Historic perspectives and future challenges: the impacts of wildfires on high-elevation forests in Glacier National Park, British Columbia, Canada

By

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ABSTRACT

Wildfire activity in western Canada is changing, with trajectories moving towards more frequent and severe wildfires. Increased wildfire ignitions, growing drought conditions, and historical forest management practices are leading to shorter intervals between fire events (e.g., < 30 years) in some forest ecosystems. Studies describing the impacts of wildfire on forest ecosystems is a growing field of research, however, the number of studies focused on mountain forests is comparatively less. Wildfire in mountain forests is generally infrequent and often burns at high intensity leading to severe ecological effects. Considering the anticipated increases in wildfire activity in western Canada, studies focused on wildfire effects in these mountain forests are needed. High-elevation coniferous forests in western Canada are home to many ecologically important species such as whitebark pine (*Pinus albicaulis*), a keystone and foundation species for many subalpine forests. Whitebark pine is a long-living species (1000+ years old) that is considered endangered in Canada. Many studies describe the effects of blister rust disturbance and mountain pine beetle disturbance, but few studies describe effects of wildfire disturbance and climate. The sensitivity of whitebark pines to climate, and the presence of historical wildfire disturbance in these forest ecosystems are still not fully described. To understand how future wildfire regimes may impact forest regeneration in whitebark pine ecosystems, foundational knowledge and understanding of historical wildfire regimes and climate is critical. The two goals of this study are to (1) improve our understanding of historical wildfire activity in high-elevation forests and assess the relationship between climate and the growth of whitebark pine. This provides a foundation to then (2) determine the impacts of future wildfire frequencies on forest regeneration. In a high-elevation forest in the Beaver Valley, Glacier National Park, Canada, I collected cross sections from fire-scarred trees and cores from whitebark pine trees to document past wildfires and assess the relationship between climate and whitebark pine tree growth. I found that whitebark pine tree growth prefers warm and dry climate during the growing season; I also found a greater presence of historical wildfires at these elevations than previous studies described. To determine contemporary wildfire impacts on forest regeneration, I characterized tree and understory regeneration at a site affected by a single wildfire (2017) and a short-interval reburn (1992 and 2017). From these surveys I found that high burn severity had a greater impact to regenerating plant abundance (trees and understory) compared to the number of wildfires that burned a forest (e.g., single burn vs. short-interval reburn). Pre-fire composition remained unchanged after a single wildfire, but in regions that experienced the greatest disturbance (e.g., high severity wildfire followed by high severity wildfire) an increased presence of pioneer species such as lodgepole pine (*Pinus contorta*) and deciduous species was detected. Fire management agencies in western Canada can use these insights to better manage the presence of wildfire in whitebark pine ecosystems to preserve whitebark pine trees and promote high-elevation forest resiliency. My findings highlight the importance of understanding both historical and contemporary wildfire impacts to high-elevation coniferous forests and provides baseline ecological information about the response of whitebark pine forests to increased wildfire activity.

TABLE OF CONTENTS

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DEDICATION

I would like to dedicate this work to the community of women working in the wildfire space.

"I stand
On the sacrifices of a million women before me
Thinking
What can I do
To make this mountain taller
So the women after me
Can see farther"
-Rupi Kaur

The completion of this thesis would not have been without your sacrifices or your support.

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LIST OF FIGURES

LIST OF TABLES

CHAPTER 1: Introduction

High-elevation forests in British Columbia

The high-elevation subalpine forests of interior British Columbia (BC) are classified by the biogeoclimatic (BEC) ecosystem classification zones (Meidinger and Pojar 1991) as Englemann Spruce-Subalpine Fir (ESSF) forest and is the third largest BEC zone in BC, covering 15.3% of the province (Chourmouzis et al. 2009; Hamann et al. 2005). This zone extends across interior BC from 49-57° in latitude, and in southern BC can range in elevation from 1,500-2,300 m above sea level (asl). These high-elevation forests are dominated by coniferous trees, herbaceous plants, and shrubs; and provide important ecosystem services such as snow retention, soil stabilization, and wildlife habitat (Meidinger and Pojar 1991).

High-elevation ESSF forests in southern interior BC are dominated by subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmanni*), whitebark pine (*Pinus albicaulis*), and, in disturbed or very dry sites, lodgepole pine (*Pinus contorta*). Broadleaf trees are uncommon in high-elevation subalpine regions (Meidinger and Pojar 1991). Common shrubs and herbaceous plants include many vaccinium species (e.g., *Vaccinium scoparium*, *Vaccinium membranaceum*, etc.), pink and white mountain heather (*Phyllodoce empetriformis* and *Cassiope mertensiana*), sitka valerian (*Valeriana sitchnesis*), and one-leaved foam flower (*Tiarella unifolia*). Whitebark pine is considered a foundation and keystone species in this ecosystem and is an endangered species in Canada (Achuff and Wilson 2010; Tomback et al. 2022). It is an important tree island and habitat initiator, with high-water use efficiency and hardy seeds (Tomback and Achuff 2010; Tomback et al. 2001, 2022; Tomback 1982). Whitebark pine possesses traits that allow it to establish and tolerate arid, windy conditions, and poor soil environments at upper elevations (Tomback and Achuff 2010; Tomback et al. 2001, 2022;

Wagner et al. 2018). A unique mutualistic relationship exists between the whitebark pine tree and a species of bird called the Clark's nutcracker (*Nucifraga columbiana*). The Clark's nutcracker caches seeds from whitebark pinecones for future food supply, often in burned landscapes or high-elevation terrain (Tomback et al. 2001; Wagner et al. 2018). Although brown bears (*Ursus arctos*) roaming the area are reported to opportunistically eat the seeds from these cones, the Clark's nutcracker remains the most abundant disperser of seeds from whitebark pinecones (Tomback 2003).

Glacier National Park

Glacier National Park (GNP) is found among the tall, snowy ranges of the Purcell's and Selkirk's mountains that form the first tall mountain barrier east of the Coast Mountains in BC (Parks Canada 2024). Old-growth stands of ESSF forests are often found at higher elevations in GNP and the interior-cedar hemlock (ICH) BEC zone at lower elevations. The Beaver Valley is in GNP and forms a significant north-south orientated landscape feature in the park about five km wide and 40 km long. GNP was established in 1886 just after the completion of the transcontinental Canadian Pacific Railway (CPR) line. The establishment of the park and visitor facilities was in part to entice travelers to the picturesque natural landscapes and to make use of the newly developed railway line. The nearby Illecillewaet Glacier was historically a major tourist attraction and brought in international visitors to witness or climb the mountains and glaciers in the area (Parks Canada 2024). Prior to 1962, transport corridors within GNP were limited to the railway line and small trails before the establishment of the Trans-Canada Highway. Prior to the opening of the Trans-Canada highway, passage from Revelstoke to Golden took place on the "Big Bend Highway" which travelled 305 km north of Revelstoke through the

Selkirk mountains following the Columbia River, before heading south again to Golden (Parks Canada 2024).

The construction of the CPR line through GNP involved numerous landscape disturbances including deforestation, railway fires, excavation, and blasting (Longworth 2009; Marsh 1972). The steep mountainous terrain that characterizes GNP challenged railway construction and other infrastructure development by means of flooding, landslides, and avalanches. The creation of the railway line through GNP connected western Canada to the interior, driving colonial settlement, tourism, agricultural development, mining, and logging (Longworth 2009; Marsh 1972). Among these disruptions was the occupation of colonial settlers on Indigenous land and the illegalization of their traditional practices which include cultural burning and hunting (Longworth 2009). The construction of the CPR brought more settlers into the prairies east of GNP and into the Columbia River valley west of GNP and forced Indigenous people in the surrounding landscapes onto reserves (Longworth 2009). Although historical written records in western science and literature have purposely not recognized the occupancy and traditional territory of Indigenous peoples within GNP (Longworth 2009), their oral history describes the traditional and unceded territory of the Ktunaxa, Secwépemc, Sinixt, Sylix, and Stoney Nakoda as overlapping and extending across the park.

Climate and wildfire in Glacier National Park

Seasonal climate in GNP is described by warm, moderately dry summers, and cold, snowy winters. In the summer months (June-September) temperatures range from 5 to 15℃ and precipitation varies between 100-125mm in the form of rain. During the winter months

(November-March) temperatures drop to -7°C to -15°C (or sometimes colder) with heavy amounts of precipitation (175-300mm snow water equivalent) in the form of snow (Environment Canada 2024). Upper elevations of exposed subalpine forests are often harsh environments for plant growth and can be subject to strong winds, variable temperatures (Meidinger and Pojar 1991; Tomback 2003; Wagner et al. 2018), and on steeper slopes, landslides and/or avalanches.

Warming conditions driven by climate change are shifting forest dynamics; these changes can include increased moisture stress and changes in vegetation composition (Coop et al. 2022; Davis et al. 2020; Seidl et al. 2017). In subalpine stands, elevational shifts of species' ranges and shifts in composition are observed (Davis et al. 2020). For example, elevated drought conditions can favor the establishment of early-successional tree species such as lodgepole pine in subalpine forest stands (Case and Peterson 2007) to the detriment of more shade tolerant species such as subalpine fir or Englemann spruce.

Wildfire regimes are defined by the characterization (frequency, intensity, return interval, size etc.) of fire events over a described area and period, and the cumulative spatial and temporal impacts of wildfire (Agee 1996; Baron et al. 2022; Parisien et al. 2023). Historical wildfire regimes of subalpine ESSF forests in BC are not yet fully described. To my best knowledge, only one study in GNP describes wildfires occurring once every 100-150 years (Johnson et al. 1990). Anthropogenic climate change is leading to more fire-conducive conditions, increasing fire season length, and wildfire activity across western North America (Baron et al. 2022; Coop et al. 2020; Ellis et al. 2021; Parisien et al. 2023) and driving more frequent and severe wildfires (Ellis et al. 2021; Parisien et al. 2023; Wang et al. 2020). With elevated drought conditions, increased forest density, woody fuels (Hessburg et al. 2019), and increased lightning ignitions (Coop et al. 2020), more extreme wildfire behavior and burned area are expected (Baron et al. 2022; Ellis et al. 2021; Parisien et al. 2023). These projections are expected to increase wildfire activity in high-elevation coniferous stands of interior BC and increase the occurrence of short-interval reburns (e.g., <30 years). How these changes in projected wildfire activity will impact forest regeneration and dynamics in high-elevation forests remains uncertain.

Although it is generally thought that high-elevation forests were impacted by low frequency, high severity wildfires in the past, little is known about the historical presence of wildfires at upper elevations of subalpine (whitebark pine) stands in GNP. These stands are generally found in drier sites on south-facing slopes and could have been impacted by fire more frequently in the past (relative to more mesic sites in similar settings). Although whitebark pine is a long living species in these stands and has strong prospects for use in dendrochronology, few studies document the history of past wildfires using this species (Johnson et al. 1990; Morgan and Bunting 1990; Murray and Siderius 2018).

Further, the growth of whitebark pine has been related to climate variability in BC (Carlson et al. 2018; Wong and Daniels 2017; Youngblut and Luckman 2013), where growth is mostly related to warm conditions during the growing season. However, the sensitivity of whitebark pine growth to climate parameters over time has not been explored. Such analyses and insights would provide information on the changing relationship between tree growth and climate during this most recent period of observed climatic warming.

Establishing historical baselines (wildfire history and tree growth-climate analyses) will provide insights to contextualize how forest stands are changing due to climate change and provide a point of historical comparison when assessing the impacts of future wildfire. I ask the following research questions to better characterize the historical and contemporary presence and impacts of wildfire and climate at upper elevations of forest stands at a study site in GNP:

1. What is the historical presence of wildfires in forests stands of high-elevation forests of the Beaver Valley, BC, and is whitebark pine growth sensitive to climate? (Chapter 2)
2. What are the impacts of more frequent and severe wildfires to forest regeneration at the upper elevations of the Beaver Valley, BC? (Chapter 3)

To answer these questions, I performed a field-based study at a study site in the Beaver Valley of GNP, BC. Coupled with remote sensing imagery and tree-ring analysis at a laboratory at the Thompson Rivers University, two studies were conducted to address my research questions. Chapter 2 answers the first question above and will be reduced and formatted as a short submission as a Research Report (~1,500 words) to the journal *Tree-Ring Research*. Chapter 3 answers the second research question and is formatted as a manuscript for a planned submission as an Original Research Article to the journal *Fire Ecology*. To summarize the outcomes of both studies, Chapter 4 discusses the main contributions of my thesis.

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CHAPTER 2: Fire history and climate-growth relationships using whitebark pine (*Pinus albicaulis*) in Glacier National Park, Canada

ABSTRACT

In high-elevation coniferous forests across interior British Columbia (BC), endangered whitebark pine (*Pinus albicaulis*) trees grow at upper elevational limits where they can experience disturbance from climatic variability, white pine blister rust fungus (*Cronartium ribicola*), mountain pine beetle (*Dendroctonus ponderosae*), and wildfires. Although many studies capture the effects of biotic disturbances on whitebark pine (Campbell and Antos 2000; Wong and Daniels 2017), few studies have examined the relationship between climate and whitebark pine growth in BC, and even fewer have reconstructed fire history using fire-scarred trees from high-elevation forest stands. Although whitebark pine trees are at high risk of extirpation in Canada, historical climate impacts on growth and wildfire regimes in these forests are poorly understood. Glacier National Park is located in interior BC and is characterized by mountainous landscapes and high-elevation coniferous forests (whitebark pine habitat) that experience long, cold, and snowy winters and short, dry summers. The goal of this study was to reconstruct past wildfire activity in the Beaver Valley, Glacier National Park, and assess the relationship between climate parameters and whitebark pine growth. Over the interval of 1786-1977, 12 wildfire events were recorded using cross sections from eight fire-scarred trees; only one fire (1937) was recorded in more than one sample. Lightning likely ignited these wildfires, as historical records of railway fires and mining fires did not coincide with fire events recorded in our study. To assess climate-growth relationships, a tree-ring chronology was constructed with series from 14 individual trees (interseries correlation: 0.417). Between 1901 and 2022, a significant positive association was found between tree growth and monthly (e.g., July) and monthly aggregate (e.g., June-July) temperature variables during the growing season and negative associations found with growing season precipitation and monthly Standardized Precipitation Evaporation Index (SPEI). These findings suggest that whitebark pine trees at the study site experience the most growth during years with warm and dry summer conditions. Temporal stability of climatic parameters was observed in the later part of the 20th century, but did not remain stable over the entire period. Management agencies that monitor the vitality of whitebark pine trees can incorporate our findings of historical wildfires in whitebark pine habitat to inform the application of wildfire (e.g., prescribed burns) to these forests and other similar landscapes. This study provides baseline ecological information on the sensitivity of whitebark pine trees to climate parameters and highlights the need for more studies exploring these relationships.

Keywords: Canada, climate, dendrochronology, fire history, fire-scarred trees, Glacier National Park, tree rings, Whitebark pine.

BACKGROUND

Whitebark pine (*Pinus albicaulis*) trees are a keystone and foundation species in subalpine forests of interior British Columbia (BC), forming tree islands at upper elevations and new forest habitat for more shade tolerant species such as subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmanni*) (Tomback et al. 2001; Youngblut and Luckman 2013). Although whitebark pine is considered an early successional species (Tomback 2003), it is a poor competitor and is thus often found at the edges of subalpine forests at higher elevations on steep, south-facing slopes (Murray and Siderius 2018). Whitebark pine has a mutualistic relationship with the Clark's nutcracker (*Nucifraga columbiana*); of which the seed caching behaviour of Clark's nutcracker strongly affects the distribution and recruitment of whitebark pine trees (Tomback 1982, 2003; Tomback et al. 2001, 2022, Tomback and Achuff 2010). In some cases, Clark's nutcracker may cache in fire-affected landscapes where predation is lower, allowing for the early establishment of whitebark pine in these regenerating stands (Perkins 2015; Tomback 1982; Tomback et al. 2001, 2022).

Whitebark pine communities across North America are endangered according to the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) assessment and status report (Achuff and Wilson 2010), and have been negatively impacted by multiple disturbances including blister rust fungus (*Cronartium ribicola*), mountain pine beetle (*Dendroctonus ponderosae*), increased drought conditions, and changing wildfire regimes (Carlson et al. 2018; Murray and Siderius 2018; Tomback et al. 2022; Tomback and Achuff 2010; Wong and Daniels 2017). Whitebark pine trees are moderately adapted to wildfire with intermediate bark thickness (1-2 cm thick) that can protect the cambium tissues from low severity wildfires, and in some cases better than other tree species of subalpine forests (e.g., Engelmann spruce) (Murray and Siderius 2018).

Although wildfires in subalpine forests are infrequent and often stand replacing (Bowman et al. 2009; Hoecker et al. 2020; Johnson et al. 1990), smaller and localized low severity wildfires at these locations may only damage parts of whitebark pine trees leaving a fire scar. Fire-scarred trees preserve annual, sometime seasonal records of wildfire in the rings of the tree (Baisan and Swetnam 1990; Dieterich and Swetnam 1984), characterizing to certain extents the history of wildfire occurrence (Swetnam et al. 1999). By removing sections from fire-scarred trees, fire events can be dated to produce a reconstruction of past wildfire activity (e.g., Brookes et al. 2021; Harvey et al. 2017). In the case of whitebark pine, few studies have examined fire-scarred trees to reconstruct fire history (Johnson et al. 1990; Morgan and Bunting 1990; Murray and Siderius 2018).

Previous reconstructions of wildfire history using tree-rings from whitebark pine trees in subalpine regions characterize widely variable fire intervals of anywhere between 10-200+ years (Morgan and Bunting 1990; Murray and Siderius 2018). Airey and Taylor (2024) found fire return intervals of 60 years at a site in the Soldier Mountains, Idaho, Morgan and Bunting (1990) found fire occurring on average every 50 years for a site on Russell Peak in Shoshone National Forest, Wyoming, USA, and Murray and Siderius (2018) found fire occurring on average every 50 years for sites across the North Cascades National Park, Washington, USA. In Glacier National Park, BC, Johnson et al. (1990) found fire occurring on average every 110 years relying on tree-rings and aerial photography. Site-specific characteristics such as latitude, elevation, aspect, and composition of nearby trees and understory species likely attributed to the variability in fire history reported (Larson et al. 2009; Morgan and Bunting 1990; Murrary and Siderius

2018; Johnson et al. 1990). This variability in fire history for whitebark pine ecosystems highlights the need for further research investigating past wildfire activity in these ecosystems in BC. In the context of changing wildfire regimes, establishing a historical baseline of wildfire activity can provide a point of comparison to expected future wildfire activity.

In addition to providing a record of past wildfire events, tree-ring datasets from whitebark pine trees can be used to assess the growth response of trees to climate variability (Wong and Daniels 2017; Youngblut and Luckman 2013). Past research investigating climate-growth relationships of whitebark pine indicate growth is positively associated with growing season temperatures (Larocque and Smith 2005; Wong and Daniels 2017; Youngblut and Luckman 2013). The relationship between whitebark pine growth and precipitation is perhaps more complex, with some studies indicating a negative association with growing season precipitation (Carlson et al. 2018), while others report a positive relationship with growing season precipitation (Wong and Daniels 2017). Tree-ring studies include approaches to examine the stability of climate-growth relationships over time (e.g., Griesbauer et al. 2021); however, to the best of our knowledge, no studies have assessed the stability of climate-growth relationships over time using whitebark pine trees in BC. This highlights another gap, in addition to historical wildfire regimes, in the understanding relationships between whitebark pine and environmental variability.

The goal of this study is to gain insights on the ecology of a high-elevation whitebark pine stand by investigating past wildfire activity and determining the dominant climate parameter(s) driving the growth of whitebark pine. The specific objectives are: 1) characterize wildfire activity using fire-scarred whitebark pine trees and 2) detect any relationships between annual radial growth of whitebark pine and climatic parameters including temperature, precipitation and an index of drought. The key findings from Johnson et al. (1990) describe wildfire activity in Glacier National Park as infrequent, stand replacing, and lightning driven wildfires that occur on average about once every 110 years. Therefore, we hypothesize that wildfire occurrence at our study site will be historically infrequent. Previous research examining the effects of climate variability on whitebark pine tree growth from nearby regions reported a positive relationship between growing season temperature (Youngblut and Luckman 2013) and a positive relationship with moisture (Wong and Daniels 2017), therefore we hypothesize that both summer temperature and precipitation will be positively related to whitebark pine growth. Lastly, regional tree-ring studies of coniferous forests limited by growing season temperature in BC describe strengthening relationships with climatic parameters in the last century (Griesbauer et al. 2021), therefore we hypothesize that the relationship between whitebark pine growth and our climate parameter(s) will strengthen over time.

METHODS

The study area is located in the Beaver Valley, Glacier National Park, BC. Glacier National Park was established in 1886 and covers 1,359 km^2. This area is the largest federally protected park in BC and encompasses forested and mountainous terrain, alpine meadows, and glaciated regions. Subalpine forests in the Beaver Valley are comprised of largely subalpine fir, Engelmann spruce, and whitebark pine at higher elevations, but also include lodgepole pine (*Pinus contorta*) on drier and recently disturbed sites. The study area was selected to avoid influences from historical and contemporary logging or prescribed burning, and in an area where past wildfires burned with minimal to no suppression. The sampling site is located on a southwest facing slope at ~ 1,900 m asl (Fig. 1), and is historically snow-free as early as June.

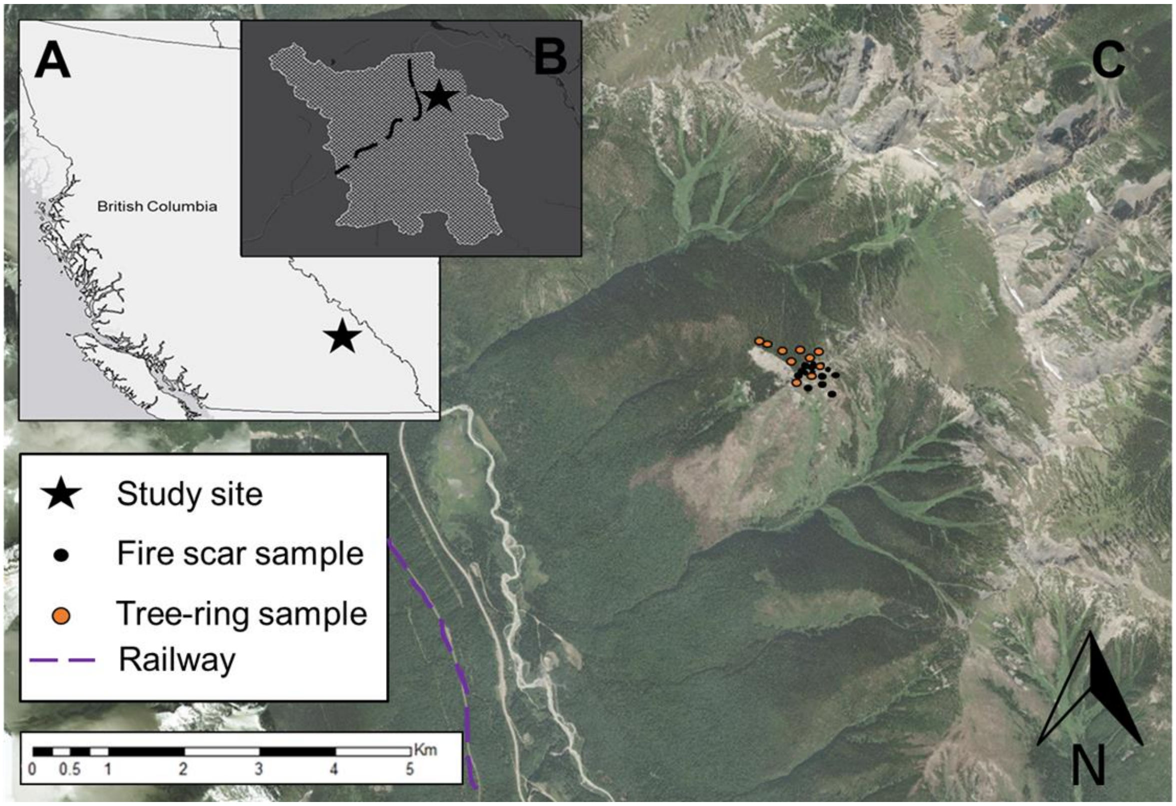

Fig. 1. "A" (top left)" The study site (star on inset map) in Glacier National Park, British Columbia, Canada. "B" (middle left): The national park boundary. "C": The location of tree-ring (orange circles) and cross sections of fire-scarred trees (fire scar samples) (black circles).

Sample collection

Field sampling was completed in July 2022. To reconstruct fire history, fire-scarred trees were visually identified and opportunistically sampled in the study area. The study area is extremely steep so access was gained by helicopter and the sampling area was constrained to areas that could be accessed and sampled safely. In total, eight cross sections from standing dead trees, stumps, and fallen logs were collected using a chainsaw.

A site-level tree-ring chronology was required to crossdate our cross sections, date fire events from fire scars, and to investigate climate-growth relationships of whitebark pine. Two increment cores were extracted from 14 trees (28 cores) at 1.3 m above the ground and in the same area where the cross sections of fire-scarred trees were collected. We targeted both living and dead whitebark pine trees to generate a longer tree-ring chronology.

