THESIS

THE ECOLOGICAL EFFECTS OF MULTIPLE DISTURBANCES ON SUBALPINE FOREST

STRUCTURE AND RECOVERY IN A CHANGING CLIMATE

Submitted by

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ABSTRACT

THE ECOLOGICAL EFFECTS OF MULTIPLE DISTURBANCES ON SUBALPINE FOREST

STRUCTURE AND RECOVERY IN A CHANGING CLIMATE

Due to the shifting global climate, the severity, size, and frequency of climate-driven disturbances are increasing, inevitably causing disturbances to interact in time and space. Bark beetle epidemics and wildfires have historically shaped the disturbance regimes of western North American forests. Their interactive effects on stand dynamics and recovery are inadequately studied in Engelmann spruce (*Picea engelmannii*)- subalpine fir (*Abies lasiocarpa*) dominant forests; understanding these interactions is imperative to the management and health of forested ecosystems. Tree seedling densities and species composition, surface fuel loading, and stand structure characteristics were compared across 80 sites that experienced either high tree mortality from epidemic spruce beetle outbreaks (>50% affected basal area), high-severity wildfire (>90% tree mortality), post-outbreak high-severity wildfire (1-3 years post-outbreak), or no disturbance (control) in northern Colorado and southern Wyoming. The beetle-affected sites span multiple years post-outbreak from 1996-2017, ultimately comprising a chronosequence of beetle-affected stands. Structural changes in subalpine stands following spruce beetle outbreaks include species compositional shifts in overstory trees, and significant increases in fuel loading over time-since-outbreak. Tree seedling densities among outbreak and control sites differ significantly from burned areas, indicating that wildfires override the effects of repeated disturbances on regeneration. While a cursory assessment of post-outbreak regeneration based on height resulted in the appearance of consistent and stable forest recovery, subsequent aging techniques shed

additional light on the drivers of subalpine tree establishment. Subalpine tree regeneration may remain suppressed in the understory for over a century; post-outbreak recovery dynamics cannot be fully understood through the use of height as a proxy for seedling age. Given the strong correlation between Engelmann spruce and subalpine fir establishment with cool and moist growing conditions, there remains significant uncertainty about post-disturbance recovery and the persistence of spruce-fir forests in a warming and drying world. It is critical to understand post-disturbance fuel dynamics and stand recovery to identify hazards for subsequent fire suppression, implement treatments to enhance forest resilience, and to understand the potential consequences of climate-induced shifts in disturbance regimes on forest health.

ACKNOWLEDGEMENTS

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INTRODUCTION

Subalpine forests constitute a significant portion of high-elevation conifer forests in the western United States, extending from southern Canada to New Mexico. The subalpine zone ranges from 1275m in northern latitudes to 3355m in the southern extent (Eyre 1980), located directly below treeline. Subalpine forests are dominated by Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), and to a lesser extent quaking aspen (*Populus tremuloides*), and lodgepole pine (*Pinus contorta*). Rocky Mountain subalpine forests are characterized by warm, dry summers and cold, wet winters, with the majority of precipitation occurring in the form of snow (USDA NRCS 2020).

Disturbances have been the historic driver of subalpine forest succession and composition. Historic disturbance regimes of subalpine forests are characterized by climate-driven, high severity events such as wildfires and spruce beetle (*Dendroctonus rufipennis*) outbreaks, and wind driven, blowdown events (Veblen 2000). Wildfires in subalpine zones are typically high-severity or stand-replacing, occurring at intervals of 300-600 years (Romme and Knight 1981; Veblen 2000). Historic spruce beetle activity varies in severity, with high-severity outbreaks occurring at intervals of 100-250 years over the past several centuries (Veblen 2000). Blowdown events occur at an irregular frequency; however, subalpine species may be particularly susceptible to severe blowdowns due to shallow roots, rugged terrain, and greater exposure to wind (Veblen 2000).

Disturbances in subalpine forests can have interactive effects on one another. Disturbances can be linked, when one event influences the occurrence or severity of a subsequent disturbance, or compounded, when multiple disturbances alter post-disturbance

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recovery compared to the recovery trajectory after a single event (Harvey et al. 2013).

Blowdown events in subalpine stands can be linked to spruce beetle outbreaks by creating large amounts of host material for spruce beetles to brood in, enabling beetle population growth and ultimately increasing the probability of live host tree infestation (Hebertson & Jenkins 2007). Similarly, blowdown events have been shown to affect subsequent fire severity in subalpine stands (Kulakowski & Veblen 2007; Buma & Wessman 2012). Blowdown events result in an accumulation of surface fuels and ladder fuels, which contribute to fire spread, canopy fires, and tree mortality. The relationship between beetle kill and subsequent wildfires is not as straightforward. Multiple studies have shown that spruce beetle outbreaks are not linked to subsequent fire severity (Andrus et al. 2016; Kulakowski & Veblen 2007), or at most have a moderate effect depending on the stage of outbreak recovery a stand is in when it burns (Harvey et al. 2014). Indirect effects of fuel accumulation from beetle-caused tree mortality may reduce post-fire vegetation recovery (Carlson et al. 2017). However, subalpine stands have characteristically high fuel loads despite bark beetle presence; fires in this forest type are characteristically severe and are not fuel limited. Additionally, fire behavior is highly variable based on fine-scale fuel characteristics and dynamic effects of stand structure on fire behavior (Hoffman et al. 2015). Across numerous studies in recent literature, climate is a significant driver of fire extent and post-fire recovery in subalpine systems (Andrus et al. 2016; Kulakowski & Veblen 2007; Kulakowski et al. 2003).

Changes to climate over the past two decades have altered historic disturbance regimes in subalpine systems. In western forests, climate change has caused earlier and longer dry seasons, higher temperature minimums and maximums, and larger climatic water deficits (Seager et al. 2007; Abatzoglou & Barbero 2014). Correspondingly, subalpine systems have had an increase in

fire severity and area burned relative to the historic fire regime (Westerling et al. 2006; Schoennagel et al. 2017). Intensifying drought conditions related to a changing climate have altered the severity, frequency, and size of fires in western subalpine forests.

Warmer and drier conditions associated with climate change have also been causally linked to bark beetle outbreaks (Hart et al. 2014). Drought conditions weaken tree defenses against insect attacks (Raffa et al. 2008). Additionally, warmer temperatures associated with drought conditions influence bark beetle population levels. Overwintering beetle adults and larvae cannot survive temperatures below -26°C and 34°C, respectively (Massey & Wygant 1954). Warmer winter temperatures due to climate change favor overwintering survival rates and enable significant beetle population growth (Hart et al. 2014). Dendrochronological reconstructions have shown that drought conditions have driven historical outbreaks, and recent epidemic bark beetle outbreaks were by warmer temperatures (Hart et al. 2014; Hebertson and Jenkins 2008). Higher temperature minimums and increased drought conditions are making forests more susceptible to severe bark beetle epidemics on a landscape scale.

Alterations in disturbance regimes in conjunction with a changing climate raise concerns about forest resilience and recovery. Subalpine forest resilience depends on the ability of trees to regenerate and recover ecosystem functioning following high-severity disturbances (Johnstone et al. 2016). Warming and drying trends associated with climate change have been documented to cause regeneration failure, particularly following high-severity disturbances (Flatley & Fulé 2016; Hansen et al. 2018; Stevens-Rumann et al. 2018). Seedling regeneration in moisture-limited systems, such as subalpine forests, are particularly vulnerable to moisture deficits from increasing temperatures and reduced soil moisture from early-season snowmelt (Kueppers et al. 2017; Lazarus et al. 2017; Andrus et al. 2018). Moisture deficits, reduced precipitation, and high

temperatures are correlated with lack of establishment (Andrus et al. 2018), or post-disturbance regeneration failure (Harvey et al. 2016). According to climate model projections, increasing water deficits and maximum temperatures are expected to persist (Rangwala & Miller 2010; Williams et al. 2013; Novick et al. 2016; Yuan et al. 2019). Changing climatic conditions and unprecedented disturbance regimes may erode subalpine forest resilience, alter recovery trajectories, and create novel changes to ecosystem structure and functioning.

Climate-driven changes in disturbance regimes have created significant concerns for forest managers. Larger, high severity disturbances result in greater tree mortality across the landscape. An increase in disturbance frequency will inevitably lead to disturbance interactions. Altered disturbance regimes and subsequent interactions have the potential to have novel effects on ecosystem functioning. The effects of high severity wildfires and bark beetle outbreaks on forest structure, distribution, and regeneration in the face of climate change pose considerable uncertainties about the future of our forests. This study focuses on disturbances in subalpine forests of the Rocky Mountains. The first chapter considers structural changes in subalpine forests after bark beetle outbreaks, high severity wildfires, and their spatial interactions. The second chapter evaluates drivers of subalpine tree establishment and elucidates recovery dynamics of post-disturbance tree regeneration. Together, these chapters assess the impacts of changing disturbance regimes on forest structure and resilience, and the implications for the persistence of these forests in the future of unprecedented climatic conditions.

BEETLEMANIA: IS THE BARK WORSE THAN THE BITE? THE ECOLOGICAL EFFECTS OF BARK BEETLES AND WILDFIRES IN ROCKY MOUNTAIN SUBALPINE FORESTS[1]

2.1 Introduction

Subalpine forests are dominant in high-elevation or cold temperature sites across western North America. This far-reaching ecosystem historically experienced infrequent high severity disturbances, including wildfires and bark beetle outbreaks (Kulakowski et al. 2003; Veblen 2000). High-severity disturbances, such as wildfires and bark beetle outbreaks, are drivers of subalpine forest succession and composition, and fuel accumulation and changes. These disturbances have shaped these ecosystems for millennia but increasing extent of these disturbances in recent years has led to concerns about recovery from these disturbances and the potential interacting effects of these biotic and abiotic disturbances.

High severity disturbances in subalpine ecosystems historically occurred on the century scale and have predominantly been driven by climate (Bessie and Johnson 1995). Wildfires in these forests are relatively infrequent, typically high-severity or stand-replacing occurring at intervals of 300-600 years (Romme and Knight 1981; Veblen 2000; Schoennagel et al. 2004). Fire exclusion in subalpine forests has had minimal effects on historic fire regimes, particularly in the Rocky Mountains due to fire return intervals that span centuries (Romme and Despain 1989; Sherriff et al. 2001). Unlike forests at lower elevations, subalpine forests are not fuel limited; fires in subalpine forests are climate-driven and are often associated with drought conditions (Sherriff et al. 2001). Meanwhile, historic spruce beetle (*Dendroctonus rufipennis*)

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outbreaks varied in severity, with high-severity outbreaks occurring at intervals of 100-250 years

over the past several centuries (Veblen 2000). Dendrochronological reconstructions have shown

that drought conditions have driven historical outbreaks, and recent epidemic bark beetle

outbreaks were preceded by warmer temperatures (Hart et al. 2014; Hebertson and Jenkins

2008). In addition, reconstructions have shown widespread synchronicity of outbreaks,

indicating a regional driver such as climate (Hart et al. 2014). Climate change may be altering

the disturbance regimes of both wildfire and bark beetle outbreaks in subalpine forests with

documented evidence of increasing fire season length, greater areas burned, and even more fire

starts (Abatzoglou and Williams 2016; Dennison et al. 2014; Schoennagel et al. 2017;

Westerling et al. 2006) and may also play a role in the extent and severity of bark beetle

outbreaks in this system (Hart et al. 2014; Dell and Davis 2019).

These two disturbances significantly alter fuel complexes over time with large

implications on subsequent disturbances. High severity wildfires alter fuels both through

consumption of burnable fuel and the creation of a new dead fuels. Due to the severity of

subalpine wildfires, postfire surface fuels consist of coarse woody debris and downed logs. Slow

decomposition rates contribute to the persistence of postfire surface fuels on the landscape for

decades to centuries. Similarly, bark beetle caused mortality may have long-lasting impacts on

forest structure, stand recovery, and future disturbances. Canopy and surface fuel components

can change dramatically as the Englemann spruce (*Picea engelmannii)* move from the "yellow

phase" (1-3 years after bark beetle attack) when needles lose foliar moisture content, to the "gray

stage" (3-10 years after attack) when needles and fine branches fall, to the "old stage" (10+ years

after attack) when standing dead snags fall to the forest floor (Andrus et al. 2016). The

conversion of standing trees to downed logs is associated with an accumulation of combustible

and often continuous coarse woody surface fuel loads (Stephens et al. 2018). Additionally, several studies found that higher elevation surface fuels tend to be denser and more continuous than other forest types, contributing to characteristic stand-replacing fires in subalpine forests (Taylor and Fonda 1990; Fryer and Johnson 1988). Outbreak severity, rate of mortality, and spatial arrangement of host trees within a stand can further influence the alteration of fuel complexes throughout space and time in beetle-affected stands (Hoffman et al. 2015; Sieg et al. 2017). The effects of bark beetle caused mortality on fire behavior varies greatly throughout evolving outbreak stages (Hoffman et al. 2015; Sieg et al. 2017); the variable impacts of fuel moisture and spatial arrangement at the time of burning are important concerns for land managers and fire managers to consider.

In addition to changes in fuels complexes, spruce beetle outbreaks and wildfires alter regeneration dynamics and species recovery. Following the loss of mature Engelmann spruce trees, species dominance shifts toward subalpine fir. Post-outbreak recovery depends on the release of tree regeneration already present on site, taking decades for Engelmann spruce to attain basal area dominance (Veblen et al. 1991). On the other hand, species recovery following stand-replacing wildfires requires seed dispersal from unburned area for new recruitment cohorts (Veblen et al. 1991). Lodgepole pine and quaking aspen quickly and prolifically colonize burned subalpine stands. Serotinous lodgepole pine relies on an aerial seedbank for seed dispersal, and quaking aspen is able to resprout from extensive root systems that can survive high-severity fires (Mitton and Grant 1996; Harvey et al. 2016). Engelmann spruce preferentially establishes on bare mineral soil, allowing early, but slow, postfire recruitment (Johnstone and Chapin 2006). Due to litter layer requirements for establishment, subalpine fir is typically one of the last species to colonize a post-fire landscape (DeRose & Long 2010; Harvey et al. 2016). As postfire

recovery develops, spruce and fir attain basal area dominance over shade-intolerant lodgepole pine and quaking aspen and become climax community dominants. While lodgepole pine and quaking aspen are fire- and drought-tolerant species, spruce and fir seedlings are particularly sensitive to postfire moisture stress and large burn patches, slowing their postfire recovery following large fires and droughted conditions (Coop et al. 2010; Harvey et al. 2016). This has important implications for the future of subalpine stands; altered disturbance regimes and changing climatic conditions create uncertainty about the persistence of spruce-fir forests. Furthermore, it is unknown how these forests will respond to both spruce beetle and wildfire disturbances, requiring further investigation.

Few studies in recent literature have analyzed the potential of compounded disturbance effects on conifer regeneration in the Rocky Mountains (Carlson et al. 2017; Harvey et al. 2013; Harvey et al. 2014*a*; Kulakowski et al. 2013; Stevens-Rumann et al. 2015). In upper montane mixed-conifer forests, Harvey et al. (2014*a*) found that pre-fire beetle outbreaks can reduce post-fire regeneration if outbreak severity is high enough to diminish seed sources. However, in these lodgepole pine dominated stands, viable seeds of serotinous cones can persist in the aerial seedbank, contributing to post-fire regeneration despite pre-fire outbreaks (Harvey et al. 2014*a*). In dry mixed-conifer forests dominated by Ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziesii*), Stevens-Rumann et al. (2015) found no compounded effects from bark beetle outbreaks and wildfire on post-disturbance regeneration, while in similar systems Harvey et al. (2013) did found compounded effects on regeneration following high-severity beetle outbreaks coupled with low-severity fire, due to a reduction of pre-fire *in situ* seed sources. Finally, in subalpine forests, Carlson et al. (2017) found that there may be a reduction in post-fire tree regeneration due to pre-fire spruce beetle outbreaks. This effect of linked disturbances on

post-fire regeneration was attributed to differences in vegetation recovery because of post-outbreak surface fuel effects on fire behavior (Carlson et al. 2017). The effects of multiple disturbances on post-disturbance recovery varies by forest type and disturbance severity. Although most studies have indicated that climate has a critical impact on post-disturbance regeneration, there is considerable uncertainty in the literature regarding the nature of bark beetle-fire interactions and associated regeneration dynamics.

This study focused on the effect of spruce beetle outbreaks, high-severity fires, and their interactive effects on subalpine forests in Northern Colorado and Southern Wyoming, USA. We constructed a chronosequence of beetle-affected stands in various post-outbreak stages in order to analyze how fuels change over time following the spruce beetle epidemic. We chose to focus on outbreaks that occurred from 1996 until 2017 due to the resulting widespread mortality from these events, as well as widespread discrepancies in the scientific literature on interacting disturbances and recovery dynamics in these systems. The goals of this study were to answer the following questions: 1) how does time-since-outbreak affect stand and fuel structures in subalpine forests? 2) how does the recovery trajectories and fuel complexes differ between wildfires, outbreaks, or a combination of the two disturbances? and 3) what are the site-specific drivers of post-disturbance fuels and tree regeneration?

2.2 Methods

2.2.1 Study Area

Subalpine forests range in latitude from southern Canada to New Mexico, typically directly below the tree line. The subalpine zone in the Central US Rockies is characterized by warm, dry summers, and cool, wet winters with the majority of annual precipitation in the form

of snow. These forests commonly consist of long-lived shade-tolerant species such as

Engelmann spruce and subalpine fir (*Abies lasiocarpa)*, and to a lesser extent quaking aspen

(*Populus tremuloides*) and lodgepole pine (*Pinus contorta*) at earlier seral stages.

Study sites were located in northern Colorado and southern Wyoming in subalpine forests

in the Arapaho-Roosevelt National Forests, Routt National Forest, and Medicine Bow National

Forest (Figure 2.1). Sites were located in subalpine stands at a range of elevations from 2,591 to

3,326 meters above sea level and were predominately composed of Engelmann spruce and

subalpine fir, and to a lesser extent quaking aspen and lodgepole pine. On average, study sites

received 97.03 centimeters of precipitation per year, ranging from 48.77 to 115.32 centimeters

over the timespan of the outbreak under study (USDA NRCS 2020). The average temperatures

for study sites range from a mean low of -8.11° C to a mean high of 13.83° C (USDA NRCS

2020). A large-scale (5,261 ha (13,000 ac)) blowdown event occurred in 1998 in the Hahns

Peak/Bears Ears Ranger District of the Routt National Forest in northern Colorado (Schaupp et

al. 1999). This event initiated spruce beetle infestations in healthy, standing Engelmann spruce

trees, triggering a landscape-scale epidemic outbreak, which has been exacerbated by warmer

and drier conditions.

