

THESIS

THE EFFECTS OF BARK BEETLE-FIRE DISTURBANCE INTERACTIONS ON
POST-DISTURBANCE FOREST REGENERATION

Submitted by

Jean L. Fleming

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Master's Committee:

Advisor: Jason Sibold

Jill Baron

N. Thompson Hobbs

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ABSTRACT

THE EFFECTS OF BARK BEETLE-FIRE DISTURBANCE INTERACTIONS ON POST-DISTURBANCE FOREST REGENERATION

Disturbances in forested ecosystems create ecological legacies that can affect future disturbances and these disturbance interactions influence post-disturbance establishment. In addition, disturbances can become compounded and cause drastic ecosystem changes including decreased post-disturbance establishment, regeneration of unexpected species assemblages, or shifts to alternative stable states. I studied the post-disturbance establishment of five tree species following two interacting disturbances, a bark beetle outbreak and a high-severity fire. The goal of my research was to identify the factors that influence post-disturbance seedling establishment, and to determine how bark beetle-fire interactions affect forest regeneration. I evaluated seedling establishment at 98 study sites across the Cow Creek fire in Rocky Mountain National Park. Two bark beetle species, mountain pine beetle (*Dendroctonus ponderosae*) and spruce beetle (*Dendroctonus rufipennis*), caused epidemic scale tree mortality in the five years before the fire. I created a Bayesian mixture model for each tree species to assess the independent variables that influenced the abundance of the species' establishment. The variables that influenced mean seedling abundance were different for each species. Forest age, distance to a seed source following the fire, and disturbance interactions affected the seedling abundance for most of the species. The presence of recent bark beetle activity had a measurable affect on post-disturbance

establishment for three species. *P. contorta* and *P. tremuloides* mean abundance increased by a factor of 3.1 and 1.4, respectively, in areas with mountain pine beetle disturbance. The mean abundance of *P. engelmannii* seedlings was 3.8 times greater in areas where spruce beetle had caused tree mortality before the fire. This increase in seedling abundance in areas with bark beetle presence was independent of the other studied factors, including fire severity and elevation. The increased seeding abundance I recorded following bark beetle and fire disturbance suggests that interacting disturbances can increase the likelihood that forests will recover to their original species assemblages. The results of this study should be utilized to inform future forest management and to avoid unnecessary management action.

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Committee members:

Jason Sibold, Jill Baron, and Tom Hobbs

2013 field assistants:

Kelly Brady, Pete Gadomski, Nick Fleming, Catherine Kordesch, and David Fryefield

2014 field assistants:

Aaron Sidder, Amanda Farias, Ilana Araujo, Ian Smith, Mackenzie Platt, Nicole Luchetta, and Westin Pease

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INTRODUCTION: DISTURBANCE IN ROCKY MOUNTAIN SUBALPINE FORESTS

Disturbances play an important role in ecosystems; they influence vegetation dynamics by changing the age and species composition of forest patches (White 1979, Veblen et al. 1994). In addition, the lasting ecological patterns created by disturbances can affect how future disturbances influence the landscape (Dale et al. 2001, Bebi et al. 2003). These disturbance interactions are especially important in areas where disturbances are common, such as Rocky Mountain subalpine forest ecosystems. Disturbances that occur in subalpine forests include blowdown, avalanche, wildfire and bark beetle outbreak (Veblen et al. 1994). Individually, these disturbances have been well researched. Many studies have focused on the frequency, extent, severity, and return interval of the different disturbance types (Schmid and Frye 1977, Veblen et al. 1989, 1991b) with fewer studies focusing on the ecological consequences of disturbances.

In subalpine ecosystems, wildfire is one of the largest and most frequently studied individual disturbances. The fire regime is defined by large, high-severity burns, with a > 200 year return interval (Sibold et al. 2006). Subalpine fires are generally driven by drought and other climatic conditions (Schoennagel et al. 2004, Sibold et al. 2007). Stand-replacing fires are common, especially in areas dominated by fire adapted *Pinus contorta* (lodgepole pine) (Kipfmueller and Baker 2000, Sibold et al. 2006, Jenkins et al. 2008). These high-severity, stand-replacing fires generally lead to the regeneration of even-aged *P. contorta* stands (Kipfmueller and Baker 2000, Sibold et al. 2006, Jenkins et al. 2008). Bark beetles also cause landscape-scale disturbances in subalpine forests,

that affect canopy composition differently than fire disturbances. Unlike fire, bark beetle disturbance causes mortality in individual tree species, and can shift the composition of the forest canopy (Schmid and Frye 1977). Bark beetles preferentially kill large old trees, especially those stressed by drought or damage (Raffa et al. 2008). Beetle disturbance has a long return interval because beetles need host trees of a certain age class (older than 80 years) to propagate (Paine et al. 1984). Following a bark beetle outbreak, the disturbed forest must recover before it can sustain another epidemic outbreak (Raffa et al. 2008). Similar to bark beetle disturbance, blowdown occurs most commonly in old growth forests (Veblen et al. 1989). The severity of blowdown disturbance can vary from affecting a few interspersed trees to replacing entire landscapes (Kulakowski and Veblen 2002). Blowdown can influence species dynamics by allowing for advanced regeneration of shade tolerant species (Veblen et al. 1989, Kulakowski and Veblen 2003). Blowdown also plays an important role in initiating spruce beetle outbreaks. When present at endemic levels, spruce beetle (*Dendroctonus rufipennis*) use downed trees as hosts. The large number of downed trees present following a blowdown allows spruce beetle populations to rise to epidemic levels (Schmid and Frye 1977). The unique characteristics of fire, bark beetle, and blowdown create ecological legacies that can interact with future disturbances.

Disturbance interactions affect landscape patterns differently than individual disturbances. The patterns that disturbances create on the landscape can last through multiple future disturbances, and as these disturbances interact they create landscape heterogeneity that allows for greater species diversity (Veblen et al. 1994). The ecological legacy of wildfire can reduce the severity of future fire disturbance and can

decrease mortality from beetle attacks (Veblen et al. 1994). High-severity fire resets the age of a forest, and reduces the number of trees that beetles can use as hosts (Veblen et al. 1994). Blowdown affects forest floor fuel load which can increase the severity and size of fire disturbance (Kulakowski and Veblen 2007). The effect of beetle disturbance on forest fire is more complicated than other disturbance interactions. Some research indicates that bark beetle disturbance can increase fire severity (Bigler et al. 2005), while other research suggests a decrease in fire severity. (Simard et al. 2011). Additional studies suggest that the difference in these findings is related to the change in canopy fuels over time following a beetle attack (Jenkins et al. 2008).

Disturbance interactions affect forests in complex ways, and frequently result in forest conditions that differ from those created by individual disturbances. More research is needed in order to fully understand the effects of disturbance interactions on forests. I completed a study focused on a bark beetle outbreak followed by a wildfire in a subalpine forest ecosystem in Northern Colorado. Past research of bark beetle-fire interactions have focused primarily on the effects of bark beetle outbreaks on the extent and severity of subsequent fire. However, few studies have focused on how disturbance interactions affect forest regeneration. The goal of my research is to understand how bark beetle-fire interactions influence post-disturbance establishment.