Sample processing

Cross sections and cores were air dried and then sanded with progressively finer sandpaper until the xylem cellular structure was visible under magnification. Ring boundaries of cross sections and cores were measured using the program WinDendro (Regent Instruments Incorporated), visually crossdated, and then statistically verified using COFECHA (Grissino-Mayer 2001). Crossdating was also verified using the whitebark pine tree chronology from nearby McMurdo Mountain (Youngblut and Luckman 2013).

Fire events were dated from fire scars on the cross sections and when possible, were dated based on the position of the scar tissue in the annual ring (Dieterich and Swetnam 1984; Harvey et al. 2017). Considering the long, cold winters and short growing seasons that characterize these high-elevation mountain environments, we interpreted scars that occurred in the latewood, and at the ring boundary, as summer fires. All records of fire events were then imported into the Fire History and Exploration System software (FHAES) (Brewer et al. 2016; Sutherland et al. 2017). We used historical records of fire events reported by Johnson et al. (1990) in Glacier National Park to cross-reference any fire dates from our samples with historical records of fire events nearby in the Beaver Valley.

Tree-ring measurements from cores were processed to create a site-level chronology. Core series were averaged per individual tree and a negative exponential spline was used to detrend all raw crossdated tree-level series to remove non-climatic influences on growth (e.g., age-growth trends). A chronology was constructed using a bi-weight robust mean; this chronology was used to crossdate partial cross sections from fire-scarred trees, and in the climate-growth analysis. Cores with too much rot were excluded from analysis.

Fig. 2. Left: Dead standing fire-scarred whitebark pine tree at the study site. Middle: Cutting a cross section of a fire-scarred whitebark pine tree. Right: Cross section from a standing dead whitebark pine tree at the study site. The individual tree records seven fire events between 1786-1977.

Fire and climate relationships

We relied on data from ClimateNA to derive monthly measures of maximum, minimum, and mean temperature and monthly precipitation sums from 1901-2022 using ClimateWNA (Wang et al. 2016). Potential Evapotranspiration (PET) was derived using the Thornwhaite equation with the R package *SPEI* (Begueria et al. 2013) and monthly Standardized Precipitation Evaporation Index (SPEI) values were calculated using monthly precipitation sums, average temperature, and derived PET, hereafter referred to as ‘SPEI1’.

To identify relationships between climate and tree-ring growth over the interval of analysis (1901-2022) we calculated the correlation coefficients between the standard chronology and monthly climate variables. Correlation analyses were performed separately for each month over a 12-month period and for mean aggregates of monthly climate variables (e.g., mean June-July temperature of current year). Additionally, the stability over time of the strongest climate-growth relationships was assessed using a moving window correlation analysis to test their consistency through time. For this analysis, we used a 40-year interval offset by two years between 1901-2022. All data analyses were completed in R (R core Team 2024), for chronology processing we used the R packages *dplR* (Bunn 2008) and *treeclim* (Zang and Biondi 2015).

RESULTS

Fire history

A total of eight cross sections were removed from fire-scarred trees in our study site. These cross sections spanned from 1671 to 1990. Our eight cross sections from fire-scarred whitebark pine trees identified 15 individual fire events, for a total of 12 unique fire events from 1786-1977 (Fig. 3). We did not assign seasonality to each fire scar because the seasonal precision of fire scars was difficult to determine, only annual dates were assigned to the calendar year in which the scar formed. Only one fire year was found in four individual cross sections of fire-scarred trees (1937), the rest of the fire years were only found in a single cross section (i.e., not co-recorded in >1 sample) (Fig. 3). To boost the strength of our fire history study we investigated historical reports of wildfires that occurred within the Beaver Valley (Table 2) Johnson et al. 1990). Using these historical records, three fire events matched our samples (Fig. 3).

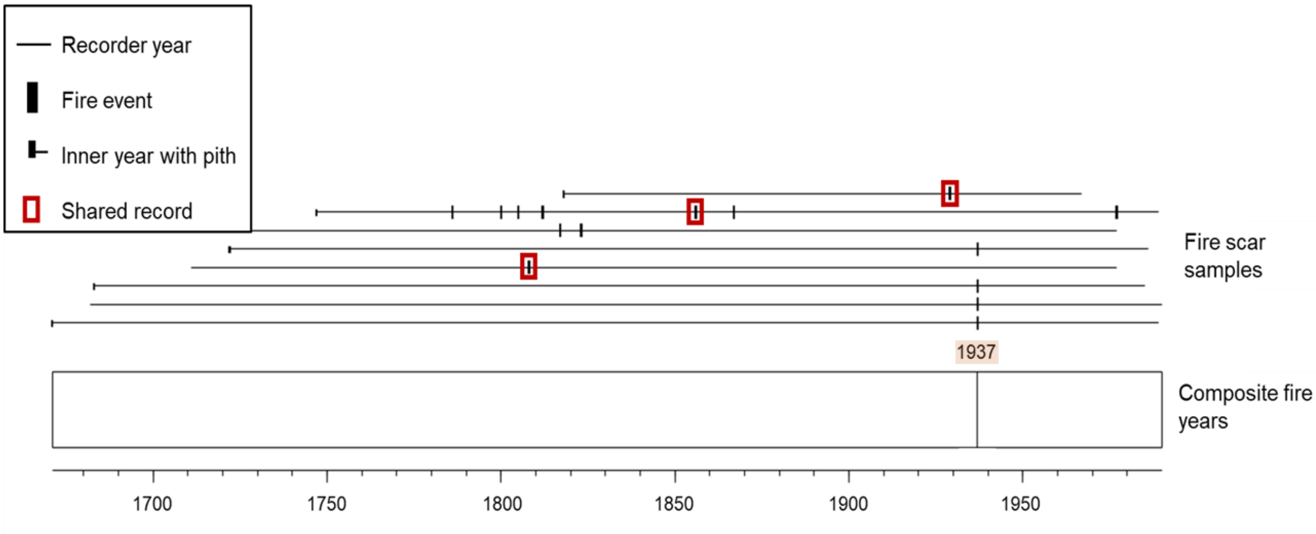

Fig. 3. Fire events from the Beaver Valley based on eight cross sections of fire-scarred trees. Vertical tick marks represent fire years from our study which range from 1786-1977. The year 1937 is highlighted above, as it is the only year that was recorded from our study from at least two individual cross sections of fire-scarred trees. The red outline around the vertical tick marks represents shared records of fire events from Johnson et al. (1990) that were recorded from the Beaver Valley, Glacier National Park.

Table 1. Comparison of fire events recorded from our cross sections of fire-scarred trees and historical records of wildfire in Glacier National Park from Johnson et al. (1990).

Year of fire event	Number of fire records from cross sections
1786	1
1800	1*
1805	1
1808	1
1812	1
1817	1
1823	1
1855	1*
1867	1
1930	1*
1937	4
1977	1

*Fire records shared by Johnson et al. 1990

Climate-growth relationships

The tree-ring chronology was constructed using 28 cores from 14 trees and spanned 1722 to 2022 (Table 1). The mean interseries correlation was 0.417.

Table 2. Characteristics for the whitebark tree-ring chronology.

Characteristic	Value
Coordinates	51.385ºN, 117.396ºW
Elevation	2053-2100 m asl
Tree-ring chronology	1722-2022
Number of trees	14
Number of segments	28

Significant positive associations were found between whitebark pine tree growth and growing season temperature (Fig. 4). The strongest positive climate-growth associations between whitebark pine growth and temperature were found for July minimum temperature ($r = 0.492$, $p < 0.05$), mean temperature ($r = 0.470$, $p < 0.05$), and maximum temperature ($r = 0.351$, $p < 0.05$) (Fig. 4). Followed by mean aggregates of monthly maximum temperatures of June-July ($r = 0.309$, $p < 0.05$), July-August ($r = 0.299$, $p < 0.05$), and June-August ($r = 0.299$, $p < 0.05$), as well as mean aggregates of monthly mean temperatures of June-July ($r = 0.396$, $p < 0.05$), July-

August ($r = 0.411$, $p < 0.05$), and June-August ($r = 0.402$, $p < 0.05$), and mean aggregates of monthly minimum temperatures of June-July ($r = 0.361$, $p < 0.05$), July-August ($r = 0.384$, $p < 0.05$), and June-August ($r = 0.340$, $p < 0.05$). Significant negative associations were found between whitebark pine tree growth and growing season precipitation and SPEI1. The strongest negative climate-growth associations between whitebark pine tree growth and precipitation were found for July ($r = -0.231$, $p < 0.05$), as well as for mean aggregates of monthly mean precipitation of June-July ($r = -0.229$, $p < 0.05$), June-August ($r = -0.242$, $p < 0.05$), and June-August ($r = -0.257$, $p < 0.05$) (Fig. 4). The strongest negative climate-growth associations between whitebark pine tree growth and SPEI1 were found for July ($r = -0.313$, $p < 0.05$), as well as for mean monthly aggregates of monthly SPEI1 for June-July ($r = -0.290$, $p < 0.05$), July-August ($r = -0.295$, $p < 0.05$), and June-August ($r = -0.310$, $p < 0.05$) (Fig. 4).

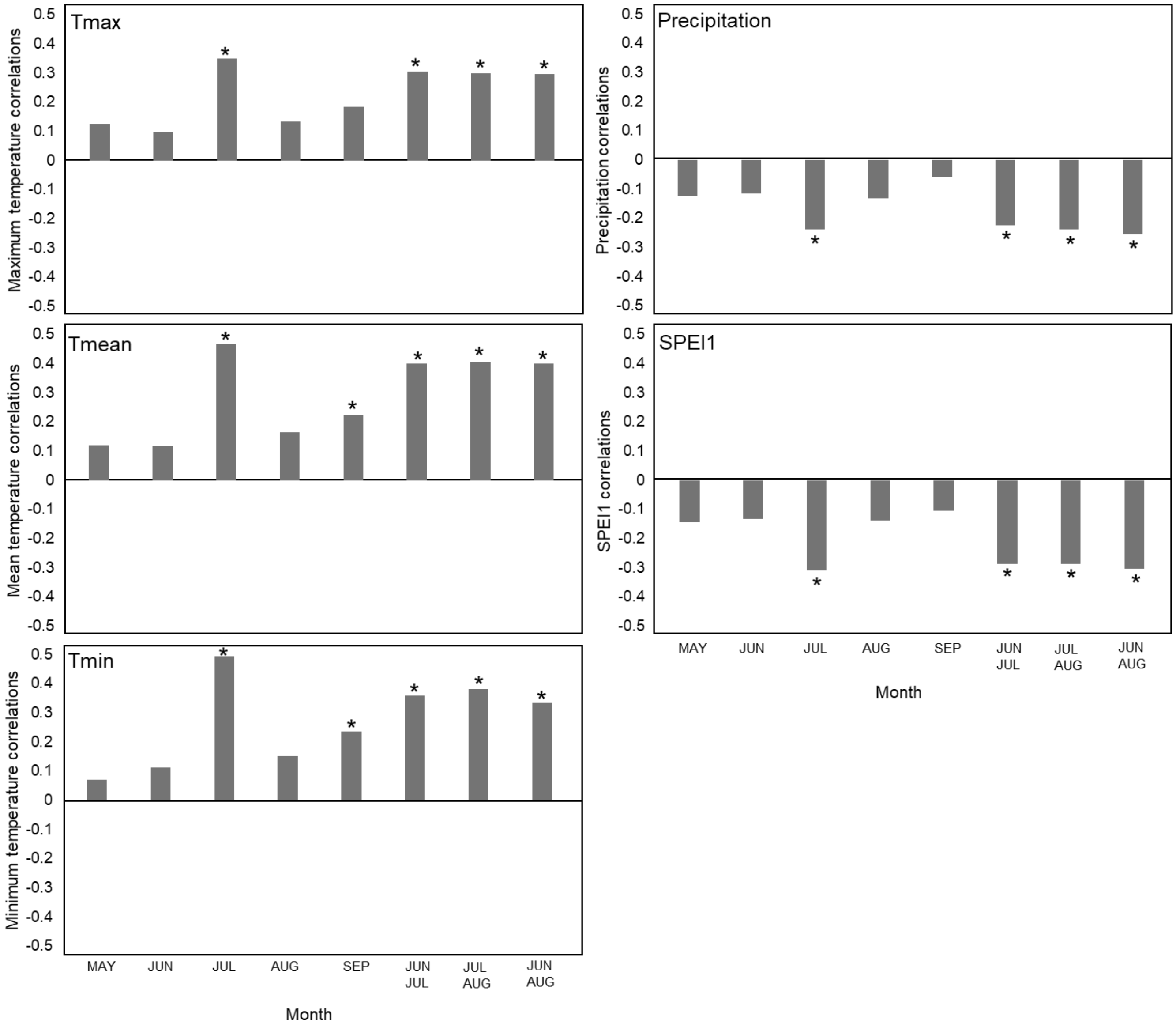

Fig. 4. Results from climate-growth correlation analyses for monthly maximum, mean, and minimum temperature, SPEI1, and precipitation in the growing year. Stars presented above or below bars represent significant values $p < 0.05$. Bars with two hyphenated months listed represent the correlation with the mean aggregates of monthly climatic variables for those months (see text).

Temporal stability of climate-growth relationships

July temperature was the climate parameter with the greatest influence on growth. We assessed the stability of the influence of mean, minimum, and maximum July temperature on tree growth over the 1901-2022 interval. Most notably, the relationship between minimum July temperature shifted from weak and insignificant associations to a positive relationship towards the later part of the 1901-2022 period, but the association was only significant between 1948 and 1989 (Fig. 5). The effect of maximum temperature on tree-ring growth in July showed a slightly declining sensitivity over the interval of analysis, with only a short significant period from 1901 to 1947 (Fig. 5). Mean temperature correlations in July were not found to be significant in the 1901-2022 period (Fig. 5). A significantly negative relationship between tree growth and July SPEI1 was found in the beginning of the 1901-2022 period, but a possible weakening sensitivity to this parameter is noted over the interval of analysis (Fig. 5)

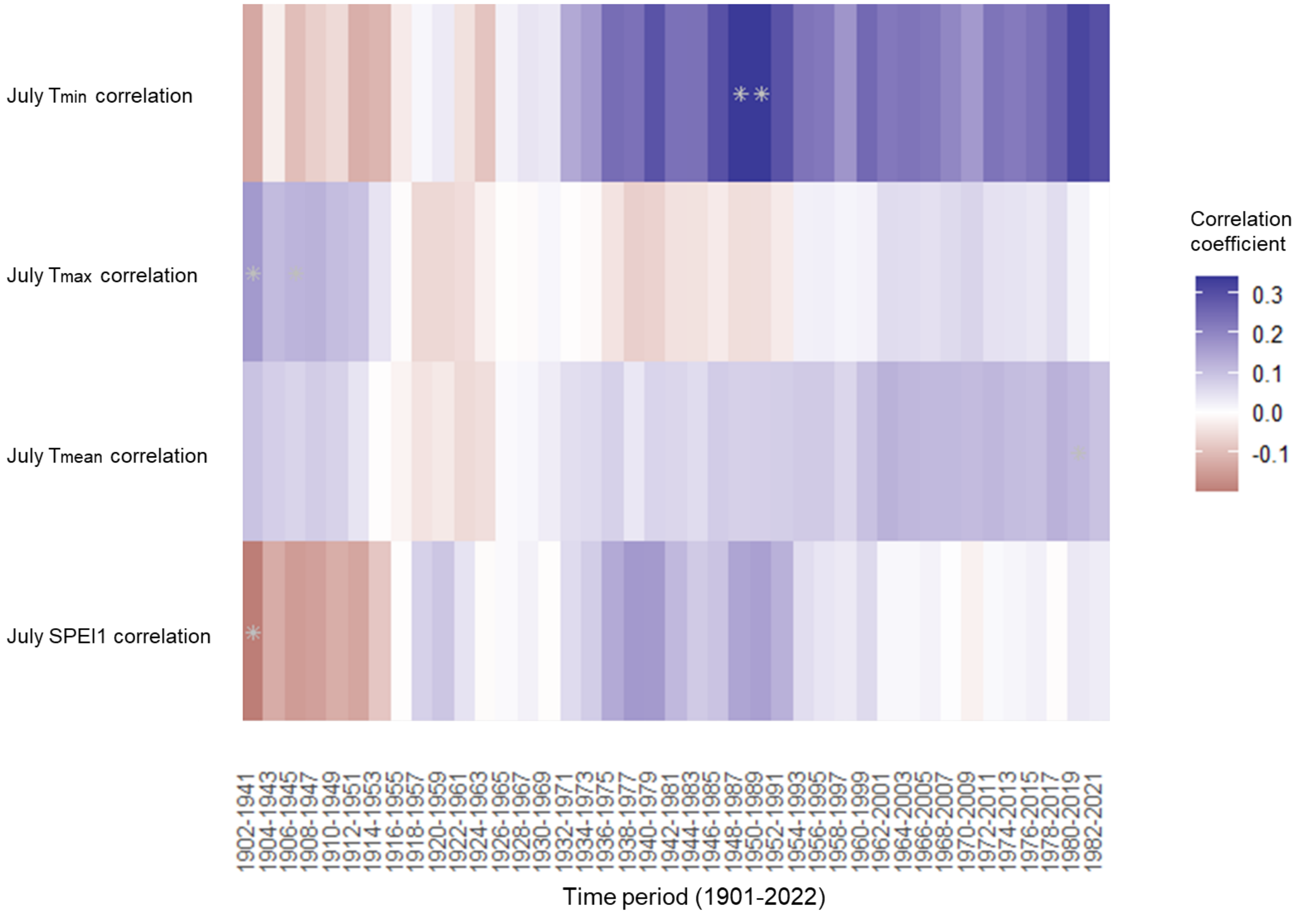

Fig. 5. Temporal stability of maximum, mean, and minimum temperature and SPEI1 for July effect on tree-ring growth of whitebark pine during the period 1901-2022, using the moving correlation function with a 40-year time window offset by two years. Stars indicate significance ($p < 0.05$).

DISCUSSION

Fire history

In this study we sought to characterize wildfire activity in a whitebark pine ecosystem in Glacier National Park. Previous research indicates that wildfires are generally infrequent in these settings (Johnson et al. 1990), however, our findings may indicate a history of more frequent wildfire activity. Fires recorded in 1800, 1855, 1930 and 1937 (Table 1), were recorded in multiple samples or corroborated by scientific sources (Johnson et al. 1990). The remainder of the fires we identified (Table 1), were recorded in a single sample, which is not ideal in fire history studies and, therefore, these fire events should be interpreted carefully. Nonetheless, our study recorded more fire events at our study site than was expected, given that the earlier study by Johnson et al. 1990 found fire return intervals of 110 years in Glacier National Park. This is an important insight when considering the heterogeneity of mountain forest landscapes and the role of whitebark pine-dominated ecosystems in this patchwork.

Sources of fire ignitions could have occurred from three sources: the Canadian Pacific Railroad (only after its construction in 1886; railway located ~ 4 km across the valley from the study site; Fig. 1), lightning, and Indigenous fire stewardship. First, numerous fires ignited during the period of railway construction (1882-1886) in Glacier National Park (Johnson et al. 1990) were not recorded in our samples. Thus, we consider the railway to have had minimal impacts on our fire history. The exception to this would be the 1937 lightning caused fire that was recorded in four samples. Although not corroborated by historical sources, it is plausible this was a railway ignited fire event. Second, over the past ~150 years, 86 known wildfires have been recorded in Glacier National Park, and of those events, 82 were ignited by lightning (Johnson et al. 1990; Natural Resource Canada 2024). Considering the dominance of documented lightning-documented wildfires overs the past ~150 years, the fire events we identified were likely also lightning ignited. Lastly, we did not find colonial records of Indigenous burning or fire stewardship for this site. Indigenous burning was widely practiced throughout BC (Hoffman et al. 2017; Hoffman et al. 2021), and although we do not possess observations (colonial or from Indigenous sources), further investigation will be supported if local Nations desire.

Anecdotally, all of the fire scar samples taken were from dead trees. Blue-stain fungus, commonly found in association with mountain pine beetle disturbances (Wong and Daniels 2017), was identified on our fire scar samples. This observation likely indicates that mountain pine beetle disturbance killed most of our sampled fire-scarred whitebark pine trees. Of the samples where we detected signs of blue stain fungus (n=6), the outermost rings were ~ 1985. These observations coincide with historical reports of mountain pine beetle outbreaks in Glacier National Park which peaked in 1995 (Parks Canada 2024), as well as mountain pine beetle activity which peaked in the 1970's in Waterton Lakes National Park (Wong and Daniels 2017). These findings further underscore the complexity of biotic and abiotic disturbances facing whitebark pine trees at our study site.

Response to climate

The growth of whitebark pine at our study site was significantly related to climate. Significant positive association between tree growth and temperature, and negative associations with precipitation and SPEI1, in the growing season, suggest that whitebark pine trees at the study site experience the most growth during warm and dry summer conditions (Fig. 4). These findings were consistent with other tree-ring studies of whitebark pine trees and climate-tree growth associations in the region (Youngblut and Luckman 2013). However, other regional tree-ring studies of whitebark pine trees and climate-growth relationships reported opposing findings (Wong and Daniels 2017). In the study by Wong and Daniels (2017) conducted in Waterton Lakes National Park, Alberta, an oscillating relationship with temperature is reported. Their findings report significantly positive correlations with warm summer temperatures (June-August) from 1900-1940, before shifting to a negative correlation with warm, dry summer conditions from 1940-1970, and then shifting again to a positive correlation with warm summer temperatures. By contrast, our findings found the strongest, positive relationship between minimum temperature and whitebark pine growth from 1940-1970 (Fig. 5). The variation of positive/negative relationships between tree growth and temperature that Wong and Daniels reported (2017) were attributed to the phases of the Pacific Decadal Oscillation (PDO) over the interval of 1900-2010. The only variable relationship with tree growth that our study observed was a shifting relationship between minimum temperature and tree growth detected from our moving window analysis (Fig. 5). Our findings reported a negative relationship between minimum temperature and tree growth in the early 1900’s before shifting to a positive relationship with the most significant and positive period between 1940-1970 (Fig. 5). Our findings lend support to the conclusions drawn from other regional studies that the relationship of whitebark pine trees to climate parameters may be modulated by site-specific conditions (Carlson et al. 2018; Murray and Siderius 2018; Wong and Daniels 2017; Youngblut and Luckman 2013).

CONCLUSION

Understanding the relationships between historical climate and whitebark pine trees can provide a historical baseline for climate in these regions and provide a point of comparison for the response of whitebark pine trees to future climatic conditions. Additionally, information on historical wildfire activity in whitebark pine habitats is not only important to understanding how to use prescribed burns effectively in these locations by agencies such as Parks Canada, but will also provide an idea of how wildfire regimes are changing with increased wildfire activity. Our findings present the potential of using whitebark pine trees for recording wildfires in high-elevations environments, and highlight drawbacks (e.g., instability in climate-growth relationships over time) to potentially using whitebark pine in tree-ring based reconstructions of climate variability. Although more research is needed to fully understand how future climate may impact the growth of whitebark pine trees and how wildfires may affect these regions, the findings from our study provide baseline ecological knowledge that can support the management of these important species in western Canada.

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CHAPTER 3: Short-interval reburns lead to shifts in species composition in a high-elevation forest, British Columbia, Canada

ABSTRACT

More frequent wildfire ignitions, increased drought conditions, and historical forest management practices are leading to shorter intervals between fire events (e.g., < 30 years) in some forest ecosystems. When these short-interval reburns occur in high-elevation forest ecosystems that are adapted to infrequent and stand-replacing wildfires, impacts on vegetation regeneration can lead to ecological changes in forests such as reduced tree densities, shifts in community composition, and in some cases regeneration failure. The goal of this study is to characterize forest regeneration at a high-elevation forest site affected by a single wildfire (2017) and a short-interval reburn (1992 and 2017). Our results indicate that successive wildfires (i.e., short-interval reburns) variably impact regenerating tree and understory diversity and lead to species-specific reductions in regenerating tree counts (seedlings and saplings) and understory plant cover. Pre-fire composition remained unchanged after a single wildfire; however, forest composition of young trees and understory plants differed in regions impacted by a short-interval reburn. In regions that experienced the greatest disturbance (e.g., high severity wildfire followed by high severity wildfire) little to no pre-fire coniferous species were found, however, an increased presence of pioneer species such as lodgepole pine (*Pinus contorta*) and deciduous species was detected. Although the forests we studied are still in early stages of post-fire regeneration, these early shifts in canopy and understory composition may persist if short-interval reburns continue to occur.

Keywords: British Columbia, Canada, climate change, drought, forest regeneration, Glacier National Park, high-elevation forest, short-interval reburns, wildfire.

BACKGROUND

Wildfires are important disturbance agents that shape ecosystem heterogeneity, alter vegetation composition and structure, and for some forest types, increase the resiliency of forests to future wildfires (Buma et al. 2022; Hoecker and Turner 2022; Stevens-Rumann and Morgan 2016; Turner et al. 2019). However, past fire suppression practices and increasing drying trends driven by climate change (Coogan et al. 2021; Ellis et al. 2021; Littell et al. 2009; Marlon et al. 2012; Stephens et al. 2014), are elevating extreme wildfire activity and increasing wildfire frequency (Parisien et al. 2023: Wotton et al. 2017). This increase in wildfire activity can lead to short-interval reburns (i.e., successive wildfires occurring less than ~ 30 years apart) where fuel-driven controls are overwhelmed by extreme burning conditions (Buma et al. 2022; Parks et al. 2017; Whitman et al. 2019). In forests adapted to infrequent high-severity wildfires (e.g., high-elevation coniferous forests), accelerating trends of wildfire frequency and severity are shifting forests outside of their historical wildfire regime (Buma et al. 2022; Hanes et al. 2019; Harvey et al. 2016; Turner et al. 2016). Although projections indicate increases in the size and frequency of wildfires (Parisien et al. 2023; Whitman et al. 2019; Wotton et al. 2017), it remains unclear how these changes will impact forest regeneration (Coop et al. 2020; Weber et al. 2022).