2.2.2 Site Selection

We used Aerial Detection Survey (ADS) data of spruce beetle outbreaks that have

occurred from 1996 to 2017 collected by the USDA Forest Service, Forest Health Protection and

its partners, to identify areas with beetle caused mortality (USFS 2017). ADS data is collected

from an aircraft, from which the collector manually indicates forest changes on a map. Due to

this methodology's nature, bark beetle outbreaks are not detected until after the tree needles start

to fade and change color. Therefore, there is typically a 1-3 year lag between initial infestation

and detection through aerial surveys, thus we used the year of initial detection above 10% tree mortality as the outbreak year. We used Monitoring Trends in Burn Severity (MTBS) data on wildfires in spruce-fir forests (MTBS Data Access 2017).

ArcMap (10.6) was used to generate random points within outbreak polygons across a gradient of time-since-outbreak, as well as within burned areas. Outbreak plots were defined as >50% of stand basal area (m^2/ha) affected by spruce beetle. We used MTBS data to map high-severity fires since 1996, as well as post-outbreak high-severity fires. All plots were located at least 50 meters from any trail or road. Both severity and bark beetle mortality were field verified.

The outbreak plots were categorized into five different groups based on the year the outbreak was detected: 1996-2004, 2005-2008, 2009-2010, 2011-2014, 2015-2017. Post-outbreak fire sites were sites where a spruce beetle outbreak was detected 1-3 year prior to a high-severity wildfire (Burn Ridge Fire, 2002; Hinman Fire, 2002; Wolverine Fire, 2005) and high-severity fire sites were burned in 2002 without previously detected outbreaks (Big Fish Fire, Lost Lakes Fire, Hinman Fire). Control plots were defined as <25% stand basal area colonized and/or dead. Ten sites were established in each of the five outbreak groups as well as in high severity burned sites, post-outbreak fire sites, control sites for a total of 80 plots with equal representation in each group. This chronosequence of outbreaks represents the spread of epidemic outbreaks over time; the earliest outbreaks started in the Routt National Forest and subsequently spread to the Medicine Bow National Forest, Arapaho National Forest, and Roosevelt National Forest. Given, the time from infestation to detection, as well as the progressive nature of outbreaks, in that all trees at a particular site likely did not die in the same year, the "year of outbreak" is somewhat of an estimate, thus we used outbreak time groups. All data was collected in the summers of 2018 and 2019, resulting in a chronosequence of 1 to 21

years post outbreak sites, while post-outbreak fire sites and high severity burned sites were measured 14-17 years post-fire.

2.2.3 Sampling Design

We modeled our plot design after Ott et al. (2018), establishing 0.08-ha circular fixed area plots. Topographic characteristics were collected at each plot, using smartphone Global Positioning System for elevation and aspect collection and a clinometer for slope collection. Within each plot, measurements were taken for each standing tree ($\geq$ 12.7cm diameter at breast height (DBH). Species, DBH, crown base height (on living trees), tree health, spruce beetle and other insect impacts were recorded. Tree health was ranked on a scale from 1-8 to quantify live, dead or dying status (modified from Forest Inventory and Analysis National Core Field Guide, USDA 2017). We used live basal area as a proxy for canopy cover. Standing Engelmann spruce trees were flagged or tagged for future monitoring. Pre- and post-disturbance basal area and density was calculated by species.

We established four 16.1m long transects, within each fixed area plot, that extended in the cardinal directions from the plot center. Following Brown (1974), we tallied woody surface fuels in 1- (<0.6cm), 10- (0.6-2.5cm), and 100-hour (2.5-7.6cm) size classes along the transects. 1-hour fuel data were collected for seven meters on each transect. 10- and 100-hour fuels were counted along the entire length of the transects (16.1m). A total of 20 litter and duff depths were taken along the four transects. Point intercept sampling was employed along each transect for a total of 100 points to identify life forms of understory growth (shrub, forb, graminoid, tree) and the corresponding substrate (litter, woody debris, moss/lichen, rock, bare ground).

We established two types of subplots. For 1000-hour fuels (≥7.6cm) (coarse woody debris), we established 0.015-ha (6.9m radius) circular subplots located at the plot center. We measured end diameters and length of each downed log; if a log extended outside of the subplot, we took the end diameter at subplot edge. We modeled transect sampling lengths and the coarse woody debris subplot area after Sikkink and Keane (2008) to bolster plot representativeness. To quantify tree regeneration, we established five 0.004-ha (3.6m radius) subplots: one center subplot and one at the end of each transect. In each regeneration subplot, we counted and classified all tree regeneration (any living tree <2m height) by height and species.

2.2.4 Statistical Analyses

Statistics and graphics were completed in R (R Core Team 2019). To answer question one, we used a simple linear model (Gaussian family) to analyze the effect of time since outbreak on different forest structural parameters, including overstory mortality, stand structure, and fuel loading (Table 1). The presence of insect mortality agents other than spruce beetle was negligible in all sites and was not included in analyses. To answer question two, we used one-way analyses of variances (ANOVAs) using disturbance groups as the predictor variable with similar response variables as those to answer question one. Tukey-adjusted comparisons were used to compare ANOVA groups using the emmeans package in R (Lenth 2019). There was no observed change in total seedling densities, Engelmann spruce seedling densities, nor subalpine fir seedling density across outbreak groups ($F<0.7$, $P>0.40$). For this reason, analyses on seedling densities were performed on disturbance type (bark beetle, post-outbreak fire, high severity fire, control), rather than across the chronosequence of time since outbreak in both ANOVAs and GLMs by species.

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For question three, generalized linear models (GLM; Gaussian family) were used to assess site specific drivers on seedling density by species, stand structure characteristics and fuel complexes. Aspect was transformed using Beer's transformation for analyses. The control group was used as the reference for the disturbance groups in the GLM analyses. Individual models were developed for different tree seedling species; all significant predictors were incorporated into larger, inclusive generalized linear models. Due to differences in life history traits, corresponding live standing densities were included in the GLM analyses for drivers of lodgepole pine and quaking aspen regeneration.

We tested the assumptions that these sites were comparable by assessing pre-outbreak basal area. We included all bark beetle killed stumps to retroactively composite a pre-outbreak basal area and performed an ANOVA to assess differences in basal area among disturbance groups. We assessed the assumptions of normality and variance with Shapiro-Wilks and Levene's tests. Due to the widespread variability within and among groups of seedlings, log-transformed seedling densities were used in analyses in order to satisfy normality assumptions for ANOVA and regression models. We also tested assumptions of autocorrelation among plots due to the clustering of plot locations by including it as a factor in a generalized linear mixed model and it represented less than 1% of the variance and thus was excluded. A threshold of $\alpha=0.05$ was used to designate statistical significance, and each study plot was a sample unit (N=80).

2.3 Results

Across all post-outbreak sites, mean pre-outbreak basal area was 60.5 ± 19.6 m^2/ha, with Engelmann spruce and subalpine fir as codominant overstory. Lodgepole pine and quaking aspen made up 2.48% and 0.60% of pre-disturbance density, respectively. Pre-disturbance basal area

were similar across groups (F=1.34, P=0.268). Beetle-affected trees (either dying or dead, hereafter referred to as snags) ranged from 50% to 96% of plot basal area, with an average of 65% affected plot basal area. The quadratic mean diameter of beetle-killed trees was 41.7$\pm$10cm.

2.3.1 Time-Since-Outbreak Influences Stand Structure and Fuel Complexes

Time-since-outbreak significantly impacted many fuels and stand structure characteristics. The abundance of standing Engelmann spruce snags was lowest in the oldest outbreak group (1996-2004), and highest in the intermediate outbreak group (2009-2010) (F=4.742, P=0.003). Sites in the youngest outbreak groups had moderate levels of standing Engelmann spruce snags (Figure 2.2). The proportion of standing live Engelmann spruce density in plots decreased with increasing time-since-outbreak. In control sites and newly infested bark-beetle sites, live standing Engelmann spruce dominated stand density over subalpine fir. In the oldest outbreak sites, live Engelmann spruce density dropped by as much as 94% compared to pre-outbreak Engelmann spruce density (F=60.714, P<0.0001). Beetle-killed trees begin to fall ~8-9 years following spruce beetle outbreak detection (R^2=0.142, P=0.007), This corresponded to an increase in dead woody surface fuels especially in the larger size classes (Figure 2.3).

Total downed woody fuel loading increased with time-since-outbreak (Figure 2.3e). This relationship was not observed in 1-hour fuels but is apparent in all other fuel size classes (Figure 2.3a). Woody fuels in the 10-hour, 100-hour, and 1000-hour size classes all have a positive linear relationship with increasing time-since-outbreak (Figure 2.3b, c, d).

2.3.2 Disturbance Type Impacts on Forest Structure and Fuels

Total fuel loading is highest in the oldest outbreak group (1996-2004) and high-severity fire group (F=4.85, P<0.001, Figure 2.4a). 1-hour fuel loading is lowest in high-severity burn sites and highest in the oldest outbreak site (F=2.66, P=0.02). Fuels in the 1-hour size class are similar across control, post-outbreak fire, and recent outbreak groups (Figure 2.5). 10-hour fuel loading is greatest in oldest outbreak sites, which is not statistically different than 10-hour fuel loading in either burn group (F=4.61, P<0.001; Figure 2.5). 10-hour fuel loading is significantly lower in recent outbreak and control groups compared to the oldest outbreak sites. Fuels in the 100-hour size class were greatest in the oldest and post-outbreak fire sites, but were not statistically different in the intermediate outbreak and high severity burn groups. The lowest 100-hour fuel loading was found in the two most recent outbreak groups and control sites (F=5.283, P<0.001; Figure 2.5). Similarly, coarse woody debris fuel loading (1000-hour size class) was highest in the oldest outbreak and the high severity burn group, but were not statistically different in the intermediate outbreak years, post-outbreak fire, and control groups (F=4.52, P<0.001; Figure 2.5). Coarse woody debris makes up a large proportion of total downed woody fuel loading; the patterns observed in 1000-hour fuels mirror total woody fuel loading trends.

Understory vegetation cover remained consistent across groups, showing no relationship with increasing time-since-outbreak. Similarly, litter and duff depths remained constant across outbreak groups but were significantly reduced in burned groups (F=2.96, P=0.009; 2.47, P=0.02). Litter depth is highest in control sites (mean=2.95cm), and lowest in high severity fire and post-outbreak fire sites (1.37cm and 1.66cm, respectively) (F= 2.96, P=0.009). Duff depths are lowest in both burn groups (mean depth of 3.2cm-3.6cm) and highest in outbreak and control groups (mean depth of 6.1cm-7.0cm) (F=2.47, P=0.02).

Tree seedling densities were significantly reduced in both burn groups (F=6.31, P<0.0001) (Figure 2.4b). Seedling densities in outbreak and control groups were not statistically different from each other (F=9.17, P<0.0001). Engelmann spruce seedling densities in control sites are statistically similar to burn groups and bark beetle sites (Figure 2.6a). Subalpine fir seedlings are significantly lower after wildfire and post-outbreak fire than in bark beetle and control sites (F=15.52, P<0.0001; Figure 2.6b). Subalpine fir seedling densities are statistically similar in bark beetle and control sites. Engelmann spruce seedling densities are significantly lower in both burn groups than in bark beetle sites (F=5.29, P=0.002). However, this pattern of seedling densities was not observed for other species, such as lodgepole pine and quaking aspen regeneration, that comprised a smaller proportion of tree seedling densities across our sites. Lodgepole pine seedling densities are either lowest or absent in bark beetle sites, and highest in post-outbreak fire sites (F=6.66, P<0.001). Lodgepole pine seedling densities in high-severity fire and control sites are not statistically different than bark beetle or post-outbreak fire sites (Figure 2.6c). Quaking aspen regeneration densities are lowest in bark beetle sites, and highest in post-outbreak fire sites (F=3.49, P=0.02). Similar to lodgepole pine, quaking aspen regeneration densities in high-severity fire and control sites are not statistically different from bark beetle or post-outbreak fire sites (Figure 2.6d).

2.3.3 Site Specific Drivers of Forest Structure

Elevation (P=0.15), aspect (P=0.44), and slope (P=0.28) are not significant in predicting total woody fuel loading when experimental groups are included in the model (Table 2.1). The oldest outbreak group (P=0.01) and high-severity fire group (P=0.003) are both positively correlated with total woody fuel loading relative to the control group. Elevation (P=0.16), aspect (P=0.83), slope (P=0.16), and group are not correlated with 1-hour fuel loading. Elevation is

negatively correlated with woody fuel loading in the 10-hour size class (P=0.002). Aside from correlations with time-since-outbreak and burn groups described above, neither aspect (P=0.85) nor slope (P=0.47) were correlated with woody fuels in the 10-hour size class (Table 2.2). Similarly, elevation has a negative correlation with fuels in the 100-hour size class (P=0.0006). Aside from correlations with disturbances, neither aspect (P=0.67) nor slope (P=0.33) have significant correlations with woody fuel loading in the 100-hour size class. Finally, aside from correlations with disturbances, there were no significant abiotic predictors of woody fuels in the 1000-hour size class (elevation: P=0.22; aspect: P=0.43, slope: P=0.31; Table 2.2).

For each species, disturbance type was a significant predictor of seedling densities (P<0.009) (GLM, Table 2.3). Additionally, live basal area was strongly correlated with total seedling density (F=17.23, P<0.0001). Live basal area, used as a proxy for canopy cover, was not included in the GLM analyses due to the correlation between live trees and disturbance type.

Similar trends were observed in both dominant subalpine species. Disturbance type was the only significant variable correlated with Engelmann spruce seedling density. High severity fire (P=0.006) and post-outbreak fire (P=0.009) were both negatively correlated with Engelmann spruce seedling densities (Table 2.3). Live basal area was strongly correlated with Engelmann spruce seedlings; greater live tree coverage was correlated with higher seedling densities (P=0.001). Contrary to our expectations, elevation (P=0.77), aspect (P=0.38), slope (P=0.17), and total fuel loading (P=0.68) were not correlated with Engelmann spruce seedling densities. Similarly, disturbance type was the only significant predictor of subalpine fir seedlings; high severity fire (P<0.0001) and post-outbreak fire (P<0.001) groups were negatively correlated with subalpine fir densities. Elevation (P=0.90), aspect (P=0.57), slope (P=0.30), litter cover (P=0.74), and total woody fuel loading (P=0.36) were not correlated with subalpine fir seedling densities.

Live basal area had a strong positive correlation with subalpine fir seedlings (F=20.45, P<0.0001).

Different predictors were observed for lodgepole pine and quaking aspen seedling density (Table 2.3). As elevation increased lodgepole pine seedling density decreased (P=0.009) and similarly as total woody fuel loading increased lodgepole pine seedling density declined (P=0.05). Disturbance type and standing lodgepole pine density (P<0.004) were both positive predictors of seedling densities. Specifically, post-outbreak fire (P=0.002) sites were positively correlated with lodgepole pine regeneration. Similarly, elevation was the only negative predictor of quaking aspen regeneration (P=0.002); there were fewer regenerating aspen at higher elevations. Disturbance type and standing aspen density were positively correlated with aspen regeneration density (P<0.0001 for both). Both high severity fire (P=0.006) and post-outbreak fire (P<0.001) sites were positively correlated with quaking aspen regeneration densities.

2.4 Discussion

Forest disturbances, such as bark beetle outbreaks and wildfires, leave ecological legacies that can influence the occurrence and behavior of future disturbances (Johnstone et al. 2016). This study improves our understanding of the recovery trajectories following bark beetle outbreaks, wildfires and overlapping disturbances, 1-21 years following these disturbances. Post-outbreak fuel loading, across all size classes except 1hr fuels, increased linearly with time-since-outbreak. Similarly, high fuel loads accumulate substantially after high-severity wildfires. High post-disturbance fuel loads and their lasting effects will persist on the landscape for decades into the future. Subalpine tree seedling densities were significantly lower following wildfires than bark beetle outbreaks, with no observed evidence of compound effects from multiple disturbances on tree seedling densities. Tree seedling densities were consistent over time-since-

outbreak, indicating that beetle-affected stands will slowly recover to spruce-fir dominated forests in the absence of fire.

2.4.1 Forest Composition

The abundance of Engelmann spruce snags initially increased as beetles successfully killed host trees and were initially identified as "dying" but not fully dead and then decreased with increasing time-since-outbreak as trees fell and accumulated as woody surface fuels. The greatest density of standing snags were present 6-9 years after spruce beetle outbreak, before snags began to fall, which is similar to post-outbreak structural changes in other forest types such as Douglas fir and Ponderosa pine forest types (Negrón et al. 2009; Hoffman et al. 2012; Donato et al. 2013; Jenkins et al. 2014).

The loss of host trees in beetle-affected stands resulted in an increase of subalpine fir percent composition over time-since-outbreak. This creates subalpine fir-dominated stands until Engelmann spruce regeneration matures into the canopy (Veblen et al. 1991). In stands unaffected by bark beetles, Engelmann spruce had stand density dominance over subalpine fir. However, species dominance switched to favor subalpine fir with increasing time-since-outbreak. This switch in species dominance can result in long-term changes to subalpine forest structure if there is reduced Engelmann spruce regeneration as expected with warming and drying conditions (Lazarus et al. 2017). Consistent with other studies on post-outbreak subalpine structure in different geographic areas, we observed higher subalpine fir tree regeneration densities in most bark beetle stands, though Engelmann spruce was still a component of the regeneration (DeRose and Long 2010). The reduction in mature Engelmann spruce trees will shift host tree size distribution to smaller size classes, and decrease stand susceptibility to subsequent spruce beetle infestations for as long as 60 years (Hart et al. 2015)

2.4.2 Fuel Complexes

Constructing a chronosequence of changing fuel structures over time allowed us to substitute space for time and study the effect spruce beetle outbreaks through time in the Rocky Mountains. Others have used this method in examining fuel complex changes following wildfires, but not outbreaks (e.g. Roccaforte et al. 2012, Stevens-Rumann et al. 2020). As expected, there was an overall increase in total downed woody fuel loading with increasing time-since-outbreak. The highest woody fuel loading was in the oldest outbreak site. This correlation was not observed with 1-hour fuel loading, nor was the expected peak in fine woody fuels observed with the onset of the "gray stage" (Andrus et al. 2016; Jenkins et al. 2012). This is likely due to the high spatial variability of 1-hour fuel loading in subalpine forests. Subalpine forests are characteristically dense; the continual loss of fine twigs from the overstory to the forest floor could obscure any initial pulse in 1-hour fuel loads. Additionally, these forests have very slow rates of organic matter turnover and decomposition, leading to consistent accumulation of fine woody fuels over time (Meyer 2013). For the 10-hour fuel loads, there was a larger increase in fuel loading ~17 years after outbreak detection. At this point in post-outbreak recovery, beetle-induced fuel accumulation was distinct from background variability in fine woody fuel loading. There was a gradual increase in 100-hour fuel loading after ~8 years post-outbreak detection. This is consistent with the end of the "gray stage" transitioning into the "old stage" of post-outbreak recovery. This trend was observed in 1000-hour fuel loading as well, as standing dead trees begin to fall ~10 years after outbreak detection and continue to fall as more years pass; this finding is consistent with post-outbreak treefall in Douglas-fir and Ponderosa pine forests as well (Donato et al. 2013; Hoffman et al. 2012). This pattern in the larger fuel size classes drove total downed woody surface fuel loading for the post-outbreak trajectory of

subalpine stands, contributing to a marked increase in total fuel loading after 10 years following outbreak detection. Due to the slow decomposition rates characteristic to subalpine stands, accumulated downed woody surface fuels from bark beetle outbreaks will persist on the landscape for decades to a century (Mietkiewicz et al. 2018).

