Fire and whitebark pine recovery strategies: drivers of post-fire natural regeneration

by

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A thesis submitted in partial fulfillment of the requirements for the degree of

Master of Science

in

Forest Biology and Management

Department of Renewable Resources
University of Alberta

ABSTRACT

Whitebark pine (*Pinus albicaulis* Engelmann), a tree species of high elevation forests in western North America, is listed as an endangered species in Canada. Prescribed burns have been employed by conservation agencies as a recovery strategy to create open habitats free of competition and to increase regeneration opportunities. However, questions remain with respect to the success of prescribed burns for the restoration of whitebark pine and best practices of this technique, as well as to what role wildfire plays in whitebark pine communities at the northern limits of its range. Understanding what drives whitebark pine post-fire regeneration and how it responds to fire severity is important for guiding future burn prescriptions and managing wildfire to effectively implement Alberta's provincial recovery plan at a landscape scale. Therefore, this research project aimed to better understand how: (i) site, stand and plot level factors, and (ii) fire severity influences the natural regeneration occurrence and abundance of whitebark pine in post-fire environments. Five prescribed burns and four wildfires across the federal and provincial mountain parks in western Alberta were sampled and information on environmental variables and whitebark pine regeneration was collected. Generalized mixed effect models were used to test individual predictors and perform model selection.

Whitebark pine post-fire regeneration was shown to be a complex process linked to a variety of biological processes at multiple spatial scales. Regeneration occurrence increased in the first 18 years after fire, mainly at stands with larger whitebark pine basal area. Seedling density increased up to 18 years on wildfires, while it declined after 10 years on prescribed burns, indicating that regeneration abundance was probably driven by the existence of favourable seedbeds and understory conditions at smaller scales. This creates a challenge in predicting regeneration abundance because of the multitude of factors that can influence post-fire conditions, such as fire severity, burning season, post-fire weather and pre-forest composition. At a plot level, decaying wood cover and litter cover up to 25 % and 9 cm depth, respectively, and medium shrub cover up to 30% were positively correlated with seedling density. Fire was not a requirement for regeneration to occur as post-fire seedling densities in the unburned plots (320.8 seedlings/ha) were higher than in the burned plots at 50 m from forest edge (288.5 seedlings/ha). We observed both beneficial and detrimental effects of fire on whitebark pine regeneration. The lower post-fire and advanced seedling densities in the burned plots may suggest that fire is not beneficial for regeneration, while the colonization of burned stands that had no mature whitebark pine trees pre-fire may suggests that fire creates new habitats for regeneration. Proximal seed sources were important as they increased the probability of regeneration occurrence. However, the current increase in tree mortality caused by white pine blister rust and mountain pine beetle threatens remaining whitebark pine stands and raises the question for how long seed sources will remain viable to sustain natural regeneration. After 18 years post-fire, regeneration densities were lower than in previous studies that looked at recent and advanced regeneration in undisturbed stands (463 – 1082 seedlings/ha) or similar to fires up to 60 years old (0 – 406 seedlings/ha). If conservation agencies are to use those densities as reference values during restoration efforts, long term post-fire occupancy surveys and artificial planting will likely be necessary to complement lack of natural regeneration in burned areas and achieve restoration goals, particularly at stands experiencing high tree mortality caused by blister rust and mountain pine beetle.

DEDICATION

I dedicate this thesis to:

Whitebark pine

You have taught me that despite all the harsh life conditions we can possibly find ourselves in, there is always a way to grow, even if very slowly. Inch by inch, we can all become strong, tall and deep-rooted trees able to stand tall and survive any challenge. Every step I`ve given to find you in the high mountains made me stronger.

Jasper

This wonderful place in nature and the people who dwell in it made me feel so alive and welcome. There, I had the best days in my life and found a deep connection with nature. I could contemplate the mountain peaks being lit by the sunrise, unbelievable blue-turquoise lakes, the trails through montane and subalpine forest, the vast openness of alpine meadows, and the unique wildlife. You are paradise.

Brenda Shepherd, Landon Shepherd and Dave Smith

It was a simple "Yes", but you have opened the door to a new life for me since the day you accepted me as a volunteer intern in Jasper. You gave me the opportunity to live and work in a place that I consider home. You have believed in my abilities and went out of your way to support me before and during my graduate program. You have my sincere and eternal gratitude!

Mike Flannigan and Vernon Peters

Thank you for your patient guidance, encouragement and understanding throughout my time as your student. I was extremely lucky to have had supervisors who cared about my work and personal growth. It is a debt that won`t be able to pay so soon. Thank you so much!

ACKNOWLEDGMENTS

Two pages are not enough to thank the large group of people and organizations who provided support and helped me during this journey, and to whom I am greatly indebted. First and foremost, I would like to thank my supervisors Dr. Mike Flannigan and Dr. Vernon Peters for their financial and academic support, guidance, patience, understanding and encouragement throughout my program. Your help went above and beyond. You have my gratitude for everything.

To the Alberta Conservation Association, Natural Sciences and Engineering Research Council of Canada (NSERC), Alberta Agriculture and Forestry, thank you for the financial support.

Big thanks to all staff from Parks Canada, Alberta Environmental and Parks, BC Parks and Alberta Agriculture and Forestry who provided us with in-kind support. Thank you to Helen Purves, Heather Daw, Matt Rance, Scott Jevons, Ryan Good, Jed Cochrane, Kris Beattie, Jane Park, Wayne Van Velzen, Joyce Gould, Jodie Krakowski, Pam Melnick, Margriet Berkhout and Kelsy Gibos for providing logistical support, information on sites and GIS data. My sincere and special thanks to Brenda Shepherd, Landon Shepherd and Dave Smith from Jasper National Park for going out of their way to support this project and me during my graduate program.

Thank you to all my field assistants Brendan Middel, Karambir Singh and Nathan Oostenbrink, and volunteers Sara Barszczewski and Daniel Knop who came along on strenuous hikes with me to collect data during my field seasons.

Thank you to all staff from the Department of Renewable Resources and Field Research Office for their services. Special thanks to Peter Blenis for making time to help me with statistics and for Kim Schaerer from the Field Research Office for being a great friend and keeping me safe from the bears.

Personal Friends

Thank you to all my lab mates and staff from the Western Partnership for Wildland Fire Science Group. Thanks to Ellen, Karen, Xinli, Xianli, François, Kate, Kiera, Jinhan, Oleg, Hugh, and Piyush for their presence and assistance. My sincere and special thanks to Denyse and Rodrigo for their exceptional friendship, emotional support, for providing comments on my thesis, for always listening to my complaints and problems and for lifting me up.

A big thanks to my counsellor Richard for helping me to navigate through emotionally difficult times, to learn more about my own insecurities and fears, how to be more compassionate with myself, and to believe that I am good enough.

I am grateful to all my roommates. Thanks to Andrés, Krishna, and Dani for being eternal friends. Thanks to Cass and Morag for teaching me a lot about mental health and for all the good memories at Usalama. Thanks to Dubhe for being family, letting me annoy her when I was bored and for taking me on incredible hikes.

Thank you to all my friends in Edmonton and Jasper. Thanks to Abiola and Joni for keeping me positive about life. Thanks to Renata for reminding me of home and sharing many cheese buns. Thanks to Jaime, Dante, Rodriguinho, Natalia, Denyse, Manoela, Shuwen and Arenna for all the gatherings and good conversations. Thanks to Heidi, Kim, Jasmine and Sarah for making my days in Jasper fun and brighter.

A final thanks goes to my family and friends in Brazil. Thanks to Bruninha, Amandinha, Amana, Vicente, Caiafa, Mari, Indira, Juh, Thaís Diniz, Serafim, Marcelo Almeida and Cassinha for nurturing our friendship despite the distance and time. Thanks to my aunt Junia, my brothers Gilberto, Rodrigo and André, and my sister-in-law Juliana. Special thanks to my mother Andrea and father César, for giving me this life and for making me believe that I am strong and capable and that I can always go beyond my limits.

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CHAPTER 1 - INTRODUCTION

1.1 THE STUDY PROBLEM

Populations of whitebark pine (*Pinus albicaulis* Engelmann*)*, an important tree species of high elevation forests of western North America, have been declining dramatically across their entire geographical range for the past century because of shifts in the historical disturbance regime directly or indirectly caused by human activities and global warming (Schwandt *et al.* 2010; Esch 2012; Keane *et al.* 2017; Shepherd *et al.* 2018). In light of the recent and projected population declines and its ecological importance, whitebark pine was designated as an endangered species in Alberta under Alberta's Wildlife Act in 2009 (Government of Alberta 2014) and in Canada under the Species at Risk Act in 2012 (COSEWIC 2010; Government of Canada 2018). In the United States of America (U.S.), whitebark pine is still a candidate species for listing under the Endangered Species Act (USDOI Fish and Wildlife Service 2011, 2018).

Concern for conserving and restoring the species is growing and provincial and federal agencies in Canada have been working to achieve this goal. Multiple recovery plans, including the *Alberta Whitebark Pine Recovery Plan 2013-2018* (Alberta Whitebark and Limber Pine Recovery Team 2014) and the recently proposed *Recovery Strategy for the Whitebark Pine (Pinus albicaulis) in Canada* (Environment and Climate Change Canada 2017), identify research priorities and knowledge gaps, and provide strategies for conservation and restoration of the species (Keane *et al.* 2012, 2017).

These recovery plans recommend prescribed burns as a mean to restore the historical fire regime and to create more favourable habitats, free of competition, for natural regeneration to occur (Keane and Arno 2001). Prescribed burns have been applied on the landscape over the past 30 years in Canada. However, they are expensive tools and can cause the mortality of valuable mature cone-producing whitebark pine trees if not carefully and properly applied. Lastly, not many monitoring studies have evaluated the success of these projects, posing the question whether prescribed burns are really successful in restoring the species.

Fire may not play the same ecological role across the geographical range of whitebark pine because of differences in community types and fire regimes. In stands where whitebark pine is easily outcompeted by other tree species, fire may be more important to maintain whitebark pine as a main forest component in the landscape. On the other hand, in cold and dry areas, where harsh conditions limit the growth of competing species, whitebark pine may prevail as a climax species without the need of fire. In addition, fire regimes vary across the species range. Most studies looking at the effects of fire on whitebark pine were completed in the United States, where mixed-fire regimes prevail. Therefore, it is not correct to assume that the fire effects on regeneration are the same for every community type and that all findings from studies in the U.S. can be applied in the northern limit of the species in Canada, where crown fire regimes may predominate. Understanding the role of fire in whitebark pine systems in high elevation subalpine forests in Alberta and what drives regeneration in post-fire environments is necessary to inform managers on best application practices of prescribed burns on the landscape and to successfully achieve local conservational goals (Alberta Whitebark and Limber Pine Recovery Team 2014).

1.2 BACKGROUND INFORMATION

1.2.1 WHITEBARK PINE BIOLOGY

Whitebark pine is a long-lived and keystone species of high elevation forest of western mountain regions of North America. It is a slow growing tree which produces its first cones around 25 to 30 years of age, but sizable cone crops start usually after 60 to 80 years (McCaughey and Tomback 2001). It is considered a stone pine species in the subsection *Cembrae,* which are characterized for having indehiscent cones, wingless seeds, five needles per fascicle, and for having its seeds dispersed by birds of a specific genus (*Nucifraga*). A discussion of whitebark pine would be incomplete without mentioning the close and important mutualistic relationship with Clark`s Nutcracker (*Nucifraga columbiana*), which is the main seed disperser of whitebark pine.

Nutcrackers collect seeds from whitebark pine during late summer and early autumn and cache them in multiple locations for later retrieval. Seeds that are not retrieved represent the main source of whitebark pine regeneration. Preferable caching locations are sites closer to source trees, but Clark`s can travel over 20 km to distant sites (Lorenz *et al.* 2011). Tragically, if cone production falls below certain thresholds, mainly caused by white pine blister rust infection (*Cronartium ribicola)*, Clark`s may be less likely to visit stands and will probably forage on alternative seed sources, such as other coniferous species, such as Douglas-fir (*Pseudotsuga menziesii*) (Tomback and Linhart 1990; McKinney *et al.* 2009; Barringer *et al.* 2012).

Whitebark pine is not a species of great commercial value, but it provides many ecological benefits and services to the environment where it occurs. Its seeds have a high-energy content that serve as an important food source for small mammals, birds, and bears (Tomback and Kendall 2001). It regulates spring runoff, reduces local erosion (Tomback *et al.* 2001) and facilitates the establishment of shade-tolerant tree species such as subalpine fir (*Abies lasiocarpa*) and engelmann spruce (*Picea engelmannii*) by alleviating harsh conditions for their development (Callaway 1998).

1.2.2 THREATS TO WHITEBARK PINE POPULATIONS

Populations of whitebark pine have been declining dramatically across their entire geographical range for the past decades because of shifts in the historical disturbance regime directly or indirectly caused by human activities and global warming.

Fire and mountain pine beetle (*Dendroctonus ponderosae*) are examples of natural disturbances that have been altered. Fire suppression policies adopted in the past century allowed other tree species to outcompete and replace whitebark pine in more productive sites (Keane 2001), but to a lesser extent in high elevation forests, where historical fire return intervals are usually longer (Sherriff *et al.* 2001; Larson *et al.* 2009). Outbreaks of mountain pine beetle are occurring more frequently across western Canada and causing increased mortality of pine species, including whitebark pine, as a consequence of warmer mean winter temperatures and the abundance of continuous old pine forests have created perfect conditions for mountain pine beetle survival (Campbell and Antos 2000; Logan *et al.* 2010).

Among all the factors threating whitebark pine, the disease white pine blister rust can be listed as an important one. Levels of blister rust infection in whitebark pine populations have been increasing across its range (Campbell and Antos 2000; Zeglen 2002; Smith *et al.* 2013; Shepherd *et al.* 2018). This disease is caused by *Cronartium ribicola*, a fungus accidentally introduced to western Canada in the early 19th century, which kills young seedlings and cone producing mature trees. It has a complex life cycle, alternating between two hosts: five-needle white pines (e.g. whitebark and limber pine) and *Ribes* species (e.g. currants). After initial infection caused by basidiospores that land on leaves, the fungus grows in the bark and phloem of tree branches and stem, blocking the transport of water and nutrients (McDonald and Hoff 2001). Tree mortality and loss of seed production significantly reduce regeneration potential.

In addition, climate change is also predicted to pressure whitebark pine populations by directly affecting establishment and survival, and influencing natural disturbance regimes (Hansen *et al.* 2016; Keane *et al.* 2017). Predicted warmer temperatures may facilitate mountain pine beetle outbreaks, the occurrence of more severe fires (Flannigan *et al.* 2005) and growth of competing vegetation at higher elevations. Consequently, suitable habitats for whitebark pine are likely to decrease in the next decades across its range, pushing the species to northern and higher areas (Coops and Waring 2011).

1.2.3 WHITEBARK PINE COMMUNITY TYPES

The geographical distribution of whitebark pine is extensive (Appendix 15). In Canada, it covers a large portion of the Coastal and Cascade Mountains in British Columbia, and the Rocky and Columbia mountains in western Alberta and eastern British Columbia

(Ogilvie 1990). In Alberta, it extends from Waterton National Park to Kakwa Wildland Park and stands usually occur in a patchy and discontinuous distribution. The elevational range varies with latitude, but on average it can be found 1950 m to 2250 m (Achuff *et al.* 2002).

A result of its broad geographical and altitudinal range is the occurrence of different community types which whitebark pine forms. In areas where conditions are warmer and wetter, whitebark pine tends to play a seral role, where it is a major forest component until more shade-tolerant species develop and out-compete it. Otherwise, if conditions are drier and colder, it tends to form climax communities, where it remains as a major forest component as harsh environmental conditions limit the establishment of other co-occurring tree species that could eventually compete with it, such as Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*) and lodgepole pine (*Pinus contorta*) (Arno and Hoff 1989; Arno 2001). Differently from the whitebark populations in most part of United States, whitebark pine is usually a minor component in subalpine forests in Canada, where it tends to form climax/co-climax communities near the treeline.

Those differences in community types are important to understanding what role fire plays in whitebark pine recovery. In the case of seral communities, fire may be necessary to maintain whitebark pine in the landscape by eliminating competitors and reinitiating the successional process (Weaver 2001). On the other hand, in climax communities, where whitebark pine can regenerate and remain as a major forest component over the long term without major competition, fire may not be essential. In other words, communities may not respond to fire in the same way across its range.

This is the reality of whitebark pine in the northern limits of Alberta. It is suggested that the species usually grows at high elevations and forms climax or co-climax communities that remain open without fire as a consequence of the harsh conditions that limit the growth of competitors (Wong *et al.* 2008; Wong 2012). So, is fire a requirement for natural regeneration to occur? Can fire bring benefits to these communities? Studying post-fire regeneration of whitebark pine can help us answer those questions and better understand the role of fire on whitebark pine populations in Alberta, which is of extreme importance to plan effective fire management actions to restore the species.

1.2.4 VARIABILITY IN FIRE REGIMES ACROSS WHITEBARK PINE RANGE

Fire has been naturally occurring in whitebark pine ecosystems for at least the past 14,000 years (Minckley *et al.* 2007; Murray and Siderius 2018). Fire frequency and severity are highly variable across the geographical range of whitebark pine (Campbell *et al.* 2011). In summary, the three main types of fire regimes reported in whitebark pine communities are: (i) infrequent high-intensity stand-replacing fires, (ii) mixed-severity fires and (iii) frequent low severity surface fires. Each one of these fire regimes is believed to have different effects on whitebark pine dynamics.

Low severity surface fires, for example, mostly consume understory fuels, including seedlings of trees species, but it can kill individual trees by heating the cambium (a live tissue inside the bark) to lethal temperatures. Engelmann spruce and subalpine fir may be more affected than whitebark pine trees because of their thinner bark (Ryan and Reinhardt 1988; Morgan and Bunting 1990). In this case, the main service provided by surface fires seems to be the reduction of competition from understory and overstory trees while keeping mature whitebark pine trees alive. This type of fire usually occurs in the southern range of the species or on dry ridges (Morgan *et al.* 1994).

High severity stand-replacing fires, on the other hand, cause high or complete mortality of understory and overstory vegetation, including whitebark pine, returning the succession process back to an initial state over large areas. They usually originate in lower elevation forests and spread upslope when weather and fuel conditions are favourable for fire spread. Stand-replacing fires are infrequent and their return interval is usually over 250 years in the northern Cascades, Greater Yellowstone Area, and Rocky Mountains (Morgan and Bunting 1990; Keane *et al.* 2012). The advantage this type of fire provides to whitebark pine comes from the fact that the species can still colonize the interior of such large fires because of the longer dispersal abilities offered by Clark`s Nutcracker, while the seed dispersal of co-occurring wind-dispersed tree species is limited to short distances from surviving trees. In that way, emerging whitebark pine seedlings can grow without competition for some time within the burn perimeter.

Lastly, mixed-severity fires are reported as the most common fire regime in whitebark pine ecosystems (Campbell and Antos 2003; Larson *et al.* 2009), and they are a mix of the low-intensity surface fires and high severity stand-replacing fires. They create a complex mosaic of post-fire conditions on the landscape (Arno *et al.* 2000; Siderius and Murray 2005), which is believed to be the most beneficial for whitebark pine (Murray 2007; Campbell *et al.* 2011). Their return interval can vary from 60 to over 300 years depending on fuel conditions and drought cycles (Arno and Hoff 1989).

Fire regimes across whitebark pine's range can thus be understood as inherently complex and variable. Considering these differences is important when using prescribed burns as a restoration tool since their goal is to mimic the effect of historical fires. Information on fire regimes in subalpine forests and fire effects on whitebark pine regeneration are not lacking, but most existing studies were undertaken in the United States, where ecological and environmental conditions and whitebark pine community types are likely to differ from the ones at the Canadian northern limit of the species. Therefore, again, it comes down to the question of what role fire plays on northern whitebark pine systems and how fire drives regeneration in post-fire environments.

1.2.5 WHITEBARK PINE POST-FIRE REGENERATION

There are important stages that regeneration of whitebark pine, or of any other tree species, has to go through before it establishes: (i) Seed dispersal/delivery, (ii) seed germination, and (iii) seedling survival. In the case of whitebark pine, for example, Clark`s nutcracker needs to cache seeds in locations that will support seed germination and long-term seedling survival. Burned areas provide favourable conditions for regeneration establishment, such as lower litter cover (McCaughey 1990) and competition from other conifer species that are physiologically less tolerant of environmental exposure (Maher and Germino 2006; Bansal *et al.* 2011), and greater availability of soil nutrients (Perkins 2015). On the detrimental side, the more open conditions within the burn may expose seedlings to greater insolation and cause heat scorching of young whitebark pine seedlings, which, in turn, can lead directly to mortality (Weaver 2001; Moody 2006; Larson and Kipfmueller 2010). Fire can also affect soil ectomycorrhizal communities important for whitebark pine growth, but impacts vary according to fire intensity, forest type and other factors (Cairney and Bastias 2007; Trusty and Cripps 2011).

Seed dispersal by Clark`s nutcracker offers whitebark pine a great advantage when colonizing the interior of large fires. There is a perception that the bird prefers caching in recent burns, even though there is no research published testing this hypothesis. Since Clark`s nutcracker uses spatial memory to locate cache seeds (Bednekoff and Balda 2014), fires may provide preferable structural cues. Another factor may be the earlier snow melt in more open areas (i.e. recent burns), facilitating access to cached seeds.

After seeds are dispersed, they still need to germinate and survive to become fully established. Balanced levels of available moisture and temperature seem to be important factors controlling both of these stages. Higher germination rates in burned areas were associated with higher spring precipitation (Tomback *et al.* 1993), mesic sites (Tomback *et al.* 1993; Moody 2006), and higher maximum July surface temperatures (Mellmann-Brown 2005). At the same time, extremes in temperature and moisture may be detrimental to survival. Heat scorching and desiccation are the main causes of seedling mortality (McCaughey 1990; Larson and Kipfmueller 2010). With that susceptibility, it is not surprising that whitebark pine regeneration in burned areas has been commonly found close to nurse objects that create microsites favourable, such as logs, rocks, and woody debris (Izlar 2007; Klutsch *et al.* 2015). Medium levels of vegetation cover have also been reported to favour seedlings by protecting them from those adverse conditions (Maher *et al.* 2005; Maher and Germino 2006; Tomback *et al.* 2011; Leirfallom *et al.* 2015). In the end, it is noticeable that whitebark pine regeneration is influenced by post-fire conditions.

Post-fire conditions and the effects of fires are not uniform across a landscape. They are complex and vary depending on burn characteristics (i.e. season, type of fire, duration, frequency, and severity), post-fire weather, and the community burned. Fire severity, a measure of biomass consumed by a burn (or in other words, the amount of ecological change), can influence the post-fire seedbeds and plant regeneration (Greene *et al.* 2005). High severity stand-replacing fires have very different post-fire conditions than low severity surface fires, for example. Therefore, fire severity may also play a fundamental role on whitebark pine regeneration; however, not many studies explore this association in depth.

1.3 OBJECTIVES AND SIGNIFICANCE OF STUDY

The broad goal of this study is to expand our understanding about the role of fire on whitebark pine dynamics at its northern limit by exploring fire, stand and plot level factors driving whitebark pine occurrence and abundance in early post-fire environments. Some of the more specific questions for which we want to provide evidence are:

(i) What drives regeneration in post-fire environments? Is regeneration explained by fire, stand or plot level factors?
(ii) Do prescribed burns have similar effects as wildfires on promoting post-fire regeneration?
(iii) Does fire severity influence post-fire regeneration of whitebark pine?

The questions surrounding whitebark pine post-fire regeneration are not new. However, most studies seem to concentrate on the U.S. range, where whitebark pine communities and ecological and environmental conditions probably differ. Studies focusing on the northern limits of the species range are warranted, particularly now, when global warming is expected to increase fire frequency and intensity in many parts of Canada. This study will build upon the knowledge of post-fire regeneration of whitebark pine, helping us understand the role fire plays for northern whitebark pine communities. Understanding the complexity of factors at multiple spatial scales controlling tree regeneration is essential for management practices and restoration actions for an endangered species such as whitebark pine.

CHAPTER 2 - METHODOLOGY

2.1 STUDY AREA

Our study area is located in the Rocky mountain region of western Alberta, Canada, spanning provincial and federal mountain parks, including Jasper National Park, Banff National Park, Kootenay National Park, Willmore Wilderness Park, Spray Valley Provincial Park, and the forest land use zone R11 Management Area (i.e. North Saskatchewan Crossing area). We sampled recent (< 20 years old) wildfires and prescribed burns that occurred within the whitebark pine range of these provincial and federal mountain parks. Ideally, we wanted to limit study sites to a smaller geographical area, avoiding large variability in environmental conditions; however, the number of burns that met our criteria was limited within small scale regions. Therefore, we decided to explore study sites at a broader geographical range across the parks to increase the number of fires available, and to test fire differences explicitly.

The latitudinal range of our study goes from 50° 52` N (Spray Valley Provincial Park) to 53° 47` N (Willmore Wilderness Park). See Table 1 for detailed information on fires and Figure 1 for their distribution. The elevation range of the study sites varied from 1600 to 2370 m. Fires north of Jasper town (Vine Creek, Sheep Creek and Jackpine) had the lowest elevation averages (1600 m - 2000 m). Fires also varied in age (5 – 18 years) and size (12 ha – 16000 ha).

Study sites were within the subalpine natural sub-region, characterized by cold winters with high snowfall and short cool summers, with occasional hot and dry weather in summer (Natural Regions Committee 2006). According to the databases from provincial weather stations, monthly minimum temperatures during our 2016 field season were relatively similar between regions in summer months, ranging from 0 °C to 1.5 °C in July 2016. Maximum summer temperatures varied more among regions. Weather stations closer to the Vermilion Pass and Helen Lake fires report maximum temperatures of 18 °C – 20 °C in July 2016, while stations nearer the other sites show maximum temperatures varying from 27 °C – 30 °C. In 2016-2017, mean total precipitation during the growing season (April – September) at Grand Cache, Kootenay Plains and Spray Valley Provincial Park was 552.65, 265.8 and 328.9 mm, respectively.

