Post-fire regeneration of endangered limber pine (*Pinus flexilis*) at the northern extent of its range

by

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ABSTRACT

Limber pine *(Pinus flexilis),* an ecologically important species of the montane and subalpine regions of western Canada and the United States, is endangered in Alberta. Limber pine is thought to regenerate following fire, due to its relationship with a bird, the Clark's nutcracker (*Nucifraga columbiana*), which has long been celebrated for preferentially caching pine seeds in open areas. High-severity fire is thus thought to open new areas for colonization, and prescribed fire has been proposed as a recovery tool to stimulate natural limber pine regeneration. Few studies, however, have examined regeneration of limber pine after fire, especially at the northernmost limits of its range. In this study, I examined natural limber pine regeneration within two Alberta burns to determine if limber pine recruitment is occurring following fire, describe how ecological processes influence seedling occurrence and abundance, and define how fire affects the availability of substrates important to limber pine regeneration. I accomplished this by establishing plots within stands where, prior to fire, limber pine had been dominant and plots in limber pine habitat that had not contained dominant limber pine. This was done to test whether fire provided limber pine an opportunity to colonize new habitat, or if recruitment simply occurred in areas in which limber pine had already held a pre-disturbance presence. I also established plots within unburned limber pine stands acting as a seed source to provide a regeneration baseline as a point of comparison. Limber pine regeneration was tallied in each plot and biophysical characteristics of the plot measured.

I found only six post-fire limber pine seedlings within the burns, as compared to 124 similarly aged seedlings found in unburned plots. Seedlings within the burns were all found within 250 m of an unburned limber pine stand. To illuminate the cause of such low

regeneration numbers within the burn, I used a likelihood-based approach to compare hypotheses of ecological processes influencing recruitment. These hypotheses, including seed dispersal, substrate availability, microclimate, and competing vegetation, were modelled against seedling occurrence and abundance in plots. Akaike information criterion (AIC) values and weights provided strongest support for insufficient seed dispersal as the cause of low seedling occurrence within the burn. Due to the low number of seedlings in the burn, the abundance analysis was performed on only the unburned dataset; model selection here showed that when seed distance is small, strong support is found for substrate variables in driving abundance, though seed dispersal variables remain important. Finally, the availability of substrates found to be important to limber pine seedling abundance in the unburned plots was compared by stand type. Similar availability of desirable substrates within the burn as in the unburned plots suggests that safe sites for limber pine regeneration occur within the burn, indicating that these areas may simply not be receiving seed from Clark's nutcracker distribution. Seed dispersal by Clark's nutcrackers may be limited to short distances in the areas studied, despite studies showing far-ranging caching behaviors of nutcrackers for other pine species. Overall, these results indicate that fire may not stimulate limber pine regeneration in some contexts, questioning the proposition of using prescribed burning in Alberta as a recovery tool, unless burning is supplemented by plantings of limber pine seedlings.

DEDICATION

To all the wild places where limber pine grows:

> "The love of wilderness is more than a hunger for what is always beyond reach; it is also an expression of loyalty to the earth, the earth which bore us and sustains us, the only paradise we shall ever know, the only paradise we ever need, if only we had the eyes to see….

> Wilderness is not a luxury but a necessity of the human spirit, and as vital to our lives as water and good bread. A civilization which destroys what little remains of the wild, the spare, the original, is cutting itself off from its origins and betraying the principle of civilization itself."

> — Edward Abbey, Desert Solitaire

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CHAPTER 1. INTRODUCTION

1.1 Project overview

The Rocky Mountains of Alberta are home to a gnarled beauty of a tree- a sentinel of wilderness and symbol of durability and hardiness. Limber pine (*Pinus flexilis*) is an endangered species in the province whose loss could come with dire consequences due to the foundational ecological services it provides (Alberta Whitebark and Limber Pine Recovery Team 2014a). Tragically, it has been grossly understudied, and we thus have large knowledge gaps concerning its ecology, and by extension, mechanisms that could be used to aid its recovery. One of those key gaps concerns its relationship to natural disturbance, namely, fire. We have reason to believe that fire stimulates natural limber pine regeneration (Webster and Johnson 2000), and prescribed fire has thus been proposed as a potential recovery tool (Alberta Whitebark and Limber Pine Recovery Team 2014a). However, we are ignorant of the conditions that will best encourage post-fire recruitment, as no studies have yet been conducted on limber pine's post-fire regeneration niche in Alberta. In addition, we have limited understanding of the relative importance of the proposed mechanisms by which fire would increase regeneration. Is the creation of new limber pine stands limited by dispersal, adequate substrate for germination, or a combination of both? How does fire influence dispersal and substrates for limber pine? All these questions are important to answer before using an expensive tool like prescribed fire which carries the risk of accidental fire mortality of seed source individuals and young recruits should prescribed fire escape.

1.2 Limber pine ecology and endangered status

Limber pine is a five-needled white pine native to the montane and subalpine regions of Alberta. Its entire range stretches from California to its northernmost stands located near the Kootenay Plains Ecological Reserve in the west-central portion of Alberta (Steele 1990). It has a broad elevational tolerance, ranging from approximately 1300 to 2200 m in Alberta (Alberta Whitebark and Limber Pine Recovery Team 2014a), and 900 to 3800 m throughout its range (Steele 1990), giving it the widest elevational range of any conifer in the Rocky Mountains (Schoettle and Rochelle 2000).

Limber pine's broad ecological tolerance extends to a tolerance for an equivalently wide range of ecosystems, including often steep, rocky, or otherwise droughty habitats inhospitable to most other tree species. It is this characteristic of limber pine which makes it so ecologically important. In these harsh environments, the twisted boles of limber pine act as a stabilizing force, reducing erosion, mitigating avalanche potential (Tomback and Achuff 2010), and promoting snow drift accumulation that, in turn, positively influences moisture retention (Baumeister and Callaway 2006). It provides habitat and food for many species, including bears, rodents, and birds, (Tomback and Kramer 1980; Benkman et al. 1984; McCutchen 1996) and, when it lives in more mesic areas where a mixture of limber pine and other tree species are found, is thought to colonize post-disturbance and facilitate establishment of other species (Rebertus et al. 1991; Donnegan and Rebertus 1999; Webster and Johnson 2000).

Limber pine's ability to perform these important ecological roles is currently threatened. The species was listed as endangered by the Government of Alberta in 2008 under the Wildlife Act (Alberta Whitebark and Limber Pine Recovery Team 2014a), evaluated as endangered by the Committee on the Status of Endangered Wildlife in Canada in 2014 (COSEWIC 2014), and is currently being assessed for listing federally under the Species at Risk Act (Species at Risk Public Registry 2018). This endangered status is mainly due to the spread of an introduced fungus (*Cronartium ribicola*) that produces the lethal disease white pine blister rust (WPBR). Introduced to eastern North America in the late 19th century (Kinloch 2003), this disease was first reported in Alberta's limber pine population in 1952 (Bourchier 1952). Infection by WPBR has spread rapidly throughout the range of limber pine, affecting an estimated 88% of Alberta's stands, and on average 43% of trees within those stands (Smith et al. 2013). The disease creates cankers that girdle and kill the affected branch, eventually reaching and killing the main stem (McDonald and Hoff 2001). The initial death of branches inevitably leads to lowered cone production, placing an expiration date on an infected tree's reproductive potential long before the tree itself is killed by the disease (Maloney et al. 2012).

Reduction in cone production due to WPBR infection is especially problematic for five-needled pines due to their heavy reliance on Clark's nutcracker (*Nucifraga columbiana*),

a corvid bird primarily responsible for the distribution of limber pine seeds (Lanner and Vander Wall 1980). Nutcrackers scatter-hoard the large seeds in shallowly dug caches across the landscape (Tomback and Kramer 1980), returning to the caches in winter and spring until other food sources, such as insects, are once again readily available (Tomback 1978). A single nutcracker typically caches between two to three times its caloric needs, leaving some seeds that can subsequently germinate if they were cached in a favorable location (Tomback 1982). In another five-needle pine species, whitebark pine (*Pinus albicaulis*), Clark's nutcrackers are attracted to stands with a threshold density of cones; the smaller number of cones produced by trees infected by WPBR may thus not be sufficient to attract Clark's nutcrackers to the stand (McKinney and Tomback 2007; McKinney et al. 2009; Barringer et al. 2012). This effect may be intensified by red squirrel (*Tamiasciurus hudsonicus*) predation on limber pine cones in infected stands (Benkman et al. 1984; McKinney and Tomback 2007; Siepielski and Benkman 2007; Siepielski and Benkman 2008), although this relationship is dependent on temporal processes such as masting (Peters et al. 2017) and the presence of other cone-bearing trees that can act as an alternate squirrel food resource (McKinney and Fiedler 2010; Peters et al. 2017)

There is a degree of genetic resistance to WPBR naturally present in limber pine populations (Schoettle et al. 2014; Sniezko et al. 2016), and a large portion of the recovery strategy for the species involves growing and planting rust-resistant seedlings (Kinloch 2003; Schoettle and Sniezko 2007; Burns et al. 2008; Alberta Whitebark and Limber Pine Recovery Team 2014a). Unfortunately, however, WPBR does not represent the only risk to limber pine stands. Mountain pine beetle (*Dendroctonus ponderosae*), a bark beetle that primarily attacks lodgepole pine (*Pinus contorta*) and pondersosa pine (*Pinus ponderosa*) (Logan and Powell 2001), will also attack and kill limber pine (Wood 1963; Langor 1989). Stands infected by WPBR may have increased susceptibility to mountain pine beetle attack (Schwandt and Kegley 2004). Mountain pine beetle could also kill trees harboring blister rust resistance, thereby simultaneously reducing stand resilience to WPBR.

1.3 Limber pine and fire

The relationship between limber pine and fire has been little studied, but what studies there are suggest that fire stimulates natural limber pine regeneration and can be used to

combat some of the losses of limber pine to WPBR. Fire, of course, also presents a threat to limber pine, especially if by ill-luck fire were to occur in and kill stands harboring trees genetically resistant to WPBR. The recruitment of new limber pine stands, however, has been assumed to be fire-dependent, in large part due to limber pine's relationship with Clark's nutcracker.

In areas dominated by high-severity, stand-replacing fires, fire is thought to clear out competitor species, providing new habitat for stands of limber pine to establish (Arno and Hoff 1990). In a stand-reconstruction study in the Kananaskis Valley of Alberta, Webster and Johnson (2000) found rapid recruitment of limber pine following high-severity fire in existing limber pine stands, along with establishment of limber pine in areas that it seemingly had not occupied prior to fire. Their main finding was that following infrequent fire-induced extinction events, limber pine is quick to distribute to and recolonize burned sites from unburned stands outside the burned area. Similar findings from the Colorado Front Range showed limber pine colonizing new areas after fire (Veblen 1986; Rebertus et al. 1991; Donnegan and Rebertus 1999).

This recruitment following fire stems from limber pine's dispersal by Clark's nutcracker, which is thought to provide an advantage over wind-dispersed species in the recolonization of burned areas. Wind-dispersed species are obligated to recruit from burn edges or unburned remnants within a burn, thus typically experiencing a steep decline in seed dispersal, and therefore recruitment, with distance from seed-producing adult trees (Greene and Johnson 2000). As a bird-dispersed species, limber pine can disperse far greater distances than can seeds of their wind-dispersed competitors, allegedly allowing them to recolonize even the deep interior of large burns which may not be reached by wind-dispersed seeds (Tomback and Linhart 1990; Coop and Schoettle 2009; Keane and Parsons 2010). Clark's nutcrackers have been observed dispersing seeds at distances of up to 32.6 kilometers from the parent seed source (Lorenz et al. 2011), although shorter dispersal distances are more frequently reported (Tomback 1978; Tomback and Linhart 1990).

There is some evidence that Clark's nutcrackers prefer caching in burned areas. Studies have found that nutcrackers often cache seed in open areas, such as those created by fire, perhaps to capitalize on the enhanced rate of snowmelt or removal of snow by wind that

provides earlier and easier access to cached seed (Vander Wall and Balda 1977; Tomback 1978; Hutchins and Lanner 1982; Tomback 1982). It has also been speculated that the large amount of downed woody debris produced by a fire can be used as a memory trigger by nutcrackers to assist in later retrieval of their caches (Keane and Parsons 2010). Nutcrackers are known to use pattern recognition to reclaim seed from caches, often caching near objects such as logs, snags, or rocks (Hutchins and Lanner 1982; Tomback et al. 1993). A study examining caching of limber pine in an approximately 110-year-old burned area found that limber pine had been distributed to the burn by nutcrackers from limber pine stands approximately 3 km away (Lanner and Vander Wall 1980). Nutcrackers have also been observed caching seed above ground in tree hollows and crowns and caching near trees rather than in openings (Lorenz et al. 2011); as such, the extent to which they preferentially utilize burned areas for caching is unknown.

1.3.1 Fire suppression

If mosaics of fire-created openings in the landscape provide opportunities for limber pine establishment, fire suppression policies may inadvertently reduce the likelihood of new stand establishment. Fire suppression originated as a policy in Canada's Rocky Mountain national parks in 1945 (Woodley 1995). This was followed in 1979 by an acknowledgment of the importance of fire in natural ecosystems and the inclusion of prescribed fire in parks management (Woodley 1995); however, in many areas in Alberta's southern Rockies, the current fire return interval length exceeds the historic baseline (Rogeau et al. 2016). Fire suppression has had the greatest impact in areas prone to low-severity fire, as low-severity fires are typically most easily extinguished. However, the historical fire regime typical to Alberta's limber pine stands is uncertain. As a primarily montane species, limber pine may have experienced low to mixed severity fire regimes, especially as their more open forest structure provides little fuel to carry and spread crown fire (Rogeau et al. 2016). However, in many Albertan limber pine stands, the severe, rocky slopes contain so little vegetation that low-severity fire would be highly fuel limited, with very slow fuel accumulation likely unaffected by fire suppression. Fire suppression may be leading to less available habitat for new limber pine stand establishment in Alberta, potentially requiring management

intervention via prescribed burning to restore historic rates of fire, but the exact effects of fire suppression on limber pine are difficult to state and require further study.

A secondary concern in the wake of fire suppression is the threat of eventual successional replacement of limber pine in established stands by shade-tolerant, competitive species. Limber pine thrives in many environments due to its high-stress tolerance (Schoettle and Rochelle 2000) but is often believed to be a poor competitor against other species. To make matters worse, limber pine facilitates the establishment of other species by providing shelter from the wind and sun (Rebertus et al. 1991; Baumeister and Callaway 2006). Studies from the Colorado Front Range show that these competitors eventually grow larger than the slow-growing five-needle pines, shading out the shade-intolerant pine seedlings, and causing successional replacement as older trees die (Veblen 1986; Rebertus et al. 1991; Donnegan and Rebertus 1999). This prevention of new limber pine recruitment could cause an eventual, slow march of limber pine decline on the landscape as old limber pine die off and are not replaced.

1.3.2 Post-fire regeneration niche

Prior to using prescribed fire as a tool, it is important to understand the regeneration potential of the species after fire. Few studies have examined the survival and recruitment of limber pine in burned areas. The first of these, Coop and Schoettle (2009), examined natural regeneration of limber pine on sites of different burn severities in Colorado. They did find an increase in limber pine regeneration in areas with complete overstory mortality, as compared to unburned areas, but only when data was pooled from all three of their study areas. Looking at each area separately produced more mixed results, with two of the three study areas displaying poorer regeneration in the more severely burned interior of the fire than in partially burned areas, and one of the three study areas showing more regeneration in unburned plots than in either partially or fully burned plots. There did seem to be an association between limber pine seedling presence and more open canopies, a condition which could be caused by more severe fire. Results of this study, although suggestive of a positive relationship between limber pine establishment and burns, highlights the complex nature of regeneration after fire.