CHAPTER 1. THE EFFECTS OF BARK BEETLE-FIRE DISTURBANCE INTERACTIONS ON POST-DISTURBANCE FOREST REGENERATION

INTRODUCTION

Disturbances drive landscape patterns by altering the age and species composition of ecosystem patches (White 1979). In forested ecosystems, disturbances increase light and resource availability, which can create an opportunity for the establishment of new individuals (White 1979, Peterson and Vose 2014). The ecological legacies of past disturbance create a mosaic of forest patterns that shape both the likelihood and characteristics of future disturbances (Veblen et al. 1994), and influence the patterns of post-disturbance regeneration (Sibold et al. 2007). The effect of disturbance interactions on post-disturbance regeneration is potentially more significant when disturbances occur close together in time (Paine et al. 1998). When a disturbance event occurs in an area that has not yet recovered from a prior disturbance the result can be a compounded disturbance that can shift species assemblages or push ecosystems into novel stable states (Paine et al. 1998). Compounded disturbances have been identified in many ecosystems, and in most cases have been found to reduce the likelihood that regeneration will follow the patterns of the pre-disturbance ecosystem (Paine et al. 1998, Kulakowski et al. 2013, Harvey et al. 2013). Regeneration of species assemblages that are different than pre-disturbance patterns is worrisome due to the unpredictable nature of ecosystem shifts, and the possibility that shifts to alternative stable states could lead to species extinctions or loss of economic resources (Scheffer et al. 2001). Concern over compounded disturbances is currently growing

because climate change is predicted to increase the frequency and extent of disturbances over the next century (IPCC 2007), which will increase the potential for compounded disturbances. As compounded disturbances become more common, effective ecosystems management will require a greater understanding of their ecological consequences (Dale et al. 2001, IPCC 2007, Peterson and Vose 2014). The goal of my research was to investigate how the bark beetle outbreaks, wildfire, and other environmental factors interact to shape post-fire regeneration in subalpine forests of Rocky Mountain National Park (RMNP), and to assess the effects of compounded bark beetle and wildfire disturbance on post-disturbance regeneration.

Bark beetle (*Dendroctonus*) outbreaks in Rocky Mountain subalpine forests periodically result in extensive areas of species-specific mortality (Schmid and Frye 1977, Shore et al. 2006). Low amounts of tree mortality occur when beetles are present at endemic levels, but when forest conditions are conducive to a mass attack beetle populations can rise to epidemic levels and cause extensive tree mortality at a landscape scale (Raffa et al. 2008). Ideal bark beetle host trees are older than 80 years, larger than 15 cm diameter at breast height (dbh), and are located in dense stands with more than 750 stems per acre (Paine et al. 1984). Age and resource competition tends to weaken these trees and make them less able to defend against beetle attacks (Shore and Safranyik 1992, Hicke and Jenkins 2008). Bark beetle outbreaks have lasting ecological legacies that influence forests for years following an outbreak (Veblen et al. 1991a). Because bark beetles target specific host species, outbreaks can shift species dominance to non-host species that were present in the forest before the outbreak (Raffa et al. 2008). Trees infested and killed by bark beetles also influence the

ecological legacy of the forest; attacked trees undergo changes for decades following an outbreak (Simard et al. 2011, Schoennagel et al. 2012). These forest changes can be classified in four stages: green-attack, red, gray, and silver. Green-attack stage begins when trees are first infested by adult beetles and lasts for < 1 year; during the green-attack stage needles on infested trees lose their moisture quickly but are retained in the canopy (Simard et al. 2011, Hicke et al. 2012, Schoennagel et al. 2012). Red stage occurs 1-2 years after trees are infested; trees begin to lose needles to the forest floor and needles that remain in the canopy lose their green color (Simard et al. 2011, Hicke et al. 2012, Schoennagel et al. 2012). Within a single forest stand bark beetles infest trees over multiple years, therefore within the first few years of an outbreak, forest stands will be in a mixture of green-attack and red stage (Harvey et al. 2014a). In the 2-15 years following the start of an outbreak stands shift into the gray stage, in which needles fall to the forest floor, boles remain standing, and no new tree infestations occur (Simard et al. 2011, Hicke et al. 2012, Schoennagel et al. 2012). Silver stage (*i.e.* old outbreak stage) occurs 25-30 years after an outbreak, at which point the majority of trees killed during the outbreak have fallen down and are present on the forest floor (Simard et al. 2011, Hicke et al. 2012, Schoennagel et al. 2012). Disturbance interactions between bark beetle outbreaks and wildfires are highly influenced by the time elapsed since the bark beetle outbreak (Harvey et al. 2014a, 2014b). As disturbed forests move through different post-bark beetle stages, fuel availability and flammability change significantly (Simard et al. 2011). In the last two decades, Colorado subalpine forests have experienced extensive high-severity outbreaks of two bark beetle species, mountain pine beetle (*Dendroctonus ponderosae*) and spruce beetle (*Dendroctonus*

rufipennis) (US Forest Service 2012). The mountain pine beetle outbreak began in 1996 and has affected more than 1.3 million hectares of Colorado forest (US Forest Service 2012). Mountain pine beetles utilize multiple pine species as hosts; in subalpine forests they cause mortality in both *Pinus contorta* and *Pinus flexilis* (Amman and Cole 1983). The recent spruce beetle outbreak began in the early 2000s and has killed *Picea engelmannii* in over 0.76 million hectares of Colorado forest (Samman and Logan 2000, US Forest Service 2012).

In Colorado, fire regimes and their effect on post-fire species regeneration is generally well understood, outside the scope of beetle influence. Wildfires in subalpine forests of Colorado play a central role in shaping forest patterns (Veblen et al. 1994, Mckenzie et al. 2011). The subalpine fire regime is characterized by high-severity stand-replacing fires, that burn areas larger than 300 hectares, and have a fire rotation time > 200 years (Romme 1982, Kipfmueller and Baker 2000, Sibold et al. 2006). *P. contorta* can quickly recolonize areas that have been severely burned because it is adapted to regeneration in open sites with mineral soil, and has serotinous cones that do not open until they are exposed to temperatures > 45° C (Lotan 1976). *Populus tremuloides* is also adapted to high-severity fires due to its ability to re-sprout suckers from underground root systems within the first year following a fire (Mitton and Grant 1980, Suzuki et al. 1999). In the Rocky Mountain region *P. tremuloides* regeneration occurs most often through re-sprouting, and germination of *P. tremuloides* from seeds is believed to be rare (Kay 1993, Night 1994). In contrast to *P. contorta* and *P. tremuloides*, *P. engelmannii* and *Abies lasiocarpa* require seed trees to be present following a fire in order to disperse seeds (Johnson and Fryer 1989, Little and Peterson 1994). Although

these species are generally less abundant in the initial floristics following a high-severity fire, they can become more common in the canopy over time due to their ability to tolerate the low-light understory following the initial post-fire regeneration (Day 1972).