As time passes after a spruce beetle outbreak, standing snags are transferred to dead surface fuels. This causes canopy fuels to be discontinuous as live interconnecting canopy fuels were reduced. There are still ladder fuels that maintain connectivity between fuel complexes due to dense, suppressed regeneration that makes up the understory and subcanopy of subalpine forests. This change in fuel distribution throughout the fuel layers is not expected to enhance the risk of fire spread due to reduced canopy bulk density and fuel continuity, although increased wind penetration can override these effects (Black et al. 2013; Jenkins et al. 2008; Sieg et al. 2017). Instead, fire spread is likely to change from wildfires that predominately spread throughout the crown, to surface fires with long residence times (Donato et al. 2013). Standing snags also pose a risk to firefighters as they fall, especially if they become fire weakened. Thus, it is important to allocate human resources carefully in these bark beetle affected areas, especially 6-9 years post-outbreak, when snag fall rates begin to accelerate.

In addition to altered fire behavior, beetle-caused fuel accumulations can impact nutrient cycling and wildlife habitat. Downed logs persistent on the landscape can significantly increase soil carbon (C) and inorganic nitrogen (N) pools (Wiebe et al. 2014). Increased soil C:N results in elevated immobilized nitrogen that is unavailable for plant uptake until decomposition ensues (Edburg et al. 2012). Due to slow decomposition rates, reduced soil fertility from fuel accumulation may impede vegetation growth for decades to a century (Edburg et al. 2012). Implications of fuel accumulations of wildlife habitat vary significantly by species. Small

mammals, such as the red-backed vole (*Clethrionomys gapperi*), selectively use areas with abundant coarse woody debris (Ucitel et al. 2003). On the other hand, Rocky Mountain elk (*Cervus canadensis*) avoid beetle-killed forests, which results in a loss of viable habitat (Lamont et al. 2019). Fuel prescriptions in beetle-affected forests will have highly variable effects on ecosystem functioning; managers must consider differing impacts when prioritizing treatment objectives.

Wildfires in subalpine stands left greater total woody surface fuel loads on the landscape than control stands; this study is one of very few recent publications to document post-fire fuel characteristics in Rocky Mountain subalpine stands. These burned sites had greater proportions of 100- and 1000-hour fuels, while 1- and 10-hr fuels were unchanged compared to control sites. Burned sites had high coarse woody debris loads because low intensity surface fires will have high severity effects in subalpine stands, as Engelmann spruce and subalpine fir are thin-barked species that are easily killed by fire (Starker 1934). Up to 100% overstory mortality led to significant tree fall and coarse woody debris accumulation 14-17 years post-fire. While few recent studies document post-fire fuel loads in subalpine stands, our findings were consistent with Romme (1982), who found that high post-fire fuel loads in subalpine forests were mainly comprised of fire-killed stems, which can take decades to centuries to decompose. Abundant litter and 1-hour fuels contribute to initial fire spread, while coarse woody debris and duff layers can perpetuate smoldering and soil heating effects (Romme 1982), however we did not see litter and duff depths similar to control sites even 14+ years after wildfires and 1-hr fuels were similar to control sites. Some hypothesize that following a wildfire could take up to 100 years for these fine fuel layers to develop from litterfall (Romme 1982). Consequently, recently burned stands

may have reduced susceptibility to subsequent fires or beetle outbreaks for 100 years or more (Kulakowski and Veblen 2007).

Post-outbreak fire sites had fuel loads that were slightly lower than high-severity sites though not significantly so, but higher than recent outbreak and control sites. This could be due to the consumption of downed fuels from beetle-killed trees. However, the post-outbreak fire sites analyzed in this study capture fires that occurred 1-3 years after the bark beetle outbreak. At this stage after the outbreak, snags had likely not yet begun to fall, and substantial coarse fuels had not accumulated. Additional data on fires that occurred in later stages of outbreak recovery may provide different conclusions about compounded disturbances on fuel complexes and subalpine tree regeneration. Although, numerous empirical studies have found weak or non-significant relationships between beetle-kill fuels and subsequent fire severity in terms of canopy mortality, increased coarse woody surface fuels from beetle-killed trees may result in extended smoldering over a larger surface area, increased heat release from surface fires, and detrimental impacts on soil health (Brown et al. 2003; Certini 2005; Harvey et al. 2014a; Carlson et al. 2017). Assessing heating effects on soils was beyond the scope of this study given the long time-since fire used in this study. Further studies in subalpine forests are needed to understand the influence of increased fuel loads due to spruce beetle outbreaks on burning conditions, high residence times, soil heating effects, and ultimately plant community responses.

2.4.3 Tree Regeneration

Total tree seedling densities were similar among outbreak groups and controls. This trend was observed in Engelmann spruce and subalpine fir seedling densities as well. Seedling densities in the oldest outbreak group are consistent with densities in the newest outbreak group. The lack of significant differences in tree seedling densities across the chronosequence of beetle-

affected stands could be due to the shade tolerant nature of Engelmann spruce and subalpine fir. Subalpine tree species do not need canopy openings for seedling establishment, which differs from the tree regeneration response after bark beetle outbreaks in other forest types (Hawkins et al. 2013; Collins et al. 2011). Conversely, canopy cover was a significant predictor of subalpine tree seedlings, as shaded, moist microclimate conditions favor subalpine fir and Engelmann spruce. This relationship with canopy cover could also be indicative of seed source. Both species can persist in the subcanopy or understory for many years. This role of overstory trees as facilitators of subalpine species seedling survival in spruce beetle-affected stands is consistent with recent studies in subalpine stands of southwestern Utah (Pettit et al. 2019). Although the spruce beetle outbreaks observed in this study were high-severity disturbances, there were still some live mature Engelmann spruce remaining in or nearby affected stands. Middle-aged, cone bearing Engelmann spruce that have not been killed by spruce beetles will continue to produce seeds, allowing for early cohorts of Engelmann spruce tree seedlings in beetle-affected stands, though the quantity of seed fall has certainly changed following outbreak. This indicates that the sampled outbreak stands will continue to persist as spruce-fir forests. However, there is not an observed increase in subalpine tree regeneration over time-since-outbreak. These findings of low post-outbreak tree regeneration are consistent with Carlson et al. (2020) and may be attributed to reduced snowpack and increased moisture deficits observed in western subalpine forests (Andrus et al. 2018; Lazarus et al. 2017). Ultimately, we are unable to fully assess the true dynamics of subalpine tree regeneration without aging every seedling that was measured. Insight into establishment dates through dendrochronological techniques may clarify the difference between suppressed advanced regeneration and post-outbreak recovery in these stands (Schapira et al. in

preparation). Assessing the tree seedling data as it is now, these stands will continue to regenerate as spruce-fir forests in the absence of large fire events.

Engelmann spruce and subalpine fir seedling densities were dramatically reduced in both burn groups compared to outbreak and control groups. However, subalpine tree seedling densities were similar after high-severity burns and post-outbreak burns. There was no evidence of compounded effects from multiple disturbances on subalpine tree species regeneration. This finding is consistent with studies in subalpine forest types (Kulakowski et al. 2013), as well as other forest types in the Rocky Mountains (Harvey et al. 2014*b*; Stevens-Rumann et al. 2015). Wildfires in subalpine stands are characteristically severe; viable seed sources within burn patches are limited, if existent at all. Recolonization of the burned area will depend on seed delivery and establishment from unburned Engelmann spruce and subalpine fir seed sources, which can be impeded by large burn patch sizes (>150m to live seed source), reduced soil moisture and climatic water deficit from warming conditions (Andrus et al. 2018; Harvey et al. 2016). Harvey et al. (2016) documented significantly reduced Engelmann spruce and subalpine fir post-fire establishment associated with severe post-fire drought conditions. Reforestation of burned subalpine stands may take decades to centuries (Rodman et al. 2019), as subalpine tree species have episodic seed production dependent on climatic conditions (Beuchling et al. 2016). If subalpine burned areas were to reburn at higher frequencies than the system is historically adapted for, there may be major shifts in forest structure. Repeated burns in subalpine forests can reduce material legacies (e.g., coarse woody debris) that facilitate seedling survival, increase patch sizes that reduce seedling establishment, and kill off subalpine tree species before seed production (Coop et al. 2010; Harvey et al. 2016*a*; Harvey et al. 2016*b*; Turner et al. 2019).

Climate-induced fire regime shifts can result in unprecedented conversions of subalpine forested ecosystems to non-forested systems.

Conversely, lodgepole pine and quaking aspen regeneration densities were highest after spruce beetle outbreak and fire. Lodgepole pine seedling establishment was dependent on pre-disturbance stand structure; if viable seed sources are present, post-fire conditions favor lodgepole seedling recruitment due to exposed mineral soil, lack of shade by other seedlings, and light seeds that can be dispersed easily by wind (Harvey et al. 2016; Johnstone and Chapin 2006). Additionally, lodgepole pine is a drought tolerant species; post-fire seedling establishment is unaffected by post-fire drought (Harvey et al. 2016). Quaking aspen regenerates prolifically after high-severity fires, through which other seedlings that may compete for light availability are removed. Quaking aspen have underground root systems that can remain viable for hundreds of years despite aboveground tree mortality (Peet 2000). This vegetative life strategy allows aspen to resprout after high-severity fires, quickly attaining stand dominance while other conifers may be reduced due to dispersal distances, post-fire climate, and reduced soil moisture. The climatic predictions of increased high-severity fires in subalpine stands will favor aspen dominance (Kulakowski et al. 2013). Additionally, given the serotinous nature of lodgepole pine, repeated fires can perpetuate lodgepole pine dominance (Harvey et al. 2016). However, the proportion of serotiny across all of our sites is unknown and highly variable. There were fewer quaking aspen regeneration and lodgepole pine seedlings at higher elevations, which corresponded with fewer overstory aspen and lodgepole pine trees. However, climate change models predict range shifts upward in elevation; furthermore, faster range shifts in high elevation ecotones are expected relative to lower elevation forests (Kroiss and HilleRisLambers 2015). A

warming climate coupled with changing disturbance regimes may result in unprecedented losses to subalpine tree species.

Contrary to other studies in subalpine forest types (Andrus et al. 2018; Coop et al. 2010; Harvey et al. 2016), we did not observe any effect of elevation, aspect, nor slope on subalpine climax species seedling densities. This could be because cool and moist growing conditions were pervasive throughout the subalpine stands that were sampled. Plots were not established on the range edge of the subalpine zone, which may explain why we did not observe the expected trend of Engelmann spruce and subalpine fir moving upward in elevation with warming climates (Kroiss and HilleRisLambers 2015). Moreover, abiotic factors may have a weakened effect on seedling densities as warming conditions hinder seedling survival. Seedlings from the experimental groups of this study have been destructively sampled and aged using dendrochronological techniques, in order to pinpoint establishment dates (Schapira et al. in preparation). These ages will provide a clear understanding of how, or if, subalpine stands are recovering from these disturbances. Data on distance to seed source may elucidate structural drivers of seedling establishment. Long term, post-disturbance climate data may elucidate broad-scale drivers of reduced seedling establishment.

2.4.4 Management Implications

Forest managers can implement different tactics to mitigate detrimental consequences of shifting and interacting disturbance regimes. Fuel treatments within the first decade of outbreak detection can reduce total fuel accumulation caused by beetle-killed overstory trees. This may reduce residence times and prolonged smoldering during subsequent burning, mitigating detrimental impacts on soil health and seedling establishment (Carlson et al. 2017; Certini 2005). However, prescriptions for fuel treatments depend on management objectives. If managing for

fire behavior, removal of large beetle-killed trees and ladder fuels within the first decade of an outbreak may be beneficial. However, special consideration should be given to fine fuel accumulation that has been found to accumulate after salvage logging, as fine surface fuels may increase the risk of surface fire spread (Donato et al. 2013*b*). Additionally, there may be negative repercussions of fuel treatments on wildlife habitat. For example, the Canada lynx selectively use outbreak stands with large diameter trees, and its prey, the snowshoe hare, prefers understory connectivity in subalpine stands (Squires et al. 2020). Fuel reduction treatments aimed at reducing fire behavior may have negative implications for listed wildlife species. If managing for resistance, proactive landscape scale removal of large diameter host trees may improve stand resistance to epidemic bark beetle outbreaks (Jenkins et al. 2014; Temperli et al. 2014) and potentially influence the subsequent fuel loading observed in this study. However, treatments at this scale may be costly and result in removing valuable timber product (Temperli et al. 2014). Silvicultural techniques including tree planting and shelterwood treatments may increase stand resiliency to bark beetle outbreaks by creating favorable microsite conditions to promote spruce regeneration (DeRose and Long 2014). More broadly, post-disturbance tree planting may promote stand resiliency and the persistence of subalpine species on the landscape, though long-term patterns of tree regeneration are unknown given the centuries long recovery time scale.

2.4.5 Conclusions

Climate change is altering forest disturbance regimes, which are corresponding with heightened canopy mortality (Allen et al. 2010, Johnstone et al. 2016). An increase in the extent of disturbances will inevitably result in an increase in the interactions of disturbance events. Despite disturbance interactions, though all studied sites had tree regeneration, low post-fire seedling density following wildfires, regardless of previous outbreaks, is consistent with other

studies in the Rocky Mountains (Harvey et al. 2016*a*; Stevens-Rumann et al. 2018). While this

study did not support compounded or additive effects from interacting disturbances, low post-fire

Englemann spruce and subalpine fir regeneration in the Rocky Mountains may promote

structural shifts to favor drought- and fire-tolerant species such as lodgepole and aspen.

Continued high severity disturbance events may reduce forest resiliency and result in state shifts

to altered forest types or non-forested ecosystems, particularly in slow-growing subalpine stands