A second study, conducted by Smith et al. (2011), was a seed and seedling planting experiment conducted in Waterton Lakes National Park in Alberta. Burned and unburned soil was one of four paired treatment types used in their protocol. Seedlings planted in burned

plots were marginally healthier than those planted in unburned plots. Between these results and those of Coop and Schoettle (2009), there are no definitive answers about the mechanisms by which limber pine seedlings regenerate and survive in burned areas.

1.3.3 Seed dispersal vs. substrate limitations to regeneration

At present, we have a handful of retrospective studies using dendrochronological methods that suggest established limber pine stands initiated after a fire (Veblen 1986; Rebertus et al. 1991; Donnegan and Rebertus 1999; Webster and Johnson 2000). However, these findings are not evidence that limber pine will regenerate on all fires, nor do they tell us the conditions under which fire might maximize regeneration potential. What is needed are more "bottom-up" examinations of natural seedling establishment in burned areas to define fire's impacts on the dispersal and regeneration niche of limber pine.

Plant species are subject to a series of bottlenecks on successful recruitment. Sufficient viable seed must first be available for dispersal, and dispersal then must occur. A subset of dispersed seeds will arrive in a "safe space" for germination, but not all will successfully germinate. An even smaller fraction yet of germinants will survive through to adulthood. Each bottleneck is influenced by different processes, such as climate, abundance of seed predators, availability of adequate substrate for germination, and dispersal methods, and ideal conditions for each stage may differ (Clark et al. 1999). For instance, sites suitable for germination and seedlings may not be ideal for adults or may change over time to no longer support the species (Turnbull et al. 2000).

Disentangling these processes for limber pine is a difficult undertaking, further complicated by limber pine's relationship with Clark's nutcracker. Presence of seedlings at a site far from adult limber pine necessitates that the site was desirable to nutcrackers as a caching location and that conditions at the site were adequate for seed germination and survival. Lack of seedlings at a site, however, may suggest either 1) that the site is not desirable for caching- in which case the adequacy of the site for germination is unknown, or 2) that the site was desirable for caching, but was not a safe germination site. The debate about seed or substrate limitation to seedling recruitment represented here is a classic challenge examined by many plant ecology studies (Eriksson and Erlhén 1992; Clark et al. 2007), but

no studies have focused on their relative importance for the establishment of limber pine following fire disturbance.

1.4 Study Objectives

In 2014, the first iteration of Alberta's Limber Pine Recovery Plan identified crucial research and actions that must be taken to avert the decline of limber pine in Alberta. Recovery efforts are multi-pronged and include protection of stands harbouring potential rust-resistance, alongside actions to encourage regeneration on the landscape, both naturally and through the planting of rust-resistant seedlings. Use of prescribed fire to remove competitor species and stimulate natural regeneration, while simultaneously creating areas potentially conducive to planting rust-resistant seedlings, is an attractive option for encouraging limber pine recovery. Alberta's limber pine recovery plan suggests prescribed fire could be used as a recovery tool but acknowledges further research must first be done to understand how fire affects limber pine's regeneration niche and where prescribed fire may most successfully stimulate regeneration (Alberta Whitebark and Limber Pine Recovery Team 2014a). Prescribed fire is an expensive and time-consuming undertaking (Burr et al. 2001). Managers require detailed information about whether prescribed fire will be successful to maximize efficiency and mitigate expense associated with this recovery tool.

This project aims to address these knowledge gaps by examining limber pine regeneration on one prescribed fire and one wildfire that occurred within dispersal distance of limber pine stands. Specifically, I focus on three questions:

1) Is limber pine recruitment occurring within these burned areas?
2) Which of seed dispersal, availability of substrate, microclimate, or presence of competing vegetation are most driving limber pine seedling occurrence and abundance?
3) How do the variables driving seedling abundance compare between burned and unburned areas?

To answer these questions, I established plots within the burns in stands that had been dominantly limber pine prior to the burn, as well as within stands that had either not contained limber pine or had a minor component of limber pine prior to burning. I also established plots in unburned seed sources to determine a regeneration baseline for seedling establishment

within my study regions and compare this baseline to the number of seedlings found in the burn. I then crafted a series of statistical model hypotheses, each representing one of the driving ecological processes described in question 2 and used an AIC-information theoretic approach to compare their ability to explain seedling occurrence and abundance. Finally, I compare the variables driving seedling abundance across stand types and regions to see how availability of these important factors differ between my burned and unburned study sites. By examining these differences in more detail, I can identify whether burned sites provide a substantially different habitat for limber pine seedlings than do unburned sites, further refining how burning affects the potential for limber pine recruitment. In doing so, I aim to help fill the knowledge gap concerning the role of fire in limber pine recruitment and inform the use of fire in recovery planning for this endangered species.

CHAPTER 2. METHODS

2.1 Study area

Limber pine regeneration was surveyed within two regions containing recent burns in Alberta's R11 Forest Management Unit (FMU) (Figure 1). The R11 FMU includes limber pine's northernmost distribution throughout its entire range. Within this boundary, I focused on areas that had burned from the 2001 Dogrib Creek wildfire (51.67° N 115.42°W, ~10,000 ha), and the 2009 Upper Saskatchewan prescribed fire (52.03°N 116.60°W, ~5,600 ha), as well as surrounding unburned limber pine seed sources. These fires were selected for their age, (being neither so old that regeneration would be difficult to age, nor so young that insufficient time would have transpired for regeneration to occur), size, and most importantly, proximity to adult limber pine that could potentially act as a seed source for regeneration within the burn.

The portion of the Dogrib Creek fire examined occurred primarily in the montane, within a coniferous forest dominated by white spruce (*Picea glauca*) and lodgepole pine (*Pinus contorta*), with scattered small stands of limber pine interspersed throughout rockier, less hospitable regions (Table 1). This fast-spreading crown fire occurred in October under unusually high drought conditions and very high winds (up to 130 km/h). The Upper Saskatchewan fire, as a spring prescribed burn, occurred in a different season than the Dogrib fire. Within its perimeter, substantially large areas burned at high severity, but many patches were left unburned. The mix of montane and subalpine sites surveyed at the Upper Saskatchewan fire had been predominately lodgepole with a minor component of spruce, with larger limber pine stands occurring along ridges, at cliff edges, and along the banks of the nearby North Saskatchewan River (Table 1).

Limber pine seed source dynamics of each burn reflected these pre-burn conditions. The Dogrib fire perimeter contained several small limber pine patches (4.4-8.8 ha) that escaped crown-fire. A few similarly sized limber pine stands are also present outside of the burn perimeter, within the known nutcracker dispersal distance. The Upper Saskatchewan fire, alternatively, was not found to have any substantive surviving limber pine within the interior of the fire perimeter that could act as a seed source. Instead, the burn perimeter is bordered to

the east by an unusually large limber pine stand (~388 ha), with a few small stands to the south and east along the North Saskatchewan River.

2.2 Field sampling

Limber pine regeneration was sampled at three stand types, with abbreviations given in parentheses- limber pine present prior to fire (burned LP), limber pine absent or a very minor stand component prior to fire (burned absent), and unburned limber pine control (unburned). These stand types were chosen to determine if limber pine would re-colonize sites post-disturbance, if disturbance allowed limber pine to colonize new areas previously occupied by competitor species, and to establish a baseline of potential limber pine regeneration within each region. Only sites deemed to be suitable for limber pine establishment were selected, based upon the site's basal area of remaining trees and topography. Mesic, flat sites with high regeneration density of other species (particularly lodgepole) were excluded as limber pine was not expected to effectively compete in these locations (Steele 1990).

At each stand type for each fire, six sites composed of four 50 x 4 m plots were established. Sites were chosen in areas in which four plots could be placed within relatively homogeneous habitat, although occasionally plots did need to be placed in less appropriate locations due to size constraints. Plots were oriented perpendicular to the slope and typically placed along an elevation gradient. The first plot start point was chosen to allow subsequent plots to follow within homogenous habitat whenever possible. I then randomized the distance to the subsequent plot starts using a random number generator of between 25-75 m. When this random number would place plots in unsuitable habitat or in inaccessible topography, the plot was moved to the nearest suitable location or a new random number was drawn.

Data collected within each plot included elevation, aspect, and slope. Elevation was read from a Garmin 64S. Slope was derived from a clinometer. Aspect was read from a declination corrected compass pointed in the direction of the predominant aspect. This was later translated to Heat Load Index as in equation 3 of McCune and Keon (2002):

Heat load index (HLI) = 0.339 + 0.808 * cos(latitude) * cos(slope) – 0.196 * sin(latitude) * sin(slope) – 0.482 * cos (π – absolute((π- absolute(aspect- π)- π*1.25)) * sin (slope)

This equation rescales aspect to a scale of zero to one in which zero is the coolest slope and one the warmest, while also taking into consideration the effects of slope and latitude on incoming solar radiation.

To characterize the plot, I established five 1m x 1m micro-plots at 5, 15, 25, 35, and 45m along the main plot. Within each of these micro-plots, I measured ground cover broken into 13 cover categories (tree regeneration, shrub, ground shrub, herb, live grass, dead wood, rock, bedrock, exposed mineral soil, lichen, litter, moss, and other). In addition, soil texture and litter depth were measured by digging a small hole in the center of each micro-plot. Soil texture was classified using the flowchart from Archibald et al. (1996). Basal area was measured to species at each micro-plot using a basal area prism (factor 2), with separate tallies for living and dead trees of each species. Dead trees were identified using their silhouette form, knowledge of the dominant species present at the site prior to the burn, and other clues such as remnant cones and habitat type. Dead limber pine, which tends to have a more open growth form than lodgepole pine, was occasionally difficult to distinguish from lodgepole pine. In these situations, a final species assignment was made using contextual clues, or alternatively, the tree was classified as "unknown". Snags taller than breast height that were not recognizable were also placed in this category. Measurements were later converted to the variable "proportion limber pine", describing the proportion of living and standing dead basal area that was limber pine within each plot, quantitatively identifying plots that had contained limber pine prior to fire, and "proportion dead", describing the proportion of dead trees of known and unknown species within the total living and dead basal area. A spherical densiometer was used to determine live canopy cover. These values were then averaged to arrive at an overall basal area, ground cover, canopy cover, and soil profile for the plot. Soil texture values were converted to numerical classes from 0 to 5, 0 being the coarsest, to allow averaging of the values for the plot (Table 2).

A complete search for regeneration was conducted in the 50 x 4 m plot. Seedlings of all tree species were tallied; a stem was included in this tally if it was less than 1.4m tall. Trees

greater than this height were considered saplings and included in the basal area measurement, when applicable. Extra data was gathered for any limber pine seedlings found. Caching by Clark's nutcrackers can sometimes result in several limber pine seedlings growing in a cluster. The number of seedlings within a cluster was thus noted, with the height of all seedlings described. For the purpose of statistical analysis in this thesis, number of or occurrence of "seedlings" or "regeneration sites" refers to the number of or occurrence of seedling clusters, as all individuals within a cluster represent a single nutcracker caching event, as in Leirfallom et al. (2015). Most seedlings found were single individuals, justifying the use of this method.

I then aged the tallest seedling in a cluster by counting the annual growth whorls present on the stem. These whorls can be difficult to see, especially in seedlings taller than 50 cm. I attempted to age all seedlings encountered but typically did not arrive at an age estimate for seedlings taller than the 50 cm threshold. These age estimates were then used to differentiate regeneration sites that had germinated in the time since fire period from older seedlings that were advanced regeneration (established prior to the fire) in both the burned and unburned plots. Only seedlings from the post-fire age class were used in the analyses. Since the counting of annual growth whorls can be inaccurate, there is a possibility of misclassifying the age group of seedlings whose true age was near the fire age.

The distribution of limber pine in Alberta is currently not thoroughly mapped. To address the challenge of missing potential seed sources, a helicopter survey of both the Upper Saskatchewan and Dogrib regions was conducted. Good potential habitat for limber pine in these regions was first found using ArcGIS and flagged for examination during the flight. Areas with limber pine were spotted from the helicopter and marked on GPS for later investigation on the ground. Several previously unknown limber pine stands within the Dogrib region were identified. I later mapped each of these stands by foot, using a Garmin 64S GPS to regularly mark stand boundary points. No new limber pine stands were found in the Upper Saskatchewan; polygons of these stands had already been mapped and were obtained via the Alberta Conservation Information Management System (ACIMS).

Using the boundary points mapped in the Dogrib Region, polygons for each stand were produced in ArcGIS to determine the approximate size of each stand. Stand size was also calculated for the stand polygons from the ACIMS database for the Upper Saskatchewan

region, after slight changes to the polygons based upon ground truthing of stand boundaries and satellite imagery. These sizes were then multiplied by the average basal area measured within each of these seed source stands to derive the variable *seed strength*. This variable was used as an estimate of the area of total living limber pine available to act as a source of seed to nearby plots. The distance from each plot's centroid to the nearest of these seed source stands was also calculated using planar distance via the "Generate Near Table" in the Analysis Tools, Proximity toolbox to arrive at the variable *seed distance*. This variable was later found to suffer from quasi-complete separation in the analyses, leading to highly inflated and biased parameter estimates (Zhao and Iyengar 2010). Nutcrackers most frequently cache seeds within 100 m of a seed source, with occasional longer distance trips (Hutchins and Lanner 1982). Seed distance was thus later categorized into plots placed at either greater than or less than 100 m of a limber pine stand to reflect this nutcracker caching tendency and avoid statistical issues due to quasi-complete separation.

2.3 Data analysis

2.3.1 Formulation of hypotheses

To test the relationship between limber pine occurrence, abundance and potential drivers of those processes, I proposed four competing hypotheses of environmental/biotic factors to determine which had the strongest explanatory power for the observed data. The four hypotheses (with abbreviations listed in parentheses) were: 1) seed availability and distribution by Clark's nutcrackers (seed), 2) abiotic substrate type (soil), 3) variables affecting and that could act as a proxy for moisture availability and solar radiation (microclimate), and 4) presence of competing vegetation (vegetation).

To identify variables to be included in each of the hypotheses, exploratory data analysis was conducted as suggested in Zuur et al. (2010). The variables lichen, moss, seedling regeneration, and bedrock measured as a component of the percent cover plots were found to be either rare, did not vary substantially, or did not capture information relevant to the hypotheses above, and were excluded from further analysis. Examination of the derived variable seed strength revealed that the one large stand of limber pine in the Upper Saskatchewan strongly dominated that region as it was vastly larger than all other stands,

creating a sharply bimodal and nearly categorical distribution. This variable was thus removed from further analysis. Pair-plot correlation coefficients and variance inflation factors (VIF) were then used to assess potential collinearity of variables and ensure no variables included within one hypothesis category had a VIF greater than 3 or correlation coefficients greater than 0.7 (Zuur et al. 2010; Dormann et al. 2013) (Appendix 1, Table 11 & Table 12). Rock cover, litter depth, and litter cover were found to exceed this threshold; litter cover and litter depth were thus combined to create the variable "litter volume" as described in Table 2 which decreased its collinearity with rock cover to an acceptable level. Total living basal area, proportion of dead basal area, and basal area of living limber pine were also considered and found to be highly collinear (Appendix 2, Table 13, Fig. 6); basal area of living limber pine was chosen of these to represent the locally available seed source. All variables assigned to and considered within each hypothesis and explanation of each are given in Table 2, with a description of variables excluded provided in Table 14.