While it is clear that prior disturbance influences the likelihood and characteristics of subsequent disturbances in Rocky Mountain subalpine forests (Veblen et al. 1994, Bebi et al. 2003, Bigler et al. 2005), the ecological consequences of these interactions are not as well understood. In the context of bark beetle-fire interactions, research has focused primarily on whether bark beetle disturbance changes the likelihood, extent, or intensity of subsequent wildfires (Bebi et al. 2003, Bigler et al. 2005, Kulakowski and Veblen 2007). In Rocky Mountain subalpine forests, bark beetle disturbance can influence future fire behavior, especially the likelihood that a fire will burn as a ground or crown fire (Jenkins et al. 2008, Simard et al. 2011, Schoennagel et al. 2012). However, the significance of the disturbance interaction is determined by a mixture of factors including time since beetle attack, beetle outbreak severity, and burn conditions (Harvey et al. 2014a). For example, when a forest fire burns during extreme weather conditions, fire severity is less influenced by other factors (Harvey et al. 2014a). Under moderate weather conditions fire severity is influenced by the outbreak stage of past bark beetle disturbance; when compared to forests without beetle disturbance, fire severity is greater for forest patches in green-attack/red stage and less for forest patches in gray stage (Simard et al. 2011, Harvey et al. 2014a, 2014b). The influence of beetle disturbance on fire severity increases as bark beetle outbreak severity increases (Harvey et al. 2014a). In severe fire weather conditions when the presence of bark beetles does not influence fire severity, some aspects of fire behavior can still be

influenced by bark beetle outbreak stage (Schoennagel et al. 2012). Fire behavior can affect the regeneration following a fire by changing the post-disturbance seed source (Turner et al. 1999). Due to the ecological importance of these interactions I focused my research on a wildfire that had burned through a forest recently disturbed by bark beetles (mixed green-attack/red stage). More specifically, I investigated the post-disturbance seedling establishment following a wildfire in an area with ongoing mountain pine beetle and spruce beetle outbreaks. My research focused on the following question: what factors, including potentially compounded bark beetle-fire disturbance interactions, influence seedling abundance and species composition following wildfire?

STUDY AREA

My study area was located within a designated wilderness area surrounding the West and Fox Creek drainages in northeastern Rocky Mountain National Park. The land use of my study area includes multiple anthropogenic disturbances before and after the 1915 establishment of Rocky Mountain National Park (Buchholtz 1983). Mining and ranching were both common within the Rocky Mountains in the early 1900s, and likely occurred within my study area, although these practices were halted when the park was established (Buchholtz 1983). Fire suppression began within the park boundary in 1915 and continued until the 1970's when fire was reintroduced to the park through controlled burns (Buchholtz 1983). This 55-year fire suppression period did not have a significant influence on my study area due to the naturally long fire return interval (>200 years) of

Colorado subalpine forest ecosystems (Sibold et al. 2006). Effects from park tourism are minimal within my study area, which is located more than two miles from the nearest public trail (Schuster et al. 2004).

My study area has a characteristic continental climate. Precipitation is primarily introduced to the site as snow during winter storms, and through localized summer convective storms (WRCC 2014). The closest weather station to my study area is located approximately 11 km away in Estes Park, Colorado; at an elevation 350 meters lower than the lowest point within my study area (WRCC 2014). The mean annual precipitation in Estes Park is 400 millimeters (WRCC 2014). The precipitation during summer storms falls in the form of hail, rain, or snow (WRCC 2014). Lightning will often accompany these summer storms and can act as the ignition source for wildfire (U.S. Fish and Wildlife Service et al. 2010). Summer mean temperatures from 1981-2010 measured in Estes Park were 17° Celsius, while winter means were -2° Celsius (WRCC 2014). The topography of the West Creek drainage is mountainous which, allows for localized weather patterns depending on aspect and elevation (USGS-NPS 2005).

My study plots are located within the perimeter of the 2010 Cow Creek fire, which burned as a high-severity fire for the majority of its extent (USGS 2010). Some lower-severity burned areas were present within the fire, located near the burn edges and low in drainages (USGS 2010). The fire burned 485 hectares of forest from 2700 to 3550 meters in elevation during two distinct periods: 390 hectares burned between June 24th and July 13th, and an additional 100 hectares burned between September 5th and September 27th (USGS 2010). Approximately 90% of the area burned was dominated by subalpine forest and I focused my sampling within that ecosystem type. The pre-fire

subalpine canopy was dominated by *P. contorta* at elevations below 2900 meters and was dominated by *A. lasiocarpa* and *P. engelmannii* forest at elevations above 3200 meters (USGS-NPS 2005). *A. lasiocarpa* and *P. engelmannii* also made up the dominate canopy cover in lower elevation areas in close proximity to West Creek (USGS-NPS 2005). Mixed conifer (*P. contorta*, *P. engelmannii*, *A. lasiocarpa*, and *P. flexilis*) canopy covered elevations from 2900 to 3200 meters (USGS-NPS 2005). *P. tremuloides* and several *Pinus ponderosa* were also present within the extent of the burned subalpine forest (USGS-NPS 2005). Based on fire history research in the area the majority of the forest that burned in the Cow Creek fire was initiated following a stand-replacing fire that occurred in 1646, with the exception of a section of land between West and Fox Creek that was initiated following a fire in 1861 (Buechling and Baker 2004).

Before the 2010 fire, mountain pine and spruce beetles caused large-scale tree mortality within the burn area as part of greater regional outbreaks that began in 1994 and 2002 respectively (US Forest Service 2012). In 2007 the USFS aerial detection survey identified mountain pine beetle as the cause of mortality in the area (US Forest Service 2012). By early 2010 the outbreak had spread through a majority of the forest and had killed many of the large pine (US Forest Service 2012). *P. contorta* was the primary host of mountain pine beetle, although many *P. flexilis* were also killed in the attack (US Forest Service 2012). Spruce beetle outbreaks are difficult to detect in aerial surveys because the needles turn a dull green color after being killed (Schmid and Frye 1977). Consequently, the severity and extent of outbreaks based on aerial surveys are often underestimated (Schmid and Frye 1977). Moreover, when beetle disturbance is

detected by aerial surveys it means that beetles have been present for at least one year within the trees (Schmid and Frye 1977). In the summer of 2010, the aerial detection survey recorded evidence of spruce beetle mortality in valleys adjacent to my study area (US Forest Service 2012). In 2011, approximately 245 hectares of the West Creek drainage directly adjacent to the fire was recorded as affected by spruce beetles (US Forest Service 2012). Due to the lag time between when beetles kill a tree and when that mortality can be identified by an aerial survey this data suggests that the beetle outbreak was in green-attack/red outbreak stage in the area before the fire began in the summer of 2010.

METHODS

Field methods

I used a stratified random sampling method to identify study points within the fire perimeter. Within each plot I collected species data for all conifer seedlings or saplings and all *P. tremuloides* suckers. I estimated the age of seedlings and suckers through the presence of annual nodes (Urza and Sibold 2013). For all stems in the plot, I recorded species and status (alive or dead) and documented evidence of pre-fire bark beetles by checking for beetle galleries on all dead *P. contorta*, *P. flexilis*, and *P. engelmannii*. Sites with any evidence of either mountain pine or spruce beetles were classified as beetle active sites. Given the number of trees killed by beetles in the surrounding forest and the 2008-2011 USFS aerial detection survey data, I assumed that any mountain pine or

spruce beetle galleries found within the fire were the result of the most recent bark beetle outbreak and that the trees were killed by beetles between 2008 and 2010 (US Forest Service 2012).