Tree species composition varies between whitebark pine stands. In the Rocky mountain region of western Alberta, engelmann spruce, subalpine fir, and lodgepole pine are usually the most common forest overstory components that occur with whitebark pine. Subalpine larch (*Larix lyalli*) and Douglas-fir (*Pseudotsuga menziesii*) can be observed as well, but they are less common. Limber pine (*Pinus flexilis*) is found in the forest land use zone R11 Management Area. Common understory species that can be found in whitebark pine stands are: *Chamaenerion sp.* (fireweed), *Arctostaphylos sp.* (bearberry), *Rhododendron albiflorum* (white-flowered rhododendron), *Rhododendron menziesii* (False azalea), *Vaccinium scoparium* (grouseberry), and *Phyllodoce sp.*(mountain heather). Soils in subalpine whitebark pine stands are typically regosols, characterized by its young age, underdeveloped soil profile and thin organic layers (Holland and Coen 1982).

Infection levels of white pine blister rust in whitebark pine stands vary across the Canadian Rockies (Smith *et al.* 2008, 2013; Shepherd *et al.* 2018). Specific infection levels for each sampled fire in our study is not available. Smith *et al.(*2013) provide an average of percentage of live trees infected for three geographical regions in the Canadian Rockies: (i)

Waterton National Park, with 83% of all live sampled trees infected; (ii) northern region of Banff National Park, where 36% of live trees were infected, and (iii) Jasper National Park and McBride, British Columbia, with an average of 49 % of trees diseased. Current infection levels likely increased since 2013. The probability of infection is higher at stands located west of the continental divide and at sites with a longer growing season (Shepherd *et al.* 2018).

The fire regimes in whitebark pine communities are complex. Although mixed-severity and high severity stand-replacing fires are reported to occur across whitebark pine range (Larson 2005; Larson *et al.* 2009; Murray and Siderius 2018), all fires visited were only high severity stand-replacing fires, with high tree mortality and with just a few remaining tree islands within the burn perimeter.

2.2 SITE SELECTION

The first step for selecting sites was to find, in advance, recent fires less than 20 years old that occurred within whitebark pine range by using provincial or federal historical fire data bases and communication with staff from management areas (i.e. Parks Canada, Alberta Parks and Alberta Agriculture and Forestry). From all fires of suitable age and within whitebark pine range, we selected a subset of prescribed burns and wildfires in order to capture variability in burning conditions and to test the effect of burn origin on regeneration.

Selected burns were less than 20 years old in order to enable us to observe fire severity indicators, such as tree mortality, heat scorch, tree branch consumption and changes in understory vegetation. The disadvantage of this decision was that it reduced our chances of finding post-fire regeneration of whitebark pine within the burn. Although new whitebark pine seedlings can establish even 3 - 5 years after fire, it can take over 10 years to reach good levels if conditions remain favourable (Tomback *et al.* 1993). Among the nine sampled fires, five were at least 10 years old, while four were younger.

We gave priority to fires in proximity to known whitebark pine stands to increase chances to find regeneration. Personal communication with staff from the provincial and federal parks, information on the location of health monitoring plots used by Smith *et al.* (2013) and on previous research by Moody (2006) were used to identify whitebark pine stands. Only the Jackpine wildfire in Willmore was not within known whitebark pine range. It was still visited as an attempt to find new populations of seedlings that could reflect dispersal by Clark`s Nutcracker.

Accessibility to high elevation whitebark stands is difficult and time demanding; therefore, it not only affected our fire selection, but also the decision of which specific locations within a fire we could sample. More easily accessible stands were given priority in sampling, and most of them were accessible by 2 - 3-hour hike.

2.3 SURVEY METHODS

2.3.1 SAMPLING DESIGN

Fires were sampled in the summer of 2015 and 2016. We used Geographical Information System (ArcGIS version 10.5) fire perimeter and digital elevation model (DEM) layers and information on fire progression (when available) from local agencies to identify locations within each fire that burned on different days, aspects and meso-habitat (i.e. open upper subalpine or closed lower subalpine forests). We tried to sample more than one location within each burn according to the differences in the fire conditions listed above, but that was not possible for smaller fires, which was the case for most prescribed burns. For this study, these multiple locations are referred to as stands.

Stands within the same burn were on average one to two kilometres apart. They were considered to be our independent units because we believed that most of the variation in burning conditions occurred at this level as a consequence of the differences in aspect and forest structure between stands. Within each stand, we selected three to four locations, in advance, along the fire perimeter to establish sampling transects. We gave priority to areas in higher elevations (i.e. usually > 1,800 m above sea level) to increase chances of finding whitebark pine regeneration, as well as a preference for more accessible locations to reduce travel time between transects. The distances between transects were on average 150 – 200 m apart.

Along most transects, we established four plots, one at each -15 m (unburned forest), 0 m, 15 m, and 50 m from forest edge to try to capture a smaller scale variation in fire severity, assuming the plots at the forest edge (0 m) were the least severe and the ones at 50 m were the most severe. At some transects, we were able to establish only two or three plots, thus creating an unbalanced experimental design (Table 3). Plots were 50 m long by 4 m wide, with longest axis always being perpendicular to the transect and parallel to the forest edge. At each plot, we assessed the occurrence and abundance (density) of post-fire whitebark pine regeneration, and multiple stand- and plot-level predictors, including tree basal area, aspect, seedbed and understory competition cover. Within each plot, seedbed quality and understory competition information was collected at five 1 m x 1 m quadrats established at 5, 15, 25, 35 and 45 m along the plot. Tree basal area was estimated at 5 and 45 m within each plot using basal area prisms. See Figure 2 for transect and plot scheme and Table 2 for predictors and their respective descriptions.

2.3.2 POST-FIRE WHITEBARK PINE REGENERATION OCCURRENCE AND ABUNDANCE

At each plot, we assessed post-fire whitebark pine regeneration occurrence and abundance. We first determined if regeneration was present or absent. When present, we counted the number of seedlings and calculated the density per hectare (seedlings/ha) by dividing the count of seedlings by the plot area (in hectares) Every seedling was counted as one unit regardless of whether it was in a cluster or by itself (e.g. one cluster with 12 seedlings was counted as 12 instead of only one). To determine if a seedling was post-fire regeneration, we estimated its age by counting the number of annual whorls. If the number of annual whorls was less than the age of the burned site, we considered the seedling as part of the post-fire regeneration. Otherwise, we considered it as advanced regeneration and didn`t include it in the data analysis.

Counting annual whorls, especially in young seedlings, can be very difficult because they may be close together or are not always visible. Although whorl counts and actual seedling age are positively correlated, counting whorls is not always accurate and it can underestimate the age (Gelderman 2014; Klutsch *et al.* 2015). Therefore, mainly at plots in the undisturbed forest and at the fire edge, some seedling may have been classified as post-fire regeneration when they were actually advanced regeneration, or vice-versa.

2.3.3 FIRE AND STAND LEVEL FACTORS

Time since fire, fire weather index (FWI), fire size and burn origin were used as our fire level factors. Whitebark pine basal area, total tree basal area of all tree species, and aspect were our stand level factors. Exploring stand variables provides insight on which stand types whitebark pine is more likely to regenerate in after a fire.

Fire Weather Index (FWI) is a numeric rating of fire spread potential and it is calculated based on fuel moisture and weather conditions, such as temperature and wind speed (Van Wagner 1987). Higher FWI values indicate that conditions are more favourable for a fire to spread, such as warmer temperatures, stronger winds and drier fuels. Therefore, chances are that higher severity fires are likely to occur. FWI is not a direct measure of fire severity, but it provides an indication of how severe a fire might have burned. If a study site burned for multiple days, we obtained multiple FWI values. In some cases, FWI was retrieved directly from fire managers of local management areas. For other fires, FWI information was not readily available. In those cases, we had to retrieve FWI values from historical database of the closest provincial or federal weather station. Weather stations were usually at lower elevations or more than 30 km away from sampling locations. Therefore, we suspect that some FWI values may not be entirely accurate.

Burn origin refers to whether the fire was a prescribed burn or wildfire. We assumed they were different in size, seasonality and intensity because prescribed burns are usually applied in the landscape when conditions are cooler and moister for better control. Wildfires are usually naturally ignited by lightning strikes during summer when the weather conditions are usually warmer and drier. Those differences are reflected in variability in fire severity.

Total live and dead basal area for each tree species, and total percent canopy cover were estimated at 5- and 45-m within every plot, using a basal area prism and a convex densitometer, respectively. The two estimations were averaged and used in analysis. The basal area prism factor (2, 5, or 10 Basal Area Factor) was chosen according to stand density. The total basal area was calculated in m^2/ha by multiplying the number of tree counts by the chosen basal area factor. At the start point of each plot elevation and aspect were determined with a hand-held GPS unit and a compass, respectively. Because aspect values measured in degrees are not suitable for analysis, they were later rescaled to Heat Load Index, which is a linear measure with values ranging from zero to one, with one being the warmest aspect (southwest) and zero being the coldest aspect (northeast)(McCune and Keon 2002). The formula used was:

$$Heat\ Load\ Index = \frac{1-\cos(\theta-45°)}{2}$$, where θ is the plot aspect in degrees.

2.3.4 PLOT LEVEL FACTORS

Seedbed and understory vegetation cover were used as our plot level factors and they were tested so we could better understand under which conditions early whitebark pine regeneration occurred in post-fire environments. Soil lfh depth (litter, fibric and humic organic matter), exposed mineral soil cover, decaying wood cover and moss cover were assessed as seedbed quality predictors, while the percentage cover of herbs, tree seedlings (i.e.

mainly *Picea engalmannii, Abies lasiocarpa, Pinus contorta*), and shrubs, and tree seedling density were assessed as understory competition predictors.

The percentage cover of exposed mineral soil, decaying wood, moss, tree seedlings (< 1.3 m height), shrubs and herbs was visually assessed within 1 m x 1 m quadrats that were established at 5, 15, 25, 35 and 45 m in each plot. The average taken from the five quadrats was used for analysis. Shrubs were subdivided into three height classes to provide a better representation of the vertical structure of the understory vegetation. Those classes were: Large shrubs (>50 cm), medium shrubs (between 20 − 50 cm), and grounds shrubs (<20 cm). Large shrubs were rarely found in our plots, so we decided to exclude them in the analysis. Soil lfh depth was taken by digging a hole in the soil at each quadrat and measuring from the interface between the organic layer and mineral soil to the top of the lfh surface. The number of seedlings per hectare of other tree species (excluding whitebark pine) was calculate by dividing the count of seedlings by the plot area.

2.4 DATA ANALYSIS

Our data analysis comprised two steps: (i) use of logistic and zero-truncated negative binomial (ZTNB) regression to test the effect of individual variables and to identify which predictors had a stronger association with post-fire whitebark pine regeneration occurrence and abundance (response variables); and (ii) use of the most significant variables (identified in step 1) in different combinations to perform linear mixed effect model selection. The only data point removed from the statistical analysis (and figures) was from one plot at Vermilion

Pass (stand VP1), which was considered an outlier, since its regeneration density was over ten standard deviations larger than the overall mean.

Neither of our two response variables for whitebark pine regeneration followed a normal distribution. Regeneration occurrence followed a binomial distribution and regeneration density, which was count data, followed a poisson distribution. Another characteristic that needed to be considered for our data was that observations had multiple clustering levels (i.e. fires, stands and transects) and spatial auto-correlation between observations. Therefore, we used generalized linear mixed effect models (glmm) to account for the lack of independence between observations (i.e. the existence of clustering levels) and for the non-normal distribution of the data (Bolker *et al.* 2008). Some models failed to converge when all random factors were included (i.e. fire, stand and transect). We suspected it was likely because of the complexity of models and the few numbers of observations. Ideally, all clustering levels would be adopted as random factors in our mixed effect models to account for lack of independence, but we decided to use only stand. We believed most of the environmental and burning conditions occurred at this level since stands were primarily selected according to their aspect, elevation and meso-habitat (i.e. open/upper subalpine or closed/lower subalpine forest). Predictors fell into one of the three scales: fire, stand, and plot.

We first ran a logistic regression to test for relationships between regeneration occurrence and the various predictors. In this stage, all data points were considered in the analysis. In a second step, we considered only data points where regeneration was present and ran a zero-truncated negative binomial regression to further test the relationship between regeneration density and the same predictors. The ZTNB regression was chosen to account for the overdispersion (i.e. larger variation than expected in the data) in regeneration density and for the fact that plots with no regeneration were removed from dataset at this stage (Hilbe 2014).

After running the regressions and identifying stronger predictors, we performed model selection. We used an approach suggested by Hosmer and Lemeshow (2000) and adopted in a similar study (Coop and Schoettle 2009). Predictors were tested one-by-one using the appropriate glmm (i.e. first stage of the analysis) and only predictors at $p < 0.25$ were selected to build subsequent models. The models were tested and ranked according to their Akaike's Information Criterion (AIC), Evidence Ratio (ER), Akaike Weight (w_i), Cumulative Akaike Weight (acc wi) and the number of parameters estimated (k_i) (Burnham *et al.* 2011).

Evidence Ratio (ER):

$$ER = \frac{\exp(-\frac{1}{2} * \Delta best)}{\exp(-\frac{1}{2} * \Delta i)}$$

Akaike Weight (Wi):

$$Wi = \frac{\exp(-\frac{1}{2} * \Delta i)}{\sum_{r=1}^{R} \exp(-\frac{1}{2} * \Delta i)}$$

All analyses were conducted using R software version 3.2.2 (R Core Team 2015). For the logistic regression, we used the function *glmer*, from the package *lme4*. The *glmmTMB* package was used to fit zero-truncated negative models with the regeneration density data (Bolker 2016).

Data visual exploration was an important complement to analysis. Only the best predictors were further explored. In many graphs, regeneration occurrence data was summarized by stand as a way to represent presence-absence data.

CHAPTER 3 – RESULTS

In total, 9 fires, 25 stands, 71 transects and 241 plots were sampled. 40.5% of the plots had at least one whitebark pine seedling present. Seedling density ranged from 0 to 1400 seedlings per hectare, and the mean and median were equal to 148.8 and 0 seedlings per hectare, respectively when considering all plots. The standard deviation was high, totalling 273.3, which indicates the overdispersion in the data set. When only plots with regeneration were considered (n = 97), the distribution was still skewed, but the difference between the variance and mean was smaller (mean = 369.6; standard deviation = 322.9) (Figure 1). Although not represented in data analysis and figures, an extreme high regeneration density episode with 3250 seedlings/ha was observed in the stand VP1, at Vermillion Pass wildfire.

Regeneration density and the proportion of plots with seedlings present varied between and within burns, regardless of burn origin (Table 4; Figure 13). Moab Lake and Vermillion Pass wildfires and Saskatchewan Crossing and Buller Creek prescribed burns had the highest regeneration responses, having 40.6 – 69.2% of their plots occupied with regeneration and density means ranging from 159.4 to 257.8 seedlings per hectare. Vine Creek and Mount Nestor prescribed burns, and Sheep Creek wildfire had lower mean densities (25 - 79.4 seedlings/hectare), and proportion of plots with regeneration (11.1 – 22.5 %). Jackpine wildfire was the only fire where whitebark pine recruitment was absent in all plots.

3.1 MULTIPLE SCALE FACTORS LINKED TO REGENERATION

3.1.1 REGENERATION OCCURRENCE MODEL

After testing all the variables individually with the appropriate generalized linear mixed effect model, we listed them according to increasing AIC values (Table 5). The models converged for all variables, except for the herb cover and fire size. Moss cover, whitebark pine basal area, time since fire, FWI and medium shrub cover were the only variables that had a p-value lower than 0.25; all of them showed a positive relation with regeneration occurrence. Fire, stand and plot scales had at least one variable with p-value <0.25 and a difference in AIC < 2 compared to the best variable. The best variables of the fire, stand and plot scales were time since fire, whitebark pine basal area and moss cover, respectively.

In the second stage of the model selection, multiple models were tested using variables at p<0.25 and later ranked according to their AIC values (Table 6). Eight models were listed within the 95 % confidence interval (i.e. cumulative wi < 0.95). Model I was selected as a final model for having the lowest AIC and at least one variable at the fire, stand and plot scale. Model I had moss cover, time since fire, whitebark pine basal area and FWI as predictor variables and all of them showed a positive correlation with whitebark pine regeneration occurrence (Table 10). Understory competition was not represented by any variable within the selected occurrence model.

Estimates from logistic regression characterize the relationship between the predictor and response variable on a log-odds scale, which doesn`t provide meaningful information. Therefore, we calculated the exponential of each coefficient. With that, we were able to interpret the effect of every one-unit increase in selected variables on regeneration probability.

One-unit increase in moss cover, time since fire, whitebark pine basal area, or FWI will increase the probability of regeneration occurrence by 1.8%, 18.8%, 8.9% and 7.1%, respectively (Table 9). It is important to remember that the positive correlations between the predictors and regeneration occurrence found in this study apply only within the range of values sampled for each predictor.

3.1.2 REGENERATION ABUNDANCE MODEL

Among the 18 variables tested in relation to regeneration abundance, nine showed a $p<0.25$. Whitebark pine basal area, medium shrub cover, and mineral soil cover were positively related with regeneration abundance, while decaying wood cover, total basal area, depth of soil lfh layer, time since fire, and regeneration density of other tree species (*Pinus contorta, Abies lasiocarpa, Picea engelmannii*) displayed a negative correlation (Table 7). There was a significant difference between prescribed burns and wildfires. Fire, stand and plot scales had at least one variable with p-value <0.25. The best variables of the fire, stand and plot scales were time since fire, whitebark pine basal area and decaying wood cover, respectively.

Variables at p-value< 0.25 were tested in various combinations and, ranked according to their AIC values (Table 8). Whitebark pine basal area, decaying wood cover and medium shrub cover were present in most models within the 95% confidence interval. Competing models with a difference in AIC< 2 may be considered as good as the best model (Symonds and Moussalli 2011, but see also Burnham *et al.* 2011; Richards *et al.* 2011). Therefore, although model I has the lowest AIC, it is more complex (i.e. larger number of estimators) compared to simpler models with a difference in AIC <2. We selected model VII as a final model because it has at least one variable of each scale, in which time since fire and whitebark pine basal area were also present in the occurrence model.

In model VII, whitebark pine basal area and medium shrub cover were positively correlated with regeneration density, while decaying wood cover and time since fire had a negative correlation (Table 10). Similar to the logistic regression, a poisson model is in log form; therefore, calculating the exponential of each coefficient helped us with the interpretation of results. For every one-unit increase in whitebark pine basal area, decaying wood cover, time since fire and medium shrub cover, we can expect a change of 3.1, -4.8, -5.2 and 1.8 in seedlings per hectare, respectively. The correlations between the predictors and regeneration abundance apply only within the range of values sampled for each predictor.

Figure 3 shows the comparison of the fitted values against observed values and Figure 4 displays the model residuals. We observed under predictions for lower densities and over predictions for higher values and that residuals scale with the mean.

3.2 DIFFERENCES IN REGENERATION BETWEEN PRESCRIBED BURNS AND WILDFIRES

Regeneration occurrence did not vary significantly according to burn origin, while regeneration abundance differed between prescribed burns and wildfires (Figure 5, Table 5 and 7). The proportion of plots with whitebark pine regeneration in wildfires (46.5%) was 1.35 higher than prescribed burns (34.4%). When considering only plots where regeneration was present, the mean abundance in prescribed burns (430.2 seedling/ha) was 1.34 higher than in wildfires (321.3 seedlings/ha), yet they both had seedling density ranges of 50 – 1350 seedlings/ha. At a stand level, regeneration was present in 71.4 % and 81.8 % of the burned stands at prescribed burns and wildfires, respectively. Amongst the 10 burned stands with no mature whitebark pine present, five of them still had whitebark pine regeneration, showing that proximal seed sources were not always a requirement.

Some other fire level factors may have interacted with burn origin and were taken into account, such as FWI, burning season and time since fire. All wildfires and two of our prescribed burns occurred in the summer, while two other prescribed burns burned in the spring and one in the fall. Burning season did not come up as a significant variable for occurrence or abundance (p-values 0.21 - 0.524; Figure 5), yet we still can observe a higher regeneration occurrence in the fall burns and higher seedling density in spring and summer burns. Fall burns had a conflicting response, where they showed the highest proportion of plots with regeneration (>60%), but lowest seedling densities (<250 seedlings/ha).

Regeneration occurrence seemed to respond positively to FWI values up to 56.5 (Coef=0.06472 and p-value = 0.0932; Figure 6). The rise of one FWI unit increases the probability of regeneration occurrence by 6.7%. The effect of FWI on regeneration density was not statistically significant (p-value = 0.382), but Figure 6 still suggested a positive relationship between them. The response of regeneration occurrence and abundance to lower severity fires is unclear since the FWI values only ranged from 21.8 to 56.5. Mean FWI in prescribed burns (39.4) was higher than in wildfires (27.6) (Appendix 5).

Fires varied from 5 to 18 years old at the time of sampling and, on average, wildfires were older than prescribed burns; mean fire age was equal to 6.9 and 12.1 years, respectively. In overall, regeneration occurrence increased over time (coefficient = 0.1993; p-value = 0.0761), but regeneration density declined (coefficient = -0.0499; p-value = 0.0602). Although it was not statistically tested, an interaction between time since fire and burn origin seems to be present (Figure 7). Regeneration occurrence was positively influenced by time since fire in both prescribed burns and wildfires. After fire, regeneration abundance increased in wildfires up to 16 years, while it decreased after 10 years on prescribed burns.

3.3 IMPORTANCE OF SEED SOURCE AND STAND BASAL AREA

When individually tested, whitebark pine basal area, which also works as an indicator for the presence of local seed sources, was positively correlated with whitebark pine regeneration occurrence (coefficient = 0.07074; p-value = 0.0822; Table 5) and abundance (coefficient = 0.03215; p-value = 0.00217; Table 6) in post- fire environments. Considering those coefficients and the range of whitebark pine basal area sampled, the increase in 1 m^2/ha in whitebark pine basal area would raise the probability of regeneration occurrence and its density by 7.3% and 3.3%, respectively. 10 out of 25 sampled stands had no whitebark pine basal area, and 5 of them still had post-fire regeneration present (Table 4).

When looking at forest structure, represented by the total tree basal area of all species together, we can observe that regeneration occurrence and density were lower in stands with higher basal area (Figure 6). The effect of total basal area on regeneration abundance was statistically significant, with coefficient= -0.04997 and p-value= 0.0602, meaning that an increase of 1 m^2/ha in the total basal area can reduce density by 4.9%. Although occurrence decreases at increasing total basal areas, the effect was not significant (coefficient= 0.007576; p-value=0.494).

Heat load index, where values closer to 1 represent warmer aspects and values closer to 0 represent cooler aspects, did not show any significant linear correlation with regeneration occurrence (p-value=0.555) or density (p-value=0.883) (Appendix 6).

3.4 REGENERATION BETWEEN UNDISTURBED FOREST AND BURN INTERIOR

There was a decrease in seedling density at increasing distances into the forest or into the burn, where densities were highest at the forest edge (0 m), intermediate at 15 m, and lowest at 50 m and within undisturbed forest (- 15 m) (Figure 8). When considering only plots with regeneration, mean seedling density of plots at -15 m, 0 m, 15 m and 50 m was equal to 320.8, 446.4, 371.9 and 288.5 seedlings/ha, respectively. However, the range of seedling density among plots at – 15 m, 0 m and 15 m was similar (50 – 1350 seedlings/ha). The pattern between distance classes and regeneration density varied depending on fire (Appendix 3), and differences were more evident on prescribed burns than in wildfires. The stand VP1, at Vermillion Pass wildfire, had a plot at 15 m with a density of 3250 seedlings/ha.

Differences in occurrence between distance classes were present as well. Plots at -15 m, 0 m and 15 m showed similar regeneration occurrence, having around 45% of their plots with at least one whitebark pine seedling, whereas plots at 50 m from the fire edge had on average only 25% of plots with regeneration, half of the occurrence at the other distance classes. The pattern between distance classes and regeneration occurrence varied depending on fire (Appendix 4).

Higher fire severity reduced the survival of advanced regeneration. Advanced regeneration was present in approximately 10 % of plots at 15 m and 50 m within the burn, 37 % at 0 m and 50 % at the unburned forest. Advanced regeneration abundance also varied between distance classes, with a continuous decrease in density from the undisturbed forest towards the burn interior (Appendix 13). Mean seedling density of advanced regeneration per hectare and ranges at the unburned forest, 0 m, 15 m and 50 m were, respectively, 241.9 (0 – 2850), 104.2 (0 – 900), 17.6 (0 – 600) and 6.1 (0 – 200). When considering only plots with regeneration, post-fire regeneration densities in plots at the forest edge (446.4 seedling/ha) and at 15 m into burn (371.9 seedling/ha) were higher compared to advanced regeneration at our undisturbed plots (241.9 seedling/ha).

The variation in regeneration abundance between distance classes may have been controlled by differences in seedbed and understory vegetation conditions. There was a clear decrease in LFH depth, moss, medium shrub and tree regeneration cover, and an increase in mineral soil and herb cover as we moved away from the forest edge. Cover percentage of small shrubs and decaying wood did not vary significantly among distance classes (Figure 10 and 11). According to the logistic and poisson regressions at the model selection stage, some seedbed and understory vegetation variables showed a significant effect on regeneration (Table 5 and 7). Occurrence was positively correlated with moss cover (coefficient= 0.01797; p-value=0.0313) and medium shrub cover (coefficient=0.03898; p-value=0.1748). Abundance had more variables correlated to it. Exposed mineral soil (coefficient= 0.0138; p-value= 0.0752) and medium shrub cover (coefficient= 0.027; p-value= 0.0117) were positive covariates, while decaying wood cover (coefficient= -0.048; p-value= 0.0114), LFH depth (coefficient= -0.074; p-value= 0.045) and tree regeneration density (coefficient= -0.0025; p-value= 0.126) were negative covariates (See Figures A7 – A10).