2.3.2 Description of analyses

I then conducted four analyses on the data as summarized in Table 3. First, seedling density was compared by region and stand type. This described the differences in regeneration processes between these stands and areas studied, though in this analysis regeneration was not corrected for time since fire, to aid interpretability of differences in results.

Each hypothesis set then was evaluated against the occurrence of limber pine seedlings in all stands (analysis 2). This allowed identification of the ecological factors which best explain observed presence and absence of regeneration sites in plots across the landscape. Stand type was considered for inclusion in this analysis but found to be collinear with many of the tested variables, which effectively defined the differences between stands. Multicollinearity between variables creates many issues in regression analyses, including biased parameter and standard error estimation, which can affect variable significance (Farrar and Glauber 1967; Graham 2003). Stand type was thus not included in the models to reduce collinearity (Dormann et al. 2013); instead, the hypothesis sets described above were created to include quantitative variables that may differ by stand type and describe ecological processes which might be driving seedling occurrence.

Then, the explanatory strength of the same hypothesis sets was assessed for abundance of limber pine seedling clusters (analysis 3). The abundance analysis was limited to unburned stands due to the low number of limber pine seedlings found in the burn. Abundance models performed across all stand types using both quantitative variables and stand type were considered but again suffered from high multicollinearity between stand type and other variables resulting in biased parameter estimates, significance values, and poor model fit (Farrar and Glauber 1967; Graham 2003) (Appendix 3, Table 15, Fig. 7). Excluding stand type from these models still resulted in poor model fit and under-dispersed data (Appendix 3, Table 16, Fig. 8), likely due to problems of zero-inflation as there were very few seedlings found in the burn. Restricting the analysis to the unburned stand type allowed me to avoid these problems of zero-inflation and offered greater exploration of variables important to limber pine regeneration when the hurdle of seed distribution distance is minimized, while also preventing the exaggeration of importance of variables associated with unburned stands (Zuur and Ieno 2016). Zero-inflated and zero-altered models were also considered but ultimately rejected as a methodology because the above limitation provided a simpler paradigm in which to examine seedling abundance. The variable *seed distance* was removed from the seed hypothesis for this analysis, as all unburned plots contained living adult limber pine that could act as an immediate seed source.

In the fourth analysis, variables determined to be important to abundance in the unburned stands were then compared across stand types to examine if those variables differed between burned and unburned plots. This analysis was necessary for identifying whether factors important for limber pine recruitment in the unburned plots were available within the burned area, providing additional clarification to the processes driving limber pine regeneration.

Overall, in the first analysis, I compare the difference in regeneration by stand type. In the following two analyses I compare the strength of evidence of the four proposed ecological process hypotheses (seed distribution, microclimate, soil substrate, and competing vegetation) on seedling occurrence between the two burned and one unburned stand types and abundance in the unburned stand type. Due to little data found in the two burned stand types, the occurrence analysis primarily evaluates which of these ecological processes may be most

limiting seedling occurrence. For this same reason, the abundance analysis was limited to the unburned stand type. The fourth analysis relates the variables found as important to limber pine regeneration in the unburned stand type back to those found in the burn, describing their availability and thus potential for affecting limber pine regeneration following fire.

2.3.3 Statistical methodology

All analyses were performed in R version 3.4.3 (R Core Team 2017) using generalized linear mixed effects models fit with the package glmmTMB (Brooks et al. 2017). Random intercepts were allowed by site to account for lack of independence between plots clustered within each site. Prior to fitting the models, all continuous explanatory variables were standardized so each had a mean of zero and standard deviation of one. This simultaneously allows variables at different scales to be more easily compared while also improving model convergence (Zuur et al. 2009). Logistic regression occurrence models were fit using a binomial distribution to define the probability of seedling occurrence, given variables in each hypothesis. Comparison of seedling density by stand type and abundance models were fit using a log-linked Poisson distribution. For these analyses, the dispersion statistic for the top-performing models was calculated and compared to the dispersion statistics in 1,000 simulated data sets, given the estimated parameters of each model. In each case, the true dispersion statistic was well within the realm of potential values, suggesting the data was not over-dispersed and the Poisson distribution provided sufficient variation to fit the data. Finally, abundance models included an additional offset variable for the age of the fire. Poisson distributions assume discrete count data, thus preventing explicit correction of seedling abundance for the different times since fire in the Dogrib and Upper Saskatchewan regions. Use of an offset allowed for better comparison of abundance data between the two regions, while still allowing the response variable to be in the form of discrete counts. Note, however, that the response in these models is thus technically counts of seedling clusters per year since fire, due to the use of the offset.

Hypotheses for the occurrence and abundance analyses were compared using Akaike information criterion (AIC). AIC provides a measure of the relative strength of evidence for each hypothesis, while also penalizing model complexity which otherwise could provide greater model fit (Burnham and Anderson 2002). Variables within each hypothesis category

as described in Table 2 were iteratively removed based upon principles of reducing AIC and model parsimony. This was accomplished by eliminating variables which did not contribute to ΔAIC>2. Removal of extraneous variables ensured that no individual hypothesis was unduly penalized for complexity which did not substantially improve model fit, while also providing an opportunity to evaluate which of the variables within each hypothesis category best explained the response. Pseudo-R^2 values were calculated for each parsimonious model as in Magee (1990) as an additional objective measure of model fit. This measure of fit compares the likelihood ratio of the fitted model to a null model including random effects and thus represents the variance explained by the fixed effects. Adjustments were accounted for such that the likelihood ratio would achieve 1 at its maximum (Nagelkerke 1991). Pseudo-R^2 values were calculated using the MuMIn package in R (Barton 2018).

Each hypothesis category's AIC was then compared, as a measure of which ecological process best described the observed data. However, seedling regeneration is not a product of any one of these processes alone. Retained variables were then added to a combined model to examine variable significance and the relative strength of each variable on seedling cluster occurrence and abundance, as judged by their coefficients, when used in combination to model the response.

Finally, variables retained in the top performing abundance models from the unburned stands were compared across stand types to examine how their availability differed between unburned and burned plots. In these models, each variable indicated as important to abundance was taken as the response variable and modelled against region and stand type. Interactions between region and stand type were considered and retained when significant. Since many of these variables were bounded (i.e. percent cover values ranging between 0-1), a beta-distributed GLMM was used. Site was again used as a random effect to account for lack of independence of plots within sites. Because the beta distribution requires values to be greater than zero and less than one, a slight transformation was applied to each environmental variable so as to convert values to something very near their original value, while removing all instances of zeros and ones (Cribari-Neto and Zeileis 2010).

CHAPTER 3. RESULTS

3.1 Seedlings found by stand type

After searching 144 plots (2.88 ha), 96 (1.92 ha) of those in the burned stand types and 48 (0.96 ha) in the unburned control, I found a total of six post-fire aged limber pine regeneration sites in the burn (Table 4). In comparison, 124 similarly aged regeneration sites were found in the unburned limber pine plots. Of the post-fire regeneration sites found in the burn, five were found in the burned limber pine stand type and one was found in the burned limber pine absent stand type (Fig. 2Figure 2). Statistical comparison of seedling cluster density found significant differences between the burned absent and burned LP stand types and the unburned stand type by region (Table 5, Fig. 3). No statistical difference was found between the burned absent and burned LP stand types.

The number of regeneration sites found in the Dogrib and Upper Saskatchewan was similar after accounting for time since fire. Four of the six seedlings clusters were found in the Dogrib region; two were found in the Upper Saskatchewan, aligning with the doubling of time since the Dogrib fire (16 years) than had elapsed for the Upper Saskatchewan prescribed burn (8 years). It is unlikely that seedling regeneration occurs linearly with time since disturbance in this manner, but differences in the time since fire period are important to consider in comparing the two regions. In the unburned control, of the 124 post-fire aged seedling clusters found, 88 were found in Dogrib and 36 were found in Upper Saskatchewan (Table 4). The percentage of seedlings from both unburned regions found in clusters was comparable; in Dogrib, 26% of the seedlings found were in clusters, while in Upper Saskatchewan clusters comprised 28% of the seedlings in the unburned stand (Table 4). In the burned plots, 1 of the 6 regeneration sites found was in a cluster; this was found in the burned limber pine stand type in the Upper Saskatchewan (Table 4).

From a cursory look at the data and before running models, distance to seed source appeared to have a large effect on the presence of seedlings at the burned plots. The six post-fire aged regeneration sites found in the burned stand types were found over four plots, each of which were located within approximately 250 m of a limber pine seed source (Fig. 4). The closest of these plots to an unburned limber pine stand contained 3 seedlings; the other three

plots contained one seedling each. Note that of the plots in the two burned stand types, 24% were within 250 m of an unburned limber pine stand. Plots in the two burned stand types were placed between 21 m to 4125 m away from unburned limber pine stands, all well within the known distribution distance of Clark's nutcracker. Sixty percent of plots were placed within 1000 m of an unburned limber pine stand, with other plots placed at greater distance to capitalize on good potential habitat and determine whether seedlings might occur at greater distances (Appendix 4, Fig. 9).

3.2 Ecological processes influencing seedling occurrence

Of the hypotheses of ecological processes affecting seedling occurrence, seed distribution was found to have more support than the other three proposed models (AIC_{wt}= 0.83; Table 6). Microclimate performed similarly well to this top model (ΔAIC= 3.2, AIC_{wt}= 0.17), with a similar variance explained by the fixed effects by both the seed and microclimate hypotheses (pseudo-R^2= 0.36, 0.33 respectively) despite the strong AIC_{wt} given to the seed hypothesis.

Competing vegetation and soil as alternative hypothesis candidate models had ΔAIC values of >10, a threshold past which a hypothesis is typically considered to have little to no support in comparison to the superior hypothesis. Akaike weights for these models further supported their lack of evidence, as they were negligible for both hypotheses (AIC_{wt}= 0.00, Table 6). Each model did still explain variation somewhat better than the null, with better explanatory power provided by the soil hypothesis (pseudo-R^2= 0.17, Table 6) than the vegetation hypothesis (pseudo-R^2= 0.09, Table 6)

Within each model hypothesis, only variables providing substantial contribution to model fit, while still accounting for parsimony, were retained from the full models proposed in Table 2. From the seed hypothesis, only seed distance was retained, while in the microclimate model, only canopy cover was retained. Of the variables proposed in the soil and competing vegetation hypotheses, litter volume, downed wood, and herb cover were found to be the variables which best contributed to the model (Table 6).

Seed distance and canopy cover were found to have the greatest impact on the probability of seedling presence when modelled in combination with other retained variables

(Table 7). Seed distance had a strongly negative effect on the probability of post-fire seedling presence, with distances greater than 100 m decreasing the log odds of finding a seedling at a plot by 5.566. Translated to probability, the probability of finding a seedling at greater than 100 m from a seed source given the combined model (while holding all other variables at their mean) was 0.4%, while the probability of finding a seedling in a plot less than 100 m from a seed source stand was 29.0%. Canopy cover was associated with a greater likelihood of finding a seedling, with each unit of increase in canopy cover from the mean associated with a 1.557 increase in the log odds of seedling presence. Presence declined with greater values of downed wood cover, with a marginal amount of significance ($p=0.067$, Table 7). Neither herb cover nor litter volume was found to have a significant influence on seedling presence when modelled in combination with the better explanatory variables from the other, more competitive hypothesis categories of seed distribution and microclimate.

3.3 Ecological processes influencing seedling abundance in unburned stands

Only the seed and soil models were found to have support for driving seedling abundance in the unburned stands. Soil had the definitively strongest support ($AIC_{wt}= 0.98$, Table 8), though seed distribution did provide some explanation of the variation seen in abundance across plots (pseudo-$R^2= 0.30$), despite the low weighting given the hypothesis ($AIC_{wt}= 0.02$). The microclimate and vegetation final models performed approximately as well as one another ($AIC= 209.0$, 211.2 respectively) and were found to have some explanatory power as compared to the null, with greater explanation provided by the vegetation hypothesis (pseudo-$R^2= 0.19$) than the microclimate hypothesis (pseudo-$R = 0.10$). However, the large ΔAIC between these and the top two hypotheses suggests that vegetative competition and microclimate do not play strong roles in limiting or promoting limber pine seedling recruitment within unburned stands where limber pine predominates.

From the soil hypothesis, soil texture, rock cover, and exposed mineral soil cover were all selected as variables important to seedling abundance. Taken at the mean value of all other variables included in the model, a change in mineral soil cover, soil texture, and rock cover by one unit would translate to a -0.607, 0.477, and 0.400 in the log abundance of limber pine seedling clusters per year since fire (Table 9). In the seed model, basal area of alive limber pine was retained and found to have a positive association (coefficient= 0.481, Table 9) with

seedling abundance. From the less competitive vegetation and microclimate models, grass, number of other regenerating seedlings and canopy cover were retained and did not have a significant effect on seedling cluster abundance when analyzed in combination with the other variables.

3.4 Comparison of substrate availability between stand types

Following the abundance analysis, all variables retained in the top hypothesis (soil) were compared by region and stand type. This step was performed to determine if the relative absence of limber pine seedlings in the burn may be attributable to differences in these characteristics between stand types since the abundance analysis was only conducted on the plots from the unburned stand type. Variables from the second-best performing hypothesis (seed) were not compared, as the only retained variable (alive limber pine basal area) was known to differ between burned and unburned plots.

Soil texture and percent covers of exposed mineral soil and rock were compared. Percent cover of exposed mineral soil and rock differed significantly by region, with soil cover values tending to be larger in the Upper Saskatchewan region and rock cover values larger in the Dogrib region (Fig. 5**Error! Reference source not found.**, Table 10). Soil texture values t ended to be similar between the regions, except for somewhat finer soil textures in the burned absent stand type in the Dogrib region than those found in the Upper Saskatchewan region.

More importantly, however, within each region soil cover and rock cover values did not differ significantly by stand type, suggesting that the pre-fire environmental conditions were similar, and neither fire nor post-fire regeneration had a long-term effect on changing the availability of these substrates (Fig. 5**Error! Reference source not found.**, Table 10). W hether these variables differed immediately following fire and had an effect on the availability of potential limber pine seedling germination sites cannot be stated. Soil texture did differ significantly by stand type, but only in the burned limber pine absent stand type in the Dogrib region. As soil texture would not be affected by fire, this was an artefact of sampling design and in this region may simply demarcate the difference in where limber pine typically grows, as the unburned limber pine and burned limber pine stands had nearly identical soil texture values. The lack of significant differences between these values between stand types in each

region suggests that good limber pine seedling microsites may be available in the burned area but that seed distribution to these safe germinating sites is not occurring with regularity, or that an unmeasured factor is preventing seedling germination and survival if they are being distributed to the burned areas.