Data analysis

I used existing GIS datasets to incorporate pre-fire vegetation (USGS-NPS 2005), burn severity (USGS 2010), beetle presence (US Forest Service 2012), and stand age (Buechling and Baker 2004) in my analysis. I completed statistical analysis using the R statistical environment for statistical computing and graphics (R Core Team 2013) and QGIS Geographic Information System (QGIS Development Team 2014).

I analyzed the effect of eight independent variables on post-fire seedling abundance. I selected these variables because previous research has shown their ability to influence post-disturbance regeneration in similar ecological systems (Turner et al. 1997, 1998, Paine et al. 1998). Seven of the eight variables were calculated in the same manner for all species. Three of the variables were continuous: elevation, northness, and slope. The additional four variables were categorical: mountain pine beetle (present, absent), spruce beetle (present, absent), year of last stand-replacing burn (1646, 1841, neither), and burn severity (low, medium-low, medium-high, and high). Burn severity was calculated for each site based on the Burn Area Reflectance Classification of the fire (USGS 2010). I verified the burn severity at each plot using the following metric: low (<10% tree mortality), medium-low (10%-50% tree mortality), medium-high (50%-90% tree mortality), or high (>90% tree mortality). The final variable I included in my analysis was distance to seed or root source. Distance to seed or root

source was calculated in one of two ways depending on the life-history traits of each species. For *P. tremuloides* and serotinous *P. contorta*, I calculated distance to seed or root source to the closest forest patch where that species was present, dead or alive (USGS-NPS 2005). I calculated the distance to seed source of *P. engelmannii*, *A. lasiocarpa*, and *P. flexilis* as the distance from the plot to the closest patch of live vegetation (unburned or low/medium-low fire severity) where that species was present based on the 2005 vegetation map (USGS-NPS 2005). I also included six ecologically relevant variable interactions in my analysis, five of which accounted for possible disturbance interactions within my study area (fire severity * year of last stand-replacing burn, mountain pine beetle presence * year of last stand-replacing burn, spruce beetle presence * year of last stand-replacing burn, mountain pine beetle presence * fire severity, spruce beetle presence * fire severity). One additional variable interaction, fire severity * elevation, was included due to the known influences that elevation can have on fire severity (Bigler et al. 2005).

I calculated Pearson's correlation coefficients for each set of variables to test for collinearity between variables (Ott and Longnecker 2010). I created a Bayesian regression model of seedling abundance for the five most common species identified in my study sites. I modeled seedling abundance with a zero inflated Poisson model specified as:

$$\begin{aligned}
y &\sim \begin{cases} \text{Pois}(\lambda_i), & z_i=1 \\ 0, & z_i=0 \end{cases} \\
z_i &\sim \text{Bern}(P) \\
\beta &\sim N(\mu, \Sigma) \\
\lambda_i &= e^{X\beta}
\end{aligned} \tag{1}$$

In my model, λ_i is the abundance likelihood, informed by the vector β of regression coefficients that relate to the vector X of explanatory variables. P is the presence probability for the species. A mixture model was used to account for the multitude of sites in which one or more of the species were absent (Royle and Dorazio 2008). I wrote a Monte Carlo Markov Chain algorithm (MCMC) in the R statistical environment, using Gibbs samplers and Metropolis Hastings algorithms when appropriate; I used the MCMC algorithm to fit each of my five species models to my seedling abundance data. I centered and scaled all non-categorical predictor variables and modeled categorical variables with more than two categories as multiple binary variables. For each species, I completed model selection using a 10-fold cross validation with a best-first search to optimize mean squared error. I fit the selected model to the full data set using 100,000 MCMC iterations. For each variable included in the model I calculated the derived quantity e^β which allowed me to consider the multiplicative affect of the model parameters on mean seedling abundance.

RESULTS

I sampled a total of 98 sites within the Cow Creek fire (Table 1). The Cow Creek fire burned at high-severity for most of its extent, however, patches of lower-severity burn were present within the fire. Of the sites I sampled, there were 45 high-severity, 21 medium-high severity, 18 medium-low, and 14 low-severity sites. Mountain pine beetle was present in 70 of my study sites. There were 41 total sites where *P. contorta* was the dominant canopy species, and mountain pine beetle was present in 35 of those sites. Spruce beetle was much less common within the Cow Creek fire perimeter; I found *P. engelmannii* that showed sign of pre-fire spruce beetle presence at 23 of the 98 sites. Spruce beetle was present in 5 of the 13 sites dominated by *P. engelmannii*.

Plots where mountain pine beetle was present before the fire (n=70) had more post-disturbance seedling abundance of *P. contorta* and *P. tremuloides* than sites in which mountain pine beetle was not present. When considering only sites dominated by *P. contorta* (n=41), the mean abundance of *P. contorta* regeneration in plots where mountain pine beetle was present (n=35) was 1059 seedlings per hectare. Sites dominated by *P. contorta* with no mountain pine beetle presence (n=6) had a mean abundance of 600 *P. contorta* seedlings per hectare (Figure 2a). The mean abundance of *P. tremuloides* was also higher in sites with evidence of pre-fire mountain pine beetle (Figure 2b). A similar pattern was evident when all sites in which *P. contorta* was present (n=82) were included. The mean abundance of *P. contorta* in sites with mountain pine beetle (n=61) was 801 seedlings per hectare while a mean 218 seedlings per hectare

occurred in sites where mountain pine beetle was not present (n=21) (Figure 2f-g). *P. engelmannii*, *A. lasiocarpa*, and *P. flexilis* showed a decrease in mean seedling abundance after fire in sites with pre-fire mountain pine beetle (Figure 2). *P. engelmannii* was the dominant canopy species in 13 sites. Within these sites there was a higher abundance of *P. engelmannii* and *A. lasiocarpa* seedlings when pre-fire spruce beetle was present (n=5) in comparison to sites with no spruce beetle (n=8) (Figure 3c-d). *P. contorta* and *P. tremuloides* seedling abundance was lower in sites with spruce beetle versus sites without (Figure 3 a-b). When all sites with *P. engelmannii* in the canopy were taken into account (n=54) the same patterns were present (Figure 3).

