StataCorp, 2017) were used to test for differences in line regeneration heights (square root transformed) in units of cm.

6.3.4 Effects of fire and seismic line on regeneration

Here, regeneration density was defined as any tree in the seismic line or adjacent forest that was < 5 cm DBH for a more direct comparison between seismic line and adjacent forest regeneration (only 4.2% of regeneration density on the seismic line had a DBH ≥ 5 cm). To visualize the main experimental effects, I first plotted the mean and standard errors of regeneration density (per ha) for all tree species against the presence of fires and seismic line location (versus adjacent forest). Mixed-effects negative binomial models (*xtnbreg* command in STATA 15.1/SE; StataCorp, 2017) were used to test for differences in regeneration density (trees per 100 m^2) of wildfire (burnt versus unburnt) and seismic line presence. Site ID was used as a random effect to account for the paired nature of the seismic line and adjacent control forest plots within a single site. Separate binary dummy variables were used to represent the presence (1) or absence (0) of a recent wildfire, and seismic line (1) or adjacent forest (0) plots. Control plots and reference conditions for categorical contrasts of variables in models were therefore sites in mature, undisturbed forests. Model selection of predictor variables was limited to the interaction of two main treatment variables (fire presence and seismic line presence versus adjacent forest), regardless of their significance.

Initial collinearity among variables was assessed using Pearson correlations with only two variables, stand height and stand age, being highly colinear ($|r| = > 0.7$) at $r = 0.74$. I therefore did not include stand height and stand age in the same model, but potentially one of the variables. Coefficients are reported for negative binomial models, but I also interpret them as percent change in regeneration per one unit change in the predictor variable by exponentiating them, subtracting one, and multiplying by 100% ([exp[var] -1]×100%). Finally, a mixed-effects negative binomial model was used with the combination of presence/absence of wildfire and seismic line presence (burnt line, unburnt line, burnt forest, unburnt forest) to predict regeneration density and a pairwise test with a Bonferroni adjustment (*pwcompare mcompare(bonferroni)*; STATA 15.1/SE StataCorp, 2017) used to test significance between treatments. Model assumptions were examined for independence, normality of response variables and presence of outliers, and correlations ($r > |0.7|$) among independent variables. Variables were removed and/or modified (transformed) to meet model assumptions.

6.3.5 Relationship between stand, fire severity, and seismic line characteristics on regeneration

For this analysis, regeneration density was defined as any tree on the seismic line regardless of its DBH since analysis was restricted to only seismic line plots. This allowed me to examine the effects of fire severity and seismic line characteristics, such as line orientation and line (forest gap) width since such variables are not representative of adjacent forests. I also considered the effect of the adjacent stand characteristics on regeneration density on seismic lines by including stand height, stand basal area, stand age, and their interaction with seismic line (forest gap) width and orientation. Since I removed the adjacent forest plot from the paired design (random effect) from the above section resulting in a single plot per site, I used standard negative binomial regression models (*nbreg* command in STATA 15.1/SE; StataCorp, 2017). Model selection of predictor variables was based on the inclusion of variables for seismic line and stand characteristics only if significant (at $\alpha = 0.05$). Line width varied between 3 and 14 m ($\bar{x} = 6.4$ and SE = 0.2), while line orientation represented the compass bearing of seismic lines transformed to an index between 0 (east-west orientation) and 1 (north-south orientation) following the methods of van Rensen et al. (2015). Most lines in the area were on north-south and east-west axes (80%). In addition to line characteristics, I examined the effects of graminoid, dwarf shrubs, woody debris, lichen, bare ground, bryophyte, and open water (graminoids and dwarf shrubs were found to be significant and used in models) on regeneration density using average percent cover within six sequential quadrats (2 × 5 m) along each transect. Again, all analyses of regeneration density were at a scale of stems per 100 m^2.

6.4 Results

6.4.1 Relationship between fire, seismic line, and bulk density on regeneration density height

Bulk density ranged from 0.12 to 1.47 g/cm^3 ($\bar{x} = 0.59$, SE = 0.02) and was 34% higher on seismic lines than in adjacent forests ($p < 0.001$), 10% higher on burnt seismic line than on unburnt seismic lines, but this difference was not significant ($p = 0.162$), and 11% higher in burnt forests than in unburnt forests, but again not significant ($p = 0.154$) (Table 6.2; see Appendix Table 6.A1 for results by ecosite).

Affects of bulk density on regeneration density and line regeneration height gave contrasting results and appeared to vary by ecosite. For all ecosites, a 1 g/cm^3 increase in bulk density increased regeneration density by 33% and was marginally significant ($p = 0.067$), while a 1 g/cm^3 increase of bulk density significantly decreased line regeneration height by 5% ($p = 0.027$). When ecosites were separated for evaluating regeneration density and line regeneration height, only two, out of the eight, models were significant with all others having a $p > 0.300$. In medium hygric, a 1 g/cm^3 increase in bulk density increased regeneration density by 5% and was marginally significant ($p = 0.067$). In medium xeric, a 1 g/cm^3 increase in bulk density significantly decreased line regeneration height by 16% ($p < 0.001$) (Figure 6.3). When removing the first, and then the second, most likely outliers from the medium-hygric model (Figure 6.3, pink points in the top right), the result was no longer significant ($p > 0.118$ and $p = 0.657$, respectively) suggesting caution in interpreting the significant trend. In contrast, when removing the first, and then the second, most likely outliers from the medium-xeric model (Figure 6.3, brown points in the top left), significance remained more consistent ($p < 0.004$ and $p = 0.116$, respectively). Overall, there does not appear to be a conclusive relationship with bulk densities and regeneration density or line regeneration height counter to my predictions.

Table 6.2: Mean, standard error, and results of a paired *t*-test comparing bulk densities (g/cm^3) for all lines with all forests, burnt lines with unburnt lines, and burnt forests with unburnt forests.

Statistic	All		Line only		Forest only	
	Line	Forest	Burnt	Unburnt	Burnt	Unburnt
Mean	0.67	0.50	0.70	0.64	0.53	0.48
Standard Error	0.03	0.02	0.04	0.04	0.03	0.03
n	146	146	78	68	78	68
t	5.59		0.99		1.02	
df	145		144		144	
p-value	< 0.001		0.122		0.144	

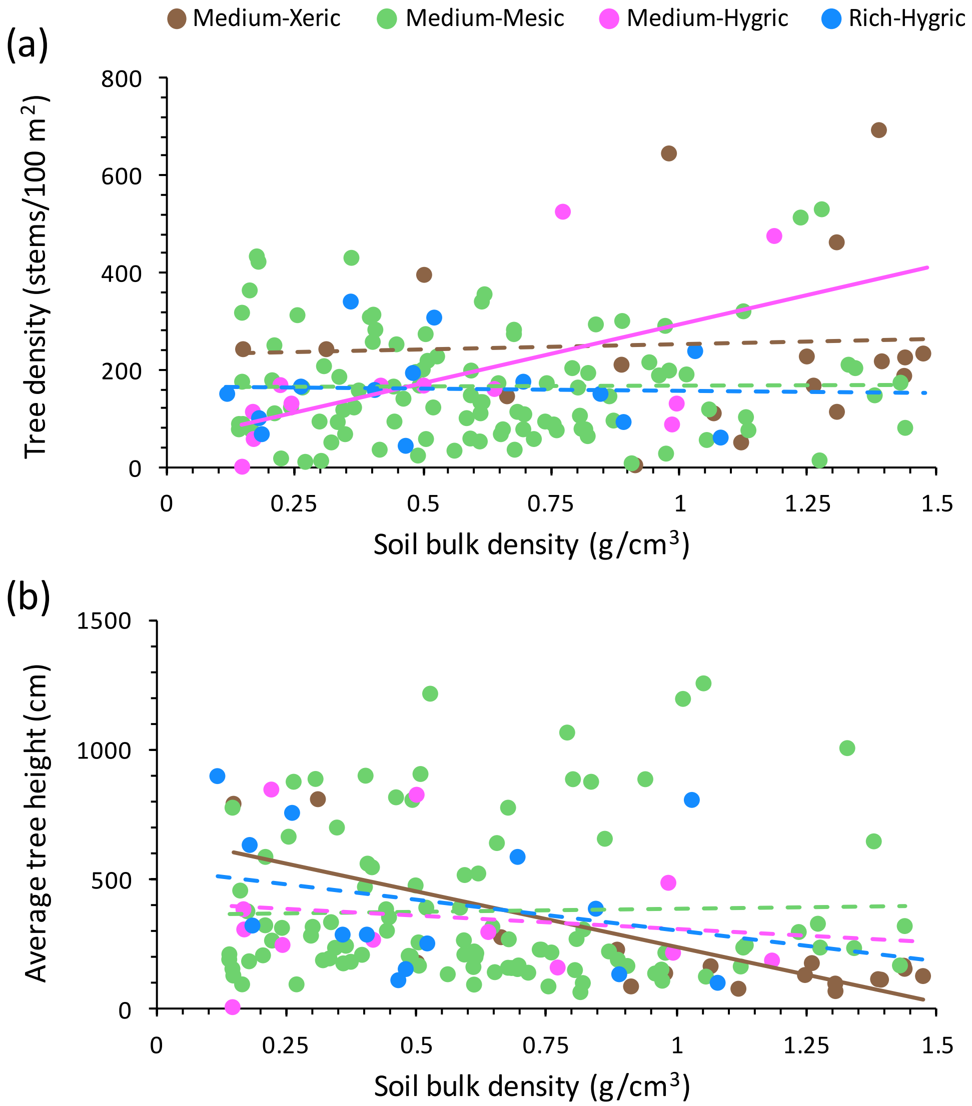


Figure 6.3: Tree density (a. top) and average tree height (b. bottom) on seismic lines as a function of soil bulk density separated by four ecosites common to mesic upland forests of northeast Alberta, Canada. Solid lines represent significant ($p < 0.050$) linear trends between soil bulk density and either height or density for that ecosite, while dashed lines are non-significant trends. Note that significance of the trend in tree density for the medium-hygric model is lost when removing the two high outliers.

6.4.2 Effects of fire and seismic line on regeneration

Preliminary analyses demonstrated clear increases in regeneration density after recent wildfires (≤ 23 years), including in the 2-year-old wildfire. Moreover, the interaction between seismic line (vs. forest) and presence of wildfire within the last 23 years on regeneration density was significant and positive (Figure 6.4 and Table 6.3; see Appendix Figure 6.A1 and Table

6.A2 for results by ecosite). On average, burnt lines had 19,622 regenerating stems/ha (SE = 1,626), unburnt lines had 11,870 regenerating stems/ha (SE = 1,130), the adjacent burnt forests had 16,739 regenerating stems/ha (SE = 1,253), and the adjacent unburnt forest had 6,934 regenerating stems/ha (SE = 740). Burnt lines, therefore, had 65% more regenerating stems per hectare than unburnt lines ($p < 0.001$), 17% more regenerating stems per hectare than burnt forest, but was not significant ($p = 0.603$), and 183% more regenerating stems per hectare than unburnt forest ($p < 0.001$) (Figure 6.4). Burnt forests had 140% more stems per hectare than unburnt forests ($p < 0.001$) and 41% more stems per hectare than unburnt lines ($p = 0.025$). Finally, unburnt lines had 71% more regenerating stems per hectare than unburnt forests ($p = 0.048$). There were, therefore, more regenerating tree stems on burnt seismic lines, compared to unburnt lines, adjacent burnt forest, and adjacent undisturbed forests illustrating that wildfires, regardless of their severity or timing, promote substantial natural regeneration (passive restoration) on most linear disturbances in mesic-upland boreal forests. Overall, regeneration density was 141% higher in burnt versus unburnt sites, 57% higher on seismic lines versus adjacent forest, but 30% less for the interaction of burnt and seismic lines (see Figure 6.4 and Table 6.3). Average regeneration rates were always higher than the recommended standards of 1,000 stems/ha.

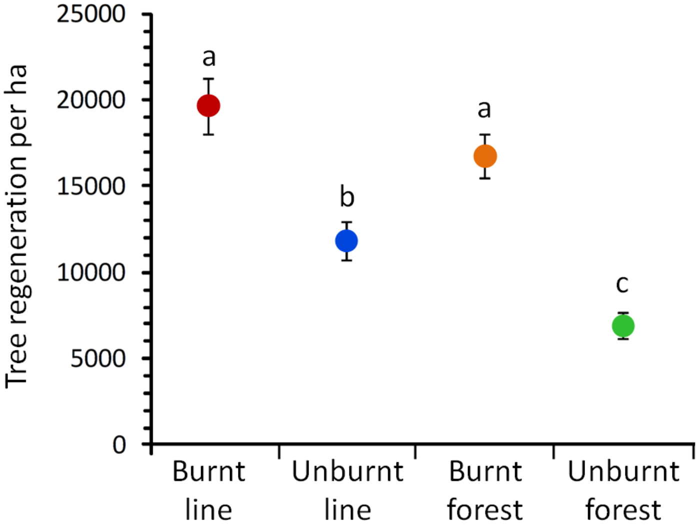


Figure 6.4: Regeneration density (DBH < 5 cm) per hectare by seismic line or adjacent forest and presence/absence of recent (≤ 23-yrs.) wildfire. Significance of treatments within each category was based on a pairwise comparison (Bonferroni adjustment) with different letters indicating significant ($p < 0.0125$) differences between categories.

Table 6.3: Mixed-effects negative binomial regression model parameters (coefficient, β; and standard error, SE) relating regeneration density per hectare (DBH < 5 cm) to presence of fire and seismic line (vs. adjacent forest control). Both fire and seismic line presence were included regardless of significance given that they were study design (treatment) variables. *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$.

Tree density (stems/ha)	β (SE)
Constant (intercept)	0.74 (0.14)***
Fire variables	
Presence	0.88 (0.12)***
Presence × Seismic line	-0.35 (0.12)**
Seismic line location variable	
Seismic line plot	0.45 (0.10)***
Model statistics	
n	292
Log likelihood	-1,672
Wald χ^2	67.71
Prob > χ^2	< 0.001

6.4.3 Relationship between stand, fire severity, and seismic line characteristics on regeneration

When eliminating the adjacent paired forest plots and only assessing regeneration on seismic lines using surrounding stand characteristics (basal area, stand height, stand age), line characteristics of width (gap) and bearing, fire severity, and ground cover, patterns in regeneration density on seismic lines were more apparent. Age of wildfire (stand) was not always significant with a simple binary variable of fire presence and fire severity often being a better predictor of regeneration density. This remained true even when considering interactions between wildfire age and fire severity, suggesting that time since fire is less important than site and disturbance characteristics in predicting regeneration. Species composition of regeneration density is similar on the seismic line to the adjacent forest, both of which is similar to the mature stand in the adjacent forest (Figure 6.5; see appendix Figure 6.A2 for results by ecosite). Jack pine, in particular, was a good indicator for distinguishing local moisture regimes, where high, medium, and low jack pine densities represented low, medium, and high site moisture. Regeneration rates on lines increased by 1% per 1 unit (%) increase in fire severity, increased by 9% per 1 m^2/ha increase in jack pine basal area, decreased by 0.1% for each one unit change in the interaction of fire severity and jack pine basal area, increased by 2% per 1-m increase of stand height, and decreased by 0.8% per 1% increase in graminoid ground cover (Table 6.4; see appendix Table 6.A3 for results by ecosite).

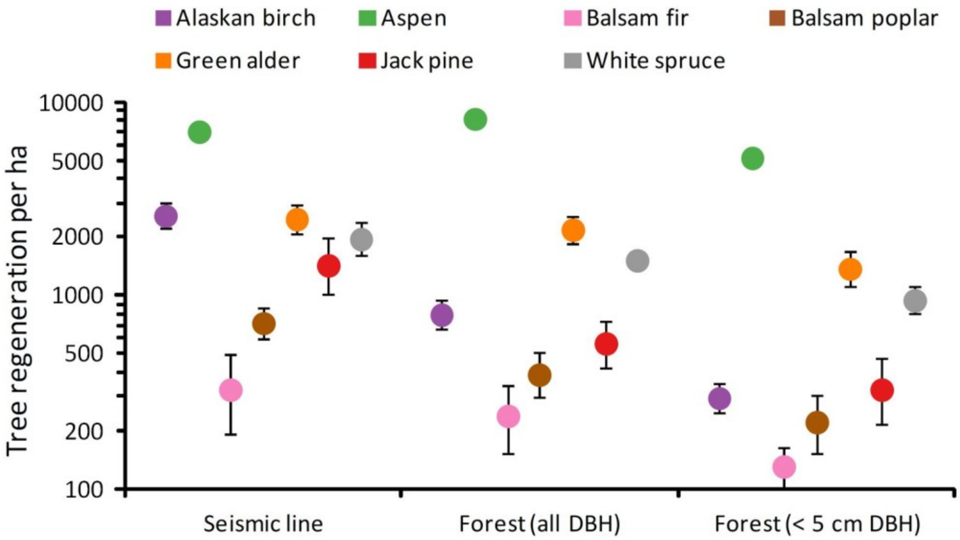


Figure 6.5: Regeneration density on seismic lines [all diameter at breast height (DBH) classes] and adjacent forests (all DBH classes and < 5 cm DBH) for the seven most common species found in upland mesic forests of northeastern Alberta, Canada. Error bars are represented by one standard error; error bars not visible have ranges smaller than the point that represents their origin. Note that the y-axis is in $\log_{10}$ scale.

Table 6.4: Standard negative binomial regression model parameters (coefficient, β; and standard error, SE) relating regeneration density of all tree species on seismic lines to fire severity (% tree mortality), line characteristics, stand variables (BA represents basal area in m^2/ha), and percent ground cover in northeast Alberta, Canada. *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$.

Tree density (stems/ha) seismic line only	β (SE)
Constant (intercept)	4.210 (0.212)***
Fire variables	
Severity (% tree mortality)	0.010 (0.001)***
Jack pine BA × severity	-0.001 (0.0003)**
Stand variables	
Height (m)	0.024 (0.009)**
Jack pine BA (m^2/ha)	0.086 (0.021)***
Ground Cover (%)	
Graminoid	-0.008 (0.003)*
Model statistics	
n	146
LR χ^2	57.13
Prob > χ^2	< 0.001

6.5 Discussion

6.5.1 Relationship between fire, seismic line, and bulk density on regeneration density and height

Bulk density measures were low overall ($\bar{x}$ = 0.59 g/cm^3), perhaps due to the high organic matter typically of boreal forests. In this region, organic matter ranges between 0 to 50% ($\bar{x}$ = ~15%) (Grigal 1989; Périé and Ouimet 2008; Hossain et al. 2015). Maximum bulk density in this study was only 1.47 g/cm^3, with only 6 sites being over 1.40 g/cm^3, below the bulk density where negative effects begin to affect tree establishment, growth, and survival in aspen boreal forest soils (1.55-1.65 g/cm^3) or at comparable textures (Daddow and Warrington 1983; Sealey and Van Rees 2019). Bulk density was 36% higher on seismic lines supporting observations from industry, government, and researchers (Revel et al. 1984; MacFarlane 2003; Lee and Boutin 2006). An additional factor that may account for increases in bulk density is the repeated use of lines by wildlife forming wildlife trails (Latham et al. 2011b; Tigner et al. 2014, 2015; Dickie et al. 2020). Seismic lines also experienced a compounding effect from wildfires, where bulk densities further increased by 13%, although this was not significant. Adjacent forests also experienced increases in bulk density post-fire, but at a slightly lower rate of 12% and again were not significant. This suggests that wildfires can compact soils by approximately the same rate regardless of the initial level of compaction pre-fire, but that compaction levels vary substantially between sites and overall are not significant. Contrary to suggestions from others (Revel et al. 1984; MacFarlane 2003; Lee and Boutin 2006), seismic line compaction does not appear to affect regeneration density or line regeneration height, at least for mesic boreal forests where lines are not extensively disturbed by ATV use. These findings are similar to other studies examining regeneration density, survival, and stand height to bulk density in aspen forests (Kabzems and Haeussler 2005; Ampoorter et al. 2011; Kabzems 2012; Sealey and Van Rees 2019). Sites extensively used by ATVs may, however, have different results, but it is apparent that the majority of seismic lines in these ecosites are not limited by soil compaction.

6.5.2 Effects of fire and seismic line on regeneration

Both fire and seismic line increased regeneration density in mesic-upland forests, with fires having a larger effect (141% increase) than seismic lines (57% increase) when compared to unburned sites and adjacent forests, respectively. Contrary to some reports pointing to arrested succession with little to no tree development on seismic lines in mesic-upland forests (MacFarlane 2003), unburnt seismic lines had higher regeneration rates than the adjacent forests illustrating an expected response to early seral conditions. A similar pattern was observed in peatland forests, although at much lower densities (Filicetti and Nielsen 2020 [Chapter 5]). Seismic lines, either burnt or unburnt or of any ecosite, have regeneration densities well over 1,000 stems/ha, the minimum suggested regeneration density for upland sites from the Alberta guidelines for seismic line deactivation (Government of Alberta 2017).

Although comparing seismic lines to paired adjacent forests have limitations, they do provide for broad comparisons and control for local site conditions. As seismic lines represent narrow clear-cut openings, they have higher levels of sunlight and wind (Stern et al. 2018), and are next to readily available seeds/suckers from the adjacent forest and thus are useful comparisons. Given these conditions, we would expect seismic lines to have higher regeneration rates due to the early seral conditions of the site, yet many report in other ecosites a near lack of regeneration (Lee and Boutin 2006; van Rensen et al. 2015; Filicetti et al. 2019 [Chapter 4]; Filicetti and Nielsen 2020 [Chapter 5]). However, many seismic lines are still easy to traverse, particularly unburnt lines, and thus require more time to "fill in" and mature. This may be a much longer process due to attrition rates not accounted for in clear-cut studies as the small gap size of seismic lines can be kept shaded if the overstory is large enough, the repeated usage of animals can result in trampling, and the higher bulk densities may result in reduced growth that can take 5 or more years to be detected (Kabzems and Haeussler 2005; Ampoorter et al. 2011; Kabzems 2012; Sealey and Van Rees 2019). This is similar to other reports in wetter ecosites, where it is believed that a high water table and a lack of microsites restrict tree regeneration and growth (Lee and Boutin 2006; van Rensen et al. 2015; Filicetti et al. 2019 [Chapter 4] [Chapter 3]; Filicetti and Nielsen 2020 [Chapter 5]). However, the dense patterns of regeneration post-fire suggest that seismic lines minimally damage roots/suckers and site availability.

6.5.3 Relationship between stand, fire severity, and seismic line characteristics on regeneration

Age of wildfire was related to tree regeneration on seismic lines, but was not always a better predictor than a simple binary variable of fire presence and always worse than fire severity. This is similar to results for xeric jack pine stands (Filicetti and Nielsen 2018 [Chapter 2]), and treed peatlands (Filicetti and Nielsen 2020 [Chapter 5]), where most seed abscission post-fire occurs within the first few years (Greene et al. 2013) and points to a reoccurring observation that time since disturbance on lines for at least the last few decades is less important than the severity of the disturbance and site characteristics. Aspen, which accounts for 43% of the regeneration density observed in this study, regenerated at higher rates post-fire, mostly from suckering (Greene and Johnson 1999; Frey et al. 2003; Jean et al. 2020), where > 95% of recruitment occurs within the first 3 years post-fire (Greene et al. 2004). Aspen tend to increase their proportional abundance in a stand post-fire and thinning can occur within the first few years post-fire (Greene and Johnson 1999). Other species tend to occupy different niches, like balsam fir and white spruce that are less adapted to fires, but are able to establish seedlings post-fire with aerial seeds banks (de Groot et al. 2013). Regardless, immediately after a wildfire competition to colonize and establish new sites is high and recruitment after the first couple of years is minimal.