(Gill et al. 2017; Turner et al. 2019; Andrus et al. 2020).
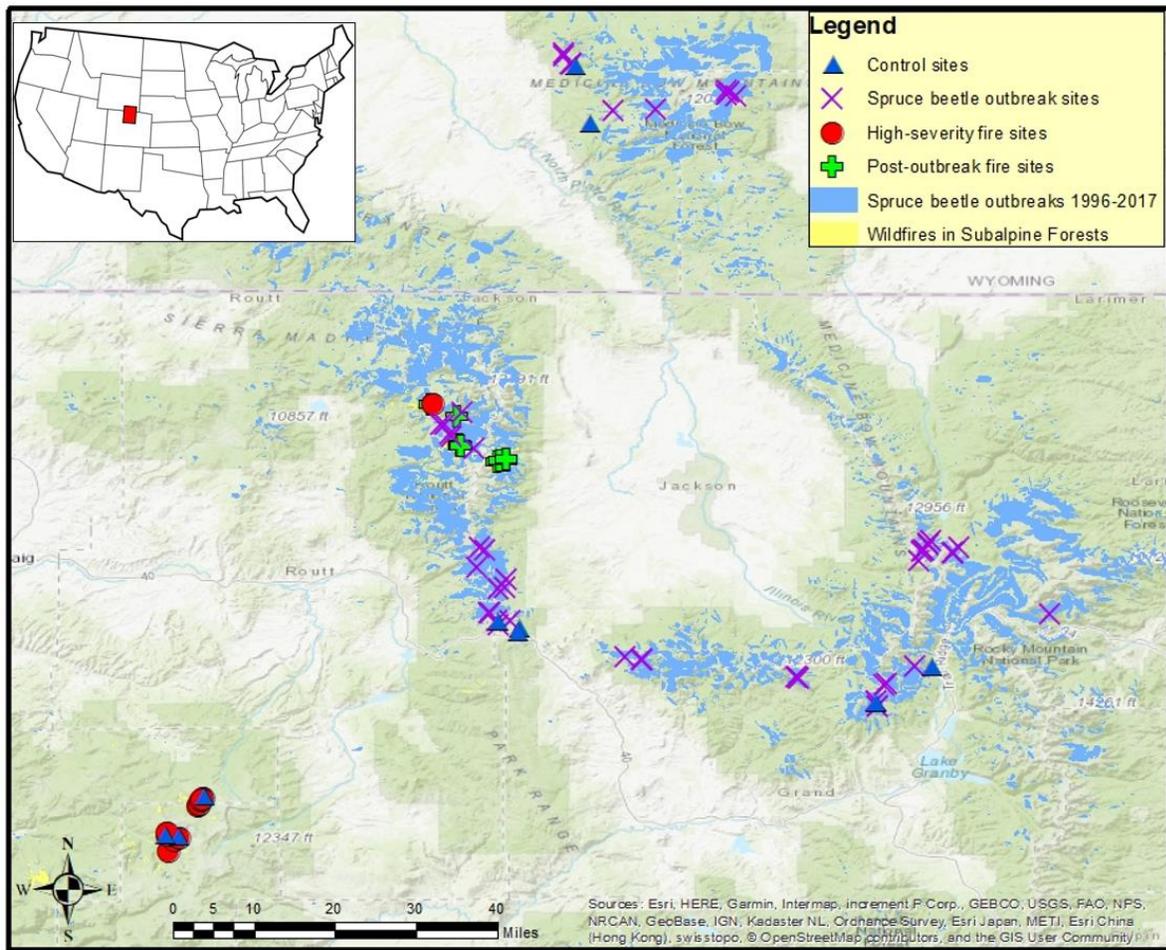
Figure 2.1: Map of study sites in Northern Colorado and Southern Wyoming.
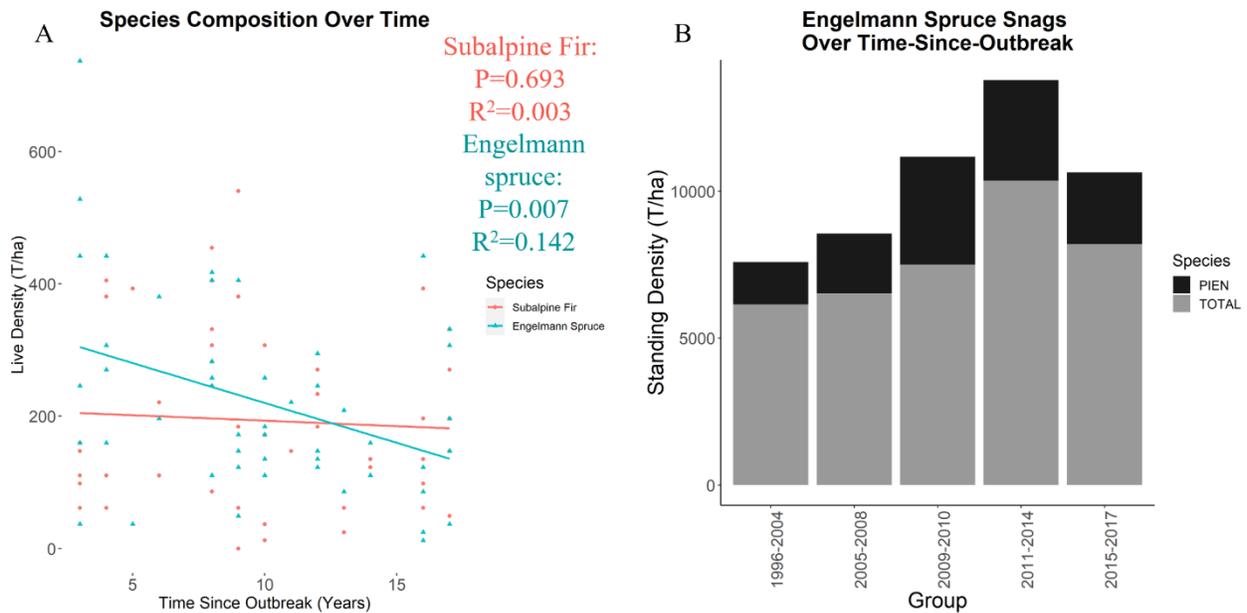
Figure 2.2: Standing Engelmann spruce dynamics. A) Live standing Engelmann spruce decreases over time as live standing subalpine fir remains constant. B) Standing Engelmann spruce snags density compared to total density. Engelmann spruce snags decrease in older outbreak groups, there may also be some spruce trees continuing to experience infestation in earlier groups as those were not captured in the "dead and dying" tree rating system. Snags shown as a proportion of total standing trees. Some living trees in total standing density were beetle infested and will die over time.
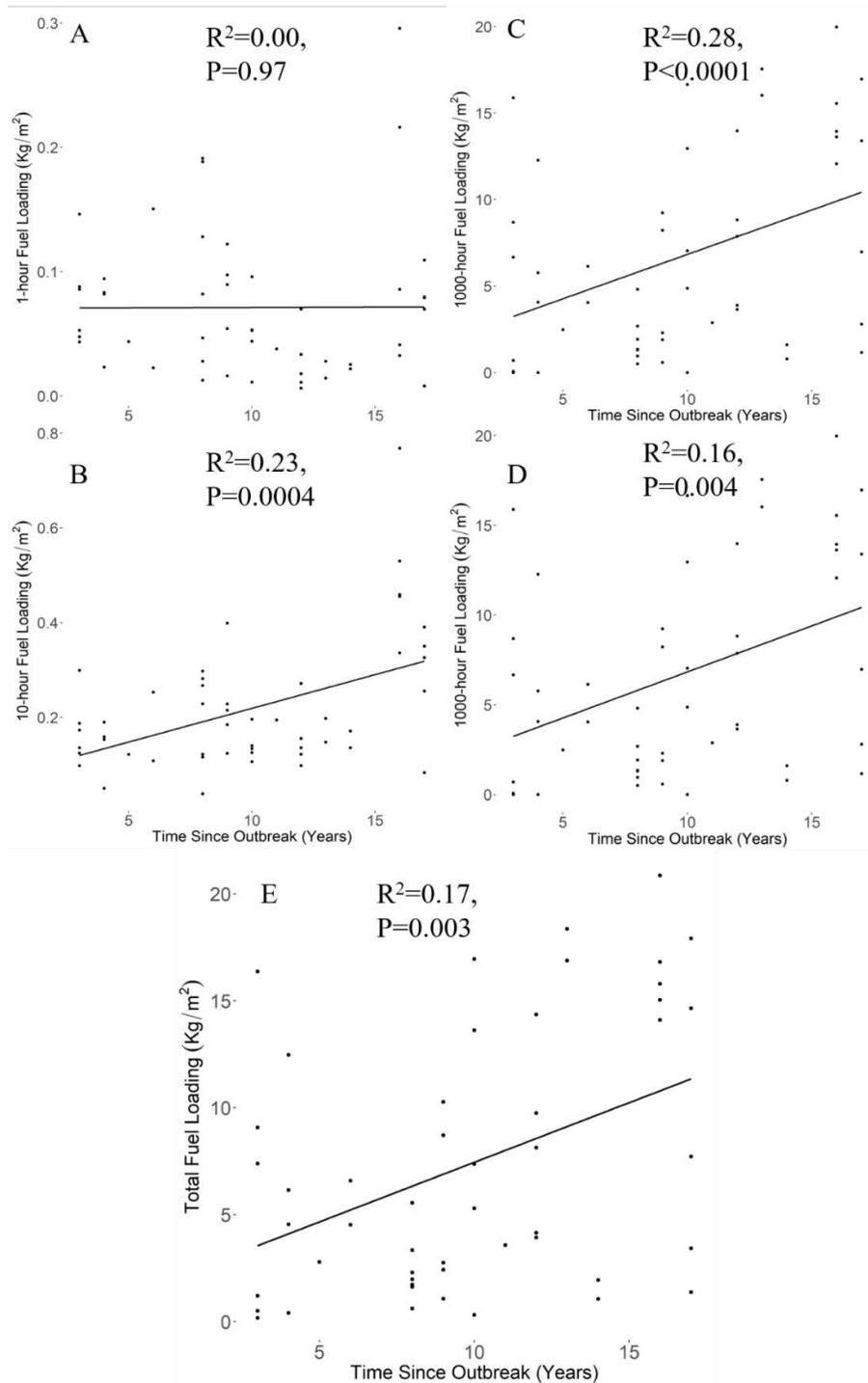
Figure 2.3: Fuel loading (Kg/m^2) over time in spruce beetle-affected subalpine stands with fitted linear regression. A) 1-hour fuel loading over time; B) 10-hour fuel loading over time; C) 100-hour fuel loading over time; D) 1000-hour fuel loading over time; E) Total fuel loading over time.
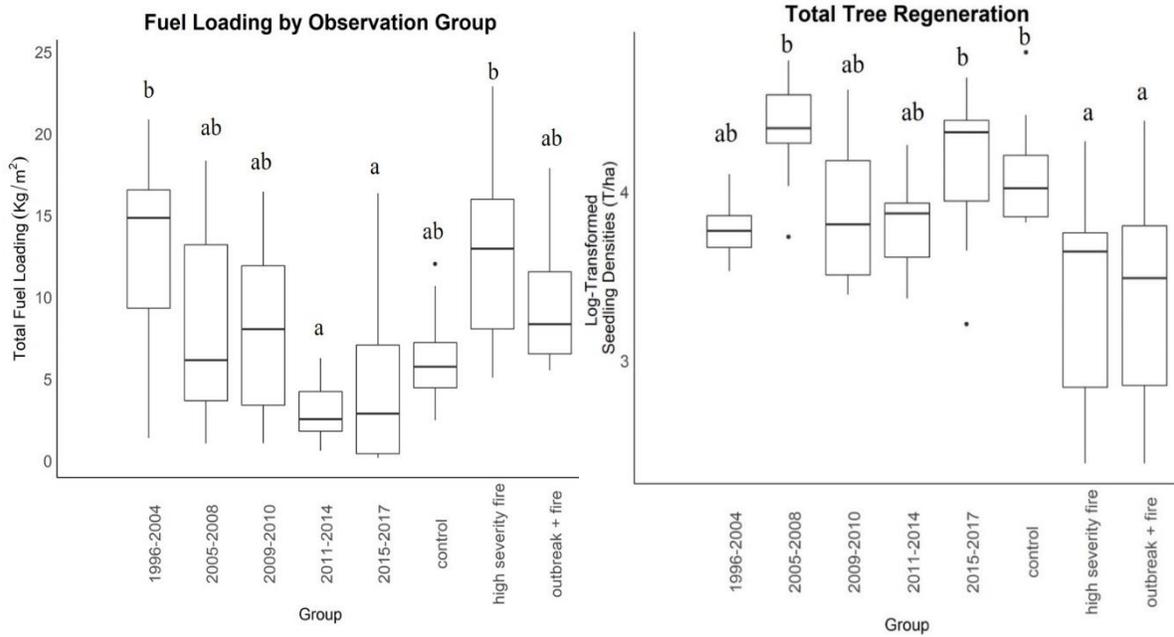
Figure 2.4: *A*. Boxplots of total fuel loading by group. *B*. Boxplot of total tree seedling densities including all species (log) in each disturbance group. Horizontal bars represent mean fuel loading of each disturbance group, height of boxes represent spread of 75% of data. Different letters indicate statistically significant differences between groups from a Tukeys HSD analysis.
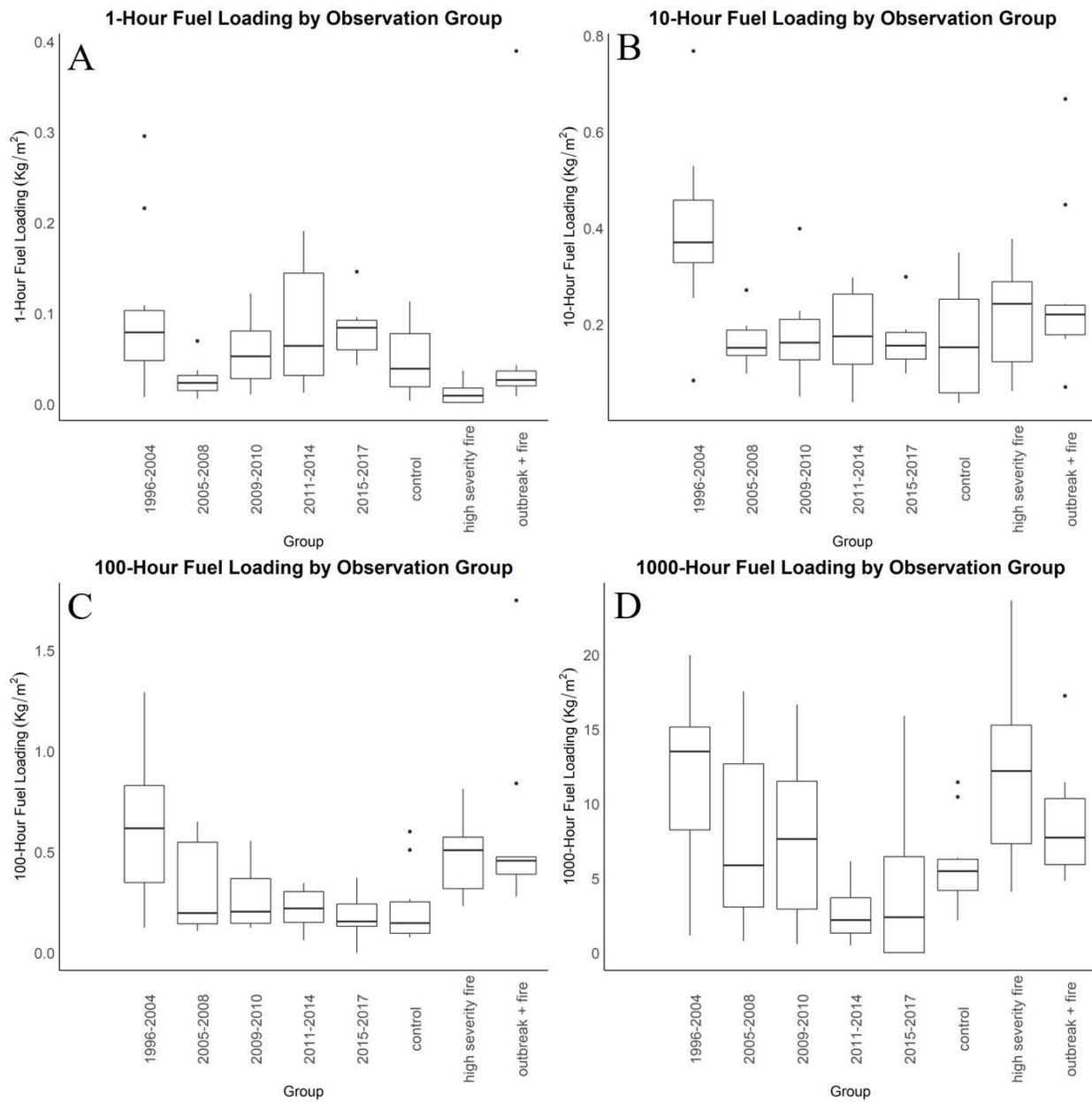
Figure 2.5: Boxplot of fuel loads by group for A) 1-hour fuels, B) 10-hour fuels, C) 100-hour fuels, and D) 1000-hour fuels.
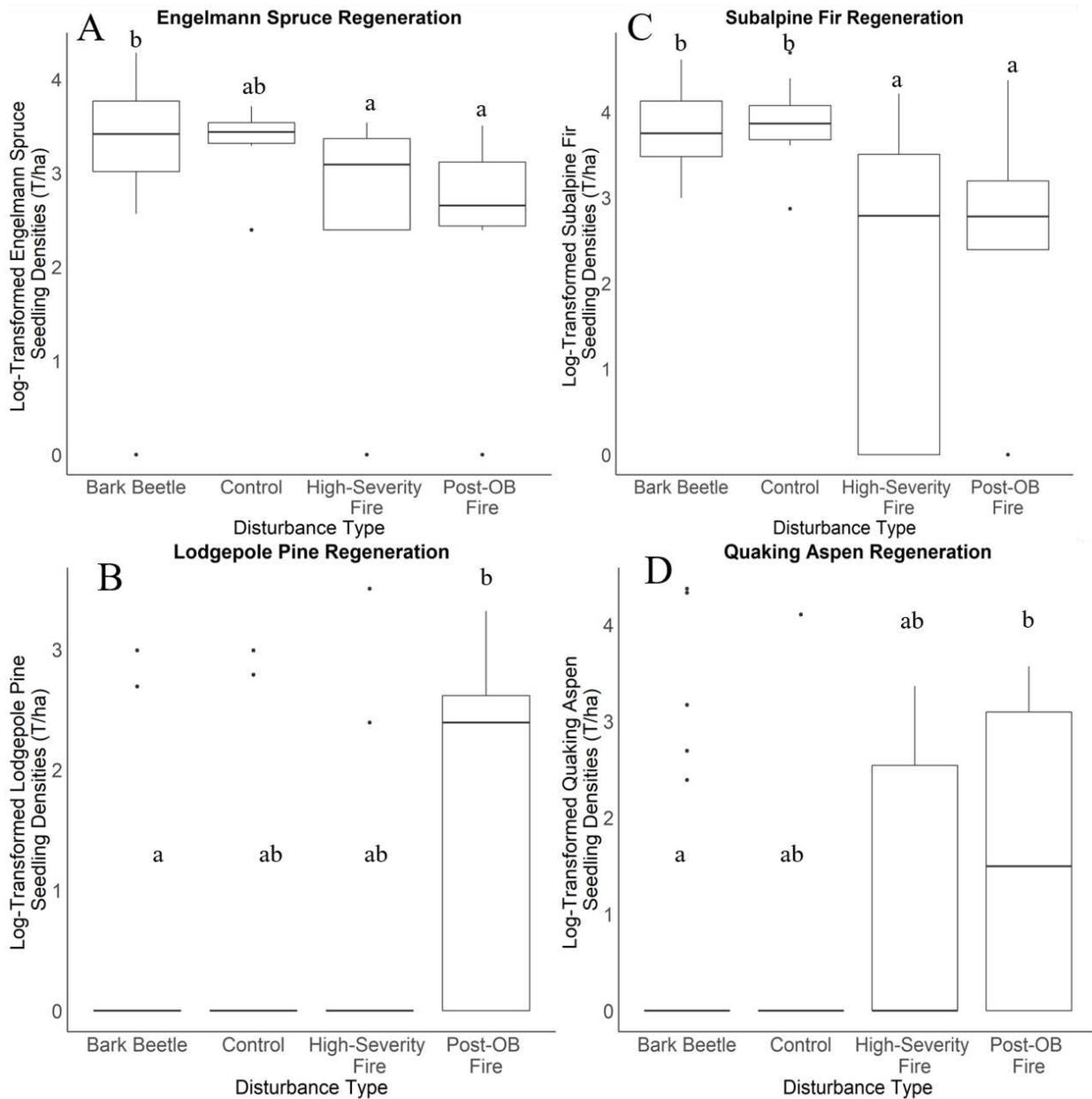
Figure 2.6: A) Engelmann spruce, B) Subalpine fir, C) Lodgepole pine, D) Quaking aspen tree log-transformed seedling densities by disturbance type. Lowercase letters indicate significant differences observed among disturbance types using Tukey's HSD test.
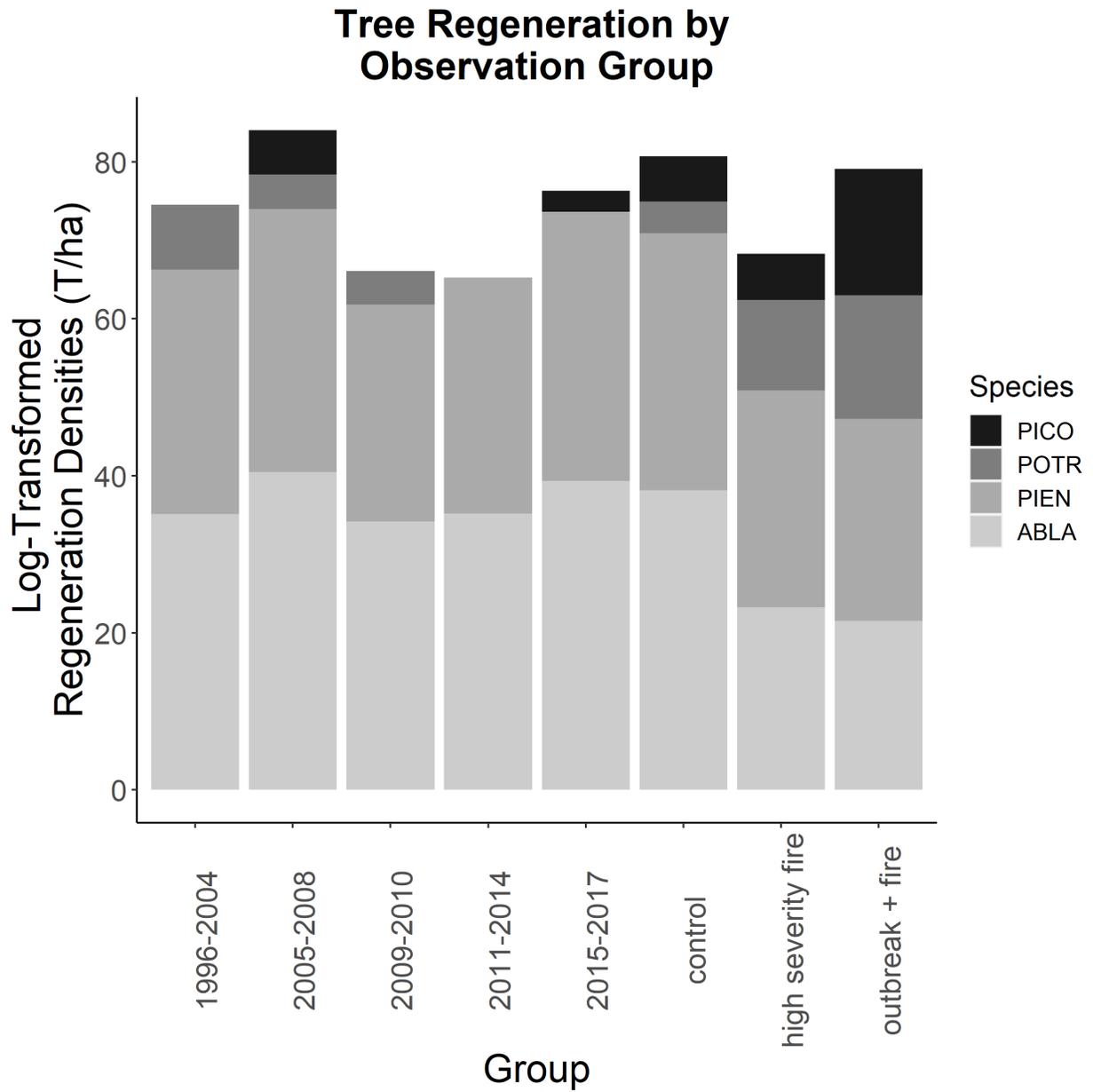
Figure 2.7: Tree seedling densities for each species by observation group. Seedling densities are log-transformed.