The Pearson's correlation coefficients suggested a lack of collinearity between all sets of variables (correlation coefficients < 0.5). I used my models to assess the patterns identified in my field data and to compare the importance of bark beetle presence to my 14 additional variables. My use of k-fold cross validations selected models with a lower mean squared error than both the full and null models, showing an increase in predictive power. The explanatory variables that influenced the model were different for each species (Table 3). For *P. contorta* the mean abundance (intercept) value was $e^{\beta} = 9.3$ per 400 m² plot. The presence of mountain pine beetle in a plot before the fire increased the mean abundance 3.1 fold. The abundance of *P. contorta* seedlings decreased as distance to seed source increased and in plots where spruce beetle was present (Table 3). *P. contorta* abundance was not significantly affected by fire severity. The model for *P. engelmannii* abundance had an intercept of 2.12, and nine additional variables affected seedling abundance. The multiplicative effect of spruce beetle presence was 2.48. Mean abundance was lower in areas of high-severity burn

and decreased as slope and distance to seed source increased. Three variable interactions influenced *P. engelmannii* seedling abundance. Abundance was lower in plots that burned at medium-low severity in 2010 and were burned by a stand replacing fire in 1646. Abundance was greater in plots where spruce beetle interacted with the 1646 fire, and where mountain pine beetle interacted with medium-high severity fire (Table 3). *A. lasiocarpa* abundance was significantly affected by one individual variable and six interacting variables. Seedling abundance decreased as elevation increased. The interaction of fire severity with year of last stand replacing fire and the interaction of fire severity with the presence of spruce beetle increased *A. lasiocarpa* seedling abundance. The presence of mountain pine beetle with medium-high burn severity decreased seedling abundance. For *P. tremuloides*, the mean abundance ($e^{\beta} = 5.1$) was greater in areas with presence of mountain pine beetle ($e^{\beta} = 3.4$). The fire of 1861, distance to root source, and slope also influenced abundance. The interaction of burn severity and elevation increased shoot abundance (Table 3). *P. flexilis* had a mean abundance of 1.0. The abundance decreased as distance to seed source increased. *P. flexilis* abundance was greater in plots where mountain pine beetle presence interacted with the stand-replacing fire of 1861 (Table 3)

DISCUSSION

The lasting ecological legacies of disturbance interactions can determine the landscape patterns of forests for hundreds of years (Veblen et al. 1994). Multiple studies have shown the ability of disturbance interactions to compound and cause ecological

surprises in post-disturbance regeneration, including novel species assemblages or alternative stable states. (Paine et al. 1998, Buma and Wessman 2011, Kulakowski et al. 2013). These changes, initiated by compounded disturbances, are of concern to ecosystem managers because of their unpredictable nature (Paine et al. 1998). There can be negative economic and social consequences of species or ecosystem shifts, including loss of ecosystem services (Folke et al. 2004). Concern over the effects of compounded disturbances has led to research which suggests that, even when alternative stable states or novel species assemblages do not occur, compounded disturbances reduce post-disturbance regeneration (e.g. Paine et al. 1998, Kulakowski et al. 2013, Harvey et al. 2013). The results of my study lead to the opposite conclusion, that compounded disturbances can act as a stabilizing force by facilitating the establishment of pre-disturbance species assemblages.

My analysis of post-fire seedling establishment shows an increase in mean seedling abundance of three species in areas where bark beetles were present before the fire (Figure 2-3). Mountain pine beetle disturbance before the Cow Creek fire increased the abundance of *P. contorta* seedlings 3.1 fold. The mean abundance of *P. engelmannii* was 2.5 fold greater in areas where spruce beetle was present before the fire, and *P. tremuloides* regeneration increased in areas with mountain pine beetle presence before the fire ($e^{\beta} = 3.4$). The effect on the regeneration of these three species suggests that that the disturbance interactions of bark beetle and fire can affect both host and non-host species (Table 3). The influence of the beetle-fire compounded disturbance on the sucker abundance of *P. tremuloides*, a species that was not directly influenced by the first disturbance, reaffirms the importance of understanding the full

effects of compounded and interacting disturbances on post-disturbance regeneration. My results show that suppressed regeneration following compounded disturbance should not be expected in all cases. It is important that forest management plans do not assume that compounded disturbances will always lead to reduced regeneration.

Disturbance interactions affecting regeneration

My research reinforces previous studies that suggest bark beetle and fire disturbances can interact and that those interactions can affect post-disturbance forest regeneration. The interactions between time since last stand-replacing burn, bark beetle presence, and 2010 fire severity were identified as important to post-disturbance seedling abundance in a variety of the species models I created. The significance of these variables shows the long lasting effect that disturbance interactions can have on species regeneration. The interaction between time since last stand-replacing burn and fire severity influenced species regeneration of *P. engelmannii*, *A. lasiocarpa*, and *P. tremuloides* (Table 3). The stand-replacing nature of fire in subalpine forests makes long-term disturbance interactions possible (Veblen et al. 1994, Sibold et al. 2006). Even after 350 years, the 1646 fire interacted with the 2010 fire severity and influenced species abundance (Table 3). The disturbance interaction between previous stand-replacing fires and 2010 fire severity had a large effect on both *A. lasiocarpa* and *P. tremuloides* regeneration. Seedling abundance of *A. lasiocarpa* was the highest in areas that burned in 1646 and at low severity in 2010. *P. tremuloides* had high regeneration in areas that burned in 1861 and at medium-high severity in 2010. This interaction reinforces previous understanding of species composition and forest age in subalpine

forests. Subalpine forests that are composed of *P. engelmannii* and *A. lasiocarpa* species generally burn less frequently and at lower temperatures than *P. contorta* and *P. tremuloides* forests (Rebertus et al. 1991). *A. lasiocarpa* seed trees will be present at a greater density in older forests that burn at low severity, while *P. tremuloides* root structures are more common in areas that burn more frequently and at higher severity (Rebertus et al. 1991).

The ecological legacy of stand-replacing fire is known to interact with bark beetles through forest age and composition (Veblen et al. 1994). Forests must have enough large host trees to sustain a bark beetle outbreak, and therefore recent post-fire forests cannot not support epidemic-scale outbreaks (Veblen et al. 1994, Raffa et al. 2008). In older post-fire forests, beetle outbreaks become more likely due to the homogeneity of tree age (Raffa et al. 2008). However, the influence of fire-beetle interactions on post-disturbance forest regeneration has not been studied. My research suggests that spruce beetle presence and the year of last stand-replacing burn has a significant influence on the regeneration of some tree species. I found higher than average regeneration of *P. contorta* and *P. engelmannii* occurred in areas with spruce beetles present that initiated following a fire in 1646. This interaction is specific to spruce beetles; I did not find any significant interactions between presence of mountain pine beetles and the 1646 fire for any species. The presence of recently downed trees in the forest may facilitate this interaction. Downed trees are used as host trees by spruce beetle, while mountain pine beetle use only live standing trees (Schmid and Frye 1977). In the forest that initiated in 1646, spruce beetle could be more common in areas

with a large number of downed trees. The presence of downed trees would influence the fire behavior when the forest burned in 2010 and in doing so affect the regeneration abundance of tree species.