Regeneration density of trees on seismic lines were also positively related to basal area of jack pine and the interaction with fire severity. This is likely for two reasons: (1) drier sites, that are associated with jack pine, regenerate at higher rates because they have more jack pine and aspen, which both regenerate well post-fire compared to hygric and less fire-adapted species such as balsam poplar and balsam fir; and (2) hygric sites tend to burn less often and at lower severity and therefore are less likely to initiate early seral conditions. This is similar to findings in treed peatlands where fens did not regenerate trees on seismic lines as well as bogs and poor mesic ecosites (Filicetti and Nielsen 2020 [Chapter 5]).

The positive relationship with stand height possibly reflects that larger trees: (1) are a good indicator that the site is more suitable for trees (supply of available nutrients, water, etc.) and is therefore likely to have more available microsites for regeneration; (2) tend to produce more seeds (Greene et al. 1999); and (3) have larger reserves of carbohydrates in the root system and thus higher sucker dispersal and density (Greene et al. 1999, 2004).

Graminoid ground cover was negatively related to tree regeneration density, like that of seismic lines in treed peatlands (Filicetti et al. 2019 [Chapter 4]; Filicetti and Nielsen 2020 [Chapter 5]). Several studies in central and northern Alberta show negative effects of graminoids on tree regeneration in aspen forests. For instance, belowground growth of aspen decreased with smooth brome (*Bromus inermis* Leyss.) competition as this grass rapidly spreads to available rooting space inhibiting water and nutrient availability (Bockstette et al. 2017). Another grass common to boreal forests of Alberta, *Calamagrostis canadensis*, can compete and inhibit tree regeneration and growth in several ways. *C. canadensis* competes for sunlight and nutrients, while its thick growth and litter reduces soil temperatures resulting in reduced access to nutrients and water due to a shorter thaw period and growing season (Hogg and Lieffers 1991). Presence of *C. canadensis* can inhibit aspen sucker emergence by 30% and suckers that do emerge have 40% less leaf area and are smaller resulting in reduced aspen regeneration and growth (Landhäusser and Lieffers 1998).

6.6 Management implications

Seismic lines in mesic-upland forests have more compacted soils compared to adjacent forest controls. Regardless, the compaction on seismic lines appears to have negligible effects on tree regeneration and line regeneration height. Therefore, any mitigation efforts to alleviate this compaction will likely result in a resetting the regeneration already started suggesting that: (1) sites in need of restoration need to be identified first before widely applying restoration treatments; and (2) perhaps the more effective strategy is restricting human access to more open lines. Restoration of seismic lines is considered to be a billion-dollar issue (Hebblewhite 2017) with triage needed for when and where to spend limited restoration dollars to being efficient and effective. The Government of Alberta has suggested 1,000 stems/ha to designate an upland seismic line as deactivated, but this value seems rather low for mesic uplands which already have densities much higher without any active restoration efforts. Regardless, 1,000 stems/ha is likely sufficient to develop forest structure consistent with natural and post-harvest stands. In this study, most unburnt lines were restoring well on their own, yet some sources have suggested otherwise, this may be due to regeneration having poor growth and survivability due to compaction and shading on some sites studied. In particular, selecting open lines for study creates substantial selection bias that I caution researchers to be careful of when extrapolating results beyond their study of open lines. Wildfires bestow an increase in regeneration density in a much shorter time-frame and can provide a potential option for low cost passive restoration under certain circumstances. As pointed to by Filicetti and Nielsen (2020) [Chapter 5], there are substantial variations in fire frequency within a landscape due to features such as dominant tree species (Larsen 1997), fuel loads (Johnston et al. 2015), natural landscape features (Nielsen et al. 2016), and time since last fire (Beverly 2017). It is also believed that climate change will bring more frequent, more intense, and larger wildfires to much of the world, including northeast

Alberta (Flannigan et al. 2009a, 2009b). Therefore, I propose that sites that are recently burnt, and areas that have a high likelihood of experiencing a wildfire in the short-term, should not be actively restored as wildfires will do the restoration work at no cost but time until the return of fires (use of prescribed fire for restoration in this system is unlikely). However, controlling human access (ATV and snowmobile use) on lines where these activities occur or are likely is crucial to allowing natural recovery and much less expensive than site preparation, stem bending, and tree planting associated with current restoration practices.

Appendix

Table 6.A1: Mean, standard error, and results of a paired *t*-test comparing bulk densities (g/cm^3) for among four mesic ecosite on all lines and forests sampled in northeast Alberta, Canada.

Statistic	Medium xeric		Medium mesic		Medium hygric		Rich hygric	
	Line	Forest	Line	Forest	Line	Forest	Line	Forest
Mean	1.06	0.85	0.64	0.49	0.54	0.28	0.55	0.37
Standard Error	0.10	0.07	0.03	0.03	0.11	0.06	0.09	0.06
n	18	18	102	102	12	12	14	14
t	2.74		4.00		2.76		1.78	
df	17		101		11		13	
p-value	0.007		< 0.001		0.009		0.049	

Table 6.A2: Mixed-effects negative binomial regression model parameters (coefficient, β; and standard error, SE) relating regeneration density per hectare (DBH < 5 cm) of all tree species to presence of fire and seismic line location (vs. adjacent forest control) in northeast Alberta, Canada. Both fire and seismic line binary treatment variables were included regardless of significance. *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$.

Tree density (stems/ha)	Medium xeric β (SE)	Medium mesic β (SE)	Medium hygric β (SE)	Rich hygric β (SE)
Constant (intercept)	0.58 (0.43)	0.77 (0.16)***	1.98 (0.78)*	1.1 (0.41)**
Fire variables				
Presence of fire	0.8 (0.39)*	1.13 (0.14)***	-0.29 (0.54)	-0.05 (0.35)
Fire × Seismic line	-0.05 (0.44)	-0.35 (0.14)*	-0.99 (0.32)**	-0.41 (0.43)
Seismic line location variable				
Seismic line plot	0.35 (0.40)	0.4 (0.12)***	1.03 (0.23)***	0.6 (0.22)**
Model statistics				
n	36	204	24	28
Log likelihood	-217.37	-1147.04	-132.62	-150.31
Wald χ^2	9.55	77.99	22.98	9.24
Prob > χ^2	0.02	0.00	0.00	0.03

Table 6.A3: Standard negative binomial regression model parameters (coefficient, β; and standard error, SE) relating regeneration density of all tree species on seismic lines to fire severity, line characteristics, stand variables (BA represents basal area in m^2/ha), and percent ground cover in northeast Alberta, Canada. *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$.

Tree density (stems/ha) seismic line only	Medium xeric β (SE)	Medium mesic β (SE)	Medium hygric β (SE)	Rich hygric β (SE)
Constant (intercept)	5.14 (0.33)***	4.03 (0.27)***	3.86 (0.51)***	3.62 (0.38)***
Fire variables				
Severity (% tree mortality)		0.01 (0.002)***		
Jack pine BA × severity		-0.002 (0.001)*		
Line characteristics				
Line Width (m)	0.15 (0.05)**			0.15 (0.05)**
Bearing			-1.31 (0.49)**	
Stand variables				
Height (m)		0.026 (0.011)*		
Aspen BA (m^2/ha)	-0.11 (0.02)***			
Jack pine BA (m^2/ha)		0.27 (0.09)**		
Ground Cover (%)				
Graminoid		-0.01 (0.004)*		
Dwarf shrub			0.10 (0.03)***	0.04 (0.02)*
Model statistics				
n	18	102	12	14
LR χ^2	17.68	50.91	10.56	9.30
Prob > χ^2	< 0.001	< 0.001	0.005	0.010

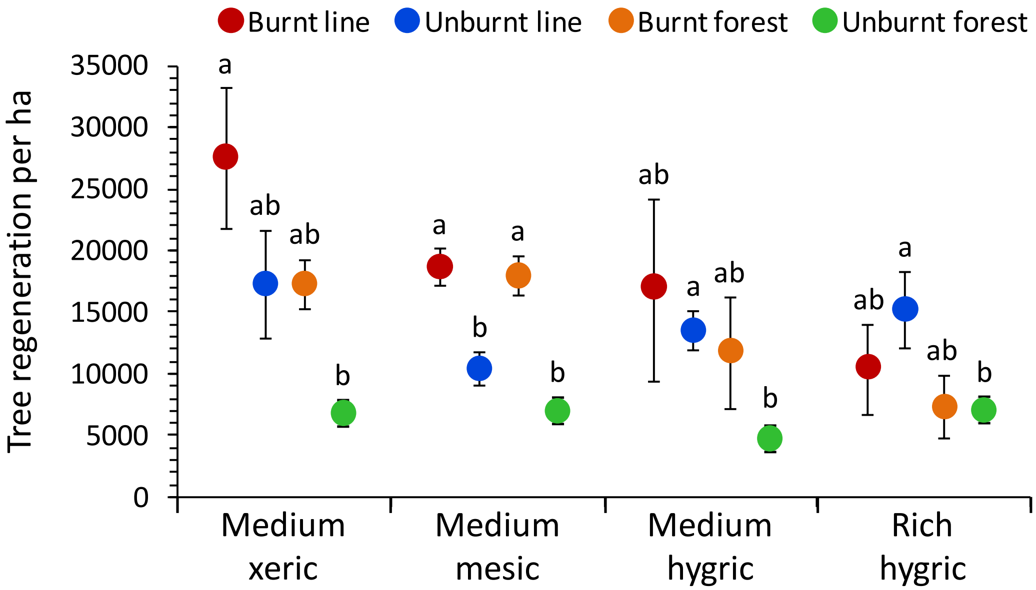


Figure 6.A1: Regeneration density [diameter at breast height (DBH) < 5 cm] (stems/ha), across four ecosites and wildfire presence in northeast Alberta, Canada. Significance of treatments within each ecosite was tested with a pairwise comparison (Bonferroni adjustment) with different letters indicating significant (*p* < 0.0125) differences within an ecosite.

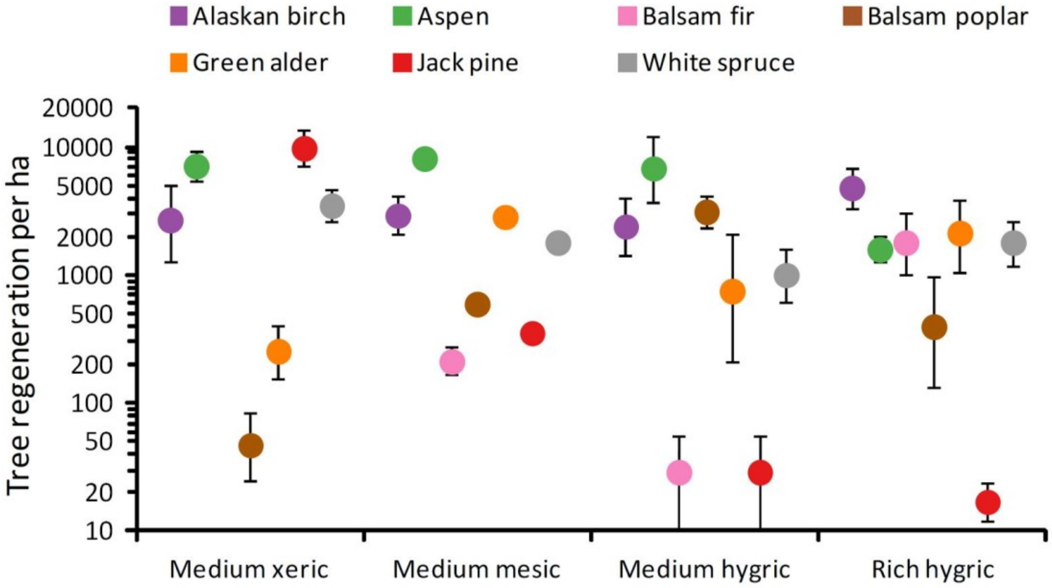


Figure 6.A2: Regeneration density for the seven most common species [all diameter at breast height (DBH) classes] found on seismic lines in the four upland mesic ecosites of northeast Alberta, Canada. Error bars are represented by one standard error; error bars that are not visible have ranges smaller the point that represents their origin.

Chapter 7: Predicting reforestation of linear disturbances in the boreal forests of Alberta: Identifying sites for passive vs. active restoration

7.1 Abstract

In western Canada, linear disturbances used for petroleum exploration (“seismic lines”) are one of the largest contributors to boreal forest fragmentation. Many of these lines have failed to recover decades after disturbance, altering forest dynamics and biodiversity. Some species suffer the effects of seismic lines, most notably the threatened woodland caribou (*Rangifer tarandus caribou*). While governments and industry are acting to facilitate forest recovery, restoration is expensive and needed across vast areas (i.e., 1.7 million km of lines for an estimated cost of $6.8 billion CAD). Guidelines for active restoration treatments also lack details, particularly to reflect differences between forest types, and the possible benefits of natural disturbance of fire as a passive form of restoration. This passive form of restoration relies on natural regeneration, and/or disturbance regimes (e.g., wildfire), complements active restoration strategies, but their effectiveness remains poorly understood. Here, I compare trajectories for density and height of trees on 375 seismic lines in northeast Alberta, Canada, across nine forest types (ecosites) in either recently burned or unburned conditions. Results suggest that most seismic lines with passive recovery meet suggested guidelines for density, with many achieving a 5 m height recovery within 20 years. Most exceptions to these patterns occur in forested peatlands, particularly fens where densities meet guidelines but heights lag behind other ecosites although this partly reflects the shorter nature of mature forests (~7 m mature forest heights) in these systems.

7.2 Introduction

Anthropogenic disturbances in forests are increasing globally as populations, industrial development, and living standards rise (Foley et al. 2005; Gauthier et al. 2015). In boreal regions, natural resource extraction (timber, minerals, and oil and gas) is the main source of disturbance (Thom and Seidl 2016). Many of the footprints in boreal regions are linear in nature (e.g., roads, transmission lines, and pipelines), with the vast majority in western Canada being seismic lines that are used for petroleum exploration (Dabros et al. 2018). Seismic lines result in high levels of forest dissection even in areas with low overall forest loss (Arienti et al. 2009; Schneider et al. 2010; Pattison et al. 2016; Riva and Nielsen 2020), reaching densities as high as 40 km of lines per km^2 of forest (Filicetti et al. 2019 [Chapter 4]). Many seismic lines, especially those within woodland caribou range, have been targeted for restoration with a conservative cost of $12,500 (CAD) per km of restored line (Pyper et al. 2014; Filicetti and Nielsen 2018 [Chapter 4]; Filicetti et al. 2019 [Chapter 5]; Johnson et al. 2019). Nevertheless, with ~1.7 million km of seismic lines, the total cost for restoration of all lines (assuming they were targeted) would be $20.4 billion (CAD) in Alberta, Canada alone (Timoney and Lee 2001). This estimate increases by $35.9 million (CAD) annually when considering ~ 2,875 km of lines are added each year (this was an average for the period of 1992–2008, a potential high point) (Komers and Stanojevic 2013). Even if only a fraction of seismic lines require restoration, restoration costs would still be substantial. One study estimates one-third of lines require restoration as two-thirds recovery naturally (van Rensen et al. 2015), suggesting a total restoration cost of $6.8 billion (CAD). Therefore, triage of which seismic lines require active restoration and the most efficient ways of applying restoration are needed given limited restoration dollars (Schneider et al. 2010; Wiens et al. 2012; Hebblewhite 2017).

Since seismic lines do not follow typical natural successional trajectories after disturbance (Lee and Boutin 2006; van Rensen et al. 2015), understanding the conditions in which natural recovery is more likely will be critical for planning restoration. Yet, many factors influence successional pathways on seismic lines, with the composition of trees and their dynamics in boreal forests being affected by changes in microtopography, soil compaction, hydrology, climate, natural disturbance regimes, and the seed bank (Bonan and Shugart 1989; Lieffers et al. 1996; Greene et al. 1999). Changes in these drivers can lead to a loss of resilience in the forest and long-term ecological shifts (Beck et al. 2011). Although these narrow disturbances were initially assumed to be harmless given their localized footprint, they fragment the boreal forests affecting landscape connectivity *sensu lato*, movement of species, and alter biodiversity (e.g., Tigner et al. 2014, 2015; Riva et al. 2018; Roberts et al. 2018; Shonfield and Bayne 2019). Predators, particularly wolves, use these linear features leading to increases in interactions with prey species, which has likely contributed to declines in woodland caribou populations (James and Stuart-Smith 2000; Latham et al. 2011a; Dickie et al. 2017b; Finnegan et al. 2018), a species-at-risk that largely drives current restoration efforts.

Slowing the movement of organisms on seismic lines depends, in the long-term, on seismic lines recovering to a later successional stage, or in the short-term on some type of structural blocking (Spangenberg et al. 2019; Serrouya et al. 2020). Dense vegetative growth would best slow movements of wolves, but defining the stage at which seismic lines can be considered ‘recovered’ remains challenging using either the goals of functional or ecological restoration targets. Prior work has used a vegetation height of 3 m as a benchmark for seismic line regeneration (van Rensen et al. 2015), as it can be measured in the field or via remote sensing (e.g., LiDAR), is higher than most shrubs (thus indicating tree recruitment), and is already used in forestry standards established for assessing value to wildlife (van Rensen et al. 2015; Alberta Agriculture and Forestry 2016). Other work suggests that vegetative heights as short as 0.5 m could be considered functionally recovered for caribou since this vegetation height slows wolf movements, yet other areas required heights as high as 4.1 m (Dickie et al. 2017a). These height thresholds do not consider differences between forest types, as treed peatlands are often characterized by short, dense, stands of trees and shrubs that are especially effective in slowing movements of animals (Tigner et al. 2014). Arguably, vegetation density is a more important factor than vegetation height in providing resistance to movement along seismic lines. Therefore, the combination of horizontal and vertical structure is key to ecological restoration, as well as to the more short-term objective of slowing wolf movements.

In parallel to the factors used to define recovery (e.g., tree height vs. density), it is critical to estimate the time required for trees to reach particular heights and densities based on site conditions, stand characteristics, and site history. Typical growth rates are known for most common species of trees growing in the boreal forests where seismic lines have been cleared. Yet there are no studies of growth rates on seismic lines, where gap sizes are small (3–12 m wide) and environmental conditions are atypical. Indeed, seismic lines affect tree establishment, survival, and growth rates (Timoney and Lee 2001; Lee and Boutin 2006; Kemper and Macdonald 2009b, 2009a; Caners and Lieffers 2014), often leading to arrested succession (van Rensen et al. 2015).

With these considerations in mind, my objective here is to describe abundance (density) and height (growth) of nine common boreal tree species on seismic lines in northeast Alberta, Canada where the oil sands footprints are most extensive. Specifically, I am interested in relating recovery patterns to: (i) age of seismic line, approximated by measuring the oldest tree observed on the line; (ii) fire history (recent presence of fire, fire severity, and time since fire); (iii) adjacent stand characteristics (stand height); (iv) line characteristics (line width); and, for height recovery, (v) regeneration density (competition). Such information can be used to prioritize future linear feature restoration efforts by identifying where recovery has or is likely to occur naturally (passive restoration) or not (thus targets for active restoration), and what the trajectories of that recovery are.

7.2 Methods

7.2.1 Study area

The study area lies in northeast Alberta, Canada encompassing ~30,000 km^2 of the Athabasca Oil Sands (Figure 7.1). Forests types (ecosites) common to the area vary in their nutrient (poor, medium, rich) and moisture regimes (xeric, mesic, hygric, and hydric) resulting in differences of tree/shrub species composition (Hart and Chen 2008) and hence regeneration patterns post disturbance. I sampled tree recovery on seismic lines that were either recently (≤ 23-years) burned or unburned (> 65-years since fire) across 9 ecosites using nutrient-moisture regime combinations (i.e., poor-xeric, poor-mesic, poor-hydric, medium-xeric, medium-mesic, medium-hygric, medium-hydric, rich-hygric, and rich-hydric) based on the Alberta Biodiversity Monitoring Institute ecosite classification (Alberta Biodiversity Monitoring Institute 2018), Table 7.1. The most common tree species in the area were: black spruce (*Picea mariana* (Mill.) B.S.P.), aspen (*Populus tremuloides* Michx.), jack pine (*Pinus banksiana* Lamb.), white spruce (*Picea glauca* Moench. Voss), Alaska birch (*Betula neoalaskana* Sarg.), tamarack (*Larix laricina* (Du Roi) K. Koch), and balsam poplar (*Populus balsamifera* L.); while the most common large shrubs (i.e., that can reach heights > 3 m; from here defined as trees) were: willow (*Salix* spp.) and green alder (*Alnus crispa* (Ait.) Pursh), see Table 7.A1 in Appendix A.

Table 7.1: Defintion of forest types (ecosite) using common overstory and understory species and mature stand heights.