Stand-replacing wildfires in old-growth coniferous forests can burn through deep organic layers in the forest floor and reduce soil and aerial seed banks (Buma et al. 2022; Gill et al. 2020; Hayes and Buma 2021; Nathan et al. 2022; Whitman et al. 2019). Compared to mature, old-growth stands, coniferous trees in recently burned forests have less than a quarter of the available seeds per meter squared, lowered dispersal distance from a tree (especially if they are small in height) and offer inadequate seed delivery from forest edge (concentrated within 10 m from living forest) (Buma et al. 2022; Gill et al. 2020; Nathan et al. 2022; Turner et al. 2019). Reburns that impact regenerating trees, before they’ve reached maturity, can deplete already reduced soil and aerial seed propagules even further and drive forest regeneration to rely entirely from seed dispersal from living forest edges, where continuous unburned forest may be further away (Gill et al. 2022; Nathan et al. 2022; Whitman et al. 2019). High-severity fires, and especially high-severity short-interval reburns create large patches of severely burned landscapes, increasing landscape homogeneity (Harvey et al. 2023). Forests converted to homogenous burn patches, can alter the behavior of animal dispersers in caching and dispersal of propagules, reshaping previous regeneration pathways (Gill et al. 2022; Nathan et al. 2022). Collectively, these effects of short-interval reburns on seeds, seed banks, and dispersal may alter forest structure, create landscape homogeneity, and change regeneration pathways (Gill et al. 2022; Gill et al. 2020; Nathan et al. 2022; Stevens-Rumann and Morgan 2016; Turner et al. 2019).

The short-term effects of reburns are not yet fully described, but can include delayed forest regeneration, changes to early forest composition, and/or forests converting to other ecosystems (Buma et al. 2022; Moritz et al. 2012; Stevens-Rumann and Morgan 2016; Stevens-Rumann et al. 2022). Landscapes affected by a short-interval reburn are not hospitable for regenerating seedlings/saplings from more shade tolerant species of firs, spruces, and pines (Hoecker et al. 2020). Drought conditions favor the disturbance-resilient plant traits that seral and early pioneer species possess (Rowe 1983). Fast regeneration of certain poplar species and lodgepole pine (*Pinus contorta*) can be found in early stands after a short-interval reburn occurs, quickly outcompeting tree species that previously dominated high-elevation forests such as subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmannii*), and whitebark pine (*Pinus albicaulis*) (Rowe 1983). In the face of warmer and drier microsite conditions and increased drought stress driven by climate change (Coop et al. 2020; Parisien et al. 2023), reburned landscapes can host lowered species richness if more shade tolerant species are unable to survive these changing conditions (Hoecker et al. 2020; Hoecker and Turner 2022; Whitman et al. 2019). Although high-elevation coniferous species in the western cordillera are adapted to infrequent stand-replacing wildfires (Hoecker et al. 2020; Stevens-Rumann and Morgan 2016; Turner et al. 2019), shorter intervals between fire events (e.g., < 30 years) may reduce conifer densities more than deciduous species (Buma et al. 2022). Species-specific resiliencies to recurring wildfire may bias regeneration and shift canopy composition or richness in the short-term, but have long-lasting ecological consequences (Buma et al. 2022; Coop et al. 2020; Hayes and Buma 2021; Stevens-Rumann et al. 2022). Additionally, early and severe changes to both coniferous forest structure and composition may have longer lasting ecological effects on ecosystem services including carbon storage, hydrology, and aesthetics (Turner et al. 1994; van Wagtendok et al. 2012; Westerling et al. 2011).

Most studies on the effects of wildfires on forest regeneration focus on trees with few studies in western North America reporting on the effects of wildfires on understory plant communities (Dawe et al. 2022; Dickson-Hoyle 2024; Hart and Chen 2007). Even fewer studies investigate the impacts of short-interval reburns on understory vegetation (Hoecker et al. 2020; Kiel et al. 2023; Whitman et al. 2019). The understory plant community plays an important role in the forest ecosystem and can support the stability and resiliency of trees and forest dynamics (Dickson-Hoyle 2024; Hart and Chen 2007; Kiel et al. 2023). Post-fire regeneration in the understory is often driven by the presence of seed propagules and rhizomes, plant growth characteristics (Dawe et al. 2022; Rowe 1983), and climatic conditions (Kiel et al. 2023). Similar to tree species, short-interval reburns not only reduce the availability of seed sources for many canopy species, but also burn through organic material in the soil where rhizomes and seed propagules for understory plants are found, impacting recovery for both canopy and understory (Kiel et al. 2023; Turner et al. 2019). Homogenous patches of burned forested landscapes can further exacerbate regeneration conditions for understory plants with the absence of canopy species that can buffer temperature, moisture, and wind disturbances. High-elevation coniferous forests that experience a short-interval reburn offer disturbance conditions that favor rapid colonizers or plants with surviving rhizomes. Colonizing plants may readily outcompete reduced populations of local vegetation and shift early post-fire species composition in the understory (Kiel et al. 2023) or result in lowered species richness. While studies describing the impacts of short-interval reburns on forest canopy exist in the literature (e.g., Agne et al. 2023; Gill et al. 2022; Hansen et al. 2018; Hayes and Buma 2021; Hoecker and Turner 2022; Kemp et al. 2016; Saberi and Harvey 2023; Prichard et al. 2017; Stevens-Rumann et al. 2022; Turner et al. 2019; Whitman et al. 2019), how these impacts will specifically affect both high-elevation forest canopy and understory story species in ESSF forests of interior British Columbia (BC) is not yet described.

In this study, we examined how a short-interval reburn influences forest regeneration at a high-elevation site in the Beaver Valley, Glacier National Park, Canada. We surveyed young (regenerating) tree counts, understory plant percent cover, and species presence across a forest affected by a single wildfire (2017) and areas affected by two wildfires (1992 and 2017, a short-interval reburn). Specifically, we aimed to determine: (1) if a short-interval reburn will affect the counts of young trees and understory plant percent cover and species richness compared to a single wildfire, and (2) if burn severity (from a single wildfire) and varying combinations of burn severities (from a short-interval reburn) affect young tree counts and understory plant percent cover or richness differently. We hypothesized that counts of young trees and understory plants will be reduced in regions affected by a short-interval reburn due to the increased combustion of the aerial and soil seed bank, resulting in decreased seedling recruitment and lowered species richness (Gill et al. 2020; Stevens-Rumann et al. 2022; Turner et al. 2019; Whitman et al. 2019). High-severity wildfires will burn forest canopy, consume understory plants, and burn deeper into surface organic layers (Gill et al. 2022; Stevens-Rumann and Morgan 2016), therefore the combined effects of one high-severity wildfire followed by another moderate or high severity wildfire will result in lowered plant richness, percent cover, and reduced counts of young and mature trees compared to plots that experience a low-severity wildfire followed by another low-severity wildfire.

METHODS

For this study, high-elevation forests (1,300-2,200 m asl) are described as occurring primarily in the Engelmann Spruce-Subalpine Fir (ESSF) biogeoclimatic (BEC) ecosystem classification zone, with lower elevation range limits transitioning into the Interior Cedar Hemlock (ICH) zone. At the upper range limits (~1,900-2,200 m asl), high-elevation forests are commonly composed of subalpine fir, Engelmann spruce, and whitebark pine (*Pinus albicaulis*). At the lower range limits (~1,300-1,900 m asl) forests are largely composed of Engelmann spruce and subalpine fir. Subalpine fir dominates forest community composition at upper range limits, while Engelmann spruce dominates canopy at lower range limits. A common minor species in most regions of ESSF is lodgepole pine, found primarily in early seral stands following wildfires or on drier sites (Buma et al. 2022; Gill et al. 2020; Nathan et al. 2022).

The study site is located in Glacier National Park, BC, Canada (Fig. 1). The Park is located in the Selkirk and Purcell Mountain ranges in east-central BC about 46 km east of Revelstoke, and covers 1,349 km^2 in area, the largest national park in BC. Wildfires in the Park are often left to burn without suppression and are not replanted following wildfire. The study site is in the northeast corner of the park boundary, located in the Prairie Hill Mountain range of the Beaver Valley and includes two wildfires that burned in 1992 (211 ha) and 2017 (3,111 ha). The first wildfire was caused by lightning on June 26th, 1992. The second wildfire was also caused by lightning on July 10th, 2017, and burned for two months before it was extinguished naturally by precipitation. This study site was selected because it includes two wildfires with a large area of reburn (~100 ha), that reburned within a short-interval (25 years), and two wildfires that burned at varying levels and combinations of severity (e.g., low severity wildfire followed by low severity wildfire, high severity wildfire followed by low severity wildfire, etc.).

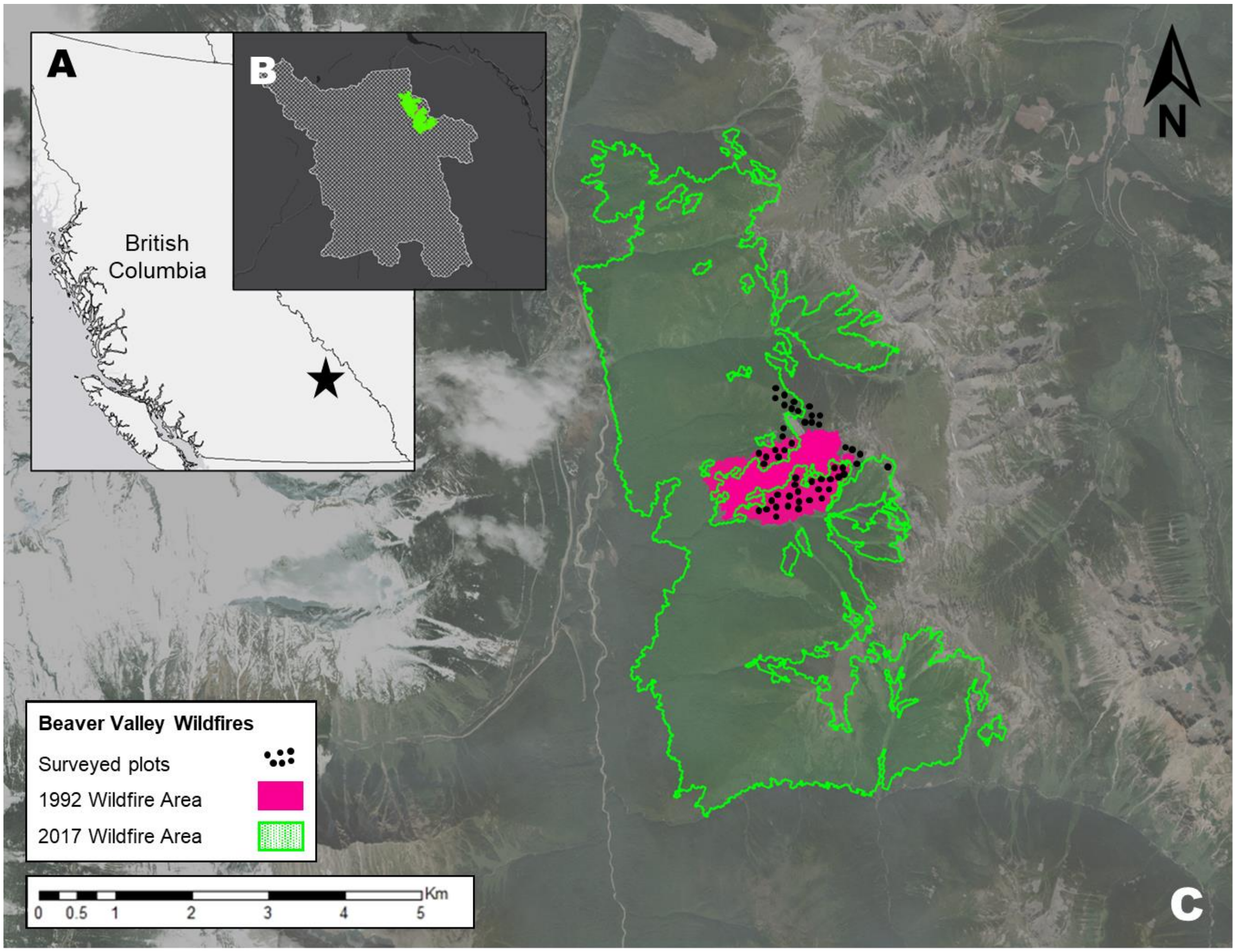

Fig. 1. "A" (top left): The study site (star on inset map) in Glacier National Park, British Columbia, Canada. "B": The national park boundary and 2017 wildfire (green). "C": The 1992 wildfire (pink shaded area) and the 2017 wildfire (green outlined area). Surveyed plots are marked by black circles.

We used a measure of severity called the Relativized delta Normalized Burn Ratio (RdNBR) with offset, defined as a ratio to assess changes in reflectance of healthy vegetation, soils, and soil moisture from a wildfire relative to pre-fire conditions and interannual variation (Key and Benson 2006; Whitman et al. 2020), as a basis for subsite selection. RdNBR burn severity layers were derived for both wildfires using satellite imagery from Landsat 9 collection 2 at 30 m spatial resolution and following Parks et al.'s (2018) methods in Google Earth Engine (Appendix Table 2). We converted continuous RdNBR values into categorical variables of unburned, low, moderate, and high using a threshold established by Key and Benson (2006). Due to the minimal area of high severity followed by high severity reburn (area < 30 m^2), we adjusted the thresholds to group low with moderate-low, and high with moderate-high (Stevens-Rumann and Morgan 2016); we refer to both hereafter as low or high severity. We also ensured that subsites from the low or high categories had significantly different RdNBR values. We selected seven subsites: two subsites affected by a single wildfire in 2017, at either low or high severity, four subsites affected by both wildfires (e.g., 1992 low severity followed by 2017 high severity, 1992 high severity followed by 2017 high severity, etc.), and lastly a single subsite affected by no known records of wildfires in the last ~150 years (Fig. 2 and Table 1). All subsites are located on south to southwest-facing slopes and across an elevational range of 1,700-2,200 m asl and do not have a history of human (settler) disturbance. Plots for each subsite were selected using stratified random sampling methods in ArcGISPro. Vegetation surveys of plots were collected over two field seasons in 2022 and 2023 between mid-July to early August, four to six weeks after snowmelt. Between 7-16 plots were sampled in each of the subsite types (Table 1), for a total of 75 plots surveyed.

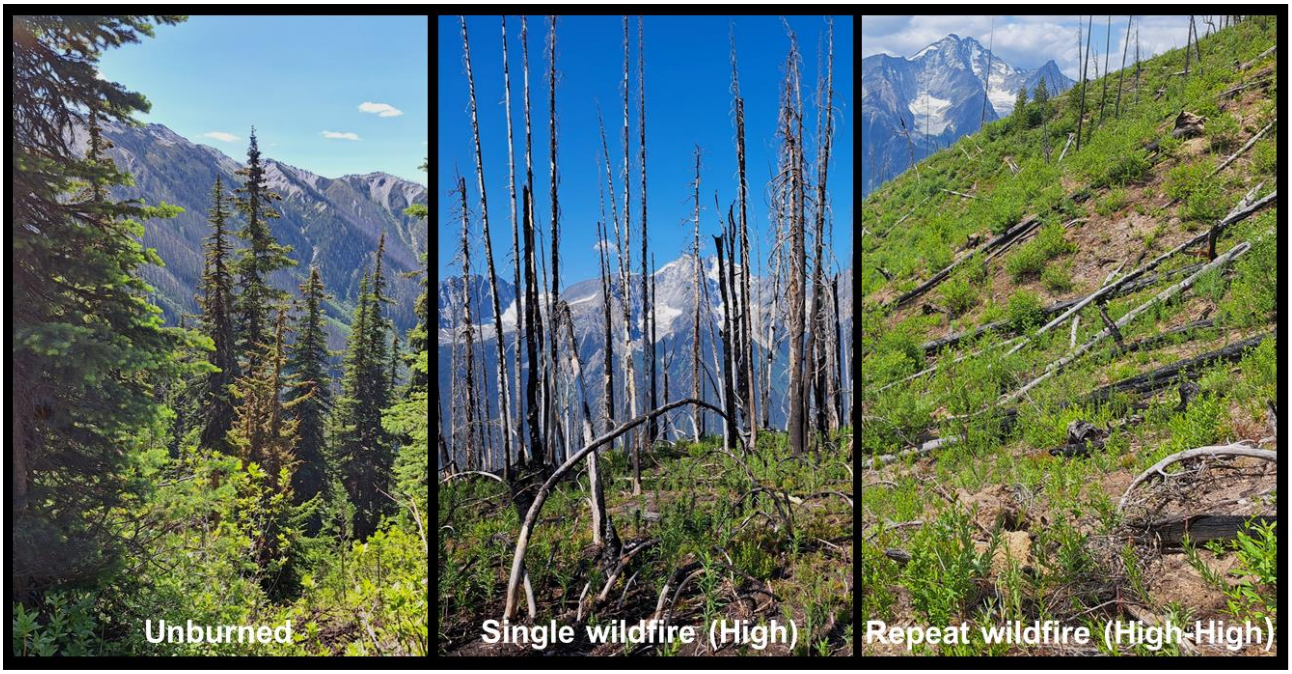

Fig. 2. Subsites in the Englemann Spruce-Subalpine Fir biogeoclimatic zone, dominated by subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmanni*), and whitebark pine (*Pinus albicaulis*). Left: unburned subsite that did not experience any wildfires in the last ~150 years. Middle: high severity subsite that experienced a single high severity wildfire (2017). Right: subsite affected by a short-interval reburn at high severity in 1992 and high severity in 2017. Photo credit: Natalie Maslowski.

Table 1. Summary of environmental characteristics for each subsite.

Subsite type	Burned in 1992	Burned in 2017	Total plots surveyed	Mean elevation (m)	Mean aspect	Mean slope angle (◦)	Mean seed source distance (m)	Mean 1992 RdNBR value	Mean 2017 RdNBR value
Unburned	No	No	10	2070	W	21	1	0	0
Low	No	Yes	7	1951	W	21	20	0	326
High	No	Yes	16	2001	SW	26	58	0	743
Low-Low	Yes	Yes	12	1878	SE	35	41	301	341
Low-High	Yes	Yes	10	1759	S	34	201	200	711
High-Low	Yes	Yes	11	1796	S	35	84	880	356
High-High	Yes	Yes	9	1674	S	38	99	895	565

Field methods

Vegetation surveys within each plot included subplots to survey trees and understory plants (Fig. 3). Surveys of young trees (regenerating seedlings and saplings) took place in the smallest circular subplots (3.99 m radius) located 15 m from plot center in each cardinal direction, and at plot center (Fig. 3). Young trees were tallied by species, status as living or dead, and size. The size classes used included: seedlings (height ≤ 30 cm) and saplings (30 cm < height ≤ 130 cm). To assess pre-fire forest structure, small and large trees were recorded in the unburned subsite. For small trees (height > 1.3 m, but diameter at breast height (DBH) ≤ 12.5 cm), plot radius depended on tree density. To sample small trees a subplot with a radius of 5.64 m (A subplot) was used, but if tree density was high (> 20 trees), then a subplot with a radius of 3.99 m (C subplot) was used (Fig. 3). For each small tree, species, height, DBH, and status as living or dead were recorded. To sample large trees (DBH > 12.5 cm) a subplot with a radius of 11.28 m (B subplot) (Fig. 3) was used. For each large tree, species (if possible), height, DBH, and status as living or dead were recorded. To assess understory plant composition, a 1 m x 1 m quadrat was randomly placed inside each of the C subplots (Fig. 3). Inside each quadrat, species percent cover for each shrub and vascular plant, and a general percent cover for bryophytes and lichen was recorded (Appendix Fig. 2).

Environmental data was also recorded at each plot. This included aspect, elevation, and slope angle. Seed source distance was measured for each plot using GIS software between the centers of each plot and the closest edge of continuous unburned forest (Kemp et al. 2016) (Appendix Table 8).

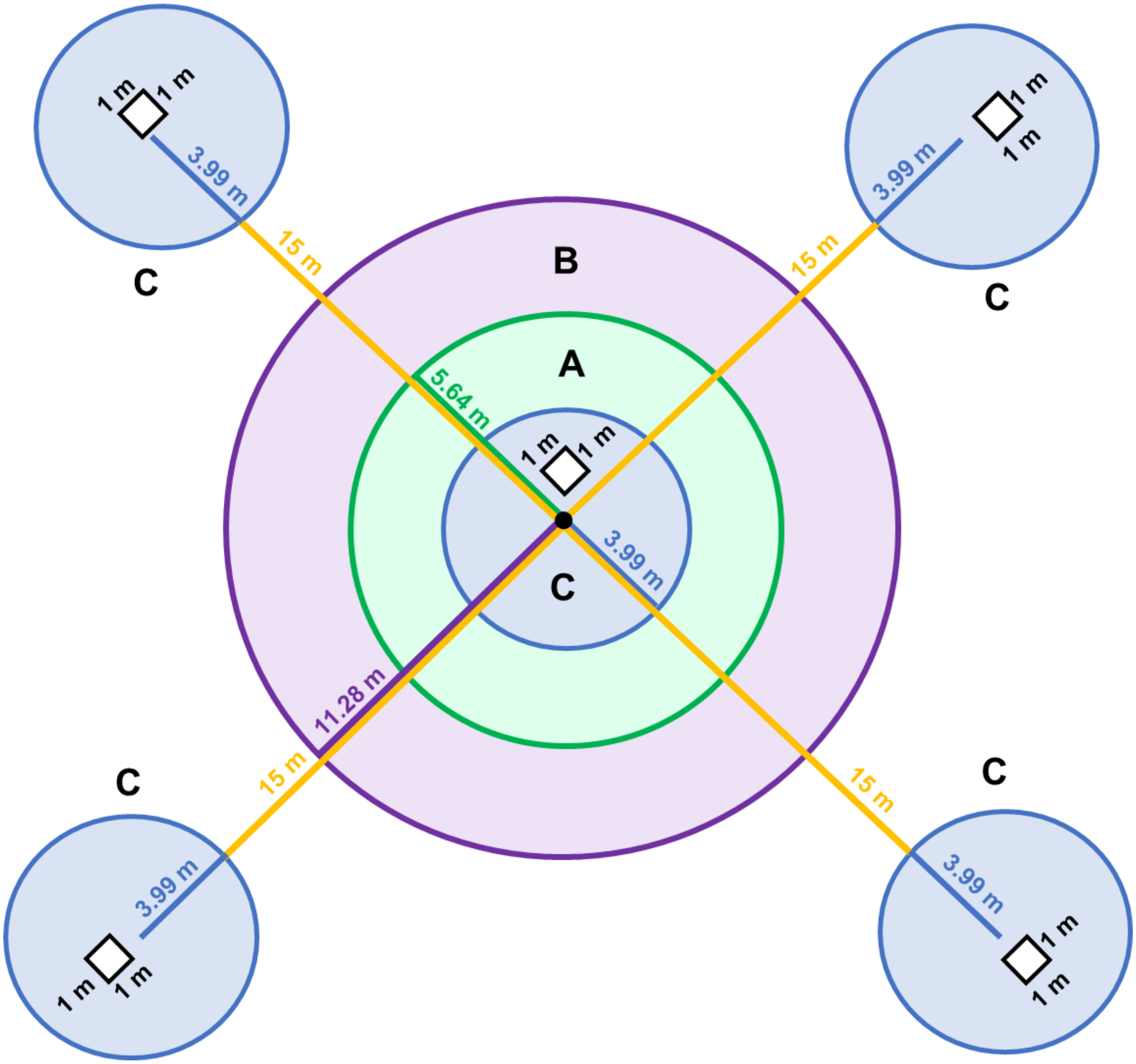

Fig. 3. Plot design to assess vegetation measurements of under- and overstorey species at the plot level. Circular subplots in blue (subplot C; *r* = 3.99 m) were used to assess species measurements of young trees < 130 cm in height. Within each circular subplot, a quadrat (1 m x 1 m) was used to assess understory species measurements. Circular subplots in green (subplot A; *r* = 5.64 m) were used to assess species measurements of small trees with height > 130 cm, and DBH <12.5 cm where tree density is n < 15-20, and circular subplots in purple (subplot B; *r* = 11.28 m) were used to assess species measurements of large trees with DBH >12.5 cm.

Statistical analyses

To visually assess differences in young trees (all trees < 130 cm in height) and understory plant composition between different subsite types (beta diversity), we performed non-metric multidimensional scaling (NMDS) using counts (young trees) or percent cover (understory) data using the R package *vegan* (Oksanen et al. 2022) and the Jaccard similarity index. A three-dimensional solution was selected by plotting stress against the number of dimensions to optimize dimensionality and model fit. For both young trees and understory, a Wisconsin double standardization transformation was performed, after which distance was calculated using the Jaccard similarity metric. The NMDS converged after 42 iterations with a stress of 0.121 for young trees; after 112 iterations with a stress of 0.174 for understory plants. Species scores were added to the final solution as weighted averages. We added gradient colors to visualize groupings by subsite type. We compared community composition among subsite types (unburned, low, high, low-low, low-high, high-low, and high, high) using a permutational multivariate analysis of variance using a pairwise adonis test with Jaccard similarity distance and 999 permutations using the package *pairwiseAdonis* (Martinez-Arbizu 2020).