CHAPTER 4 - DISCUSSION

4.1 MULTIPLE SCALE FACTORS LINKED TO REGENERATION

At least one variable at a fire, stand and plot scale was present in the final occurrence and abundance models (Tables 9 and 10), indicating that whitebark post-fire regeneration is a complex process linked to factors at multiple spatial scales. This apparent influence of many scale-dependent factors on whitebark pine regeneration was not a surprise. Whitebark pine regeneration has already been reported to be influenced by stand or fire scale factors, such as health, distance and size of seed sources (McKinney and Tomback 2007; Barringer *et al.* 2012; Leirfallom *et al.* 2015), growing season length, post-fire precipitation and moisture regime (i.e. dry vs. moist sites) (Moody 2006). Smaller scale factors, such as canopy gaps in closed forest (Gelderman 2014; Gelderman *et al.* 2016), shelter objects, such as logs and rocks, (Lonergan *et al.* 2014) and seedbed conditions (McCaughey 1990) are also correlated with post-fire whitebark pine regeneration. The association with multiple scale factors coupled with the fact that whitebark pine is dispersed by Clark`s Nutcracker, and thus regeneration may also be greatly related to caching behaviours and preferences of this bird, underscore the difficulty in predicting regeneration in burned areas.

Stands with larger whitebark pine basal area had greater regeneration occurrence and abundance, suggesting that Clark`s nutcracker also uses seed sources as caching sites. However, the colonization of 5 stands where mature whitebark pine trees were not present pre-fire may suggest that fire may create new habitats for whitebark pine. Other studies observed that the health and distance to whitebark pine seed sources were also correlated with regeneration in post-fire environments (Moody 2006; Leirfallom *et al.* 2015). This might be explained by the influence of these factors on the activity of Clark`s Nutcracker. Although the bird can fly great distances and harvest seeds at multiple locations, it is more likely to visit areas with greater cone production (Barringer *et al.* 2012), which is influenced by the size, age and health of stands. Closer and larger seed sources can increase the probability of regeneration as long as the health conditions of mature trees allow for sustainable cone production. However, stands highly infected by white pine blister rust will have decreased cone production, which in turn will attract less Clark`s Nutcrackers and reduce regeneration potential.

Regeneration abundance probably was driven by the existence of favourable seedbed or understory conditions that hold moisture and prevented heat scorch. Successful germination of whitebark pine seeds occurs more frequently in warmer microsites where enough moisture is available, but at the same time excessive heat exposure is one of the leading causes of seedling mortality (McCaughey 1990; Larson and Kipfmueller 2010). Vegetation cover of up to 30% favoured regeneration according to a study by Leirfallom *et al.(*2015), but for values greater than 30%, understory vegetation started to play a more competitive rather than facilitative role. In our study, among the most significant seedbed or understory variables, regeneration occurrence was positively correlated with moss cover (up to 75 % cover), and regeneration abundance was positively correlated with medium shrub cover (up to 30 % cover). We believe those conditions may have provided more moisture or offered cover from heat exposure, which in turn favoured seed germination, and early survival at least in the first years post-fire while understory vegetation remains at low levels.

In overall, regeneration abundance decreased with time, while occurrence increased. We believe this means that Clark`s Nutcracker continuously cached seeds across the burn, increasing the chances of finding regeneration at older fires. However, understory vegetation and seedbed conditions change over time, affecting whitebark pine regeneration dynamics. Understory plant cover, for example, is likely to increase quickly at locations where there are surviving sources of propagules, such as in the forest edge or in lower severity fires, creating a competitive environment for whitebark pine seedlings. The long-term vegetation recovery can follow different patterns depending on post-fire weather, pre-fire stand composition and fire severity, making regeneration abundance difficult to predict.

The models showed us numerous factors associated with regeneration, but we do not recommend their use as predictive models. The model for abundance overpredicted regeneration at lower density values and underpredicted at higher values, and the residuals scaled with the mean, showing that the model still needs adjustments, such as the use of non-linear terms (Figure 3). Complementary data on whitebark pine post-fire regeneration at the same or additional recent (i.e. 5 -20 years old) prescribed burns and wildfires fires could help improving the models. Nonetheless, our model selection process was still an important tool to show that whitebark pine post-fire regeneration is a complex process linked to multiple biological processes at several scales.

4.2 DIFFERENCES IN REGENERATION BETWEEN PRESCRIBED BURNS AND WILDFIRES

Regeneration occurrence did not statistically differ between our two burn origins, whereas regeneration abundance did. Regardless of statistical differences, we observed a higher regeneration abundance on prescribed burns and a greater probability of occurrence on wildfires, however, regeneration responses varied over time. Regeneration occurrence increased in the first 18 years after fire, suggesting that Clark`s nutcrackers continuously cached seeds in the open areas created by prescribed burns and wildfires over time. On the other hand, conditions remained suitable for establishment up to 18 years on wildfires, while it appeared to decline after 10 years on prescribed burns. The variability in post-fire conditions possibly caused by differences in fire severity, burning season and fire size may explain opposite responses in regeneration abundance between wildfires and prescribed burns, making regeneration abundance hard to predict.

On average, our wildfires covered a much larger area (1,000 – 16,000 ha) than the prescribed burns (12 – 5,700 ha). Differences in forest composition and topography across large fires influence fire severity, often creating a mosaic of post-fire conditions (Broncano and Retana 2004; Alexander *et al.* 2006; Jain *et al.* 2006). We suspect that larger fires could have created a more diverse post-fire environment, increasing the existence of favourable conditions for regeneration establishment or Clark`s Nutcracker visitation. In addition, seed dispersal by Clark`s nutcracker allows whitebark pine seeds to reach greater distances within the burn interior of larger fires and escape competition with wind-dispersed tree species at sites where their seed dispersal is limited to short distances from surviving trees (Agee and Smith 1984; Coop *et al.* 2010). While our data cannot test this hypothesis since our plots were limited to distances of 50 m within the burns, and not distributed across the whole burned area, other studies showed that the probability of whitebark pine regeneration decreased until 600 m from seed sources at the forest edge, then increasing at greater distances (Leirfallom *et al.* 2015), which is well beyond the dispersal distances of subalpine fir and engelmann spruce.

4.2.1 SEASONAL EFFECT

Burns that happen at times of the year out of the historical regime can have a different impact on the ecosystem. Burning season can indirectly influence fire intensity and vegetation recovery (Knapp *et al.* 2009), which can lead to important differences in post-fire conditions on the landscape that may interact with whitebark pine establishment. A good proportion of prescribed burns tends to be conducted in cooler and wetter seasons, like during spring and fall, because of operational and safety reasons, while natural fire events in subalpine forests in the Canadian Rockies, Alberta, are usually characterized as stand-replacing burns that mostly likely occur in the summer (Van Wagner *et al.* 2006; Rogeau 2016). Among our sampled fires, prescribed burns occurred in spring, summer, and early fall, while all wildfires happened in summer. Consequently, there was a greater variability in FWI values on prescribed burns (21.8 – 56.5) than in wildfires (20.8 – 37.2), and possibly a greater variability in post-fire conditions.

One of the well documented seasonal effects of fire is on shrubs. Shrubs recover better from burns that occur in summer or fall when their carbohydrates reserves are at higher levels when compared to spring (Kauffman and Martin 1990; Knapp *et al.* 2009). The presence of low levels of shrub cover may benefit regeneration (Tomback *et al.* 2011; Klutsch *et al.* 2015), and our study found that medium shrub cover up to 30 % was positively associated with whitebark pine regeneration, suggesting that summer or fall burns would be better for regeneration by favouring the post-fire recovery of some shrubs. However, regeneration occurrence and abundance were not statistically different between seasons (p-values > 0.2; Figure 5). As shown in the model selection component, regeneration may be linked to many other multi-scale factors, making it hard to conclude whether or not season really had an effect on regeneration. Therefore, the effect of seasonality and its relationship with other factors needs further investigation.

4.2.2 SEVERITY EFFECT

FWI gives an indication of how intense and fast a fire can burn based on current local weather conditions, such as wind speed, cumulative precipitation and temperature (Van Wagner 1987). While it does not measure the actual fire impact and changes in the ecosystem caused by the fire, it is still a valuable indication of how severe a fire may have burned. Our prescribed burns and wildfires were different in FWI values (Appendix 5). Mean FWI of all prescribed burns (39.4) was higher than for wildfires (27.6), but the range of FWI values of both burn origins overlapped. We witnessed good regeneration responses across the FWI ranges sampled, and regression lines showed an increase in regeneration occurrence and abundance at higher FWI values (Figure 6), suggesting that higher severity fires were better for regeneration. However, all instances of FWI values greater than 50 came from stands within the same fire (North Saskatchewan Crossing prescribed burn; Table 1), which can raise the question if the high regeneration found at these stands was only explained by fire severity or other local factors. Furthermore, our study lacked low- and mixed-severity fires.

Our FWI values ranged from 20.8 to 56.5. FWI values over 20 – 25 are already considered high, where fires are likely to spread as a consequence of favourable conditions (de Groot 1987; Podur and Wotton 2011). All burns had crown fires with very high tree mortality (i.e. rarely below 100 %) and high tree bole scorches, as well as few remaining tree islands within the burn perimeter. The reduction in soil lfh depths, moss and medium shrub covers with distance from the forest edge (Figure 10 and 11) indicates that surface burning occurred, causing consumption of understory vegetation and upper surface fuels. This shows that none of our fires, be it prescribed burns or wildfires, were like the low- or mixed-severity fires usually reported in part of the southern whitebark pine range in the United States, emphasizing that the fire regime in whitebark pine stands in its northern limit probably is mostly characterized by stand-replacing fires of high severity.

An interesting observation made in the field was the mortality of mature whitebark pine trees and the low existence of advanced regeneration within the burn, at both prescribed burns and wildfires. Previous literature suggests that large whitebark pine trees are more fire-resistant than spruce and fir because of its thicker bark and deeper roots, thus often surviving medium to low-intensity fires (Arno and Hoff 1989; Arno 2001). However, in a post-fire study, Keane and Parsons (2010) found that mature whitebark pine mortality equalled that of subalpine fir in low-, mixed- and high-intensity fires. We observed a similar outcome. Our burns were high-intensity crown fires that did not allow mature trees to survive, and whitebark pine was not more fire resistant than other tree species, such as subalpine-fir and engelmann spruce. Advanced regeneration was present in approximately 10 % of plots at 15 m and 50 m within the burn and in 37 % of the plots at 0 m (Appendix 13), showing that pre-fire seedlings hardly survive high severity fires.

Although we provide evidence of beneficial and detrimental fire effects on regeneration, the influence of fire severity will need further investigation. We not only lacked low- and mixed-severity fires, but by using one FWI for each of our sampled stands we did not capture smaller scale variations in burning conditions across the whole fires caused by typical differences in topography, fuel loading, and moisture in mountain terrains (Broncano and Retana 2004; Alexander *et al.* 2006). In future studies, other alternative experimental designs may be able to better capture the variation in burning conditions, such as studies that use Relative Differenced Normalized Burn Ratios derived from satellite imageries pre- and post-fire to classify fire severity at a smaller scale (Lutes *et al.* 2006; Miller and Thode 2007; Crotteau *et al.* 2013; Kemp *et al.* 2015). For now, we observed that high severity stand-replacing fires prevailed in the northern limits of whitebark pine and that mature trees and advanced regeneration are susceptible to fires of such intensity. At the critical point in which whitebark pine populations are declining rapidly, losing mature cone-producing trees is not affordable, and knowing their susceptibility to high-intensity fires, their protection should be a priority during fire management actions.

4.2.3 TIME SINCE FIRE

Time since fire seemed to be an important driver for regeneration occurrence and abundance and it interacted with burn origin (Figure 7). We believe Clark`s Nutcracker may continuously cache seeds within the wildfires and prescribed burns with time, but the existence of favourable post-fire conditions that favour germination and survival may be driving differences in seedling density over time between prescribed burns and wildfires. Older fires, particularly wildfires, had higher regeneration occurrence, while post-fire conditions remained suitable for establishment up to 18 years on wildfire, but appeared to decline after 10 years on prescribed burns. In our study, older prescribed burns had greater tree regeneration cover than older wildfires (Appendix 12). That was the only apparent difference in conditions over time between prescribed burns and wildfires, considering the maximum distance from the forest edge sampled (i.e. 50 m). Whitebark pine seedling density was negatively correlated with tree regeneration and small shrub cover (Appendix 10), thus suggesting that the increase in competition over time may have limited regeneration abundance in the older prescribed burns we have sampled. However, we don`t know if the decrease in regeneration over time in prescribed burns was a consequence of changes in post-fire conditions, seed dispersal or other uncontrolled factors.

In other studies, post-fire whitebark pine regeneration was either found as early as 3-5 years after a burn or took over 20 years to start establishing (Tomback *et al.* 2011; Klutsch *et al.* 2015), and its density increased with time since disturbance when conditions were favorable and competitors were not a limiting factor (Tomback *et al.* 1993; Klutsch *et al.* 2015). However, Moody (2006) studied whitebark pine post-fire regeneration in fires up to 60 years old and he did not find mean regeneration densities (0 - 406 seedlings/ha) much higher than ours, showing that older fires do not always necessarily have more regeneration than younger fires.

We believe this can be partially explained by the influence of other large-scale factors, existence of unfavourable conditions or the lack of seed dispersal. Regeneration of subalpine tree species after fire is only partially correlated with time since fire. Post-fire weather conditions, proximity to seed sources and seed predation are examples of factors playing a role in regeneration (Agee and Smith 1984). Therefore, it is possible that time since fire may have interacted with some of those other fire level factors not controlled for in this study and may have confounded the effect of burn origin. More specifically for whitebark pine, greater seedling recruitment was associated with above average spring/summer precipitation (Tomback *et al.* 1993), longer growing seasons, larger and healthier seed sources (Barringer *et al.* 2012; Leirfallom *et al.* 2015), occurrence of large cone crops (also known as mast years), and moister sites (Moody 2006). A considerable amount of variation in these conditions possibly exists between our fires because our study covered a broad geographical area and many different years. Levels of blister rust infection, for example, vary depending on geographical region (Smith *et al.* 2008, 2013), but we don`t have information for each of our fires. The same applies to post-fire weather conditions (e.g. rainfall, temperature), size of seed sources, and occurrence of large cone crops. We acknowledge that such uncontrolled fire and stand level factors may have interacted with other local factors and introduced variation in the response of whitebark pine recruitment.

4.3 IMPORTANCE OF SEED SOURCE AND STAND BASAL AREA

The existence and basal area of close seed sources were strong predictors of whitebark pine regeneration occurrence in the burned stands. Larger live whitebark pine basal area has been previously reported to attract more Clark`s Nutcracker as a consequence of higher cone production (Barringer *et al.* 2012), and the proximity of seed sources to burned area seems to be a prerequisite for regeneration to occur (Moody 2006). However, twenty percent of our burned stands had regeneration even though no whitebark pine tree was present pre-fire, suggesting that fire may create new habitats for whitebark pine establishment. Although mature whitebark pine trees were not found within some sampled stands, proximal seed sources were present (i.e. within 5 km from site), except at Jackpine wildfire. We still believe that the existence of seed sources proximal to a burned area will increase the chances of post-fire regeneration success because of greater cone production and Clark`s Nutcracker visitation. However, the increased mortality caused by mountain pine beetle and white pine blister rust raises the question of how long those seed sources will remain available in the landscape to sustain natural regeneration.

Seed crops and subsequent regeneration potential have been greatly impacted by white pine blister rust (McKinney and Tomback 2007; Smith *et al.* 2008; Shepherd *et al.* 2018). By infecting the bark and phloem of stems and branches and blocking the sap transport, the fungus kills mature trees or causes significant impacts to upper branches that are responsible for cone production (McDonald and Hoff 2001). Highly infected stands are less likely to be visited by Clark`s Nutcracker as they have fewer seeds available (McKinney and Tomback 2007; McKinney *et al.* 2009). Low seed availability also leads to increased cache pilferage by secondary seed predators, such as rodents, reducing, even more, the local regeneration potential (Lorenz *et al.* 2008; McKinney and Fiedler 2010). It means that even if fire created perfect conditions for whitebark pine establishment, regeneration will not occur if enough seeds are not available for dispersion. Therefore, we believe that seed dispersal may be potentially limiting regeneration in highly infected stands as a consequence of the high mortality of cone-producing mature trees. In future burn prescriptions, knowing the health condition of close seed sources and artificial planting will be important.

Whitebark pine seedlings can be dispersed, germinate, grow very slowly and persist in the understory of closed canopy stands dominated by other tree species, but those conditions are not the most favourable for whitebark pine seedling establishment in the longer term (Gelderman 2014). In stands where other tree species tend to outgrown whitebark pine and dominate the overstory, disturbances such as fire may be required to create openings for whitebark pine. We observed that stands with higher total tree basal area (i.e. higher productivity) had lower occurrence and abundance of post-fire seedlings even after fires had completely opened up the forest canopy (Figure 6 and A11), which makes us wonder if that was a result of caching behaviour preferences of Clark`s nutcracker for open and high elevation stands or the existence of detrimental post-fire conditions, such as greater understory competition. There is considerable uncertainty in the scientific community on caching preferences of Clark`s Nutcracker. There is a widespread belief that the bird prefers caching in open areas created by fire, but other studies observed a greater use of lower elevation forests or within their home ranges, which not always are whitebark pine stands (Lorenz *et al.* 2011; Schaming 2016). In our study, Clark`s cached at both open and dense stands, burned and unburned forest, prescribed burns and wildfires, yet the decrease in regeneration occurrence at stands with higher total tree basal area may suggest Clark`s preferred to use more open stands as caching sites.

The reduction in abundance in stands with greater basal area also suggests the existence of detrimental post-fire conditions for regeneration. Post-fire conditions vary greatly according to many factors, such as moisture regime (i.e. dry vs. moist sites), pre-fire forest composition, growing season length and post-fire weather. Consequently, the response of whitebark pine regeneration will differ as well. Whitebark pine may not regenerate well in burned stands that had a great pre-fire lodgepole pine component as a consequence of intense seedling competition (Campbell and Antos 2003; Moody 2006), which provide us with an example of how pre-fire forest composition can affect post-fire conditions. Most stands with large basal area were found at lower elevations, where longer growing season and more favourable conditions may allow for rapid and better recovery of understory plants, preventing whitebark pine to establish as a consequence of competition. Regarding moisture regime, no difference in early post-fire regeneration was found between warmer and cooler aspects in our data (Appendix 6), but other studies have done so (Moody 2006). Tomback *et al.* (2011) reported high mortality rates of seedlings in moist burned sites because of deeper duff layers, while lower densities and better survival were present at drier sites. Gelderman (2014) found higher seedling densities within undisturbed forests along southwest facing slopes. Larson and Kipfmueller (2010) suggested a trade-off between germination and seedling survivorship, where germination increases on warmer sites but emerging seedlings are more susceptible to heat scorching if not located in protected microsites. Knowing that post-fire conditions can vary greatly depending on multiple factors, basal area of burned stands may not determine regeneration occurrence and abundance. When it comes down to whitebark pine restoration, it is important to understand whether fire will create conditions that will allow whitebark pine to establish better in the longer term. Is it worth burning open stands where whitebark pine may not easily experience competition? Is it worth burning dense lower elevation stands to eliminate competition? Is fire necessary for regeneration to occur?

4.4 REGENERATION BETWEEN UNDISTURBED FOREST AND BURN INTERIOR

We initially expected to find better regeneration responses within the burn, yet we found the highest densities at the forest edge, intermediate densities at 15 m and lowest values at 50 m within the burn and at the unburned forest. Although regeneration occurrence at 50 m plots was lower than unburned plots, fewer occupied plots were required to achieve similar regeneration densities, suggesting that conditions within burn are more favourable for germination and survival. Many previous post-fire studies covered distances greater than 50 m into the burn and they showed mixed results when comparing whitebark pine regeneration between unburned and burned plots. Klutsch *et al.* (2015) found higher regeneration densities in the unburned adjacent forest than in burned plots. Moody (2006) had mixed results, where some burned sites had more regeneration than undisturbed forest. McDowell (2010) found a greater probability of regeneration occurrence and a larger mean seedling density with increasing distances from the forest edge on an 11-year-old burn. Leirfallom *et al.* (2015) observed regeneration throughout their burned sites, and seedling density decreased until 600 m from seed sources located at the forest edge, but then increased at longer distances.

The presence of regeneration within the undisturbed forest shows that fire is not required for regeneration to occur. However, an important question is whether fire is beneficial. We observed evidence in favor and against this idea. The mean post-fire regeneration density at the forest edge (446.4 seedling/ha) and at 15 m into burn (371.9 seedling/ha) was greater than the mean advanced regeneration density of 241.9 seedlings/ha at our unburned plots, what shows that fire, in some cases, may allow regeneration to reach greater seedling densities compared to unburned natural stands. We also observed occasional high regeneration densities over 1000 seedlings/ha at the forest edge and at 15 m. On the other hand, the mean post-fire regeneration density we found was lower compared to other local studies. Shepherd *et al.* (2018) assessed the density of whitebark pine seedlings shorter than 1.3 m in height within unburned stands during their whitebark pine stand health monitoring in the Canadian Rockies and had a mean regeneration density of 463 seedlings/ha (range of 0 – 2254 seedlings/ha) and 94 % of their plots had at least one seedlings present. Gelderman (2014) studied whitebark pine regeneration in multiple mesohabitats and found mean regeneration densities of 743.6 and 1082.4 seedlings/ha at unburned closed canopy and open forests, respectively. Those values are higher than the ones we found in our study (mean density = 369.6 seedling/ha; 40.5 % of plots with regeneration present). Lastly, fire may have a negative effect on advanced regeneration as its occurrence decreased at greater distances into the burn. It was present in approximately 10 % of plots at 15 m and 50 m within the burn and in 37 % of the plots at 0 m (Appendix 13).

We believe our fires are too young (5 – 18 years old) to know whether post-fire regeneration within the burn will reach greater densities than unburned plots in the longer term, but Moody (2006), who assessed post-fire whitebark pine regeneration in fires up to 60 years old, observed that seedling densities within the burn did not always reach greater values compared to adjacent unburned forest. Mean regeneration densities within the burned area ranged from 0 to 406 seedlings/ha even after 30 – 60 years post-fire, suggesting that regeneration might not easily increase much beyond the densities we observed. Are post-fire conditions within the burn unfavourable for germination or survival? Is it a consequence of insufficient seed dispersal? What is limiting regeneration within the burn over time? The differences in regeneration occurrence and abundance between unburned and burned plots that we observed may still help us to better understand some of the factors influencing whitebark pine regeneration.

There is a great perception that nutcrackers prefers caching seeds in open and warmer areas, such as the ones created by burns, where there are many small structures, such as logs and rocks, used as spatial features to remember location of seed caches and where snow melts earlier in the season (Tomback and Linhart 1990; Bednekoff and Balda 2014). We observed a greater probability of regeneration occurrence at stands with larger whitebark pine basal area, suggesting Clark`s Nutcracker may use seed sources and adjacent burned areas as caching sites. However, areas where there was no whitebark pine pre-fire were also colonized. This result coupled with the fact that we found good regeneration occurrence both within the burn and undisturbed forest where mature whitebark pine trees were present suggests that Clark`s Nutcracker caches in multiple locations, regardless of burn.

We could observe a clear variation in the seedbed and understory vegetation between unburned and burned plots (Figures 10 and 11) which may have influenced differences in regeneration abundance between distance classes (Figure 8). As the distance from the unburned plots increased towards the burn interior, there was a rise in mineral soil cover and small shrubs, and a decrease in canopy cover, soil LFH depth, moss cover, tree regeneration density and medium shrub cover. Among all the tested understory and seedbed variables, lower soil organic matter (i.e. decaying wood cover and LFH layer depth), seedling density of other tree species (i.e. *Pinus contorta, Picea engelmannii, Abies lasiocarpa),* medium shrub covers up to 30 % and exposed mineral soil cover favoured regeneration (Appendix 9 and 10). Previous studies showed that seedling density increased as soil organic matter, herb cover and down woody debris decreased (McDowell 2010). Vegetation cover up to 30% increased seedling survival in a post-fire study by Leirfallom *et al.* (2015). Overall, we observed that the burned sites presented conditions that are both favourable (more exposed mineral soil and less competition from other tree species) and detrimental (less cover of small shrubs and more exposure to heat) to regeneration. Yet, whitebark pine seedling densities were higher at the forest edge, where there were usually deeper soil organic layers and more cover offered by shrubs. Our hypothesis is that the cooler and moister conditions found closer to the forest edge may have facilitated whitebark pine seed germination at least in the earlier stages of regeneration establishment. Greater quantities of young seedlings have been found in moister sites, or during years with above-average spring precipitation levels (Tomback *et al.* 1993), showing that surface moisture appears to stimulate germination. Temperature also seems to influence seed germination. In general, successful germination tends to occur on warmer sites as long as there is available moisture (McCaughey 1990; Moody 2006; Larson and Kipfmueller 2010). Those may be the conditions provided by low levels of medium shrub cover. However, we expect an increase in understory cover and regeneration of other tree species, such as subalpine fir and engelmann spruce, with time at the forest edge, raising the question whether or not whitebark pine will survive competition in the longer term.

Conditions at the burn interior may provide better conditions for seedling survival and establishment by escaping competition from tree species on the longer term. Greater distances from the surviving mature trees are well documented to reduce post-fire regeneration of local wind-dispersed trees, such as subalpine fir (*Abies lasiocarpa*) and engelmann spruce (*Picea engelmanni*) (Agee and Smith 1984; Coop *et al.* 2010). On the other hand, seeds of bird-dispersed species, such as whitebark pine, can reach greater distances from the parent tree, offering them the advantage to colonize the interior of large fires and escape competition of wind-dispersed trees species. Our plots were limited to distances 50 m from the forest edge, where seeds from wind-dispersed trees could still easily reach. Seedlings establishing at greater distances may experience environments free of tree competition unless mature lodgepole pine was present pre-fire.