Table 2.1: Predictor variables and response variables used in analyses to address each research question.

Study question	Predictor variables	Response variables
Question 1) how does time-since-outbreak affect stand and fuel structures in subalpine forests?	Time since outbreak	Englemann spruce mortality Snag density Live tree density QMD 1hr 10hr 100hr 1000hr Total fuel loading
Question 2) how does the recovery trajectories and fuel complexes differ between wildfires, outbreaks, or a combination of the two disturbances?	Disturbance groups	Litter and duff 1hr 10hr 100hr 1000hr Understory vegetation cover Total seedling density
	Bark beetle, control, high severity fire, and post-outbreak fire	Log_{10}(Seedling density) (by species)
Question 3) what are the site specific drivers of post-disturbance fuels and tree regeneration?	Elevation Aspect Slope Disturbance group Fuel loading Litter cover Standing pre-fire species	1hr 10hr 100hr 1000hr Total fuel loading Seedling density (by species)

Table 2.2: Generalized linear model (GLM) predictors and outputs for fuel loading by size class. Significant predictors are bolded (P<0.05).

Predictors	Estimate	Std. Error	*t* value	*P*
Total fuel loading				
(Intercept)	189.2	100.61	1.88	0.06
Elevation	-0.05	0.03	-1.47	0.15
Aspect	6.26	8.19	0.76	0.45
Slope	0.72	0.66	1.09	0.28
Group				
BB (96-04)	+58.44	23.49	2.49	0.15
BB (05-08)	+26.49	23.13	1.15	0.26
BB (09-10)	+27.93	23.24	1.20	0.23
BB (11-14)	-22.41	24.50	-0.92	0.36
BB (15-17)	-0.89	24.34	-0.04	0.97
High-severity fire	**+70.55**	**23.29**	**3.03**	**0.003**
Post-outbreak fire	+37.50	23.1	1.62	0.11
1-hour fuel loading				
(Intercept)	2.07	1.22	1.70	0.06
Elevation	-0.0005	0.0004	-1.42	0.15
Aspect	0.02	0.10	0.21	0.45
Slope	0.01	0.01	1.44	0.28
Group				
BB (96-04)	+0.35	0.29	1.23	0.15
BB (05-08)	-0.21	0.28	-0.76	0.26
BB (09-10)	+0.12	0.28	0.42	0.23
BB (11-14)	+0.41	0.30	1.39	0.36
BB (15-17)	+0.43	0.30	1.44	0.97
High-severity fire	**-0.33**	**0.28**	**-1.18**	**0.003**
Post-outbreak fire	+0.15	0.28	0.52	0.11

Predictors	Estimate	Std. Error	*t* value	*P*
Elevation	**-0.002**	**0.0008**	**-3.16**	**0.002**
Aspect	0.03	0.18	0.19	0.85
Slope	0.01	0.01	0.73	0.47
Group				
BB (96-04)	**+1.88**	**0.52**	**3.59**	**0.0006**
BB (05-08)	-0.17	0.52	-0.33	0.74
BB (09-10)	+0.20	0.52	0.39	0.70
BB (11-14)	+0.44	0.55	0.81	0.42
BB (15-17)	+0.38	0.54	0.71	0.48
High-severity fire	+0.53	0.52	1.03	0.31
Post-outbreak fire	+0.93	0.52	1.79	0.08
100-hour fuel loading				
(Intercept)	**18.26**	**4.59**	**3.98**	**0.0002**
Elevation	**-0.005**	**0.002**	**-3.59**	**0.0006**
Aspect	-0.16	0.37	-0.43	0.67
Slope	0.03	0.03	0.99	0.33
Group				
BB (96-04)	**+3.45**	**1.07**	**3.22**	**0.002**
BB (05-08)	+1.02	1.05	0.97	0.34
BB (09-10)	+0.97	1.06	0.92	0.36
BB (11-14)	+0.87	1.11	0.78	0.44
BB (15-17)	+0.88	1.11	0.79	0.43
High-severity fire	**+2.98**	**1.06**	**2.81**	**0.007**
Post-outbreak fire	**+3.96**	**1.06**	**3.74**	**0.0004**
1000-hour fuel loading				
(Intercept)	160.13	99.20	1.61	0.11
Elevation	-0.04	0.03	-1.23	0.22
Aspect	6.36	8.08	0.79	0.43
Slope	0.67	0.65	1.03	0.31

Predictors	Estimate	Std. Error	*t* value	*P*
Group				
BB (96-04)	**+52.74**	**23.16**	**2.28**	**0.03**
BB (05-08)	+25.88	22.81	1.14	0.26
BB (09-10)	+26.65	22.91	1.16	0.25
BB (11-14)	-24.17	24.15	-1.00	0.32
BB (15-17)	-2.59	24.00	-0.11	0.91
High-severity fire	**+67.48**	**22.96**	**2.94**	**0.005**
Post-outbreak fire	+32.52	22.87	1.422	0.16

Table 2.3: Generalized linear model (GLM) predictors and outputs for tree seedling densities by species. Significant predictors are bolded (P<0.05).

Predictors	Estimate	Std. error	*t* value	*P*
Engelmann spruce				
T/ha (log transformed)				
(Intercept)	2.99	1.53	1.95	0.055
Elevation	0.0002	0.0005	0.33	0.74
Aspect	0.12	0.13	0.89	0.38
Slope	-0.01	0.01	-1.38	0.17
Fuel loading	0.0007	0.002	0.41	0.68
Disturbance type				
Bark beetle	-0.15	0.30	-0.51	0.61
High severity fire	**-1.13**	**0.40**	**-2.86**	**0.006**
Post-outbreak fire	**-1.01**	**0.38**	**-2.67**	**0.009**
Subalpine fir				
T/ha (log transformed)				
(Intercept)	**4.37**	**1.85**	**2.37**	**0.02**
Elevation	-0.0001	0.0006	-0.13	0.90
Aspect	0.08	0.15	0.890.58	0.57
Slope	-0.01	0.01	-1.04	0.30
Litter Cover	-0.003	0.009	-0.33	0.74
Fuel loading	0.001	0.002	0.91	0.36
Disturbance type				
Bark beetle	-0.21	0.33	-0.64	0.53
High severity fire	**-2.14**	**0.47**	**-4.54**	**<0.0001**
Post-outbreak fire	**-1.72**	**0.46**	**-3.79**	**0.0003**

Predictors	Estimate	Std. error	*t* value	*P*
Lodgepole pine				
T/ha (log transformed)				
(Intercept)	**4.80**	**1.67**	**2.88**	**0.005**
Elevation	**-0.001**	**0.0005**	**-2.67**	**0.009**
Aspect	0.08	0.14	0.60	0.55
Slope	0.001	0.01	0.11	0.91
Fuel loading	**-0.004**	**0.002**	**0.91**	**0.050**
Standing PICO density	**0.009**	**0.002**	**2.97**	**0.004**
Disturbance type				
Bark beetle	-0.25	0.31	-0.80	0.43
High severity fire	0.57	0.42	1.37	0.17
Post-outbreak fire	**1.30**	**0.40**	**3.3**	**0.002**
Quaking aspen				
T/ha (log transformed)				
(Intercept)	**6.06**	**1.8**	**3.06**	**0.003**
Elevation	**-0.002**	**0.0006**	**-3.50**	**0.0009**
Aspect	**0.32**	**0.16**	**1.98**	**0.051**
Slope	0.001	0.01	-0.16	0.88
Fuel loading	0.00	0.002	0.001	0.999
Standing POTR density	**.02**	**0.005**	**4.69**	**<0.0001**
Disturbance type				
Bark beetle	0.58	0.38	1.56	0.12
High severity fire	**1.47**	**0.50**	**2.95**	**0.004**
Post-outbreak fire	**1.69**	**0.48**	**3.52**	**0.0007**

SEEDLINGS? THE UNEXPECTED ELDERS OF UNDERSTORY TREES[2]

3.1 Introduction

Over the past several decades, the impacts of climate change have created unprecedented risks to forests across the globe and will continue to threaten ecosystem health in future climate scenarios. Warmer and drier conditions associated with climate change have resulted in drought-induced tree mortality (van Mantgem et al. 2009), changing disturbance regimes (Johnstone et al. 2016; Thom et al. 2017), and harsher growing conditions that may threaten tree seedling survival (Hansen et al. 2018; Stevens-Rumann et al. 2018). Forests in the western United States have historically been shaped by disturbance events such as wildfires and bark beetle outbreaks (Veblen et al. 1994; Veblen 2000). Climate is a major driver of these disturbances; as the climate continues to warm, increases in disturbance extent, frequency, and interactions will result in widespread tree mortality (Abatzoglou & Williams 2016; Allen et al. 2015). Forest resilience to a high severity disturbance is dependent on the ability of trees to regenerate and recover ecosystem functioning (Johnstone et al. 2016). Tree seedling germination and survival are particularly sensitive to climatic conditions; juvenile trees survive in narrower climatic conditions than those that support their adult counterparts (Dobrowski et al. 2015; Lazarus et al. 2017). Increased temperature and moisture stress associated with climate change have resulted in tree regeneration failure in some forested ecosystems, particularly following high-severity wildfires (Flatley & Fulé 2016; Hansen et al. 2018; Stevens-Rumann et al. 2018; Kemp et al. 2019). Reduced tree regeneration can erode forest resilience to disturbances and a changing climate, and may result in shifts in species dominance, novel changes to forest structure, or state shifts to non-forested

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[2] Formatted for publication in *Journal of Vegetation Science*

ecosystems (Harvey et al. 2016; Kemp et al. 2016; Stevens-Rumann et al. 2018; Coop et al. 2020).

In general, successful regeneration not only requires specific climatic conditions for viable seed production and successful germination, but their alignment in time and space (Grubb 1977; Andrus et al. 2018). Different conifer species in the Rocky Mountains have exhibited episodic recruitment, or widespread, noncyclical pulses in seed production that coincide with specific climatic conditions (Brown & Wu 2005; Buechling et al. 2016; Kroiss & HilleRisLambers 2015; Rother & Veblen 2017; Andrus et al. 2018). Seed crop production can occur at intervals of a few years to multiple decades (Keyes & González 2015; Buechling et al. 2016; Andrus et al. 2018). Episodic recruitment events have fluctuated with warming and drying conditions over the past several decades (Redmond et al. 2012; Allen et al. 2014; Buechling et al. 2016; Andrus et al. 2018). The alignment of climatic conditions required for seed production and subsequent germination can make successful recruitment very infrequent (Woodward et al. 1994; Buechling et al. 2016; Andrus et al. 2018*b*). As such, several studies have noted a decline in establishment pulses in species that require abundant moisture for seed germination and survival (Reich et al. 2016; Kueppers et al. 2017; Andrus et al. 2018). In particular, climate-driven reductions in tree establishment have been observed in high-elevation forests of the Rocky Mountains (Kueppers et al. 2017; Lazarus et al. 2017; Andrus et al. 2018).

Rocky Mountain subalpine forests are characteristically cool and moist, with a persistent snowpack that provides moisture to the soil through late spring and early summer (Westerling et al. 2006; Lukas et al. 2014). These forests are particularly sensitive to warming conditions as earlier spring snowmelt results in drier soils and increased moisture stress during peak summer temperatures. Peak summer temperatures have already increased over the past several decades in

subalpine forests by ~1° C per decade, and this trend is expected to continue with future climate change scenarios (Rangwala & Miller 2010). Temperature is positively correlated with episodic, infrequent seed production of Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*), two dominant conifer species in the subalpine zone of the Rocky Mountains (Woodward et al. 1994; Buechling et al. 2016). At the same time, above-average snowpack and late season snowmelt provide significant soil moisture during warm summer months and are strongly correlated with successful subalpine seedling germination (Andrus et al. 2018; Hill et al. 2018). Therefore, subalpine tree germination and survival will only be augmented by warming temperatures when coupled with increased summer precipitation or abundant snowpack (Gill et al. 2015; Kueppers et al. 2017; Lazarus et al. 2017; Redmond & Kelsey 2018). This requirement for the temporal alignment of high soil moisture for seed germination and warm temperatures for seed production makes the successful establishment of Engelmann spruce and subalpine fir seedlings an increasingly rare occurrence (Kroiss & HilleRisLambers 2015; Kueppers et al. 2017; Andrus et al. 2018).

Increasing summer temperatures observed in subalpine forests are typically associated with early season snowmelt, water deficits, and increased moisture stress on tree seedlings (Andreadis & Lettenmaier 2006). Drought-intolerant species in snow-dependent ecosystems are increasingly at risk of temperature-induced moisture stress (Harvey et al. 2016; Kueppers et al. 2017; Redmond & Kelsey 2018). Engelmann spruce and subalpine fir are particularly drought-sensitive during seedling establishment (Kueppers et al. 2017; Lazarus et al. 2017). Both species require abundant moisture and relatively cool temperatures during the first growing season, but subsequent drought vulnerability decreases with older tree ages (Kroiss & HilleRisLambers 2015; Lazarus et al. 2017). On the other hand, more drought-tolerant subalpine species such as

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Pinus flexilis (limber pine) and *Pinus contorta* (lodgepole pine) have shown an increase in germination rates with increasing temperatures, despite drier soil conditions (Kueppers et al. 2017*b*; Lazarus et al. 2017). As climatic conditions continue to become warmer and drier, there may be significant contractions in Engelmann spruce and subalpine fir ranges, resulting in novel changes to subalpine ecosystems (Conlisk et al. 2017; Kueppers et al. 2017).

In addition to changing climate conditions, altered disturbance regimes hinder the persistence of Engelmann spruce and subalpine fir on the landscape. Over the past two decades, warmer and drier conditions have given rise to climate-driven spruce beetle (*Dendroctonus rufipennis*) outbreaks, as well as longer fire seasons and more frequent fires (Westerling et al. 2006; Dennison et al. 2014). This combination has resulted in widespread tree mortality in the central Rocky Mountains (CSFS 2019). Typically, live overstory trees create microsite conditions that help buffer temperature extremes and moisture deficits for vulnerable germinants (Calder & Clair 2012; Stephens et al. 2019). Overstory mortality due to moderate to high-severity disturbances may therefore result in a significant loss of optimal microsite conditions for seedling survival. Some evidence suggests that the majority of post-outbreak regeneration comes from the release of suppressed saplings in the understory (DeRose & Long 2010); however, new seedling establishment may be hindered by the loss of overstory tree facilitation (Conlisk et al. 2017). While fires expose bare mineral soil that provides favorable conditions for Engelmann spruce establishment (Johnstone & Chapin 2006), the loss of overstory trees and associated refugia makes site conditions particularly harsh for drought-sensitive subalpine species (Krawchuk et al. 2020). Consequently, growing season precipitation and moisture availability immediately following a fire are crucial for Engelman spruce's successful establishment and survival (Harvey et al. 2016; Urza & Sibold 2017). An increase in disturbance frequency and/or

severity may cause further seedling mortality and a loss of viable seed sources that are critical for disturbance resilience.