The number of species detected at each plot is defined as species richness. Alpha diversity of the plots was assessed using species richness. To compare overall richness of young trees within each subsite type (alpha diversity), we used a hurdle model. The species richness data (young trees) had a high proportion of zeroes, which left the distribution strongly left-skewed (Zuur et al. 2009; Zuur et al. 2012). Following the procedures outlined by Zuur et al. (2009) for discrete and zero inflated data, we tried a square root transformation on the data, but this did not improve linearity or homogeneity of variance, as well as alternative generalized linear models. Considering the type of zeroes in our data, and the objective of our analysis, the hurdle model was considered the most appropriate model approach. The hurdle model uses a two-step modeling approach to examine richness of young trees as a function of three categories of predictor variables: subsite type (e.g., burn severity and burn severity combination), biotic environmental variables (distance to live seed source), and abiotic environmental variables (e.g., elevation, aspect, and slope). The first step of the hurdle model involves a logistic regression model to predict young tree presence or absence. The second step then uses a Poisson family distribution model to predict young tree richness. Predictor variables were compared to evaluate which one significantly influenced young tree presence or absence and species richness. Model fit was assessed visually by plotting the Pearson's residuals against the fitted values (Zuur et al. 2009; Zuur et al. 2012). Further, we also plotted residuals on a histogram to assess distribution and assessed model fit using a (hanging) rootogram plot using the package *countreg* (Kleiber and Zeileis 2016; Tukey 1977). Lastly, for the Poisson distribution portion of the hurdle model, a Tukey test was used to perform a post-hoc analysis using the package *emmeans*. Analyses were completed using the package *pscl* (Zeileis et al. 2008; Jackman 2012) for the hurdle model.

Predictor variables were compared to evaluate which one significantly influenced understory species richness. To assess overall species richness of understory plants within each subsite, a generalized linear model was selected because the data did not display any significant overdispersion of zeros. Predictor variables included three categories: subsite type, and biotic and abiotic environmental variables. A Tukey test was used for a post-hoc analysis using the package *emmeans*. Further, we also plotted residuals on a histogram to assess distribution and assessed model fit using a (hanging) rootogram plot using the package *countreg* (Kleiber and Zeileis 2016; Tukey 1977). All statistical analyses were conducted in R version 4.1.2 (R Core Team 2024) with $\alpha = 0.05$.

RESULTS

Young trees

The counts of young trees varied depending on subsite type, where the highest density of stems (counts) per plot was reported in the subsite affected by one low severity wildfire followed by the unburned subsite and the lowest density of young trees was reported in the low-high reburn subsite (Table 2). Short-interval reburns demonstrated more severe effects on the presence of young trees, except for where the study site experienced a single high severity wildfire, where abundance of young trees in this subsite were similar to those regions affected by a reburn (Table 2).

Table 2. Total counts (stems) of all young trees for all plots were converted to stems per hectare for comparative analysis across subsite types.

Subsite type	**Young tree stems estimated per hectare**
Unburned	12,056
Low	15,228
High	1,110
Low-Low	8,346
Low-High	856
High-Low	5,716
High-High	1,110

Community composition of young tree species differed among subsite types (Fig. 4 and 5). Young tree species in the unburned, single low or high severity subsite were compromised of exclusively coniferous species such as subalpine fir, Engelmann spruce, and whitebark pine (in most cases this was the same for the low-low subsite) (Fig. 4). In subsites affected by a reburn (excluding the low-low subsite) young tree species consisted of largely lodgepole pine and deciduous tree species such as black cottonwood (*Populus trichocarpa*) and trembling aspen (*Populus tremuloides*) (Fig. 4). Only native species were found.

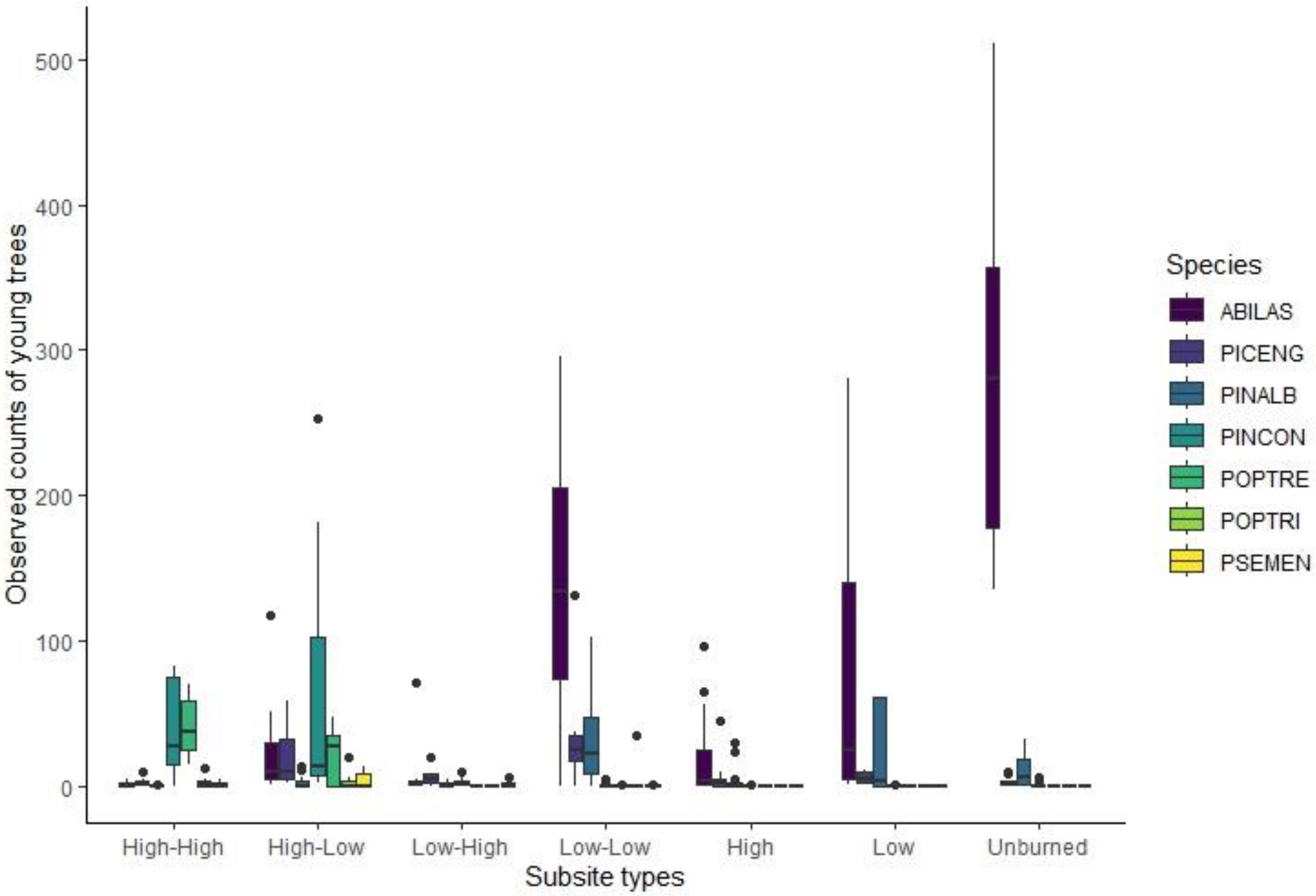

Fig. 4. Young tree counts per stem as a function of species and subsite type. Boxplots show the median, and whiskers represent the upper and lower interquartile range. Dots are considered outliers. Rare species that appeared only once in the data were removed (Poos and Jackson 2012). Species corresponding to abbreviated species codes can be found in Appendix Table 3.

A permanova analysis showed that among the predictor variables we tested (subsite type, seed distance, and environmental variables), subsite type and seed source distance significantly explained the variation in the richness data (Fig. 5). The effects of elevation, slope, and aspect class (e.g., north, northwest, west, southwest, etc.) did not significantly explain the variation in young tree species richness among subsites (Fig. 5). Using NMDS, visual assessments showed that community composition for subsites unaffected by wildfire (unburned), affected by only one wildfire (low or high), or subsites affected by two low severity wildfires had the most significantly similar species composition (Fig. 5 and Fig. 6). Community composition was most dissimilar between these subsites and the subsite affected by two high severity wildfires (Fig. 5

and Fig. 6). Visual assessments also showed that seed source distance followed similar groupings of subsites, where seed distance was highest for subsites affected by a reburn where at least one wildfire burned at high severity (Appendix Fig. 14; Appendix Table 8). Results from the PairwiseAdonis test showed that each subsite had significantly distinct community compositions from each other (Appendix Table 7).

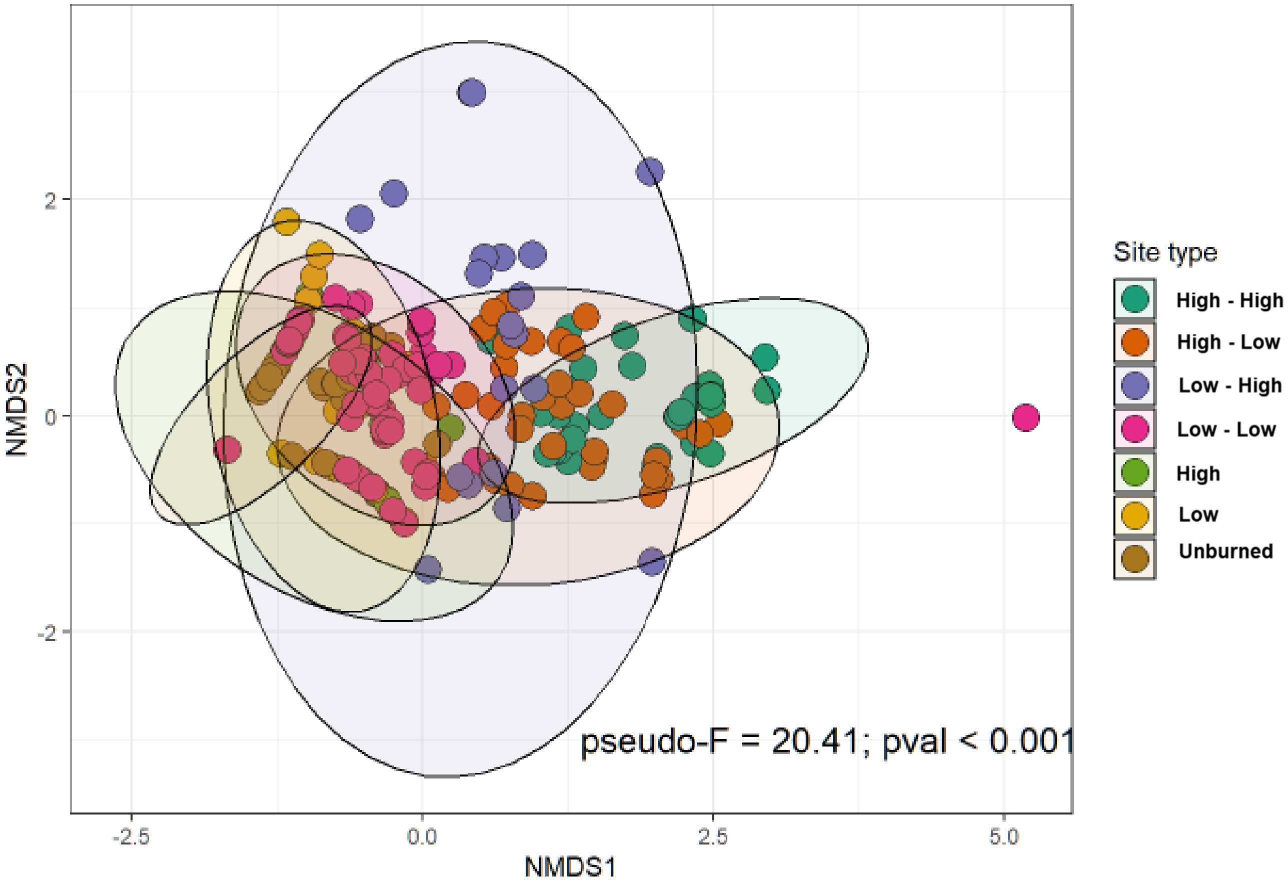

Fig. 5. Non-metric multidimensional scaling (NMDS) bi-plot of young tree composition data across the study site. Each point represents a single subplot (n=375) in a community composition space. Points closer to each other have more similar tree species composition than points farther apart. Points are colored by subsite type. Ellipses which are drawn at 95% confidence intervals are also colored by subsite type and indicate subsite composition similarity, where ellipses that are not overlapping show significantly dissimilar plant community compositions.

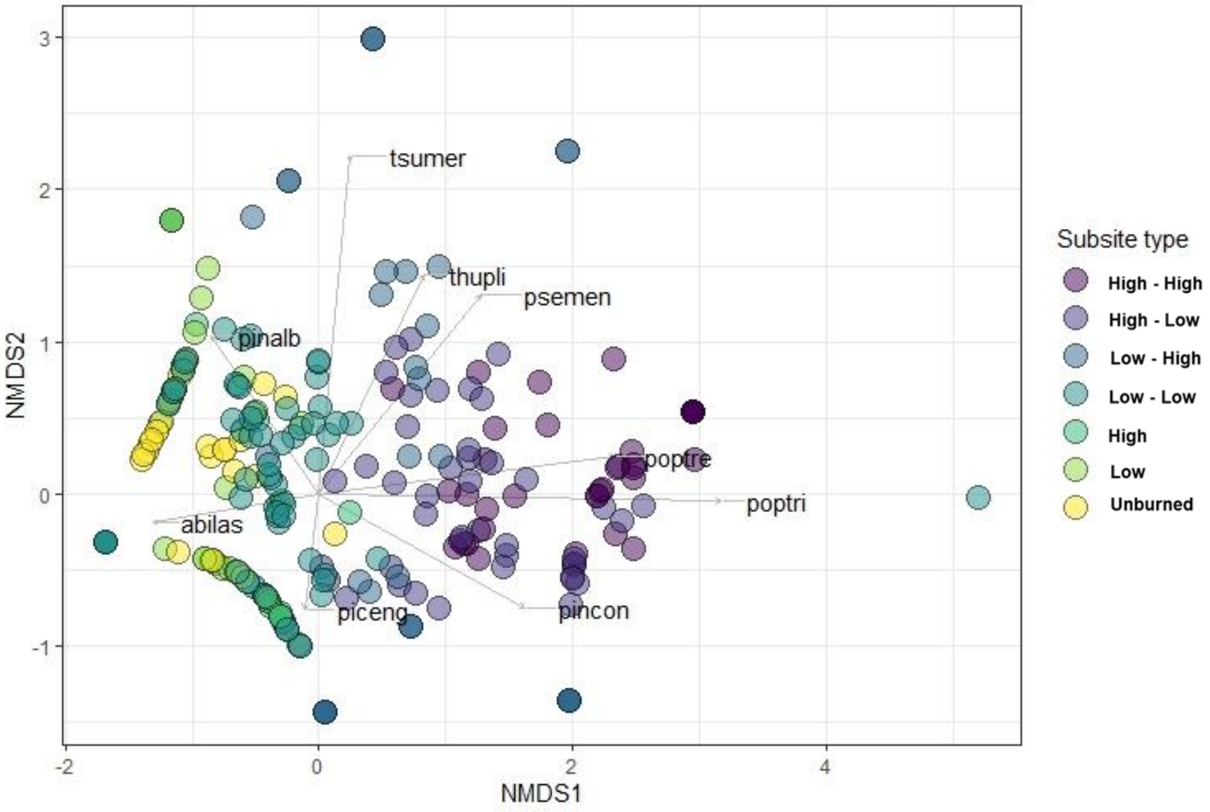

Fig. 6. Non-metric multidimensional scaling (NMDS) bi-plot of young tree composition data across the study site. Each point represents a single subplot (n=375) in a community composition space. Points closer to each other have more similar tree species composition than points farther apart. Points are colored by subsite type. Species corresponding to abbreviated species codes can be found in Appendix Table 3.

The hurdle model showed a significant relationship between the predictor variable subsite type and the species richness of young trees for both the Poisson and logistic regression steps of the hurdle model (Fig. 7 and Appendix Table 6). For the predictor variable seed distance, a significant relationship was found for only one of the two steps of the hurdle model (logistic regression) (Appendix Table 6). The hurdle model also showed slope angle as a significant predictor of tree species richness, but is not ecologically meaningful and was thus not considered further. Aspect did not significantly explain species richness and the hurdle model was unable to use elevation as a response variable because it could not reliably estimate the standard errors for some parameters.

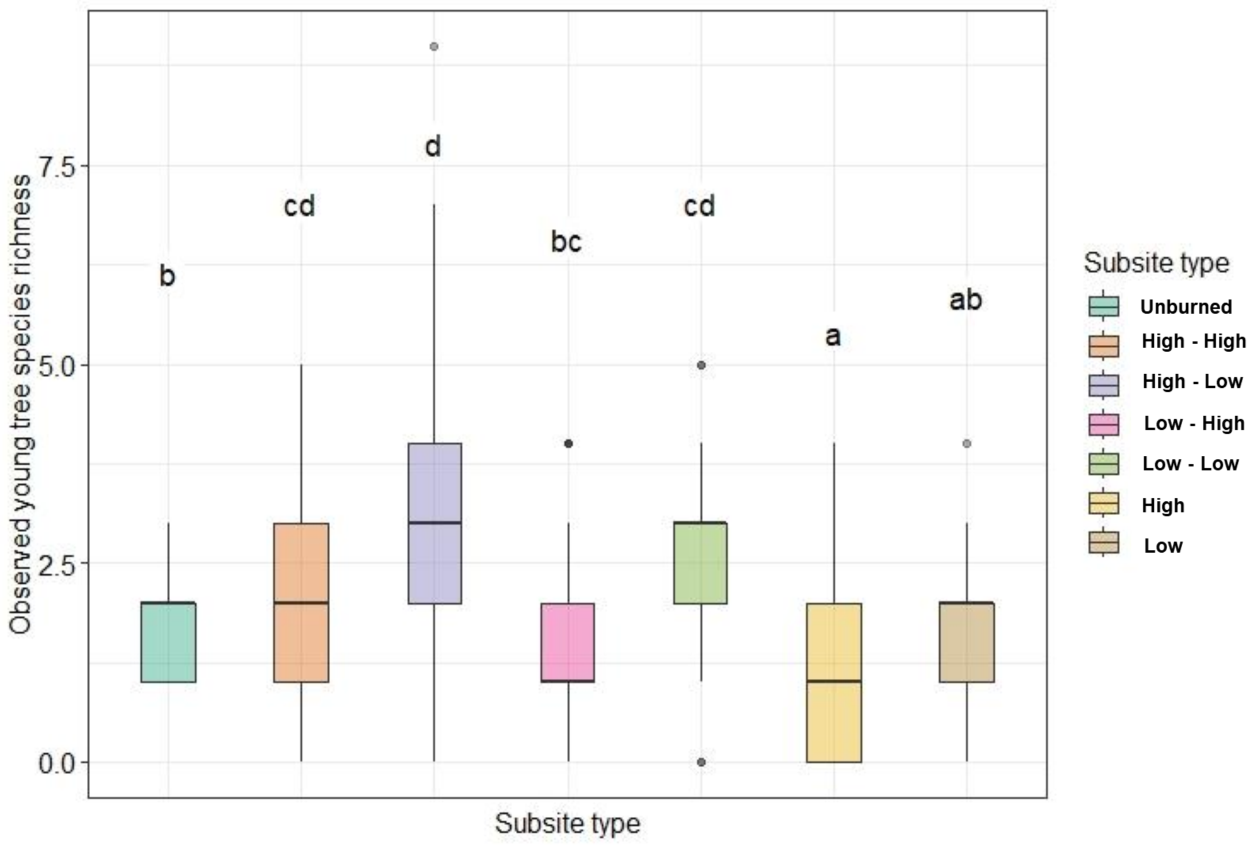

Fig. 7. Boxplot of observed young tree species richness across subsite types, where whiskers represent the upper and lower interquartile range and dots are considered outliers. A Tukey test (post-hoc analysis) was performed to determine differences in species richness: letters above each boxplot correspond to similarity in richness, where different letters represent significant dissimilarity.

Overall richness was highest in the subsite affected by a short-interval reburn (high-low) and lowest in the subsite affected by a single high severity wildfire (Fig. 7). Species richness differed among subsite types and demonstrated a variable relationship between richness and the number of wildfires (one or two) and their burn severity (high or low).

Understory plants

Total understory percent cover was highest in the single low severity subsite, and lowest in the subsite affected by a single high severity wildfire. Subsites affected by a short-interval reburn demonstrated overall lowered percent cover of understory species (Fig. 8). The only significant differences in cover were found between both the single low and the unburned subsite and the single high severity subsite. No other significant differences in cover were found.

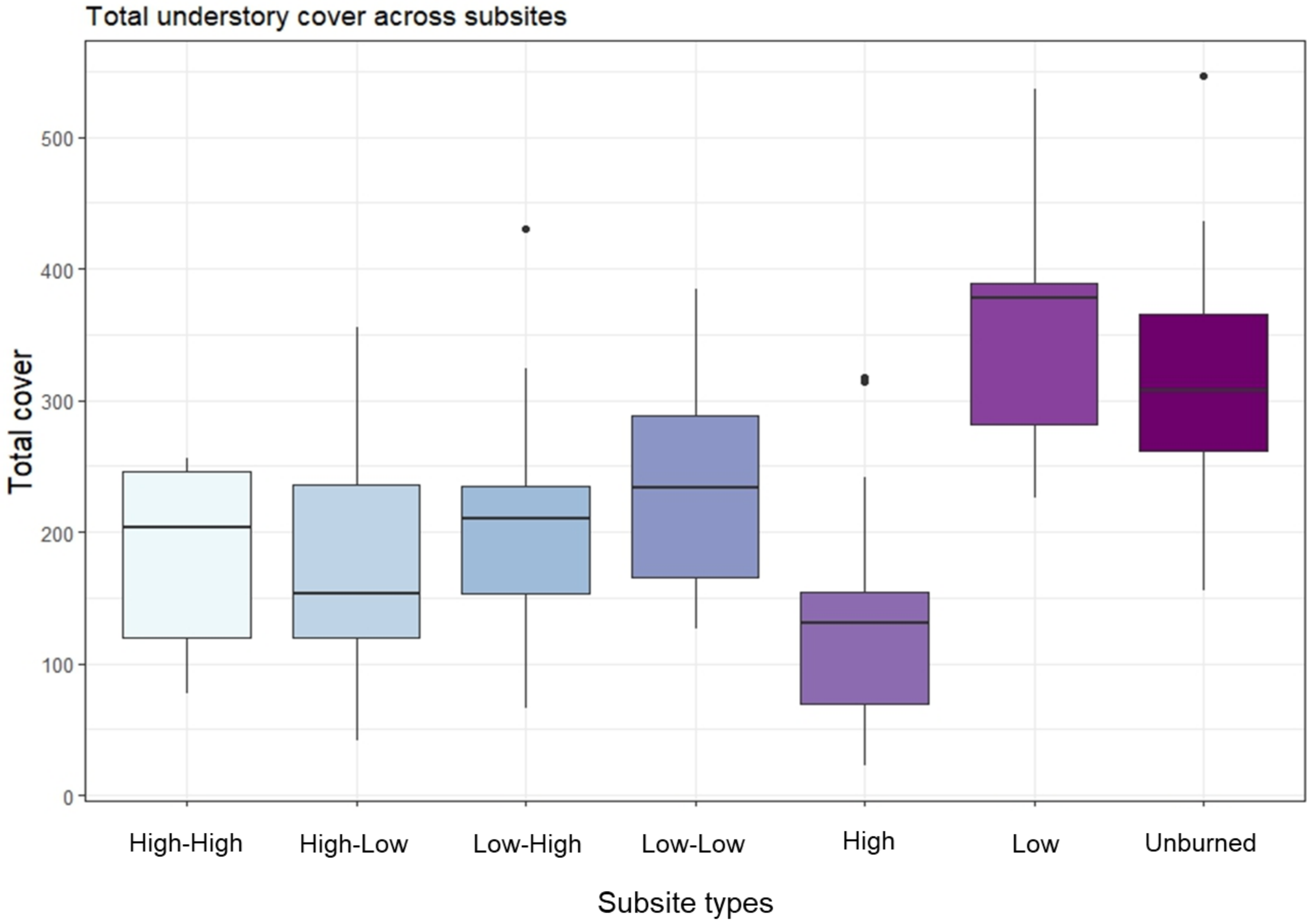

Fig. 8. Box plots depicting understory species total percent cover across subsite types. Subsites describe different ranges of fire severity combinations, from high-high to no previous fire in the last 50 years. Whiskers denote the distance to observations furthest from the nearest mean that are also within 1.5 x the inter-quartile range from the nearest quartile; and dots are observations further than the 1.5 x the inter-quartile range from the nearest quartile.