Ecosite	Common overstory species	Common understory species	Mature height (m)
Poor xeric	Jack pine	Bearberry, lichen	15 (0.48)
Poor mesic	Black spruce	Bog cranberry, feather moss	12 (0.80)
Poor hydric	Black spruce	Bog cranberry, cloud berry, peat moss	7 (0.55)
Medium xeric	Aspen & Jack pine	Bearberry, hairy wildrye, buffaloberry	18 (1.63)
Medium mesic	Aspen & White spruce	Squashberry, bunchberry, buffaloberry	20 (0.65)
Medium hygric	Balsam poplar & White spruce	Horsetail, willows, currants	21 (2.31)
Medium hydric	Black spruce & Tamarack	Bog cranberry, graminoids, peat moss	8 (0.40)
Rich hygric	Balsam fir & White spruce	Red osier dogwood, thick feather moss	21 (1.94)
Rich hydric	Black spruce & Tamarack	Graminoid dominance, peat moss	8 (0.79)

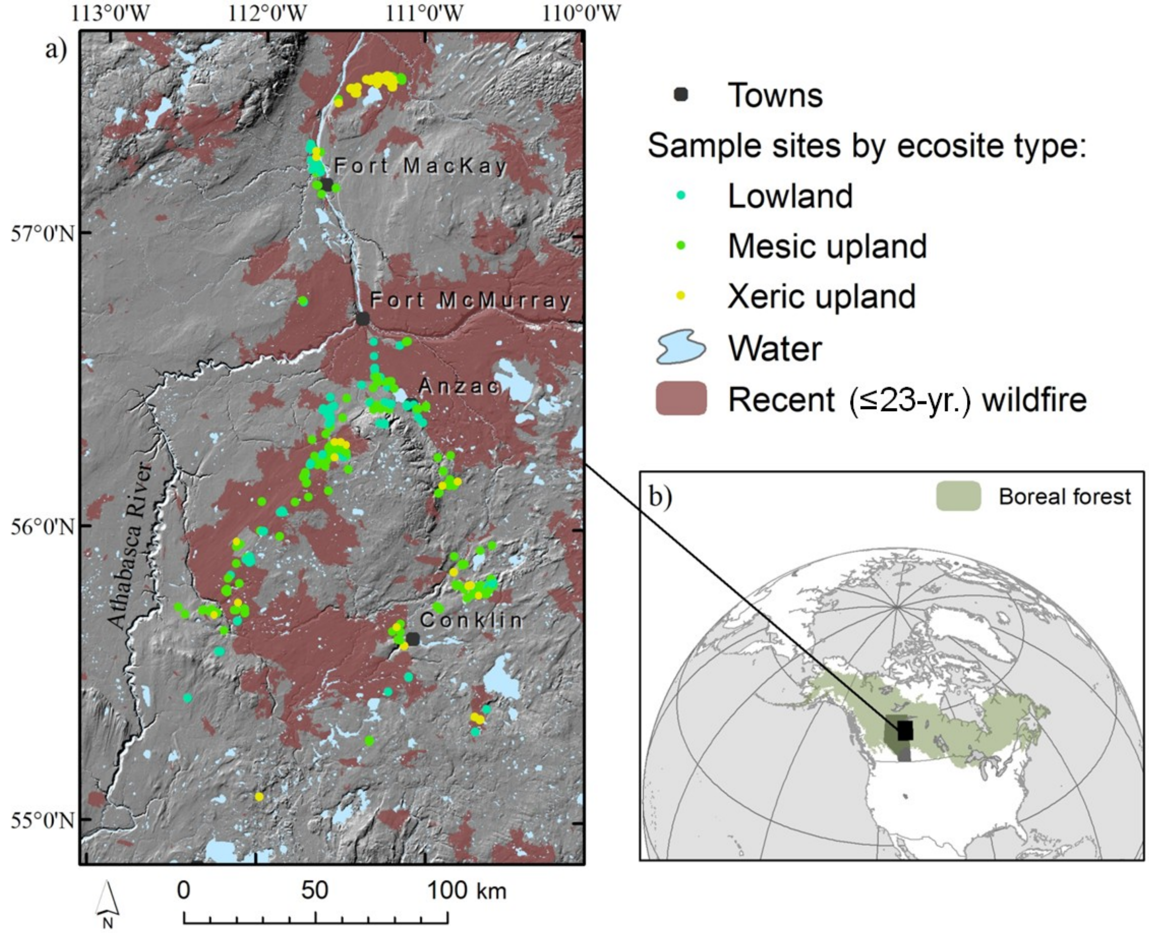


Figure 7.1: Study area map showing: (a) location of sampling sites by general ecosite (lowland, mesic upland, and xeric upland forests) within northeast Alberta, Canada with extent of recent (≤ 23-years) wildfires in dark red, general terrain, and notable population centers in dark gray ovals; and (b) outline of the province of Alberta, Canada (grey) within North America and the region of boreal forests in North America.

7.2.2 Data collection

Field work occurred in the summer months of 2016–2019 with 375 seismic lines sampled. Each year focused on different ecosites/regimes, 2016 on xeric forests dominated by jack pine (Filicetti and Nielsen 2018 [Chapter 2]), 2017 on lowlands dominated by black spruce and tamarack (Filicetti et al. 2019 [Chapter 4]; Stevenson et al. 2019 [Chapter 3]; Filicetti and Nielsen 2020 [Chapter 5]), 2018 on mesic uplands most often dominated by aspen (see Chapter 6), and 2019 involved some revisits of other ecosites to fill data gaps. Sampling effort within each year (broad ecosite) reflects the approximate area of each ecosite within the study area, with less sampling effort to rarer ecosites (i.e., 79 poor-xeric, 34 poor-mesic, 29 poor-hydric, 21 medium-xeric, 102 medium-mesic, 12 medium-hygric, 61 medium-hydric, 14 rich-hygric, and 23 rich-hydric ecosites). Additionally, each ecosite was sampled across a chronosequence of time since fire for recent (≤ 23-yrs old) wildfires relative to years in which wildfires occurred. I emphasized more recent fires to examine recovery trajectories post-fire, as most trees in this system rely on the natural wildfire regime to regenerate. Specifically, six wildfires were selected due to their size, accessibility, and age distribution (1–23 years). Out of the 375 sites, 225 sites (60%) were within recent wildfires (I define hereafter as ‘burnt’), while 150 sites (40%) did not experience a wildfire in over 65 years and thus are considered mature forests (I define this group as ‘unburnt’ although certainly these sites have burned at some point in their history). Each site had a 30 m transect established along the center of the seismic line and all regenerating trees were counted in 1-m wide belt quadrat along the transect line. Orientation (bearing) and width of each seismic line was recorded for each site with widths ranging from 2.5 to 14 m and 74% of line bearings being either north-south or east-west in orientation (for examples see Figure 7.1 and Table 7.2). None of the seismic lines in this study were replanted or treated with any silvicultural treatment or mechanical site preparation and thus represent natural recovery dynamics (i.e., leave-for-natural recovery), ranging from sites that could be considered in a state of arrested succession to expected, or even exceeding, levels of regeneration to that of adjacent forests. More detailed field methods are available in Filicetti and Nielsen (2018 [Chapter 2], 2020 [Chapter 5]).

Destructive sampling was used to measure age and height of trees for the four most common tree species at each site with two individuals selected per species. Specifically, stem cookies were collected at the base of the tree to quantify age of individual trees and its height measured with a tape measure to the nearest centimeter. Much larger trees (with a height > 5 m and a root collar > 6 cm) were cored at their base and height measured using a tape measure and/or a Haglof Vertex IV (Sweden) hypsometer to the nearest decimeter. Cookies and cores were labeled and transported to the lab where they were sanded and aged (Table 7.A3 in Appendix A). Note, I did not examine radial growth of trees on seismic lines as I was interested in the relationship between tree age and height given the restoration objectives on seismic lines focus on height and density of trees.

Stand information was collected in the adjacent forest (25 m into the forest from the seismic line edge with the side of line determined by a flip of a coin), including stand basal area by species using a 2-factor metric prism (m^2/ha), stand age of representative mature trees using dendrochronological aging via tree cores/cookies (stand ages ranged from 1 to 158 years), and representative tree height using a Haglof Vertex IV (Sweden) hypsometer (stand heights of alive trees ranged from 0 to 36 m). Fire severity, defined as percent overstory tree mortality, was also collected in the adjacent stand for recent fires along with time since last wildfire, or simply the presence-absence of recent (≤ 23 yrs.) wildfire, and dated using spatial wildfire databases (Alberta Agriculture and Forestry 2017).

7.2.3 Predictor variables

Since one aim of this study is to relate these findings to the larger landscape, I used predictor variables that could be related to geo-spatial datasets on ecosite, fire history, general stand conditions, and basic line characteristics. All variables have been found to be influential in similar studies (Hart and Chen 2008; Filicetti and Nielsen 2018 [Chapter 2], 2020 [Chapter 5]; Filicetti et al. 2019 [Chapter 4]). However, in some cases the significance of their effects were quite small ($p > 0.10$) and thus removed for parsimony. Below, I describe all variables used to explain patterns in tree density and height.

First, I considered three wildfire variables: 1) presence of a recent (≤ 23-years) fire [dummy coded as burnt (1) and unburnt (0)]; 2) fire severity defined in the field as percent overstory tree mortality; this value is correlated with common remote sensing burn severity indices (Whitman et al. 2018); and 3) time since fire. However, all three fire variables were highly correlated (Pearson correlation, $r > 0.76$, $p < 0.001$) and although fire severity can be important for ecosites with fire-dependent species (e.g., serotiny), initial analyses showed that fire severity for this study was only marginally better than presence of recent fire and not of importance for most species. Likewise, initial analyses showed that time since fire rarely improved on a simple presence of recent fire with time since fire being a poor predictor of tree density owing to seed abscission patterns post-fire occurring within the first few years (Greene et al. 2013; Filicetti and Nielsen 2018 [Chapter 2], 2020 [Chapter 5]), and the viability of tree seeds that are stored in the boreal forest floor being low (Bonan and Shugart 1989). Age of oldest tree on the seismic line was used as a proxy of minimum age of seismic lines and this was, not surprisingly, correlated with time since fire for burnt sites ($r = 0.62$, $p < 0.001$) with higher correlations for individual ecosites with species dependent on fire for seed abscission and sucker proliferation. Thus, variable selection only considered the presence of recent wildfires and minimum age of seismic line for predictions of recovery.

Three adjacent stand characteristics were measured and considered in preliminary analyses: forest age, height, and basal area. All three variables were correlated and for a number of reasons, including ease of obtaining remotely-sense data for landscape applications, I only considered stand height in models of regeneration density and height on lines. Of these three variables, stand height was the most consistent and strongest predictor and moderately correlated to stand age ($r = 0.57$, $p < 0.001$) and stand basal area ($r = 0.59$, $p < 0.001$). I also considered a quadratic term for stand height as many stand dynamics, such as sunlight through gaps or seed availability, change non-linearly as the stand grows/ages.

Three seismic line characteristics were measured and considered in preliminary analyses: line orientation, line width, and age of line. For height of trees on seismic lines, I also considered tree density on lines as a predictor to account for density-dependence processes such as competition. Orientation and width have been shown to be occasionally significant and the magnitudes of their effects can be substantial (Filicetti and Nielsen 2018 [Chapter 2], 2020 [Chapter 5]; Filicetti et al. 2019 [Chapter 4]). Both are related to the quantity of sunlight received, but also other factors such as wind, and hence seed dispersal, and precipitation. Since data of when and how specific seismic lines were cut are not publicly available, I used the age of the oldest tree on the seismic line as a proxy for age of line disturbance (i.e., minimum line age and specifically age since initial tree recovery), from here on defined as ’age of line’. I acknowledge that seismic lines were created with different machinery (e.g., bulldozers to mulchers) and with different operator instructions (e.g., remove all vegetation to remove as little as possible) with mulchers used in more recent times (a minority in this study). However, there is no known database of disturbance history for the region and it is difficult to estimate in the field, especially for older lines. Finally, an interaction between age of line and presence of recent fire was considered to control for different trajectories of older or younger lines to wildfire.

7.2.4 Analysis of density and height

I modeled the most common tree species by ecosite (see section 7.2.1) by examining their prevalence across ecosites since ecosites are related to tree species dominance (see Table 7.A1 in Appendix A). Not only did ecosites have different composition of trees, but a species across ecosites can have different patterns in density and height. Rather than use two-way or three-way interactions of ecosite with other variables, I developed models for each species by ecosite for density, but not for height since here I was more interested in general structure of the line than composition since species specific differences in abundance are provided by density models. Only species with ≥10 observations in an ecosite were considered resulting in the elimination of a number of uncommon species in each ecosite and the elimination of several uncommon species altogether. Species of trees and tall shrubs that were eliminated include balsam fir (*Abies balsamea* (L.) Mill.; pin cherry (*Prunus pensylvanica* L. f.); redosier dogwood (*Cornus sericea* (*stolonifera*) L.); river alder (*Alnus incana* (L.) Moench); Saskatoon (*Amelanchier alnifolia* (Nutt.) Nutt. ex M. Roem.); and squashberry (*Viburnum edule* (Michx.) Raf.). That left 9 species across 9 ecosites for density models, but not all species occurred in all ecosites, with a total of 35 combinations modelled (see Table 7.A6 and 7.A7 in Appendix A) Negative binomial regression models for each species-ecosite were used for estimating density (*nbreg* command in STATA 15.1/SE; StataCorp. 2017), while height was estimated by generalized linear model (*glm* command in STATA 15.1/SE; StataCorp. 2017) with a gaussian distribution and a log link function since height was log-linear in shape. Although I would expect canopy height to plateau with time, and thus require more traditional growth models (Dale et al. 1985), I did not find the heights of trees attenuating with age given the recent nature of these disturbances. Because greater than one tree was potentially sampled in each seismic line plot for measures of height, standard errors, and thus significance, was adjusted for non-independence using the *cluster* option in STATA to correctly calculate variances given non-independence. Model selection was accomplished by using backward selection, retaining significance of $p < 0.10$, of the predictor variables. Model assumptions were examined for independence, normality of response variables and presence of outliers, and correlations ($r > |0.7|$) among independent variables. Variables were removed and/or modified (transformed) to meet model assumptions.

7.3 Results

7.3.1 Thresholds to regeneration density and height (growth) on seismic lines

Field data demonstrated that most sites (96%) already had over 1,000 stems/ha, and indeed 78% of sites had over 10,000 stems/ha of trees on seismic lines (Table 7.A3 in Appendix A). Additionally, 81% of sites had at least one of the few trees sampled over 1 m tall and 51% of sites had the mean tree height over 1 m tall (Table 7.A4 in Appendix A). When considering both density and height, 51% of all sites had a combined threshold of at least 1,000 stems/ha and a mean tree height ≥ 1 m. Ecosites that consistently fell below these thresholds were all hydric sites and to some degree nutrient poor sites (Table 7.1 and Figure 7.2; Table 7.A3, 7.A4, and 7.A5 in Appendix A). However, when considering the tallest tree sampled on seismic lines, the majority of seismic lines in all ecosites still reached heights greater than 1 m.

Table 7.2: Percent of sites that meet thresholds for regeneration density (1,000 and 10,000 stems/ha) and mean site regeneration height (1, 3, and 5 meters) with maximum site regeneration height in parantheses. All values based on field observaitons that vary in seismic line and forest fire age.

Ecosite	Common species	Mature stand height (m)	1,000 (stems/ha)			10,000 (stems/ha)		
			1 m	3 m	5 m	1 m	3 m	5 m
All sites	NA	15 (0.38)	51 (79)	13 (41)	5 (24)	44 (68)	11 (36)	5 (21)
Poor xeric	Jack pine	15 (0.48)	52 (70)	0 (9)	0 (1)	44 (53)	0 (5)	0 (0)
Poor mesic	Black spruce	12 (0.80)	24 (71)	0 (38)	0 (18)	24 (68)	0 (38)	0 (18)
Poor hydric	Black spruce	7 (0.55)	31 (72)	0 (28)	0 (7)	21 (55)	0 (24)	0 (7)
Medium xeric	Aspen & Jack pine	18 (1.63)	33 (95)	10 (57)	10 (19)	33 (81)	10 (57)	10 (19)
Medium mesic	Aspen & White spruce	20 (0.65)	92 (99)	35 (81)	14 (55)	79 (83)	30 (70)	12 (49)
Medium hygric	Balsam poplar & White spruce	21 (2.31)	83 (92)	42 (92)	17 (67)	67 (75)	33 (75)	17 (50)
Medium hydric	Black spruce & Tamarack	8 (0.40)	11 (64)	0 (16)	0 (3)	11 (64)	0 (16)	0 (3)
Rich hygric	Balsam fir & White spruce	21 (1.94)	86 (100)	36 (71)	14 (71)	86 (86)	36 (71)	14 (71)
Rich hydric	Black spruce & Tamarack	8 (0.79)	9 (57)	0 (0)	0 (0)	4 (52)	0 (0)	0 (0)

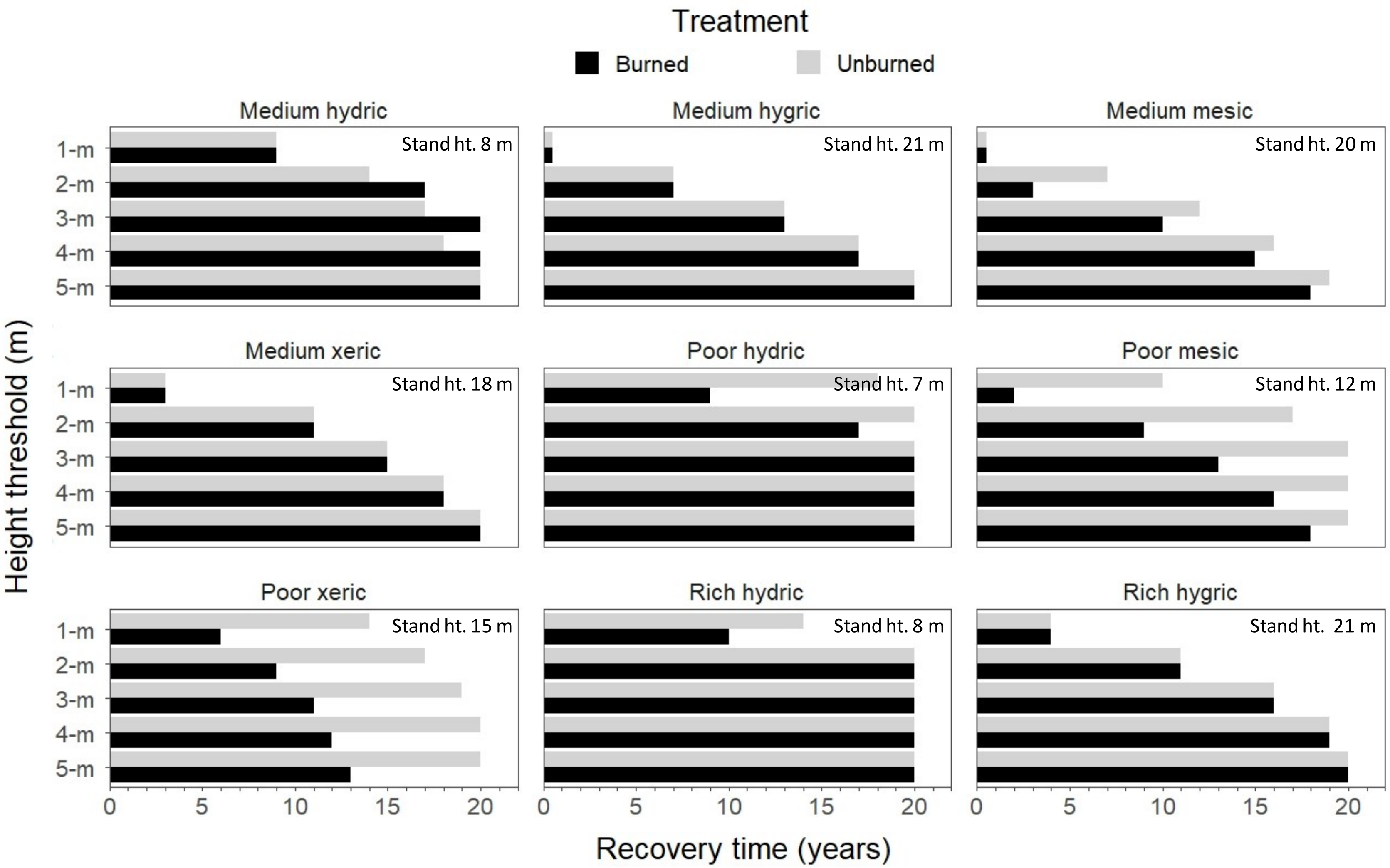


Figure 7.2: Predicted recovery time (years) for regenerating trees in each of the nine ecosites for different height thresholds (1, 2, 3, 4, and 5 meters) considering both burnt (presence of recent wildfire, black) and unburnt (absence of recent wildfire, gray) sites. Note that presence of wildfire in some ecosites was not significant and thus did not vary in predictions, but are still shown here.

7.3.2 Regeneration density on seismic lines

Regeneration density increased with age of line in poor hydric sites, was constant in poor xeric, poor mesic, medium xeric, and rich hydric sites (out to 20 years), and decreased with age of line in medium hygric, medium hydric, and rich hygric sites. In medium mesic sites, regeneration decreased for ~8 years before increasing again (Figure 7.3; Table 7.A6, Figure 7.A1, and Figure 7.A2 in Appendix A).

Wildfire increased regeneration density immediately post-fire compared to sites without fire and/or altered trajectories for five ecosites (i.e., poor xeric, poor mesic, poor hydric, medium xeric, and medium mesic), but not for the other four (i.e., medium hygric, medium hydric, rich hygric, and rich hydric). Post-fire regeneration density for the five affected ecosites were: poor xeric increased by 62-times with fire; poor hydric by 6.8-times with fire and changes in the trajectory (increasing to decreasing density), poor mesic by 2.5-times with fire, medium xeric by 2.0-times with fire, medium mesic by 6.0-times with fire and changes in the trajectory (to decreasing density) (Figure 7.3; Table 7.A6, Figure 7.A1, and Figure 7.A2 in Appendix A).

A few ecosites, especially medium hydric and rich hydric, had high stem counts, partly owing to the inclusion of willow (Figure 7.3). However, even when excluding willow, stem counts were still well above 1000 stems/ha (Table 7.A1 in Appendix A).

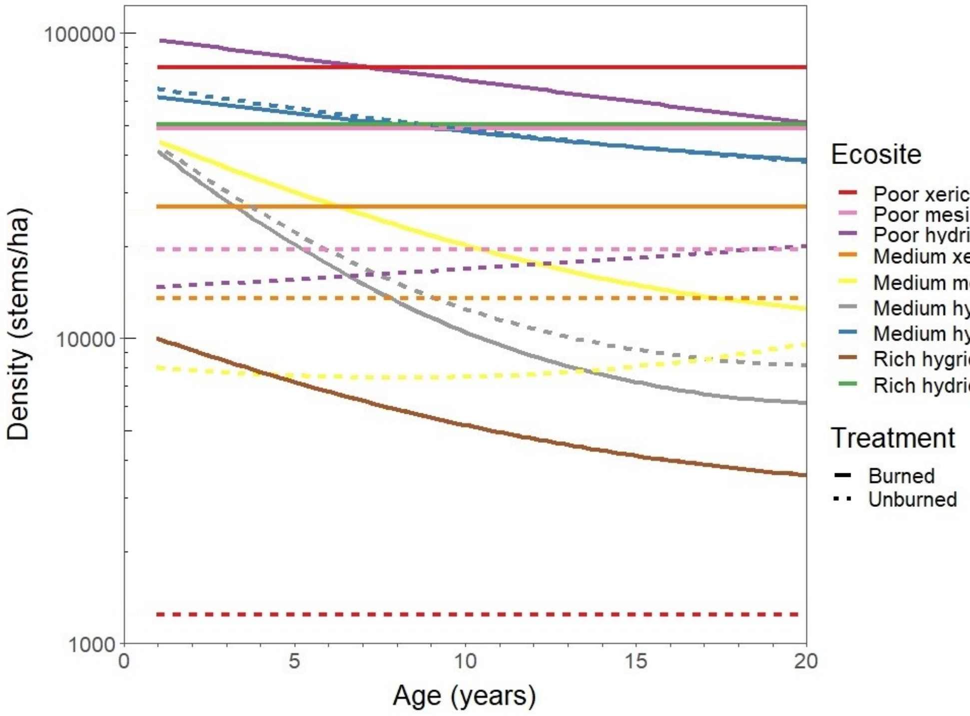


Figure 7.3: Predicted values in regeneration density by ecosite (sum of all species) with age of line (years) for nine ecosites across unburnt (a) and burnt (b) stands. Note that the y-axis is $\log_{10}$ scale to allow ease of viewing species with large differences in density. Guidelines for seismic line recovery in Alberta suggest a minimum tree density of 1000 stems/ha for productive uplands (Government of Alberta 2017) which are the graph origin (all ecosites were above this threshold without active restoration practices).

7.3.3 Height (growth) of regenerating trees on seismic lines

Poor xeric and medium hydric sites had slow early growth followed by rapid late growth, with poor xeric sites being more extreme. Poor mesic, medium xeric, medium mesic, medium hygric, and rich hygric sites had more gradual growth rates with the biggest differences being in their average heights. Poor hydric and rich hydric had the flattest growth rates with poor hydric being the flattest (Figure 7.4; Table A7 and Figure 7.A3 in Appendix A).