The interaction between bark beetle outbreaks and fire severity can also have an effect on post-disturbance regeneration. This interaction has been the focus of a large body of research due to interest in how fire severity changes when fires occur in post-beetle outbreak forests (e.g. Bebi et al. 2003, Kulakowski and Veblen 2007, Schoennagel et al. 2012). The majority of these studies have concluded that fire severity is not correlated with presence or severity of pre-fire bark beetle outbreaks. Additional studies have found that beetle outbreak presence and severity can influence fire severity in the subalpine, but only under uncommon moderate burn conditions (Harvey et al. 2014a). The Cow Creek fire burned under extreme weather conditions for 91% of its extent, and the severity of the fire was not significantly correlated with the presence of beetles. However, bark beetle and fire disturbance can interact in ways that do not influence fire severity, but do affect post-disturbance regeneration (Harvey et al. 2013). In addition, the effect that these interactions have on regeneration abundance can vary depending on bark beetle outbreak stage (Harvey et al. 2014a). The Cow Creek fire burned through forests that had been affected by a bark beetle outbreak less than three years prior (US Forest Service 2012). In the first three years following the start of a beetle outbreak, affected forest patches include a mixture of green-attack and red stage trees (Griffin et al. 2011, Harvey et al. 2014a). During the red/green attack phase fine canopy fuels dry out and begin to fall to the forest floor, changing canopy density, fuel moisture, and the micro-climate of the forest (Simard et al. 2011). The

needles, which remain in the canopy during green-attack/red stage increase the flammability of tree crowns and increase the likelihood of crown fire or torching (Schoennagel et al. 2012). My results show that the presence bark beetle did not affect the burn severity of the Cow Creek fire, however the interactions between bark beetle presence and fire severity did have a compounded effect on post-disturbance regeneration. *A. lasiocarpa* and *P. engelmannii* regeneration was less than average in areas with mountain pine beetle presence that burned at medium-high severity. In other forested systems crown fires have been shown to decrease regeneration density when compared to surface burns (Turner et al. 1999). Crown fires are much more destructive to the canopy seed source than a ground fire, even when burn severity is the same (Turner et al. 1999). This difference also explains the greater than average *A. lasiocarpa* seedling abundance that occurred in areas with spruce beetle and medium-high or medium-low fire severity.

All species were affected by at least one interacting factor related to a disturbance interaction, which reaffirms that disturbance interactions can have long term ecological legacies that influence forest regeneration. The disturbance interactions of fire-fire, fire-beetle, and beetle-fire all affected the patterns of post-disturbance regeneration. While historic fires, bark beetle outbreaks, and recent stand replacing fire were easily identified large-scale disturbances, I was unable to collect reliable data on smaller-scale disturbance such as pre-2010 non-stand-replacing fire, non-bark beetle tree parasites, or basic gap dynamics and therefore did not include these disturbances in my analysis. Future analysis of these additional disturbances is needed to identify the influence they have on regeneration.

Additional variables affecting post-fire establishment

Forest regeneration following the Cow Creek fire was influenced by multiple variables. My findings show the importance of both abiotic and biotic factors in determining how forests will regenerate. Different individual and interacting variables affected each of the five species models (Table 3). The presence of bark beetles in plots before the fire increased the mean abundance of *P. contorta*, *P. engelmannii*, and *P. tremuloides*. Based on previous research and model selection, fire severity was included in the regeneration models of both *P. contorta* and *P. engelmannii*. Fire severity is a well-studied factor in the regeneration of subalpine species. In *P. contorta* dominated forests high-severity fires favor regeneration of *P. contorta* by opening the serotinous cones and releasing a large crop of fast growing seeds (Turner et al. 1999). Other subalpine species, such as *P. engelmannii* and *A. lasiocarpa*, are more likely to regenerate following a medium-low or low-severity burn in which not all seed producing trees are killed. As expected, my results show that *P. engelmannii* regeneration abundance was 73% less in plots that burned at high-severity. However, *P. contorta* seedling abundance was not significantly affected by the presence of high severity fire.

Distance to seed trees or root structures significantly influenced the regeneration abundance of all of the study species except *A. lasiocarpa*. Plots that were closer to the seed trees or root structures of each species had a higher mean abundance of that species. Without the presence of seed trees or root structures, post disturbance regeneration is conditional on rare long-distance dispersal events (Turner et al. 1998). My model showed that regeneration abundance decreased as distance to seed or root source increased. However, my analysis of seed trees did not take into account live-

residual trees in high or medium-high severity areas that could have acted as seed trees. Live-residual trees were occasionally present in areas of my study site that burned at high or medium-high severity, especially in areas with highly heterogeneous terrain. Although I did not take these individual live trees into account in my analysis of distance to seed source, my calculations did act as a reasonable estimation for distance to a significant seed source, where many live seed trees were present.

My analysis focused on initial seedling establishment, which cannot be used to perfectly predict how the future forest canopy will develop. Some subalpine species are slower to colonize but may become more abundant over time (Johnson and Fryer 1989). Due to self-thinning, herbivory, and resource competition many of the seedlings that were present during my sampling will not survive to become part of the forest canopy (Kashian et al. 2005). Although research on initial seedling growth is imperfect, the patterns in my data clearly show the significant effect of multiple variables that will likely influence the forest in the long term.

Site productivity

This study highlights the importance of understanding disturbance interactions and the many influences they can have on post-disturbance regeneration. However, other factors that can affect forest regeneration should be considered in future research. Measurements of site productivity, nutrient and moisture availability, and soil type were not included in my research but likely have significant effects on the germination and survival of seedlings. Site productivity could be the mechanism that led to the unexpected increase in seedling abundance of *P. contorta*, *P. tremuloides*, and *P.*

engelmannii in plots where bark beetles were present before the 2010 Cow Creek fire. Bark beetles preferentially attack large trees, which are generally found at sites that are highly productive (Raffa et al. 2008). Regeneration abundance may also have been greater than average in those sites due to the high site productivity. Additional research on soil nutrient and moisture content as well as micro-climate analysis would help quantify the importance of productivity on post-disturbance regeneration.

Compounded disturbance interactions

In past research compounded disturbances have been considered a cause of extreme negative effects on ecosystem regeneration (e.g. Paine et al. 1998, Kulakowski et al. 2013, Harvey et al. 2013). My research shows that disturbances can interact and create compounded effects on post-disturbance regeneration that do not negatively affect the stable state of the ecosystem. The assumption that compounded disturbances result in system change was not true in the case of the Cow Creek fire. While it is clear that compounded disturbances can have negative effects on ecosystem regeneration, it is now also apparent that there are other possible outcomes.

Management implications

The management of forests before and after compounded disturbance events is complex due to the unpredictable nature of disturbance interactions. Fear of state changes and slow regeneration fuels public and political requests for active management following large-scale disturbances (Dale et al. 1998). Concern over the consequences of compounded disturbances has led to management which attempts to

preemptively reduce the likelihood of compounded disturbances (Jenkins et al. 2008, Buma and Wessman 2012). Post-disturbance management is also becoming more common following compounded disturbances in an effort to return the ecosystem to pre-disturbance vegetation (Dale et al. 2001). The results of my study show that active management is not always required following compounded disturbances. The regeneration of pre-disturbance species can be facilitated by disturbance interactions. Unnecessary management is expensive, and can even be detrimental to ecosystem recovery (Dale et al. 2001). The patterns formed by post-disturbance regeneration are important for ecosystem heterogeneity and biodiversity; unneeded active management can change these patterns and in doing so influence the ecological legacy of the disturbance (Dale et al. 1998, 2001). Areas that have undergone a single disturbance do not necessarily need to be protected from future disturbances in fear of compounded disturbance affects. Compounded disturbances can be beneficial to re-establishment of historic vegetation assemblages and should not be considered purely negative.

CONCLUSION

My research shows that the interactions of multiple disturbances can be a stabilizing force on post-disturbance regeneration and that a short timespan between disturbances does not necessarily lead to negative effects. In my study the interaction of bark beetle disturbance followed by fire disturbance increased post-disturbance seedling establishment of three subalpine tree species. The surprising nature of my findings suggests that more research on post-compounded disturbance regeneration is

required to fully understand the ecological consequences of disturbance interactions. My research focused on just two of the many disturbance types that could have compounded effects on subalpine regeneration, additional research on other disturbance types would improve our ability to predict how forests will regenerate following compounded disturbance.