CHAPTER 4. DISCUSSION

Given the expanding threat and mortality induced by WPBR infection in Alberta's limber pine stands (Smith et al. 2013), stimulation of natural regeneration of limber pine through use of prescribed fire is an attractive restoration strategy. My study provides much-needed insight into the post-fire regeneration dynamics of limber pine in the northern extent of its distribution and reflects the variability in limber pine successional processes that are to be expected across its diverse geographic and elevation range (Steele 1990; Coop and Schoettle 2011). Overall, the overwhelmingly low numbers of limber pine I found within the burned areas suggest prescribed fire may not be an effective recovery tool in some contexts and burned areas may require supplementary limber pine seedling plantings to achieve restoration goals. Occurrence of limber pine regeneration across both burned and unburned areas was best explained by variables related to seed dispersal, while abundance of limber pine seedlings in the unburned areas was best explained by the abiotic substrate availability, most notably the soil texture and cover of rock and soil. Availability of these substrates did not tend to differ by stand type, suggesting that 1) suitable substrates may be available within the burn but are not receiving seed and 2) fire did not have long-term effects on these variables within this system.

4.1 Limitations to limber pine recruitment in burned areas

The finding of only five limber pine seedling clusters at the burned limber pine plots and one limber pine seedling cluster at the burned limber pine absent plots was contrary to expectation. As there were so few post-fire seedlings found and stand type was multicollinear with many variables, models exploring the ecological variables between the unburned, burned limber pine, and burned absent stand types were of limited value (Appendix 3, Tables 15 & 16, Figs. 7 & 8). However, comparison of seedling cluster density by stand type and region showed that unburned limber pine stands had significantly greater regeneration than the two burned stand types, which did not differ significantly from one another (Fig. 3). My results (Fig. 2, Table 4), and mixed model analysis (Table 5), show that fire did not effectively stimulate limber pine regeneration within either burned stand type. All limber pine seedling clusters found within the burn were near the burned edge, with surviving limber pine no more than 250 m away.

There is a dominant narrative about how fire benefits five-needle pines based on the limited handful of studies which have been conducted on the species. Of these, dendrochronological studies examining limber pine stands have previously described limber pine as an early-successional colonist (Rebertus et al. 1991). When fire occurs, limber pine is expected to be distributed by Clark's nutcrackers to those spaces, where it establishes and then, especially in xeric areas, facilitates establishment of other species (Rebertus et al. 1991; Donnegan and Rebertus 1999). Following facilitation and establishment, these competing species are expected to potentially successionally replace limber pine when stands are not subjected to re-occurring fire.

It was thus surprising to find so little regeneration within the burn. Burned limber pine stands were expected to be re-colonized by limber pine via distribution to the site from outside of the burn (Webster and Johnson 2000), as these areas were demonstrably good habitat for limber pine. In areas where competing species were cleared out from good limber pine habitat, limber pine's mutualistic relationship with Clark's nutcracker was expected to provide limber pine a competitive advantage over other species which do not have long-distance dispersal mechanisms (Rebertus et al. 1991). This simple narrative is compelling, but growing evidence suggests that the relationship between five-needle pines and fire is more complex than this.

Studies of limber pine showing establishment after fire have been dendrochronological studies (Rebertus et al. 1991; Donnegan and Rebertus 1999; Webster and Johnson 2000) or done at close distance to the burned edge (Coop and Schoettle 2009). Results of dendrochronological studies, though powerful in explaining processes of species establishment and growth, are often used to describe stochastic, system-dependent processes as deterministic. There is growing appreciation among both general ecologists and the five-needle pine community that processes once thought to be constant, such as post-disturbance establishment and succession, are far more elastic and unpredictable, depending greatly on the suite of weather conditions, co-occurring vegetation, severity of disturbance, and other often unpredictable elements which may change the trajectory of colonization and subsequent succession of the stand (Campbell and Antos 2003; Eliot 2007; Amberson et al. 2018). Although my findings of little regeneration in the burned areas would seem to be at odds with these dendrochronological studies describing limber pine as an early disturbance colonist, this

element of stochasticity and localized differences in processes such as seed dispersal and substrate availability must be taken into consideration. In addition, the low regeneration numbers found in the burn in this study describe conditions that may not be targeted in a dendrochronological study of limber pine, which would be unlikely to focus on areas of limber pine absence. Re-establishment or post-disturbance colonization of sites certainly happens in some conditions, but may not occur in all, depending on other factors such as overall forest type and co-occurring vegetation, climate, and nutcracker caching behavior in relation to these more variable factors.

One of the factors not considered by the narrative of competitive advantage of limber pine in recolonizing burn interiors is the importance of aerial seed banks and, in large fires, residual tree islands of limber pine's competitors. Both can provide seed for post-fire regeneration of competitors to limber pine. In my study areas, the predominant competitors to limber pine are lodgepole pine and white spruce (Table 1). In large burned areas dominated prior to fire by species with aerial seed banks, such as lodgepole pine, pre-fire forest composition is predictive of post-fire regeneration regardless of distance (Johnson 1992; Greene and Johnson 1999). Recruitment of wind-dispersed species, like white spruce, theoretically ought to decline substantially with distance from the nominal burned edge (Greene and Johnson 2000). Greene and Johnson (2000) however, found that in practice, burns typically leave residual surviving spruce, with average distance between random points within large burns and residual tree islands of 150 m. High regeneration densities for wind-dispersed species have been found out to distances of 400 m from a stand edge (Donato et al. 2009). In practice, therefore, seed of species functioning as competitors to limber pine may have a substantial advantage in recolonizing burned areas. This effect theoretically could be amplified when residual stands of limber pine are not of sufficient size to attract nutcrackers (McKinney et al. 2009; Barringer et al. 2012), a problem not present for wind-dispersed seeds of species like spruce. This effect is highlighted by my finding of regeneration of lodgepole and white spruce within the burn with limited recruitment of limber pine (Appendix 6, Fig. 10). By studying sites that extended from seed sources to 4000m distant from seed harvest stands, I show that limber pine, at the mercy of nutcracker caching whim, may, in fact, be at a disadvantage when colonizing large burns, contrary to the popular narrative.

In addition, much of the support for a close relationship between fire and five-needle pines comes from studies focused on whitebark pine. Whitebark and limber pine are ecologically similar species, differing primarily in their elevational distribution and dependence on nutcrackers for dispersal. Both five-needle pines live in mountainous environments and share nutcracker dispersal, and it is thus tempting to apply findings from the far better-studied whitebark pine to limber pine management. These studies show nutcrackers often caching whitebark seed in openings (Tomback 1978; Hutchins and Lanner 1982; Tomback 1982), along with frequently greater seedling success of whitebark pine seedlings in areas following disturbance (Tomback et al. 1993; Larson and Kipfmueller 2010; Tomback et al. 2011; Klutsch et al. 2015; Perkins 2015). This greater success rate is often attributed to release from shade, which may have otherwise suppressed seedlings.

Despite the temptation to lump them together based on these similarities, differences in habitat and co-occurring vegetation between whitebark and limber pine may translate to different relationships with fire. Alberta's whitebark pine is found as a typically co-dominant component of subalpine mixed forests (Arno 2001; Alberta Whitebark and Limber Pine Recovery Team 2014b) and tends to be self-replacing at upper treeline or exposed sites where fire is rare (Natural Regions Committee 2006). This is an important distinction from limber pine, which in Alberta is more often found in open forests within the drier, warmer aspects of the montane or highly rocky and exposed regions of the subalpine (Alberta Whitebark and Limber Pine Recovery Team 2014a). These differences in forest types, and thereby fuel availability, lend themselves to important differences in prevailing fire regime. Lower availability of fuel in the montane has historically resulted in frequent, low-severity fires with the occasional high severity fire, whereas the subalpine region typically enjoys a longer fire return interval with a resulting increase in fire severity (Rogeau et al. 2016). In the most extreme, rocky environments of the montane and subalpine (such as those sometimes occupied by limber pine), fuel would be so sparse as to make fire events occur at extremely long intervals.

These are especially important differences when considering nutcracker caching behavior. Nutcrackers caching subalpine whitebark pine seeds may be more dependent on infrequent fires to open the canopy for caching events in which nutcrackers converge on the

newly created openings, though studies of nutcracker caching in burned area's in Alberta found approximately equal regeneration within unburned seed sources and up to 50m within the burn perimeter (Drummond 2018). However, in Alberta's montane ecoregion, the predominant habitat for limber pine, a generally more open forest structure may decrease the overall importance of high-severity fire in creating suitable caching locations. Fire may thus be less important for regenerative processes in Alberta's limber pine forests than for whitebark pine found in mixed stand types.

It should be noted that limber pine seedlings were found at typically healthy densities in the unburned stand type within the post-fire time period for both the Upper Saskatchewan and Dogrib regions (Table 4; 75 seedling clusters/ha for Upper Saskatchewan, 183 seedling clusters/ha for Dogrib). Regeneration densities were comparable to or better than those found in other limber pine studies (Lanner and Vander Wall 1980; Coop and Schoettle 2009; Cleaver et al. 2016), especially after accounting for differences in time since disturbance and that other studies included all stems, rather than clusters, in their density measurements. This implies that the lack of seedlings in the burned stands was due to differences in seed dispersal or germination potential between the stand types, rather than a result of general reproductive failure across the region.

Lack of regeneration in the burn was also unlikely to have resulted from low seed availability. A mast year was observed directly in the Upper Saskatchewan region and more broadly across Alberta in 2010 (Peters et al. 2017), the year following fire in the Upper Saskatchewan, and again in 2013 (VS Peters, personal communication). Mast years are known to occur in limber pine every two to three years (Alberta Sustainable Resource Development and Alberta Conservation Association 2007), suggesting that several mast years had also occurred in the Dogrib region between the 2001 fire and my regeneration surveys conducted in 2017. Both regions were thus exposed to large seed crops in the time since fire period, suggesting that low regeneration of limber pine in the burns was not a result of lack of seed for caching.

4.2 Seed distance and other factors influencing seedling absence from the burns

Comparison of the hypotheses for limber pine seedling occurrence indicates a strong influence of seed distribution on the presence of limber pine regeneration (AIC_{wt}= 0.83; Table 6). Model selection on the seed hypothesis highlighted the sizeable importance of seed distance, as this was the only variable retained. All seedlings found within the burn were within 250 m of a seed source. The importance of seed distance as a variable is thus somewhat unsurprising, though 250 m is a relatively short distance for Clark's nutcracker to travel to cache seed.

Nutcrackers have been observed caching seed at distances up to 32.6 km from a seed source stand (Lorenz et al. 2011). Much emphasis has been placed on these long-distance dispersal events, especially as a basis for stocking of areas following disturbance. Nutcracker cache location choices, however, are being revealed to be based upon a balance of short-term and long-term energetic requirements (McLane et al. 2017). Dispersal of seed at longer distances represents a series of trade-offs: does the potential future accessibility of seed dispersed at distance provide enough mitigation of long-term risk to offset the energy and time expenditure (Bonte et al. 2012)?

A recent radio-telemetry study of Clark's nutcracker provided insight into other factors affecting nutcracker caching choice. Of these, proximity of caching locations to nutcracker breeding and nesting grounds was found to greatly determine nutcracker caching locations (Lorenz et al. 2011). Prior studies acknowledged the importance of proximity of cached seed to reproductive habitat for nutcrackers to capitalize on short trips during a time when energy demands for reproduction are high, while food availability is low (Vander Wall and Balda 1977). Possible attack by aerial predators also greatly affected nutcracker choice, with odds of a site being selected for caching decreasing by 13% for every 1m distance from a tree that could provide concealment and thereby reduce predation risk (Lorenz et al. 2011). Finally, nutcracker cache site preference may also change with elevation, an important consideration for potential differences in caching of whitebark and limber pine where the two co-occur (Lorenz et al. 2011). Cache site selection in openings that provide easier and earlier access to seed due to snowmelt and wind removal, though well-documented in the literature, is thus only one of many factors influencing nutcracker choice. The complexity of nutcracker choice

and high degree of home range fidelity led Lorenz et al. (2011) to conclude "management techniques designed to encourage seed caching by nutcrackers (e.g. thinning and prescribed burning) may not affect the caching behavior of residents".

My finding of a strong relationship between seedling occurrence and distance from a seed source is not unlike findings from the whitebark pine literature. Several studies have found a strong, typically negative exponential relationship between seed distance into a burn and seedling occurrence or abundance, though the maximum distance at which seedlings were still found varied from a few hundred meters to several kilometers (Tomback et al. 1990; Moody 2006; Klutsch et al. 2015; Leirfallom et al. 2015). Hutchins and Lanner (1982) found nutcrackers primarily caching limber pine seeds within 100m of a seed source stand, with some subsequent re-caching of seed at one location approximately 3.5 km away. The only other study of natural limber pine regeneration following fire also found a negative association between seed distance and regeneration occurrence, but plots in this study were placed at a maximum of 100m from the unburned edge (Coop and Schoettle 2009).

Though these studies seem to contrast with findings of long-distance caching behavior (Vander Wall and Balda 1977; Vander Wall 1988; Lorenz et al. 2011), I suggest a simple explanation to reconcile the differences. Long-distance flights of nutcrackers may occur when a home range providing good breeding habitat, protection from predators, and retrieval opportunities due to rapid snow removal is found at distance. This would thereby justify the greater energy, time, and opportunity cost necessitating fewer total caches being made. By extension, if seed harvest stands are within a nutcracker's home range and fulfill all the necessary requirements, shorter distance caching would be the most efficient strategy. As such, nutcracker dispersal may not be as uncoupled from distance to seed source as we like to believe. I echo the suggestion from Moody (2006) that "perhaps too much emphasis has been placed on the long-distance seed dispersal abilities of Clark's nutcracker and not enough [on] the more likely shorter distance dispersal tendencies." Approximately 27% of seedlings in both regions I surveyed were found in clusters, showing that nutcrackers are actively caching within unburned stands within the systems I surveyed. The percentage of seedlings found in clusters in my study would suggest that unburned stands surveyed may fulfill the requirements of a nutcracker home range, thus requiring fewer out of stand trips by nutcrackers.

The microclimate hypothesis, though secondary in importance to the seed hypothesis, did have some degree of support ($AIC_{wt}= 0.17$, Table 6). This may have implications for either nutcracker caching choice or seedling germination potential. Selection of canopy cover as the most important variable of those proposed in the microclimate hypothesis could be indicative of nutcrackers preferentially caching in unburned areas which are associated with greater canopy cover values. This could be by virtue of the greater protection from predators and home range choice as suggested above (Lorenz et al. 2011). Alternatively, this could indicate some benefit of canopy for seedling survival. Limber pine has been described as relatively shade intolerant and does thrive in severe environments with open canopies (Steele 1990). Opening up the canopy by burning was found to have a positive influence on limber pine regeneration in Colorado (Coop and Schoettle 2009). Canopy cover, however, offers greater thermoregulation and protection from direct solar radiation (Maher et al. 2005), important factors for ameliorating site conditions which may be important to limber pine seedlings in a more northern context. In a seedling planting study, denser canopy cover improved limber pine seedling survival for their first four growing seasons, especially in cases where a protective nurse object was not available (Casper et al. 2016). My study sites were quite open even prior to fire (Table 1, Appendix 5- Table 17) and thus may experience more benefit from the protective influence of intermittent canopy cover than detriment due to shading.

Burning, in these study areas, has not seemed to stimulate a limber pine regeneration response as expected. By breaking the unburned and two burned stand types down to the ecological processes that may differ due to fire, my model comparisons rank their explanatory power for the observed patterns of presence and absence of limber pine seedlings. This effectively answers why the differences in seedling regeneration were observed between the unburned and two burned stand types while avoiding problems due to multicollinearity that were present if stand type was included as a variable (Dormann et al. 2013). This process identified seed availability, as described by the retained variable seed distance, as having strong support for explaining seedling presence and absence in the study areas.