Regeneration failures and changing disturbance regimes have raised concerns about understanding the processes that govern seedling establishment and post-disturbance recovery. An important mechanism for elucidating these processes is determining seedling establishment dates, which can provide information about stand age and drivers of recruitment. Counting bud scars is a common method for dating seedlings, as it is nondestructive, time-efficient, and can be implemented in the field (Urza & Sibold 2013; Hankin et al. 2018). However, this method may only act as a proxy for true age. Terminal bud scars can become indistinguishable as a seedling grows, and scar visibility can vary by species (Urza & Sibold 2013). Another method to achieve establishment dates is to destructively sample seedlings and count annual rings, although this kills the seedling and can be time-consuming (Telewski 1993; Rother & Veblen 2017; Andrus et al. 2018). However, this method provides improved accuracy and an annual resolution that helps understand the climatic drivers of seedling establishment (Hankin et al. 2018). Dendrochronological techniques are particularly useful in subalpine forests, where shade-tolerant species may remain suppressed in the understory and exhibit stunted growth for decades, making terminal bud scars imperceptible (Veblen 1986). Gaining insight into establishment dates is vital for understanding growth patterns and recovery dynamics of subalpine forests as climate change continues to create unprecedented disturbance regimes and hostile growing conditions.

In this study, we destructively sampled seedlings to examine post-disturbance regeneration dynamics of Engelmann spruce and subalpine fir from subalpine stands in northern Colorado and southern Wyoming to answer the following questions: 1) how does seedling age correspond to seedling height and non-destructive methods of aging following stand-replacing

versus moderate severity disturbances? and 2) what is the effect of yearly climatic conditions on establishment dates? Understanding the drivers of tree regeneration establishment and success in these subalpine forests is critical for understanding recovery trajectories and identifying areas of divergent recovery pathways either because of post-disturbance site conditions or changes in broad-scale climate patterns.

3.2 Methods

3.2.1 Study Area

We collected samples from 30 sites in subalpine forests from northern Colorado and southern Wyoming. Sites were located in the Arapaho-Roosevelt, Routt, and Medicine Bow National Forests, at elevations ranging from 2,649 to 3,326 m above sea level (Figure 3.1). Subalpine stands were co-dominated by Engelmann spruce and subalpine fir, and contained lesser proportions of lodgepole pine and quaking aspen (*Populus tremuloides*). The subalpine zone is characterized by cool, wet winters and warm, dry summers, with the majority of annual precipitation in the form of snow (USDA NRCS 2020). On average, site locations received 970mm of precipitation per year from 1958 to 2019 across sites (Abatzaglou et al. 2018). Average annual temperatures for study sites range from a mean low of -6.3° C to a mean high of 21.2° C (Abatzaglou et al. 2018).

3.2.2 Site Selection

Seedling samples were collected from a subset of study sites used in chapter 1. We used Aerial Detection Survey (ADS) data of spruce beetle outbreaks that occurred from 1996 to 2017 in USFS Region 2 to identify areas with beetle caused mortality (collected by the USDA Forest Service, Forest Health Protection and its partners) (USFS 2017). We used Monitoring Trends in

Burn Severity (MTBS) data on wildfires in spruce-fir forests (MTBS Data Access 2017).

ArcMap (10.6) was used to generate random points within the outbreak and burn polygons.

Outbreak plots were defined as >50% of stand basal area (m^2/ha) affected by spruce beetle. We

used MTBS data to map high-severity fires since 1996. All plots were located at least 50 meters

from any trail or road to minimize human impact on plot data.

The outbreak plots comprise a chronosequence of stands that reflect a range of post-

disturbance recovery conditions from 21- years to 1-year post-outbreak detection. Burn areas

include high-severity wildfires in addition to post-outbreak fires. High-severity fire sites were

burned in 2002 (Burn Ridge Fire, Hinman Fire, Big Fish Fire, Lost Lakes Fire). Post-outbreak

fire sites also burned in 2002, 1-2 years after bark beetle outbreak detection (Burn Ridge,

Hinman Fire). Samples were collected from 20 bark beetle outbreak sites and 10 burn sites

(Table 1).

3.2.3 Sampling Design and Field Measurements

Site locations in this study were a subset of fixed-area plots established in chapter 1

(design adapted from Ott et al. 2018). Five circular subplots (0.004-ha (3.6m radius)) were

established within the fixed-area plot to count tree regeneration. Seedling samples were collected

from regeneration subplots. The first two seedlings of differing height classes encountered in

each subplot were selected for destructive sampling. After height measurements and terminal

bud scar counts (Urza & Sibold 2013), each sample was excavated to approximately 10 cm

below the root collar and cut to obtain the root-shoot boundary. We collected 229 tree seedling

samples across 30 sites. Ninety-three subalpine fir and 89 Engelmann spruce seedlings (182

samples) were collected across a range of height classes from 20 spruce beetle outbreak sites.

Additionally, 22 subalpine fir and 25 Engelmann spruce (47 samples) were collected across a

range of height classes from 10 burned sites, with approximately equal proportions from burned only and post-outbreak burned sites. Seedlings were only collected from plots with 2,500 seedlings/ha or more to limit the impact on site recovery.

3.2.4 Sample Processing

Establishment dates were determined from the maximum count of annual rings on cross-section cuts from each tree seedling (Telewski 1993; League & Veblen 2006; Rother & Veblen 2017). Seedling samples were cut into at least three cross-sections at 2.5cm intervals beginning below the estimated root-shoot boundary (typically below ground level, above root collar). Each cross-section's top surface was sanded with progressively finer sandpaper (i.e., from 120 to 3000 grit) and examined under a microscope for the presence of pith; pith is not present in roots but is visible in the shoot of the tree (Telewski 1993). The first cross-section cut with the presence of pith is indicative of the oldest tissue, or the sample with the maximum ring count. We counted annual rings from the outer ring to the center pith. Half of the samples were photographed with an AxioCam color camera on a stereomicroscope (up to 50x zoom), and rings were subsequently counted. The other half of the samples were counted in real-time under a stereomicroscope (30x zoom). The maximum annual ring count was recorded as the age for that sample if it corresponded with the first appearance of pith; if not, the ring count in the cross-section cut with the first appearance of pith was used. A subset of samples was randomly selected for recount and age verification. A third count was performed to achieve a final age if there were discrepancies in annual ring counts. Seedlings with unclear ring boundaries were not included in analyses.

3.2.5 Data Analysis

Statistics and graphics were completed in RStudio1.3.1093 (R Core Team 2019). Graphics were created using the ggplot2 package (Wickham 2016). A threshold of α=0.05 was used to designate statistical significance. Simple linear models were used to determine correlations between height and bud scar counts to true age. Significant predictors were incorporated into a generalized linear model (GLM) to assess predictors of seedling age. Outbreak sites were used as the baseline for GLM analyses, in order to model the correlation of height, disturbance type, and bud scar count on seedling age. The difference between bud scar count and seedling age ($count - age$) was used to quantify error from using bud scar counts as a proxy for age for both species. Accuracy of bud scar counts was calculated as the percentage of samples of which bud scars predicted the exact age. Simple and general linear models were performed using the base R package.

Climate data for each plot from 1958 to 2019 was used to identify drivers of seedling establishment (Abatzoglou et al. 2018). Maximum temperature (°C), minimum temperature (°C), precipitation (mm), and soil moisture (mm) were averaged over May-September of each year for growing season values. Average annual values of vapor pressure deficit (VPD, in kPa) and climatic water deficit (CWD, in mm) were used in analyses. VPD describes the amount of water vapor in the air at a given temperature, independent of precipitation or soil moisture, and is used as a metric of the atmospheric water demand for plants (Yuan et al. 2019). CWD is defined as the evaporative demand that exceeds available soil moisture, integrating solar radiation, precipitation, and evapotranspiration at a given air temperature (Stephenson 1998). CWD is different from VPD in that it is directly affected by snowpack and precipitation; CWD is used as a metric for drought stress on soils and plants (Stephenson 1998; McCullough et al. 2016).

Twenty-seven seedlings were established before 1958 and consequently were not included in the climate variable analyses.

Z-scores were calculated for each climate variable for each site in order to standardize comparisons across sites. Each variable's long-term average is in the 50th percentile of data and has a z-score of 0. Establishment pulses were identified as years with abundant seedling establishment across all sites. Years in which establishment occurred across all study sites were used to identify broad-scale climatic drivers of establishment pulses. Seedling establishment was grouped by the percentage of all (229) seedlings established per year. Four establishment pulse thresholds were defined as years in which 5%, 2%, <2%, and 0% of total seedlings were established in that year. Each climate variable was averaged across sites during years of establishment pulses for each species and threshold group. Kruskal Wallis tests were used to identify if significant differences were present in climate variable z-scores between threshold groups for each species. Dunn's Test was used to compare groups and identify statistically different groups using the dunn.test R package (Dinno 2017).

3.3 Results

All GLM predictors (height, disturbance type, and bud scar) were significant and explained 82% variability in Engelmann spruce seedling age and 80% variability in subalpine fir seedling age (Tables 2 and 3). Height was a significant predictor of age for both species (P<0.02 The burn disturbance group was a significant predictor of seedling age for both species (P<0.03); burned sites had a negative correlation with seedling age compared to the baseline group. Bud scar counts were the most significant predictors of age for both species (P<0.0001). The accuracy of bud scar counts in predicting seedling age was similar between both species; on average, bud scars underestimated seedling age of both species by 9 years.

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3.3.1 Height Classification

Seedling height was a significant predictor of age for both species and in both

disturbances (P<0.02; R^2>0.24). However, correlations between height and age were weaker

with taller seedlings. Height of seedlings that were shorter than the median height (35cm in

outbreak sites, 30cm in burn sites) was significantly, positively correlated with age for both

species, from both disturbance types (P<0.001; R^2>0.365). On the other hand, the height of taller

seedlings (greater than the median) was not a significant predictor of seedling age for either

species from both disturbance types (P>0.24; R^2<0.14).

3.3.2 Terminal Bud Scar Counts

Terminal bud scar counts were significant predictors of seedling age for both species and

in both disturbances (P<0.003; R^2>0.33) (Figure 2). Bud scar counts accurately predicted the

exact tree age for 6% of seedlings from outbreak sites, and 17% of postfire seedlings (Table 3.4).

On average, bud scars underestimated the true age of seedlings from outbreak sites by 11.1 years,

although estimates ranged from underestimates of 76 years to overestimates of 12 years.

Conversely, the average bud scar estimate of post-fire seedling age was an underestimate by 1

year. Age estimates of post-fire seedlings ranged from underestimates of 3 years to overestimates

of 7 years.

The error of bud scar predictions of true age increased linearly with increasing age for

both species (Figure 3.3) (R^2>0.84) (negative error indicates underestimates, larger magnitudes

indicate a greater error). Bud scar counts of Engelmann spruce seedlings from beetle-affected

stands over ~30 years old started to deviate from the fitted regression line (Figure 3.2b, Figure

3.3b). Similarly, the accuracy of bud scar counts on subalpine fir seedlings from beetle-affected

stands older than ~28 years decreased substantially (Figure 3.2a, Figure 3.3a). Bud scar counts as a proxy for true age did not differ with age in post-fire seedlings (Figures 3.2c and 3.2d). The error rate of bud scar predictions of true age increased with increasing height for both species (R^2<0.3); however, the relationship was relatively weak compared to the strong correlation between seedling age and bud scar count error.

3.3.3 Broad-Scale Establishment Events

Comparisons of climate variable z-scores yielded significant differences between years with establishment pulses and years with no establishment. Growing season temperature minimums, precipitation, annual VPD, and annual CWD were significantly different between establishment pulse groups. These climate variables were also significant drivers of individual establishment years. During years of establishment pulses for both subalpine tree species, growing season maximum temperatures (P>0.1) and growing season soil moisture (P>0.3) did not exhibit significant correlations with threshold groups. Large establishment pulses were synchronous across sites, and many were consistent among both species (Figure 3.4).

Growing season minimum temperatures were significantly lower in years with abundant establishment (5% threshold group) compared to years with less or no establishment of both subalpine fir (P<0.03) and Engelmann spruce (P<0.0001) (Figure 3.5a). Years with 0% establishment had the highest temperature minimums of all groups (z-score=0.2036; 58th percentile). In years with the most subalpine fir establishment, minimum temperatures were far below the average of long-term temperature data, and the lowest of all establishment groups (z-score= -0.5283; 30th percentile). Years with low subalpine fir establishment (<2%) had temperature minimums significantly lower than years with no establishment (P=0.0331). Years

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with moderate subalpine fir establishment (<2% and 2% threshold groups) were not statistically different from one another (P=0.2764) but had mean z-score values between the highest and lowest establishment groups. A similar trend was observed for Engelmann spruce establishment pulses. Years with abundant Engelmann spruce establishment (5% group) had the lowest growing season temperature minimums of all groups (z-score= -0.8719; 19th percentile) (P<0.002). The intermediate establishment groups were not significantly different from one another or years of no establishment (P>0.9); however, years with no establishment had the highest mean temperature minimum of all groups. Years of abundant subalpine tree establishment had significantly lower growing season temperature minimums than the long-term mean values.

Precipitation was significantly different among establishment threshold groups for both species (P<0.0001) (Figure 3.5b). Years with no establishment had the lowest growing season precipitation z-scores of any establishment group, and mean precipitation lower than the long-term average (z-score= -0.4538; 32nd percentile). Subalpine fir seedling establishment pulses above the 5% threshold occurred in years with above-average precipitation (z-score=0.30, 62nd percentile). The 5% group had the highest growing season precipitation than any other subalpine fir establishment group and was significantly different from years with no establishment (P<0.0001). Years with moderate subalpine fir establishment (<2% and 2% groups) were not significantly different from one another (P=0.1945). The <2% and 2% groups had greater precipitation than years with no establishment (P<0.0001, P=0.12; respectively). Years with abundant Engelmann spruce regeneration (5% threshold group) had the highest growing season precipitation of any group, and mean precipitation above the long-term average (z-score=0.3439; 63rd percentile). Years with the highest Engelmann spruce regeneration had significantly greater

growing season precipitation than years with no establishment (P<0.0001) and moderate

establishment (2% group) (P=0.0017). Years with above 2% Engelmann spruce establishment

were not significantly different from years with no establishment (P>0.9). There is a clear

correlation between above-average precipitation and abundant subalpine tree establishment.

Annual VPD values were significantly different between establishment groups for both

subalpine tree species (P<0.0001) (Figure 3.5c). For both species, years with no seedling

establishment (0% group) had the highest VPD values of all groups and higher mean VPD than

the long-term average (z-score=0.4727; 68th percentile). Years with abundant subalpine fir

establishment (5% group) had significantly lower VPD values than years with no establishment

(P=0.035). Both groups of years with low and moderate subalpine fir establishment (<2% and

2%, respectively) were significantly lower than years with no establishment (P<0.001) but were

not different from one another (P=0.8253) or years with abundant establishment (P>0.1). All

threshold groups of Engelmann spruce establishment had significantly lower VPD values than

years with no establishment (P<0.04). Years with low and moderate Engelmann spruce

establishment were not significantly different from one another or years with abundant

establishment (P>0.9). All groups of years with seedling establishment for both species had

significantly lower annual VPD values than non-establishment years.

Annual CWD was significantly different between establishment groups of both species

(P<0.0001) (Figure 3.5d). For both species, years with no establishment had the highest CWD

values, with mean CWD higher than the long-term average (z-score=0.445; 67th percentile).

Years with abundant subalpine fir establishment and years with low establishment had

significantly lower CWD mean values than years with no establishment (P<0.0001). Groups of

years with low and moderate subalpine fir establishment were not significantly different from

one another (P=0.1188). Abundant subalpine fir establishment occurred in years with below-average CWD values (z-score= -0.4831; 31st percentile). Similarly, years with large Engelmann spruce establishment pulses (5% group) had the lowest CWD values of all spruce establishment groups, and lower values than the long-term average (z-score=-0.4486). Groups of years with low and moderate Engelmann spruce establishment were not significantly different from one another (P=0.0937). Subalpine tree establishment occurred in years with below-average annual CWD, while years of no establishment are correlated with high annual CWD values.

3.4 Discussion

Climate drives broad-scale tree seedling establishment in dominant subalpine species. Growing season temperature and precipitation, annual VPD, and CWD were limiting factors to subalpine tree establishment. Height and terminal bud scar counts were both significant predictors of seedling age for both species. However, the strength of correlation decreased as seedling height and age increase. The age distribution of post-disturbance regeneration indicates low levels of semi-continuous establishment pre- and post-spruce beetle outbreaks. However, large Engelmann spruce and subalpine fir establishment pulses occur in favorable growing years, which may warrant concern with continued drying and warming trends.

3.4.1 Aging Method: Height Classification

Subalpine fir and Engelmann spruce are both shade-tolerant species that can remain suppressed in the understory or subcanopy for decades to centuries. Because of this growth trait, height classes are not accurate proxies for the true age of either subalpine tree species. For example, the oldest seedling aged was 126 years old and 103.6cm tall at the time of collection, while another seedling aged in this study was 27 years old and 106.7cm tall at the time of

collection. This is true for short seedlings from beetle-affected stands as well; a 13-year-old seedling and a 4-year-old seedling would both be counted in the smallest height class. Although there is a strong positive relationship between height and age (older trees *tend* to be taller), there can be exceptions to this correlation. Spatial variability in canopy openings that provide light to the forest floor may result in the release of some seedlings and not others within the same stand (Antos et al. 2000). Although regeneration of differing height classes was found in these outbreak sites (see chapter 1), the variable age of short seedlings from beetle-affected stands disavows conclusions of post-outbreak regeneration. Seedlings in subalpine stands tend to be multi-aged with variable growth rates; classification based solely on height as a proxy for relative age does not provide sufficient information to assess post-disturbance recovery dynamics.

The difference in age-height slopes between post-fire and post-outbreak establishment reflects the contrasting growing conditions for seedlings following moderate severity vs. stand replacing disturbances. After moderate severity outbreaks, there are live adult trees that remain in the overstory. Canopy cover is patchy, and seedlings may stay suppressed despite some canopy openings (Antos et al. 2000). A higher age-height slope coefficient in outbreak stands compared to burned stands indicate the older age distribution of seedlings typical in spruce-fir forests (Figure 3.6a). On the other hand, the lower age-height slope coefficient in burned stands relative to beetle-affected stands indicates the younger age distribution of post-fire seedlings. Subalpine species are fire-sensitive, and wildfires tend to be stand replacing in subalpine forests; without canopy cover and dense understory vegetation, Engelmann spruce and subalpine fir grow quickly over short temporal scales given high light levels. Post-fire seedlings in subalpine stands will exhibit high rates of growth until they reach maturity or receive shade from overstory

trees (Veblen 1986). This rapid growth may explain why the correlation between height and age is much lower in burned areas than in outbreak areas. For example, a 16-year-old seedling was measured at 36.6cm, while a 9-year-old seedling of the same species from the same site was measured at 56cm. Compared to outbreak sites with suppressed growing conditions, seedlings of a given age are generally taller in burn areas than in beetle-affected stands.