Wildfire changed the growth height patterns for 6 ecosites (poor xeric, poor mesic, poor hydric, medium mesic, medium hydric, and rich hydric). Wildfire increased growth height patterns for 5 of these ecosite (poor xeric, poor mesic, poor hydric, medium mesic, and rich hydric), where the first 20 years of the trees life had higher growth height patterns than trees in unburnt sites. The differential of growth height patterns between the unburnt and the burnt only got larger as the trees aged for all of these ecosite except medium mesic, where the unburnt and burnt become similar at about 20 years of age. Medium hydric is the only ecosite to experience larger growth height patterns in the first 9 years followed by a slower growth height patterns after the first 9 years.

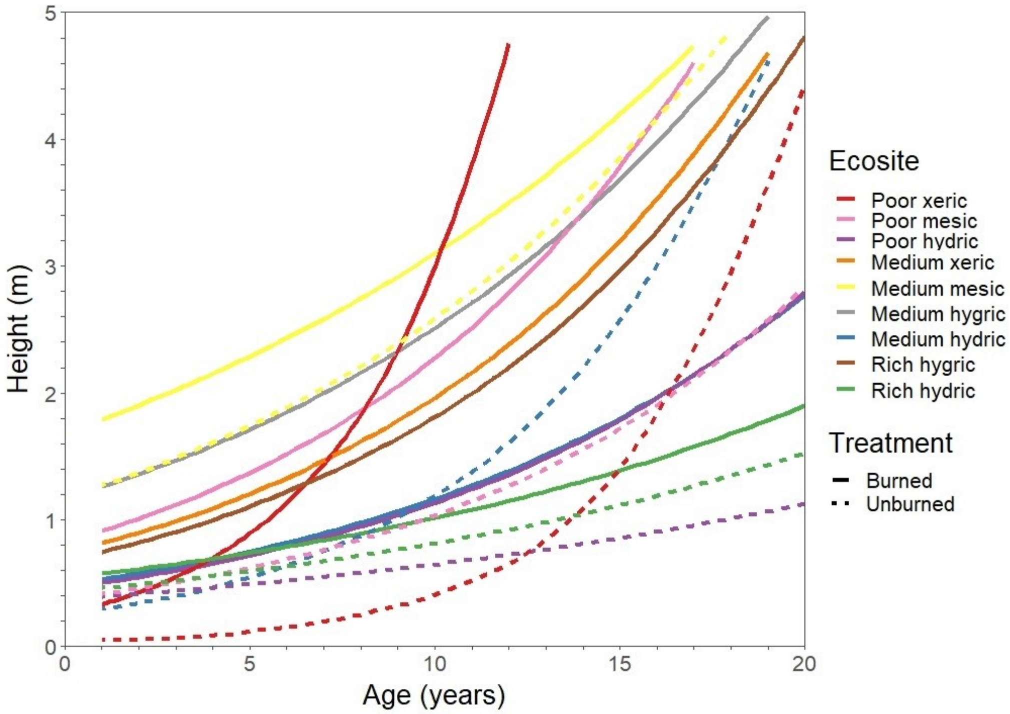


Figure 7.4: Predicted values in regeneration height by ecosite with tree age (years) for nine ecosites across unburnt (a) and burnt (b) conditions. Guidelines for seismic line recovery in Alberta suggest advanced regneration to be a tree height of 5 meters (Government of Alberta 2017) which most ecosites reach within 20 years without active restoration practices.

7.4 Discussion

7.4.1 Thresholds to regeneration density and height (growth) on seismic lines

The Alberta guidelines for seismic line deactivation is 1000 stems/ha for upland and 800 stems/ha for xeric or lowland sites (Government of Alberta 2017). These thresholds are well below the densities observed in all the ecosites assessed in this study, either in burned or unburned plots, questioning the value of current active restoration efforts applied at substantial expense (Filicetti et al. 2019 [Chapter 4]). My results suggest that, if the restoration target is a minimum density of tree stems, there seems little reason to invest in restoration efforts. When planning active restoration to 'erase' seismic lines, slow animal movement and eliminate animal trails, it may be prudent to: (i) discover what stem density thresholds are required; much higher density trees may be more beneficial in the short-term especially with high tree mortality rates;

and (ii) have more specific guidelines for individual ecosites. However, vertical structure of regeneration is also important and was often not meeting those guidelines.

Thus far, most research has focused on vertical tree structure (height) over that of density, likely owing to the ease of measuring heights remotely. My results suggest that there is more merit on focusing on regeneration height since regeneration density is suitable based on government standards. However whether these density standards result in recovery for wildlife remains unclear. Recommendations for regeneration height to be 'recovered' range from 0.5 – 5.0 m (van Rensen et al. 2015; Dickie et al. 2017a; Government of Alberta 2017) and depend on functional or ecological restoration targets. Most ecosites have the potential to reach a 5 m height within 20 years with the exception being lowland ecosites (Figure 7.2 and 7.4), but it is worth noting that lowland ecosites naturally have lower tree heights in mature stands (as low as 3 m), with regeneration growth rates often below 10 cm per year (Table 7.A2 in Appendix A). Therefore, there is a marked difference of maximum and average tree heights within and across ecosites (Table 7.1). This suggests that in most cases trees on seismic lines have potential to grow much taller, but there may be limited microsites, increasing competition, or too much shading from adjacent canopies as the seismic line gap is small (3–12 m). Mortality of regenerating stems may also be high, particularly in lowlands, resulting in high densities but limited heights.

7.4.2 Regeneration density on seismic lines

Several processes affect tree density patterns in disturbed boreal forests, particularly (i) seed abscission, seed dispersal, and seed bed conditions, (ii) competition and stand thinning, and (iii) water table depth and hydrological connectivity (Bonan and Shugart 1989; Lieffers et al. 1996; Greene et al. 1999). In this study of seismic line regeneration, different processes in different ecosites appear to influence observed patterns in regeneration. Poor xeric forests dominated by jack pine have low seed abscission and low recruitment in unburnt conditions; here, wildfires release the jack pine seed bank from the serotinous cones, consequently, regeneration almost exclusively occurs post-fire (de Groot et al. 2004). Since many poor xeric sites in this study burned in 2011, competition and stand thinning should not have played a role in the density of this stand (Figure 7.3), because these processes occur typically in later seral stages (Chen and Popadiouk 2002; Filicetti and Nielsen 2018 [Chapter 2]).

Mixed upland forests (medium xeric, medium mesic, medium hygric, rich hygric) are dominated by competition and stand thinning, which is more pronounced in the wetter spectrum of these ecosites, possibly owing to taller adjacent stands and/or fewer and less severe wildfires experienced in these ecosites (Larsen 1997). Mixed upland forests tend to regenerate well post-fire, with regeneration density positively correlated with dry conditions, but here wildfire is not required to initiate regeneration (Figure 7.3).

Lowland forests (poor mesic, poor hydric, medium hydric, and rich hydric) are dominated more by complex interactive effects between water table depth, hydrological connectivity, and the organic layer. Here, the creation of the seismic line often leads to a simplified and depressed surface that reduces depth to water (Stevenson et al. 2019 [Chapter 3]), which limits available microsites and tree regeneration (Filicetti et al. 2019 [Chapter 4]; Filicetti and Nielsen 2020 [Chapter 5]). Additionally, by removing fuel (trees) and reducing depth to water, seismic lines experience lower fire severities and/or promote fire skips at the ground surface level (Riva et al. 2018b, 2020; Filicetti and Nielsen 2020 [Chapter 5]). Therefore, in lowland forests, fires often do not destroy existing trees on the line, nor the organic layer, leaving inferior seedbed conditions. Among the lowland sites, poor mesic sites have the greatest depth to the water table and recovery from seismic line creation here mostly depends on the depth of the organic layer (seed bed), and to some extent competition and shading from the adjacent canopy, which is removed post-fire (Filicetti et al. 2019 [Chapter 4]; Filicetti and Nielsen 2020 [Chapter 5]) (Figure 7.3).

Poor hydric sites are hydrologically isolated, relying on precipitation to accumulate water (Vitt 2008), thus having a water table that is more sensitive to inter-annual fluctuations in precipitation and generally drier than fens (medium hydric and rich hydric) (Lukenbach et al. 2017; Nelson et al. 2021). Interestingly, poor hydric sites were the only sites displaying a consistent increase in regeneration density for the first 20 years post-line creation (Figure 7.3). It is possible that poor hydric sites fare better in recovery compared to poor mesic owing to less competition and shading from the adjacent canopy.

An interesting pattern emerging from this study is that increases observed in immediate post-fire regeneration for poor hydric sites are followed by consistent declines in density, the opposite of what occurs in unburnt conditions (Figure 7.3). This may be related to: (a) stand thinning with time due to competition for sunlight and underground resources, although it seems to occur too suddenly; and/or (b) post-fire conditions result in mass evaporation of the hydrologically isolated water table resulting in short-termed exposed microsites, which begin to become inundated as the site slowly accumulates water from precipitation (Lukenbach et al. 2017; Nelson et al. 2021).

Finally, medium hydric and rich hydric are the most hydrologically connected ecosites. Projections indicate that medium hydric sites lose tree density post-line creation but this pattern decreases in magnitude with time. It may take well over 20 years for medium hydric sites to recover from line creation, likely while accumulating organic matter and increasing distance to the water table. Rich hydric sites showed no evidence of recovery and may require more years than medium hydric to return to natural hydrological dynamics. The reduced depth to water also leads to a shift from typical boreal 'trees', such as black spruce and tamarack, to that of dwarf birch (*Betula pumila* L.) and large 'shrubs' of willow. In fact, the dominant tree observed on lines in rich hydric sites was willow, accounting for 87% of all stems. Wildfires do not alter the recovery patterns of tree density in these sites (Figure 7.3). This may be owing to the simplified and depressed lines being too close to the water table, having minimal microsite available which a wildfire cannot alleviate, as it does in poor hydric sites, as the water table quickly returns to similar levels pre-fire due to the highly hydrologically connected nature of these sites (Lukenbach et al. 2017; Nelson et al. 2021).

7.4.3 Height (growth) of regenerating trees on seismic lines

Growth patterns seem to be determined by typical life history traits related to stress, such as shade tolerance, nutrient regime, and moisture regime (Bonan and Shugart 1989; Lieffers et al. 1996; Greene et al. 1999; Hart and Chen 2006b). Poor xeric sites are dominated by jack pine, a shade-intolerant species that showed slow growth rates and high mortality rates in understory conditions (Yarranton and Yarranton 1974; Cayford and McRae 1983). Post-fire, after the overstory canopy is reduced, growth rates become exceptionally high (Filicetti and Nielsen 2018 [Chapter 2]).

Mixed upland forests (medium xeric, medium mesic, medium hygric, rich hygric) generally showed high regeneration heights, reaching a 5-m height within 20 years, with the exception of rich hygric sites that reached, on average, 4.8 m in 20 years (Figure 7.4). Wildfire had surprisingly little affect on growth rates for these ecosites, the one exception being medium mesic sites that observed a spurt of growth for the first 5 years post-fire, which became negligible by 18 years. Based on these results, I speculate that competition and overstory shading are the main limiting factors in these ecosites.

Lowland forests (poor mesic, poor hydric, medium hydric, and rich hydric) demonstrated the slowest and most complex growth rates. Most lowlands did not reach a 5-m height threshold within 20 years. Yet, wildfire was beneficial to growth rates in these forests and the magnitude of this benefit seems positively related to the distance to the water table. Moreover, many of these lowland forests are quite short in mature tree heights making a 5 m recovery threshold much closer to adjacent forest heights. Medium hydric sites seem to be an exception to this pattern, with an early spurt for 2-3 years post-fire followed by much slower growth, and the height in unburnt sites overtaking that of burnt sites in ~ 9 years (Figure 7.4). I speculate that this pattern may be related to hydrological connectivity; where medium hydric sites may experience a reduced water table post-fire, while the return to pre-fire levels may only take a few years.

7.4.4 Implications

Understanding when and how seismic lines should be restored will be a necessary step to optimizing the protection of the natural heritage of Canadian boreal forests (Dabros et al. 2018; Riva et al. 2020) and of forests in other parts of the world (Rosa et al. 2017). My results demonstrate that density and height of regenerating trees vary heterogeneously across the different ecosites typical of the Alberta boreal biome and that general guidelines referring to the Alberta boreal forest as a homogeneous system are not appropriate to assess regeneration success within these anthropogenic footprints. Additionally, natural regeneration density in all ecosites was higher than the Alberta recommended guidelines for restoration, suggesting that the guideline thresholds are either too low or only applicable to sites damaged from line creation and/or areas that have naturally very low tree densities. Natural regeneration height was highly variable, with clear ecosite differences that suggest the importance of identifying height targets by ecosite. Many lowland ecosites naturally have mature stands of low tree heights with growth rates below 10 cm per year (Table 7.A2 in Appendix A). Our study confirms that natural regeneration, density and height growth, is often higher in burnt sites (Figure 7.2, 7.3, and 7.4), suggesting that burnt sites and/or sites likely to burn in the near future should be given a lower restoration priority. Finally, when considering restoration of caribou habitat associated with peatlands, priority should be given to the wettest sites that are unlikely to experience wildfires and are less likely to return to forest conditions in a short-term period, although I note that these sites can also contain less dense and less tall forests suggesting that individual restoration guidelines are needed here. This would limit restoration to key places where it would be most effective at hastening recovery knowing that many sites will recover on their own given enough time.

Appendix

Table 7.A1: Density (stems per ha) of common tree species found on seismic lines in northeast Alberta, Canada.

Ecosite	Species	Min.	Median	Max.	Mean (S.E.)	Count
Poor xeric						
	Alaskan birch	0	0	24,333	371 (313)	79
	Aspen	0	0	12,333	827 (262)	79
	Balsam poplar	0	0	3,000	80 (43)	79
	Black spruce	0	0	15,000	194 (190)	79
	Green alder	0	0	11,333	700 (222)	79
	Jack pine	0	15,667	535,333	55,443 (10,754)	79
	Tamarack	0	0	0	0 (0)	79
	White spruce	0	0	333	4 (4)	79
	Willow	0	0	8,333	329 (127)	79
Poor mesic						
	Alaskan birch	0	333	19,333	1,716 (746)	34
	Aspen	0	0	5667	804 (277)	34
	Balsam poplar	0	0	3000	225 (111)	34
	Black spruce	0	8,334	95,667	16,765 (3,778)	34
	Green alder	0	0	28,333	833 (833)	34
	Jack pine	0	0	86,667	4,382 (2,622)	34
	Tamarack	0	0	9,000	637 (343)	34
	White spruce	0	0	7,000	206 (206)	34
	Willow	0	4,667	84,333	10,814 (2,913)	34
Poor hydric						
	Alaskan birch	0	0	3,000	241 (118)	29
	Aspen	0	0	4,667	310 (208)	29
	Balsam poplar	0	0	333	11 (11)	29
	Black spruce	667	12,000	155,667	35,770 (7,664)	29
	Green alder	0	0	0	0 (0)	29
	Jack pine	0	0	12,000	1,322 (583)	29
	Tamarack	0	0	667	69 (38)	29
	White spruce	0	0	0	0 (0)	29
	Willow	0	0	52,667	6,874 (3,006)	29

Table 7.A1 *Cont.*

Ecosite	Species	Min.	Median	Max.	Mean (S.E.)	Count
Medium xeric						
	Alaskan birch	0	0	31,667	2,333 (1,507)	21
	Aspen	0	3,667	26,667	5,619 (1,366)	21
	Balsam poplar	0	0	333	48 (26)	21
	Black spruce	0	0	7,667	365 (365)	21
	Green alder	0	0	1,333	238 (1,06)	21
	Jack pine	0	5,667	50,667	85,71 (2,951)	21
	Tamarack	0	0	333	16 (16)	21
	White spruce	0	667	12,667	3,048 (870)	21
	Willow	0	0	5,667	1,079 (379)	21
Medium mesic						
	Alaskan birch	0	0	17,000	1,176 (285)	102
	Aspen	0	2,500	38,000	5,052 (778)	102
	Balsam poplar	0	0	5,000	363 (87)	102
	Black spruce	0	0	1,667	26 (18)	102
	Green alder	0	0	28,000	2,879 (540)	102
	Jack pine	0	0	3,667	137 (50)	102
	Tamarack	0	0	333	3 (3)	102
	White spruce	0	0	44,667	1,559 (478)	102
	Willow	0	1,000	29,333	2,556 (396)	102
Medium hygric						
	Alaskan birch	0	667	16,000	21,39 (1,279)	12
	Aspen	0	0	31,667	5,944 (3,498)	12
	Balsam poplar	0	1,000	6,000	1,500 (528)	12
	Black spruce	0	0	0	0 (0)	12
	Green alder	0	0	11,333	1,167 (950)	12
	Jack pine	0	0	333	28 (28)	12
	Tamarack	0	0	0	0 (0)	12
	White spruce	0	333	5,667	1,056 (487)	12
	Willow	0	1,500	12,667	3,417 (1,179)	12
Medium hydric						
	Alaskan birch	0	0	21,333	1,011 (411)	61
	Aspen	0	0	15,667	645 (303)	61
	Balsam poplar	0	0	2,667	153 (63)	61
	Black spruce	0	6,000	39,333	8,399 (1,147)	61
	Green alder	0	0	0	0 (0)	61
	Jack pine	0	0	2,333	76 (45)	61
	Tamarack	0	1,000	47,333	4,295 (1,001)	61
	White spruce	0	0	0	0 (0)	61
	Willow	0	27,333	138,000	32,191 (3,717)	61

Table 7.A1 *Cont.*

Ecosite	Species	Min.	Median	Max.	Mean (S.E.)	Count
Rich hygric						
	Alaskan birch	0	667	17,000	3,357 (1,341)	14
	Aspen	0	333	3,667	1,143 (374)	14
	Balsam poplar	0	0	3,667	310 (260)	14
	Black spruce	0	0	667	48 (48)	14
	Green alder	0	167	17,333	2,452 (1,388)	14
	Jack pine	0	0	0	0 (0)	14
	Tamarack	0	0	0	0 (0)	14
	White spruce	0	667	7,000	1,595 (627)	14
	Willow	0	1,000	10,333	2,405 (844)	14
Rich hydric						
	Alaskan birch	0	0	3,000	217 (132)	23
	Aspen	0	0	1,000	72 (47)	23
	Balsam poplar	0	0	333	14 (14)	23
	Black spruce	0	333	7,000	1,580 (492)	23
	Green alder	0	0	1,000	43 (43)	23
	Jack pine	0	0	1,667	72 (72)	23
	Tamarack	0	667	14,000	3,159 (903)	23
	White spruce	0	0	0	0 (0)	23
	Willow	1,333	31,000	95,667	35,536 (4,947)	23

Table 7.A2: Descriptive statistics by species of height (cm), age (yr.), and growth rate (cm/yr.).

Ecosite	Species		Min.	Median	Max.	Mean (S.E.)	Count
Poor xeric							
	Jack pine						
		Height	7	122	730	129 (4.39)	339
		Age	1	6	24	6 (0.11)	339
		Growth	3	19	46	20 (0.48)	339
Poor mesic							
	Alaskan birch						
		Height	2	154	870	235 (44.76)	27
		Age	3	7	25	9 (1.06)	27
		Growth	0	21	49	24 (2.78)	27
	Aspen						
		Height	30	154	790	223 (63.12)	12
		Age	2	8	24	9 (1.79)	12
		Growth	6	22	44	24 (3.52)	12
	Black spruce						
		Height	2	51	670	108 (22.56)	42
		Age	1	6	33	9 (1.05)	42
		Growth	0	8	30	11 (1.21)	42
	Jack pine						
		Height	4	161	750	251 (52.12)	19
		Age	2	7	27	10 (1.46)	19
		Growth	0	23	66	26 (3.4)	19
	Willow						
		Height	1	84	290	105 (11.45)	40
		Age	1	6	24	7 (0.74)	40
		Growth	0	16	37	17 (1.46)	40
Poor hydric							
	Alaskan birch						
		Height	38	156	359	188 (41.2)	8
		Age	6	13	21	13 (1.87)	8
		Growth	6	13	31	14 (2.88)	8
	Black spruce						
		Height	3	57	710	106 (17.44)	54
		Age	3	10	47	11 (1.24)	54
		Growth	0	7	29	9 (0.82)	54
	Jack pine						
		Height	1	198	560	200 (29.53)	25
		Age	2	9	27	10 (1.01)	25
		Growth	0	15	50	19 (2.34)	25
	Willow						
		Height	8	59	280	100 (26.38)	12
		Age	4	6	12	7 (0.8)	12
		Growth	1	14	33	15 (2.99)	12

Table 7.A2 *Cont.*

Ecosite	Species		Min.	Median	Max.	Mean (S.E.)	Count
Medium xeric							
	Alaskan birch						
		Height	40	275	1,036	392 (123.56)	8
		Age	3	9	25	12 (3.21)	8
		Growth	10	33	41	30 (3.55)	8
	Aspen						
		Height	40	191	1,214	301 (43.24)	36
		Age	2	8	48	10 (1.44)	36
		Growth	8	31	55	32 (2.08)	36
	Jack pine						
		Height	28	119	813	171 (33.5)	30
		Age	2	5	19	7 (0.81)	30
		Growth	4	20	49	23 (2.12)	30
	White spruce						
		Height	1	39	296	61 (14.32)	22
		Age	2	7	13	7 (0.64)	22
		Growth	0	7	25	9 (1.15)	22
Medium mesic							
	Alaskan birch						
		Height	93	400	1,370	489 (34.25)	81
		Age	4	14	34	15 (0.73)	81
		Growth	9	30	69	33 (1.34)	81
	Aspen						
		Height	68	310	1,800	466 (28.55)	174
		Age	2	10	31	12 (0.56)	174
		Growth	9	38	71	39 (0.97)	174
	Balsam poplar						
		Height	97	311	1,080	418 (44.69)	44
		Age	3	9	28	11 (1.13)	44
		Growth	19	37	63	37 (1.56)	44
	Green alder						
		Height	131	314	610	325 (13.19)	76
		Age	4	11	27	12 (0.54)	76
		Growth	15	28	54	30 (1.01)	76
	Jack pine						
		Height	83	360	1,200	524 (93.64)	18
		Age	4	13	23	12 (1.61)	18
		Growth	14	39	56	37 (3.06)	18
	White spruce						
		Height	22	145	1,001	207 (23.59)	72
		Age	4	12	32	13 (0.76)	72
		Growth	4	12	44	14 (0.96)	72

Table 7.A2 *Cont.*

Ecosite	Species		Min.	Median	Max.	Mean (S.E.)	Count
	Willow						
		Height	92	258	954	321 (25.33)	60
		Age	3	12	30	12 (0.87)	60
		Growth	10	27	51	28 (1.33)	60
Medium hygric							
	Alaskan birch						
		Height	118	358	740	366 (50.81)	14
		Age	5	13	25	13 (1.53)	14
		Growth	12	30	42	30 (2.24)	14
	Aspen						
		Height	163	353	1,340	577 (140.62)	10
		Age	4	7	32	14 (3.52)	10
		Growth	32	43	65	44 (3.06)	10
	Balsam poplar						
		Height	121	610	1,300	618 (89.69)	16
		Age	3	16	28	16 (1.9)	16
		Growth	20	40	66	40 (2.86)	16
	Willow						
		Height	182	315	710	385 (58.91)	10
		Age	5	15	26	15 (2.2)	10
		Growth	20	27	36	26 (1.49)	10
Medium hydric							
	Alaskan birch						
		Height	15	96	356	130 (18.79)	28
		Age	1	8	14	7 (0.71)	28
		Growth	7	14	76	19 (2.6)	28
	Aspen						
		Height	9	40	360	82 (24.18)	18
		Age	1	4	12	4 (0.79)	18
		Growth	5	15	45	18 (2.41)	18
	Balsam poplar						
		Height	20	58	204	83 (20.94)	10
		Age	2	6	12	6 (1.01)	10
		Growth	7	12	20	13 (1.45)	10
	Black spruce						
		Height	9	44	500	73 (9.38)	75
		Age	1	9	46	9 (0.81)	75
		Growth	2	6	18	7 (0.48)	75
	Tamarack						
		Height	8	72	640	107 (14.16)	63
		Age	1	7	23	8 (0.54)	63
		Growth	3	11	38	13 (1.05)	63

Table 7.A2 *Cont.*

Ecosite	Species		Min.	Median	Max.	Mean (S.E.)	Count
	Willow						
		Height	19	73	290	88 (6.42)	92
		Age	1	5	25	5 (0.36)	92
		Growth	5	16	59	19 (0.95)	92
Rich hygric							
	Alaskan birch						
		Height	62	338	990	466 (80.94)	16
		Age	3	17	26	15 (1.75)	16
		Growth	15	24	47	28 (2.63)	16
	Aspen						
		Height	53	255	1,160	388 (88.32)	16
		Age	2	7	26	10 (1.92)	16
		Growth	18	33	73	35 (3.48)	16
	Green alder						
		Height	104	211	480	252 (43.68)	8
		Age	5	10	14	10 (0.99)	8
		Growth	10	28	34	26 (3.02)	8
	White spruce						
		Height	69	248	893	282 (65.33)	12
		Age	11	17	27	17 (1.53)	12
		Growth	4	14	33	16 (2.65)	12
	Willow						
		Height	178	323	563	341 (50.07)	8
		Age	9	18	31	17 (2.63)	8
		Growth	15	18	32	21 (1.99)	8
Rich hydric							
	Alaskan birch						
		Height	26	80	144	84 (16.62)	8
		Age	2	4	12	5 (1.19)	8
		Growth	9	15	42	19 (4.17)	8
	Black spruce						
		Height	9	38	240	55 (14.23)	17
		Age	1	6	20	8 (1.4)	17
		Growth	2	7	13	7 (0.72)	17
	Tamarack						
		Height	10	50	136	68 (11.66)	15
		Age	3	6	19	8 (1.15)	15
		Growth	3	7	21	9 (1.32)	15
	Willow						
		Height	18	104	267	104 (11.85)	30
		Age	1	6	20	6 (0.89)	30
		Growth	5	17	73	23 (2.89)	30

Table 7.A3: Percent of sites that meet thresholds for regeneration density (1,000–100,000 stems/ha).