Burning, however, may have created other, unmeasured "hidden treatments" (Huston 1997) that prevented seedling occurrence within the burned stand. These other factors associated with burned stands could explain the lack of seedling presence in the burn, while

still allowing for nutcracker caching. Keane and Parsons (2010) found little regeneration following prescribed fire, despite many observations of nutcracker caching. They attributed this to high levels of seed retrieval from the burn due to low overall seed availability in nearby, blister rust affected whitebark forests. Though I found good enough regeneration within my unburned stands to suggest that there was enough seed available for many caches to be left unconsumed, it is possible that nutcrackers cached within the burn and simply retrieved more caches from the burned rather than unburned stands. Seed pilferage by rodents may also have had an effect, with possibly increased rates of predation in the burn rather than the unburned stands where greater seed availability could satiate predators (Nathan and Casagrandi 2004; Orrock et al. 2006). Within unburned stands, fallen seed from unharvested limber pine cones may also be more easily obtained than seed buried within nutcracker caches due to greater ease of detectability (Peters et al. 2004), resulting in fewer instances of cache pilferage. Nutcracker caching at depths of up to 3 cm is thought to limit instances of seed pilferage (Hutchins and Lanner 1982), though experimental caches by researchers have found high rates of pilferage at similar depth (Pansing et al. 2017). Additionally, in the montane and subalpine regions in Alberta, fires tend to occur in the summer (Rogeau et al. 2016). Both fires surveyed occurred out of this typical season (Dogrib in fall, Upper Saskatchewan in spring), which may have effects on fire intensity and competing species seed availability (Knapp et al. 2009). This theoretically could influence limber pine seedling recovery. No studies have examined the effect of fire seasonality on limber pine post-fire recruitment, making the influence of this out of season burning on this study is difficult to assess. Most ecosystems are resilient to occasional out of season burns, however, (Knapp et al. 2009), implying that this may have had minimal effect. Finally, important mycorrhizal associates of limber pine may be absent from the burn, seriously influencing the ability of seed cached within the burn to germinate and survive (Cripps and Antibus 2011; Trusty and Cripps 2011; Jenkins et al. 2018).

These alternative explanations are important to consider and would be a good focus of future research, though they do not change the overarching management implications of my results (i.e. that fire may not stimulate natural limber pine regeneration in all circumstances). It is, however, my belief that for the reasons given above and the proximity of all found seedlings within the burn to an unburned seed source, that seed distribution is a key explanatory variable limiting seedling occurrence in the burns.

4.3 Importance of seed and substrate to seedling abundance in unburned stands

Comparison of the hypotheses for abundance of limber pine seedling clusters in the unburned plots shows that even when distance to a seed source is small, seed source dynamics play an important role in regeneration of limber pine. However, interestingly, once the hurdle of dispersal distance is lessened, substrate takes on a far more important role than it had in the occurrence analysis. The soil hypothesis, which included variables describing abiotic substrates, best explained limber pine seedling cluster abundance of the hypotheses tested (AIC_{wt}= 0.98; Table 8). The combined model of retained variables from all four hypotheses presented a positive effect of finer textured soils and rock cover and a negative effect of bare mineral soil cover (Table 9).

Rocky sites tend to not represent the best growing conditions for most conifers, often indicating conditions of low nutrient, soil, and water availability (Duryea and Dougherty 1991). These conditions may represent areas in which limber pine's high drought tolerance and adaptability provide it a competitive advantage over other vegetation, thereby leading to increased abundance on rockier sites. My results are consistent with those of Cleaver et al. (2016) who also found a positive relationship between limber pine regeneration and rocky ground cover and attributed this to the reduced competition with other vegetation provided by rocky sites. Nutcrackers have previously been found preferentially caching in rocky areas (Vander Wall and Balda 1977; Tomback 1982), and so these findings may also be indicative of nutcracker caching tendencies. Alternatively, it is possible that gravity dispersed seed landing in rocky areas can become nestled within the rocks. This may make seed predation more difficult than in cases in which seed falls on other substrates, such as soil or vegetation, where it is more likely to remain above the ground and become easy pickings for hungry birds or rodents.

Rock cover in the combined model became marginally insignificant, despite being retained in the substrate model as an important variable for seedling abundance. I attribute this to slight collinearity between rock cover and texture, basal area of alive limber pine, and grass (Appendix 1, Table 12). Although the correlation coefficient and VIF between these variables are still below the thresholds described in my methods, this multicollinearity can result in significant predictors appearing to be less significant (Graham 2003). My chosen selection

criteria of AIC identified it as an important variable for model fit, which seems substantiated by its near significance at a α=0.05 significance threshold level. Although rock cover was ranked as less important than the more highly significant variables of texture and basal area of alive limber pine (with which it is collinear), I believe it is still an important variable to consider in relation to limber pine abundance.

In contrast to the above relationship with rock, the negative relationship between mineral soil and limber pine regeneration suggests that these areas represent spaces where seeds are either unlikely to be cached or in which predation of gravity dispersed seeds sitting at the surface may be higher. A negative association between limber pine regeneration and cover of open mineral soil was also found in other studies of natural limber pine regeneration (Coop and Schoettle 2009; Cleaver et al. 2016). Though Perkins (2015) found a positive influence of bare soil created by fire on whitebark pine regeneration, an important difference exists between this analysis and mine in that open soil in the abundance analysis was not created by known recent disturbance. Plots analyzed for seedling abundance were in the unburned stands; sites of open soil were thus not left open due to disturbance, but perhaps instead due to qualities of the site not conducive to plant success (Cleaver et al. 2016).

Finer soil textures were found to improve seedling abundance. It should be noted that the soil textures of the sites surveyed typically ranged from complete bedrock or gravel and shale to finer silts and silt loams. Very few sites were found with soil textures as fine as the clays. These results thus should not be taken to suggest that limber pine abundance would be improved in very fine, less well-drained soils, as these soil types were not well-represented in the plots. Soil of finer texture will have better moisture retention than those of very coarse texture, such as the pure sands or gravel. Despite limber pine's renowned drought tolerance, greater levels of soil moisture will improve limber pine seedling survival and abundance (Moyes et al. 2013; Windmuller-Campione and Long 2016) when this does not lead to being outcompeted by other species. Taken in combination with the finding of greater seedling abundance in rocky sites, finer textures may represent a compromise of sites which have better moisture retention than sites containing pure rock, but still have high enough coverage of rock to limit competition by other, less drought-tolerant tree species.

Although the comparison of seed and substrate hypotheses found strong support for the importance of substrate on limber pine regeneration in unburned stands, seed was still an important hypothesis, with basal area of live limber pine retained as the most important variable in the most parsimonious model (Table 8). In the combined model, basal area of live limber pine was second only to cover of mineral soil in significance and degree of effect size (Table 9). The joint importance of proximal living limber pine that can act as a seed source between both the occurrence and abundance analyses highlights the importance of seed availability in limber pine forests. Other studies of limber pine regeneration echo the importance of proximal basal area of limber pine for limber pine regeneration as both a source of seed and shelter for limber pine seedlings (Cleaver et al. 2016; Windmuller-Campione and Long 2016). Nutcrackers are drawn to stands with a higher density of cones (Barringer et al. 2012). This could be easily extrapolated to suggest that sites with denser limber pine have a higher carrying capacity of nutcrackers and thus greater instances of seed caching and potential for regeneration, especially if nutcrackers are caching in close proximity to where seed was harvested. Since limber pine may potentially distribute seed through gravity along with nutcracker caching, seedlings in areas of higher limber pine basal area may also be the result of greater seed available and dropping to the ground. The importance of available seed may be enhanced in this study, as northern limber pine stands at the edge of its range have lower overall cone production than more southern stands within Alberta (Peters et al. 2017), thereby boosting the importance of overall limber pine basal area as potential sources of seed. Alternatively, areas of higher limber pine basal area may be indicative of higher overall site productivity and suitability for limber pine, thus also representing conditions most suitable to seedling germination and survival.

Overall, comparison of the hypotheses in the unburned stand demonstrate that when seed is more readily available, limber pine regeneration is most dependent on availability of suitable substrates in which it can regenerate without competitive exclusion. Interestingly, seed availability, as measured by basal area of live limber pine, was found to still play an important role even in the unburned stands, signifying that seed production is a key variable in limber pine forests. These results illuminate the factors driving limber pine regeneration in the northernmost part of its range. However, since the seedling abundance analysis was performed only on the unburned plots due to the lack of seedlings found within the burn, these

results are not directly applicable to burned areas nor do they help us substantially in directing fire management for the recovery of the species. The following analysis builds upon the results discussed above, using comparison of the driving variables of limber pine regeneration abundance by stand type to help further clarify the cause of low limber pine regeneration in the burn.

4.4 Availability of desirable substrates between burned and unburned plots

Comparing availability of soil texture, exposed soil cover and rock cover between unburned and burned plots showed that these values were similar between stand types. Burned and unburned plots were spatially homogeneous with regards to substrates that were shown to be most important to limber pine in the unburned stands, reducing the likelihood of dispersed seed reaching unsuitable habitat. Safe sites are of course a function of more than just availability of substrate, also incorporating light, moisture, nutrient availability, influence of surrounding plants, exposure, temperature, predation/ herbivory risk, and a host of other variables that can affect seedling germination and survival (Green 1983). However, the substantial ΔAIC between substrate and all other hypotheses examined in the abundance analysis (Table 8) strongly suggests that when seed is available, substrate plays a key role in determining regeneration abundance. This implies that the low regeneration found within the burn may be a function of seed-dispersal limitation, as suggested in the occurrence analysis, rather than a lack of available substrates.

Post-disturbance environments tend to be seed limited (Turnbull et al. 2000) due to a combination of removal of vegetation creating unoccupied desirable substrates and reduction in readily available seed for species without a disturbance-resistant seed bank. This seems to be especially true for limber pine, for which post-disturbance colonization is dependent on nutcrackers, whose seed dispersal behavior is neither altruistic or even impartial, but rather, facilitates the later retrieval and consumption of those seeds. Lodgepole pine and white spruce, with their reliance on aerial seed banks and wind dispersal, were found at far greater density than limber pine within the burned stands (Appendix 6, Fig. 10). Recruitment of these other species was based most strongly on the species that had occupied that stand prior to fire, with the exception of burned limber pine stands which were seemingly beginning to convert to other stand types. It would thus seem that the fires I surveyed have not created a sterilized

environment free from regeneration, but rather that when seed is available, regeneration does occur. The lack of limber pine regeneration suggests that seed is simply not reaching these safe regeneration sites and that nutcrackers may not be reliable facilitators of post-disturbance colonization in the studied fires.

The homogeneity in substrate availability between the unburned and two burned stand types is likely due to the type of limber pine forests found at the northern extent of limber pine's range. Limber pine here is typically found on steep, rocky, sites in which well-spaced limber pine is found without any significant understory (Alberta Sustainable Resource Development and Alberta Conservation Association 2007). In other regions, however, limber pine's high degree of adaptability translates to it being found in mixed stands with a wide array of other tree species (Steele 1990; Tomback and Achuff 2010). Fire occurring in or near these limber pine forest types may certainly have a greater, longer-lasting effect on substrate availability. In these circumstances, fire may be more useful as a tool for creating new habitat for limber pine. Managers wishing to use prescribed fire to stimulate regeneration should consider how fire will interact with the forest type in which they are working and whether this is likely to help achieve recovery targets (Keane 2018).

One caveat to this analysis is that site selection within the burn was done in areas that seemed suitable for limber pine regeneration and were not done randomly throughout the burn. Thus, there are certainly many sites within the burn with substrates unsuitable for limber pine regeneration. It is possible that nutcracker dispersal is occurring to these unsafe sites. Were this to be the case, however, limber pine recruitment within the burns would still be seed-dispersal limited, as nutcrackers would not be functioning as effective agents of seedling recruitment.

4.5 Future research

Any observation-based ecological study is subject to the challenge of filtration: the need to filter through the excess of possible explanatory variables to arrive at a few of greatest interest to the study (Resetarits and Bernardo 1998). My research functions as an important preliminary look at the understudied relationship between limber pine regeneration and fire. Together with its unexpected result—that fire did not effectively stimulate limber pine dispersal

and regeneration in fires−this research has identified several key elements for future study, which by necessity were filtered out of this study. Further research in the areas identified may find better explanations for the low regeneration observed in this study than my proposal of seed-dispersal limitation to recruitment.

Clark's nutcracker caching behavior has yet to be studied in Alberta and limited studies have been conducted on caching of limber pine, in general. By surveying regeneration, I was able to determine conditions which seem to promote both nutcracker caching and seedling germination and establishment. Nutcracker caching was not directly observed, however, and as such, I cannot definitively state that nutcrackers were not caching in the burn and other factors, such as the limitations mentioned in section 4.2, subsequently prevented seedling establishment. Further study of nutcracker caching behaviors in Alberta can illuminate if caching is indeed occurring within burned areas. If this is the case, the factors limiting the success of these caches must also be explored. A seed or seedling planting study, in which growth and survival of limber pine planted both within the burn and in seed source stands are compared, could simulate nutcracker caching and provide further insight into the suitability of these post-fire environments when seed is known to be available.

The regions investigated by this study had different seed source dynamics. In the Upper Saskatchewan, large stands of limber pine were present. Whitebark pine is also found in this region at higher elevations. This region presents an excellent opportunity to examine caching behavior and time allocated to harvest in areas host to multiple nutcracker target species, and to examine if this dynamic affects caching and regeneration dynamics of either species. In the Dogrib region, several smaller stands of limber pine were present, without any nearby whitebark. Comparison of nutcracker caching behavior in areas with such different seed availability would also be useful in widening the applicability of results to multiple population types.

Seed availability in this study was approximated through use of living limber pine basal area, proportion of limber pine in a stand, and distance to a seed source. Although cone counts were conducted in these stands, this data was not used due to the low number and variation in cones seen, as counting was performed in a non-mast year. Though mast years are known to have occurred in the time since fire period (Peters et al. 2017), long-term cone counts

directly identifying seed availability could strengthen future similar studies. Alberta's northernmost stands of limber pine are known to have lower cone production values than Alberta's more southern stands, despite less frequent incidence of blister rust in the north (Peters et al. 2017). Although the healthy density of limber pine seedlings in unburned stands would suggest that seed availability was adequate for regeneration in the time since fire period, overall cone production of stands may be an important selection criterion in identifying candidate areas for prescribed fire treatment.

Finally, future studies could be improved by a fuller characterization of soil variables, including the availability of nutrients, retention of water, and soil temperature, all of which are changed by fire (Certini 2005). A seed or seedling planting study, such as the one discussed above, could also investigate the alterations in availability and composition of mycorrhizal fungi in post-fire habitats and the resulting effects on limber pine regeneration.

CHAPTER 5. CONCLUSIONS

5.1 General conclusions

Fire has been considered an agent of renewal in Alberta's endangered limber pine ecosystems. Large, severe fires are thought to open habitat to which Clark's nutcrackers, as long-distance seed dispersers, will promptly cache seed, allowing limber pine to colonize new habitat. However, the relationship between limber pine and fire has received limited attention, with this study being the first to examine natural post-fire regeneration in the northern extent of its range. My finding of low regeneration within the two burns surveyed shows that fire does not stimulate new recruitment in every case. All regeneration found within the burn was within a relatively short distance of seed source stands. This has important implications for recovery targets in limber pine management. Managers wishing to use prescribed fire as a restoration tool for the species may need to consider seed source dynamics prior to burning and be aware that nutcrackers may not be reliable seed dispersers, especially to the interior of larger fires.