3.4.2 Aging Method: Terminal Bud Scar Counts

The age distributions of advanced regeneration following moderate-severity disturbances differ greatly from the age structure of new recruitment following high-severity wildfires. Moderate severity, biotic disturbances allow for continuous establishment both pre- and post-disturbance, compared to stand-replacing, abiotic disturbances that truncate the age distribution of seedlings. Establishment dates from beetle-affected stands range from 1893 to 2015, given closed-canopy conditions that permit prolonged suppressed growth. On the other hand, post-fire seedlings established in 2001 or later, resulting in a relatively young cohort of seedlings from burned areas.

In general, terminal bud scar counts explain about 76% of the variability in seedling age of establishment from beetle-affected stands. Bud scar counts resulted in providing the true age of a seedling in only 6% of cases on outbreak sites. This error rate is similar to the results of Hankin et al. (2018), who tested the accuracy of terminal bud scar counts in *Pinus ponderosa* and *Pseudotsuga menziesii* for annual precision (a requirement for accurate analyses of annual climate). For both Engelmann spruce and subalpine fir, the error between bud scar counts and true age becomes increased in older seedlings; terminal bud scar counts consistently underestimate long-lived seedlings (Figure 3.3). This trend could be due to the slow growth exhibited by older seedlings in suppressed settings. Using terminal bud scar counts may be

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limited in slow-growing species such as suppressed subalpine fir and Engelmann spruce due to the extremely small growth increments between bud scars (Urza & Sibold 2013).

Our findings of weaker predictive strength of terminal bud scar counts for true age in post-fire establishment may be due to sampling design. Specifically, the smaller sample size of seedlings from burned areas and the smaller variability in ages (Post 2001) may have biased the R^2 value. Although the R^2 value for the bud scar count – age relationship is smaller for postfire seedlings than for seedlings from outbreak sites, the range of error is much smaller (Table 3.4). This is consistent with our findings of greater accuracy of terminal bud scar counts in younger seedlings. Aside from differences in sample size, greater accuracy of bud scar counts in predicting postfire seedling age could be due to high growth rates and younger ages of seedlings from burned areas, negating the difficulty of discerning narrow growth increments. This could also explain the stronger correlation between terminal bud scar count with taller post-fire seedlings, which is supported by the findings of Urza & Sibold (2013). Although the R^2 value for the correlation between terminal bud scar counts and postfire Engelmann spruce seedling age is deceptively small, postfire spruce seedlings have the highest percent accuracy of both species from both disturbance types (Table 3.4).

3.4.3 Climatic Drivers of Establishment

Subalpine fir and Engelmann spruce establishment pulses were correlated with minimum temperature and high precipitation levels in the spring and summer months. Abundant subalpine fir and Engelmann spruce seedling establishment occurred in years with average growing season minimum temperatures below -0.1°C and -0.38°C, respectively. On the other hand, no seedling establishment occurred in years with average growing season temperature minimums of 0.49°C. Low spring temperature minimums may contribute to the persistence of winter snowpack late

into the growing season. Snowpack levels have been shown to be directly correlated with successful subalpine fir and Engelmann spruce establishment in other studies (Buechling et al. 2016; Andrus et al. 2018; Carlson et al. 2020). Because there was no correlation between establishment years and maximum temperatures, seed masting was rejected as an explanation for broad-scale establishment patterns. At the same time, cool and moist growing season conditions limit subalpine seedling establishment and provide the strongest support for our findings. Late season snowmelt provides soil moisture as evaporative demand increases with increasing temperature in the summer months (Stephenson 1998; Redmond & Kelsey 2018; Hill et al. 2018); soil moisture is critical for establishing seedlings as it is a major contributor of temperature-induced moisture stress (Brodersen et al. 2006). Surprisingly, remote sensing derived soil moisture was not a significant predictor of seedling establishment, due to wide variability in soil moisture over small spatial scales. This finding is corroborated by Andrus et al. (2018); precipitation and snowpack levels proved to be more accurate predictors of broad-scale soil moisture and associated establishment pulses. Below-average temperature minimums in occurrence with above-average precipitation creates cool and moist growing season conditions that are optimal for subalpine tree species (Gill et al. 2015; Andrus et al. 2018; Hill et al. 2018). First-year subalpine tree germinants have high turgor loss points, indicative of high drought sensitivity (Lazarus et al. 2017); thus, subalpine seedlings require abundant growing season moisture in the first year of growth. Abundant subalpine tree seedling establishment occurred in years with average growing season precipitation above 53mm, whereas no seedling establishment occurred in years with average growing season precipitation of 44mm. Above average precipitation and lower temperatures (and lower temperature-induced moisture stress)

during the first growing season can contribute to subalpine seedling survival, supporting our findings of cool and wet conditions associated with widespread establishment events.

Our results indicate that subalpine fir and Engelmann spruce establishment events are highly correlated with lower-than-average VPD and CWD. Low deficit values correspond with cooler temperatures and low moisture stress on subalpine tree seedlings, supporting our findings of preferential establishment in cooler growing conditions. This is supported by other studies in this forest type (Lutz et al. 2010; Kueppers et al. 2017; Andrus et al. 2018; Hill et al. 2018). Deficit values quantify moisture stress; low moisture deficits associated with broad-scale establishment indicate the importance of water availability for seedling germination and first-year growth. Our findings of substantial tree establishment during years of low moisture deficit is supported by other studies in this region (Andrus et al. 2018; Hill et al. 2018; Redmond & Kelsey 2018), in addition to other forest types over a broad geographic range (Stevens-Rumann et al. 2018; Davis et al. 2019*b*; Hankin et al. 2019; Rodman et al. 2020). The correlation of both temperature and moisture with deficit values underscores the importance of cool *and* moist growing conditions for the establishment and survival of subalpine tree species. Although some experimental studies have suggested that warmer temperatures in conjunction with increased precipitation will promote subalpine tree establishment (Gill et al. 2015; Kueppers et al. 2017*b*), precipitation is highly spatially variable and the observed trends in subalpine forests indicate increasing moisture stress associated with higher summer temperatures (Lutz et al. 2010; Novick et al. 2016; Yuan et al. 2019). Therefore, our findings suggest that regional warming trends may severely threaten broad-scale Engelmann spruce and subalpine fir establishment.

Years with large establishment pulses of both species (>5% total seedlings established across all sites) were strongly correlated with the climate variables detailed above. Many of the

pulse events were synchronous across sites and species, indicating broad-scale drivers of seedling establishment (Figure 3.4). We found large establishment pulses as frequent as 2-year intervals. Although there have been few studies to analyze annual drivers of subalpine tree recruitment, Andrus et al. (2018) found widespread, synchronous pulses of subalpine tree establishment at this same frequency. Some pulse events were species-specific, such as the recent Engelmann spruce establishment pulse events occurring in burn sites. Burn areas expose bare mineral soil, providing optimal substrate for Engelmann spruce germination (Johnstone & Chapin 2006), which is contrary to the thick litter layers on which subalpine fir preferentially establishes (DeRose & Long 2010). Some years with low levels of spruce-fir establishment had climatic conditions that were closer to the long-term average than years with large establishment pulses. However, these years were significantly different from years of no establishment. This could be indicative of low levels of establishment that require suitable (but not anomalous) climatic conditions in addition to site-specific conditions, such as microsite facilitation and microclimate (Kroiss & HilleRisLambers 2015). Our finding of steady, yet low density, seedling establishment in subalpine forests is consistent with Woodward et al. (1995). Many other studies in western US subalpine forests have documented the importance of microclimate in successful seedling establishment. Although microsite considerations were beyond the scope of this study, canopy cover, appropriate substrate, soil fertility, and presence of nurse logs have all been documented as components of microsites that promote subalpine tree establishment (Brang et al. 2003; Parish & Antos 2005; Hill et al. 2018; Pettit et al. 2019). Although site-specific conditions may encourage low levels of seedling establishment during moderately favorable growing years, regional conditions anomalous to long-term climate promote broad-scale establishment events.

3.4.4 Implications of Climate Change on Establishment Events

Subalpine forests have experienced rapid warming over the past several decades, driven by increasing maximum summer temperatures (Rangwala and Miller 2010). This trend of increasing summer temperatures is strongly linked to projected increases in both VPD and CWD (Lutz et al. 2010; Rangwala et al. 2013; Williams et al. 2013; Novick et al. 2016; Young et al. 2017). Moisture deficits put undue stress on trees, preventing resource allocation to growth processes in efforts to conserve water (Lutz et al. 2010; Sulman et al. 2016). Consequently, mortality rates of seedlings and adult trees are strongly linked to increasing water deficits (Das et al. 2013; Young et al. 2017). Although above-average precipitation may mitigate water stress from moisture deficits (Lutz et al. 2010), climate projections of precipitation vary considerably over spatial and temporal scales (Kelsey et al 2018; Yuan et al. 2019), while models project steady and significant increases in water deficits in snow-dependent systems (Lutz et al. 2010; McCullough et al. 2016; Young et al. 2017). Drought-induced adult tree mortality concurrent with declines in successful seedling establishment may result in range contractions (Gottfried et al. 2012), compositional shifts to drought-tolerant species (Kueppers et al. 2017, 2017*b*), or potential losses to forest cover type.

3.4.5 Research Limitations

There is an abundance of interacting factors at differing scales that affect subalpine tree seedling establishment. In addition to numerous regional climatic factors, site level variability in elevation, topography, soil conditions, and overstory stand structure can have substantial effects on tree establishment at differing capacities. In this study, we tried to encapsulate regional drivers of establishment within one forest type, and incorporating fine-scale spatial variability into analyses was beyond the scope of this project, but important for future research. There could

be a potential scale mismatch between remote sensing derived site variables, such as soil moisture, and actual site conditions that vary over narrow spatial and temporal scales. Additionally, the sample size of seedlings from burned areas was relatively small in comparison to the number of seedlings from beetle-affected stands. This discrepancy can introduce bias when comparing the two groups. Seedlings from burned areas have only established over the last two decades, while seedlings from beetle-affected stands date back to the late 19th century. There is a shorter window of establishment in burned areas, preventing observations of long-term growth trends of post-fire recruitment. Additional samples and samples from older fires would reduce bias in future analyses.