The presence of microsites, such as nurse objects, that offer more moisture and protection against direct heat exposure seems to be important for germination and survival within burns (Tomback *et al.* 1993; Lonergan *et al.* 2014; Klutsch *et al.* 2015). Therefore, it is not surprising we found that some level of understory cover promoted whitebark pine regeneration, at least in the first stages of seedling establishment. In our study, medium shrub cover was the vegetation type that was positively associated with better regeneration responses. In high elevation environments, where conditions are usually harsh and resources are limited, whitebark pine seedling establishment may be facilitated by neighbouring vegetation since they offer protection against prevailing winds and heat exposure (Callaway 1998; Maher and Germino 2006; Gelderman 2014), which are probably conditions exacerbated within burned areas. However, we believe that understory cover beyond a certain level may restrain regeneration instead of facilitating it. Since our sampling was limited to shrub covers up to 30%, we don`t know how whitebark pine seedling would respond to higher cover levels, which are likely to increase with time. This raises the question on how regeneration will respond to changes in conditions in the longer term.

It is challenging to conclude if regeneration differences between burned and unburned plots are a consequence of caching behaviour preferences or the existence of beneficial post-fire conditions for seed germination or seedling survival just through observational studies. Seed sowing and seedling planting trials can help to clarify that question. Higher germination and seedling survival were observed in burned areas rather than in unburned areas, and seedlings planted with shelter objects (stumps, logs, rocks) or inoculated with mycorrhizal treatments had higher survival than the ones without (Izlar 2007; Lonergan *et al.* 2014; Perkins 2015). Greater seedling growth rates were observed in recent burns compared to unburned forest (Perkins 2015) as a potential consequence of increased light and soil nutrients availability and earlier snow melt in spring. At the same time, higher seedling mortality has been associated with high sun exposure and drought (McCaughey 1990; Izlar 2007), therefore the conditions within a burn may be good for seedling survival, as long as regeneration is in microsites that protect them from adverse conditions, such as close to nurse objects or protected by neighbouring plants. Despite the widespread belief that Clark`s Nutcracker prefers caching at open areas created by fire, some positive effects of burned areas on regeneration reported by our study and results from seed sowing and seedling planting trials, we still observed lower whitebark pine regeneration occurrence and abundance within the fire (i.e. plots at 50 m), at least in an early post-fire environment. In face of the current increase in tree mortality at remaining whitebark pine stands caused by blister rust and mountain pine beetle, we believe that whitebark pine post-fire regeneration may be limited particularly by insufficient seed dispersal. Natural regeneration can`t happen without the existence of viable seed sources.

CHAPTER 5 - CONCLUSIONS

Understanding the role of fire and the complexity of drivers controlling post-fire regeneration of whitebark pine is essential for management practices and restoration actions for this endangered species. After exploring a variety of fire, stand and plot level factors we found that, rather than being a simple process explained by variables at a single scale, whitebark pine post-fire regeneration is linked to a variety of biological processes at multiple scales, which creates challenges in predicting regeneration outcomes. Overall, fire does not appear to be necessary for whitebark pine regeneration in northern ecosystems as we found higher regeneration abundance in plots at the unburned forest than at 50 m within the fire. However, an important question that remains is whether fire is beneficial for regeneration. We observed both beneficial and detrimental fire effects. Compared to other studies within our region, we observed lower regeneration densities than in undisturbed forests and a decrease in advanced regeneration abundance within the burns, suggesting that fire is detrimental for regeneration. On the other hand, the colonization of stands where whitebark pine was not present in the pre-fire forest composition suggests that fire creates new habitats for regeneration establishment. While we have limited power to answer this question with confidence, because our study only looked at early post-fire environments, longer-term studies suggest regeneration will not increase much beyond the densities we observed over time.

At a fire level, prescribed burns showed greater regeneration densities and lower regeneration occurrence than wildfires. Regeneration occurrence increased in the first 18 years after fire on prescribed burns and wildfires, mainly at stands with larger whitebark pine basal area, indicating that Clark`s nutcrackers were actively using the open areas created by fire as caching sites over time. On the other hand, post-fire conditions remained suitable for establishment up to 18 years on wildfires, while it appeared to decline after 10 years on prescribed burns, indicating that regeneration abundance was probably driven by the existence of favourable seedbeds and understory conditions at smaller scales. This creates a challenge in predicting regeneration abundance in prescribed burns and wildfires because of the multitude of factors that can influence post-fire conditions, such as fire severity, burning season, post-fire weather and pre-forest composition.

At a stand level, although proximal seed sources were not always required, their presence greatly increased chances of colonization of burned stands. Areas with larger whitebark pine basal area had a greater regeneration occurrence, indicating the nutcracker also used seed sources or adjacent areas as caching sites. However, the current increases in tree mortality caused by white pine blister rust and mountain pine beetle at whitebark pine stands are greatly reducing cone production and natural regeneration potential, making seed dispersal an important limiting factor for future regeneration in burned areas. In other words, seed sources may not remain viable to sustain natural regeneration in the near future.

We observed understory and seedbed conditions associated with regeneration at a plot level. Decaying wood cover and litter depths up to 25 % and 9 cm, respectively, and medium shrub cover up to 30% were positively correlated with seedling density. Partial shade provided by low covers of medium shrubs may have protected new seedlings from excessive heat exposure, which is one of the main documented causes of seedling mortality in burned areas. However, cover levels greater than that may play more of a competitive role rather than facilitative. Some of these results suggest that higher severity fires are better for regeneration, such as the negative influence of greater levels of soil organic cover on seedling abundance. In contrast, the higher regeneration abundance at the forest edge, where medium levels of canopy cover and medium shrubs were present, may suggest the opposite, namely that low- or mixed-severity fires promote better regeneration. Although FWI values and greater consumption of soil organic matter (i.e. lower soil lfh depth and decaying wood cover) were positively associated with regeneration occurrence according to our model, we observed that mature whitebark pine trees and most part of the advanced regeneration did not survive the fire, showing that high severity fires have detrimental effects on whitebark pine.

The question about the influence of fire severity on regeneration, however, will need future investigation for multiple reasons. We looked only at early post-fire environments, therefore it is unclear how regeneration will respond over a longer term. We also lacked low and mixed severity fires in our study. All prescribed burns and wildfires that we sampled were high-severity stand-replacing fires, where few or no tree islands remained within the burn perimeter. Using one single FWI value for an entire fire does not capture smaller scale differences in soil and fuel consumption, therefore future studies may want to consider the use of alternative experimental designs that can better capture the variation in burning conditions, such as studies that use Relative Differenced Normalized Burn Ratios derived from satellite imageries pre- and post-fire to classify fire severity at a smaller scale.

In the end, an existing question from conservation agencies is whether whitebark pine is adequately establishing in burned areas compared to natural stands. Answering this question is not easy and it may depend on which values of natural regeneration we use as baseline levels to be achieved during restoration efforts. Within the fire age range sampled (5 – 18 year old fires), mean post-fire regeneration densities at our burned plots (288.5 – 446.4

seedling/ha) surpassed densities of advanced regeneration at our unburned plots (241.9 seedling/ha), yet they were lower than densities from other studies at older burns and undisturbed whitebark pine stands. Moody (2006), who assessed post-fire whitebark pine regeneration in fires up to 60 years old, observed that seedling densities within the burn did not always reach greater values compared to adjacent unburned forest and mean regeneration densities within the burned area ranged from 0 to 406 seedlings/ha even after 30 – 60 years post-fire. Shepherd *et al.* (2018) found a mean regeneration density of 463 seedlings/ha < 1.3 m in height, in their health monitoring surveys at unburned whitebark pine stands. Gelderman (2014), who sampled whitebark pine stands at Jasper National Park and Willmore Wilderness Park where white pine blister rust infection levels are lower compared to southern stands, found mean regeneration densities of 743.6 and 1082.4 seedlings/ha at unburned closed canopy and open forests, respectively.

Although the post-fire regeneration abundance in our burned plots reached densities similar to our advanced regeneration, remaining seed sources that support natural regeneration are in great risk because white pine blister rust infection and mountain pine beetle outbreaks. Anticipating this problem is of extreme importance; therefore, we believe that artificial plantings are an important complementary approach during restoration efforts in burned areas now and in the future. However, one existing challenge when planning artificial plantings is the lack of information on recommended stocking whitebark pine seedling densities. Even though some studies found densities over 700 seedlings/ha in unburned stands (Gelderman 2014), these densities might not be easily achievable in artificial plantings because of the high cost of seedlings and their low availability in tree nurseries. Based on (i) the mean regeneration densities observed at our prescribed burns and wildfires (369.6 seedlings/ha), (ii) the regeneration density ranges from other studies at older burns (0 to 406 seedlings/ha) (Moody 2006), (iii) a seedling survival of 50% reported in planting trials (Keane and Parsons 2010; Keane *et al.* 2017) and (iv) the low availability whitebark pine seedlings in nurseries, we believe that planting at least 250 – 500 seedling/ha may be a feasible approach to achieve minimum densities similar to undisturbed whitebark pine stands (approximately 450 seedlings/ha) (Shepherd *et al.* 2018). Nonetheless, post-fire regeneration surveys will be important to determine whether natural regeneration has occurred on individual fires, and the planting effort required to achieve stocking objectives.

TABLES

Table 1 - List of sampled sites, fire history, and location.

BURN ORIGIN	FIRE	MANAGEMENT AREA	SEASON	FWI*	APPROXIMATE SIZE (HA)	STANDS	BURNING DATE	TIME SINCE FIRE (YEARS)	LATITUDE/ LONGITUDE
Prescribed burn	Buller Creek	Spray Valley Provincial Park	Summer	21.8	261	4	August 26, 2011	5	50°52'34.37"N / 115°19'40.44"W
	Saskatchewan Crossing	R11 Management Area	Spring	26.9 – 56.5	5700	5	May 29 –June 03, 2009	7	52° 1'21.56"N / 116°31'34.59"W
	Vine Creek	Jasper National Park	Spring	23	<20	2	June 2, 2009**	7	53° 5'45.08"N / 118° 4'54.66"W
	Mount Nestor	Spray Valley Provincial Park	Summer	24 – 26	400	2	June 28-29, 2008	8	50°54'36.26"N / 115°22'18.35"W
	Helen Lake	Banff National Park	Fall	40.9	12	1	September 16, 1998	18	51°39'56.54"N / 116°24'25.35"W
Wildfire	Jackpine	Willmore Wilderness Park	Summer	33.7	11000	1	July 5, 2006	10	53°33'54.97"N / 119°34'32.10"W
	Sheep Creek	Willmore Wilderness Park	Summer	26.2 – 34.05	13000	3	July 2-4, 2006	10	53°46'3.21"N / 119°43'4.75"W
	Vermillion Pass	Kootenay National Park	Summer	27.2 – 37.2	16000	5	August 3 – 20, 2003	13	51° 4'6.68"N / 116° 0'33.82"W
	Moab Lake	Jasper National Park	Summer	20.8 – 28.3	1000	2	July 14-15, 2000	16	52°39'57.91"N / 117°58'36.63"W

* Fire Weather Index (FWI) is a numeric rating of fire spread potential and it is calculated based on fuel moisture and weather conditions, such as temperature and wind speed (Van Wagner 1987). Higher FWI values indicate that conditions are more favourable for a fire to spread, such as warmer temperatures, stronger winds and drier fuels.

**The burn prescription of Vine Creek was completed in 2015, but area sampled was initially burned likely in 2009 based on conversation with local staff. Exact date may not be accurate.

Table 2 – List of variables and their respective units, description, and scale that they were measured at.

RESPONSE VARIABLES

NAME	UNIT	DESCRIPTION
Whitebark Pine Regeneration Occurrence	Presence/Absence	
Whitebark Pine Post-Fire Regeneration Abundance (seedling density)	Seedlings/hectare	Density of seedlings per hectare. Every seedling in a cluster was counted as one.

PREDICTORS

SCALE	NAME	UNIT	DESCRIPTION
QUADRAT* (Seedbed)	LFH depth	Centimetres	Depth of the soil litter and duff layer.
	Mineral soil cover	%	Average cover was taken from five 1 x 1 m quadrats measured within each plot.
	Decaying wood cover	%	
	Moss cover	%	
QUADRAT* (Understory Competition)	Herb cover	%	Average cover was taken from five 1 x1 m quadrats measured within each plot.
	Medium shrub cover**	%	
	Small shrub cover*	%	
	Tree regeneration cover***	%	
PLOT	Distance from forest edge	Meters	Distance from the forest edge where plot was established. There are 4 classes: -15 m, 0 m, 15 m and 50 m
	Tree seedling density	Seedlings/ha	Seedling density of tree species, except whitebark pine
	Canopy cover	%	
STAND	Whitebark pine basal area	m^2/ha	Total basal area of mature whitebark pine, dead or live
	Total basal area	m^2/ha	Total basal area of all mature trees of all species together, dead or live
	Heat load index	Class	Index form 0 to 1, 0 being the coolest aspect and 1 the warmest
FIRE	Fire Weather Index	Score	Unit. Higher values indicate drier fuel conditions at the time of the burning.
	Time since fire	Years	Years after fire
	Burn origin	Class	Prescribed burn or Wildfire
	Season	Class	Spring, summer or fall
	Fire size	Hectares	

* Values measured at 1 m x 1 m quadrats were averaged thus these variables were analyzed at the "plot" level in statistical analyses

** Medium Shrub was considered as any shrub with a height between 20 and 50 cm, while small shrubs were <20cm

***Tree regeneration was considered as seedlings smaller than 1 meter in high of any tree species, excluding whitebark pine

Table 3 – Distribution of plots sampled amongst fires and distance class. Percentage of the total is presented in brackets.

	Prescribed Burns					Wildfires				
Distance Class	Buller Creek	Mount Nestor	Helen Lake	Saskatchewan Crossing	Vine Creek	Jackpine	Moab Lake	Sheep Creek	Vermilion Pass	TOTAL
-15 m	6	3	1	11	5	3	4	8	13	54 (22.4%)
0 m	8	5	1	16	6	4	4	8	13	65 (27%)
15 m	10	4	0	14	4	4	17	8	12	73 (30.3%)
50 m	8	5	1	14	3	3	7	7	1	49 (20.3%)
TOTAL	32 (13.3%)	17 (7.1%)	3 (1.2%)	55 (22.8%)	18 (7.5%)	14 (5.8%)	32 (13.3%)	31 (12.9%)	39 (16.2%)	241

Table 4 – Sampled fires and stands, with respective information on regeneration occurrence and abundance, and local whitebark pine basal area.

Burn Origin	Fire	Time since fire (years)	Stand	N° of transects	N° of plots	Proportion of plots with regeneration	Regeneration density range min – max (mean)	Mean whitebark pine basal area (m^2/ha)
Prescribed Burn	Buller Creek	5		10	32	0.406	0 – 850 (159)	2.38
			BC1	2	5	0.400	0 – 650 (180)	1.5
			BC2	2	6	0.000	0 – 0 (0)	0
			BC3	4	15	0.467	0 – 350 (123)	0.67
			BC4	2	6	0.667	0 – 850 (392)	9.79
	Vine Creek	7		5	18	0.111	0 – 300 (25)	6.33
			VC1	2	10	0.200	0 – 300 (45)	0.28
			VC2	3	8	0.000	0 – 0 (0)	0.97
	Saskatchewan Crossing	7		15	55	0.418	0 – 1350 (206)	1.74
			SASK.C1	3	10	0.000	0 – 0 (0)	0
			SASK.C2	3	12	0.417	0 – 1350 (196)	1.39
			SASK.C3	4	15	0.133	0 – 500 (37)	0
			SASK.C4	3	11	1.000	50 – 900 (309)	3.29
			SASK.C5	2	7	0.714	0 – 1350 (721)	6.07
	Mount Nestor	8		5	17	0.176	0 – 850 (79)	0
			MN1	2	8	0.000	0 – 0 (0)	0
			MN2	3	9	0.333	0 – 850 (150)	0
	Helen Lake	18		1	3	0.667	0 – 200 (83)	0
			HL1	1	3	0.667	0 – 200 (83)	0
Wildfire	Jackpine	10		4	14	0	0 – 0 (0)	0
			JP1	4	14	0.000	0 – 0 (0)	0
	Sheep Creek	10		10	31	0.226	0 – 650 (60)	2.14
			SC1	3	12	0.083	0 – 50 (4)	0
			SC2	2	7	0.000	0 – 0 (0)	0
			SC3	3	12	0.500	0 – 650 (150)	5.52
	Vermillion Pass	13		13	39	0.692	0 – 1400 (186)	1.28
			VP1	2	5	0.800	0 – 1400 (480)	3.15
			VP2	2	7	0.429	0 – 350 (93)	10.31
			VP3	3	9	0.778	0 – 550 (200)	2
			VP4	3	9	0.556	0 – 350 (72)	0
			VP5	3	9	0.889	0 – 350 (194)	3.19
	Moab Lake	16		8	32	0.625	0 – 1000 (258)	5.57
			ML1	4	17	0.824	0 – 1000 (374)	4.62
			ML2	4	15	0.400	0 – 750 (127)	6.65

Table 5 – List of models testing the relationship between individual predictors and post-fire whitebark pine regeneration occurrence. Where AIC is the Akaike`s Information Criteria, ΔAIC is the difference in AIC between a specific model and the model with the lowest value, Wi is the Akaike Weight, and ER is the evidence ratio. Predictors were tested through logistic regression, with stand as a random factor.

Predictor	Scale	AIC	ΔAIC	Deviance	Wi	Cumulative Wi	ER	Coefficient	Std. Error	P-value
Moss Cover	Plot	270.5	0	264.5	0.256	0.256	1.000	0.01797	0.008347	0.0313
WBP Basal Area	Stand	272	1.5	266	0.121	0.378	2.117	0.07074	0.04069	0.0822
Time Since Fire	Fire	272.1	1.6	266.1	0.115	0.493	2.226	0.1993	0.1123	0.0761
FWI	Fire	272.3	1.8	266.3	0.104	0.597	2.460	0.06472	0.03856	0.0932
Medium Shrub Cover	Plot	273.3	2.8	267.3	0.063	0.660	4.055	0.03898	0.02873	0.1748
Tree Regeneration Cover	Plot	273.8	3.3	267.8	0.049	0.710	5.207	-0.02546	0.02307	0.27
Small Shrub Cover	Plot	274.3	3.8	268.3	0.038	0.748	6.686	-0.01464	0.01576	0.353
Burn Origin	Fire	274.4	3.9	268.4	0.036	0.785	7.029	*0.6693*	*0.8116*	*0.4096*
Total Basal Area	Stand	274.6	4.1	268.6	0.033	0.818	7.768	0.007576	0.011066	0.494
Canopy Cover	Plot	274.6	4.1	268.6	0.033	0.851	7.768	0.005067	0.007061	0.473
Heat Load Index	Stand	274.8	4.3	268.8	0.030	0.880	8.585	0.3744	0.6335	0.555
Mineral Soil Cover	Plot	275	4.5	269	0.027	0.907	9.488	-0.007168	0.01903	0.706
Decaying Wood Cover	Plot	275	4.5	269	0.027	0.934	9.488	-0.009938	0.036697	0.787
Tree Regeneration Density	Plot	275	4.5	269	0.027	0.962	9.488	0.001055	0.003968	0.79
LFH Depth	Plot	275.1	4.6	269.1	0.026	0.987	9.974	-0.01252	0.07756	0.872
Burn Season*	Fire	276.5	6	268.5	0.013	1.000	20.086	-	-	-
Spring x Fall	-	-	-	-	-	-	-	*-1.8221*	*2.3895*	*0.446*
Summer x Fall	-	-	-	-	-	-	-	*-1.4757*	*2.3142*	*0.524*
Herb	Plot					Failed to converge				
Fire Size	Fire					Failed to converge				

*Fall is the reference category

Table 6 – Model comparison of the combination of best predictors (Table 5) affecting post-fire whitebark pine regeneration <u>occurrence</u>. Where AIC is the Akaike`s Information Criteria, ΔAIC is the difference in AIC between a specific model and the model with the lowest value, Wi is the Akaike Weight, and ER is the evidence ratio. Predictors were tested through logistic regression, with stand being used as a random factor. The model selected as the best model is highlighted in bold.

Model ID	Model Variables	Ki	AIC	ΔAIC	Wi	Cumulative Wi	ER
I	**MOSS + TIME + WBP + FWI**	**6**	**267**	**0**	**0.264**	**0.264**	**1.000**
II	MOSS + WBP + FWI	5	267.3	0.3	0.227	0.491	1.162
III	MOSS + WBP	4	268.9	1.9	0.102	0.695	2.586
IV	MOSS + FWI	4	269.2	2.2	0.088	0.782	3.004
V	MOSS + WBP + MSHRB	5	269.8	2.8	0.065	0.847	4.055
VI	MOSS	3	270.5	3.5	0.046	0.946	5.755
VII	WBP	3	272	5	0.022	0.968	12.182
VIII	MSHRB	3	273.3	6.3	0.011	1.000	23.336

MOSS = moss cover, TIME = time since fire, WBP = whitebark pine basal area, FWI = fire weather index, MSHRB = medium shrub cover.

Table 7 – List of models testing the relationship between individual predictors and post-fire whitebark pine regeneration abundance. Where AIC is the Akaike`s Information Criteria, ΔAIC is the difference in AIC between a specific model and the model with the lowest value, Wi is the Akaike Weight, and ER is the evidence ratio. Predictors were tested through zero-truncated negative binomial regression, with stand as a random factor. Variables of each category (fire, stand, understory and seedbed) with the lowest AIC are highlighted in bold.

Predictor	Scale	AIC	ΔAIC	Deviance	Wi	Cumulative Wi	ER	Coefficient	Std. Error	P-value
WBP Basal Area	Stand	1332.2	0	1324.2	0.311	0.311	1.00	0.03215	0.01049	0.00217
Decaying Wood Cover	Plot	1332.3	0.1	1324.3	0.296	0.607	1.05	-0.04792	0.01894	0.0114
Medium Shrub Cover	Plot	1334.8	2.6	1326.8	0.085	0.692	3.67	0.02733	0.01084	0.0117
Total Basal Area	Stand	1334.9	2.7	1326.9	0.081	0.772	3.86	-0.011355	0.005184	0.0285
LFH Depth	Plot	1335.8	3.6	1327.8	0.051	0.824	6.05	-0.07487	0.03732	0.0449
Time Since Fire	Fire	1336.4	4.2	1328.4	0.038	0.862	8.17	-0.04997	0.02659	0.0602
Burn Origin	Fire	1337.3	5.1	1329.3	0.024	0.886	12.81	*-0.3136*	*0.1892*	*0.0974*
Mineral Soil Cover	Plot	1337.3	5.1	1329.3	0.024	0.910	12.81	0.013813	0.007764	0.0752
Tree Regeneration Density	Plot	1337.6	5.4	1329.6	0.021	0.931	14.88	-0.002566	0.001679	0.126
Burn Season	Fire	1339.1	6.9	1329.1	0.010	0.935	31.50	-	-	-
Spring x Fall		-	-	-	-	-	-	*0.8925*	*0.7114*	*0.210*
Summer x Fall		-	-	-	-	-	-	*0.6214*	*0.6979*	*0.373*
FWI	Fire	1339.2	7	1331.2	0.009	0.944	33.12	0.007042	0.008061	0.382
Tree Regeneration Cover	Plot	1339.2	7	1331.2	0.009	0.954	33.12	-0.01055	0.0126	0.403
Moss Cover	Plot	1339.3	7.1	1331.3	0.009	0.963	34.81	-0.002915	0.003766	0.439
Herb Cover	Plot	1339.3	7.1	1331.3	0.009	0.975	34.81	-0.006567	0.008195	0.423
Canopy Cover	Plot	1339.3	7.1	1331.3	0.009	0.984	34.81	-0.002488	0.003135	0.427
Small Shrub Cover	Plot	1339.9	7.7	1331.9	0.007	0.990	46.99	-0.0006877	0.0057596	0.905
Heat Load Index	Stand	1339.9	7.7	1331.9	0.007	0.997	46.99	0.0353	0.2404	0.883
Fire Size	Fire					Failed to converge				

Table 8 – Model comparisons of the combination of best predictors (Table 7) affecting post-fire whitebark pine regeneration <u>abundance</u>. Where AIC is the Akaike`s Information Criteria, ΔAIC is the difference in AIC between a specific model and the model with the lowest value, Wi is the Akaike Weight, and ER is the evidence ratio. Predictors were tested through zero-truncated negative binomial, with stand as a random factor. The model selected as the best model is highlighted in bold.