Overall, my results suggest that the relative lack of limber pine seedling clusters within the burn is due to low distribution of seed to the burn from nearby seed sources, rather than from a deficiency of available substrate. The comparison of hypotheses for seedling occurrence across all plots showed strong support for seed distance as an explanation for the relative absence of regeneration in the burn. Substrate availability was most important for seedling abundance in unburned areas, where seed availability was less of a hurdle. Of the substrates examined, rock cover, soil texture, and availability of exposed mineral soil were found to be most important for seedling abundance. These substrate types did not tend to significantly differ in availability between burned and unburned plots surveyed, lending further support that good limber pine seedling microsites may be available within the burn perimeter but that seed distribution to these safe germinating sites is not occurring with regularity.

5.2 Management implications

5.2.1 Management in Alberta

In Alberta, the presence of limber pine in typically xeric, open forests (Alberta Sustainable Resource Development and Alberta Conservation Association 2007) may lessen the reliance of the species on fire-opened areas to attract nutcracker caching. Open limber pine forest habitats are subject to continual recruitment (Webster and Johnson 2000), with potentially less incentive for nutcrackers to expend additional energy in caching at a distance when preferred exposed slopes are readily available at seed harvest locations. My findings of little limber pine regeneration within the burn, aside from at burn edges, suggests that prescribed fire may be an inefficient recovery tool for limber pine at the northern extent of its range in Alberta unless supplemented by restoration planting. Small prescribed burns at the edge of limber pine habitat may have some use, but would be limited as limber pine is often found in constrained areas, such as streambanks, ridges, and hillslopes in which the stand is demarcated by unsuitable habitat for limber pine (Webster 1998). The risk of overachievement of prescribed fire in close proximity to limber pine, although mitigated by good prescribed burning practices, must also be considered and weighed against the potential recovery benefit. As such, until further research is conducted to address study limitations discussed above, I would not recommend the use of prescribed fire as a recovery tool for limber pine in Alberta, unless supplemented by restoration plantings of rust-resistant limber pine seedlings or if used to create protective fuel breaks to protect limber pine from fire which could be carried into stands by surrounding, denser forest.

5.2.2 Applicability to other regions

Limber pine's distribution extends from Alberta south to eastern California, New Mexico and Arizona (Steele 1990), a vast geographic area within which limber pine's broad elevation tolerance translates into finding limber pine as an element of many forest types. Within this range, limber pine occurs at both upper and lower treeline and is found from grassy, open forests to exposed rocky slopes, and as a component of dense, mixed-conifer stands (Tomback and Achuff 2010). This wide range of ecological contexts translates to an equally broad array of resulting fire regimes, and likely, relationships to fire. Coop and Schoettle (2011) make the important observation that extensive subalpine stands in which

limber pine is a dominant, or co-dominant species are not common outside of the Colorado Front Range and Means (2010) points out that important ecological differences exist between sites where limber pine is a lower treeline species and those where it is found at treeline or on exposed subalpine slopes. Results from my study in the montane and subalpine ecoregions of Alberta, under typically mixed-severity fire regimes thus should not be generalized to other ecological contexts, in which other fire regimes, climates, co-occurring vegetation, and resulting patterns of establishment dictate limber pine regenerative processes.

TABLES

Table 1: Topographic setting and stand structure of the stand types within each burn region. Values indicate the mean value at plots, with standard error shown in parentheses.

Variable	Upper Saskatchewan (2009)			Dogrib (2001)		
	Burned LP	Burned absent	Unburned	Burned LP	Burned absent	Unburned
Topography						
Elevation (m)	1556 (17)	1619 (20)	1426 (11)	1725 (23)	1697 (24)	1705 (9)
Heat load index	0.91 (0.003)	0.91 (0.004)	0.84 (0.019)	0.88 (0.016)	0.92 (0.004)	0.91 (0.005)
Slope (°)	18 (1.1)	23 (1.4)	27 (1.0)	30 (1.3)	28 (0.8)	31 (0.9)
Total basal area (m^2 ha^{-1})*						
Total	5.2 (0.63)	5.6 (0.93)	10.4 (0.61)	5.1 (0.60)	6.6 (1.26)	7.5 (0.69)
Limber pine	2.2 (0.29)	0	8.6 (0.75)	1.8 (0.34)	0.2 (0.08)	4.2 (0.45)
White spruce	0.3 (0.12)	0.5 (0.21)	1.0 (0.25)	2.5 (0.62)	1.6 (0.33)	3.1 (0.42)
Lodgepole pine	2.7 (0.58)	4.3 (0.71)	0.67 (0.24)	0.6 (0.37)	4.0 (1.35)	0
Living limber pine basal area (m^2 ha^{-1})	0.27 (0.09)	0 (0)	6.97 (0.69)	0.10 (0.10)	0 (0)	3.58 (0.49)

* standing basal area of all living and dead trees above breast height

Table 2: Summary of predictor variables included in occurrence and abundance analyses of limber pine seedling establishment.

Model Category	Variable	Description	Units
Seed	Seed distance*	Categorical variable indicating whether an available seed source is within 100m of the plot's center	Unitless
	Basal area live limber pine	Average basal area of alive limber pine at each plot	$m^2\,ha^{-1}$
	Proportion limber pine	Proportion of standing basal area (live or dead) that is limber pine	Unitless
Microclimate	Elevation	Elevation at each plot	m
	Heat load index	Transformed aspect, slope, and latitude representing typical heat load at site (eqn 3, McCune and Keon 2002). Zero equivalent to coolest slope, one to warmest slope.	Unitless
	Slope	Slope at each plot	Degrees
	Canopy cover	Average canopy cover	%
Soil substrate	Texture	Soil texture converted to a numeric scale and averaged for the plot as below: 0=Bedrock 1=Rock, scree, gravel, etc 2=Loamy sand, sand, silty sand 3= Loam, silt loam, sandy loam 4=Silt 5=Any clay	Unitless
	Litter volume	Volume of fine dead material as measured by litter depth at microplot center multiplied by litter cover, averaged over the plot	m^3
	Rock	Average of percent cover measurements**	%
	Soil		%
	Downed wood		%
Vegetation	Other regen	Number of other seedlings found in the plot	Unitless
	Ground shrub	Average of percent cover measurements**	%
	Shrub		%
	Herb		%
	Grass		%

*used only in the occurrence analysis
**applies to soil, downed wood, ground shrub, shrub, herb, grass

Table 3: Description of analyses performed.

Analysis number	Analysis intention	Description	Model type
1	Seedling density	Comparison of seedling cluster abundance by stand type and region. Plot size used as an offset to convert abundance to density to improve interpretability. Not corrected for time since fire.	Poisson GLMM
2	Occurrence	Information theoretic approach comparing hypotheses of ecological processes that could explain presence and absence of seedling clusters from plots.	Logistic GLMM
3	Abundance	Information theoretic approach to identify explanatory power of ecological processes for seedling cluster abundance at plots. Abundance was corrected for time since fire in each region through use of an offset variable. Analysis was performed on unburned stands due to low number of seedlings in the burn.	Poisson GLMM
4	Retained abundance variable comparison	Comparison of variables identified in analysis 3 as important to seedling abundance across stand types and study regions. Done to determine whether variables important for seedling abundance in unburned areas differed within the burn.	Beta GLMM

Table 4: Summary of post-fire regeneration sites found by region and stand type.

Region	Time since fire	Stand type	Post-fire seedlings found	Percent found in clusters	Regeneration density (seedling clusters/ha)*
Dogrib	16 years	Burned LP	3	0%	5.7
		Burned absent	1	0%	1.2
		Unburned	88	26%	150.8
Upper Saskatchewan	8 years	Burned LP	2	50%	2.2
		Burned absent	0	0%	0.4
		Unburned	36	28%	58.1

*estimates calculated from Poisson GLMM analysis, with model results also shown in Table 5 & Fig. 3.

Table 5: Mixed-effect model comparison of seedling cluster density by stand type and region. The unburned stand type and Dogrib region are taken as the first level of stand type and region.

Variable	β	SE	P
Intercept	5.015	0.312	<0.001
Burned absent	-4.867	1.067	<0.001
Burned LP	-3.281	0.587	<0.001
Region (Upper Sask)	-0.954	0.437	0.029

Table 6: Comparison of ecological processes driving seedling occurrence, based on AIC for most parsimonious models within each hypothesis category.

Model category	Retained variables	K_i	AIC	ΔAIC	AIC_{wt}	Pseudo-R^{2*}
Seed	Seed distance	3	92.7	0	0.83	0.36
Microclimate	Canopy cover	3	95.9	3.2	0.17	0.33
Soil	Litter volume	4	112.9	20.2	0.00	0.17
	Downed wood					
Vegetation	Herb	3	117.8	25.1	0.00	0.09

*Pseudo R^2 value calculated from the likelihood ratio between the fitted and null model (intercept only); represents the improvement of the model from the null (Magee 1990). Adjusted such that the likelihood ratio achieves one at its maximum (Nagelkerke 1991)

Table 7: Comparison of effect size of all variables retained from each model category in Table 6 on seedling occurrence when modelled in combination. Effects standardized to facilitate comparison.

Variable	β	SE	P
Intercept	-0.895	1.044	0.391
Seed distance (>100 m)	-5.566	2.450	0.023
Canopy cover	1.557	0.776	0.045
Litter volume	1.236	0.870	0.155
Downed wood	-1.199	0.655	0.067
Herb	-1.214	0.833	0.145

Table 8: Comparison of ecological processes driving post-fire aged seedling abundance in the unburned stands, based on AIC for most parsimonious models within each hypothesis category.

Model category	Retained variables	K_i	AIC	ΔAIC	AIC_{wt}	Pseudo-R^2
Soil	Texture	5	196.7	0	0.98	0.40
	Soil					
	Rock					
Seed	Basal area live limber pine	3	204.6	7.9	0.02	0.30
Vegetation	Grass	3	209.0	12.3	0.00	0.19
	Other regen					
Microclimate	Canopy cover	3	211.7	15.0	0.00	0.10

*Pseudo R^2 value calculated from the likelihood ratio between the fitted and null model (intercept only); represents the improvement of the model from the null (Magee 1990). Adjusted such that the likelihood ratio achieves one at its maximum (Nagelkerke 1991)

Table 9: Comparison of effect size of all variables retained from each model category in Table 8 on post-fire aged seedling abundance in unburned stands when modelled in combination. Effects standardized to facilitate comparison.

Variable	β	SE	P
Intercept	-1.912	0.216	<0.001
Texture	0.477	0.188	0.011
Soil	-0.607	0.187	0.001
Rock	0.400	0.210	0.057
Basal area live limber pine	0.481	0.174	0.005
Grass	-0.288	0.164	0.079
Other regen	0.007	0.189	0.967
Canopy cover	-0.142	0.158	0.369

Table 10: Comparison of relevant substrate variables by stand type and region. In all models, the unburned stand type and Dogrib region are taken as the first level of stand type and region. Interactions between region and stand type are shown when they were found to be significant.