Ecosite	Common species	Mature stand height (m)	Regeneration density thresholds (stems/ha) 1,000	10,000	25,000	50,000	100,000
All sites	NA	15 (0.38)	96	78	48	22	7
Poor xeric	Jack pine	8 (0.40)	87	65	44	28	20
Poor mesic	Black spruce	21 (2.31)	94	74	56	32	9
Poor hydric	Black spruce	20 (0.65)	100	66	52	38	14
Medium xeric	Aspen & Jack pine	18 (1.63)	100	81	43	14	0
Medium mesic	Aspen & White spruce	7 (0.55)	99	83	27	2	0
Medium hygric	Balsam poplar & White spruce	12 (0.80)	92	75	50	8	0
Medium hydric	Black spruce & Tamarack	15 (0.48)	98	92	79	39	5
Rich hygric	Balsam fir & White spruce	8 (0.79)	100	86	21	0	0
Rich hydric	Black spruce & Tamarack	21 (1.94)	100	87	74	30	0

Table 7.A4: Percent of sites that meet thresholds for average regeneration height (1–5 meters).

Ecosite	Common species	Mature stand height (m)	Average regeneration height thresholds (m) 1	2	3	4	5
All sites	NA	15 (0.38)	51	23	13	8	6
Poor xeric	Jack pine	8 (0.40)	52	5	0	0	0
Poor mesic	Black spruce	21 (2.31)	24	6	0	0	0
Poor hydric	Black spruce	20 (0.65)	31	0	0	0	0
Medium xeric	Aspen & Jack pine	18 (1.63)	33	19	10	10	10
Medium mesic	Aspen & White spruce	7 (0.55)	93	58	36	21	15
Medium hygric	Balsam poplar & White spruce	12 (0.80)	92	58	42	25	17
Medium hydric	Black spruce & Tamarack	15 (0.48)	11	0	0	0	0
Rich hygric	Balsam fir & White spruce	8 (0.79)	86	71	36	21	14
Rich hydric	Black spruce & Tamarack	21 (1.94)	9	0	0	0	0

Table 7.A5: Percent of sites that meet thresholds for maximum regeneration height (1–5 meters).

Ecosite	Common species	Mature stand height (m)	Maximum regeneration height thresholds (m)				
			1	2	3	4	5
All sites	NA	15 (0.38)	81	61	41	30	24
Poor xeric	Jack pine	8 (0.40)	71	46	9	1	1
Poor mesic	Black spruce	21 (2.31)	71	53	38	21	18
Poor hydric	Black spruce	20 (0.65)	72	45	28	17	7
Medium xeric	Aspen & Jack pine	18 (1.63)	95	76	57	38	19
Medium mesic	Aspen & White spruce	7 (0.55)	100	97	82	72	56
Medium hygric	Balsam poplar & White spruce	12 (0.80)	100	100	92	67	67
Medium hydric	Black spruce & Tamarack	15 (0.48)	66	33	16	3	3
Rich hygric	Balsam fir & White spruce	8 (0.79)	100	79	71	71	71
Rich hydric	Black spruce & Tamarack	21 (1.94)	57	9	0	0	0

Table 7.A6: Final models for tree density (stems per 30 m^2) in nine common ecosites and nine common tree species in north eastern Alberta by using the oldest tree found on the seismic line (Age), presence of fire (Fire), stand height (Height), the quadratic of stand height (Height^2), and the interaction of Age × Fire (A × F).

Ecosite	Species	Intercept	Age	Fire	Height	Height^2	A × F
Poor xeric							
	Jack pine	-3.74 (1.28)		4.13 (0.50)	0.60 (0.16)	-0.02 (0.01)	
Poor mesic							
	Alaskan birch	1.64 (0.38)					
	Aspen	-0.33 (0.54)		1.79 (0.74)			
	Black spruce	3.01 (0.31)		1.42 (0.46)			
	Jack pine	-0.01 (0.51)		6.45 (1.10)	-0.37 (0.10)		
	Willow	3.48 (0.29)					
Poor hydric							
	Black spruce	2.95 (0.61)	0.03 (0.04)	2.66 (0.73)			-0.07 (0.04)
	Jack pine	1.38 (0.54)					
	Willow	3.03 (0.85)					
Medium xeric							
	Aspen	4.06 (0.51)			-0.08 (0.03)		
	Jack pine	-1.73 (1.49)		1.14 (0.61)	0.53 (0.15)	-0.02 (0.01)	
	White spruce	-0.08 (1.14)			0.12 (0.06)		
Medium mesic							
	Alaskan birch	-0.63 (1.03)	0.12 (0.06)	1.83 (1.19)			-0.14 (0.06)
	Aspen	1.23 (0.48)	-0.04 (0.02)	2.14 (0.45)	0.07 (0.02)		-0.09 (0.03)
	Balsam poplar	1.18 (0.60)	-0.07 (0.03)				
	Green alder	1.54 (0.84)	0.09 (0.03)		-0.06 (0.03)		
	Jack pine	-12.78 (4.31)		3.54 (1.17)	1.15 (0.49)	-0.03 (0.01)	
	White spruce	1.54 (0.23)					
	Willow	0.07 (0.51)	0.06 (0.03)	2.89 (0.66)			-0.08 (0.03)

Table 7.A3 *Cont.*

Ecosite	Species	Intercept	Age	Fire	Height	Height^2	A_×_F
Medium hygric							
	Alaskan birch	-0.70 (0.81)			0.10 (0.03)		
	Aspen	4.89 (1.07)	-0.22 (0.07)				
	Balsam poplar	2.14 (0.49)		-1.22 (0.63)			
	Willow	2.33 (0.42)					
Medium hydric							
	Alaskan birch	3.05 (0.95)	-0.11 (0.07)	-1.47 (0.76)			
	Aspen	-1.42 (0.64)		2.67 (0.81)			
	Balsam poplar	-0.78 (0.57)					
	Black spruce	3.23 (0.16)					
	Tamarack	-0.20 (1.02)	0.06 (0.04)		0.21 (0.09)		
	Willow	5.03 (0.28)	-0.04 (0.02)				
Rich hygric							
	Alaskan birch	-1.51 (1.61)			0.16 (0.07)		
	Aspen	3.18 (0.56)	-0.13 (0.03)				
	White spruce	-3.15 (1.27)			0.19 (0.05)		
Rich hydric							
	Black spruce	-3.45 (1.83)			0.85 (0.32)	-0.03 (0.01)	
	Tamarack	2.25 (0.41)					
	Willow	3.34 (0.53)			0.29 (0.10)	-0.02 (0.01)	

Table 7.A7: Final models for tree height (m) in nine common ecosites on seismic lines in north eastern Alberta by using the tree age (Age), tree regeneration density (Regen), the quadratic of tree regeneration density (Regen^2), presence of fire (Fire), stand height (Height), the quadratic of stand height (Height^2), the interaction of Age × Fire (A × F), and the interaction of Width × Height (W × H).

Ecosite	Intercept	Age	Regen	Regen^2	Fire	Width	Height	Height^2	A_x_F	W_x_H
Poor xeric	-4.15 (0.92)	0.24 (0.03)	1.15 (0.34)	-0.25 (0.08)	1.97 (0.77)	0.07 (0.03)	-0.10 (0.04)	0.003 (0.001)		
Poor mesic	-0.64 (0.30)	0.10 (0.01)			0.79 (0.11)	-0.18 (0.06)	0.06 (0.02)			
Poor hydric	-4.11 (1.38)	0.06 (0.02)	0.59 (0.16)		0.21 (0.21)	0.25 (0.11)	0.35 (0.12)		0.04 (0.02)	-0.045 (0.014)
Medium xeric	-0.57 (0.11)	0.10 (0.01)				0.08 (0.01)	-0.01 (0.01)			
Medium mesic	1.19 (0.31)	0.08 (0.01)	-0.34 (0.17)		0.36 (0.11)		-0.02 (0.01)		-0.02 (0.01)	
Medium hygric	-3.22 (0.98)	0.08 (0.01)	0.75 (0.27)			0.24 (0.06)	0.071 (0.02)	-0.001 (>0.001)		-0.005 (0.002)
Medium hydric	-1.73 (0.18)	0.15 (0.02)			0.63 (0.19)	0.07 (0.01)			-0.07 (0.02)	
Rich hygric	1.02 (0.68)	0.10 (0.02)	2.39 (0.94)			-0.62 (0.26)	-0.25 (0.09)			0.029 (0.01)
Rich hydric	-1.05 (0.13)	0.06 (0.01)			0.22 (0.11)		0.02 (0.01)			

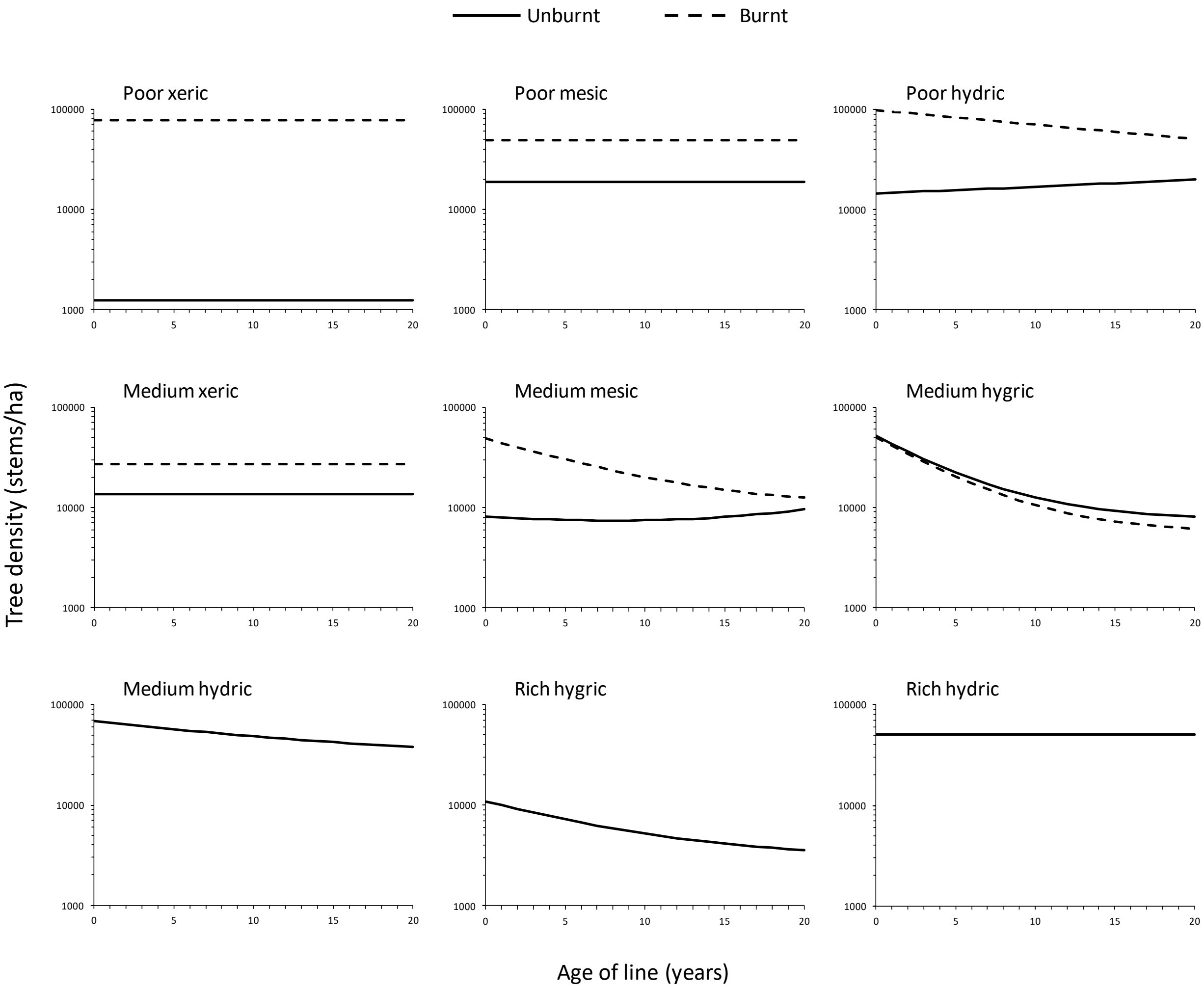


Figure 7.A1: Predicted values between regeneration density and age of seismic line in nine ecosites for unburnt (presence of recent wildfire, solid line) and burnt (absence of recent wildfire, dotted line) conditions. Figures that have no burnt (dotted) lines is owing to recent wildfires having no effect.

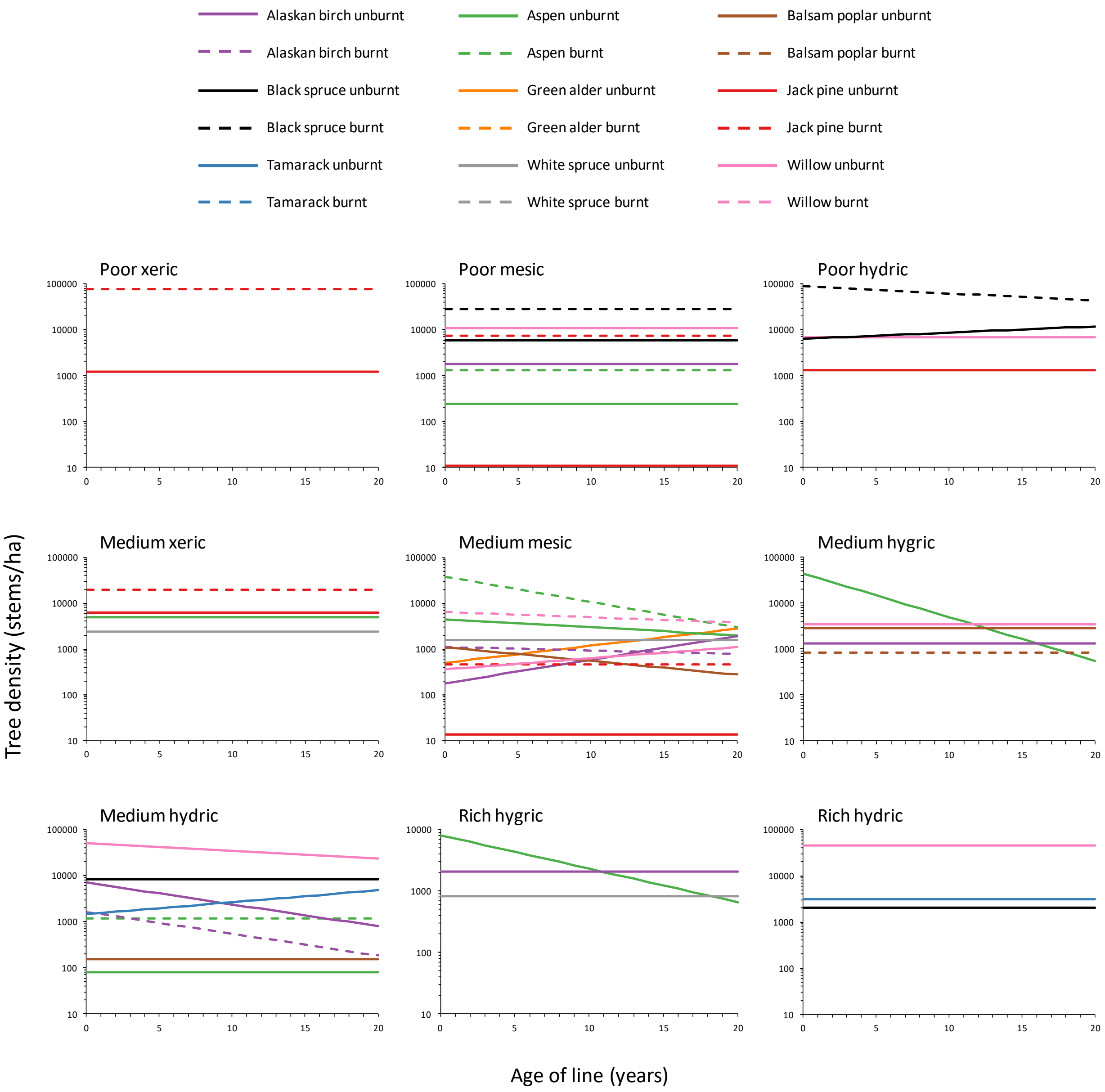


Figure 7.A2: Predicted values in regeneration density changes as the age of the line (years) increases in nine ecosites for nine common species in unburnt (presence of recent wildfire, solid line) and burnt (absence of recent wildfire, dotted line) conditions. Figures that have no burnt (dotted) lines is owing to recent wildfires having no effect.

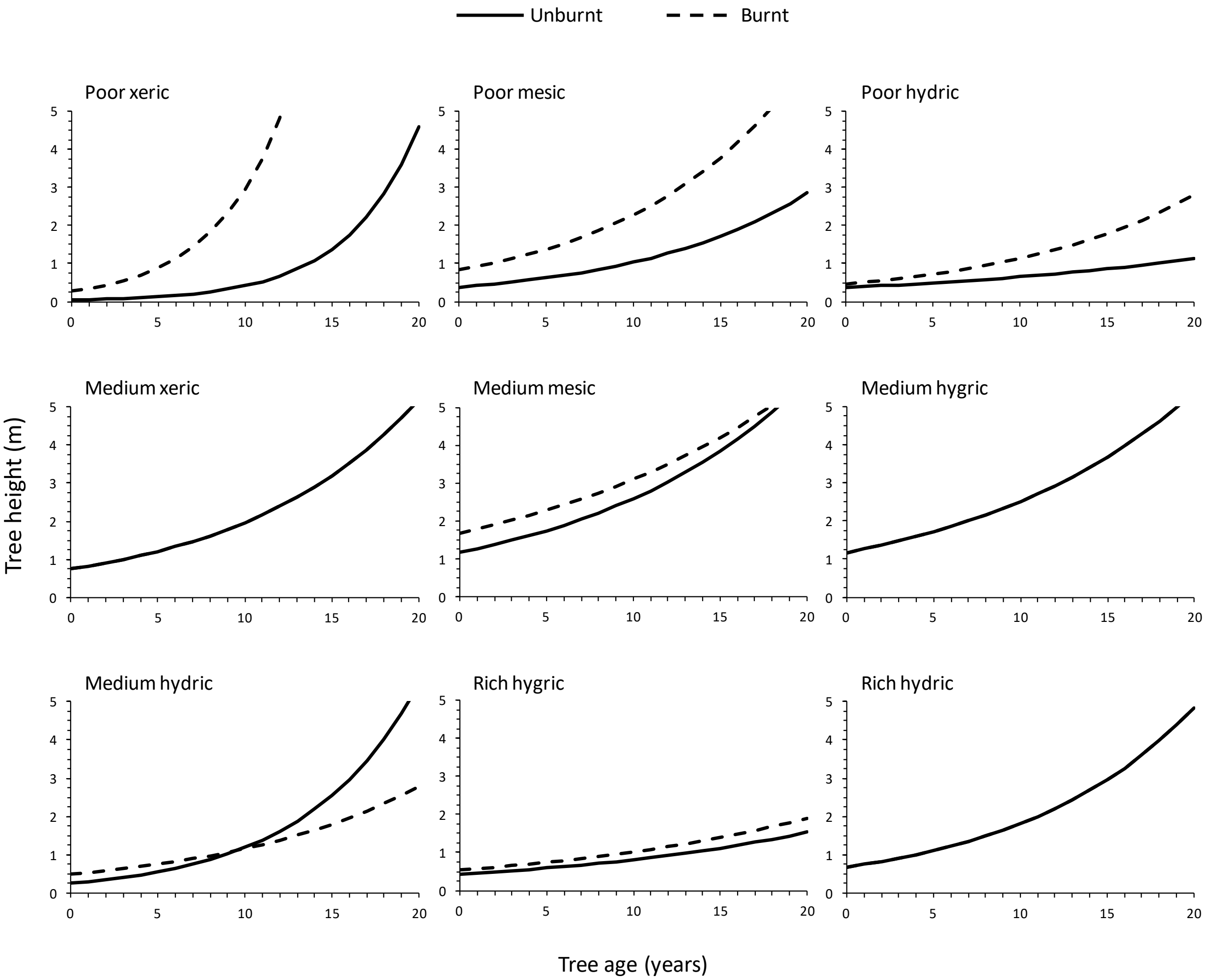


Figure 7.A3: Predicted values in regeneration tree height changes as tree age (years) increases in nine ecosites for unburnt (presence of recent wildfire, solid line) and burnt (absence of recent wildfire, dotted line) conditions. Figures that have no burnt (dotted) lines is owing to recent wildfires having no effect.