3.4.6 Conclusions

This project is one of few studies to assess annual climatic drivers of subalpine tree establishment. Our results corroborate the strong correlation between cool and moist growing conditions with successful subalpine tree establishment. Our findings suggest that broad-scale anomalous climatic conditions act as regional drivers of establishment pulses, while site-specific conditions may facilitate low-levels of establishment on short temporal scales. The use of terminal bud scar counts and height classes to predict the age of suppressed seedlings lacks a high degree of accuracy, especially in older seedlings. However, greater accuracy can be obtained in postfire establishment due to distinguishable bud scars resulting from rapid growth that is unimpeded by light availability. This is an important consideration for managers when assessing post-disturbance recovery. The critical role of first-year climate in seedling survival in conjunction with projected increases in moisture stress contribute to significant uncertainty about subalpine forests' resilience against altered disturbance regimes and changing climatic conditions.
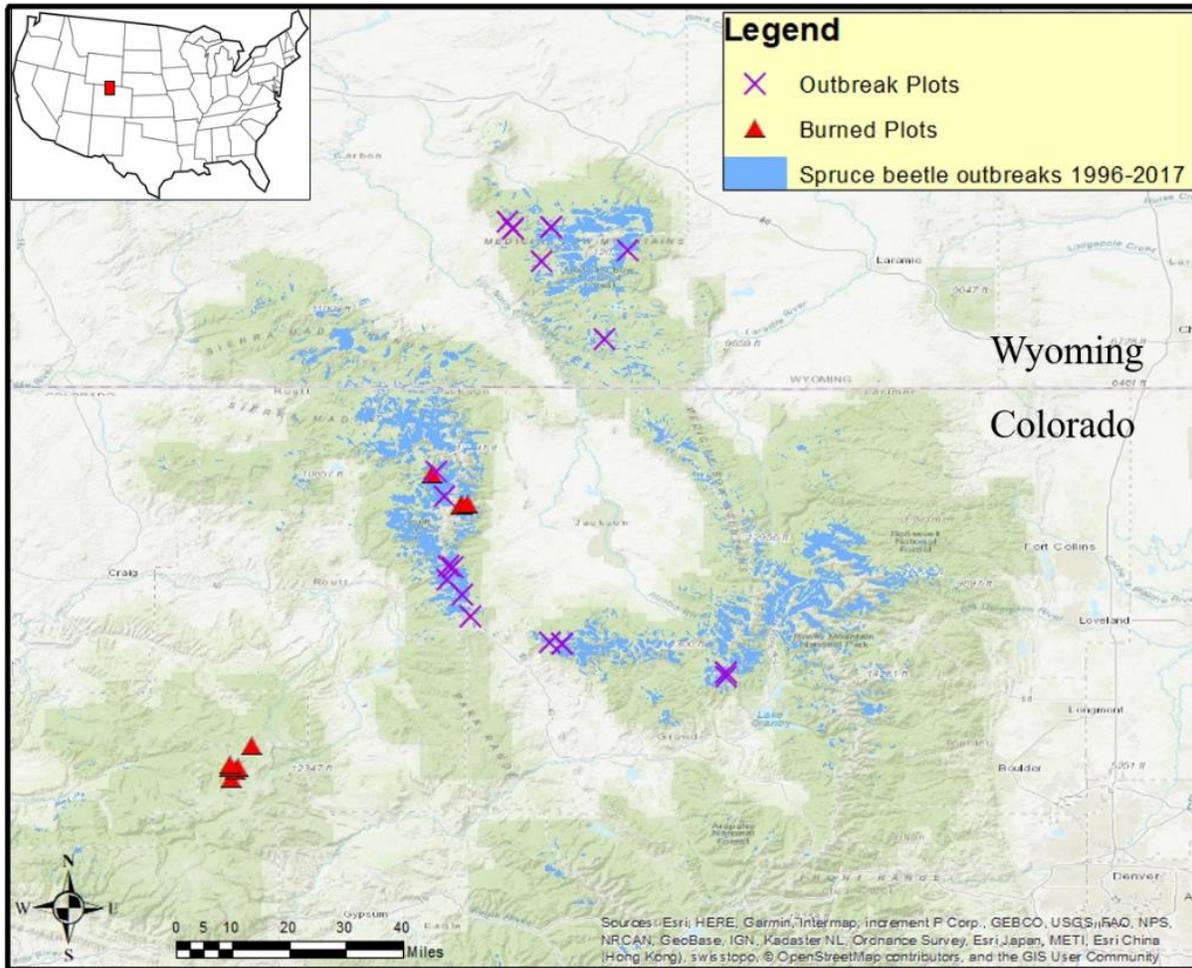
Figure 3.1: Map of site locations in Northern Colorado and Southern Wyoming.
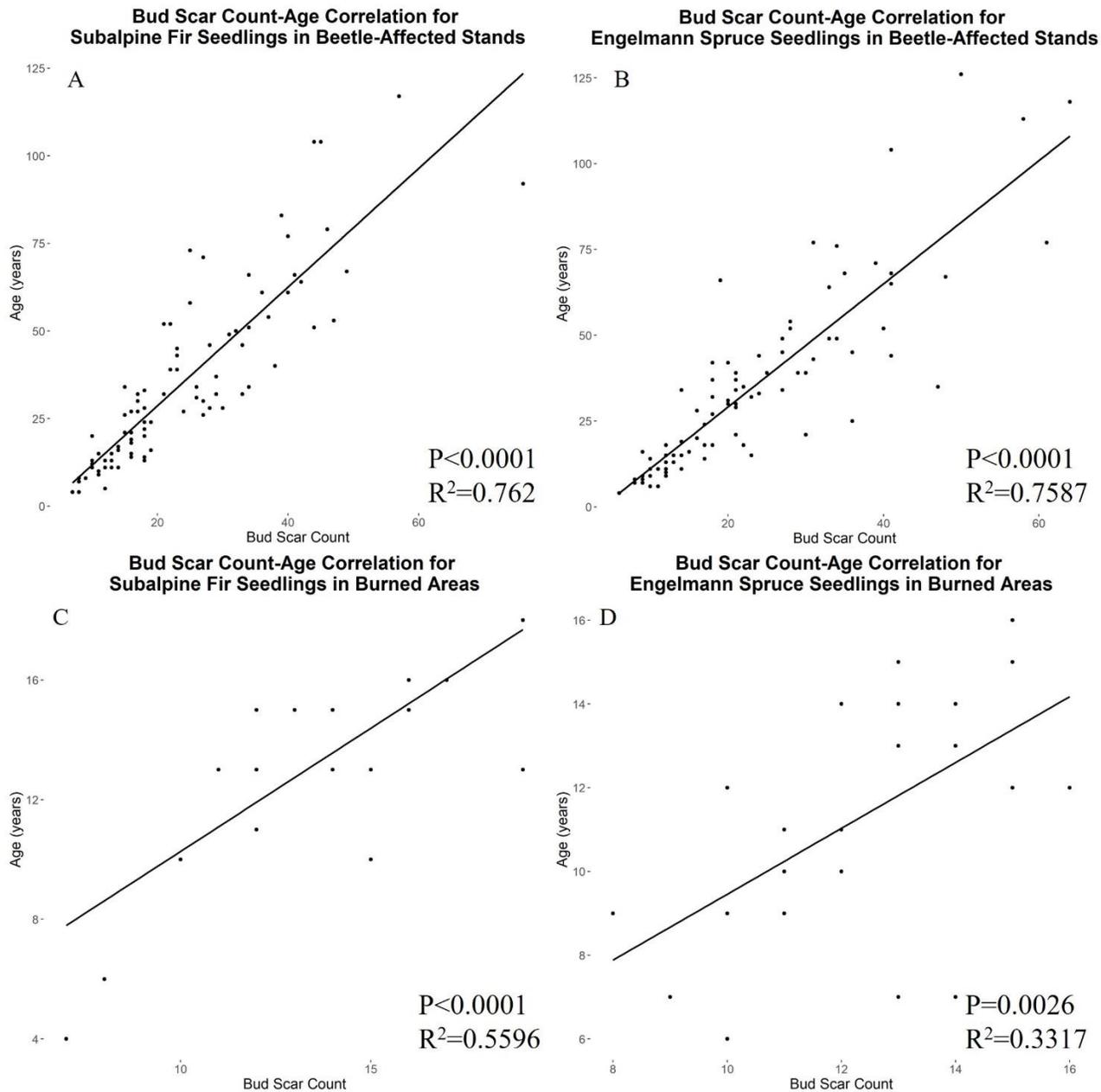
Figure 3.2: Correlation between terminal bud scar count and true age for A) subalpine fir in beetle-affected stands, B) Engelmann spruce seedlings in beetle-affected stands, C) subalpine fir in burned stands, and D) Engelmann spruce in burned stands.
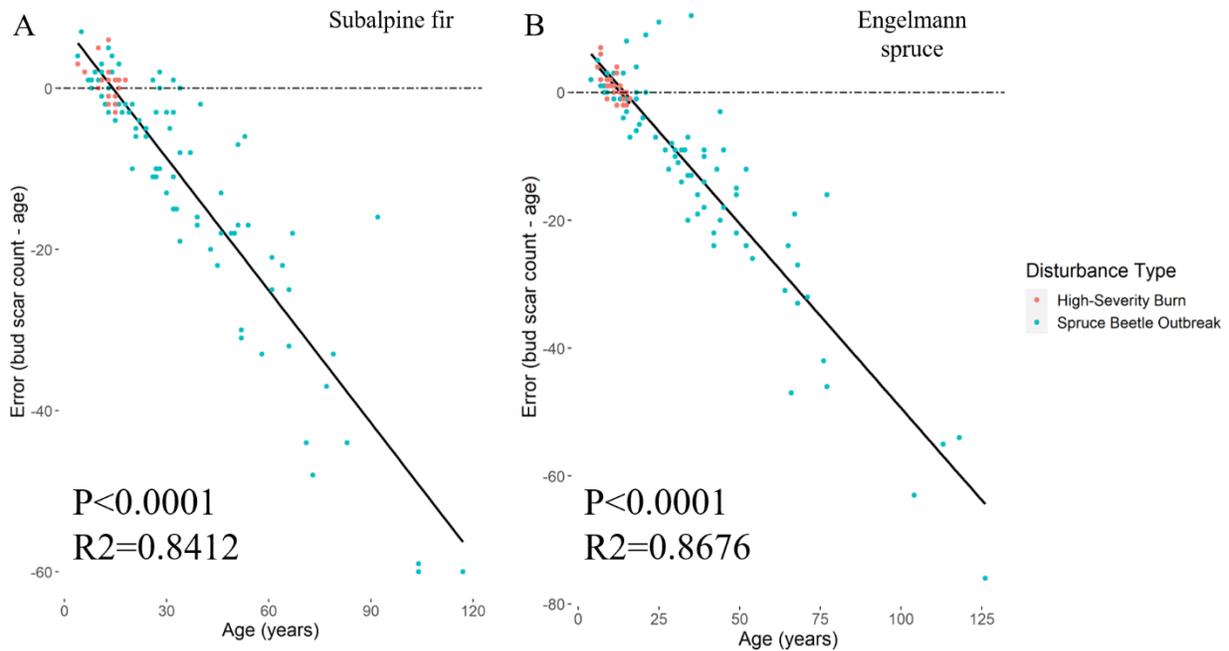
Figure 3.3: Correlation of bud scar error with true age for A) subalpine fir and B) Engelmann spruce seedlings. Negative errors indicate an underestimation of true age. The magnitude of error increases (greater absolute value) with increasing age. Horizontal dashed line indicates no error, or 100% prediction accuracy of true age.
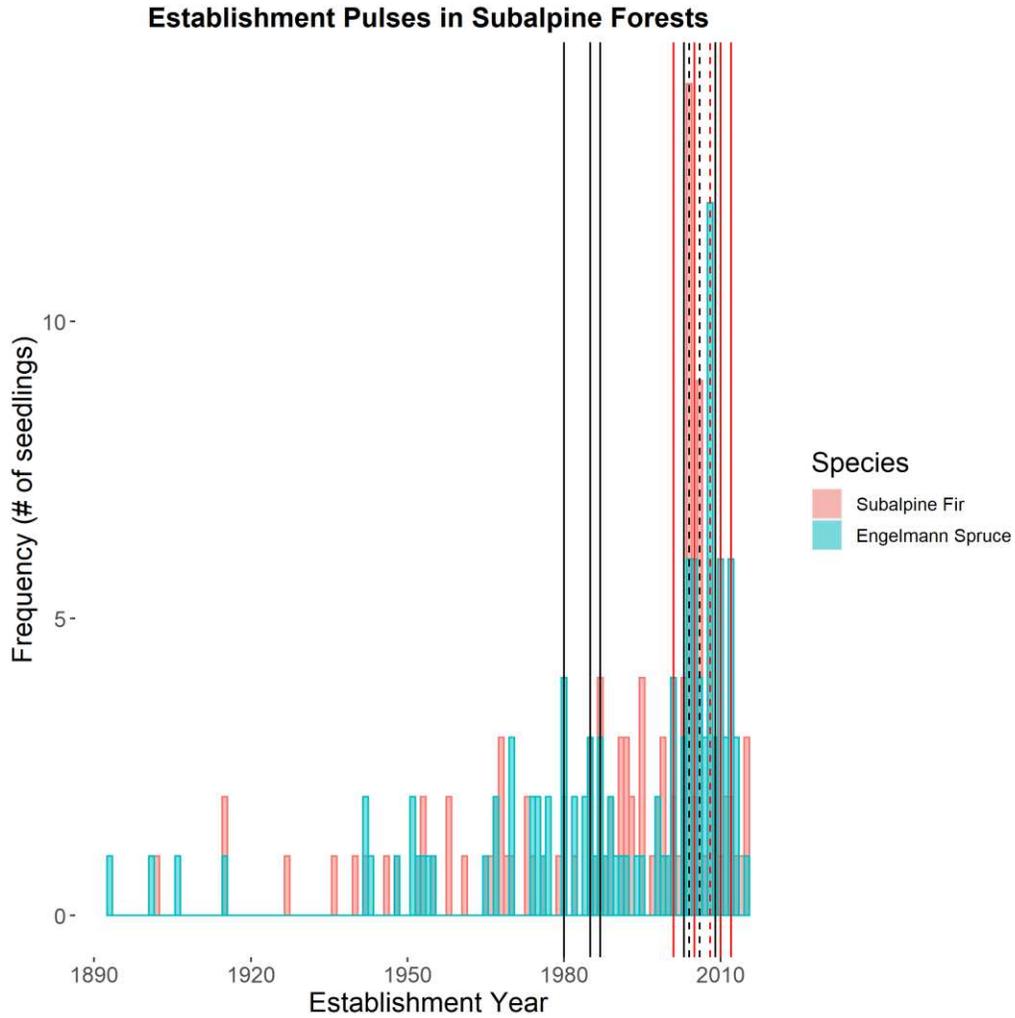
Figure 3.4: Establishment dates of both subalpine fir and Engelmann spruce. Dotted vertical lines indicate large establishment events (>5% of total seedlings). Black colored lines indicate pulse events for both species. Red colored lines indicate pulse events for Engelmann spruce.
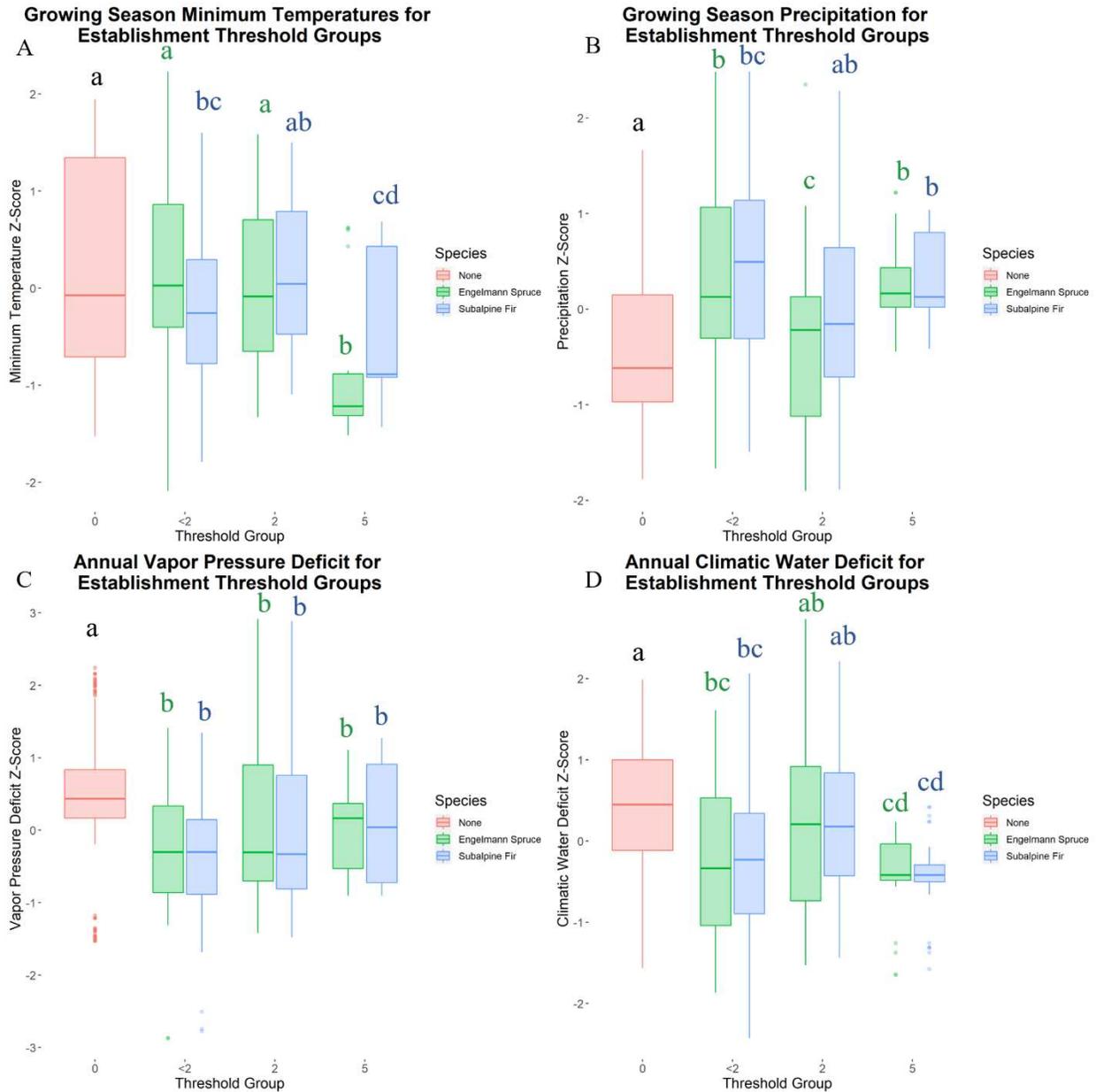
Figure 3.5: Boxplots of differences of climate variable z-scores between establishment threshold groups: A) growing season temperature minimums, B) growing season precipitation, C) annual vapor pressure deficit, D) annual climatic water deficit. Green boxes and text represent Engelmann spruce seedlings; blue boxes and text represent subalpine fir seedlings. Different letters above groups indicate statistical significance using Kruskal-Wallis tests to detect differences, and Dunn's tests to compare groups (α=0.05).

Table 3.1: Distribution of samples by species and disturbance type.

Species	Disturbance	Minimum seedlings per plot	Maximum seedlings per plot	Mean seedlings per plot
Abies lasiocarpa	Outbreak	3	6	4.65
Abies lasiocarpa	Burn	0	5	2.2
Picea engelmannii	Outbreak	2	5	4.45
Picea engelmannii	Burn	1	5	2.5

Table 3.2: Generalized linear model for predicting age of Engelmann spruce seedlings. Significant values are italicized. Outbreak sites are the baseline category. R^2=0.8158.

Engelmann spruce	Estimate	Std. error	t-value	P-value
(intercept)	-6.6190	2.3560	-2.809	*0.0059*
Height(cm)	0.1859	0.0470	3.96	*0.00013*
Bud scar count	1.4218	0.1292	11.003	*<0.0001*
Disturbance type: burn	-6.2405	2.7026	-2.309	*.02281*

Table 3.3: Generalized linear model table for predicting age of subalpine fir seedlings. Significant values are italicized. Outbreak sites are the baseline category. R^2=0.7992.

Subalpine fir	Estimate	Std. error	t-value	P-value
(intercept)	-4.6862	2.3416	-2.001	*0.0478*
Height(cm)	0.0953	0.0395	2.413	*0.0175*
Bud scar count	1.4882	0.1192	12.487	*<0.0001*
Disturbance type: burn	-7.4901	2.9357	-2.551	*0.0121*

Table 3.4: Error and accuracy of terminal bud scar counts for subalpine fir and Engelmann spruce from outbreak and burn sites. Mean error is the average of the number of years bud scar counts deviated from the true age. Accuracy is the number of times bud scar counts predicted true age. Negative error indicates underestimates of age.

Species	Disturbance	Mean Error	Accuracy
Abies lasiocarpa	Outbreak	-11.0323	4.30%
Abies lasiocarpa	Burn	0.3636	9.09%
Picea engelmannii	Outbreak	-11.191	8.99%
Picea engelmannii	Burn	1.04	24.00%

CONCLUSION

Climate-driven disturbances and their interactions have substantial impacts on subalpine ecosystem structure and resilience. An increase in climate-driven bark beetle outbreaks and wildfires has led to disturbance interactions that may alter post-disturbance recovery. Alterations in fuel structures due to beetle-caused mortality may have implications for subsequent fire behavior. Changes in overstory composition due to species-specific disturbances in conjunction with reduced tree regeneration may result in novel shifts in forest structure. While there was no evidence of compounded effects of multiple disturbances on tree regeneration, warming and drying trends coupled with increases in disturbance size and severity may result in subalpine regeneration failure (Harvey et al. 2016). Above-average growing season precipitation, below-average temperature minimums, vapor pressure deficit, and climatic water deficit are strongly correlated with subalpine tree establishment. Hence, there is significant uncertainty about the stability of forest structure and recovery dynamics given climate model projections of hotter and drier conditions in subalpine forests.

Our findings indicate that beetle-caused tree mortality results in significant increases in woody surface fuel loads over time. In particular, coarse woody debris loads increased substantially within the first decade of beetle-outbreak detection. Due to the slow decomposition rates characteristic to subalpine stands, accumulated downed woody surface feels can persist on the landscape for decades to a century (Mietkiewicz et al. 2018). The transfer of aerial fuels to surface fuels in beetle-affected stands results in a change in potential fire behavior compared to control stands. Although fuel arrangement within a stand and subsequent effects on fire weather are highly variable over spatial and temporal scales, beetle-caused fuel accumulation is likely to

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change wildfire behavior from predominate spread through the canopy to surface fires with long residence times (Donato et al. 2013). While wildfires in subalpine forests tend to be high-severity or stand replacing (Veblen 2000), altered fire behavior from increased woody surface fuel loads may negatively impact soil health and post-disturbance successional trajectories (Certini 2005; Carlson et al. 2017).

Disturbances in subalpine forests have different effects on stand structure and associated recovery dynamics. Spruce-beetle outbreaks are host-specific disturbances that result in a substantial loss of Engelmann spruce from the overstory and shift the compositional dominance toward subalpine fir. Changes in stand structure can impact post-outbreak recovery. In addition to a loss of viable seed source (Carlson et al. 2020), bark beetle outbreaks result in extensive canopy mortality. Live canopy cover facilitates subalpine tree regeneration by creating microsite conditions that buffer against temperature extremes and moisture deficits; loss of live overstory trees may reduce favorable site conditions for tree seedlings (Calder & Clair 2012; Stephens et al. 2019). Additionally, wildfires in subalpine forests tend to be stand-replacing (Veblen 2000); loss of overstory trees results in harsh post-fire growing conditions, contributing to the importance of favorable climate for post-fire seedling recruitment (Harvey et al. 2016). Climate is a critical driver of subalpine tree establishment in both beetle-affected and burned stands.

Post-disturbance recovery is contingent upon favorable growing conditions that encompass both site-specific microsite conditions, which are highly variable, and broad-scale climate trends. Although seedlings of all height classes were found consistently across time-since-outbreak, both Engelmann spruce and subalpine fir demonstrate suppressed growth in low-light conditions. Therefore, observations of seedlings in the shortest height classes do not necessarily indicate post-outbreak recovery. Post-outbreak recovery is dominated by advanced

regeneration (seedlings that were established before the disturbance). Post-fire seedling densities were severely reduced compared to control and outbreak sites, which could be due to a loss of microsite conditions and/or unfavorable post-fire climate. Large establishment events across broad spatial scales are strongly correlated to cool and moist growing conditions. Site-specific conditions may facilitate low levels of semi-continuous regeneration, while regional climate supports broad-scale pulses of subalpine tree establishment. Climate models project increasing water deficits with increasing temperatures in subalpine forests. Warming and drying trends coupled with an increase in canopy mortality due to high-severity disturbance events can create hostile growing conditions that alter the trajectory of subalpine forest recovery toward more drought- and fire-resistant species.

These studies provide valuable information to forest managers on disturbance resilience. Fuel treatment methods implemented within the first decade of bark beetle outbreak detection can minimize surface fuel accumulation. However, different management objectives may call for vastly different treatments. Silvicultural prescriptions such as planting and shelterwood cutting may improve subalpine forest recovery following high-severity disturbances, especially in burned landscapes where advanced regeneration is lacking. Due to the ability of Engelmann spruce and subalpine fir to remain suppressed in the understory for over a century, the use of height classes and terminal bud scar counts as proxies for seedling age may not be reliable methods for analyzing recovery dynamics in closed canopy stands. However, bud scars may provide accurate predictions of seedling age in burned sites; this method should be utilized over destructive sampling in order to minimize any impacts on post-fire stand recovery.

These studies had several limitations that should be taken into consideration during future research design and implementation. Soil conditions may be important predictors of seedling

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density in disturbed areas. Although highly variable over fine spatial scales, integration of within-stand soil characteristics may bolster future research on drivers of post-disturbance regeneration. Due to the spatial variability of tree mortality following disturbance events, considerations of seed source proximity may also provide further information on predictors of seedling recruitment. Larger sample sizes of burned sites in varying stages of recovery may elucidate long-term patterns of post-fire establishment and structural dynamics. Lastly, long-term monitoring of disturbed stands in subalpine forests will continue to advance our understanding of ecosystem recovery and functioning amid unprecedented climatic shifts.

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