Substrate variable	Effect	β	SE	*P*
Soil	Intercept	-2.408	0.234	<0.001
	Burned absent	-0.508	0.283	0.073
	Burned LP	-0.317	0.281	0.259
	Region (Upper Sask)	0.780	0.232	<0.001
Texture	Intercept	0.126	0.270	0.639
	Burned absent	1.271	0.385	0.001
	Burned LP	-0.061	0.381	0.873
	Region (Upper Sask)	0.530	0.382	0.165
	Burned absent x Region (Upper Sask)	-1.775	0.543	0.001
	Burned LP x Region (Upper Sask)	-0.563	0.539	0.296
Rock	Intercept	-0.357	0.269	0.184
	Burned absent	0.389	0.331	0.240
	Burned LP	0.628	0.331	0.057
	Region (Upper Sask)	-1.182	0.270	<0.001
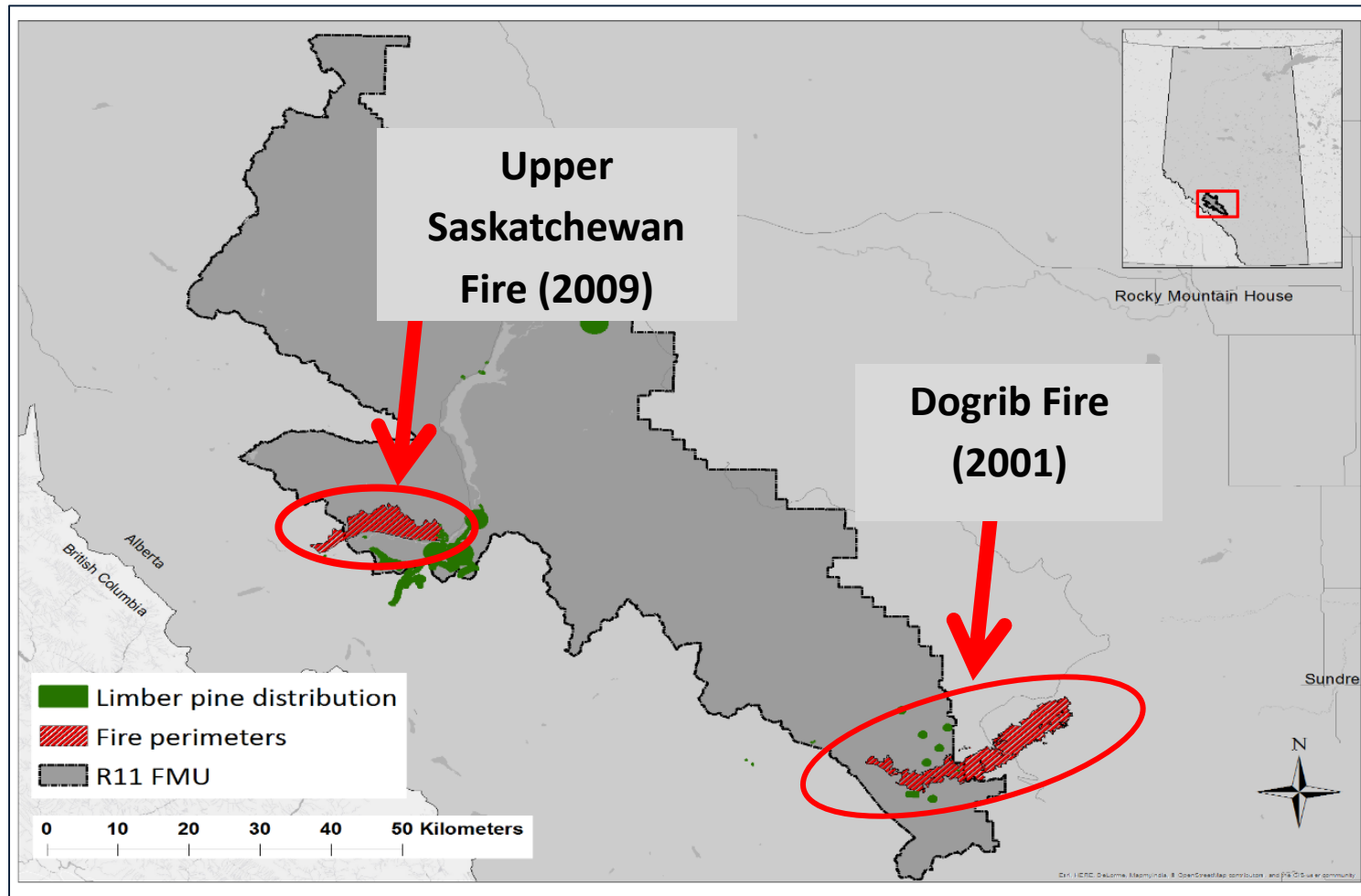
Figure 1: Map of Alberta's R11 Forest Management Unit study area and the two surveyed fires
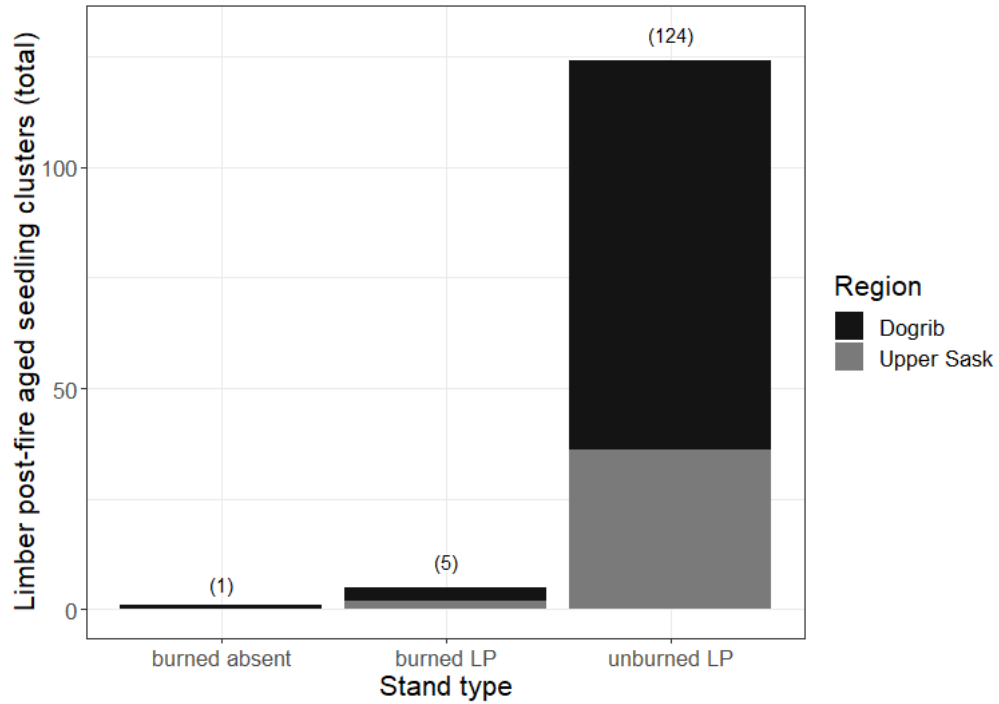
Figure 2: Total seedlings of the post-fire age group found in each stand type with colour representing the proportion found in each region.
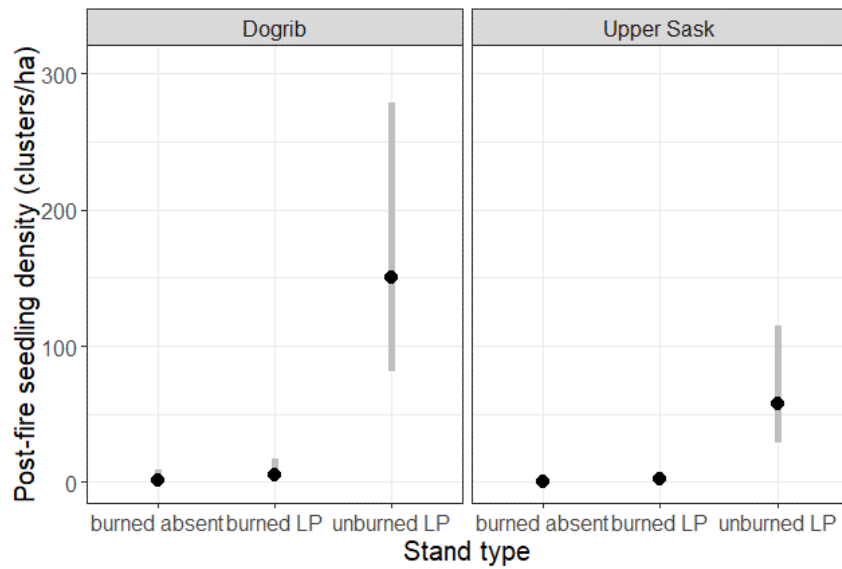
Figure 3: Seedling density found in each stand type and region as modelled by Poisson GLMM. Error bars represent 95% CI around each estimate.
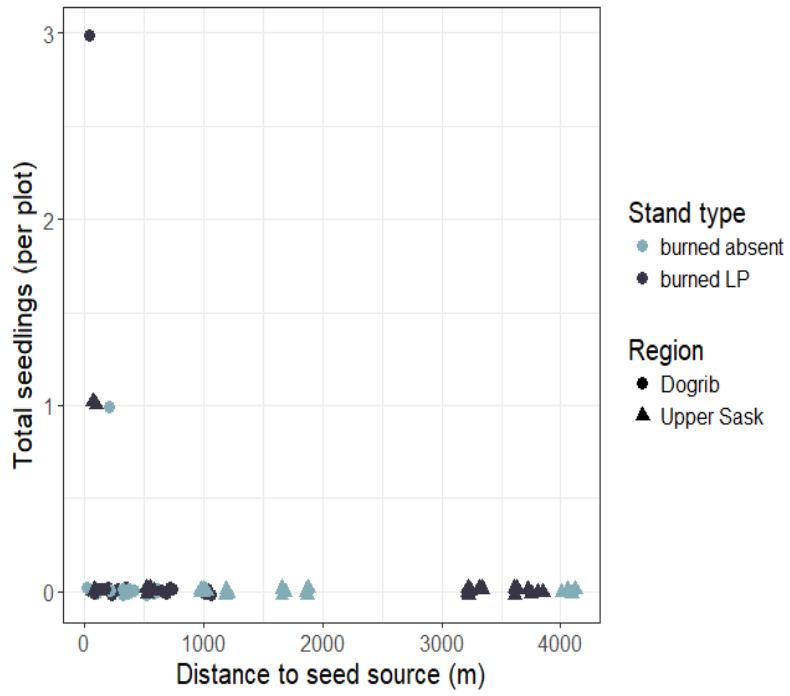
Figure 4: Distance to nearest limber pine seed source and total number of seedling clusters found in each of the burned stand types.
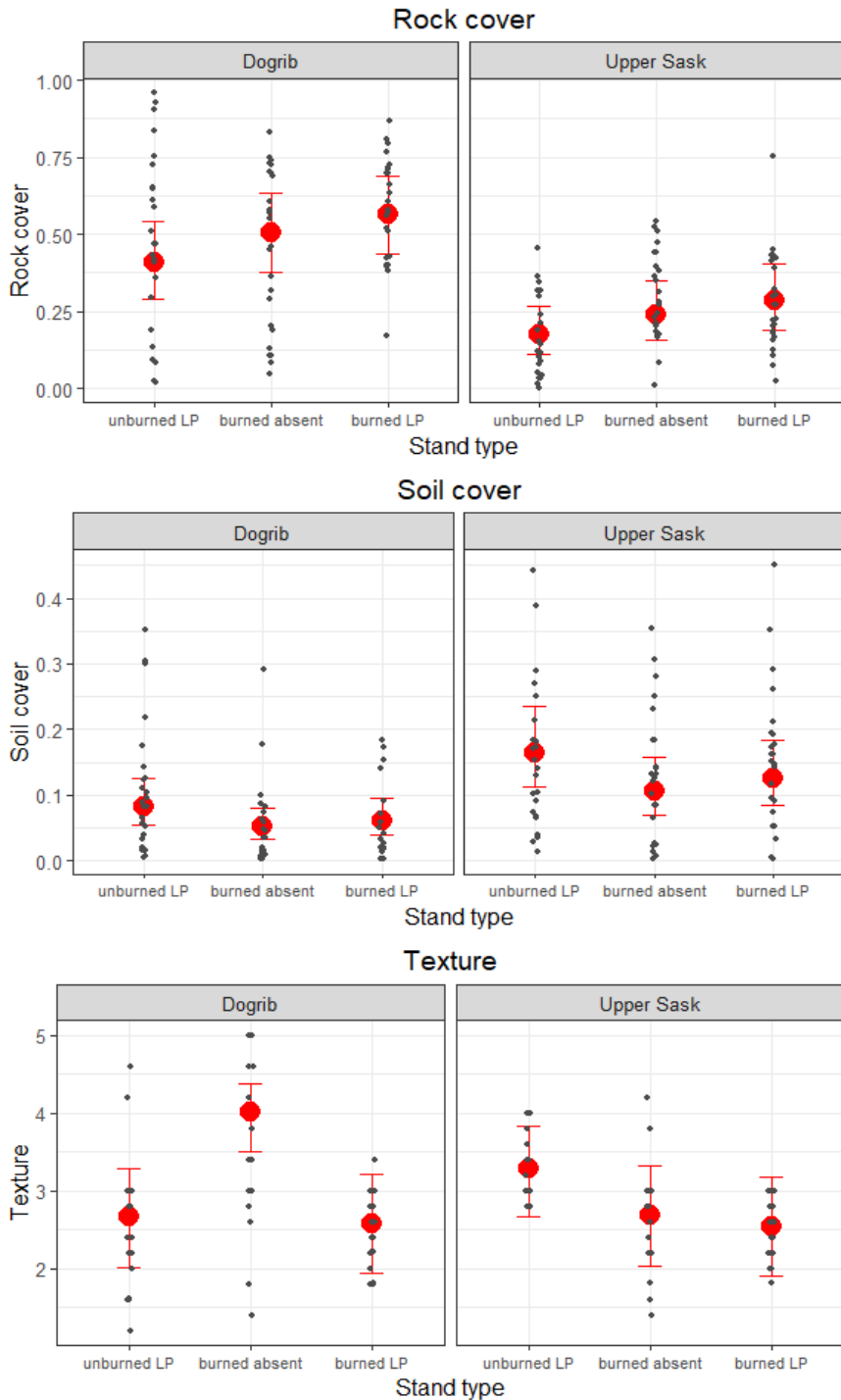
Figure 5: Comparison of key driving variables for limber pine seedling abundance between stand types as estimated by beta-GLMMs. Estimated values given by red circles with error bars representing confidence intervals. Estimates were back transformed and displayed on the level of the variable being modelled to facilitate easy interpretation and comparison.

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APPENDIX 1: VARIANCE INFLATION FACTORS FOR VARIABLES INCLUDED IN HYPOTHESES

Table 11:Variance inflation factors for variables within each model category in the occurrence analysis.

Hypothesis Category	Variable	VIF
Seed	Seed distance	2.04
	Proportion limber pine	1.65
	Basal area live limber pine	2.12
Microclimate	Elevation	1.21
	Slope	1.15
	Heat load index	1.10
	Canopy cover	1.12
Soil	Litter volume	1.83
	Texture	1.21
	Downed wood	1.10
	Rock cover	2.35
	Soil	1.64
Vegetation	Shrub	1.12
	Ground shrub	1.17
	Herb	1.16
	Grass	1.34
	Other regen	1.22
Combined model	Seed distance	1.87
	Canopy cover	2.18
	Litter volume	1.39
	Downed wood	1.09
	Herb	1.19

Table 12: Variance inflation factors for variables within each model category in the abundance analysis.

Hypothesis Category	Variable	VIF
Seed	Proportion limber pine	1.75
	Basal area live limber pine	1.75
Microclimate	Elevation	1.40
	Slope	1.10
	Heat load index	1.30
	Canopy cover	1.03
Soil	Litter volume	1.89
	Texture	2.31
	Downed wood	1.17
	Rock cover	2.63
	Soil	1.48
Vegetation	Shrub	1.03
	Ground shrub	1.34
	Herb	1.14
	Grass	1.17
	Other regen	1.15
Combined model	Basal area alive limber pine	1.57
	Texture	2.31
	Soil	1.43
	Rock	2.88
	Grass	1.45
	Other regen	1.17
	Canopy cover	1.58

APPENDIX 2: JUSTIFICATION FOR VARIABLES EXCLUDED FROM HYPOTHESES

Table 13: Variance inflation factors (VIF) of all variables originally considered in the seed hypothesis, as justification for variable exclusion. See Table 2 for final variables included.

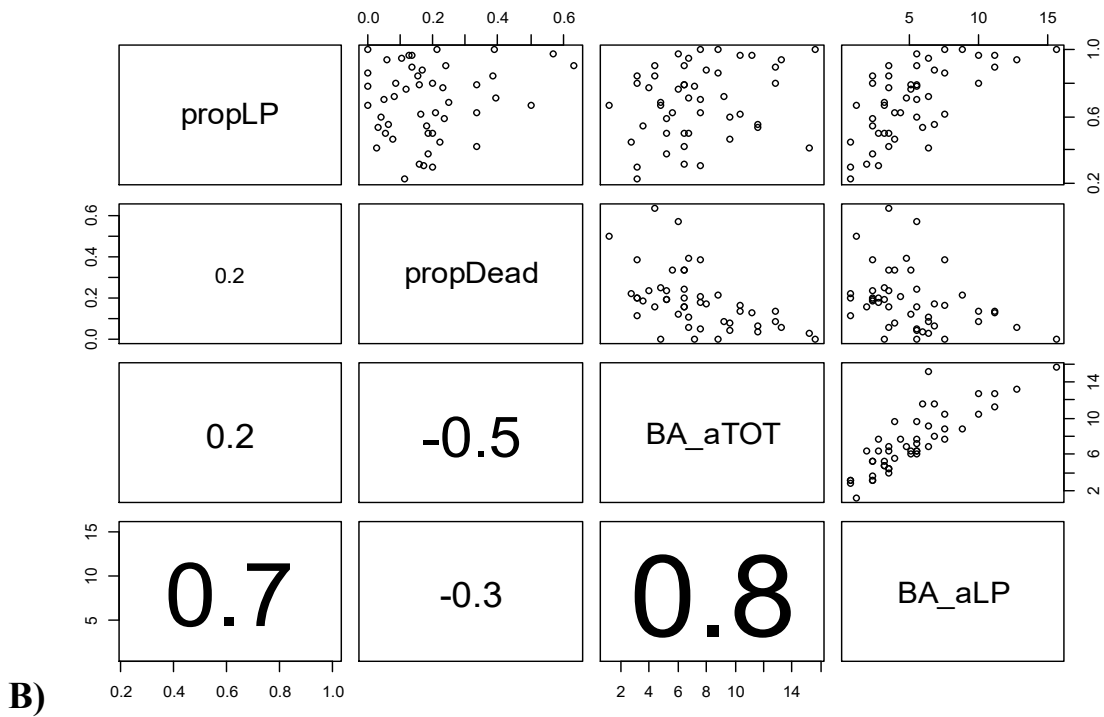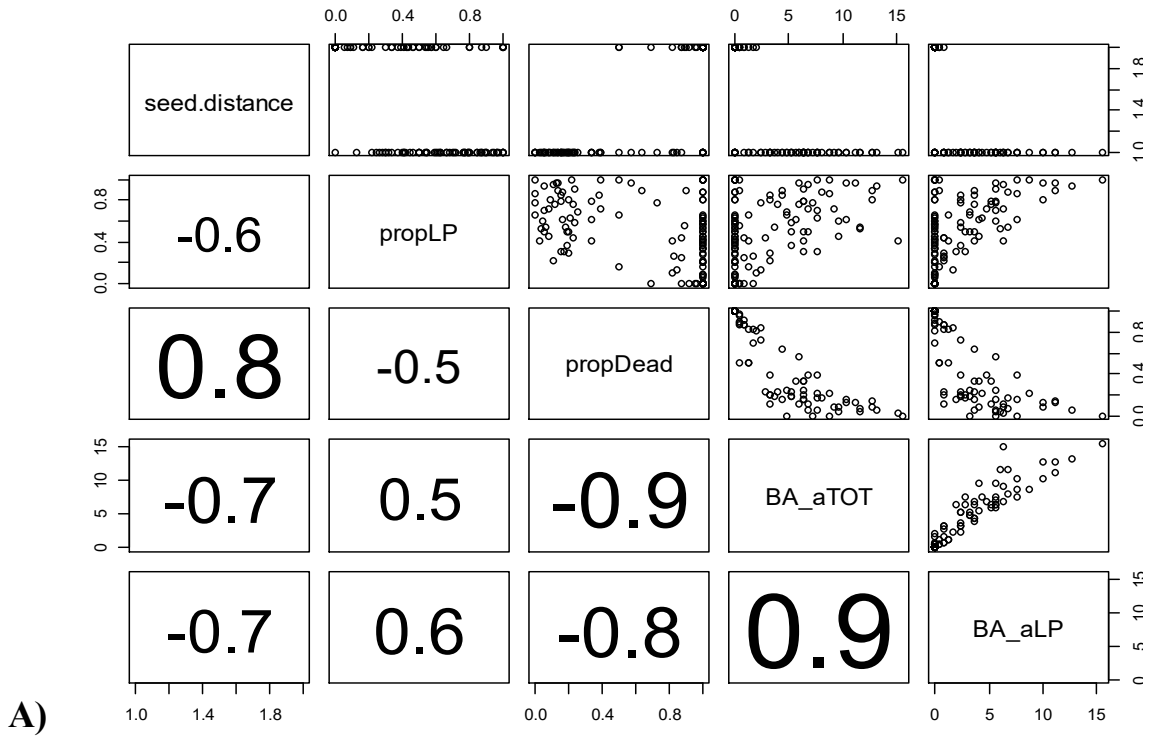| Variable	Variable Inflation Factor (VIF) in Occurrence Analysis	Variable Inflation Factor (VIF) in Abundance Analysis
Seed distance	3.23	NA
Proportion limber pine	1.80	4.71
Proportion dead	7.63	1.60
Total living basal area	18.78	8.84
Total living limber pine basal area	11.79	14.7