Model ID	Model Variables	Ki	AIC	ΔAIC	Wi	Cumulative Wi	ER
I	WBP + DECAY + MSHRB + TOTAL_BA + LFH + TIME + BURN + MSOIL + TREE_REG	12	1319.7	0	0.178	0.178	1.000
II	WBP + DECAY + TOTAL_BA + LFH + TIME + BURN + MSOIL	10	1319.8	0.1	0.169	0.347	1.051
III	WBP + DECAY + MSHRB + TOTAL_BA + LFH + MSOIL + TREE_REG	10	1320	0.3	0.153	0.500	1.162
IV	WBP + DECAY + MSHRB + TOTAL_BA	7	1320.2	0.5	0.139	0.639	1.284
V	WBP + DECAY + MSHRB + TOTAL_BA + LFH	8	1320.8	1.1	0.103	0.741	1.733
VI	WBP + DECAY + TOTAL_BA	6	1321.1	1.4	0.088	0.830	2.014
VII*	**WBP + DECAY + MSHRB + TIME**	**7**	**1321.4**	**1.7**	**0.076**	**0.906**	**2.340**
VIII	WBP + DECAY + TIME	6	1322.4	2.7	0.046	0.952	3.857
IX	WBP + MSHRB + TOTAL_BA + TIME + BURN + TREE_REGEN	9	1324.2	4.5	0.019	0.971	9.488
X	WBP + DECAY + MSHRB	6	1324.5	4.8	0.016	0.987	11.023
XI	WBP + TOTAL_BA	5	1326	6.3	0.008	0.994	23.336
XII	DECAY + MSHRB + TIME	6	1327.3	7.6	0.004	0.998	44.701
XIII	DECAY + MSHRB + LFH + TIME + BURN + MSOIL + TREE_REGEN	12	1329.8	10.1	0.001	1.000	156.022
XIV	DECAY + LFH + MSOIL	6	1332.4	12.7	0.000	1.000	572.493
XV	MSHRB + TREE_REGEN	5	1334	14.3	0.000	1.000	1274.106
XVI	TIME + BURN	5	1338.3	18.6	0.000	1.000	10938.019
XVII	WBP + MSHRB + TIME				No convergence		

BURN = burn origin, WBP = whitebark pine basal area, DECAY = decaying wood cover, TIME = time since fire, MSHRB = medium shrub cover, TOTAL_BA = total basal area, TREE_REGEN = tree regeneration density, LFH = lfh depth, MSOIL = mineral soil cover

Table 9 - Best model explaining regeneration occurrence in our study data. Predictors and respective coefficients are presented. Stand was used as a random factor. Exp(coef) = Exponential of coefficient

Model	Predictors	Coefficient	Exp(Coef)	Std.Error	P value
MOSS + TIME + WBP + FWI	Moss cover	0.0183	1.0185	0.0086	0.034
	Time since fire	0.1721	1.1878	0.1129	0.127
	WBP basal area	0.0857	1.0895	0.0434	0.049
	FWI	0.069	1.0714	0.0378	0.068

Random Effect	**Variance**	**Std. Dev.**
Stand	2.71	1.646

Table 10 – Best model explaining regeneration abundance in our study data. Predictors and respective coefficients are presented. Stand was used as a random factor. Exp(coef) = Exponential of coefficient

Model	**Predictors**	**Coefficient**	**Exp(coef)**	**Std.Error**	**P value**
WBP + DECAY + MSHRB + TIME	WBP basal area	0.030415	1.0308	0.0098	0.002
	Decaying wood cover	-0.049135	0.9520	0.0177	0.006
	Time since fire	-0.053393	0.9480	0.0238	0.025
	Medium shrub cover	0.018112	1.0182	0.0097	0.064

Random Effect	**Variance**	**Std. Dev.**
Stand	0.03618	0.1902

FIGURES

Figure 1 – Map showing study sites (in red) and the respective management areas they are located within. All fires are located in the western mountain region of Alberta, Canada. Vermillion Pass is the only fire in British Columbia.

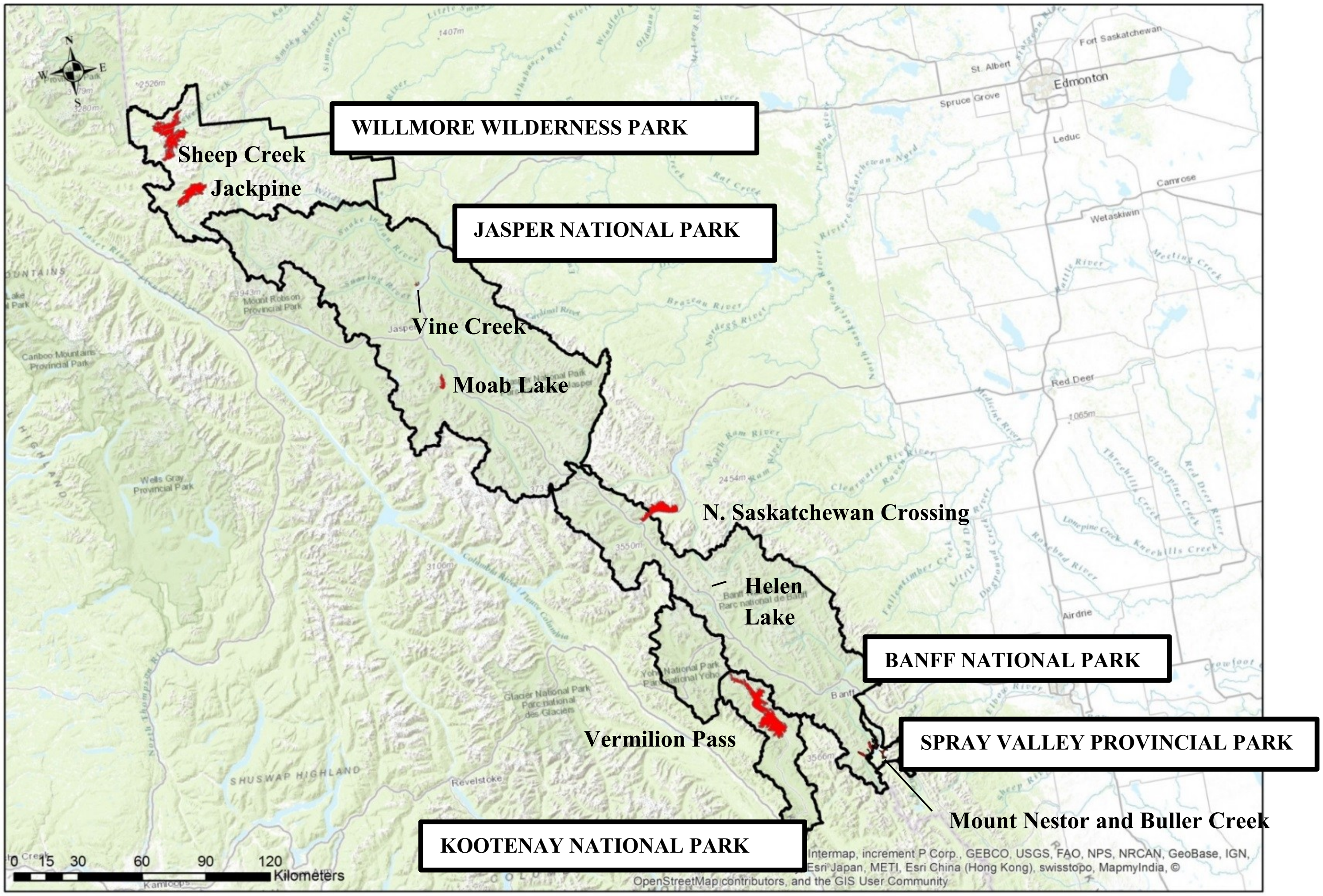


Figure 2 – Transect and plot scheme within each sampled stand. Along each transect, one 50 m by 4 m plot was established at each distance class: -15 m (unburned), 0 m (forest edge), 15 m and 50 m (burn).

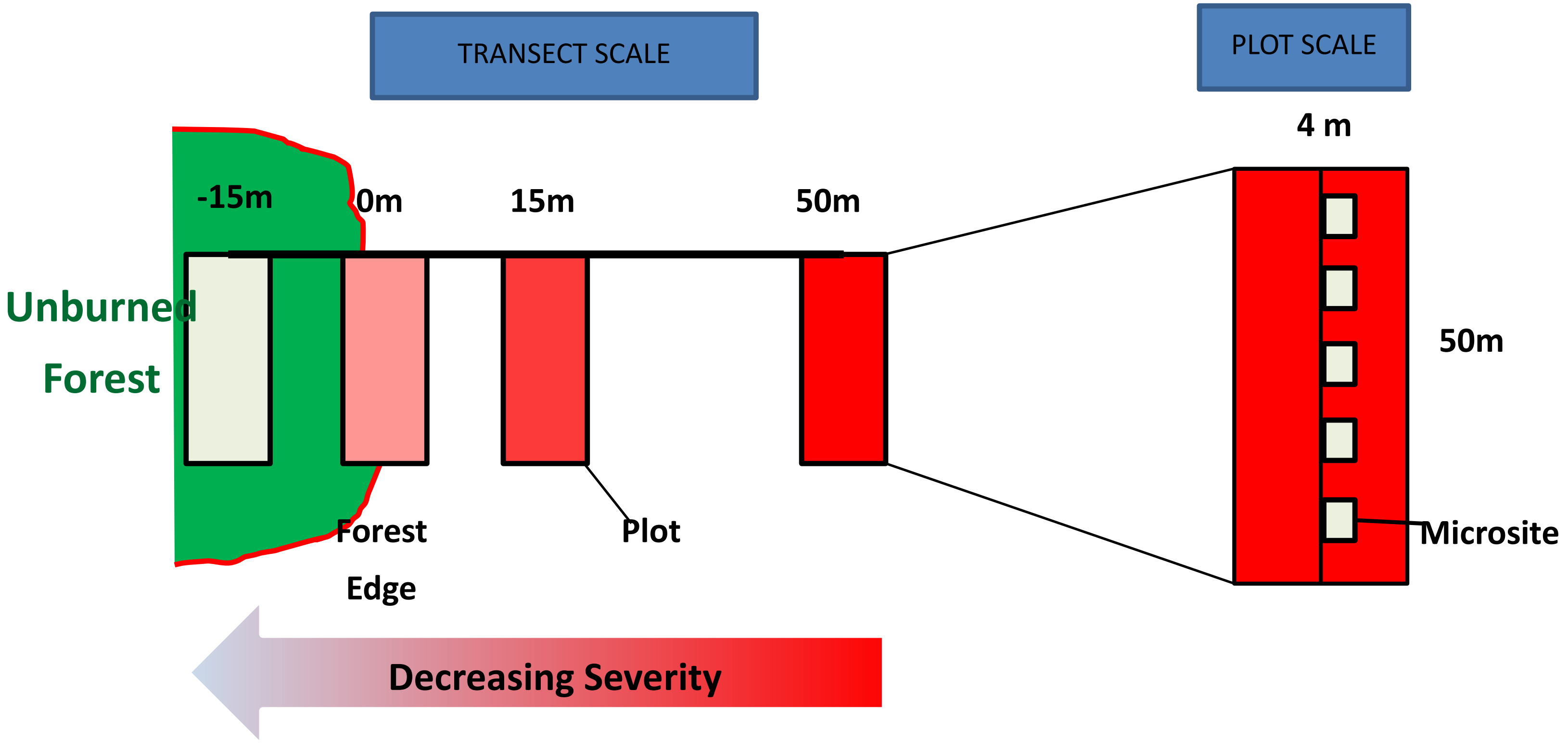


Figure 3- Fitted and observed values for the best model explaining regeneration occurrence (whitebark pine basal area + decaying wood cover + medium shrub cover + time since fire).

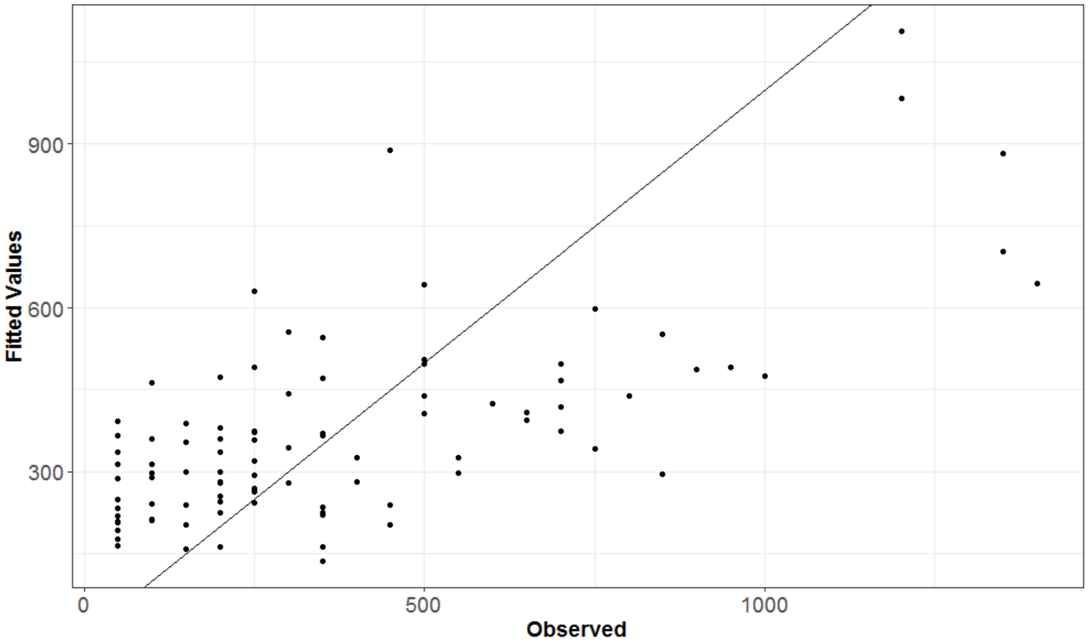


Figure 4 – Residuals and fitted values for the best model explaining regeneration occurrence (whitebark pine basal area + decaying wood cover + medium shrub cover + time since fire).

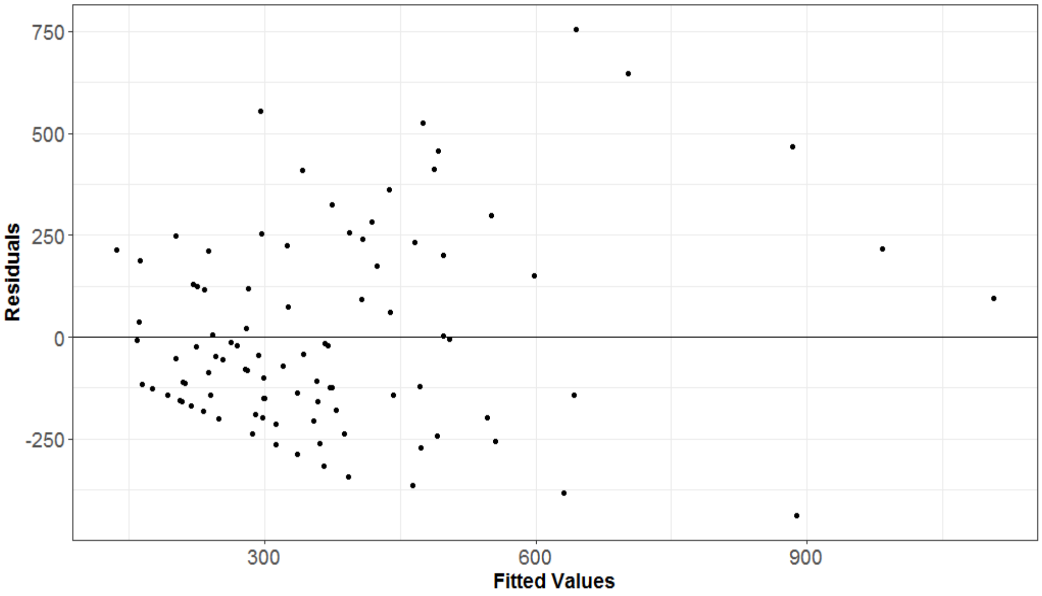


Figure 5– Proportion of plots with whitebark pine post-fire regeneration and seedling density in relation to burn origin and season. There was no significant difference (p-value<0.25) in regeneration occurrence and abundance between seasons. Burn origin only had a significant on regeneration abundance.

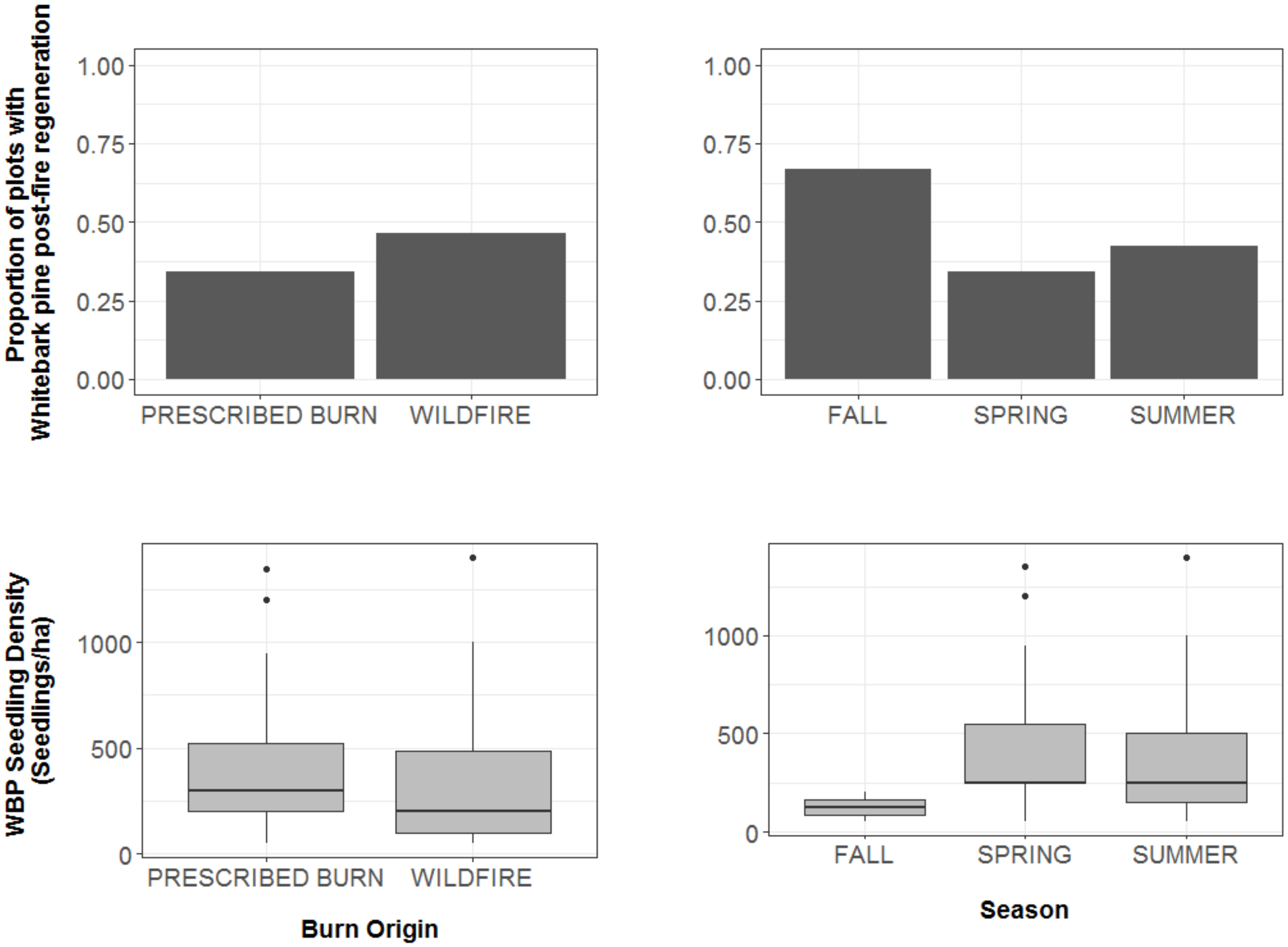


Figure 6 – Proportion of plots with regeneration (at a stand level) and seedling density (at a plot level) in relation to FWI, whitebark pine basal area, total tree basal area and medium shrub cover. On top figures, data points represent the proportion of plots with regeneration within each stand. The blue lines represent respective fitted linear models using Generalized Linear Mixed Effect Model (GLMM). Gray area around fitted line represents a 95% confidence interval.

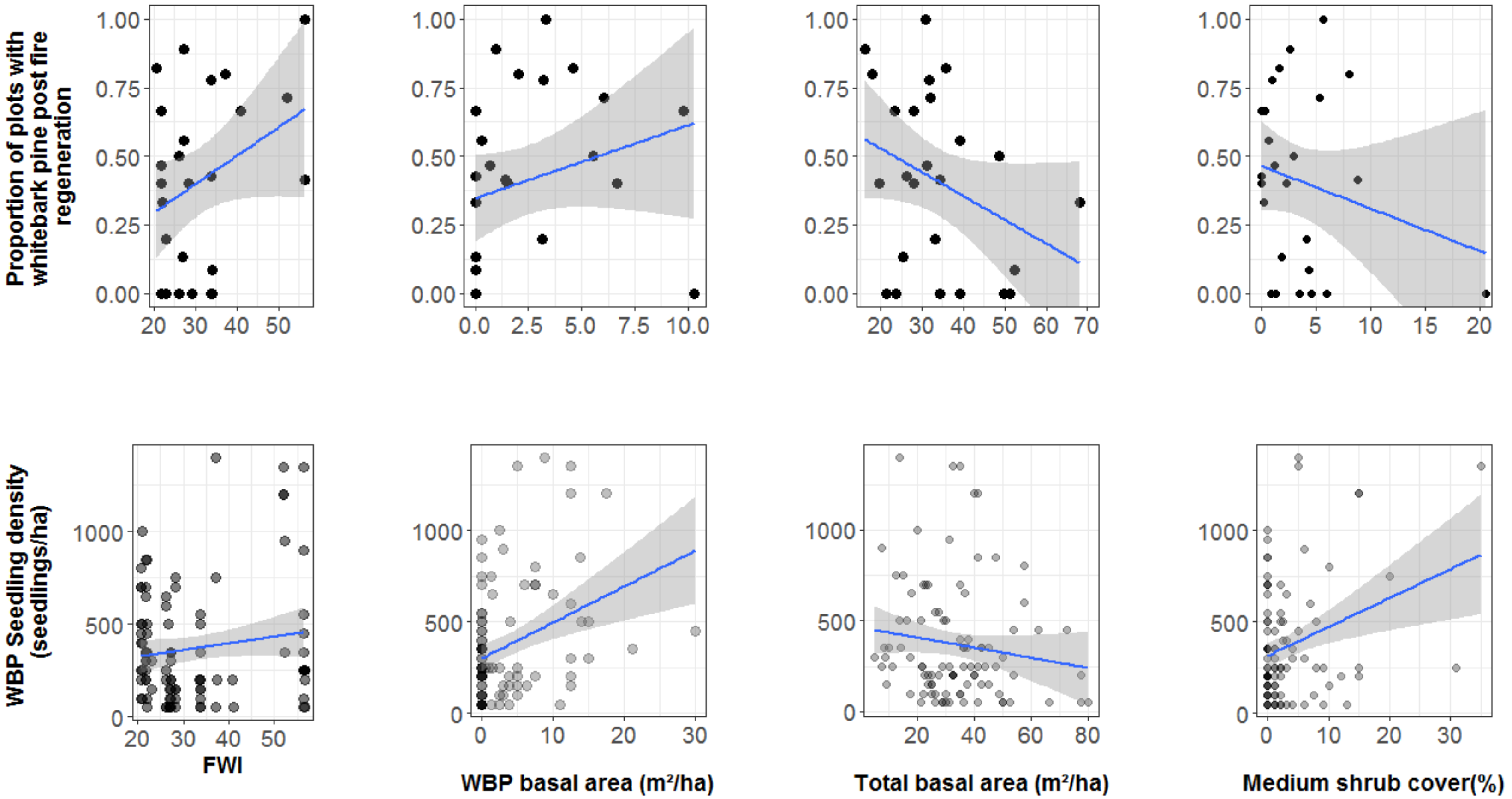


Figure 7 – Proportion of plots with whitebark pine post-fire regeneration (at a stand level) and seedling density (at a plot level) in relation to time since fire at prescribed burns and wildfires. On top figures, data points represent the proportion of plots with regeneration within each stand. The blue lines represent respective fitted linear models using Generalized Linear Mixed Effect Model (GLMM). Gray area around fitted line represents a 95% confidence interval.

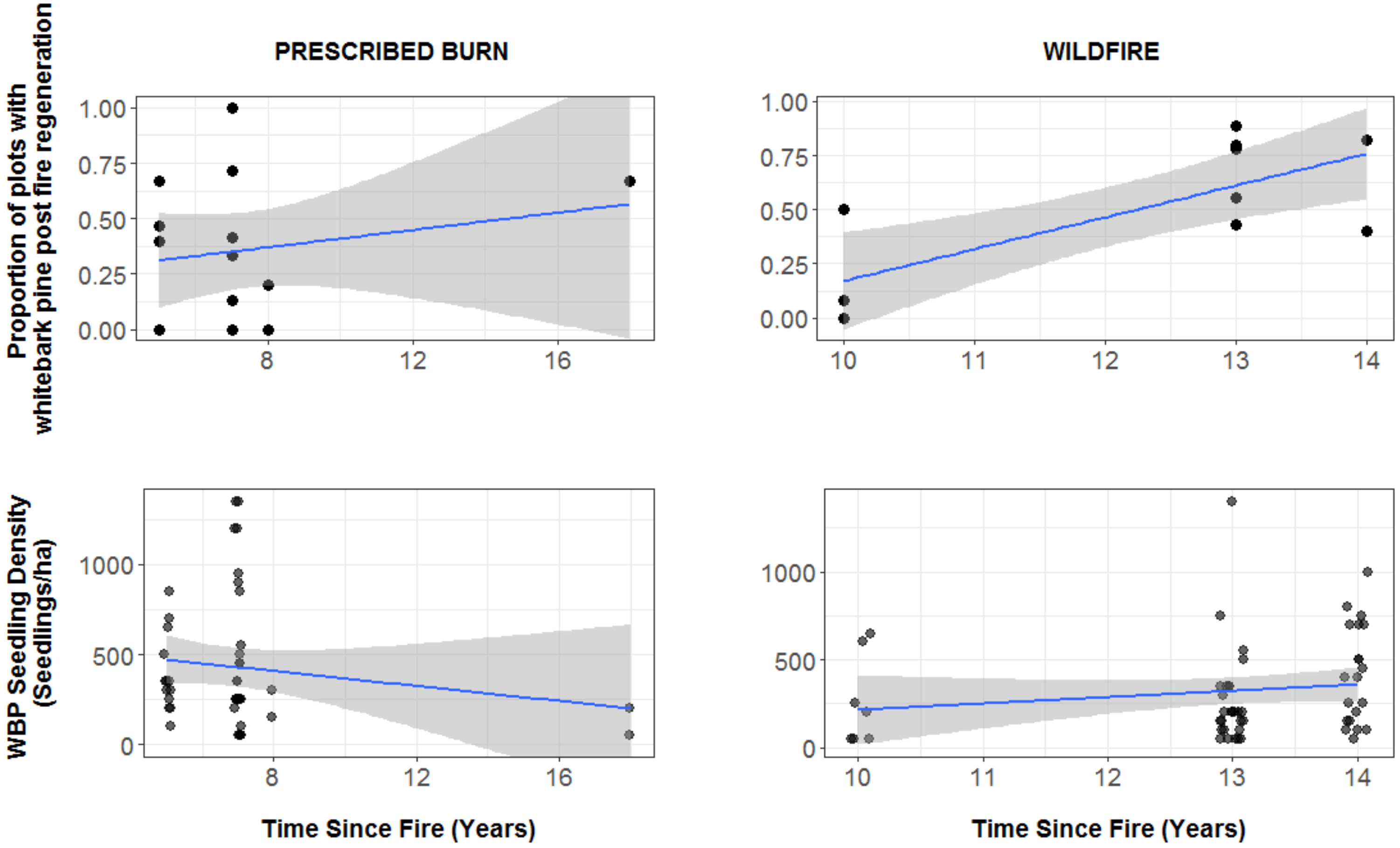


Figure 8 – Proportion of plots with regeneration (top figure) and seedling density (bottom figure) at each distance class. In the bottom graph, black dot and horizontal line within each boxplot represent the mean and median, respectively.