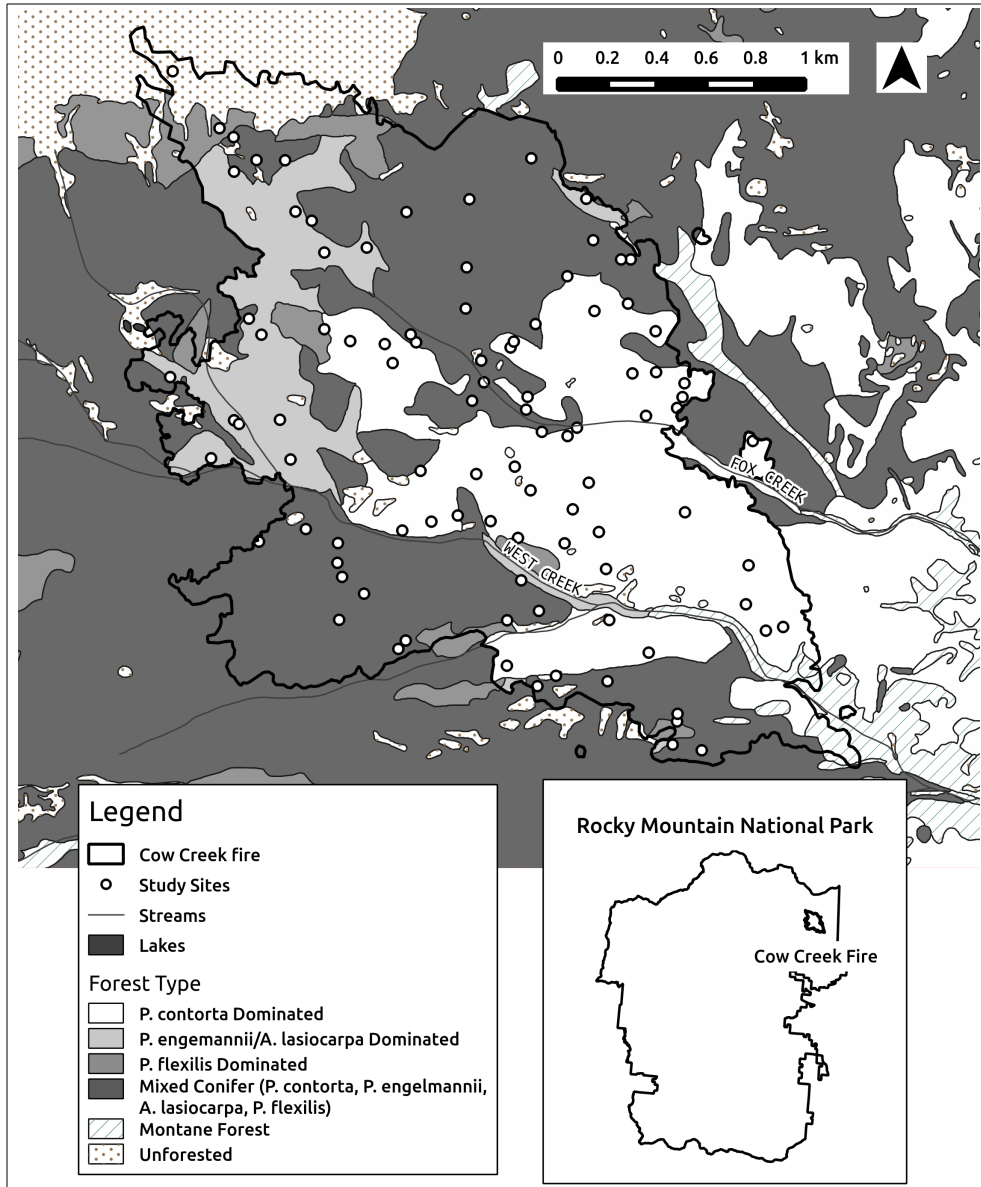


Figure 1. Study area map. Map of the Cow Creek fire extent in Rocky Mountain National Park, showing the location of the 98 sites sampled and the pre-fire forest type.

Table 1. Number of sites sampled within different pre-fire forest canopy types. Sites are categorized by the four independent categorical variables included in my analysis: fire severity, mountain pine beetle presence, spruce beetle presence, and fire history.

Variable	Total Sites	Number of Sites by Pre-fire Canopy Cover			
		<i>P. contorta</i> dominated	<i>P. contorta</i> present	<i>P. engelmanni</i> dominated	<i>P. engelmanni</i> present
Fire Severity					
High	45	23	43	1	21
Medium-High	21	10	16	4	10
Medium-Low	18	5	13	5	13
Low	14	3	10	3	10
Mountain Pine Beetle					
Present	70	35	61	6	32
Absent	28	6	21	7	22
Spruce Beetle					
Present	23	4	17	5	18
Absent	75	37	65	8	36
Fire History					
Burned in 1861	25	22	23	2	3
Burned in 1646	70	18	57	11	50
Unknown	3	1	2	0	1
Total Sites	98	41	82	13	54

Table 2. Mean variable values within different pre-fire canopy types. Mean values were calculated for the four independent continuous variables included in my analysis: distance to seed source, elevation, slope, and northness.

Variable	All Sites	Pre-fire Canopy Cover			
		<i>P. contorta</i> dominated	<i>P. contorta</i> present	<i>P. engelmanni</i> dominated	<i>P. engelmanni</i> present
Mean Distance to Seed Source (meters)					
<i>P. contorta</i>	22.11	10.40	12.55	56.84	24.85
<i>P. tremuloides</i>	359.21	272.57	341.49	430.85	415.33
<i>P. engelmanni</i>	141.22	191.60	156.45	19.93	96.90
<i>A. lasiocarpa</i>	128.34	173.67	135.51	54.91	87.14
<i>P. flexilis</i>	138.05	180.38	148.43	67.76	104.75
Mean Elevation (meters)	2947.94	2866.45	2925.88	3074.92	3006.91
Mean Slope (degrees)	19.26	17.91	19.23	19.16	20.21
Mean Northness (cosine(aspect))	-0.40	-0.59	-0.38	-0.67	-0.29