Figure 6: Correlation coefficients for all variables originally considered in the seed hypothesis in the A) occurrence analysis and B) abundance analysis. See Table 2 for final variables included.

Table 14: Justification for variables excluded from analysis.

Variable considered	Description	Reason for removal
Seed strength	Stand size of the nearest limber pine seed source multiplied by the average BA of alive LP measured within that stand. Units are in area covered by LP in m2.	Upper Saskatchewan plots dominated by one large limber pine stand; made variable sharply bimodal rather than continuous
Lichen	Percent cover of lichen in plots	Rare variable with low range (0-5%)
Moss	Percent cover of moss in plots	Rare variable
Regen cover	Percent cover of regenerating seedlings in plots	Rare variable
Bedrock	Percent cover of bedrock in plots	Rare variable
Total living tree basal area	Total basal area of all trees living within the plot	High correlation with basal area of alive limber pine
Proportion of dead trees	Proportion of the trees within a plot dead	High correlation with basal area of alive limber pine

APPENDIX 3: ABUNDANCE MODEL OUTPUTS INCLUDING ALL STAND TYPES AND STAND TYPE AND REGION AS VARIABLES

Table 15: Example abundance model including variables retained in analyses 2 &3 in a model across all stand types, including region and stand type as predictors. Stand type multicollinearity with many other variables results in marginal or no significance, despite strong significance when it is modelled alone.

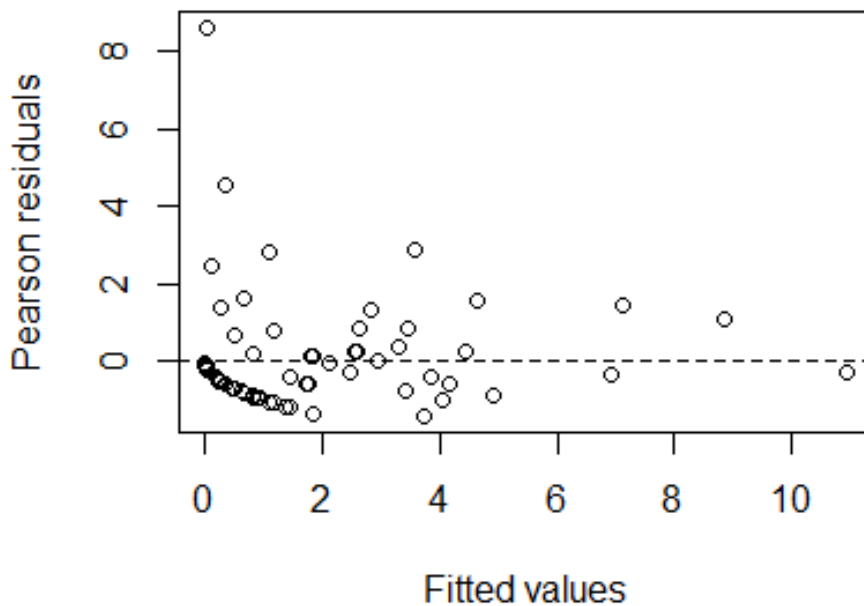| Variable	β	SE	P
Intercept	-2.133	0.356	<0.001
Burned absent	-2.437	1.265	0.054
Burned LP	-0.982	0.719	0.172
Region (Upper Sask)	-0.338	0.492	0.492
Seed distance >100m	-3.387	1.183	0.004
Basal area live limber pine	0.514	0.176	0.003
Texture	0.273	0.197	0.164
Soil	-0.419	0.167	0.012
Rock cover	0.303	0.171	0.076
Canopy cover	-0.012	0.137	0.892

Figure 7: Poor model fit of example model described in Table 15.

Table 16: Example abundance model including variables retained in analyses 2 &3 in a model across all stand types, this time excluding region and stand type as predictors. Model is under-dispersed, with dispersion statistic estimated at 0.7.

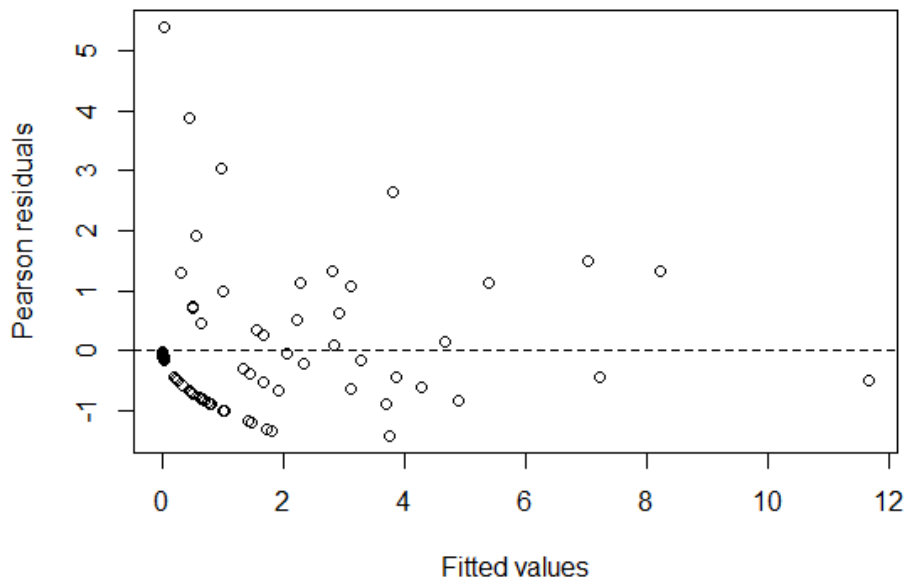| Variable	β	SE	P
Intercept	-2.675	0.303	<0.001
Seed distance >100m	-4.452	1.101	<0.001
Basal area live limber pine	0.591	0.166	<0.001
Texture	0.176	0.193	0.362
Soil	-0.394	0.173	0.022
Rock cover	0.279	0.165	0.091
Canopy cover	0.052	0.132	0.694

Figure 8: Poor model fit of example model described in Table 16.

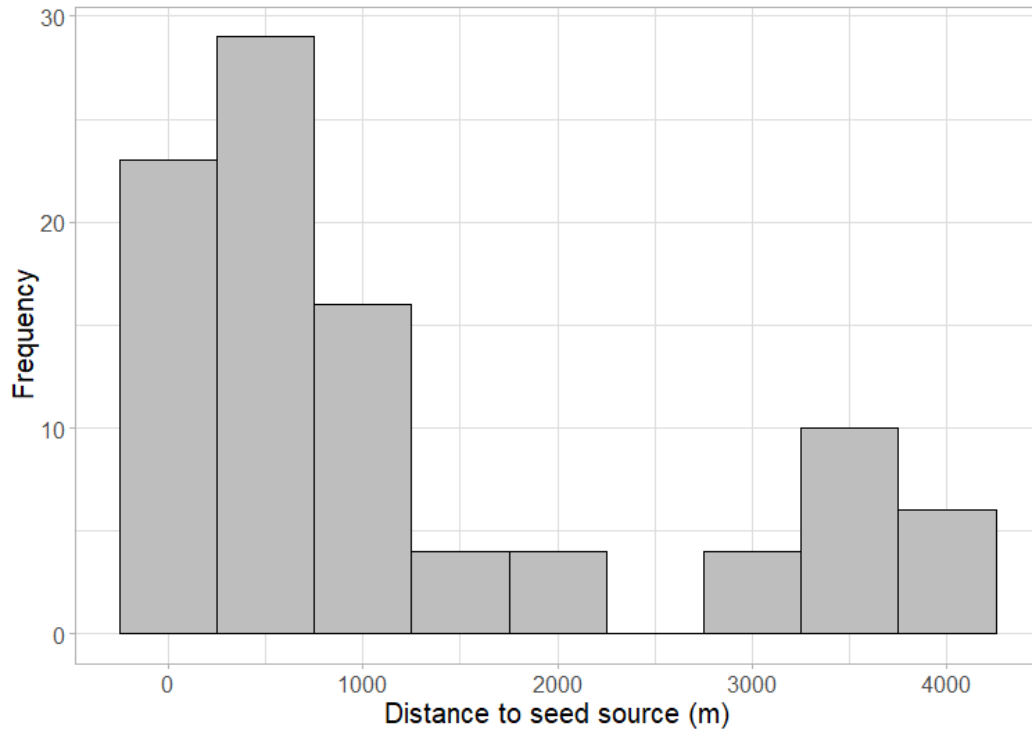**APPENDIX 4: DISTANCE TO SEED SOURCE FROM BURNED STAND TYPE PLOTS**

Figure 9: Distance from plots in the burned stand types to the nearest limber pine seed source.

APPENDIX 5: MEAN, STANDARD ERROR, AND RANGE OF VARIABLES

Table 17: Mean, standard error, and range of all values included in model hypotheses.

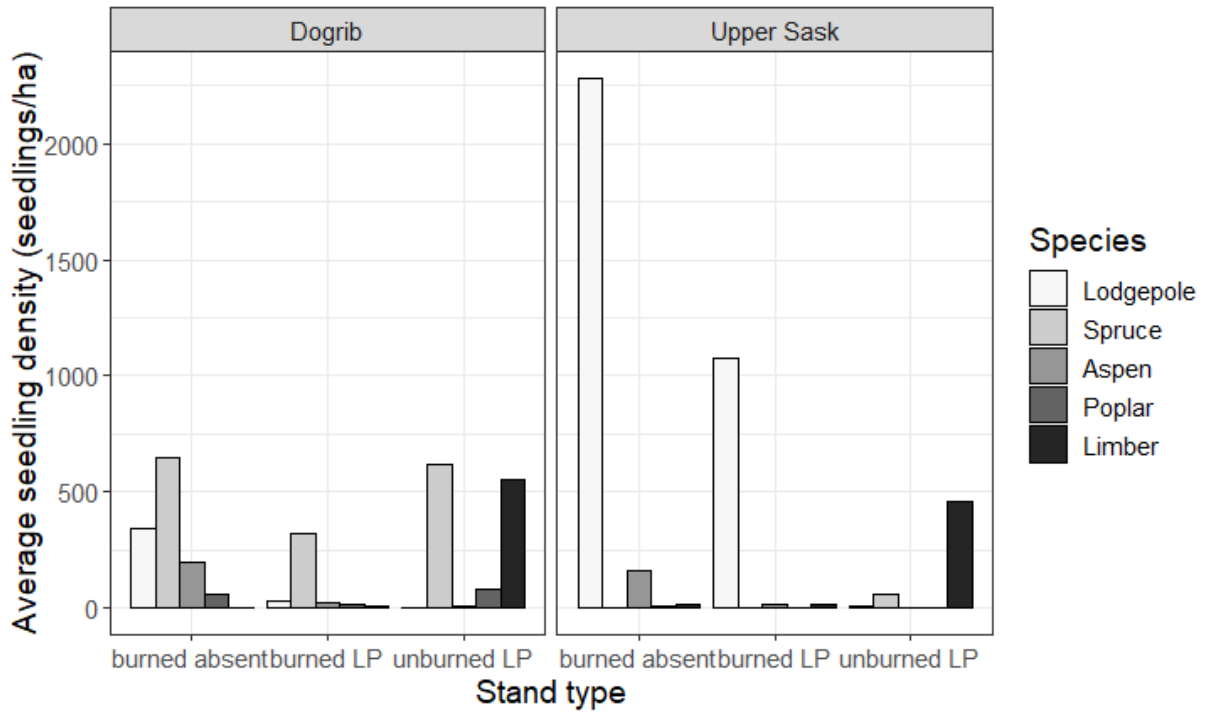|	Variable	Units	Mean (Se)	Range
Seed	Basal area live limber pine	$m^2\,ha^{-1}$	1.82 (0.3)	0-15.6
	Proportion limber pine	Unitless	0.41 (0)	0-1
	Seed distance	m	834.42 (101.6)	0-4124.2
Microclimate	Elevation	m	1621.38 (11.5)	1351-1959
	Heat load index	Unitless	0.89 (0)	0.61-0.94
	Slope	Degrees	26.1 (0.6)	1-41
	Canopy cover	%	3.39 (0.5)	0-33.33
Soil	Texture	Unitless	2.89 (0.1)	1.2-5
	Litter volume	m^3	1.62e-3 (2.0e-4)	0-0.017
	Downed wood	%	5.29 (0.4)	0-26.4
	Rock	%	37.71 (2.1)	0.04-96
	Soil	%	10.73 (0.8)	0-45.04
Vegetation	Other regen	# stems/ plot	19.94 (3.4)	0-388
	Ground shrub	%	14.97 (1.1)	0-54
	Shrub	%	4.72 (0.4)	0-19.8
	Herb	%	2.62 (0.2)	0-11.4
	Grass	%	3.81 (0.3)	0-18

Figure 10: Average regeneration density of all species by stand type and region. Limber pine seedling density includes all seedlings found (both post-fire and advanced regeneration) for easy comparison with regeneration of other species, which were not classified by age.