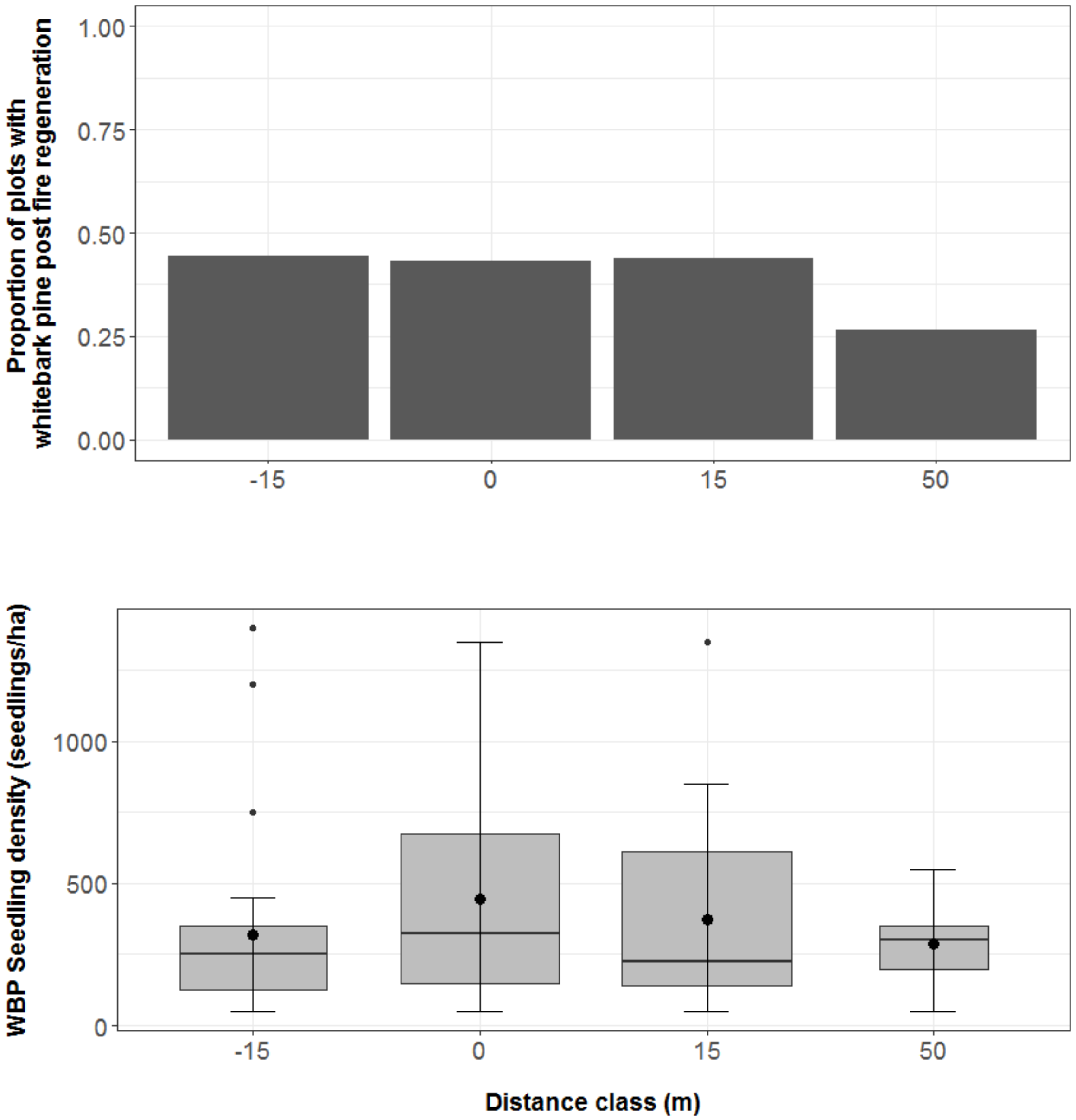


Figure 9 – Post fire whitebark pine regeneration density in relation to time since fire (years) at each distance class. Median is showed as a horizontal line within each boxplot.

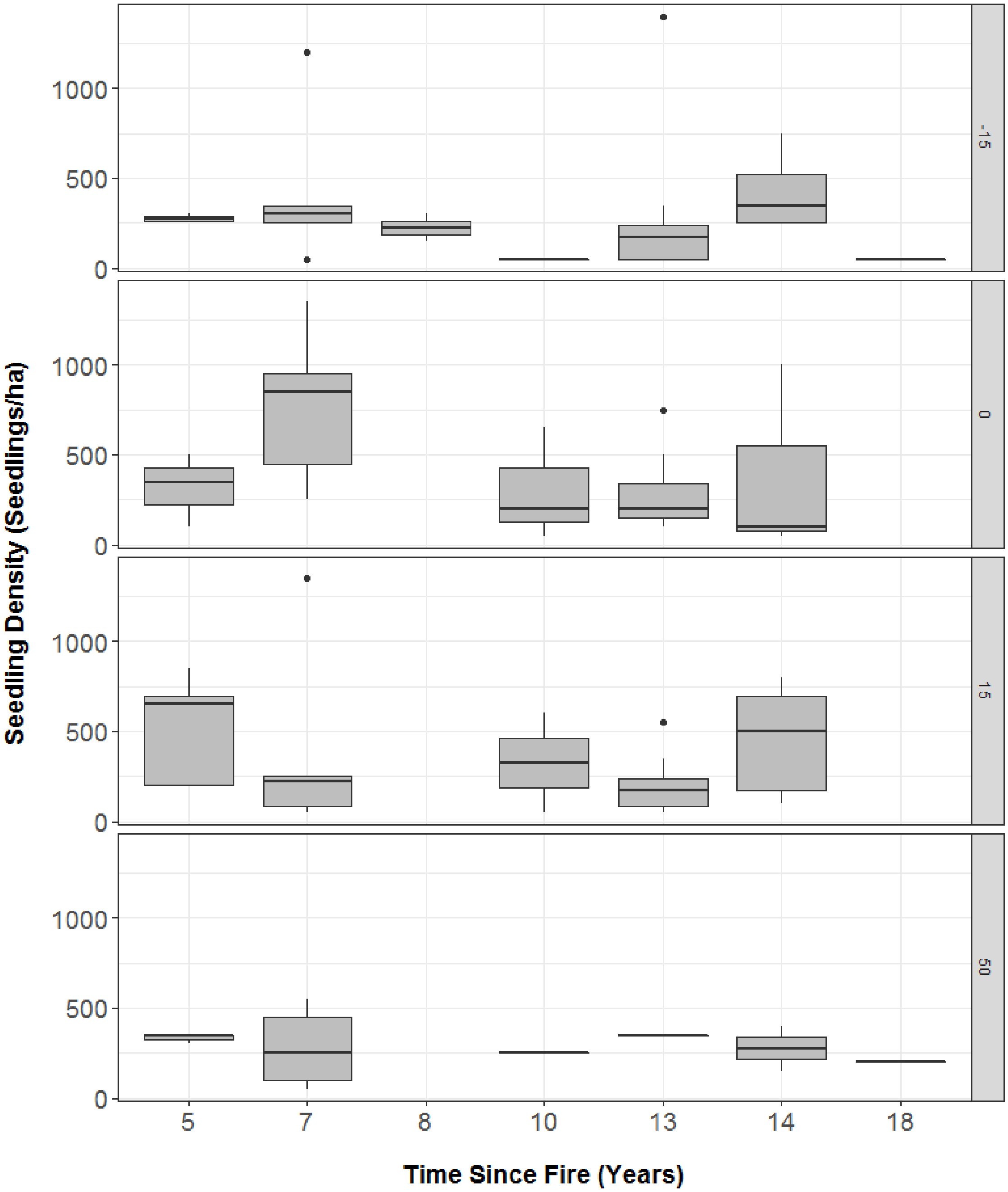


Figure 10 – Difference in LFH depth, exposed mineral soil, moss, and decaying wood cover between distance classes. Median is represented by horizontal line within each boxplot.

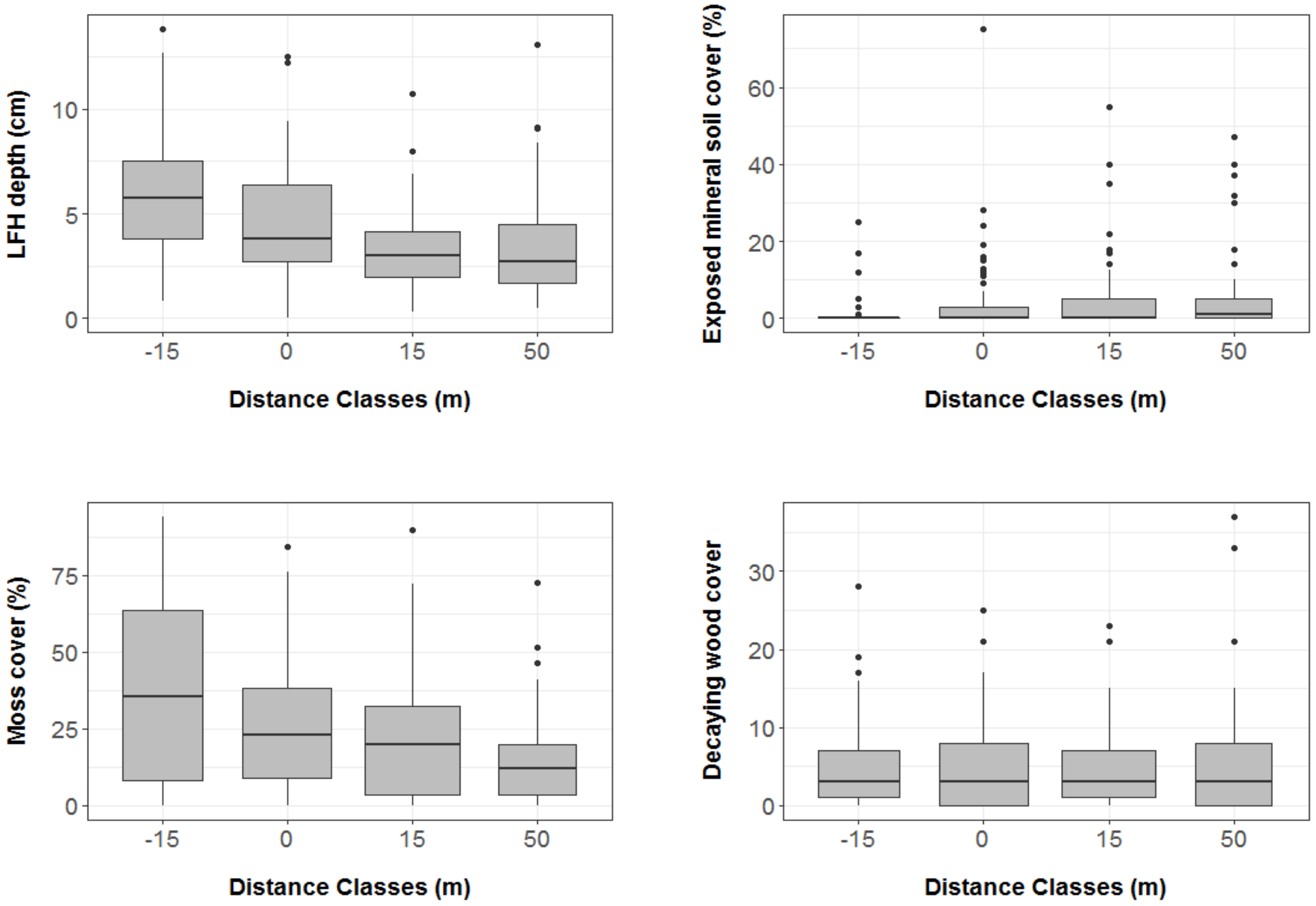
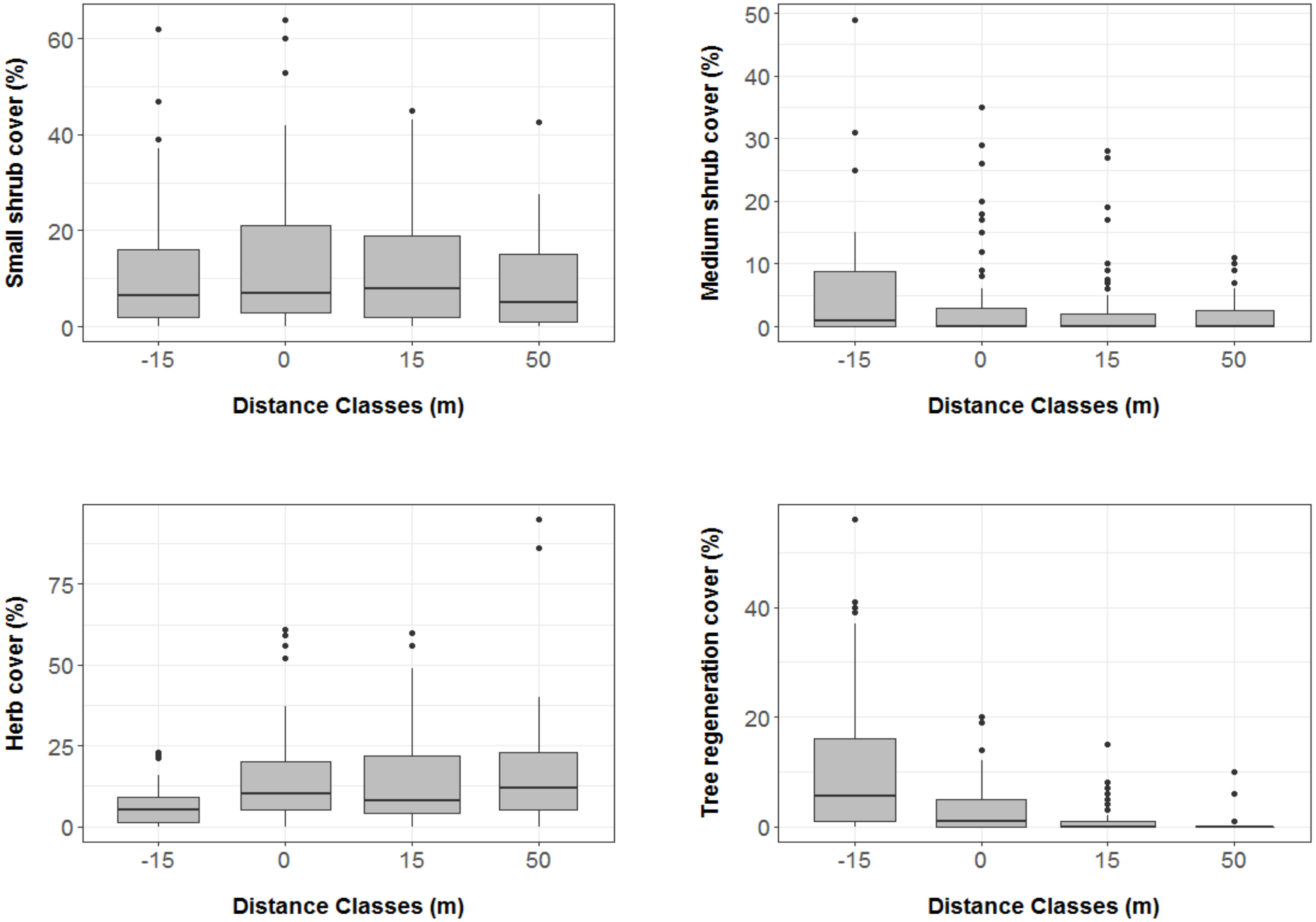


Figure 11 - Difference in small shrub, medium shrub, tree regeneration (*Pinus contorta, Picea engelmannii, Abies lasiocarpa*) and herb cover between distance classes. Median represented by horizontal line within each boxplot.



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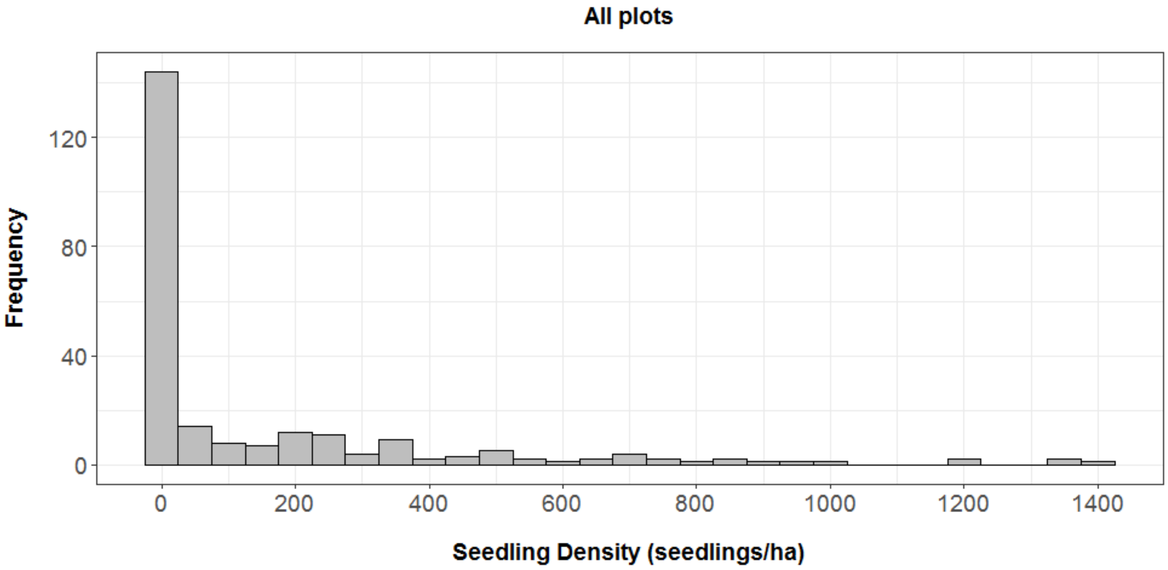
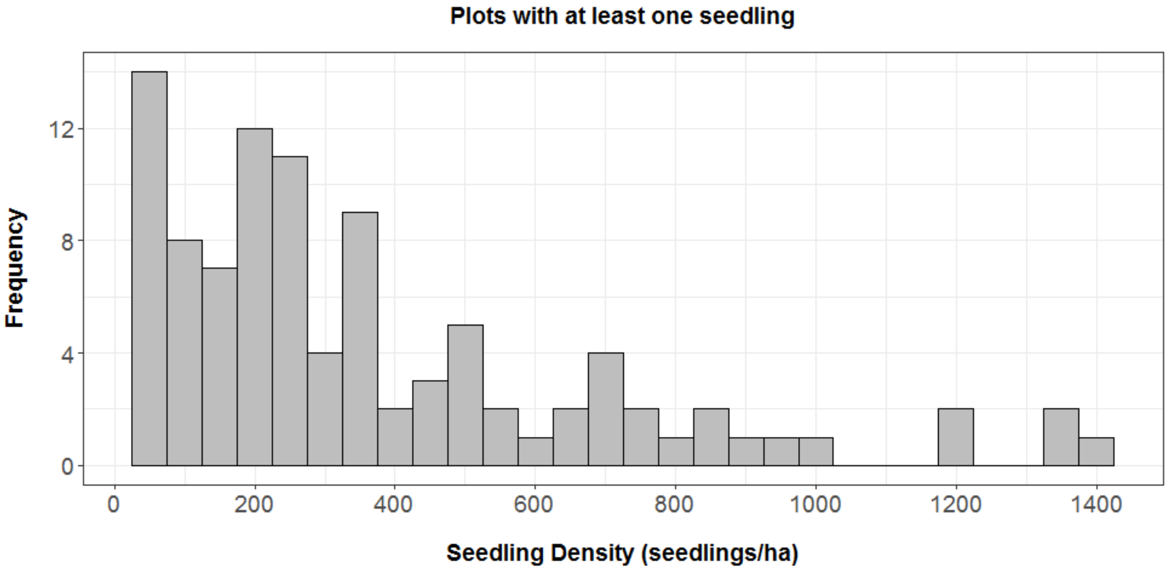
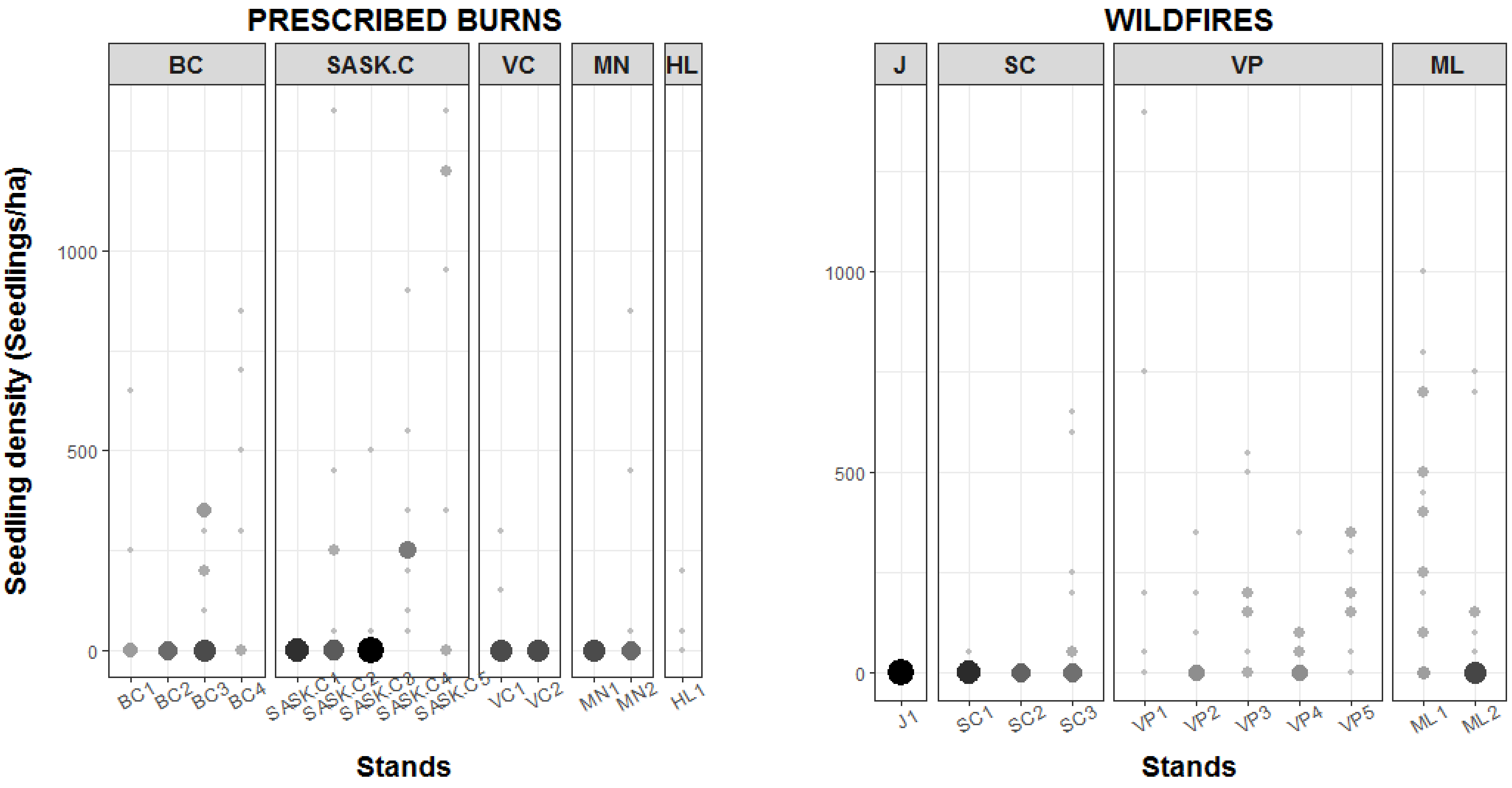
APPENDICES

Appendix 1 - Distribution of overall post-fire whitebark pine seedling density. The top figure shows the highly skewed distribution of seedling density considering all plots. The first bin indicates the number of zeros in the data. The bottom figure shows the same distribution but focuses only on plots where regeneration was present.