Chapter 8: Conclusion

8.1 Roadmap of the conclusion

The conclusion will start off with a brief summary of each chapter. The summaries will be followed by a section on broader outlook about topics alluded to but not fully covered within the prior chapters, which is then followed by a short discussion on future research. The conclusion is ended with a final conclusion.

8.2 Fire and forest recovery on seismic lines in sandy upland jack pine (*Pinus banksiana*) forests (chapter 2)

Seismic lines in sandy upland jack pine forests recover poorly due to two main mechanisms: (1) jack pine are shade intolerant; and (2) jack pine cones are fire serotinous and only release large amounts of seed, which is jack pine's main process of propagating, during and after a wildfire. Post-fire seismic lines in these forests recruit seedling densities at twice the rate as the adjacent forest, suggesting a path to recovery. This also suggests that nothing detrimental to tree regeneration has occurred to the forest floor (compaction or lack of microtopography) during/after the creation of the seismic line. Furthermore, if a wildfire occurs, no site preparation or tree plantings are required; in fact, it is quite possible that the creation of the seismic line, which removed ground biomass exposing an open seedbed, is beneficial to jack pine regeneration.

8.3 High precision altimeter demonstrates simplification and depression of microtopography on seismic lines in treed peatlands (chapter 3)

Seismic lines in tree peatlands are, on average, simplified by 20% and depressed by 8 cm compared to the adjacent forest. This demonstrates that treed peatlands experience alterations to the forest floor from seismic line creation. Furthermore, theses alterations reduce possible microsites for tree recruitment, trees that establish will likely experience reduced growth rates and survival. High precision hydrostatic altimeters show promise in quantifying microtopography which seems to be very important for allowing regeneration in this habitat.

8.4 Caribou conservation: Restoring trees on seismic lines in Alberta, Canada (chapter 4)

Seismic line creation in treed peatlands simplifies microtopography and reduces the depth to the water table limiting possible microsites for tree recruitment. Mechanical site preparation and tree plantings can overcome the detrimental effects of seismic line creation. These restoration treatments increased microtopography and increased tree density hastening recovery in treed peatlands for the short-term (< 6 years). These restoration treatments increased tree density when compared to the untreated lines, despite averaging 3.8-years since treatment application (vs. untreated lines averaging 22 years). On average, the treated lines have 1.6-times more stems than the untreated lines and 1.5-times more than the adjacent undisturbed forest, as well as having consistently more tree stems across all ecosites.

8.5 Tree regeneration on industrial linear disturbances in treed peatlands is hastened by wildfire and delayed by loss of microtopography (chapter 5)

Wildfires promote denser regeneration in treed peatlands. Regeneration density on burnt lines are 2.5-times more than unburnt lines, 1.6-times more than burnt forests, and 3.0-times more than unburnt forests. Wildfires seem to overcome detrimental effects of seismic line creation, simplified microtopography and a reduction of the depth to the water table, which limits microsites for tree recruitment in unburned sites. Wildfires are not as successful in fens to overcome detrimental effects of seismic line creation, possibly due to these areas having a higher water table, a higher fire return interval, less severe burns, or a stand with a lower proportion of fire serotinous species. Microtopography and terrain wetness explained regeneration on burnt lines, but not unburnt lines. In burnt and unburnt lines, sunlight, microtopography, and depth of water table most affected tree regeneration patterns.

8.6 Response of mesic upland boreal forests to linear disturbances, wildfires, and compaction (chapter 6)

There is clear compaction observed on seismic lines compared to adjacent forest controls yet this does not reach values high enough to impact regeneration density but may affect tree growth. Wildfires increase the compaction on seismic lines by 1.2-times but even with these higher values, compaction still does not negatively impact regeneration density. Wildfires promote denser regeneration in mesic uplands. Regeneration density on burnt lines are 1.7-times more than unburnt lines, 1.2-times more than burnt forests, and 2.8-times more than unburnt forests. Unburnt lines have 1.7-times the regeneration density than unburnt forests, suggesting that seismic lines, in mesic uplands, have reasonable regeneration density rates for clear-cut openings and are not being inhibited.

8.7 Predicting reforestation of linear disturbances in the boreal forests of Alberta: Identifying sites for passive vs. active restoration (chapter 7)

Leave-for-natural restoration has resulted in most seismic lines meeting or surpassing suggested guidelines for regeneration density and height within 20 years. Most sites that are exceptions to these patterns are in forested peatlands, particularly fens. Fen regeneration densities meet guidelines but their heights lag behind other ecosites, although, this partly reflects the shorter nature of mature forests (~7 m mature forest heights) in these systems. Wildfires quickened the pace of regeneration density and height for most sites and should be taken into consideration when making active restoration plans. If active restoration is to be focused on caribou habitat, treed peatlands, the priority should be given to the wettest sites that are unlikely to experience wildfires and are less likely to return to forest conditions in a short-term period. These sites often have less dense and less tall forests suggesting that individual restoration guidelines are needed for these ecosites. Limiting restoration to key places where it would be most effective at hastening recovery is essential for saving limited restoration dollars.

8.8 Conservation and management implications

If it is agreed that caribou and/or seismic lines require restoration, then restoration goals need to be set. One of the first items that need to be decided is what is considered restoration of a seismic line; should we aim for a complete erasure of seismic lines and have them identical to the adjacent forest or should we aim to have them on a successful trajectory with a focus on restoring trees to slow animal movement? Getting seismic lines to be identical to the adjacent forests with no signs of a disturbance is not likely to happen for many decades given that these forests are slow growing. However, fire can speed this process of ‘erasing’ a line, but results in early seral vegetation that is not favorable to caribou. Focusing on restoring trees to slow animal movement may help solve the immediate problem related to declines in woodland caribou.

Trying to reverse engineer what occurred on seismic lines is complicated. To better understand where, when, and how seismic lines need restoration there needs to be records of when lines were created, with what machinery and operator instructions, and how often the lines are re-cleared and/or used. This information should be provided to a central database and be mandatory as part of their permit. If seismic lines are required to be re-cleared, for access or safety reasons, these lines should be in a separate category compared to seismic lines that are no longer required and can be targeted for restoration.

Restoration treatments may in the short-term jump start tree density and growth, but long-term results need to be monitored. Artificial hummocks from mounding may erode and the artificial hollows can be large (1 m wide, 2 m long, 1.5 m deep) which reduces potential surface area for trees and may not recover to ground level in many decades/centuries.

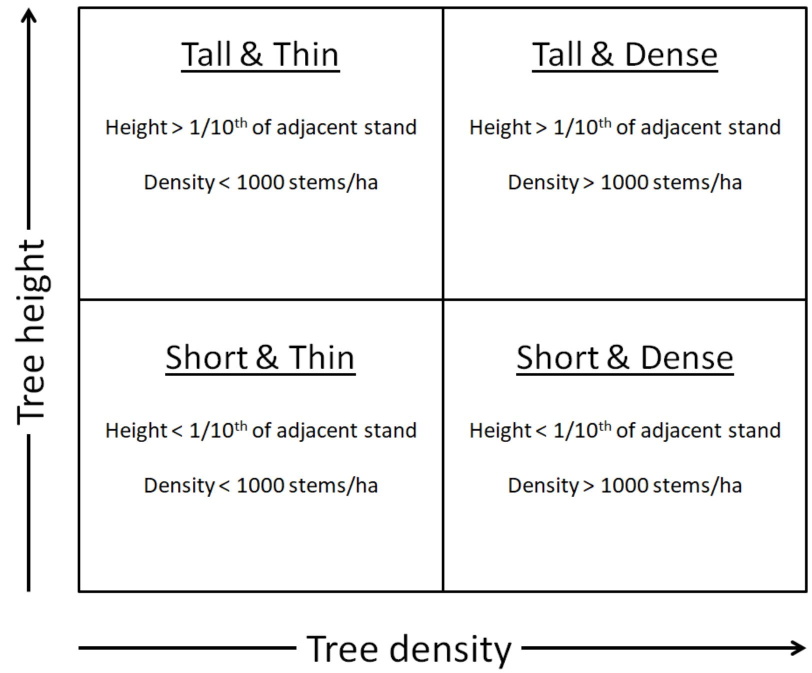
Triage of where to spend limited conservation dollars, including restoration, is an ongoing debate in conservation. Here, we are not suggesting to simply wait for wildfire to restore seismic lines. We are instead suggesting that recently burnt sites, and possibly areas likely to experience wildfires in the near future, should be considered lower priority for restoration. With climate change, large parts of the boreal forest, including northeast Alberta, are expected to receive more intense, more frequent, and larger wildfires (Flannigan et al. 2009a, 2009b). Locally, there are large variations in fire frequency within the landscape, owing to natural landscape features (Nielsen et al. 2016), dominant tree species (Larsen 1997), time since last fire (Beverly 2017), and fuel loads (Johnston et al. 2015). Areas with caribou herds, if caribou conservations is an agreed upon objective, should clearly get priority, but otherwise we do not promote widespread use of limited restoration dollars without considering trade-offs associated with natural recovery, especially with that of wildfire. Even if the interval is 70 years, you would not have to wait on average 70 years as that assumes the last wildfire was during line creation. Decent evidence suggests that even lines created 5 years post-fire will gain some benefits of the wildfire. It is also uncommon to see lines created soon after a wildfire.

If seismic lines are continuously disturbed by humans are of interest, then appropriate bodies (industry, government, hunters, parks, etc.) should keep track of usage and/or re-clearing. Most machinery in recent years have odometers and GPS and these seismic lines can be monitored using these tools. I do not think it is feasible to hire field researchers to detect and quantify the usage of these lines. There is no easy way to identify these lines without constant on the ground re-visits, although recent remote sensing may help identify the more disturbed lines. These lines could have multiple uses at any time period, which is difficult for field researchers to capture and quantify, but again remote sensing has promise for monitoring changes in the most disturbed lines. Lastly, these lines mostly occur near roads, towns, and facilities, but dwindle significantly in the interior forest (> 2 km), so the most disturbed lines are likely a minority.

8.9 Possible targets to consider

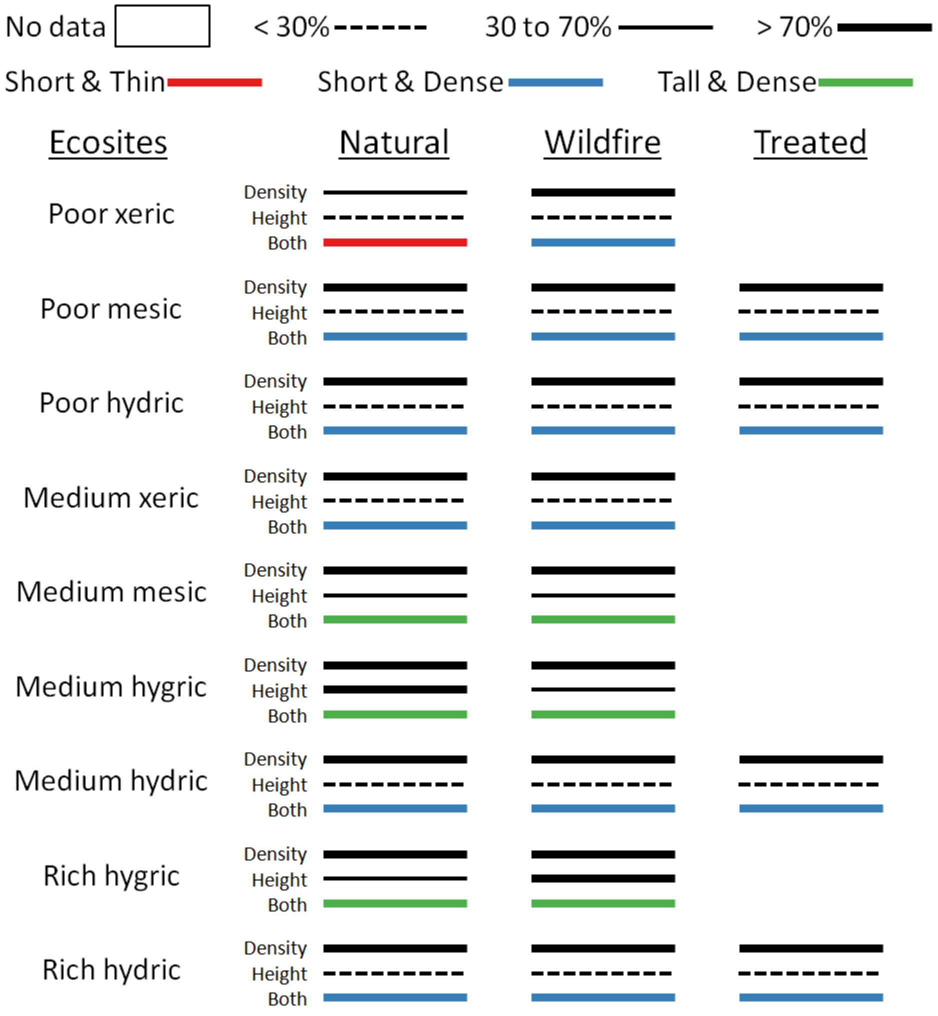
Targets should be separated into different responses, see example below. A density threshold of 1000 stems/ha is commonly used for restoration of many forests and most seismic lines appear to easily reach this threshold even without restoration or fire. Use of a height threshold, however, is more complex. I believe that the average adjacent forest height (mature and not recently disturbed) should be taken into consideration for establishment of ecosite-specific height targets. For instance, it does not make sense to expect regeneration on the seismic line to reach five meters of height if the adjacent forest height is four meters. This issue occurs in peatlands owing to their shorter tree heights due to the closeness of the water table. An additional complication that should be taken into account is the possibility that the depression and reduced distant to the water table observed on seismic lines may stunt the expected attainable height and growth rates observed in the adjacent forests. Proportional height targets, possibly 1/5th or 1/10th of the adjacent forest height, are a reasonable target for identifying trajectories of recovery. Most seismic lines struggle to reach taller heights, regardless of the threshold, and it is uncertain if this is because of high mortality rates (reduced distance to the water table, lack of sunlight due to small gap size, herbivory, etc.), which are about equal to birth rates, or owing to the age of the lines. Regardless, the main aim for restoration should be to get tree regeneration to be both Tall & Dense (Figure 8.1). When using similar thresholds for the work completed throughout this thesis, a large synthesis of this data may look like Figure 8.2.

Figure 8.1: Using regeneration height (proportion of the average adjacent forest and not recently disturbed stand height) and density thresholds (commonly used 1,000 stems/ha) to better evaluate regeneration standards.



Tall & Thin Height > 1/10th of adjacent stand Density < 1000 stems/ha	**Tall & Dense** Height > 1/10th of adjacent stand Density > 1000 stems/ha
Short & Thin Height < 1/10th of adjacent stand Density < 1000 stems/ha	**Short & Dense** Height < 1/10th of adjacent stand Density > 1000 stems/ha

Figure 8.2: Percent of sites in each ecosite that meet thresholds of: (i) regeneration density > 1,000 stems/ha; (ii) average regeneration height of the seismic line > 1/10th of average ecosite stand height (mature and not recently disturbed); and (iii) combination of density and height threshold, note no Tall & Thin category.



8.10 Broader outlook

A forest's resiliency for one type of disturbance does not necessitate resiliency for all disturbance types. Seismic line disturbances are unlike those common to the boreal forest, i.e., wildfires and insect infestations. Wildfires alter the landscape significantly by killing and removing vast amount of biomass often exposing preferential seedbed conditions for species common in the boreal (jack pine, black spruce, etc.). Similarly, insect herbivory can kill many trees but it is the increased windthrow, due to dead and compromised structural integrity of trees, that exposes preferential seedbeds.

Depending on machinery and/or operator and/or time of year, seismic line creation always kills/removes trees, yet it can either: (a) do minimal damage to the forest floor where preferential seedbeds are not exposed; or (b) do significant damage to the forest floor where compaction, depression, simplification, shortened distance to the water table, and possible root damage occurs. Both outcomes are detrimental to regeneration recruitment and growth. If minimal damage occurs to the forest floor, new stems are dependent on layering/suckering. Layering/suckering is a much slower and shorter distance mode of reproduction, hence slower recovery. If significant damage occurs to the forest floor there will be less favourable microsites for both seed and layering/suckering. The changes to the forest floor post seismic lie creation may take decades to centuries to recover.

The most common species in the boreal forests of Alberta are skewed to shade intolerant (jack pine, aspen, and black spruce), which mirrors the disturbance prone nature of these forests and the dependence of resilient colonizing/pioneering/early-successional species. Although seismic lines increase sunlight at the forest floor it does not increase as much as post wildfire or insect infestations. Lastly, wildfires initiate release of seeds en masse and/or suckering in aspen, yet seismic lines do not provide any catalyst for mass reproduction. Therefore, the boreal forest is not as resilient or adapted to the novel type of disturbance created by seismic lines and should not be expected to bounce back in a relatively short-term period (decades).

Strategies to rehabilitate forest floors post seismic line creation are already in effect. For legacy seismic lines already created, mechanical site preparation and subsequent tree plantings can occur, albeit at a high price. For newly created seismic lines, smaller/lighter machinery can be used with a mulcher set well above the surface of the forest floor to both avoid killing smaller trees and avoid compaction, depression, simplification, shortened distance to the water table, and possible root damage. Anecdotal data suggests that sites using this approach can recover faster. Zero impact seismic lines, where no trees are killed/removed, is possible and some companies are in the process of working out the details, unfortunately operator safety concerns (no machinery for quick easy movement, no line to follow, etc.) may delay or prevent implementation.

8.11 Future research

The year at which seismic lines were created would give a valuable metric to assess specific relationships of age of line to regeneration. Unfortunately, many bodies (government, industry, and academic) have reported the difficulty in obtaining dates and many suggest they are limited or do not exist. If possible, knowing the season, machinery, and operator instruction may also aid in discovering which combination is most beneficial to regeneration.

Another area of focus should be ground conditions (depth to water table, organic layer depth, microtopography, likelihood of ground wildfire and its affects, possible root damage from seismic line creation, success/failure of suckering post seismic line creation, etc.). Ground conditions are leading mechanisms for regeneration success/failure, yet minimal studies on such topics exist for boreal forests, particularly in peatlands, and even less on interactions with disturbances such as seismic lines.

8.12 Final conclusion

Seismic lines can cause a lack of regeneration density and growth but the main cause of this, in northeast Alberta, is due to seismic line creation being a novel disturbance for which the boreal forest has poor resiliency. Fens, in particular, seem to have the most difficulty in recovering post seismic line creation, which is most likely due to the loss of microtopography. Active restoration treatments have been successful in improving regeneration density and height in the short-term but longer-term studies are required to assess the longer-term success of these programs. These same active restoration treatments have proven successful in overcoming issues with the loss of microtopography. Wildfires, a disturbance the boreal forest is well adapted to, encourages rapid increases regeneration, both density and growth, on seismic lines and can be considered the best overall restoration treatment but may not overcome the loss of microtopography in fens.

References

Ahlgren, I.F., and Ahlgren, C.E. 1960. Ecological effects of forest fires. Bot. Rev. **26**(4): 483–533. doi:10.1007/BF02940573.

Alberta Agriculture and Forestry: Forestry Division. 2016. Alberta forest genetic resource management and conservation standards – third revision of STIA. Edmonton.

Alberta Agriculture and Forestry. 2016. Alberta timber harvest planning and operating ground rules framework for renewal. Alberta Agriculture and Forestry, Edmonton. doi:10.5962/bhl.title.116045.

Alberta Agriculture and Forestry. 2017. Spatial wildfire data. Available from https://wildfire.alberta.ca/resources/historical-data/spatial-wildfire-data.aspx [accessed 2 February 2017].

Alberta Biodiversity Monitoring Institute. 2018. Terrestrial field data collection protocols (abridged version) 2018-05-07. Available from http://abmi.ca/home/publications/401-450/432.html?mode=detail.

Alexandratos, N. 2005. Countries with rapid population growth and resource constraints: Issues of food, agriculture, and development. Popul. Dev. Rev. **31**(2): 237–258. doi:10.1111/j.1728-4457.2005.00064.x.

Ampoorter, E., De Frenne, P., Hermy, M., and Verheyen, K. 2011. Effects of soil compaction on growth and survival of tree saplings: A meta-analysis. Basic Appl. Ecol. **12**(5): 394–402. doi:10.1016/j.baae.2011.06.003.

Arienti, M.C., Cumming, S.G., Krawchuk, M.A., and Boutin, S. 2009. Road network density correlated with increased lightning fire incidence in the Canadian western boreal forest. Int. J. Wildl. Fire **18**(8): 970–982. doi:10.1071/WF08011.

Arseneault, D. 2001. Impact of fire behavior on postfire forest development in a homogeneous boreal landscape. Can. J. For. Res. **31**: 1367–1374. doi:10.1139/x01-065.

Bayne, E.M., Boutin, S., Tracz, B., and Charest, K. 2005. Functional and numerical responses of ovenbirds (Seiurus aurocapilla) to changing seismic exploration practices in Alberta's boreal forest . Écoscience **12**(2): 216–222. doi:10.2980/i1195-6860-12-2-216.1.

Beck, P.S.A., Juday, G.P., Alix, C., Barber, V.A., Winslow, S.E., Sousa, E.E., Heiser, P., Herriges, J.D., and Goetz, S.J. 2011. Changes in forest productivity across Alaska consistent with biome shift. Ecol. Lett. **14**(4): 373–379. doi:10.1111/j.1461-0248.2011.01598.x.

Benscoter, B.W., Greenacre, D., and Turetsky, M.R. 2015. Wildfire as a key determinant of peatland microtopography. Can. J. For. Res. **45**(8): 1132–1136. doi:10.1139/cjfr-2015-0028.

Benscoter, B.W., Wieder, R.K., and Vitt, D.H. 2005. Linking microtopography with post-fire succession in bogs. J. Veg. Sci. **16**(4): 453–460.

Bergeron, Y. 2000. Species and stand dynamics in the mixed woods of quebec's southern boreal forest. Ecol. Soc. Am. **81**(6): 1500–1516.

Beverly, J.L. 2017. Time since prior wildfire affects subsequent fire containment in black spruce. Int. J. Wildl. Fire **26**(11): 919–929. doi:10.1071/WF17051.

Bockstette, S.W., Pinno, B.D., Dyck, M.F., and Landhäusser, S.M. 2017. Root competition, not soil compaction, restricts access to soil resources for aspen on a reclaimed mine soil. Botany **95**(7): 685–695. doi:10.1139/cjb-2016-0301.

Bonan, G.B., and Shugart, H.H. 1989. Environmental factors and ecological processes in boreal forests. Annu. Rev. Ecol. Syst. Vol. 20 **3**(2): 1–28. doi:10.1146/annurev.es.20.110189.000245.

Boucher, D., Gauthier, S., and De Grandpré, L. 2006. Structural changes in coniferous stands along a chronosequence and a productivity gradient in the northeastern boreal forest of Québec. Ecoscience **13**(2): 172–180. doi:10.2980/i1195-6860-13-2-172.1.

Bouget, C., and Duelli, P. 2004. The effects of windthrow on forest insect communities: A literature review. Biol. Conserv. **118**(3): 281–299. doi:10.1016/j.biocon.2003.09.009.

Braithwaite, N.T., and Mallik, A.U. 2012. Edge effects of wildfire and riparian buffers along boreal forest streams. J. Appl. Ecol. **49**(1): 192–201. doi:10.1111/j.1365-2664.2011.02076.x.