Understory plant species differed among subsite types (Fig. 9). Species that dominated in the unburned subsite also dominated the subsites affected by only one wildfire (low or high). Among the species that most dominated these regions were partridge foot (*Luetka pectinata*), white mountain heather (*Cassiope mertensiana*), and grouse whortle berry (*Vaccinium scoparium*) (Fig. 9). Other notable species were those that dominated the reburn subsites which included Salix spp., thimble berry (*Rubus parviflorum*), and alpine groundsel (*Packera pauciflora*) (Fig. 9). A permutation test showed that among the predictor variables we tested (subsite type, seed distance, and environmental variables), subsite type significantly explained the variation in understory species richness. The effects of seed distance, elevation, slope, and aspect class (e.g., north, northwest, west, southwest, etc.) did not significantly explain the variation in young tree species richness among subsites (Appendix Table 8). Using NMDS, visual assessments of community composition described the most dissimilarity in species between the unburned and high-high/high-low/low-high severity subsites (Fig. 9 and Fig. 10), as shown by the ellipses and their minimal or non-existent overlap (Fig. 10). All other subsites overlapped significantly and demonstrate similarities in plant community composition (Fig. 10). Results from the PairwiseAdonis test (Appendix Table 9) showed that each subsite had overall distinct community composition from each other.

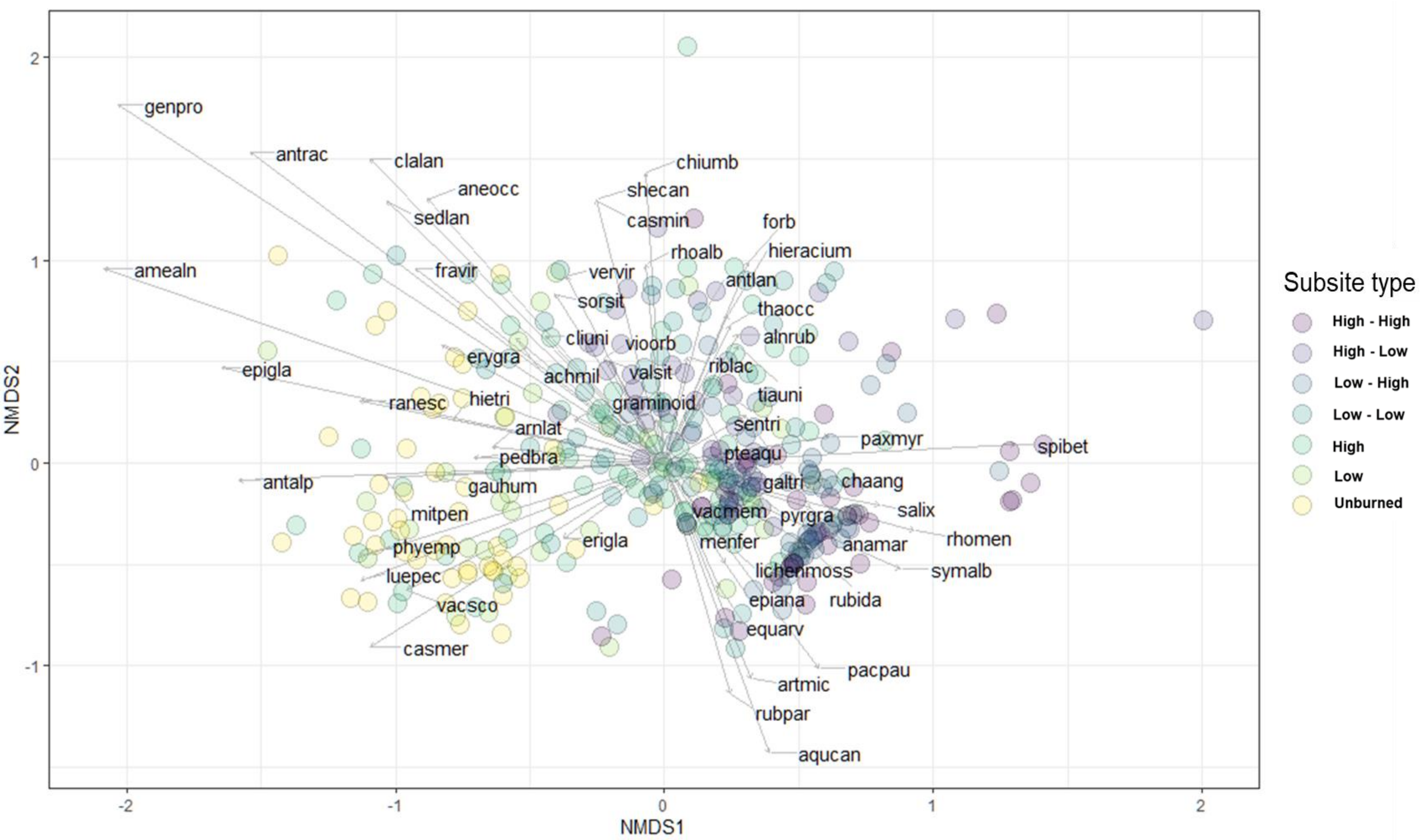

Fig. 9. Non-metric multidimensional scaling (NMDS) bi-plot of understory plant composition data across the study site. Each point represents a single subplot (n=375) in a community composition space. Points closer to each other have more similar understory species composition than points farther apart. Points are colored by subsite type. Species labels visualize abundance of species in various communities, where length of arrows correspond to greater abundance of those species. Species corresponding to abbreviated species code can be found in Appendix Table 3.

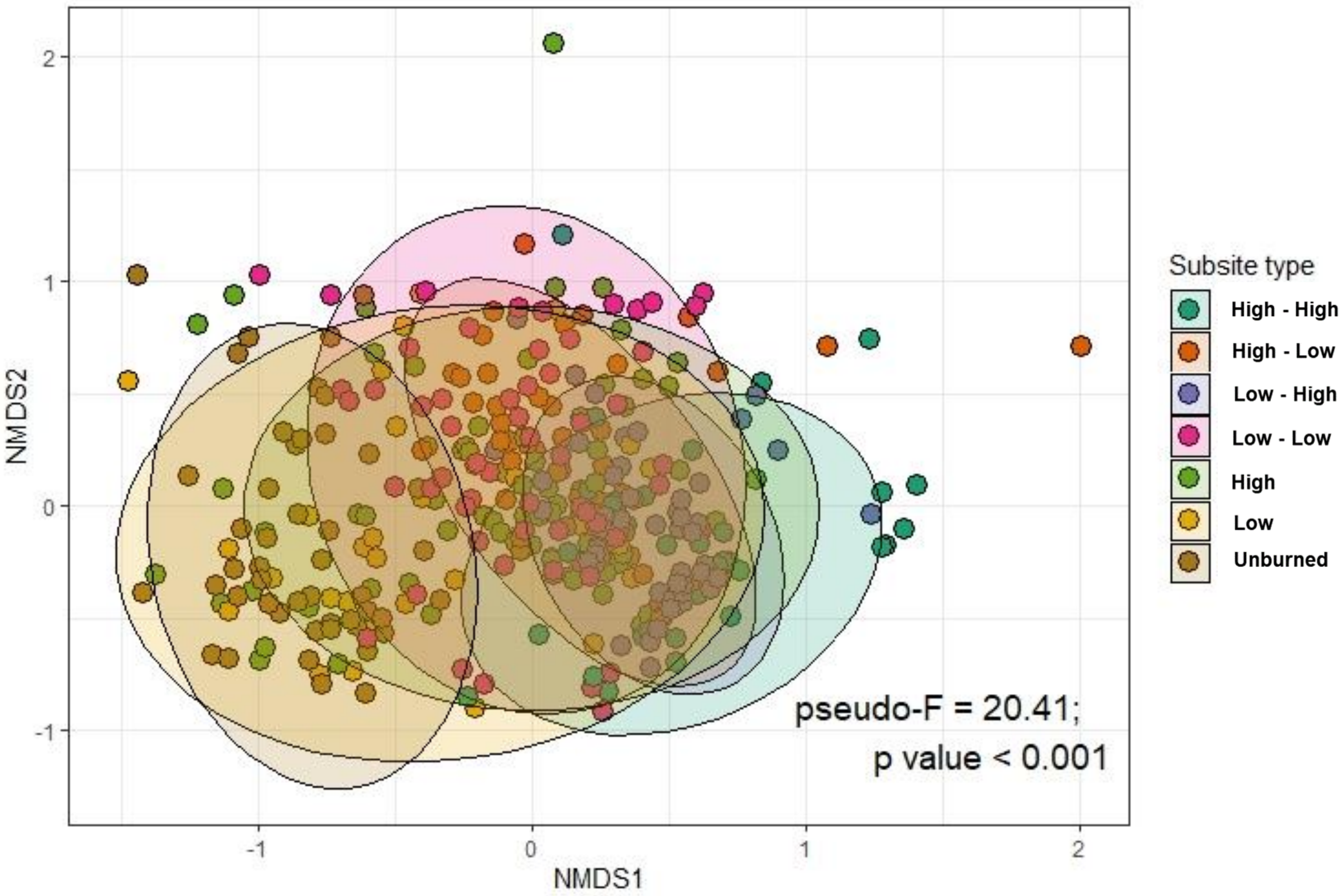

Fig. 10. Non-metric multidimensional scaling (NMDS) bi-plot of understory plant composition data across the study site. Each point represents a single subplot (n=375) in a community composition space. Points closer to each other have more similar understory species composition than points farther apart. Points are colored by subsite type. Ellipses which are drawn at 95% confidence intervals are also colored by subsite type and indicate similarity in subsite composition, where ellipses that are not overlapping show significantly dissimilar plant community compositions.

A generalized linear model (Appendix Table 10) showed that subsite types significantly explained the variation in richness The highest understory species richness was found in the subsite affected by a single low severity wildfire or the unburned subsite (Appendix Fig. 11 and Fig. 11). All other subsites did not vary significantly in species richness (Fig. 11).

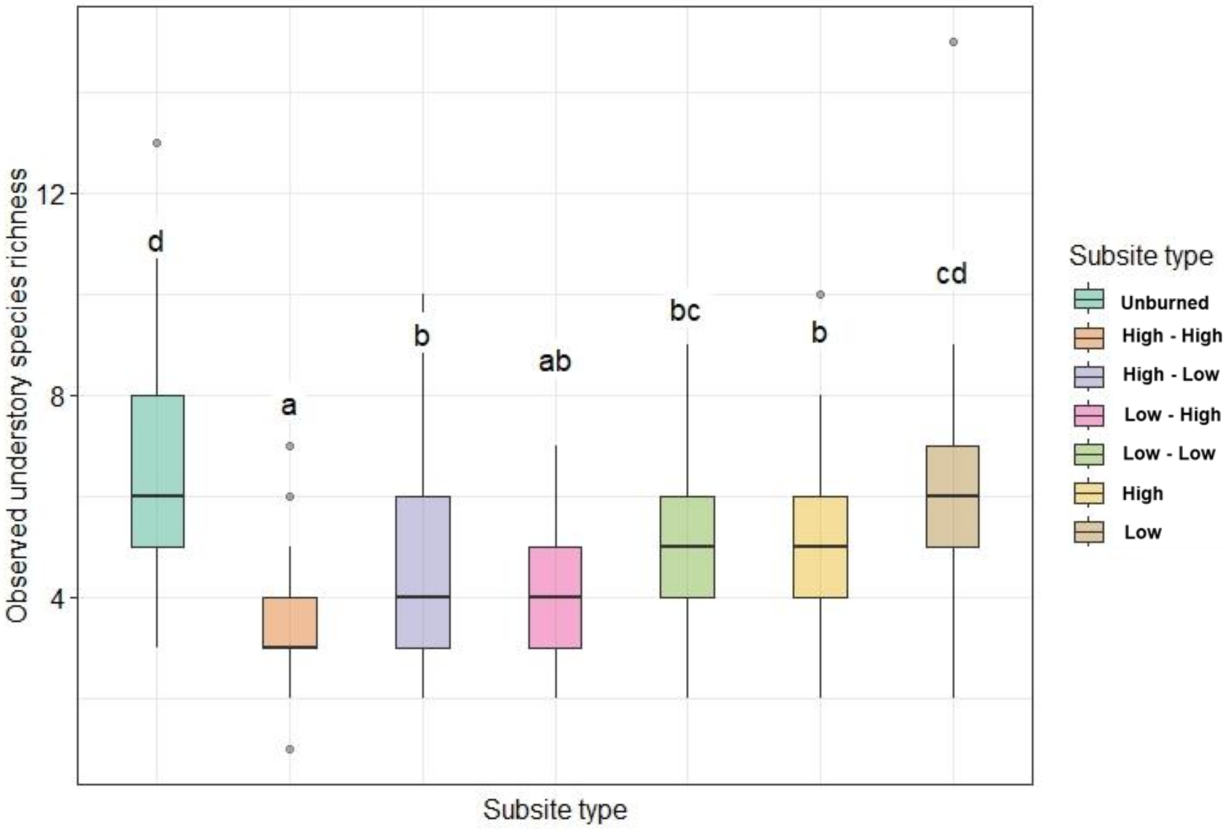

Fig. 11. Boxplot of observed understory species richness across subsite types, where whiskers represent the upper and lower interquartile range and dots are considered outliers. A Tukey test (post-hoc analysis) was performed to determine differences in species richness: letters above each boxplot correspond to similarity in richness, where different letters represent significant dissimilarity.

DISCUSSION

Our study provides new knowledge of how short-interval reburns influence high-elevation forest canopy and understory plant communities. Short-interval reburns in our study site led to different understory plant and tree species compositions, minimal reductions to understory cover, and highly variable stem (counts) density of regenerating trees compared to those observed at a similar site that burned only once (2017). All surveyed subsites experienced the same post-fire environmental (climatic) conditions and regenerated over the same period of time, but differences in plant community compositions and site-specific differences in species' abundance were significant, indicating the importance of wildfire recurrence and burn severity to early post-fire forest regeneration.

Not all types of short-interval reburns reduce regenerating tree counts and species richness

Regions that experienced a single disturbance of wildfire had variable effects on regenerating tree density (Table 2). When the recent (2017) wildfire burned at high severity, consistent and comparable reductions in stem density were recorded in nearly all subsites (including reburns). Despite our initial hypotheses, and the reported effects of reburns on tree densities (Gill et al. 2020; Hoecker and Turner 2022; Stevens-Rumann and Morgan 2016; Turner et al. 2019), not all reburns at our study site affected stem abundance in the same way, suggesting that burn severity is critical when considering effects of wildfire on post-fire tree regeneration (Table 2 and Fig. 4). Although high severity wildfires and high severity reburns reduce soil and aerial seedbanks, burn regenerating trees, and create large patches of homogenous burned landscapes (Harvey et al. 2023), low severity reburns (e.g., low-low, high-low) are often considered non-independently from high severity reburns (Hoecker and Turner 2022; Whitman et al. 2019), but have less severe effects on regenerating tree abundance than other reburns or wildfires that burn once at high severity (Table 2 and Fig 4). These different responses to wildfire suggest that although fire activity continues to increase and short-interval reburns become more prevalent at higher elevations, low severity reburns could be places of fire refugia for regenerating forest ecosystems (Meigs and Krawchuk 2018).

Our findings found that richness generally increased with the number of wildfires (Fig. 7), suggesting an early resilience of canopy species diversity to more frequent and severe wildfires. Few studies in the literature report the effects of short-interval reburns on regenerating tree species richness or diversity, while certain studies suggest lowered richness in canopy species after a reburn (Hoecker and Turner 2022), others suggest the opposite (Donato et al. 2008). This disagreement may indicate that the effects of reburns on species richness could be site specific or relate to burn severity. When forested landscapes experience a disturbance, such as a wildfire, previous dominating canopy trees are often reduced, increasing canopy openings and exposing soil nutrients (Harvey et al. 2016). These landscapes disturbed by high severity wildfires can favor the invasion of colonizer species such as lodgepole pine, or poplar species that create opportunities for their seed growth from legacy propagules in the soil seedbank (Kiel et al. 2023). These stands of seral species could thereby increase richness in the short-term, before shade tolerant species outcompete these early colonizers in later stages of forest succession. Although burn severity explained some of the differences in overall species richness found in reburned regions (Fig. 7), there was no significant variation in richness in landscapes that only burned in 2017 (whether at high or low severity), suggesting that the number of wildfires a forest experiences might better predict expected regenerating tree species richness than burn severity. Early increases in species richness of canopy species, and variable effects of reburns on regenerating tree density, suggests that high-elevation ESSF forests in interior BC that experience a short-interval reburn may resist reductions to abundance, and increase species richness in the short-term.

After a short-interval reburn understory plants may experience reduced species richness, but show resistance to changes in cover

Wildfires that burn through duff layers of the soil and burn through the forest canopy, can increase light availability and reduce competition for understory plants (Rowe 1983). These effects can increase layering of vascular plants in response to high light availability, making plant cover high following wildfire (Kiel et al. 2023; Whitman et al. 2019). Our surveys of understory plants showed consistent cover across disturbance levels, irrespective of the varying combinations of burn severity (e.g., high-high, low-low, high-low, low-high; Fig. 8; Fig. 11), which may point to certain resistance of cover in the understory to frequent wildfires (Buma et al. 2022; Hoecker et al. 2020; Kiel et al. 2023). Although some significant decreases were recorded in regions affected only by the recent high severity wildfire, no other significant changes were detected to understory cover. While burn severity appeared to influence the differences observed in regenerating canopy density, these effects were not observed in our surveys of understory cover (Fig. 8). While overall cover was lower in regions affected by a reburn, these results were not significantly different to overall cover in regions affected by a single burn.

Our study demonstrates the negative impacts of short-interval reburns to understory species richness. Unlike regenerating canopy richness which responded positively to wildfire disturbance, as disturbance impacts increased (e.g., low, followed by high, followed by low-low, etc), understory species richness appeared to decrease linearly (Fig. 11). Although certain studies suggest positive responses in understory richness following a reburn (Kiel et al. 2023), our findings were similar to other findings that suggest otherwise (Edwards et al. 2015; Whitman et al. 2019). Reductions in understory species richness could be attributed to increased soil heating (Whitman et al. 2019), or increased combustion in the soil seedbank. Altered germination conditions could favor certain colonizer species and exclude more shade tolerant varieties that were present in the pre-fire understory. High understory cover might mask as early forest resilience, but reductions in species richness suggest otherwise.

Landscapes affected by fire disturbance in high-elevation ESSF forests of interior BC may be driven by regeneration that is filtering for certain characteristics of plants in the understory that can better survive wildfires or tolerate the harsh conditions of reburned landscapes (Edwards et al. 2015; Hoecker et al. 2020). A study by Rowe (1983) classified different groups of regenerating plant species which exhibited varying fire adaptive traits. These plants were categorized as fire avoiders, those that could not survive wildfires, endurers, those that could survive wildfires, and invaders, those that dispersed to landscapes post-fire (Rowe 1983). In our study site, we found the highest presence of shrubs (e.g., salix spp., rhododendron spp., vaccinium spp., etc.), fireweed and mosses in regions affected by high levels of disturbance (e.g., high followed by high severity). These findings suggest that these plant species may exhibit certain fire adaptive traits that allow them to either disperse to disturbed sites or survive the wildfires in place (Edwards et al. 2015). This may explain the abundant presence of understory colonizer species in our high severity fire disturbed subsites. High severity burns favor the growth of shrubs and plants, such as rhododendron spp. and vaccinium spp., with deep underground rhizome plant traits, classified by Rowe's (1983) study as endurers (Edwards et al. 2015). These rhizomes can endure high severity wildfires which help them to resprout post-fire (Edwards et al. 2015). Comparatively, the reproductive tissues of many herbaceous plants, classified by (Rowe 1983) as fire avoiders, is often found in the duff layer of the forest floor and will typically burn during a higher severity wildfire. Fireweed was found most abundantly in our high severity subsites, likely because of its high dispersal ability. Rowe (1983) classified these plant species as invaders, because they could disperse across large distances to disturbed landscapes. These various colonizer species in our study site exhibited certain fire adaptive traits that may have explained their high abundance in our disturbed subsites. If a reburn occurs, plants exhibiting traits such those found in invaders or endureres may likely colonize the understory after a disturbance, outcompeting late successional, shade tolerate species which are poorly adapted to survive wildfires and fire affected landscapes.

Short-interval reburns alter plant species composition

We found significant differences to plant community composition for both canopy and understory plants between regions affected by a single burn and a reburn (Fig. 5; Fig. 10). Our study observed a large quantity of regenerating trees in regions that experienced a higher severity reburn (e.g., high severity followed by high severity wildfire) (Fig. 4). This abundant presence of regenerating trees was composed overwhelmingly by either poplar or lodgepole pine (Fig. 4), compared to regions affected only by a single burn, regenerating tree composition matched that of the stands unaffected by fire ("pre-fire forest state") nearby (e.g., subalpine fir, Engelmann spruce, and whitebark pine) (Fig. 4). Large stands of broadleaf trees, particularly trembling aspen, may outcompete (and replace) coniferous species when their environments are threatened by increased drought conditions and shorter wildfire intervals (Buma et al. 2022; Donato et al. 2008; Gill et al. 2017). Competitive traits such as rapid maturation, long living seedbanks, and strong seed dispersal ability are associated with early colonizer species such as poplar or lodgepole pine (Donato et al. 2008; Gill et al. 2022; Rowe 1983), and could explain why the community composition of reburned areas was largely represented by these colonizer species. In the context of early seral stand composition shade tolerant species, that were found in forests unaffected by wildfire ("pre-fire forest state") or affected by a single burn, may struggle to outcompete colonizer species in landscapes affected by a short-interval reburn.

Among the seral stands of poplar and lodgepole pine trees in regions affected by high levels of disturbance (e.g., high severity followed by high severity wildfire), was an increased cover of shrubs (e.g., salix species) and mosses (Fig. 9). The composition of certain understory species following wildfire is often related to burn severity (Dickson-Hoyle et al. 2024; Hart and Chen 2007). High severity reburns (e.g., high followed by high severity) favor the growth of certain plants with deep underground rhizomes that can survive intense wildfires as seen by the increased presence of Birchleaf spirea (*Spirea betulifolia*), False azalea (*Rhododendron menziesii*), and salix species in our study site (Fig. 9). In other regions, unaffected by wildfires ("pre-fire forest state") or affected by a single burn, were understory communities largely composed of shade tolerant varieties of shrubs (e.g., pink mountain heather and vaccinium species), herbaceous plants (e.g., alpine pussy toes (*Antennaria alpinus*)), and grasses (Fig. 9). These differences in community compositions between regions affected by a single burn and by a reburn were significant (Fig. 10) and could be explained by a number of factors including the increased combustion of legacy seed propagules and reproductive tissues in the duff layer where many herbaceous plants are found, increased distances to seed sources (from living forest), and differences in competitive traits between colonizer species and shade tolerant species (Kiel et al. 2023; Rowe 1983).

Wildfires that burn at high-elevation coniferous forests are often high severity, stand-replacing wildfires that burn through aerial seedbanks, and through deep organic layers in the ground and soil seedbank. Regeneration at these locations can thereby rely heavily on seed dispersal from living forest edges, and animal dispersers (Gill et al. 2020; Turner et al. 2019). Distances to living forest edges were the largest in regions with the highest levels of disturbance (e.g., high severity followed by high severity wildfire) (Appendix Table 8). These findings may support why our study observed differences in community composition at these locations where there were large abundances of poplar species and fireweed, which are species known to be strong seeders that can disperse over large distances (Rowe 1983). Subsites with the shortest distances to living forest edges (Appendix Table 8), were generally sites that experienced low levels of wildfire disturbance (e.g., one wildfire at either low or high severity, or two low severity wildfires). This may explain why presence of subalpine fir, Englemann spruce, and whitebark pine as well partridge foot, grouse whortleberry, and white mountain heather were dominant at these low disturbance regions, and why both understory and canopy composition at these subsites matched the composition of the surrounding living forest. These significant differences in the community composition between regions affected by a single burn and a reburn suggest that shifts in early forest composition are likely after a reburn and could persist if fire activity continues to increase at these locations (Buma et al. 2022; Nathan et al. 2022).

Limitations

We recognize that the main limitation to this study is that we used only one short-interval reburn site in one region of southern-interior BC, and that careful interpretation may be needed for other landscapes.

We also recognize that using satellite indices of burn severity are well tested in forests that experience a single wildfire, but that the reliability of using satellite derived indices in studies examining short-interval reburns are not fully understood. A recent study reported that satellite derived burn severity indices in locations that have experienced a short-interval reburn can either under- or over- estimate severity (Saberi and Harvey 2023). Although field measurements of burn characteristics of the 1992 and 2017 wildfires were used to ground truth satellite derived burn severity, these methods are not error free and could also explain some of the variation in our count or cover data across subsite types.

While our study design provides important comparisons of post-fire regeneration between forests of varying levels of disturbance, it is difficult to make causal links between environmental drivers and plant community responses without manipulative experiments (Kiel et al. 2023). Recent assessments of post-fire regeneration (i.e., within 10 years following a wildfire) may provide early insights into future forest species composition and structure. However, these assessments do not account for all possible succession trajectories and future impacts to forests from climate change. Despite this limitation, early assessments are critical to assessing fire effects and succession patterns that can persist over decades (Harvey et al. 2016; Turner et al.

2019), and can provide an important impression of the trajectories of future forests for contemporary and preventative management of these landscapes.