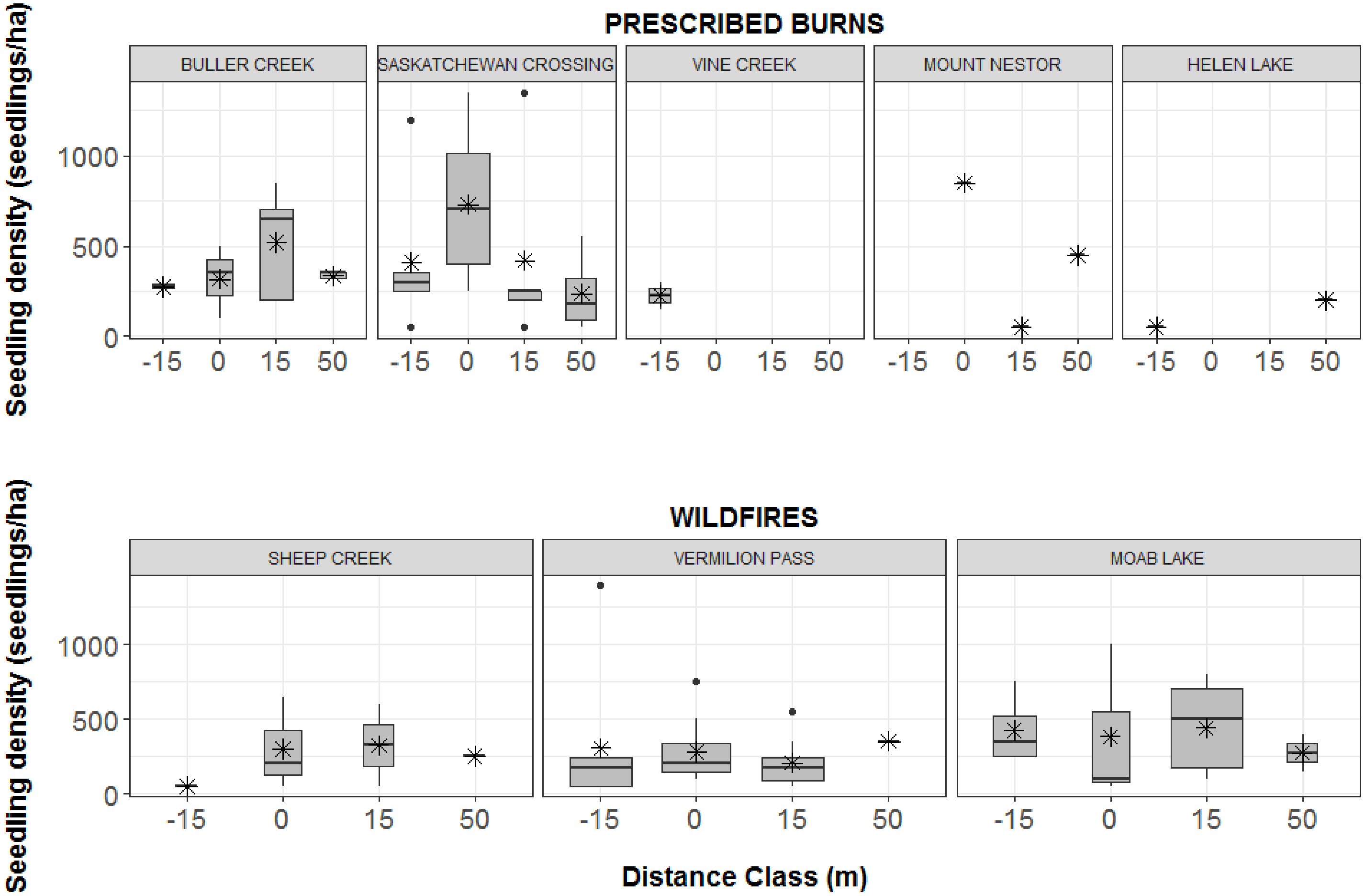




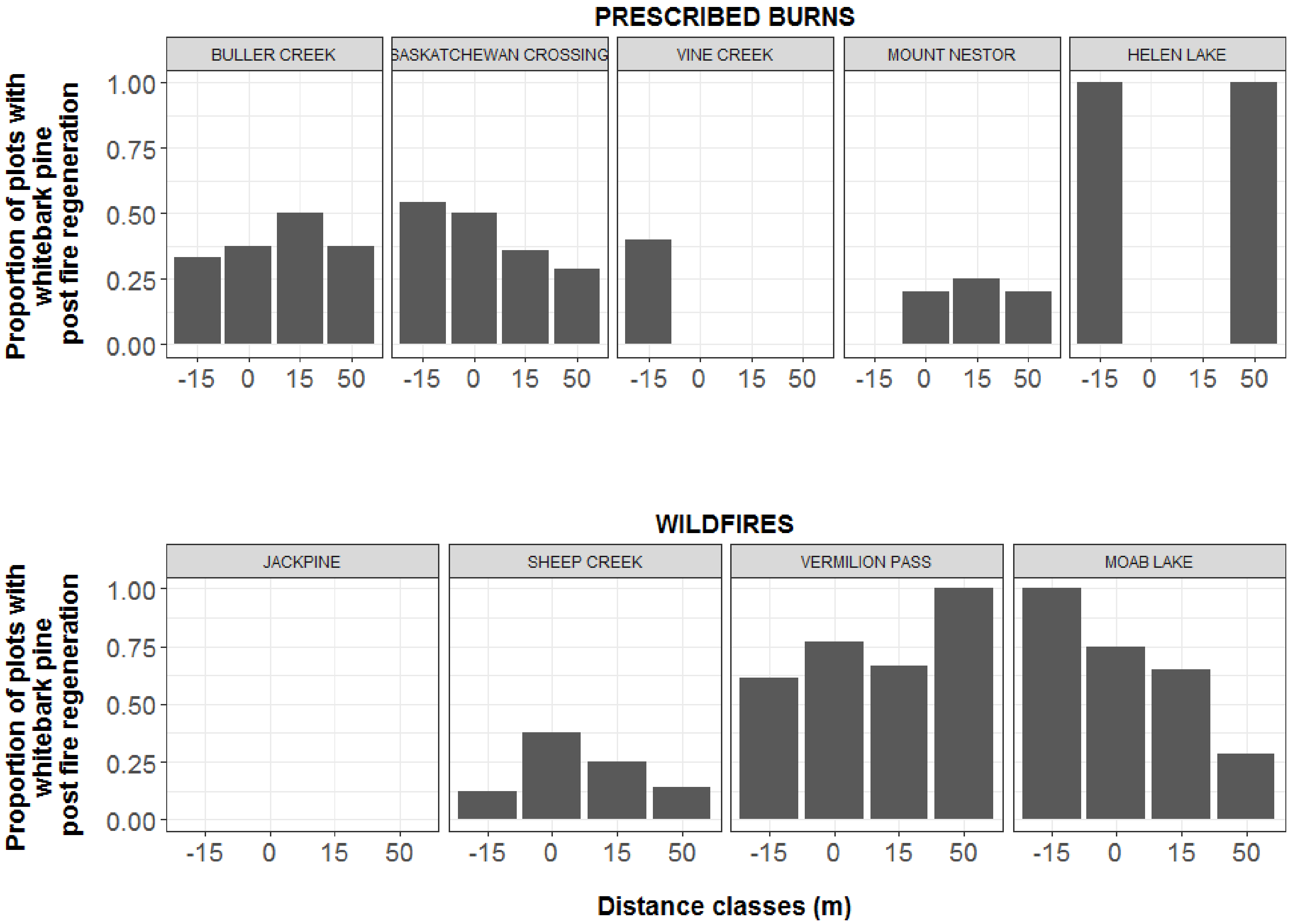
Appendix 2 -Distribution of whitebark pine post-fire seedling density between and within study sites. Fires are organized from youngest to oldest fire within each burn type. Fire Codes: BC=Buller Creek, HL=Helen Lake, J=Jackpine, ML=Moab Lake, MN=Mount Nestor, SASK.C=Saskatchewan Crossing, SC=Sheep Creek, VC=Vine Creek, VP=Vermillion Pass. Larger and darker circles indicate greater number of plots.



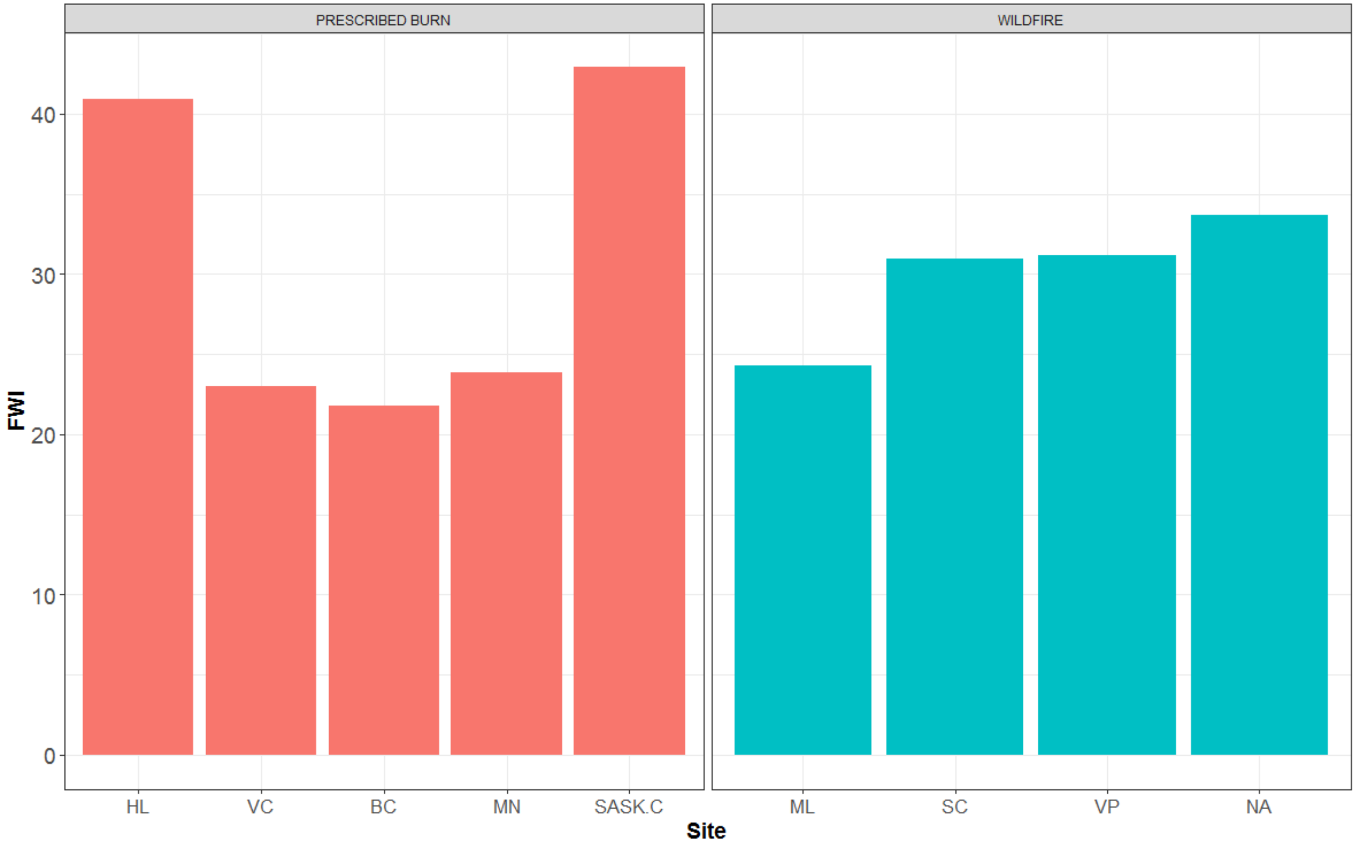
Appendix 3 - Post-fire whitebark pine regeneration density at each distance class and fire excluding plots with no regeneration. Stars and horizontal lines represent the mean and the median, respectively. Fires are organized from youngest to oldest fire within each burn type. Jackpine wildfire is not represented since no plots had regeneration present.



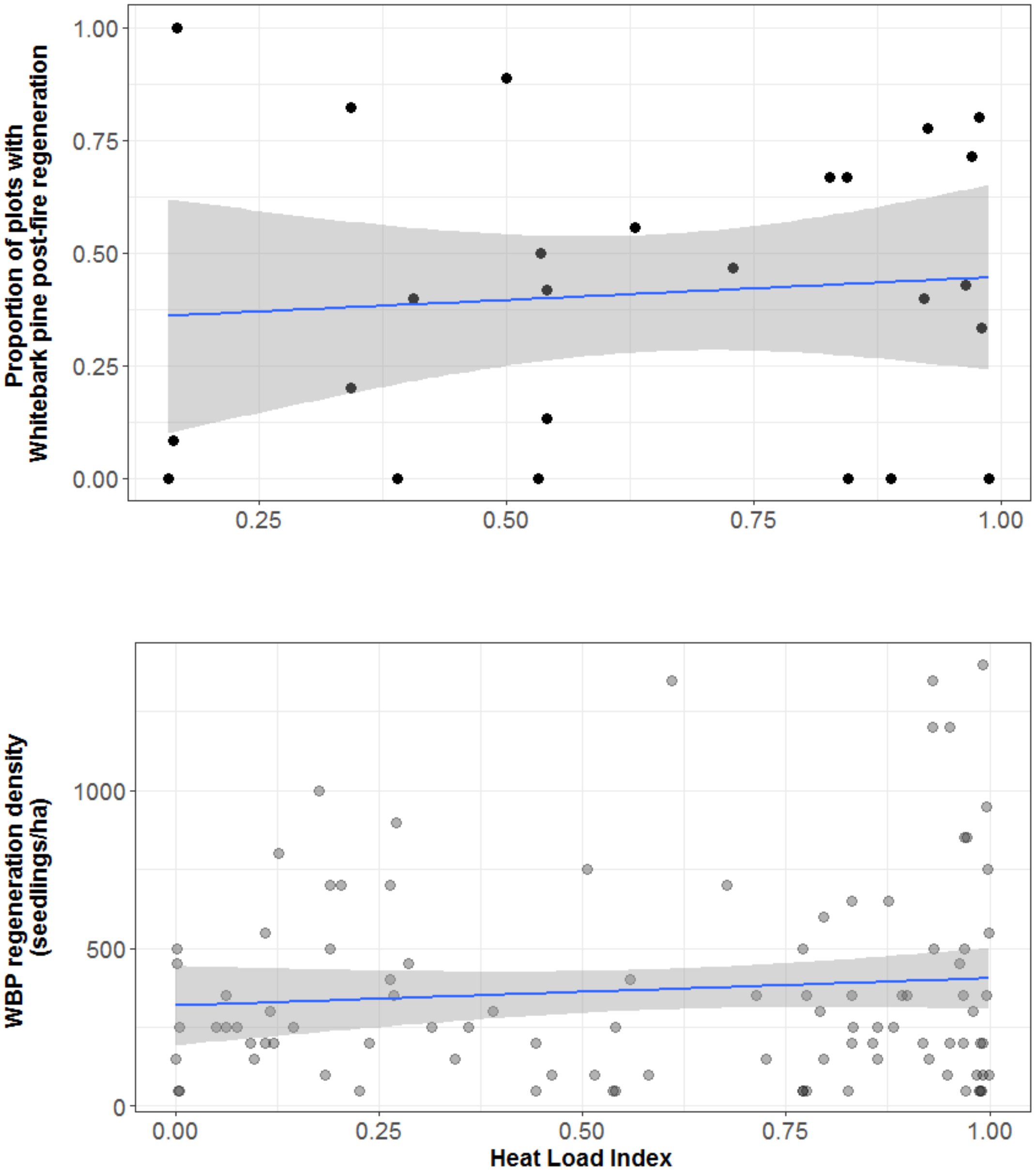
Appendix 4 - Proportion of plots with regeneration at each distance class and fire. Fires are organized from youngest to oldest fire within each burn type.



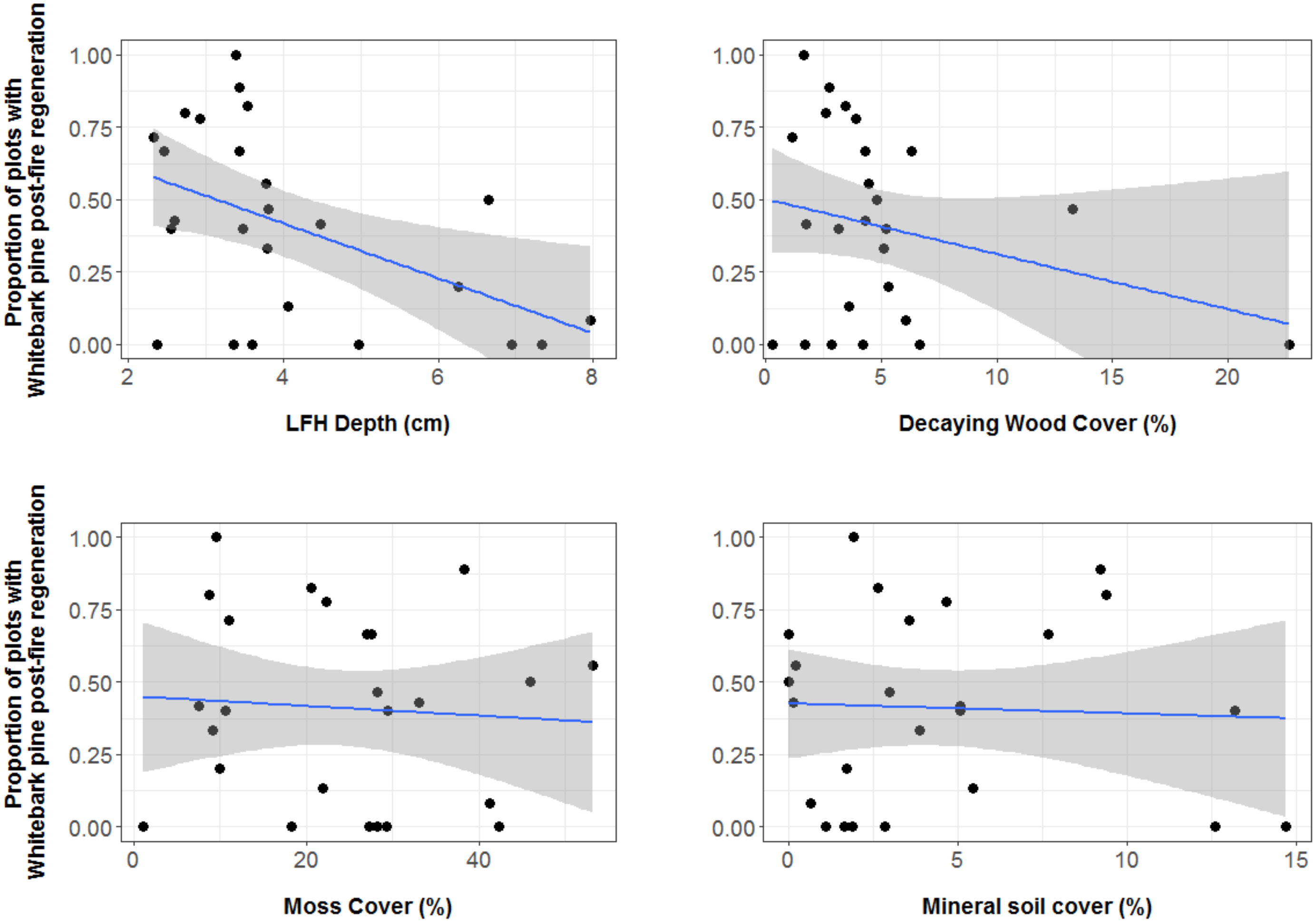
Appendix 5 - FWI values between prescribed burns and wildfire, and between sampled stands within each study fire. Fires are organized from smallest to largest fire sizes within each burn type. Fire Codes: BC=Buller Creek, HL=Helen Lake, J=Jackpine, ML=Moab Lake, MN=Mount Nestor, SASK.C=Saskatchewan Crossing, SC=Sheep Creek, VC=Vine Creek, VP=Vermillion Pass.



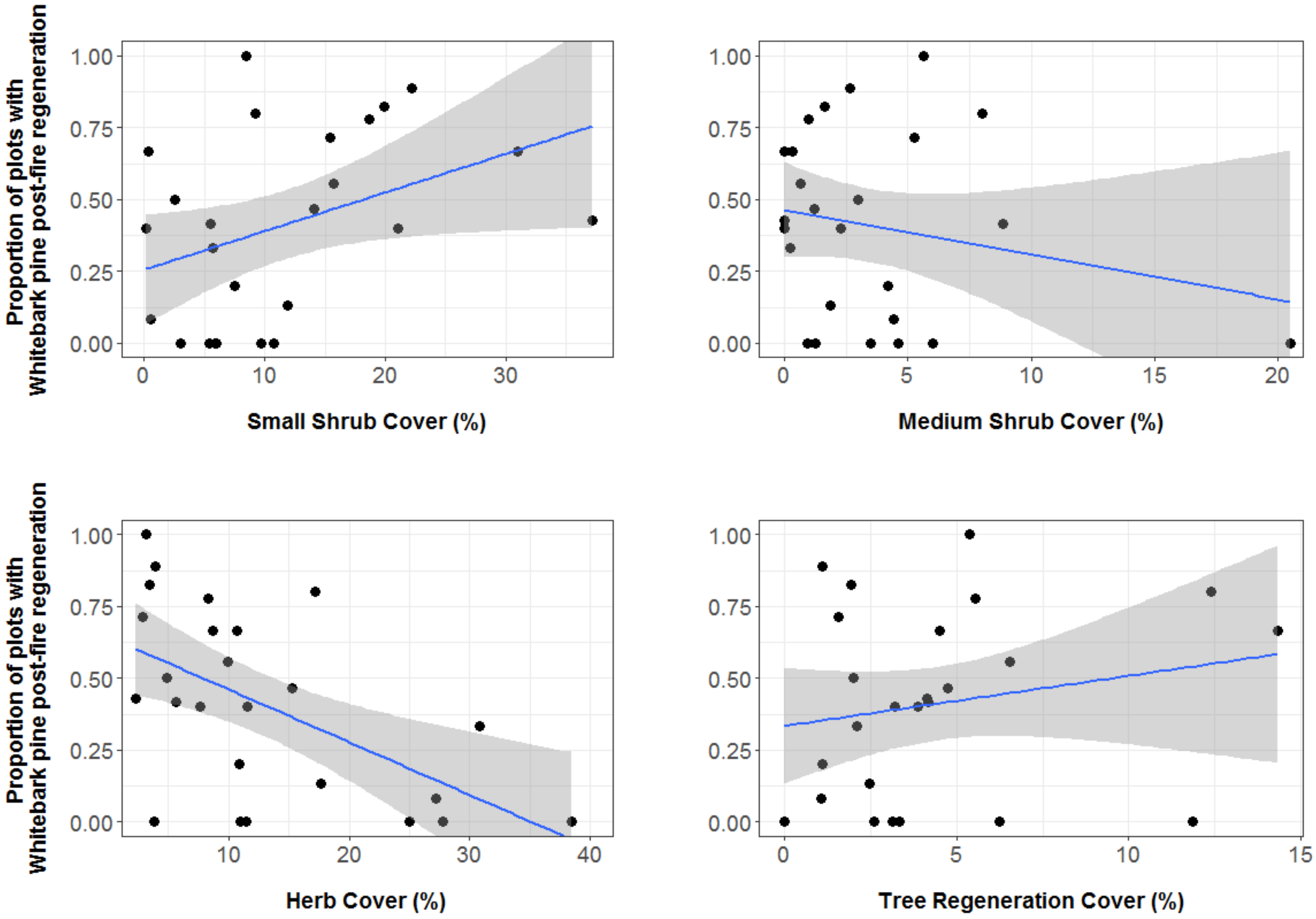
Appendix 6 - Proportion of plots with regeneration (top figure) and seedling density (bottom figure) in relation to Heat Load Index. On top figure, data points represent the proportion of plots with regeneration within each stand. The blue lines represent respective fitted linear models using Generalized Linear Mixed Effect Model (GLMM). Gray area around fitted line represents a 95% confidence interval.



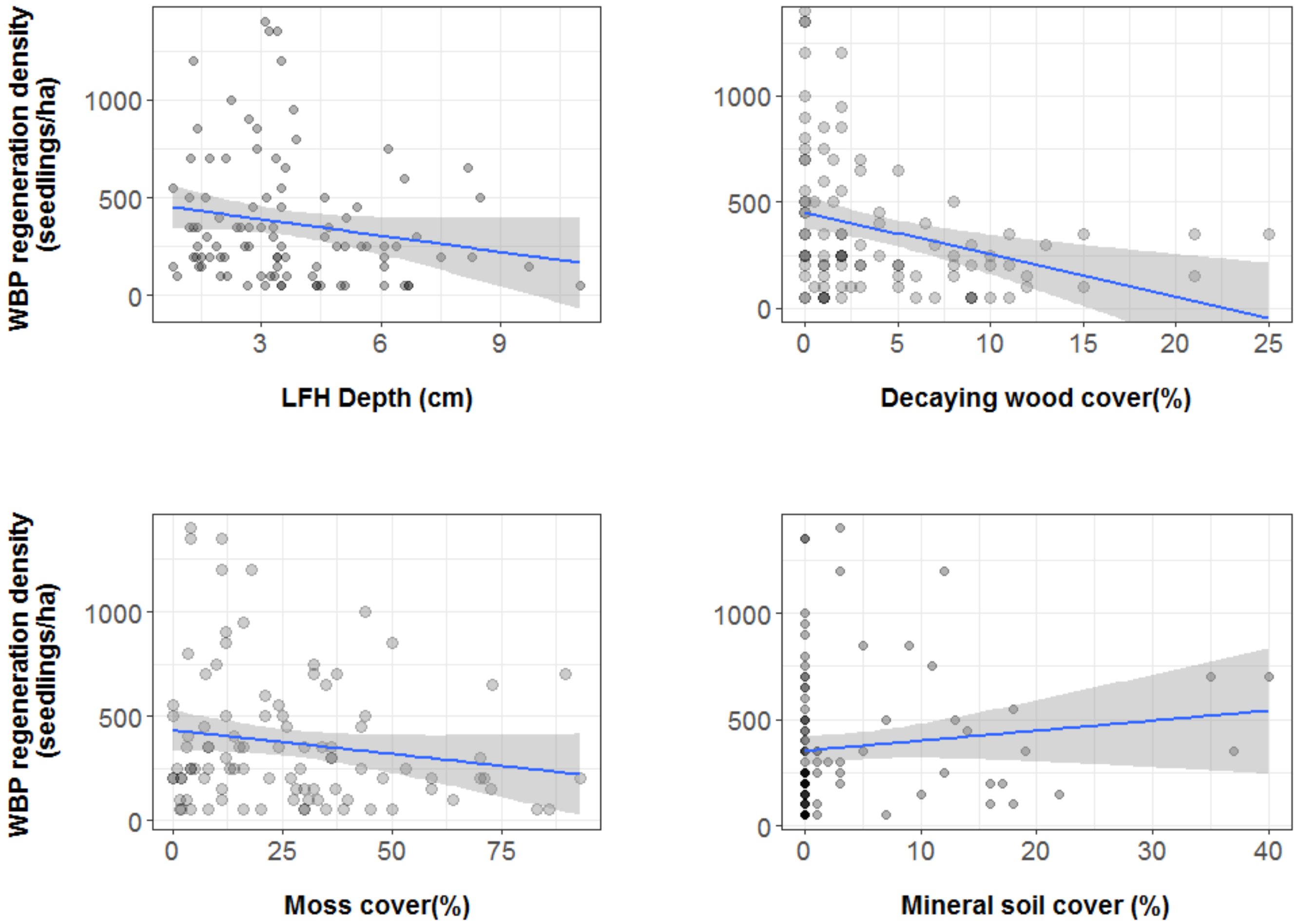
Appendix 7 - Proportion of plots with whitebark pine post-fire regeneration in relation to seedbed predictors. Data points represent the proportion of plots with regeneration within each stand. The blue lines represent respective fitted linear models using Generalized Linear Mixed Effect Model (GLMM). Gray area around fitted line represents a 95% confidence interval.