Brandt, J.P., Flannigan, M.D., Maynard, D.G., Thompson, I.D., and Volney, W.J.A. 2013. An introduction to Canada's boreal zone: Ecosystem processes, health, sustainability, and environmental issues1. Environ. Rev. **21**(4): 207–226. doi:10.1139/er-2013-0040.

Brubaker, K.M., Myers, W.L., Drohan, P.J., Miller, D.A., and Boyer, E.W. 2013. The use of LiDAR terrain data in characterizing surface roughness and microtopography. Appl. Environ. Soil Sci. **2013**. doi:10.1155/2013/891534.

Bubier, J.L. 1991. Patterns of Picea mariana (Black Spruce) Growth and raised bog development in victory basin , Vermont. Torrey Bot. Soc. **118**(4): 399–411.

Burton, P.J. 2002. Effects of clearcut edges on trees in the sub-boreal spruce zone of Northwest-Central British Columbia. Silva Fenn. **36**(1): 329–352. doi:10.14214/sf.566.

Camill, P., Chihara, L., Adams, B., Andreassi, C., Barry, A., Kalim, S., Limmer, J., Mandell, M., Rafert, G., Camill, P., Chihara, L., Adams, B., Andreassi, C., Barry, A., Kalim, S., Limmer, J., Mandell, M., and Rafert, G. 2010. Early life history transitions and recruitment of Picea mariana in thawed boreal permafrost peatlands. Ecology **2**(February 2010): 448–459.

Caners, R.T., and Lieffers, V.J. 2014. Divergent pathways of successional recovery for in situ oil sands exploration drilling pads on wooded moderate-rich fens in Alberta, Canada. Restor. Ecol. **22**(5): 657–667. doi:10.1111/rec.12123.

Carroll, S.B., and Bliss, L.C. 1982. Jack pine - lichen woodland on sandy soils in northern Saskatchewan and northeastern Alberta. Can. J. Bot. **60**(11): 2270–2282. NRC Research Press, Ottawa, Canada. doi:10.1139/b82-278.

Cayford, J.H., and McRae, D.J. 1983. The ecological role of fire in jack pine forests. Role Fire North. Circumpolar Ecosyst.: 183–199.

Chazdon, R.L. 2008. Beyond deforestation: Restoring forests and ecosystem services on degraded lands. Science (80-.). **320**(5882): 1458–1460. doi:10.1126/science.1155365.

Chen, H.Y.H., and Popadiouk, R. V. 2002. Dynamics of North American boreal mixedwoods. Environ. Rev. **10**(3): 137–166. doi:10.1139/a02-007.

Chen, J., Hapsari Budisulistiorini, S., Itoh, M., Miyakawa, T., Komazaki, Y., Dong Qing Yang, L., and Kuwata, M. 2017. Water uptake by fresh Indonesian peat burning particles is limited by water-soluble organic matter. Atmos. Chem. Phys. **17**(18): 11591–11604. doi:10.5194/acp-17-11591-2017.

Chew, S.C., and Sarabia, D. 2016. Nature-culture relations: Early globalization, climate changes, and system crisis. Sustain. **8**(1): 1–29. doi:10.3390/su8010078.

Chrosciewicz, Z. 1974. Evaluation of fire-produced seedbeds for Jack Pine regeneration in central Ontario. Can. J. For. Res. **4**(4): 455–457. doi:10.1139/x74-067.

Cortini, F., Comeau, P.G., Strimbu, V.C., Hogg, E.H. (Ted., Bokalo, M., and Huang, S. 2017. Survival functions for boreal tree species in northwestern North America. For. Ecol. Manage. **402**: 177–185. Elsevier B.V. doi:10.1016/j.foreco.2017.06.036.

Crites, S., and Dale, M.R.T. 1998. Diversity and abundance of bryophytes, lichens, and fungi in relation to woody substrate and successional stage in aspen mixedwood boreal forests. Can.

J. Bot. **76**(4): 641–651. doi:10.1139/b98-030.

Cumming, S.G., Schmiegelow, F.K.A., and Burton, P.J. 2000. Gap dynamics in boreal aspen stands: Is the forest older than we think? Ecol. Appl. **10**(3): 744–759. doi:10.1890/1051-0761(2000)010[0744:GDIBAS]2.0.CO;2.

Dabros, A., Pyper, M., and Castilla, G. 2018. Seismic lines in the boreal and arctic ecosystems of North America: environmental impacts, challenges, and opportunities. Environ. Rev. **16**(February): 1–16. doi:10.1139/er-2017-0080.

Daddow, R.L., and Warrington, G.E. 1983. Growth-limiting soil bulk densities as influenced by soil texture. Fort Collins.

Dale, V.H., Doyle, T.W., and Shugart, H.H. 1985. A comparison of tree growth models. Ecol. Modell. **29**: 145–169.

Desponts, M., and Payette, S. 1992. Recent dynamics of jack pine at its northern distribution limit in northern Quebec. Can. J. Bot. **70**(6): 1157–1167. NRC Research Press, Ottawa, Canada. doi:10.1139/b92-144.

Dickie, M., McNay, S.R., Sutherland, G.D., Cody, M., and Avgar, T. 2020. Corridors or risk? Movement along, and use of, linear features varies predictably among large mammal predator and prey species. J. Anim. Ecol. **89**(2): 623–634. doi:10.1111/1365-2656.13130.

Dickie, M., Serrouya, R., Demars, C., Cranston, J., and Boutin, S. 2017a. Evaluating functional recovery of habitat for threatened woodland caribou. Ecosphere **8**(9). doi:10.1002/ecs2.1936.

Dickie, M., Serrouya, R., McNay, R.S., and Boutin, S. 2017b. Faster and farther: wolf movement on linear features and implications for hunting behaviour. J. Appl. Ecol. **54**(1): 253–263. doi:10.1111/1365-2664.12732.

Dyer, S.J., O'Neill, J.P.., Wasel, S.M.., and Boutin, S. 2001. Avoidance of industrial development by woodland caribou. J. Wildl. Manage. **65**(3): 531–542.

Dyer, S.J., O'Neill, J.P., Wasel, S.M., and Boutin, S. 2002. Quantifying barrier effects of roads and seismic lines on movements of female woodland caribou in northeastern Alberta. Can. J. Zool. **80**(5): 839–845. NRC Research Press, Ottawa, Canada. doi:10.1139/z02-060.

Environment Canada. 2012. Recovery strategy for the woodland caribou, boreal popoulation (*Rangifer tarandus caribou*) in Canada. Available from http://www.registrelep-sararegistry.gc.ca/document/default_e.cfm?documentID=2253.

Feduck, C., McDermid, G.J., and Castilla, G. 2018. Detection of coniferous seedlings in UAV imagery. Forests **9**(7): 1–15. doi:10.3390/f9070432.

Filicetti, A.T., Cody, M., and Nielsen, S.E. 2019. Caribou conservation: Restoring trees on seismic lines in Alberta, Canada. Forests **10**(2): 185. doi:10.3390/f10020185.

Filicetti, A.T., and Nielsen, S.E. 2018. Fire and forest recovery on seismic lines in sandy upland jack pine (*Pinus banksiana*) forests. For. Ecol. Manage. **421**(October 2017): 32–39. Elsevier. doi:10.1016/j.foreco.2018.01.027.

Filicetti, A.T., and Nielsen, S.E. 2020. Tree regeneration on industrial linear disturbances in treed peatlands is hastened by wildfire and delayed by loss of microtopography. Can. J. For. Res. **50**(9): 936–945. doi:10.1139/cjfr-2019-0451.

Finnegan, L., Pigeon, K.E., Cranston, J., Hebblewhite, M., Musiani, M., Neufeld, L., Schmiegelow, F., Duval, J., and Stenhouse, G.B. 2018. Natural regeneration on seismic lines influences movement behaviour of wolves and grizzly bears. PLoS One **13**(4). doi:10.1371/journal.pone.0195480.

Flannigan, M., Stocks, B., Turetsky, M., and Wotton, M. 2009a. Impacts of climate change on fire activity and fire management in the circumboreal forest. Glob. Chang. Biol. **15**(3): 549–560. doi:10.1111/j.1365-2486.2008.01660.x.

Flannigan, M.D., Krawchuk, M.A., de Groot, W.J., Wotton, B.M., and Gowman, L.M. 2009b. Implications of changing climate for global wildland fire. Int. J. Wildl. Fire **18**(5): 483–507. doi:10.1071/WF08187.

Foley, J.A., Defries, R., Asner, G.P., Barford, C., Carpenter, S.R., Chapin, F.S., Coe, M.T., Daily, G.C., Holly, K., Helkowski, J.H., Holloway, T., Howard, E.A., Kucharik, C.J., Monfreda, C., Patz, J.A., Prentice, I.C., Ramankutty, N., and Peter, K. 2005. Global consequences of land use. Science (80-.). **309**(5734): 570–574.

Franklin, K.A. 2008. Shade avoidance. New Phytol. **179**(4): 930–944. doi:10.1111/j.1469-8137.2008.02507.x.

Franklin, S.E. 2018. Pixel- and object-based multispectral classification of forest tree species from small unmanned aerial vehicles. J. Unmanned Veh. Syst. **6**(January): 195–211.

Fraser, J.W. 1976. Viability of black spruce seed in or on a boreal forest seedbed. For. Chron. **52**(5): 229–231. doi:10.5558/tfc52229-5.

Frelich, L.E., and Reich, P.B. 1995. Spatial patterns and succession in a Minnesota southern-boreal forest. Ecol. Monogr. **65**(3): 325–346. doi:10.2307/2937063.

Frey, B.R., Lieffers, V.J., Landhäusser, S.M., Comeau, P.G., and Greenway, K.J. 2003. An analysis of sucker regeneration of trembling aspen. Can. J. For. Res. **33**(7): 1169–1179. doi:10.1139/x03-053.

Frolking, S., Roulet, N.T., Moore, T.R., Richard, P.J.H., Lavoie, M., and Muller, S.D. 2001. Modeling northern peatland decomposition and peat accumulation. Ecosystems **4**(5): 479–498. doi:10.1007/s10021-001-0105-1.

Gauthier, S., Bergeron, Y., and Simon, J.-P. 1993a. Cone serotiny in jack pine: ontogenetic, positional, and environmental effects. Can. J. For. Res. **23**(3): 394–401. doi:10.1139/x93-057.

Gauthier, S., Bernier, P., Kuuluvainen, T., Shvidenko, A.Z., and Schepaschenko, D.G. 2015. Boreal forest health and global change. Science (80-.). **349**(6250): 819–822. doi:10.1126/science.aaa9092.

Gauthier, S., Gagnon, J., and Bergeron, Y. 1993b. Population age structure of *Pinus banksiana* at the southern edge of the Canadian boreal forest. J. Veg. Sci. **4**: 783–790. Available from Botany.

Givnish, T.J. 2002. Givnish_2002.pdf. **36**(December 2000): 703–743. doi:10.14214/sf.535.

von der Gönna, M.A. 1992. Fundamentals of mechanical site preparation. FRDA Rep. 178 (Forestry Canada, Pacific Forestry Centre, Victoria, BC): 1–28.

Government of Alberta: Alberta Environment and Parks. 2017. Woodland Caribou (*Rangifer tarandus caribou*). Available from http://aep.alberta.ca/fish-wildlife/wild-species/mammals/deer/woodland-caribou.aspx [accessed 10 December 2018].

Government of Alberta. 2017. Provincial restoration and establishment framework for legacy seismic lines in Alberta. Edmonton, Alberta.

Government of Canada. 2012. Woodland Caribou (*Rangifer Tarandus Caribou*), Boreal population: Recovery strategy 2012. Available from https://www.canada.ca/en/environment-climate-change/services/species-risk-public-registry/%0Arecovery-strategies/woodland-caribou-boreal-population--2012.html [accessed 16 March 2019].

Greene, D.F., and Johnson, E.A. 1999. Modelling recruitment of Populus tremuloides, *Pinus banksiana*, and *Picea mariana* following fire in the mixedwood boreal forest. Can. J. For.

Res. **29**(4): 462–473. doi:10.1139/cjfr-29-4-462.

Greene, D.F., Macdonald, S.E., Haeussler, S., Domenicano, S., Noel, J., Jayen, K., Charron, I., Gauthier, S., Hunt, S., Gielau, E.T., Bergeron, Y., and Swift, L. 2007. The reduction of organic-layer depth by wildfire in the North American boreal forest and its effect on tree recruitment by seed. Can. J. For. Res. **37**(6): 1012–1023. doi:10.1139/X06-245.

Greene, D.F., Noel, J., Bergeron, Y., Rousseau, M., and Gauthier, S. 2004. Recruitment of *Picea mariana*, *Pinus banksiana*, and *Populus tremuloides* across a burn severity gradient following wildfire in the southern boreal forest of Quebec. Can. J. For. Res. **34**(9): 1845–1857. doi:10.1139/x04-059.

Greene, D.F., Splawinski, T.B., Gauthier, S., and Bergeron, Y. 2013. Seed abscission schedules and the timing of post-fire salvage of *Picea mariana* and *Pinus banksiana*. For. Ecol. Manage. **303**: 20–24. Elsevier B.V. doi:10.1016/j.foreco.2013.03.049.

Greene, D.F., Zasada, J.C., Sirois, L., D., K., Morin, H., Charron, I., and Simard, M.J. 1999. A review of the regeneration dynamics of North American boreal forest tree species. Can. J. For. Res. **29**: 824–839.

Grigal, D.. 1989. Bulk Density of surface soils and peat in the north central United States. Can. J. Soil Sci. Soil Sci. **69**: 895–900.

de Groot, W.J., Bothwell, P.M., Taylor, S.W., Wotton, B.M., Stocks, B.J., and Alexander, M.E. 2004. Jack pine regeneration and crown fires. Can. J. For. Res. **34**(8): 1634–1641. doi:10.1139/x04-073.

de Groot, W.J., Cantin, A.S., Flannigan, M.D., Soja, A.J., Gowman, L.M., and Newbery, A. 2013. A comparison of Canadian and Russian boreal forest fire regimes. For. Ecol. Manage. **294**: 23–34. doi:10.1016/j.foreco.2012.07.033.

Gu, L., Baldocchi, D., Verma, S.B., Black, T.A., Vesala, T., Falge, E.M., and Dowty, P.R. 2002. Advantages of diffuse radiation for terrestrial ecosystem productivity. J. Geophys. Res. Atmos. **107**(5–6). doi:10.1029/2001jd001242.

Haddad, N.M., Brudvig, L.A., Clobert, J., Davies, K.F., Gonzalez, A., Holt, R.D., Lovejoy, T.E., Sexton, J.O., Austin, M.P., Collins, C.D., Cook, W.M., Damschen, E.I., Ewers, R.M., Foster, B.L., Jenkins, C.N., King, A.J., Laurance, W.F., Levey, D.J., Margules, C.R., Melbourne, B.A., Nicholls, A.O., Orrock, J.L., Song, D.-X., and Townshend, J.R. 2015. Habitat fragmentation and its lasting impact on Earth’s ecosystems. Sci. Adv. **1**(2):

e1500052. doi:10.1126/sciadv.1500052.

Hart, S.A., and Chen, H.Y.H. 2006a. Understory vegetation dynamics of North American boreal forests. CRC. Crit. Rev. Plant Sci. **25**(4): 381–397. doi:10.1080/07352680600819286.

Hart, S.A., and Chen, H.Y.H. 2006b. Understory vegetation dynamics of North American boreal forests. CRC. Crit. Rev. Plant Sci. **25**(4): 381–397. Taylor & Francis Group, Boca Raton. doi:10.1080/07352680600819286.

Hart, S.A., and Chen, H.Y.H. 2008. Fire, logging, and overstory affect understory abundance, diversity, and composition in boreal forest. Ecol. Monogr. **78**(1): 123–140.

Hebblewhite, M. 2017. Billion dollar boreal woodland caribou and the biodiversity impacts of the global oil and gas industry. Biol. Conserv. **206**: 102–111. Elsevier Ltd. doi:10.1016/j.biocon.2016.12.014.

Hogg, E.H., and Lieffers, V.J. 1991. The impact of Calamagrostis canadensison soil thermal regimes after logging in northern Alberta. Can. J. For. Res. **21**: 387–394.

Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A.J., Vandermeer, J., and Wardle, D.A. 2005. Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. Source Ecol. Monogr. **75**(1): 3–35. doi:10.1890/04-0922.

Hossain, M.F., Chen, W., and Zhang, Y. 2015. Bulk density of mineral and organic soils in the Canada’s arctic and sub-arctic. Inf. Process. Agric. **2**(3–4): 183–190. China Agricultural University. doi:10.1016/j.inpa.2015.09.001.

James, A.C.R., and Stuart-Smith, A.K. 2000. Distribution of caribou and wolves in relation to linear corridors. J. Wildl. Manage. **64**(1): 154–159.

Jayen, K., Leduc, A., and Bergeron, Y. 2006. Effect of fire severity on regeneration success in the boreal forest of northwest Québec, Canada. Ecoscience **13**(2): 143–151. doi:10.2980/i1195-6860-13-2-143.1.

Jean, S.A., Pinno, B.D., and Nielsen, S.E. 2020. Early regeneration dynamics of pure black spruce and aspen forests afterwildfire in boreal alberta, Canada. Forests **11**(3): 1–13. doi:10.3390/f11030333.

Johnson, C.J., Mumma, M.A., and St-Laurent, M. 2019. Modeling multispecies predator–prey dynamics: predicting the outcomes of conservation actions for woodland caribou. Ecosphere **10**(3): e02622. doi:10.1002/ecs2.2622.

Johnston, D.C., Turetsky, M.R., Benscoter, B.W., and Wotton, B.M. 2015. Fuel load, structure, and potential fire behaviour in black spruce bogs. Can. J. For. Res. **45**(7): 888–899. doi:10.1139/cjfr-2014-0334.

Johnstone, J.F., and Chapin, F.S. 2006. Effects of soil burn severity on post-fire tree recruitment in boreal forest. Ecosystems **9**(1): 14–31. doi:10.1007/s10021-004-0042-x.

Jonsson, B.G., and Esseen, P.A. 1990. Treefall disturbance maintains high bryophyte diversity in a boreal spruce fForest. J. Ecol. **78**(4): 924–936.

Jutras, S., Plamondon, A.P., Hökkä, H., and Bégin, J. 2006. Water table changes following precommercial thinning on post-harvest drained wetlands. For. Ecol. Manage. **235**(1–3): 252–259. doi:10.1016/j.foreco.2006.08.335.

Kabzems, R. 2012. Aspen and white spruce productivity is reduced by organic matter removal and soil compaction. For. Chron. **88**(3): 306–316. doi:10.5558/tfc2012-058.

Kabzems, R., and Haeussler, S. 2005. Soil properties, aspen, and white spruce responses 5 years after organic matter removal and compaction treatments. Can. J. For. Res. **35**(8): 2045–2055. doi:10.1139/x05-175.

Keenan, R.J., Reams, G.A., Achard, F., de Freitas, J. V., Grainger, A., and Lindquist, E. 2015. Dynamics of global forest area: Results from the FAO Global Forest Resources Assessment 2015. For. Ecol. Manage. **352**: 9–20. Elsevier B.V. doi:10.1016/j.foreco.2015.06.014.

Kemper, J.T., and Macdonald, S.E. 2009a. Effects of contemporary winter seismic exploration on low arctic plant communities and permafrost. Arctic, Antarct. Alp. Res. **41**(2): 228–237. doi:10.1657/1938-4246-41.2.228.

Kemper, J.T., and Macdonald, S.E. 2009b. Directional change in upland tundra plant communities 20-30 years after seismic exploration in the Canadian low-arctic. J. Veg. Sci. **20**(3): 557–567. doi:10.1111/j.1654-1103.2009.01069.x.

Kettridge, N., Lukenbach, M.C., Hokanson, K.J., Devito, K.J., Petrone, R.M., Mendoza, C.A., and Waddington, J.M. 2019. Severe wildfire exposes remnant peat carbon stocks to increased post-fire drying. Sci. Rep. **9**(1): 5–10. doi:10.1038/s41598-019-40033-7.

Kneeshaw, D.D., and Bergeron, Y. 1998. Canopy gap characteristics and tree replacement in the southeastern boreal forest. Ecology **79**(3): 783–794. doi:10.1890/0012-9658(1998)079[0783:CGCATR]2.0.CO;2.

Komers, P.E., and Stanojevic, Z. 2013. Rates of disturbance vary by data resolution: Implications for conservation schedules using the Alberta boreal forest as a case study. Glob. Chang. Biol. **19**(9): 2916–2928. doi:10.1111/gcb.12266.

Kozlowski, T.T. 1999. Soil compaction and growth of woody plants. Scand. J. For. Res. **14**(6): 596–619. doi:10.1080/02827589908540825.

Kuhry, P. 1994. The role of fire in the development of *sphagnum*-dominated peatlands in western boreal Canada Author (s): Peter Kuhry Published by : British Ecological Society Stable URL : http://www.jstor.org/stable/2261453 Your use of the JSTOR archive indicates your. J. Ecol. **82**(4): 899–910.

Kuhry, P., Nicholson, B.J., Gignac, D.L., Vitt, D.H., and Bayley, S.E. 1993. Development of *Sphagnum*-dominated peatlands in boreal continental Canada. Can. J. Bot. **71**(1): 10–22.

Kuuluvainen, T. 1994. Gap disturbance, ground microtopography, and the regeneration dynamics of boreal coniferous forests in Finland: a review. Ann. Zool. Fennici **31**(1): 35–51.

Kuuluvainen, T., and Juntunen, P. 1998. Seedling establishment in relation to microhabitat variation in a windthrow gap in a boreal *Pinus sylvestris* forest . J. Veg. Sci. **9**(4): 551–562. doi:10.2307/3237271.

Lafleur, B., Paré, D., Fenton, N.J., and Bergeron, Y. 2011. Growth of planted black spruce seedlings following mechanical site preparation in boreal forested peatlands with variable organic layer thickness: 5-Year results. Ann. For. Sci. **68**(8): 1291–1302. doi:10.1007/s13595-011-0136-5.

Lamont, B.B., Lemaitre, D.C., Cowling, R.M., and Enright, N.J. 1991. Canopy seed storage in woody-plants. Bot. Rev. **57**(4): 277–317. doi:Doi 10.1007/Bf02858770.

Landhäusser, S.M., and Lieffers, V.J. 1998. Growth of *Populus tremuloides* in association with *Calamagrostis canadensis*. Can. J. For. Res. **28**(1991): 396–401. doi:10.1139/x98-006.

Larsen, C.P.S. 1997. Spatial and temporal variations in boreal forest fire frequency in northern Alberta. J. Biogeogr. **24**(5): 663–673. doi:10.1111/j.1365-2699.1997.tb00076.x.

Larsen, C.P.S., and MacDonald, G.M. 1998. Fire and vegetation dynamics in a jack pine and black spruce forest reconstructed using fossil pollen and charcoal. J. Ecol. **86**(5): 815–828. doi:10.1046/j.1365-2745.1998.8650815.x.

Larsen, J.A. 1980. The boreal ecosystem. *In* The boreal ecosystem. Academic Press, New York,NY. doi:10.1016/b978-0-12-436880-4.50002-9.

Latham, A.D.M., Latham, M.C., Boyce, M.S., and Boutin, S. 2011a. Movement responses by wolves to industrial linear features and their effect on woodland caribou in northeastern alberta. Ecol. Appl. **21**(8): 2854–2865. doi:10.1890/11-0666.1.