Management implications

Wildfire management strategies in western North America have a history of using areas affected by ‘old’ fires (~ > 50 years) as fire breaks to slow wildfires down during operational responses. Using previously burned forests as fire breaks, especially if the forest is immature/in the early stages of regeneration, as described in this study, can have severe ecological effects on forest community formation and regeneration (Agne et al. 2023; Prichard et al. 2017; Turner et al. 2019). Forest and protected area management agencies can use our findings to support their own forest resource assessments to determine if permitting, facilitating, or inhibiting reburns helps to meet their desired goals and outcomes for forest resources. Wildfire management strategies may need to shift away from traditional response tactics if we want to preserve future forests and support their resiliency to future wildfires in this changing climate.

Although our surveys did not find any invasive plants, other forested regions that experience a reburn at lower elevations, or reburns close to human transport corridors could be at risk of invasion from non-native plants. Homogenous patches of burned forest landscapes, especially at early stage of post-fire regeneration possess lower local seedbank abundance (low natural competition), and high light availability. These regions offer ideal conditions for species with plant traits that are resistant to drought conditions, and increased wind disturbance, such as invasive species (Dickson-Hoyle et al. 2024). Natural resource management agencies that protect natural landscapes may prevent and manage the invasion of non-native plants by using this study as a baseline for focusing their response tactics. Early surveys of reburned landscapes could be critical to finding, identifying, and managing any invasive species threatening sensitive ecosystems to prevent their populations from growing to unmanageable levels.

CONCLUSION

Our study provides evidence that short-interval reburns at high-elevation forests lead to different plant community compositions and cover of young (regenerating) trees compared to regions that only experience a single wildfire event. Significant differences to forest vegetation composition after a reburn foreshadows a possible departure of forest regeneration from historical recovery pathways. The trajectory of stand composition set by postfire regeneration can lead to long-lasting changes when these effects are exacerbated with increased seed dispersal distances, and increasing drought conditions, making increasingly inhospitable conditions for regenerating trees and new understory plants (Gill et al. 2022; Harvey et al. 2023 Hoecker and Turner 2022; Kemp et al. 2016; Stevens-Rumann and Morgan 2016; Turner et al. 2019; Whitman et al. 2019). Further, we provide new insights about the importance of considering the impacts of reburns and burn severity to regenerating trees or regenerating understory cover separately as their responses to these disturbances may differ. While the forests we studied are still in the early stages of post-fire regeneration, shifts in canopy species and understory composition are expected and may persist as short-interval reburns continue to occur.

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Chapter 4: CONCLUSION

Our knowledge of wildfires and their interactions with landscapes in western Canada has advanced, but important research gaps remain as climate change and anthropogenic disturbances continue to impact forest ecosystems. As wildfire activity continues to increase, understanding historical fire-climate relationships can provide valuable insights on past forest dynamics and provide context needed to describe how wildfire regimes are changing and how future impacts of wildfire will affect forests and post-fire regeneration. This study provides new ecological knowledge about the impacts of wildfire, both historical and contemporary, to a high-elevation forest in interior British Columbia (BC).

There are few studies that have examined the historical impacts of wildfire occurrence to high-elevation coniferous forests in interior BC and the relationships of climate with the trees that grow in these settings, such as whitebark pine (*Pinus albicaulis*) (Johnson et al. 1990; Carlson et al. 2018; Wong and Daniels 2017; Youngblut and Luckman 2013). The management of endangered whitebark pine trees, such as those found in Glacier National Park, BC, remain a priority for many management agencies such as Parks Canada. This study characterizes the historical presence of wildfires in the Beaver Valley, Glacier National Park, and the role of warm, dry summers on whitebark pine tree growth. Historical wildfires in subalpine coniferous forests are described as infrequent and stand-replacing (Johnson et al. 1990), by contrast my findings report a richer history of wildfires in high-elevation forests of the Beaver Valley and report previously undocumented historical wildfires that, to the best of my knowledge, have not been previously documented. Management agencies that use prescribed burns to manage whitebark pine habitat can use the findings from this study to inform their management plans and future prescribed burn plans to better preserve whitebark pine trees.

Few investigations of climate-growth relationships use whitebark pine trees (Carlson et al. 2018; Wong and Daniels 2017; Youngblut and Luckman 2013), and results from these studies are not entirely consistent. Despite opposing findings from other regional studies (Wong and Daniels 2017), my study suggests that whitebark pine growth is promoted in warm, dry summers (July) and this relationship may be strengthening in the latter part of the 20th century (Youngblut and Luckman 2013). The variation in regional findings of climate-growth relationships of whitebark pine suggests that findings could be driven in part by site-specific conditions (Carlson et al. 2018; Wong and Daniels 2017; Youngblut and Luckman 2013), and highlights the need for more local-scale research investigating climate-growth relationships of whitebark pine trees. Whitebark pine trees are sensitive to many disturbances including climate and wildfire, future impacts of drought and changing wildfire regimes to these ecosystems are not yet known, but this study provides a historical baseline for the presence of wildfire in whitebark pine ecosystems that can be used to compare to contemporary impacts of wildfire activity.

The results documented in Chapter 3 demonstrate the variable effects of short-interval reburns on regenerating high-elevation coniferous forest canopy and understory cover, suggesting that burn severity may be driving these observed differences in abundance. Despite the many reported consequences of short-interval reburns to canopy density (Hoecker and Turner 2022; Stevens-Rumann et al. 2022; Stevens-Rumann and Morgan 2016; Whitman et al. 2019), low severity reburns may offer fire refugia for regenerating forests in a future with increased fire activity. Although increased severity decreased understory plant cover in certain cases (single high severity wildfire), cover did not change significantly among other combinations of burn severity in reburned regions, demonstrating potential resistance of understory cover to reburns. While early increases in regenerating canopy and understory plant richness may indicate potential resiliency to increasing fire activity, significant shifts to plant composition after a reburn demonstrate a departure from previous historical recovery pathways. If recurring wildfires continue, shifts in canopy and understory composition are expected and may persist long-term. Without appropriate management, reburned landscapes could be at risk of loss of at-risk species such as whitebark pine trees, or invasion by non-native species. The research presented here lends support to the idea that increased wildfire frequency and severity driven by climate change are pushing recovering subalpine forests outside of their historical regime, shifting early forest composition, and altering forest recovery pathways.

Although changes to wildfire regimes are occurring across Canada, wildfire activity is increasing, and the exact impacts of future wildfires on coniferous forests are still uncertain; this study provides insights about the historical presence of wildfires and impacts of short-interval wildfires to at least one region of coniferous forests in interior BC that can be interpreted for other similar landscapes.

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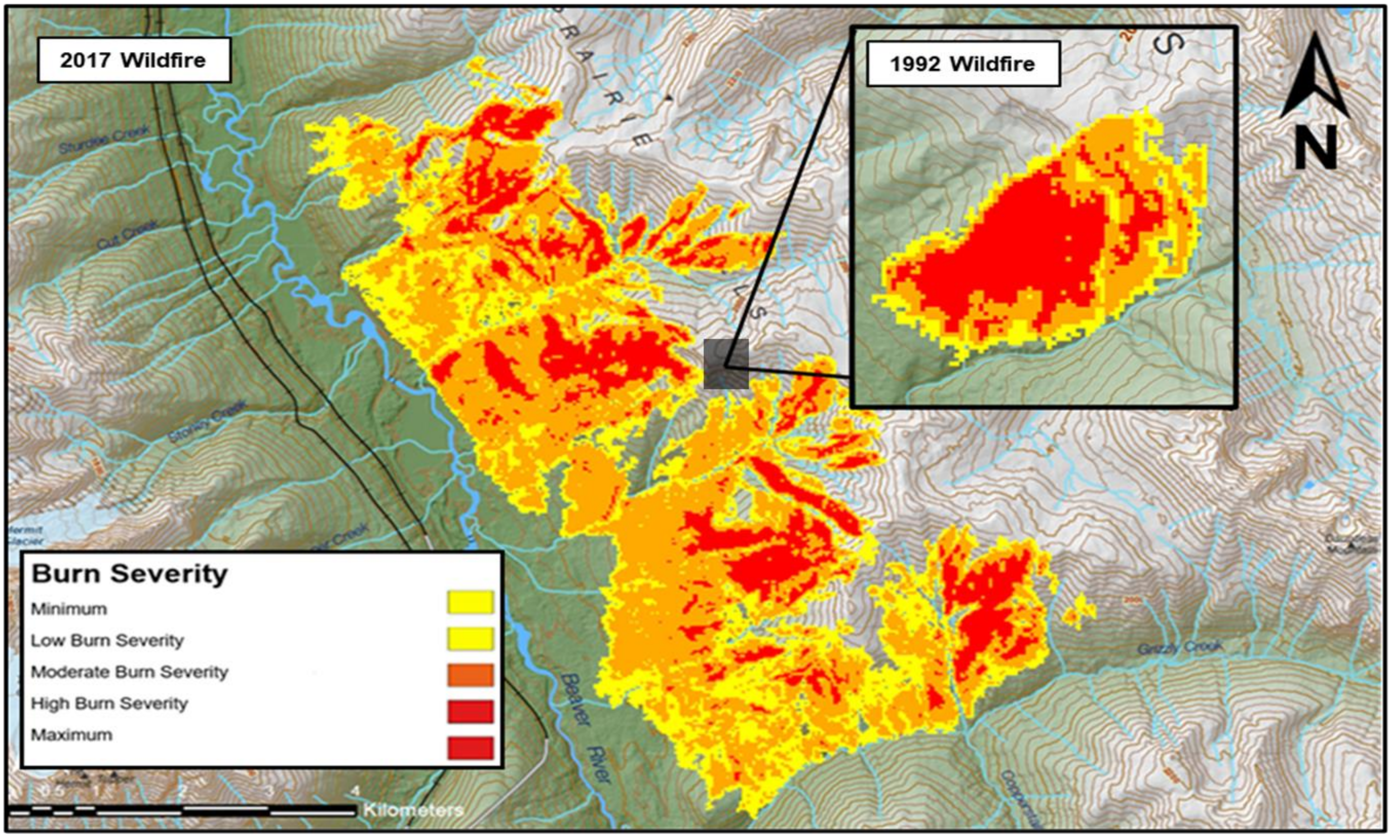
APPENDIX

Appendix Table 1. Significant correlation results for climate-growth relationships for the Prairie Hills climate chronology detrended using the modified negative exponential method.

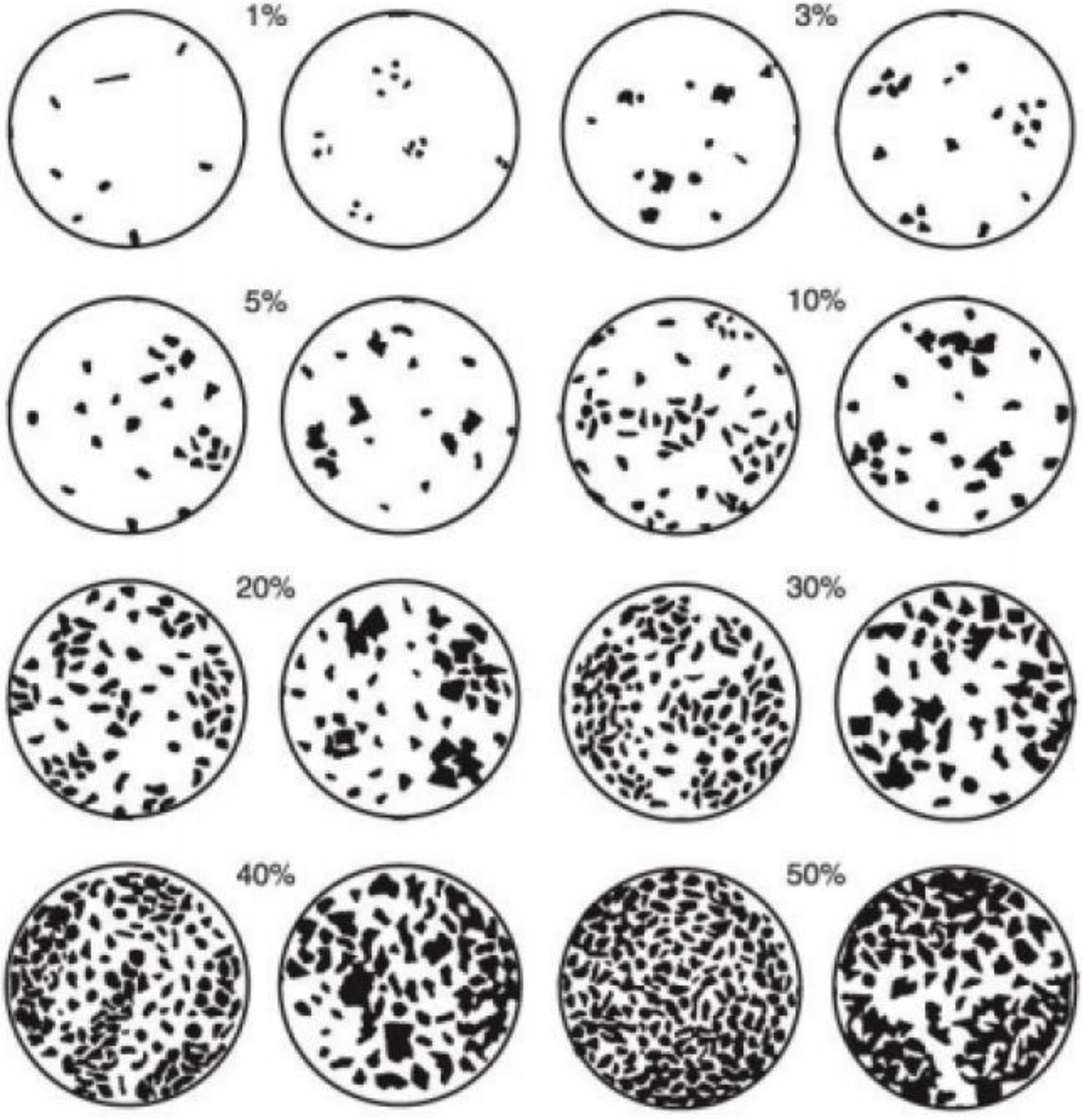
Temperature maximum	Temperature mean	Temperature minimum	SPEI1
0.348 July	0.466 July	0.491 July	-0.317 July
0.310 June-July	0.231 September	0.237 September	-0.297 June-July
0.295 July-August	0.397 June-July	0.354 June-July	-0.296 July-August
0.293 June-August	0.406 July-August	0.381 July-August	-0.308 June-August
0.300 May-July	0.399 June-August	0.331 June-August	

Appendix Table 2. Threshold values for each fire severity metric corresponding to low (CBI = 0-1.24), moderate (CBI = 1.25-2.25), and high severity (CBI = 2.25-3) using google earth engine derived severity metrics (References in Chapter 3: Key and Benson 2006). dNBR offset includes interannual variation between pre- and post-fire vegetation. In this study only high and low severity determined using RdNBR with dNBR offset. Study methods using the high and low severity categories were created by dividing the moderate severity category evenly in two and lumping this with either the low or high severity categories (e.g., low with mod-low, and high with mod-high).

		Key and Benson 2006			**Study Methods**	
		Low	**Moderate**	**High**	**Low**	**High**
Excludes dNBRoffset	dNBR	≤185	186-417	≥418	-	-
	RdNBR	≤338	339-726	≥727	-	-
	RBR	≤135	136-300	≥301	-	-
Includes dNBRoffset	dNBR	≤159	160-392	≥393	-	-
	RdNBR*	≤312	313-706	≥707	≤510	>510
	RBR	≤115	116-282	≥283	-	-



Appendix Fig. 1. Wildfire burn severity of the 1992 and 2017 wildfires in the study area. Colour scale shows the delta normalized burn ratio with offset evaluated using google earth engine using threshold values from Key and Benson 2006 (References in Chapter 3: Parks et al. 2018; Whitman et al. 2020).



Appendix Fig. 2. Reference visual guide for estimating percent cover.

Appendix Table 3. Canopy and overstory species code definitions.

Functional Group	Latin Name	Common Name	Species Code
Trees	*Abies lasiocarpa*	Subalpine fir	ABILAS
	Picea engelmanni	Engelmann spruce	PICENG
	Pinus albicaulis	Whitebark pine	PINALB
	Pinus contorta	Lodgepole pine	PINCON
	Populus tremuloides	Trembling aspen	POPTRE
	Populus trichocarpa	Black cottonwood	POPTRI
Herbs	*Achillea millefolium*	Yarrow	ACHMIL
	Anaphalis margaritacea	Pearly everlasting	ANAMAR
	Anemone occidentalis	Western anemone	ANEOCC
	Antennaria alpinus	Alpine pussytoes	ANTALP
	Antennaria lanata	Wooly pussytoes	ANTLAN
	Antennaria racemosa	Racemose pussytoes	ANTRAC
	Aqueligia canadensis	Red columbine	AQUCAN
	Arnica latifolia	Broadleaf arnica	ARNLAT
	Chamerion angustifolium	Fireweed	CHAANG
	Clintonia uniflora	Queen's cup	CLIUNI
	Epilobium glassiali	Glacial fireweed	EPIGLA
	Equisetum arvense	Field horsetail	EQUARV
	Erigeron glacialis	Glacial fleabane	ERIGLA
	Erythronium grandiflorum	Yellow avalanche lily	ERYGRA
	Fragaria virginiana	Wild strawberry	FRAVIR
	Gallium triflorum	Sweet scented bedstraw	GALTRI
	Gaultheria humifusa	Alpine wintergreen	GAUHUM
	Gentianella propinqua	Four parted gentian	GENPRO
	Hieracium spp.	Hawkweed	HIERACIUM
	Hieracium triste	Wooly hawkweed	HIETRI
	Mitella pentandra	Fivestamen mitrewort	MITPEN
	Packera pauciflora	Alpine groundsel	PACPAU
	Pedicularis bracteosa	Bracted lousewort	PEDBRA
	Pteridium aquilinum	Bracken fern	PTEAQU
	Ranunculus eschscholtzii	Subalpine buttercup	RANESC
	Sedum lanceolatum	Lance-leaved stonecrop	SEDLAN
	Senecio triangularis	Arrowleaf groundsel	SENTRI
	Thalium occidentale	Western meadowrue	THAOCC
	Tiarellia uniflora	Foamflower	TIAUNI
	Valeria sitchensis	Sitka valerian	VALSIT
	Veratrum veride	False hellebore	VERVIR
	Viola orbiculata	Western roundleaf violet	VIOORB
Shrubs	*Alnus rubra*	Red alder	ALNRUB
	Amelanchier alnifolia	Saskatoon berry	AMEALN
	Cassiope mertensiana	White mountain heather	CASMER
	Luetka pectinata	Partridge foot	LUEPEC

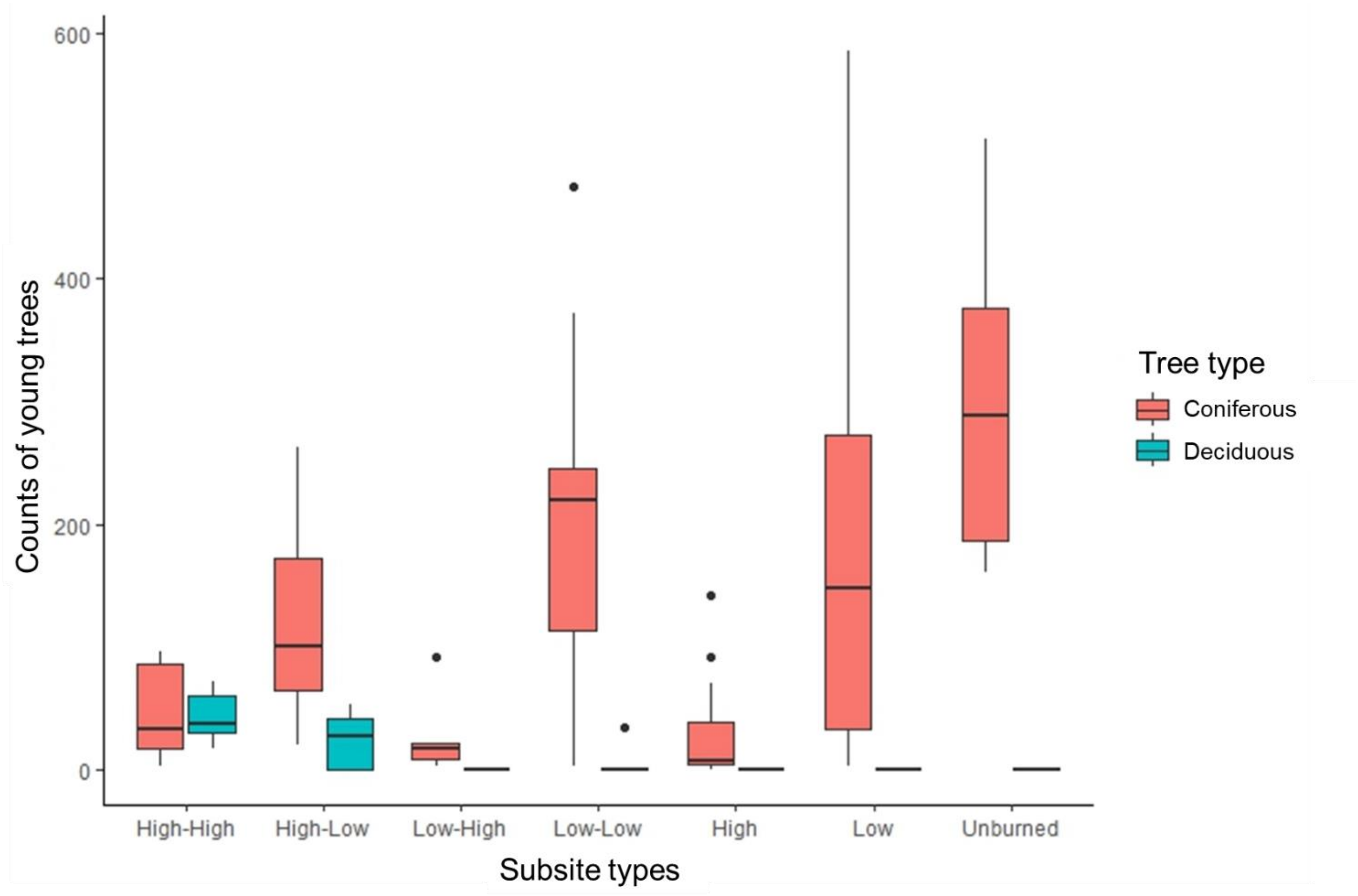
	Menziesia ferruginea	False azalea	MENFER
	Paxistima myrsinites	Falsebox	PAXMYR
	Phyllodoce empetriformis	Red mountain heather	PHYEMP
	Pyrola grandiflora	Arctic wintergreen	PYRGRA
	Rhododendron albiflorum	White rhododendron	RHOALB
	Rhododendron menziesii	False azalea	RHOMEN
	Ribes lacustre	Gooseberry	RIBLAC
	Rubus idaeus	Red raspberry	RUBIDA
	Rubus parviflorum	Thimbleberry	RUBPAR
	Salix spp.	Willow	SALIX
	Sheperdia canadensis	Buffalo berry	SHECAN
	Sorbus sitchensis	Mountain ash	SORSIT
	Spirea betulifolia	Birch leaf spirea	SPIBET
	Symphoricarpos albus	Common snowberry	SYMALB
	Vaccinium membranaceum	Black huckleberry	VACMEM
	Vaccinium scoparium	Grouseberry	VACSCO
Graminoids	-	Grasses+sedges+rushes	GRAMINOID
Cryptograms	-	Lichen+mosses	LICHENMOSS

Appendix Table 4. Mean tree seedling counts per subsite by tree type.