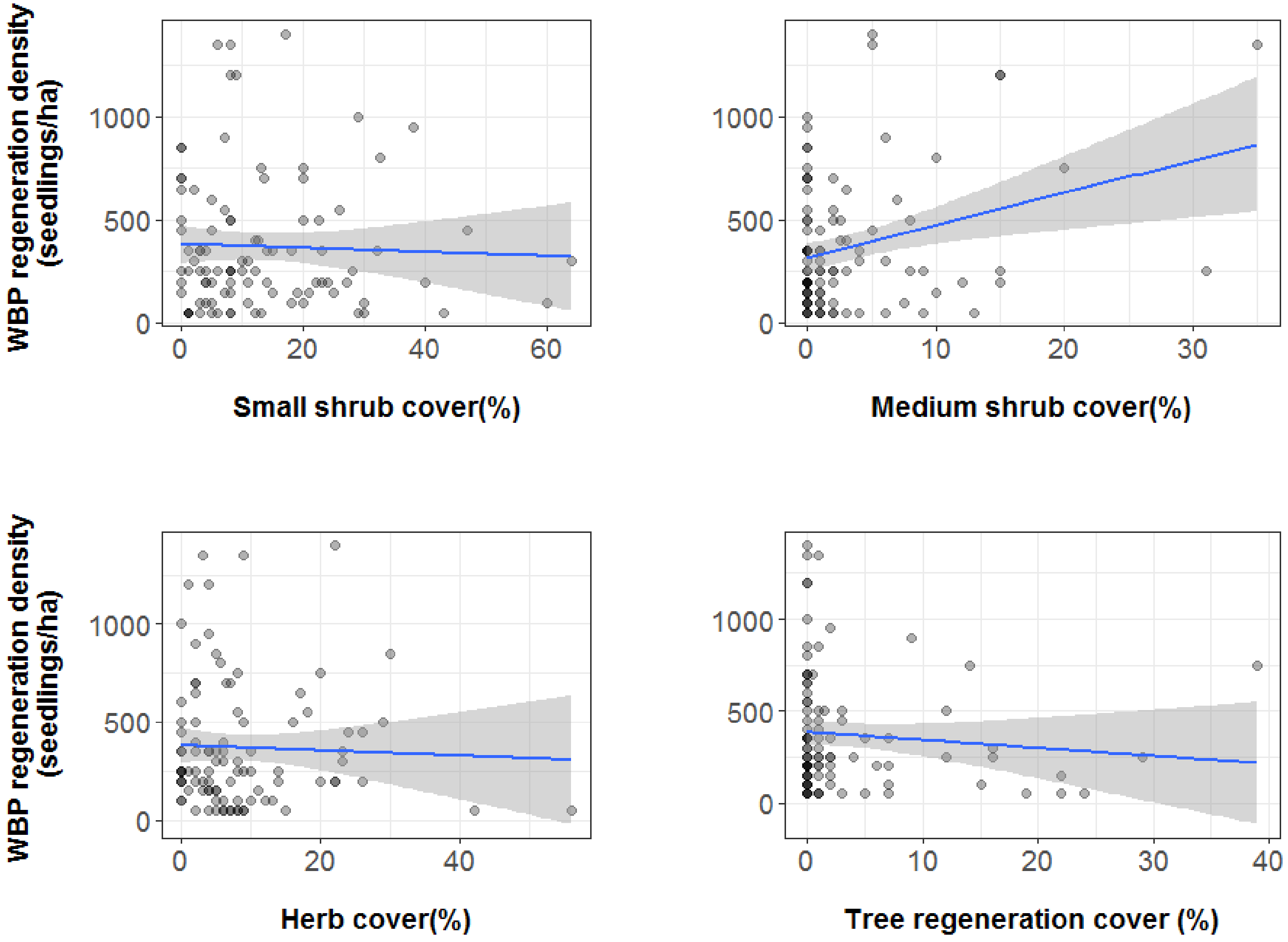
Appendix 8 - Proportion of plots with whitebark pine post-fire regeneration in relation to small shrub, medium shrubs, herb and tree regeneration (*Pinus contorta, Picea engelmannii, Abies lasiocarpa*) covers. Data points represent the proportion of plots with regeneration within each stand. The blue lines represent respective fitted linear models using Generalized Linear Mixed Effect Model (GLMM). Gray area around fitted line represents a 95% confidence interval.



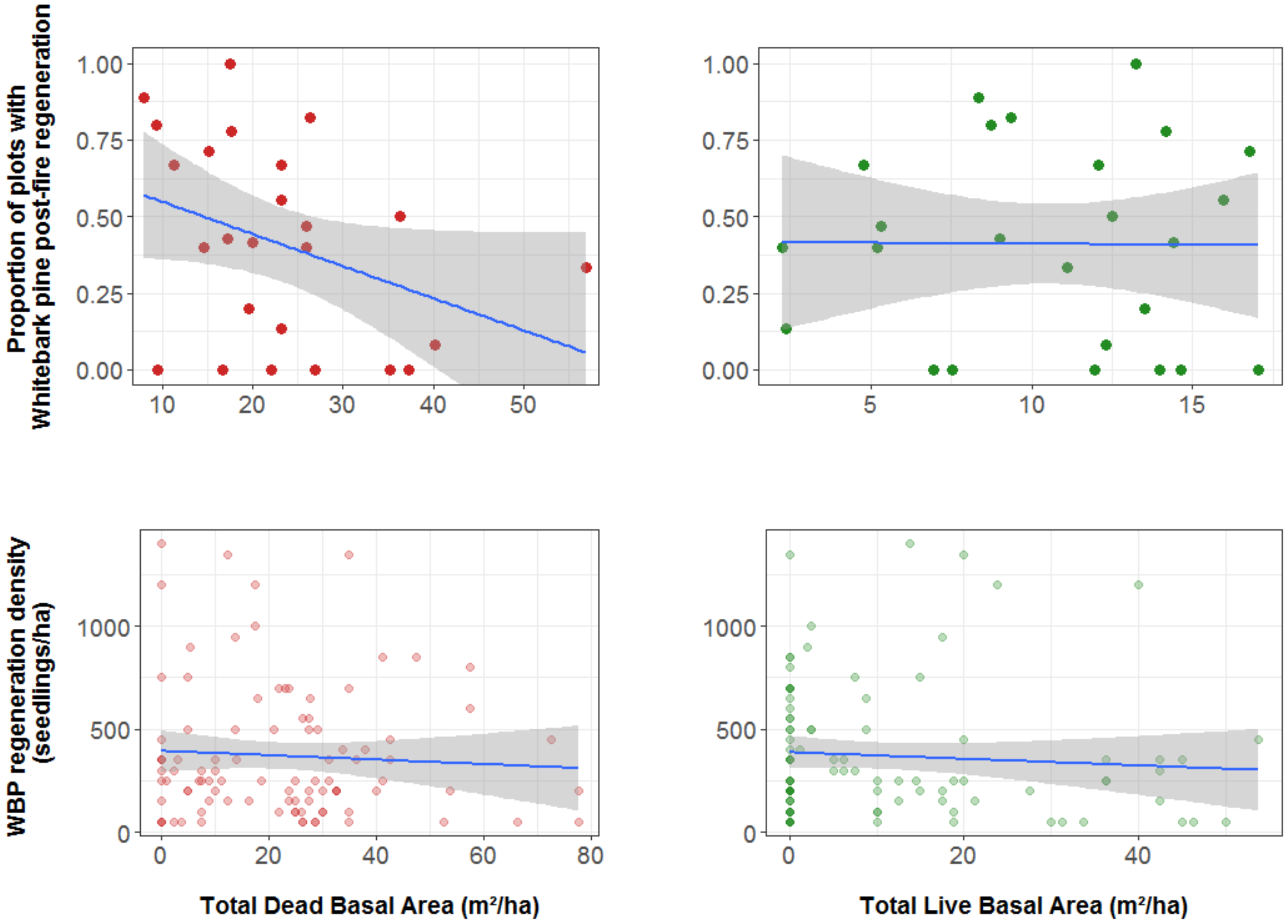
Appendix 9 - Post fire whitebark pine regeneration density in relation to lfh depth, decaying wood, moss and mineral soil covers. The blue line represents the fitted model using Generalized Linear Mixed Effect Model (GLMM). Gray area around fitted line represents a 95% confidence interval.



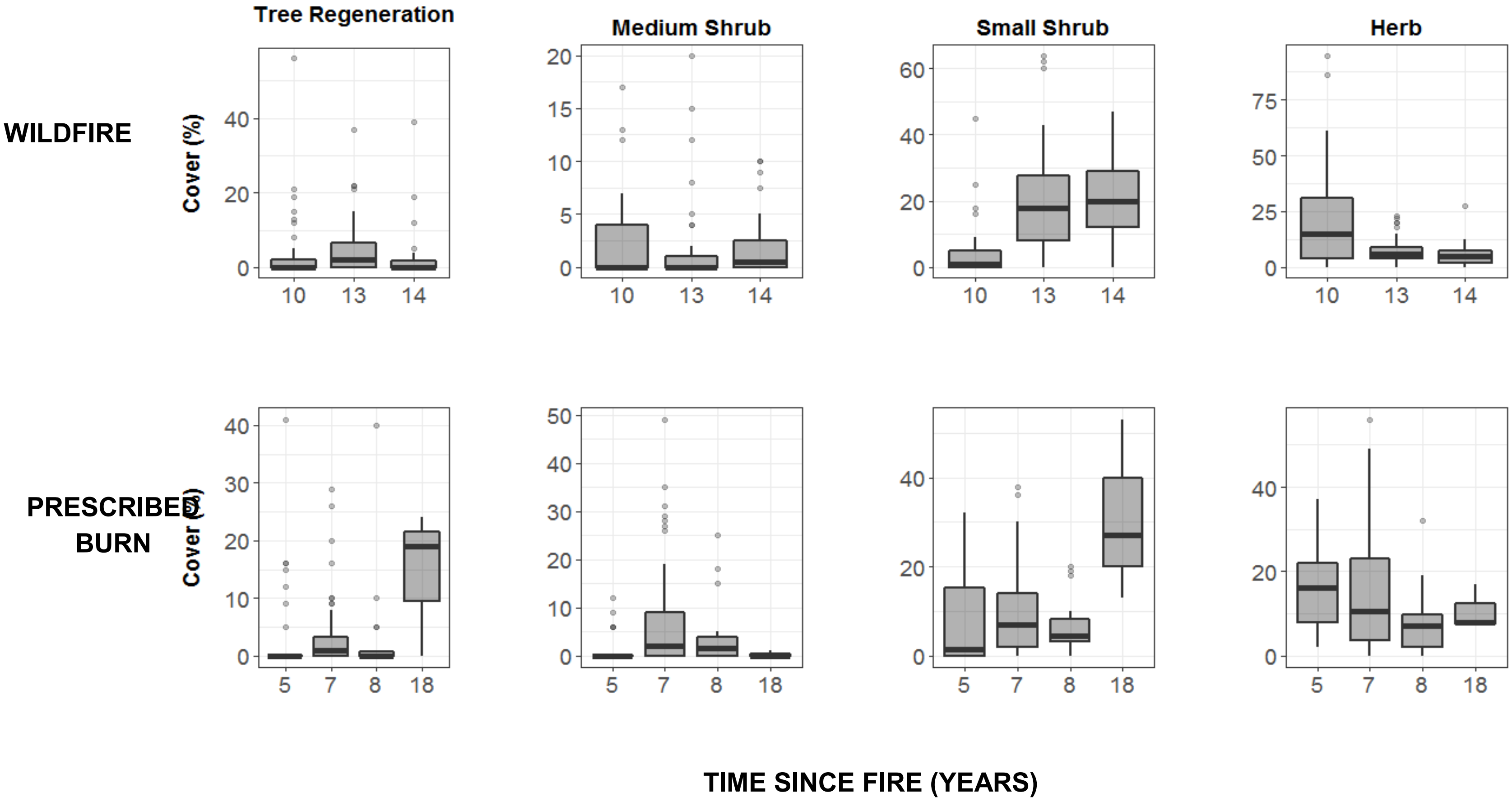
Appendix 10 - Post fire whitebark pine regeneration density in relation to small shrub, medium shrubs, herb and tree regeneration (*Pinus contorta, Picea engelmannii, Abies lasiocarpa*) covers. The blue line represents the fitted model using Generalized Linear Mixed Effect Model (GLMM). Gray area around fitted line represents a 95% confidence interval.



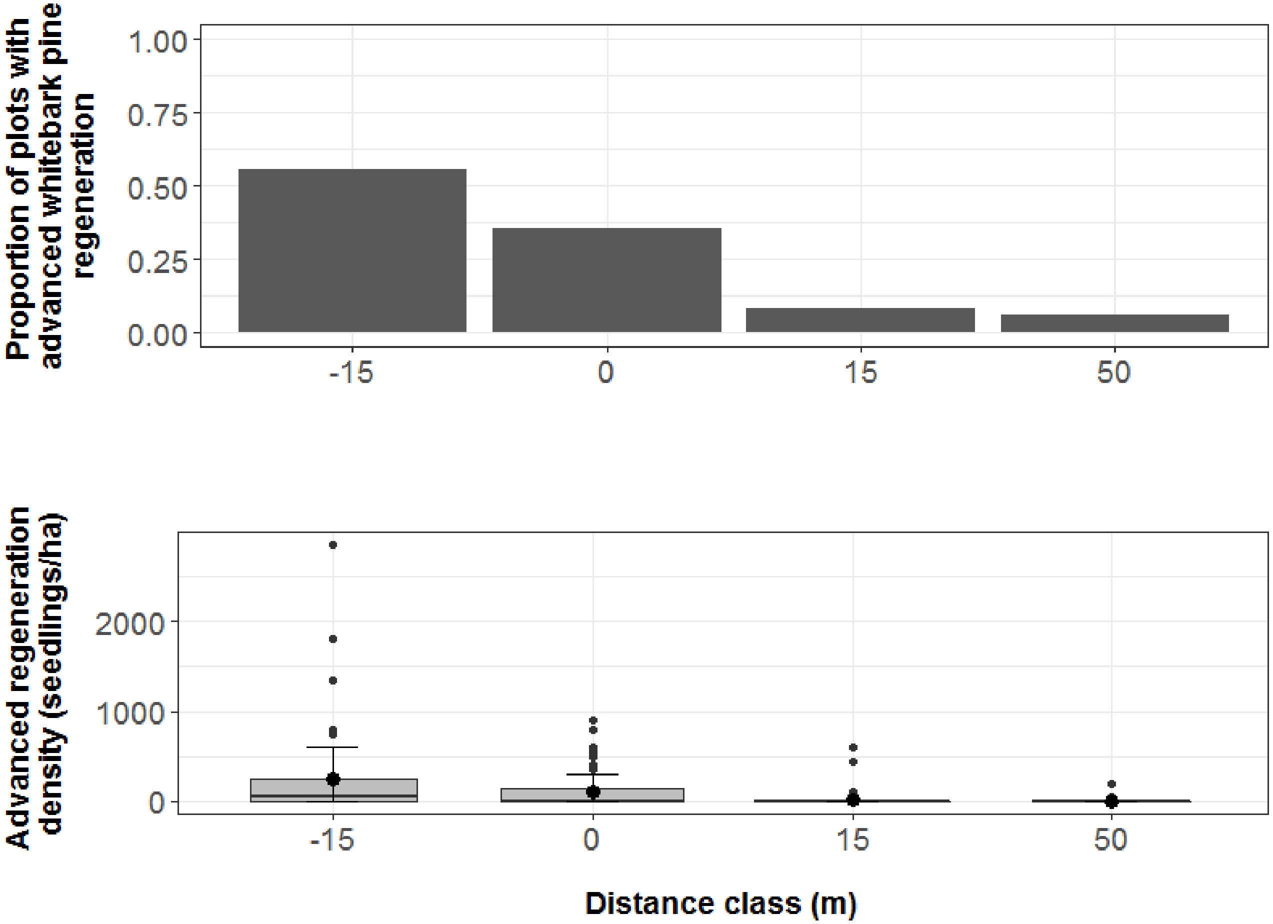
Appendix 11 - Post fire whitebark pine regeneration density and occurrence in relation to total dead and live basal area. On top figures, data points represent the proportion of plots with regeneration within each stand. The blue lines represent respective fitted linear models using Generalized Linear Mixed Effect Model (GLMM). Gray area around fitted line represents a 95% confidence interval.



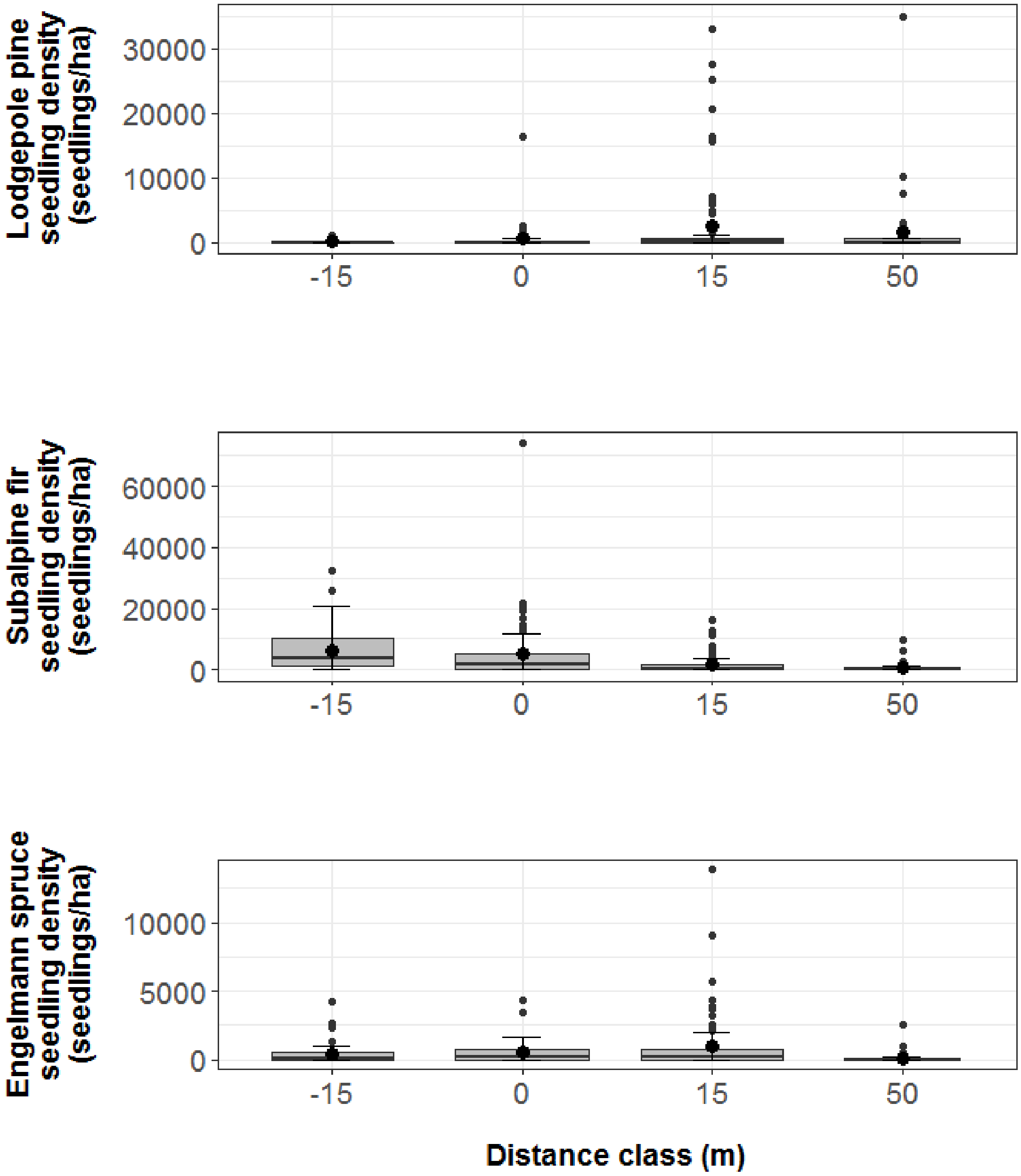
Appendix 12 - Differences in tree regeneration, shrubs and herb cover over time at prescribed burns and wildfires.



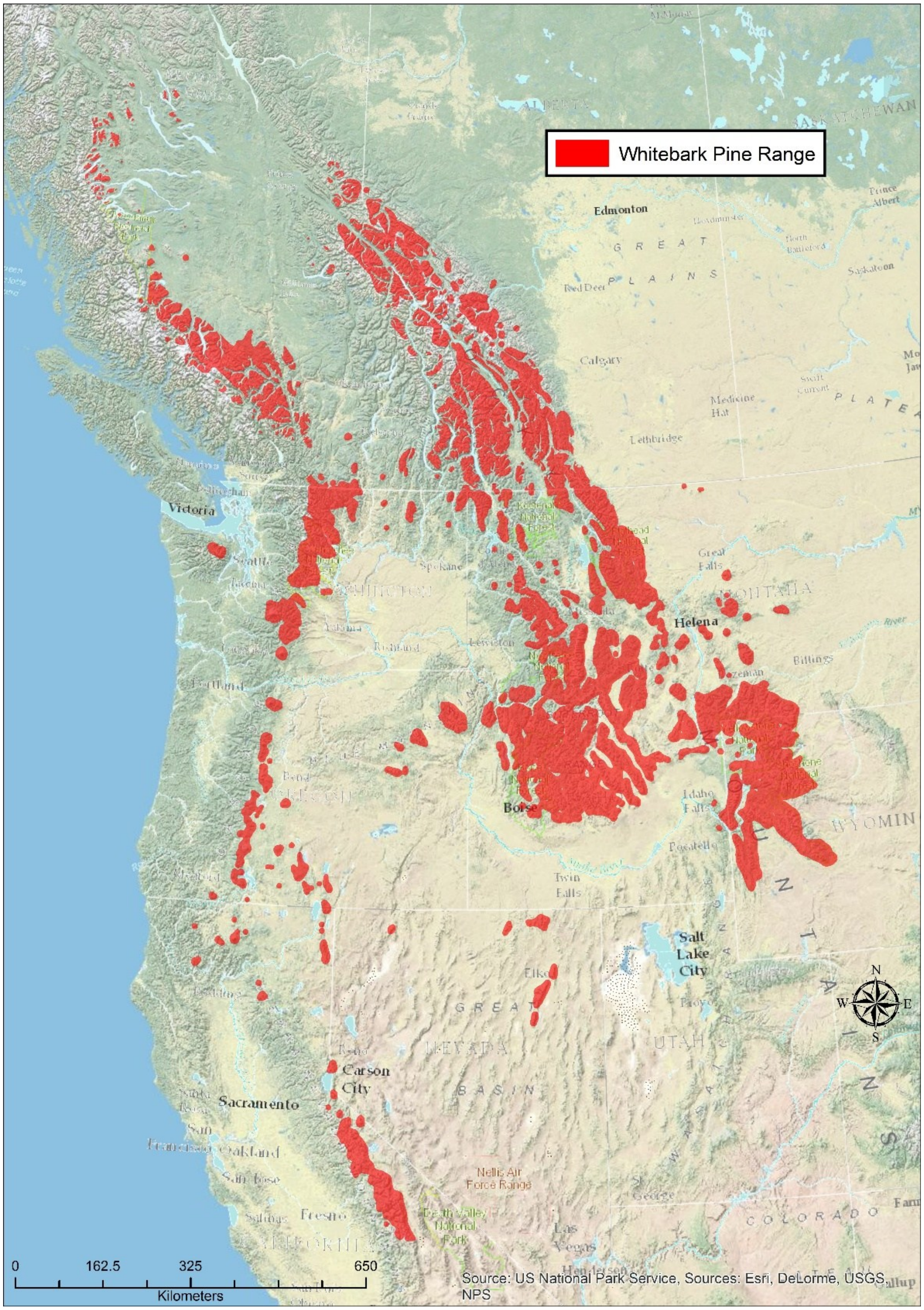
Appendix 13 - Proportion of plots with advanced regeneration (top figure) and advanced regeneration density (bottom figure) at each distance class. In the bottom graph, black dot and horizontal line within each boxplot represent the mean and median, respectively.



Appendix 14 – Seedling density of lodgepole pine, subalpine fir and Engelmann spruce at the different distance classes. black dot and horizontal line within each boxplot represent the mean and median, respectively.



Appendix 15 – Geographical distribution of whitebark pine. Source: Whitebark Pine Ecosystem Foundation (2014) and US National Park Service.



Source: US National Park Service, Sources: Esri, DeLorme, USGS, NPS