Latham, A.D.M., Latham, M.C., McCutchen, N.A., and Boutin, S. 2011b. Invading white-tailed deer change wolf-caribou dynamics in northeastern Alberta. J. Wildl. Manage. **75**(1): 204–212. doi:10.1002/jwmg.28.

Laurance, W.F., Nascimento, H.E.M., Laurance, S.G., Andrade, A., Ewers, R.M., Harms, K.E., Luizão, R.C.C., and Ribeiro, J.E. 2007. Habitat fragmentation, variable edge effects, and the landscape-divergence hypothesis. PLoS One **2**(10). doi:10.1371/journal.pone.0001017.

Lecomte, N., Simard, M., and Bergeron, Y. 2006. Effects of fire severity and initial tree composition on stand structural development in the coniferous boreal forest of northwestern Québec, Canada. Écoscience **13**(2): 152–163. doi:10.2980/i1195-6860-13-2-152.1.

Lee, P., and Boutin, S. 2006. Persistence and developmental transition of wide seismic lines in the western Boreal Plains of Canada. J. Environ. Manage. **78**(3): 240–250. Elsevier Ltd, England. doi:10.1016/j.jenvman.2005.03.016.

Lefort, P., Gauthier, S., and Bergeron, Y. 2003. The influence of fire weather and land use on the fire activity of the lake Abitibi area, eastern Canada. For. Sci. **49**(4): 509–521. doi:10.1093/forestscience/49.4.509.

Lieffers, V.J., Caners, R.T., and Ge, H. 2017. Re-establishment of hummock topography promotes tree regeneration on highly disturbed moderate-rich fens. J. Environ. Manage. **197**: 258–264. Elsevier Ltd. doi:10.1016/j.jenvman.2017.04.002.

Lieffers, V.J., and Macdonald, S.E. 1989. Growth and foliar nutrient status of black spruce and tamarack in relation to depth of water in some Alberta peatland. Can. J. For. Res. **20**: 805–809.

Lieffers, V.J., Macmillan, R.B., MacPherson, D., Branter, K., and Stewart, J.D. 1996. Semi-natural and intensive silvicultural systems for the boreal mixedwood forest. For. Chron. **72**(3): 286–292. doi:10.5558/tfc72286-3.

Lieffers, V.J., Messier, C., Stadt, K.J., Gendron, F., and Comeau, P.G. 1999. Predicting and managing light in the understory of boreal forests. Can. J. For. Res. **29**(6): 796–811. doi:10.1139/x98-165.

Lieffers, V.J., and Rothwell, R.L. 1987. Rooting of peatland black spruce and tamarack in relation to depth of water table. Botany **65**(5): 817–821. doi:10.1139/b87-111.

Linke, J., Franklin, S.E., Huettmann, F., and Stenhouse, G.B. 2005. Seismic cutlines, changing landscape metrics and grizzly bear landscape use in Alberta. Landsc. Ecol. **20**(7): 811–826. doi:10.1007/s10980-005-0066-4.

Löf, M., Dey, D.C., Navarro, R.M., and Jacobs, D.F. 2012. Mechanical site preparation for forest restoration. New For. **43**(5–6): 825–848. doi:10.1007/s11056-012-9332-x.

Logan, J.A., Régnière, J., and Powell, J.A. 2003. Assessing the impacts of global warming on forest pest dynamics. Front. Ecol. Environ. **1**(3): 130–137. doi:10.1890/1540-9295(2003)001[0130:ATIOGW]2.0.CO;2.

Lorente, M., Parsons, W.F.J., Bradley, R.L., and Munson, A.D. 2012. Soil and plant legacies associated with harvest trails in boreal black spruce forests. For. Ecol. Manage. **269**: 168–176. Elsevier B.V. doi:10.1016/j.foreco.2011.12.029.

Lovitt, J., Rahman, M.M., Saraswati, S., McDermid, G.J., Strack, M., and Xu, B. 2018. UAV Remote sensing can reveal the effects of low-impact seismic lines on surface morphology, hydrology, and methane (CH4) release in a boreal treed bog. J. Geophys. Res. Biogeosciences **123**(3): 1117–1129. doi:10.1002/2017JG004232.

Lukenbach, M.C., Hokanson, K.J., Devito, K.J., Kettridge, N., Petrone, R.M., Mendoza, C.A., Granath, G., and Waddington, J.M. 2017. Post-fire ecohydrological conditions at peatland margins in different hydrogeological settings of the Boreal Plain. J. Hydrol. **548**: 741–753. Elsevier B.V. doi:10.1016/j.jhydrol.2017.03.034.

MacFarlane, A.K. 2003. Vegetation response to seismic lines: edge effects and on-line succession. University of Alberta.

Madec, C., Walsh, D., Lord, D., Tremblay, P., Boucher, J.-F., and Bouchard, S. 2012. Afforestation of black spruce lichen woodlands by natural seeding. North. J. Appl. For. **29**(4): 191–196. doi:10.5849/njaf.11-042.

Mallik, A., and Kayes, I. 2018. Lichen mated seedbeds inhibit while moss dominated seedbeds facilitate black spruce (*Picea mariana*) seedling regeneration in post-fire boreal forest. For. Ecol. Manage. **427**(May): 260–274. Elsevier. doi:10.1016/j.foreco.2018.05.064.

Malmer, N., Albinsson, C., Svensson, B.M., and Wallén, B. 2003. Interferences between *Sphagnum* and vascular plants: Effects on plant community structure and peat formation. Oikos **100**(3): 469–482. doi:10.1034/j.1600-0706.2003.12170.x.

Malmer, N., Svensson, B.M., and Wallén, B. 1994. Interactions between *Sphagnum* mosses and field layer vascular plants in the development of peat-forming systems. Folia Geobot. Phytotaxon. **29**(4): 483–496. doi:10.1007/BF02883146.

McCullough, D.G., Werner, R.A., and Neumann, D. 1998. Fire and insects in northern and boreal forest ecosystems of North America. Annu. Rev. Entomol. **43**(1): 107–127. doi:10.1146/annurev.ento.43.1.107.

McDonald, T.P., Fulton, J.P., Darr, M.J., and Gallagher, T. V. 2008. Evaluation of a system to spatially monitor hand planting of pine seedlings. Comput. Electron. Agric. **64**(2): 173–182. doi:10.1016/j.compag.2008.04.011.

Mercier, P., Aas, G., and Dengler, J. 2019. Effects of skid trails on understory vegetation in forests: A case study from Northern Bavaria (Germany). For. Ecol. Manage. **453**(August): 117579. Elsevier. doi:10.1016/j.foreco.2019.117579.

Messier, C., Doucet, R., Ruel, J.C., Claveau, Y., Kelly, C., and Lechowicz, M.J. 1999. Functional ecology of advance regeneration in relation to light in boreal forests. Can. J. For. Res. **29**(6): 812–823. doi:10.1139/x99-070.

Moore, I.D., Grayson, R.B., and Ladson, A.R. 1991. Digital terrain modelling: A review of hydrological, geomorphological, and biological applications. Hydrol. Process. **5**(1): 3–30. doi:10.1002/hyp.3360050103.

Murray, K.J., Tenhunen, J.D., and Kummerow, J. 1989. Limitations on *Sphagnum* growth and net primary production in the foothills of the Philip Smith Mountains, Alaska. Oecologia **80**: 256–262.

Natural Regions Committee. 2006. Natural Regions and Subregions of Alberta. *Edited By*D.J. Downing and W.W. Pettapiece. Government of Alberta, Edmonton. doi:Pub. No. T/852.

Nelson, K., Thompson, D., Hopkinson, C., Petrone, R., and Chasmer, L. 2021. Peatland-fire interactions: A review of wildland fire feedbacks and interactions in Canadian boreal peatlands. Sci. Total Environ. **769**: 145212. The Authors. doi:10.1016/j.scitotenv.2021.145212.

Nielsen, S.E., DeLancey, E.R., Reinhardt, K., and Parisien, M.A. 2016. Effects of lakes on wildfire activity in the boreal forests of Saskatchewan, Canada. Forests **7**(11). doi:10.3390/f7110265.

Oglesby, R.J., Sever, T.L., Saturno, W., Erickson, D.J., and Srikishen, J. 2010. Collapse of the

Maya: Could deforestation have contributed? J. Geophys. Res. Atmos. **115**(12). doi:10.1029/2009JD011942.

Paquin, R., Margolis, H.A., and Doucet, R. 1998. Nutrient status and growth of black spruce layers and planted seedlings in responce to nutrient addition in the boreal forest of Quebec. Can. J. For. Res. **28**(5): 729–736. doi:10.1139/x98-041.

Pattison, C.A., Quinn, M.S., Dale, P., and Catterall, C.P. 2016. The landscape impact of linear seismic clearings for oil and gas development in boreal forest. Northwest Sci. **90**(3): 340. doi:10.3955/046.090.0312.

Périé, C., and Ouimet, R. 2008. Organic carbon, organic matter and bulk density relationships in boreal forest soils. Can. J. Soil Sci. **88**(3): 315–325. doi:10.4141/CJSS06008.

Pinno, B.D., and Errington, R.C. 2016. Burn severity dominates understory plant community response to fire in xeric jack pine forests. Forests **7**(4). doi:10.3390/f7040083.

Pinno, B.D., Errington, R.C., and Thompson, D.K. 2013. Young jack pine and high severity fire combine to create potentially expansive areas of understocked forest. For. Ecol. Manage. **310**: 517–522. Elsevier B.V. doi:10.1016/j.foreco.2013.08.055.

Poorter, H., Niklas, K.J., Reich, P.B., Oleksyn, J., Poot, P., and Mommer, L. 2012. Biomass allocation to leaves, stems and roots: Meta-analyses of interspecific variation and environmental control. New Phytol. **193**(1): 30–50. doi:10.1111/j.1469-8137.2011.03952.x.

Pouliot, R., Rochefort, L., and Karofeld, E. 2012. Initiation of microtopography in re-vegetated cutover peatlands: evolution of plant species composition. Appl. Veg. Sci. **15**(3): 369–382.

Pyper, M., Nishi, J., and McNeil, L. 2014. Linear Feature Restoration in Caribou Habitat : A summary of current practices and a roadmap for future programs. Submitt. to Canada's Oil Sands Innov. Alliance (COSIA). December 2014. Available from http://www.cosia.ca/uploads/documents/id24/COSIA_Linear_Feature_Restoration_Caribou_Habitat.pdf.

van Rensen, C.K., Nielsen, S.E., White, B., Vinge, T., and Lieffers, V.J. 2015. Natural regeneration of forest vegetation on legacy seismic lines in boreal habitats in Alberta's oil sands region. Biol. Conserv. **184**: 127–135. Elsevier Ltd. doi:10.1016/j.biocon.2015.01.020.

Rettie, W.J., and Messier, F. 2000. Hierarchical habitat selection by woodland caribou : Its relationship to limiting factors. Ecography (Cop.). **23**(4): 466–478.

Revel, R.D., Dougherty, T.D., and Downing, D.J. 1984. Forest growth & revegetation. The

University of Calgary Press, Calgary.

Riva, F., Acorn, J.H., and Nielsen, S.E. 2018a. Localized disturbances from oil sands developments increase butterfly diversity and abundance in Alberta's boreal forests. Biol. Conserv. **217**(April 2017): 173–180. Elsevier. doi:10.1016/j.biocon.2017.10.022.

Riva, F., Acorn, J.H., and Nielsen, S.E. 2018b. Distribution of cranberry blue butterflies (*Agriades optilete*) and their responses to forest disturbance from in situ oil sands and wildfires. Diversity **10**(4): 17–19. doi:10.3390/d10040112.

Riva, F., and Nielsen, S.E. 2020. A functional perspective on the analysis of land use and land cover data in ecology. Ambio. Springer Netherlands. doi:10.1007/s13280-020-01434-5.

Riva, F., Pinzon, J., Acorn, J.H., and Nielsen, S.E. 2020. Composite effects of cutlines and wildfire result in fire refuges for plants and butterflies in boreal treed peatlands. Ecosystems **23**(3): 485–497. Springer US. doi:10.1007/s10021-019-00417-2.

Roberts, D., Ciuti, S., Barber, Q.E., Willier, C., and Nielsen, S.E. 2018. Accelerated seed dispersal along linear disturbances in the Canadian oil sands region. Sci. Rep. **8**(1): 1–9. Springer US. doi:10.1038/s41598-018-22678-y.

Rogers, B.M., Soja, A.J., Goulden, M.L., and Randerson, J.T. 2015. Influence of tree species on continental differences in boreal fires and climate feedbacks. Nat. Geosci. **8**(3): 228–234. doi:10.1038/ngeo2352.

Rolett, B., and Diamond, J. 2004. Environmental predictors of pre-European deforestation on Pacific islands. Nature **431**(7007): 443–446. doi:10.1371/journal.pone.0156340.

Rosa, L., Davis, K.F., Rulli, M.C., and D'Odorico, P. 2017. Environmental consequences of oil production from oil sands. Earth's Futur. **5**(2): 158–170. doi:10.1002/2016EF000484.

Roy, V., Bernier, P.Y., Plamondon, A.P., and Ruel, J.-C. 1999. Effect of drainage and microtopography in forested wetlands on the microenvironment and growth of planted black spruce seedlings. Can. J. For. Res. **29**(5): 563–574. doi:10.1139/x99-024.

Royo, A.A., and Carson, W.P. 2006. On the formation of dense understory layers in forests worldwide: Consequences and implications for forest dynamics, biodiversity, and succession. Can. J. For. Res. **36**(6): 1345–1362. doi:10.1139/X06-025.

Rudolph, T.D., and Laidly, P.R. 1990. *Pinus banksiana* Lamb. – Jack Pine. *In* Silvics of North America. *Edited by* R.M. Burns and B.H. Honkala. United States Department of Agriculture (USDA), Forest Service, Washington D.C. pp. 555–586.

Ruel, J.-C. 1995. Understanding windthrow: Silvicultural implications. For. Chron. **71**(4): 434–445. doi:10.5558/tfc71434-4.

Schneider, R.R. 2002. Alternative futures: Alberta's boreal forest at the crossroads. Federation of Alberta Naturalists, Edmonton.

Schneider, R.R., Hauer, G., Adamowicz, W.L.V., and Boutin, S. 2010. Triage for conserving populations of threatened species: The case of woodland caribou in Alberta. Biol. Conserv. **143**(7): 1603–1611. Elsevier Ltd. doi:10.1016/j.biocon.2010.04.002.

Sealey, L.L., and Van Rees, K.C.J. 2019. Influence of skidder traffic on soil bulk density, aspen regeneration, and vegetation indices following winter harvesting in the Duck Mountain Provincial Park, SK. For. Ecol. Manage. **437**(November 2018): 59–69. Elsevier. doi:10.1016/j.foreco.2019.01.017.

Senici, D., Lucas, A., Chen, H.Y.H., Bergeron, Y., Larouche, A., Brossier, B., Blarquez, O., and Ali, A.A. 2013. Multi-millennial fire frequency and tree abundance differ between xeric and mesic boreal forests in central Canada. J. Ecol. **101**(2): 356–367. doi:10.1111/1365-2745.12047.

Serrouya, R., Dickie, M., DeMars, C., Wittmann, M.J., and Boutin, S. 2020. Predicting the effects of restoring linear features on woodland caribou populations. Ecol. Modell. **416**(June 2019): 108891. Elsevier. doi:10.1016/j.ecolmodel.2019.108891.

Shonfield, J., and Bayne, E.M. 2019. Effects of industrial disturbance on abundance and activity of small mammals. Can. J. Zool. **97**(11): 1013–1020. doi:10.1139/cjz-2019-0098.

Silins, U., Bladon, K.D., Kelly, E.N., Esch, E., Spence, J.R., Stone, M., Emelko, M.B., Boon, S., Wagner, M.J., Williams, C.H.S., and Tichkowsky, I. 2014. Five-year legacy of wildfire and salvage logging impacts on nutrient runoff and aquatic plant, invertebrate, and fish productivity. Ecohydrology **7**(6): 1508–1523. doi:10.1002/eco.1474.

Silva, J.A., Nielsen, S.E., Lamb, C.T., Hague, C., and Boutin, S. 2019. Modelling lichen abundance for woodland caribou in a fire-driven boreal landscape. Forests **10**(11). doi:10.3390/f10110962.

Sirois, L. 1993. Impact of fire on *Picea-Mariana* and *Pinus-Banksiana* seedlings in sub-arctic lichen woodlands. J. Veg. Sci. **4**(6): 795–802. doi:10.2307/3235617.

Skatter, H.G., Charlebois, M.L., Eftestol, S., Tsegaye, D., Colman, J.E., Kansas, J.L., Flydal, K., and Balicki, B. 2017. Living in a burned landscape: Woodland caribou (*rangifer tarandus* *caribou*) use of postfire residual patches for calving in a high fire – low anthropogenic boreal shield ecozone. Can. J. Zool. **95**(12): 975–984. doi:10.1139/cjz-2016-0307.

Smith, C.A.S., Webb, K.T., Kenney, E., Anderson, A., and Kroetsch, D. 2011. Brunisolic soils of Canada: Genesis, distribution, and classification. Can. J. Soil Sci. **91**(5): 903–916. doi:10.4141/cjss10060.

Snyman, H.A. 2005. Influence of fire on litter production and root and litter turnover in a semi-arid grassland of South Africa. South African J. Bot. **71**(2): 145–153. Elsevier Masson SAS. doi:10.1016/S0254-6299(15)30126-5.

Spangenberg, M.C., Serrouya, R., Dickie, M., DeMars, C.A., Michelot, T., Boutin, S., and Wittmann, M.J. 2019. Slowing down wolves to protect boreal caribou populations: a spatial simulation model of linear feature restoration. Ecosphere **10**(10). doi:10.1002/ecs2.2904.

StataCorp. 2017. Stata Statistical Software: Release 15. StataCorp LLC, College Station, TX, USA.

Stern, E., Riva, F., and Nielsen, S. 2018. Effects of narrow linear disturbances on light and wind patterns in fragmented boreal forests in northeastern Alberta. Forests **9**(8): 486. doi:10.3390/f9080486.

Stevenson, C.J., Filicetti, A.T., and Nielsen, S.E. 2019. High precision altimeter demonstrates simplification and depression of microtopography on seismic lines in treed peatlands. Forests **10**(4): 295. doi:10.3390/f10040295.

Sutherland, B., and Foreman, F.F. 2000. Black spruce and vegetation response to chemical and mechanical site preparation on a boreal mixedwood site. Can. J. For. Res. **30**(10): 1561–1570. doi:10.1139/x00-087.

Sutton, R.F. 1993. Mounding site preparation: A review of European and North American experience. New For. **7**(2): 151–192. doi:10.1007/BF00034198.

Taggart, R.E., and Cross, A.T. 2009. Global greenhouse to icehouse and back again: The origin and future of the Boreal Forest biome. Glob. Planet. Change **65**(3–4): 115–121. Elsevier B.V. doi:10.1016/j.gloplacha.2008.10.014.

Tedersoo, L., Suvi, T., Jairus, T., and Kõljalg, U. 2008. Forest microsite effects on community composition of ectomycorrhizal fungi on seedlings of *Picea abie*s and *Betula pendula*. Environ. Microbiol. **10**(5): 1189–1201. doi:10.1111/j.1462-2920.2007.01535.x.

Thom, D., and Seidl, R. 2016. Natural disturbance impacts on ecosystem services and biodiversity in temperate and boreal forests. Biol. Rev. Camb. Philos. Soc. **91**(3): 760–781. doi:10.1111/brv.12193.

Thompson, D.K., Benscoter, B.W., and Waddington, J.M. 2014. Water balance of a burned and unburned forested boreal peatland. Hydrol. Process. **28**(24): 5954–5964. doi:10.1002/hyp.10074.

Tigner, J., Bayne, E.M., and Boutin, S. 2014. Black bear use of seismic lines in Northern Canada. J. Wildl. Manage. **78**(2): 282–292. doi:10.1002/jwmg.664.

Tigner, J., Bayne, E.M., and Boutin, S. 2015. American marten respond to seismic lines in northern Canada at two spatial scales. PLoS One **10**(3): e0118720. Public Library of Science (PLoS), United States. doi:10.1371/journal.pone.0118720.

Timoney, K., and Lee, P. 2001. Environmental management in resource-rich Alberta, Canada: first world jurisdiction, third world analogue? J. Environ. Manage. **63**(4): 387–405. doi:10.1006/jema.2001.0487.

Triisberg, T., Karofeld, E., Liira, J., Orru, M., Ramst, R., and Paal, J. 2014. Microtopography and the properties of residual peat are convenient indicators for restoration planning of abandoned extracted peatlands. Restor. Ecol. **22**(1): 31–39. doi:10.1111/rec.12030.

Ulanova, N.G. 2000. The effects of windthrow on forests at different spatial scales: A review. For. Ecol. Manage. **135**(1–3): 155–167. doi:10.1016/S0378-1127(00)00307-8.

Veblen, T.T., Kitzberger, T., and Donnegan, J. 2016. Climatic and human influences on fire regimes in ponderosa pine forests in the Colorado front range. Published by: Wiley Stable URL : http://www.jstor.org/stable/2641025 Accessed : 25. **10**(4): 1178–1195.

Vitt, D.H. 1994. an Overview of Factors That Influence the Development of Canadian Peatlands. Mem. Entomol. Soc. Canada **126**(169): 7–20. doi:10.4039/entm126169007-1.

Vitt, D.H. 2008. Peatlands. *In* Encyclopedia of Ecology, 1st edition. *Edited by* S.E. Jørgensen and B.D. Fath. Elsevier, Oxford. pp. 2656–2664.

Weber, M.G., and Stocks, B.J. 1998. Forest fires and sustainability in the boreal forests of Canada. doi:citeulike-article-id:4422466.

Weltzin, J.F., Harth, C., Bridgham, S.D., Pastor, J., and Vonderharr, M. 2001. Production and microtopography of bog bryophytes: Response to warming and water-table manipulations. Oecologia **128**(4): 557–565. doi:10.1007/s004420100691.

Weltzin, J.F., Pastor, J., Harth, C., Bridgham, S.D., Updegraff, K., and Chapin, C.T. 2000.

Response of bog and fen plant communities to warming and ware table manipulations. Ecology **81**(12): 3464–3478. doi:10.1890/0012-9658(2000)081[3464:ROBAFP]2.0.CO;2.

Whitman, E., Parisien, M.A., Thompson, D.K., Hall, R.J., Skakun, R.S., and Flannigan, M.D. 2018. Variability and drivers of burn severity in the northwestern Canadian boreal forest: Ecosphere **9**(2). doi:10.1002/ecs2.2128.

Wiens, J.A., Goble, D.D., and Scott, J.M. 2012. Time to accept conservation triage. Nature **488**(7411): 281. doi:10.1038/488281a.

Yarranton, M., and Yarranton, G.A. 1974. Demography of a jack pine stand. Candadian J. Bot. **53**: 310–314.

Yuan, Z.Y., and Chen, H.Y.H. 2010. Fine root biomass, production, turnover rates, and nutrient contents in boreal forest ecosystems in relation to species, climate, fertility, and stand age: Literature review and meta-analyses. CRC. Crit. Rev. Plant Sci. **29**(4): 204–221. doi:10.1080/07352689.2010.483579.

Züur, A., Ieno, E., Walker, N., Saveliev, A., and Smith, G. 2009. Mixed effects models and extensions in ecology with R. Statistics for biology and health. Springer Science & Business Media.