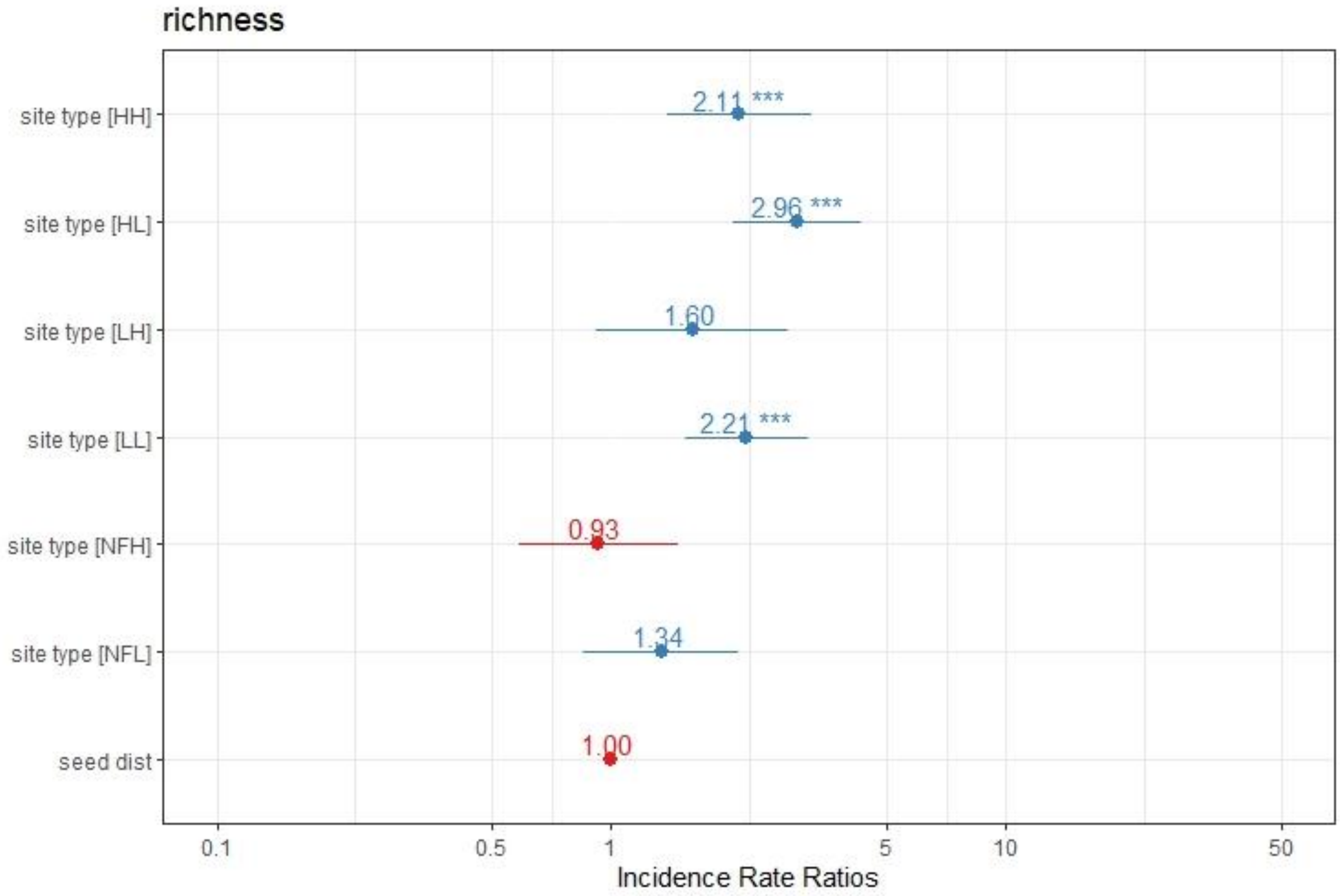
Subsite type	Mean seedling conifer density	Mean seedling deciduous density
Unburned	132	0
Low	67	0
High	22	0
Low-Low	156	1
Low-High	16	0
High-Low	89	4
High-High	34	7

Appendix Table 5. Mean tree sapling counts per subsite by tree type.

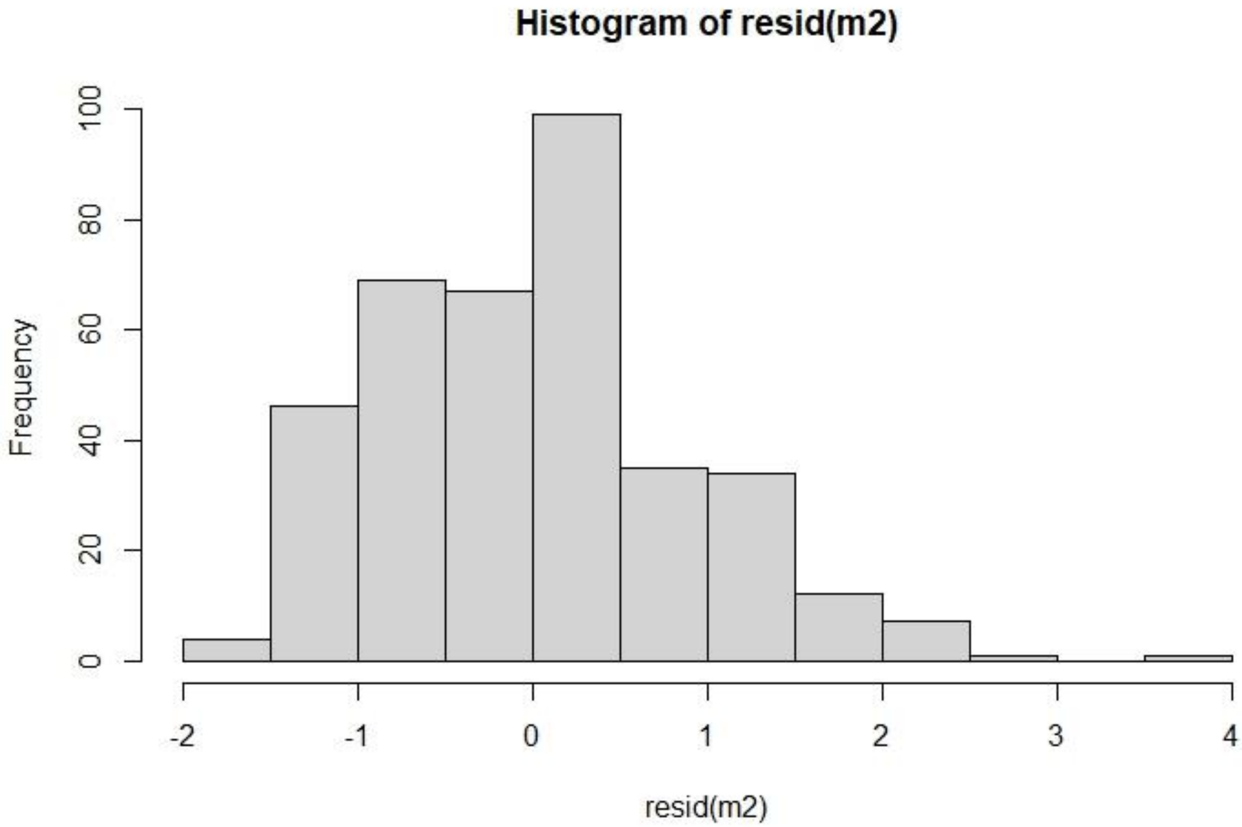
Subsite type	Mean sapling conifer density	Mean sapling deciduous density
Unburned	169	0
Low	46	0
High	6	0
Low-Low	50	2
Low-High	5	0
High-Low	31	20
High-High	10	38



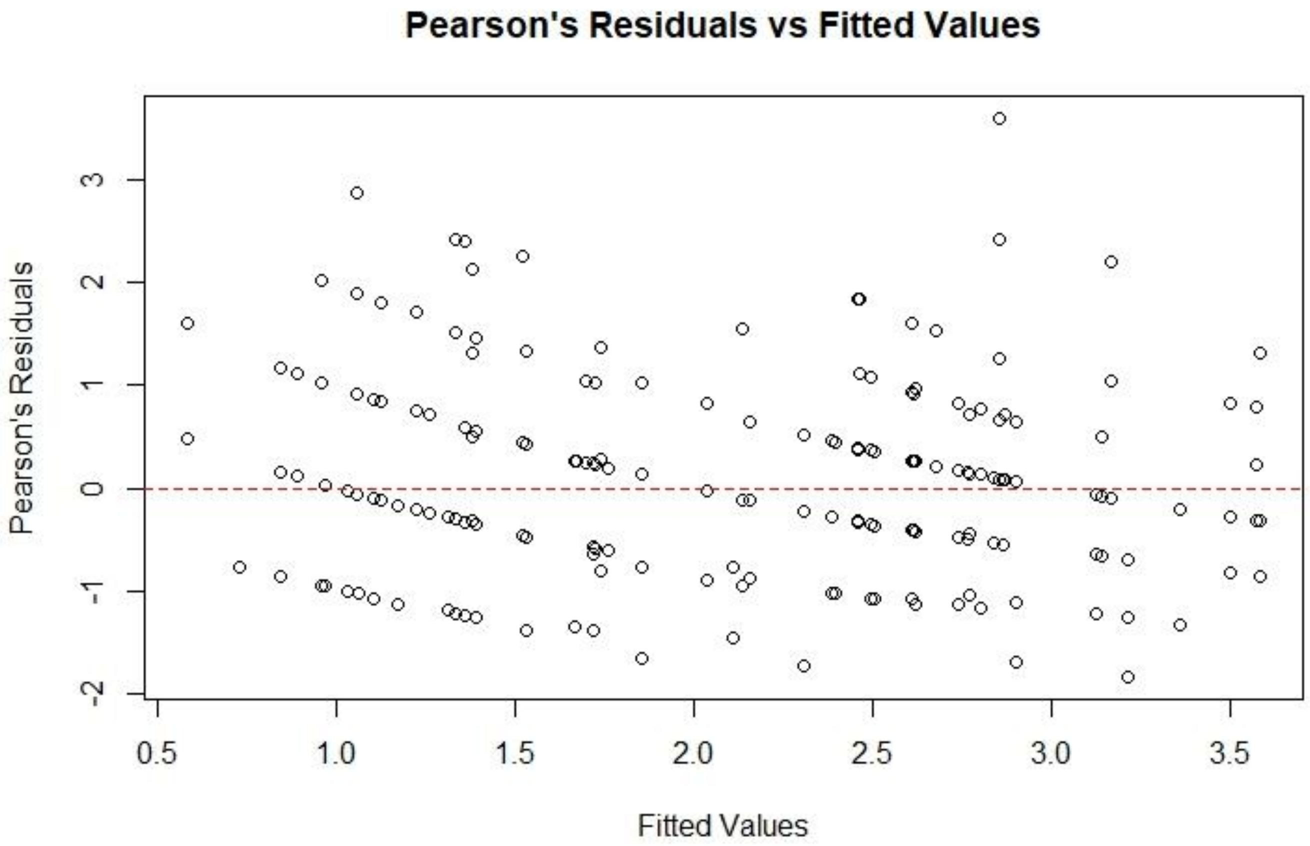
Appendix Fig. 3. Young tree counts as a function of tree type (conifer or deciduous) and subsite type. Boxplots show the median, and whiskers represent the upper and lower interquartile range. Dots are considered outliers.



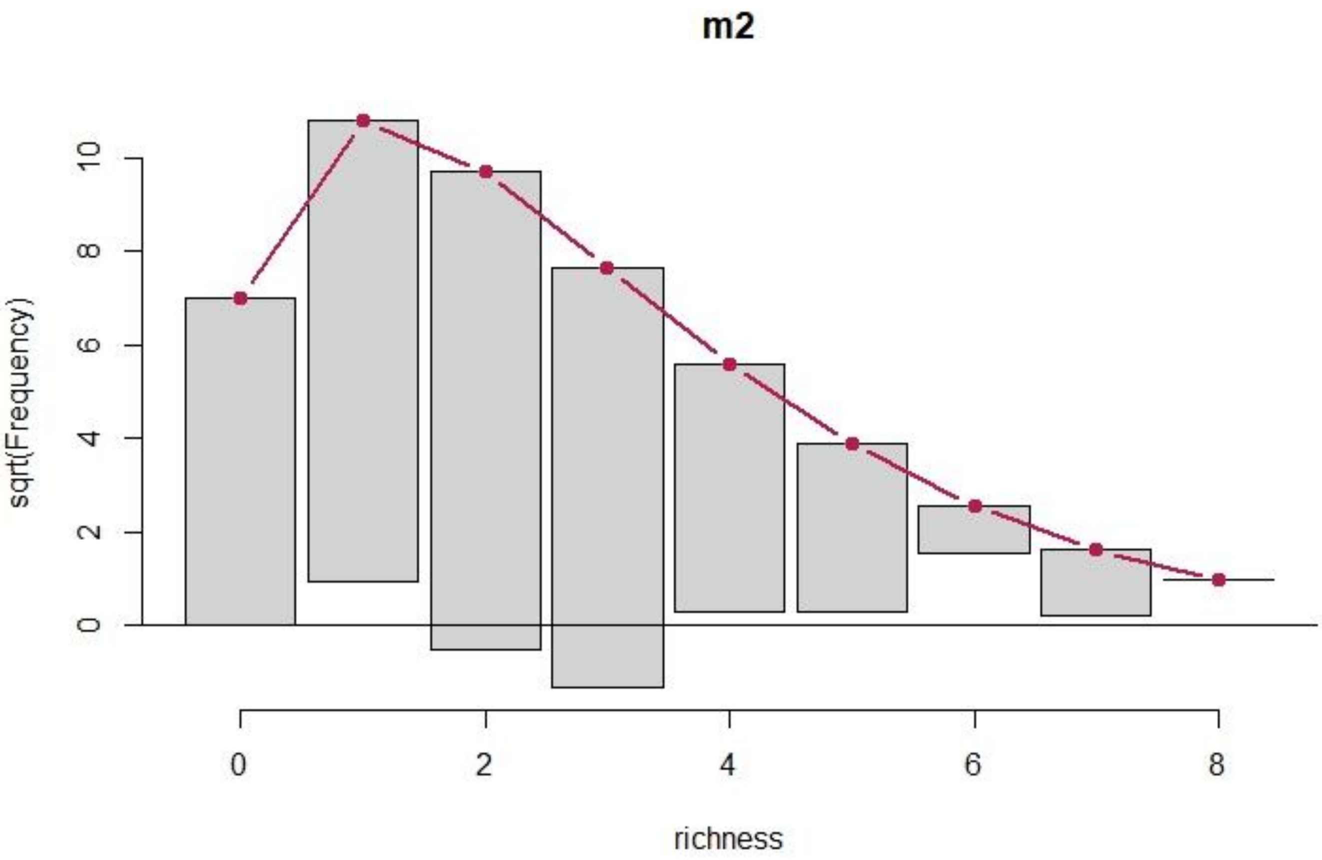
Appendix Fig. 4. Hurdle model output of the truncated Poisson.



Appendix Fig. 5. Histogram of the residuals from the hurdle model of young trees where explanatory variables are seed distance and subsite type and response variable is species richness.



Appendix Fig. 6. Plot of the pearsons residuals against fitted values (ab line shown in red) from the hurdle model of young trees where explanatory variables are seed distance and subsite type and response variable is species richness.

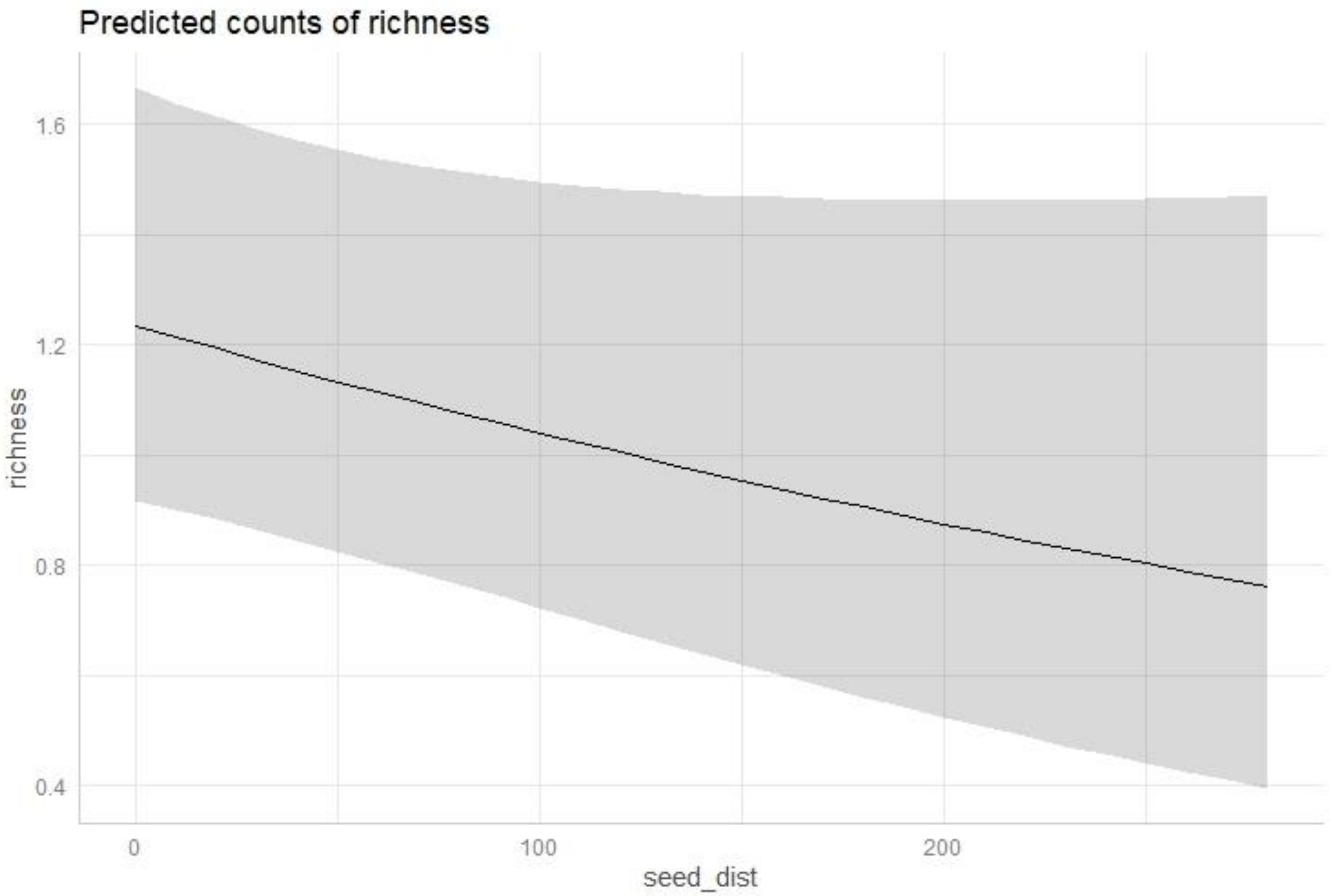


Appendix Fig. 7. Plotted rootogram to graphically compare frequencies of empirical distributions and expected (fitted) probability models (hurdle model) for young tree species richness. The observed distribution is a histogram drawn on a square root scale and superimposed with a line for the expected frequencies.

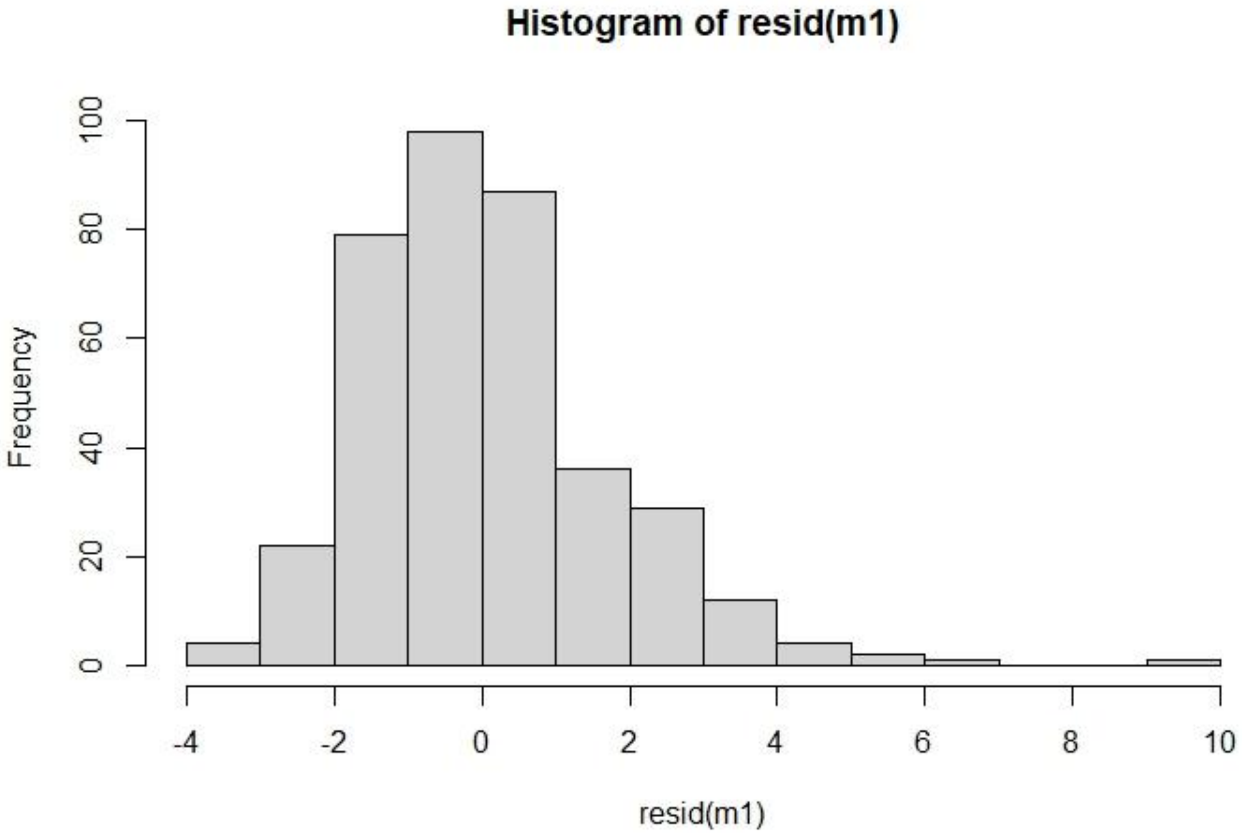
Appendix Table 6. Results from a hurdle model of young tree species richness across subsites in the study area. Species richness was modelled as a Poisson distribution and a truncated zero hurdle model to account for the overdispersion of zeroes across subsites. Subsite type (number of wildfires and burn severity), and seed source distance were included as explanatory variables. The control group (unburned subsite) is not shown below as this is the variable that was used to compare the parameters.

Model	**Variable**	**Parameter estimate**	**Standard error**	**Z**	**P-value**
Poisson	Intercept	0.211	0.153	1.382	0.167
	High-high subsite	0.746	0.215	3.47	0.000521*
	High-low subsite	1.086	0.192	5.657	1.54E-08*
	Low-high subsite	0.472	0.286	1.642	0.101
	Low-low subsite	0.791	0.18	4.387	0.000015*
	High subsite	-0.0732	0.236	-0.31	0.756
	Low subsite	0.291	0.23	1.266	0.206
	Seed distance	-0.002	0.001	-1.612	0.107
Logistic regression	Intercept	18.58	1521	0.012	0.99
	High-high subsite	-13.28	1521	-0.009	0.993
	High-low subsite	-13.94	1521	-0.009	0.992
	Low-high subsite	-13.55	1521	-0.009	0.992
	Low-low subsite	-14.43	1521	-0.009	0.992
	High subsite	-17.28	1521	-0.011	0.991
	Low subsite	-16.69	1521	-0.011	0.991
	Seed distance	-0.01425	0.005131	-2.778	0.00547

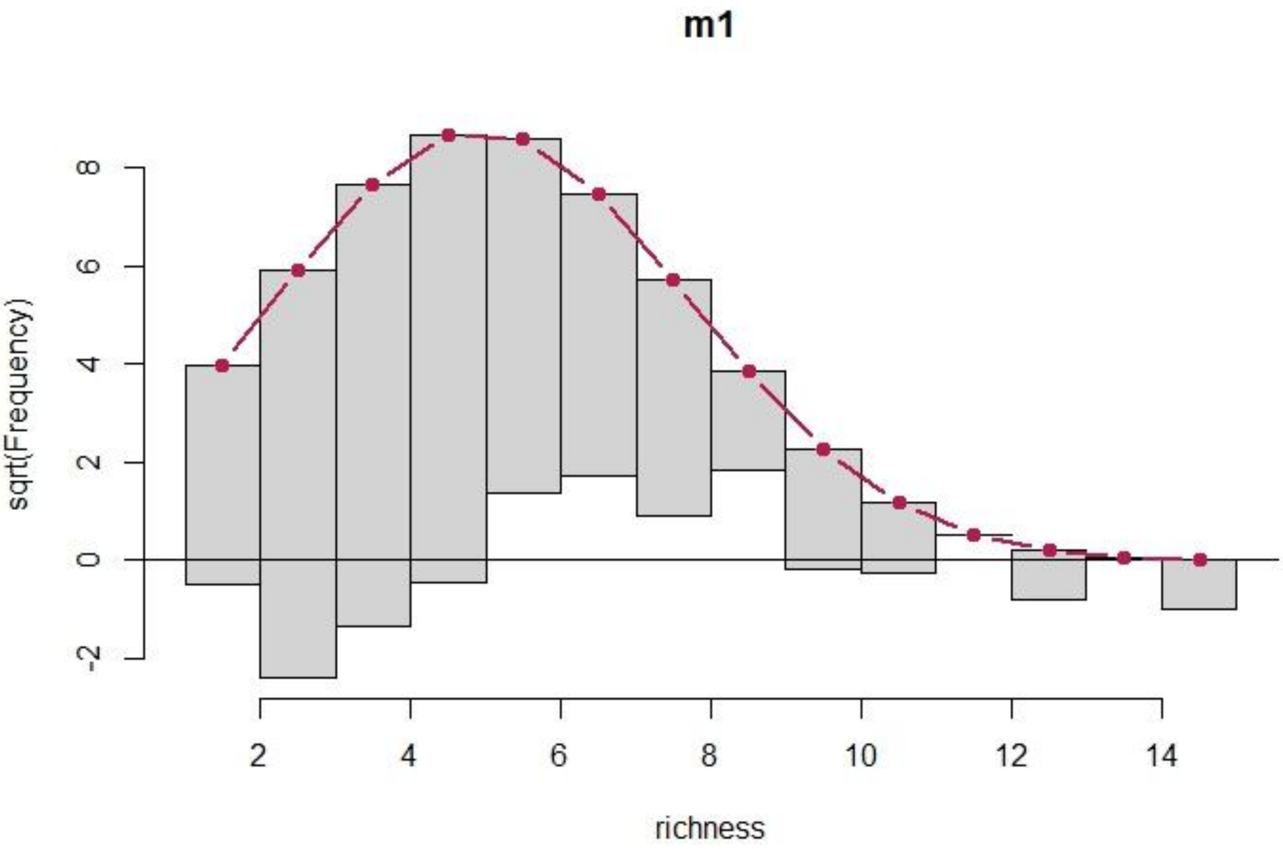
*denotes significant variables (*p*<0.05)



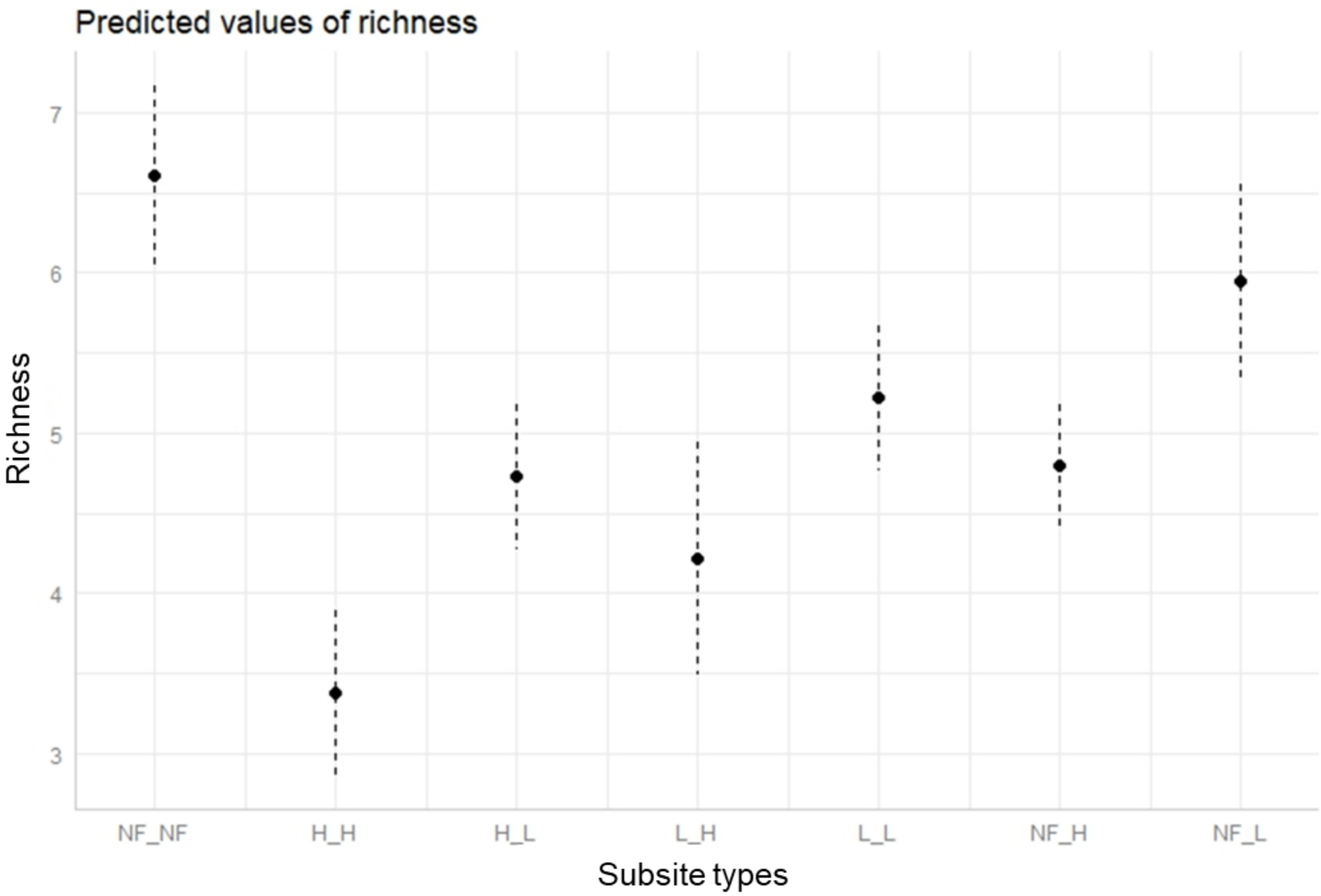
Appendix Fig. 8. Plot of predicted species richness against seed distance using the hurdle model of young tree species richness. Formulated by the package *ggeffects* from the results of the hurdle model.



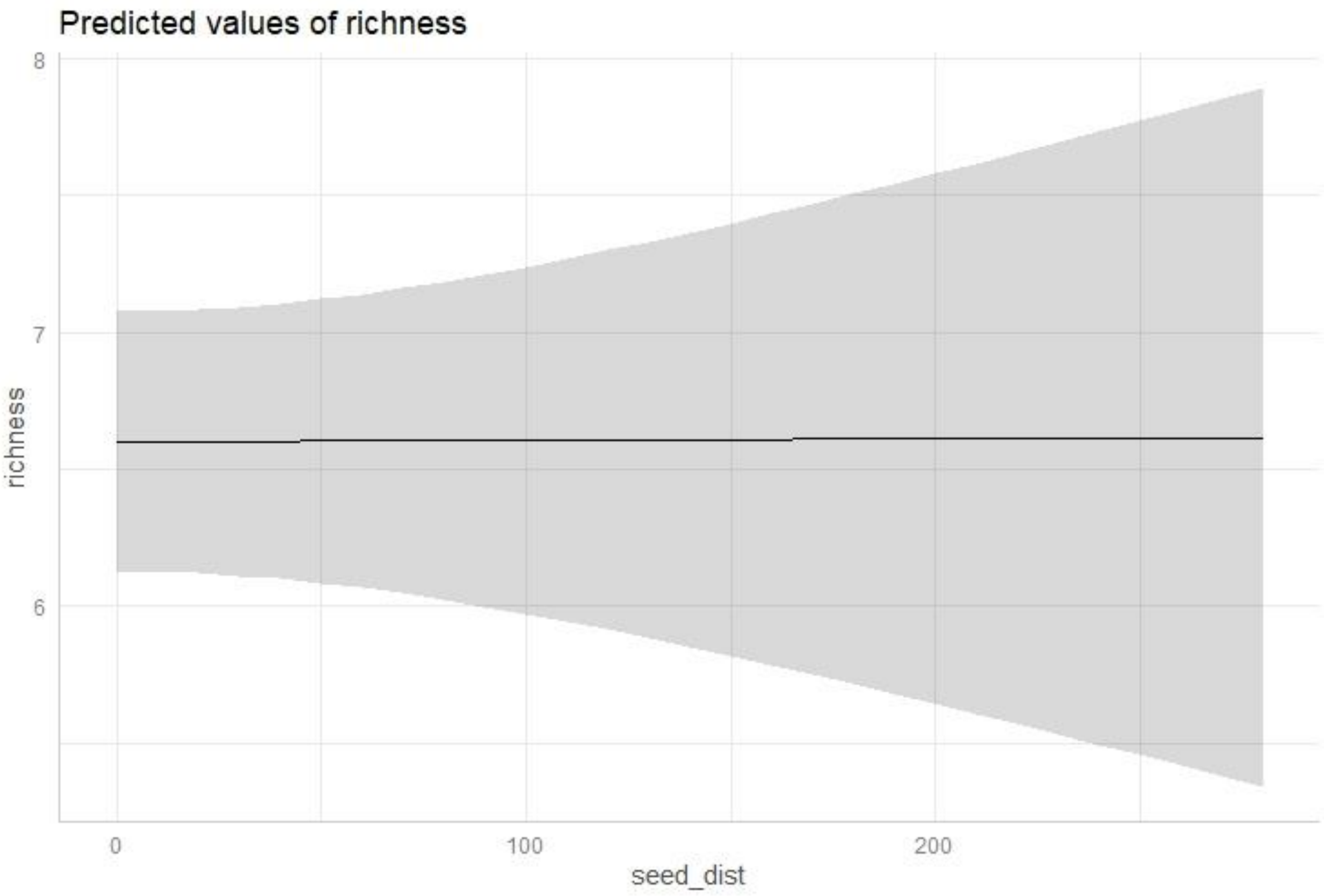
Appendix Fig. 9. Histogram of the residuals from a generalized linear model of understory vegetation where explanatory variables are seed distance and subsite type and response is species richness.



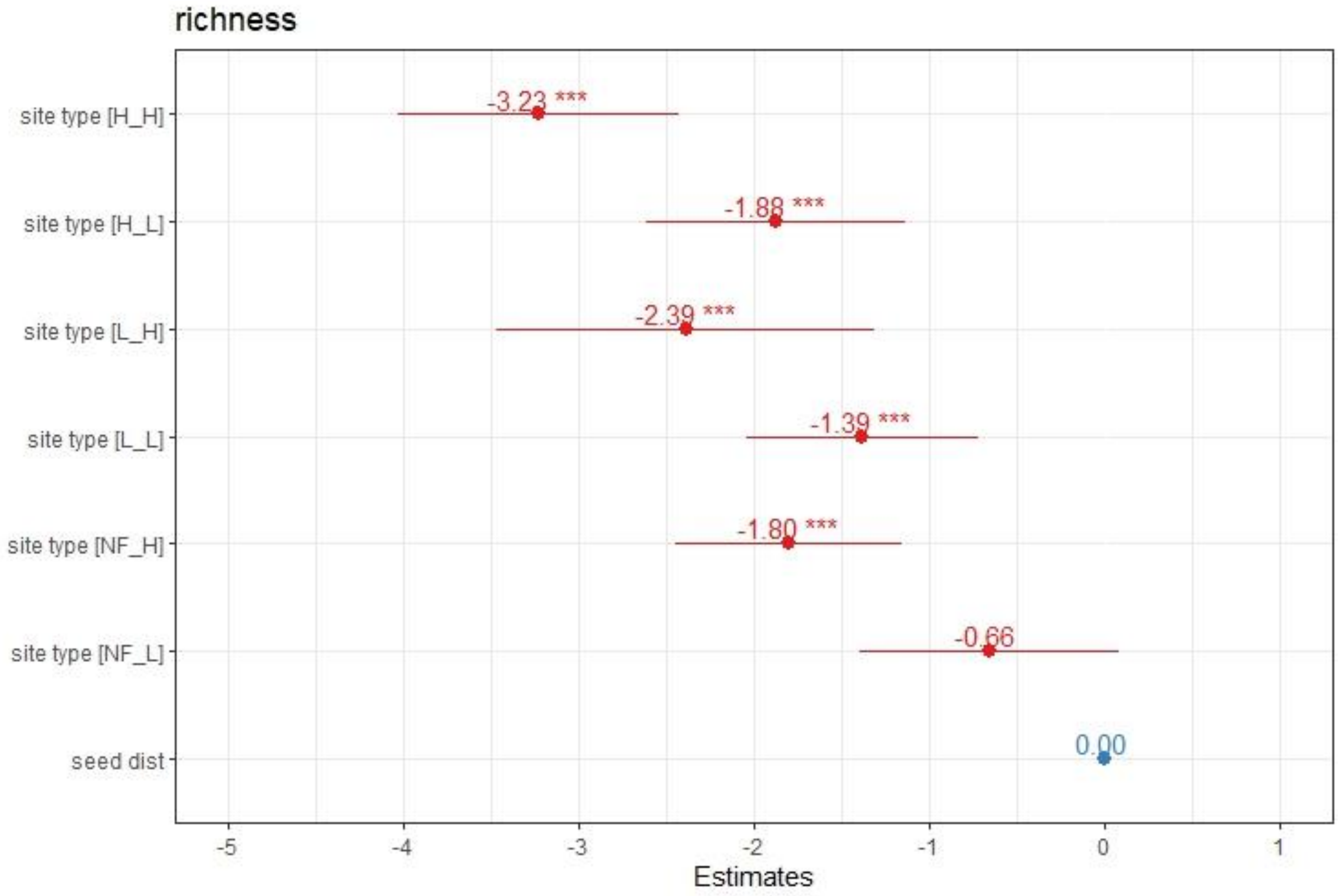
Appendix Fig. 10. Plotted rootogram to graphically compare frequencies of empirical distributions and expected (fitted) probability models (hurdle model) for understory species richness. The observed distribution is a histogram drawn on a square root scale and superimposed with a line for the expected frequencies.



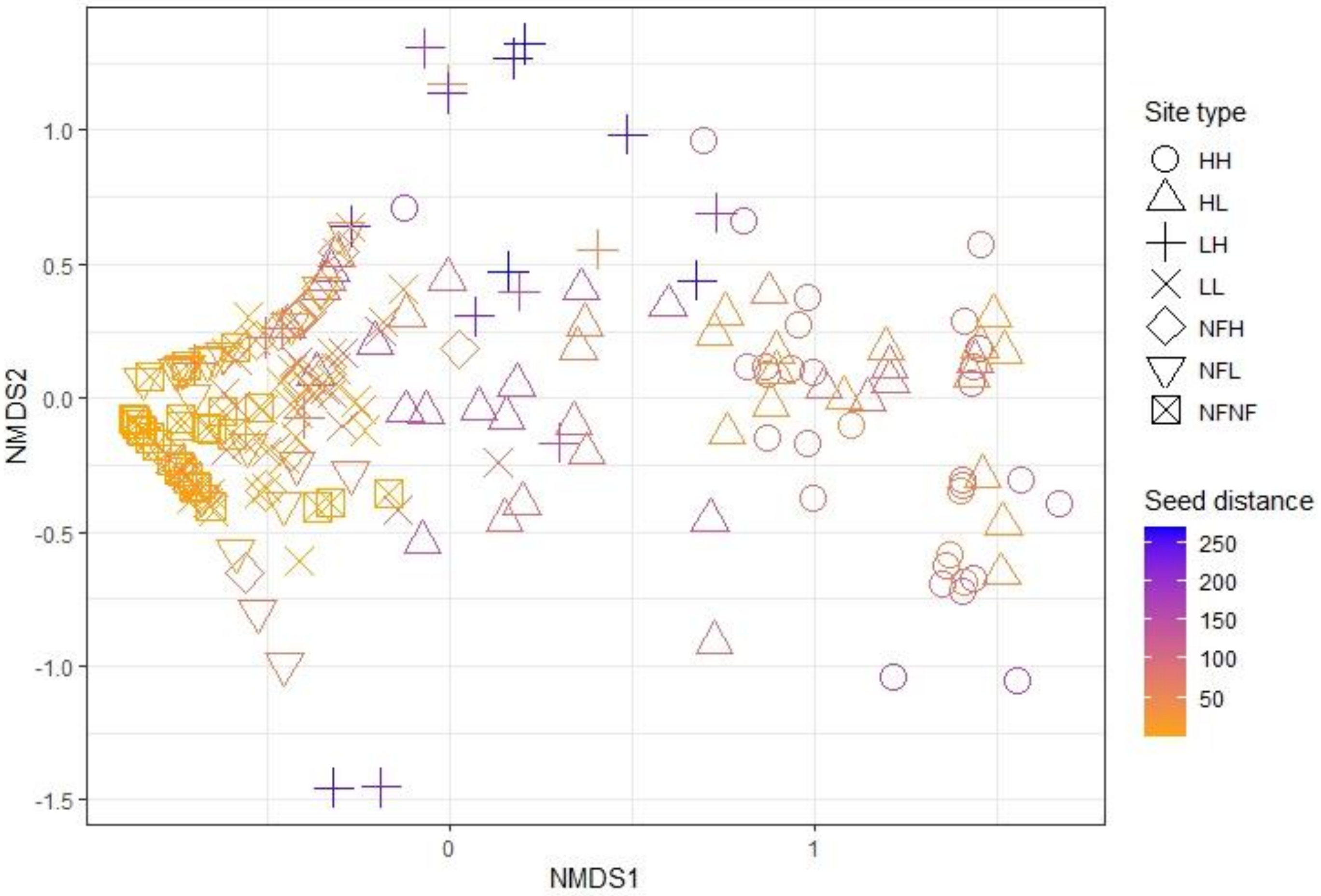
Appendix Fig. 11. Plot of predicted understory plant richness across subsite types. Formulated by the package *ggeffects* from the results of the hurdle model.



Appendix Fig. 12. Plot of predicted species richness against seed distance using the hurdle model of understory species richness. Formulated by the package *ggeffects* from the results of the hurdle model.



Appendix Fig. 13. Hurdle model output of the truncated Poisson.



Appendix Fig. 14. Non-metric multidimensional scaling (NMDS) bi-plot of young tree composition data across the study site. Each point represents a single subplot (n = 375) in a community composition space. Points closer to each other have more similar tree species composition than points farther apart. Points are colored by seed distance, and each unique shape represents a unique subsite.

Appendix Table 7. Results from the PairwiseAdonis test for young trees.

Comparison group	Variable	Degrees of freedom	Sum of squares	R^2	P-value
High-High vs Low-High	Subsite type	1	6.9173	0.22123	0.001
	Residual	85	24.3500	0.77877	NA
	Total	86	31.2673	1.0000	NA
High-High vs Low	Subsite type	1	8.2822	0.31944	0.001
	Residual	71	17.6451	0.68056	NA
	Total	72	25.9273	1.0000	NA
High-High vs Unburned	Subsite type	1	15.530	0.52068	0.001
	Residual	92	14.296	0.47932	NA
	Total	93	29.826	1.0000	NA
Low-Low vs Low-High	Subsite type	1	6.568	0.20034	0.001
	Residual	99	26.215	0.79966	NA
	Total	100	32.783	1.0000	NA
Low-Low vs Low	Subsite type	1	0.6978	0.03453	0.001
	Residual	85	19.5100	0.96547	NA
	Total	86	20.2078	1.0000	NA
Low-Low vs Unburned	Subsite type	1	2.4365	0.13101	0.001
	Residual	106	16.1609	0.86899	NA
	Total	107	18.5974	1.0000	NA
Low-High vs Low	Subsite type	1	4.4685	0.16855	0.001
	Residual	70	22.0430	0.83145	NA
	Total	71	26.5114	1.0000	NA
Low-High vs Unburned	Subsite type	1	11.121	0.37399	0.001
	Residual	91	18.694	0.62701	NA
	Total	92	29.814	1.0000	NA
Low vs Unburned	Subsite type	1	1.1543	0.08783	0.001
	Residual	77	11.9889	0.91217	NA
	Total	78	13.1432	1.0000	NA
High vs High-Low	Subsite type	1	5.361	0.16702	0.001
	Residual	100	26.736	0.83298	NA
	Total	101	32.097	1.0000	NA

High vs High-High	Subsite type	1	10.924	0.33621	0.001
	Residual	91	21.568	0.66379	NA
	Total	92	32.492	1.0000	NA
High vs Low-Low	Subsite type	1	5.0674	0.1778	0.001
	Residual	105	23.4326	0.8222	NA
	Total	106	28.5000	1.0000	NA
High vs Low-High	Subsite type	1	3.4478	0.11722	0.001
	Residual	90	25.9655	0.88278	NA
	Total	91	29.4133	1.0000	NA
High vs Low	Subsite type	1	3.8215	0.16556	0.001
	Residual	76	19.2606	0.83444	NA
	Total	77	23.0821	1.0000	NA
High vs Unburned	Subsite type	1	10.088	0.38801	0.001
	Residual	97	15.911	0.61199	NA
	Total	98	25.999	1.0000	NA
High-Low vs High-High	Subsite type	1	2.7522	0.09874	0.001
	Residual	95	25.1208	0.90126	NA
	Total	96	27.8730	1.0000	NA
High-Low vs Low-Low	Subsite type	1	6.021	0.18243	0.001
	Residual	109	26.986	0.81757	NA
	Total	110	33.007	1.0000	NA
High-Low vs Low-High	Subsite type	1	4.263	0.12619	0.001
	Residual	94	29.519	0.87381	NAN
	Total	95	33.781	1.0000	NA
High-Low vs Low	Subsite type	1	4.5423	0.16605	0.001
	Residual	80	29.519	0.83395	NA
	Total	81	33.781	1.0000	NA
High-Low vs Unburned	Subsite type	1	4.5423	0.35366	0.001
	Residual	101	22.8137	0.64634	NA
	Total	102	27.3561	1.0000	NA
High-High vs Low-Low	Subsite type	1	10.651	0.36655	0.001
	Residual	100	19.465	0.63345	NA
	Total	101	30.115	1.0000	NA

Appendix Table 8. Seed source distances across subsite types.

Subsite type	Mean distance to living forest edge (m)
Unburned	1
Low	20
High	58
Low-Low	41
Low-High	201
High-Low	84
High-High	99

Appendix Table 9. Results from the PairwiseAdonis test for understory plants.

Comparison group	**Variable**	**Degrees of freedom**	**Sum of squares**	**R^2**	**P-value**
High-High vs Low-High	Subsite type	1	1.072761271	0.049169549	4.757523827
	Residual	92	20.74483293	0.950830451	NA
	Total	93	21.8175942	1	NA
High-High vs Low	Subsite type	1	2.385362654	0.098302831	8.394523359
	Residual	77	21.88008973	0.901697169	NA
	Total	78	24.26545238	1	NA
High-High vs Unburned	Subsite type	1	4.725532945	0.16361548	17.99725339
	Residual	92	24.15640995	0.83638452	NA
	Total	93	28.88194289	1	NA
Low-Low vs Low-High	Subsite type	1	1.777415306	0.075645852	8.838335427
	Residual	108	21.71911834	0.924354148	NA
	Total	109	23.49653365	1	NA
Low-Low vs Low	Subsite type	1	1.428949102	0.058844872	5.814740752
	Residual	93	22.85437514	0.941155128	NA
	Total	94	24.28332424	1	NA
Low-Low vs Unburned	Subsite type	1	3.20297558	0.11304485	13.76489419
	Residual	108	25.13069536	0.88695515	NA
	Total	109	28.33367094	1	NA
Low-High vs Low	Subsite type	1	2.090520765	0.107361024	9.982719989
	Residual	83	17.38135735	0.892638976	NA
	Total	84	19.47187812	1	NA
Low-High vs Unburned	Subsite type	1	4.862759741	0.19831456	24.24245961
	Residual	98	19.65767757	0.80168544	NA
	Total	99	24.52043731	1	NA
Low vs Unburned	Subsite type	1	1.140627244	0.05200374	4.553088063
	Residual	83	20.79293437	0.94799626	NA
	Total	84	21.93356162	1	NA
High vs High-Low	Subsite type	1	2.142811011	0.059183312	8.366540061
	Residual	133	34.06352715	0.940816688	NA
	Total	134	36.20633816	1	NA
High vs High-High	Subsite type	1	1.745698688	0.046871845	5.999576303

	Residual	122	35.49838008	0.953128155	NA
	Total	123	37.24407876	1	NA
High vs Low-Low	Subsite type	1	2.844187543	0.072340163	10.76142573
	Residual	138	36.47266549	0.927659837	NA
	Total	139	39.31685303	1	NA
High vs Low-High	Subsite type	1	3.010423175	0.08851564	12.43027566
	Residual	128	30.9996477	0.91148436	NA
	Total	129	34.01007088	1	NA
High vs Low	Subsite type	1	2.09917081	0.061318169	7.381577921
	Residual	113	32.1349045	0.938681831	NA
	Total	114	34.23407531	1	NA
High vs Unburned	Subsite type	1	4.588732141	0.117659929	17.06878261
	Residual	128	34.41122472	0.882340071	NA
	Total	129	38.99995686	1	NA
High-Low vs High-High	Subsite type	1	1.436873562	0.056915833	5.854022397
	Residual	97	23.80871238	0.943084167	NA
	Total	98	25.24558594	1	NA
High-Low vs Low-Low	Subsite type	1	0.936699606	0.036419542	4.270954482
	Residual	113	24.78299779	0.963580458	NA
	Total	114	25.7196974	1	NA
High-Low vs Low-High	Subsite type	1	1.512195528	0.072624281	8.066095324
	Residual	103	19.30998	0.927375719	NA
	Total	104	20.82217553	1	NA
High-Low vs Low	Subsite type	1	2.184793893	0.096544009	9.403748384
	Residual	88	20.4452368	0.903455991	NA
	Total	89	22.6300307	1	NA
High-Low vs Unburned	Subsite type	1	4.208999711	0.156290854	19.07998513
	Residual	103	22.72155702	0.843709146	NA
	Total	104	26.93055673	1	NA
High-High vs Low-Low	Subsite type	1	2.427822122	0.084753538	9.4453912
	Residual	102	26.21785072	0.915246462	NA
	Total	103	28.64567284	1	NA

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Appendix Table 10. Results from a generalized linear model of understory species richness across subsites in the study area. Subsite type (number of wildfires and burn severity), and seed source distance were included as explanatory variables.

Variable	**Parameter estimate**	**Standard error**	**t**	**P-value**
Intercept	6.599943632	0.241139358	27.36983162	1.17E-90*
High-high subsite	-3.227722335	0.408700383	-7.89752706	3.33E-14*
High-low subsite	-1.877397647	0.378067666	-4.965771516	1.05E-06*
Low-high subsite	-2.391278382	0.55001242	-4.347680696	1.78E-05*
Low-low subsite	-1.385570273	0.337523794	-4.105103991	4.98E-05*
High subsite	-1.803195965	0.330812739	-5.450805713	9.22E-08*
Low subsite	-0.658225238	0.37804882	-1.741111736	0.082501987
Seed distance	5.64E-05	0.002156768	0.026135209	0.979163699

*denotes significant variables ($p < 0.05$)