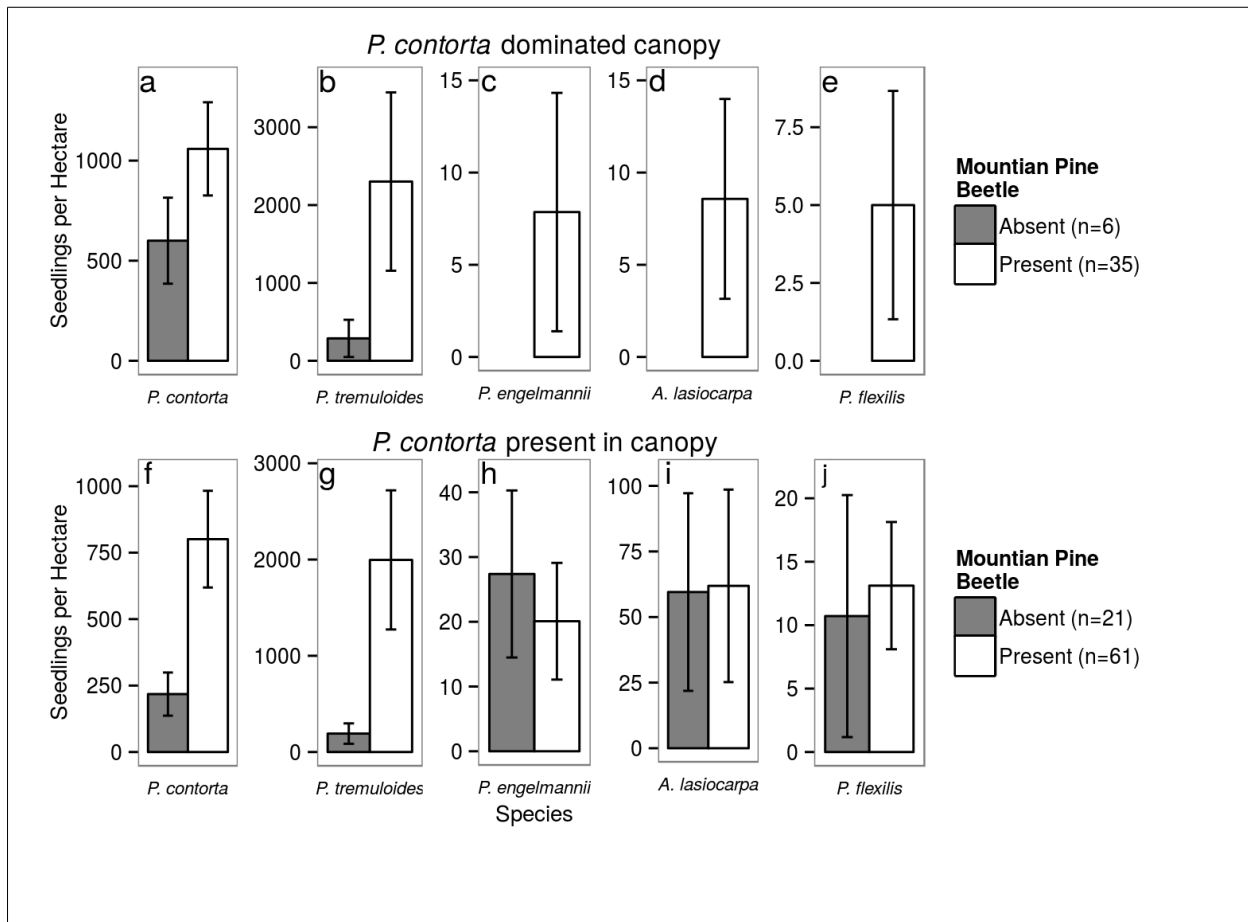


Figure 2. Mean seedling abundance in pre-fire *P. contorta* plots with and without mountain pine beetle. Comparison of mean post-fire seedling abundance in plots where mountain pine beetle was present (white) or absent (gray) before the fire. Figures a-e show mean seedling abundance of the five common subalpine species in plots dominated by *P. contorta* before the fire (n=41). Figures f-j show mean seedling abundance in plots where *P. contorta* was present in the canopy before the fire. Error bars show standard error of the mean.

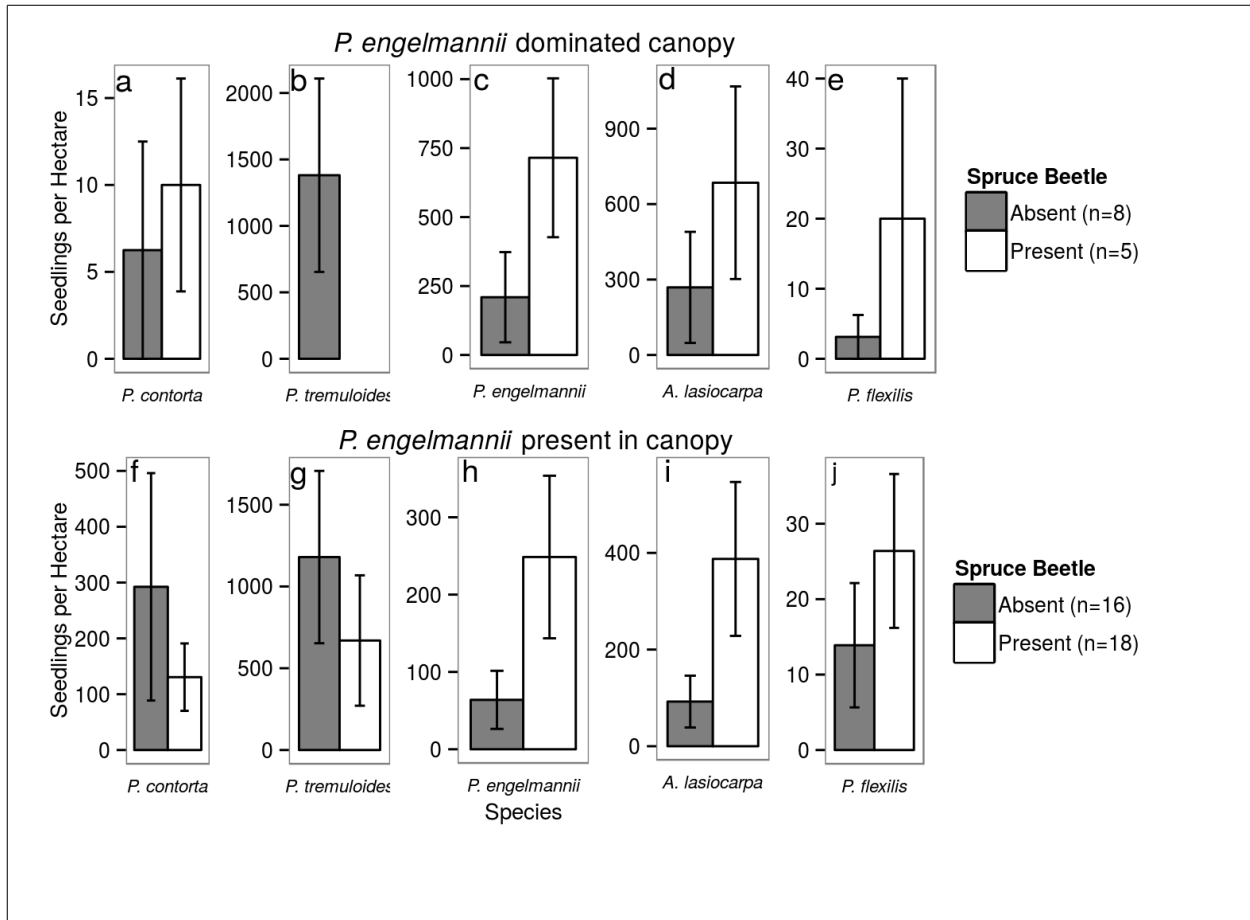


Figure 3. Mean seedling abundance in pre-fire *P. engelmannii* plots with and without spruce beetle. Comparison of mean post-fire seedling abundance in plots where spruce beetle was present (white) or absent (gray) before the fire. Figures a-e show mean seedling abundance of the five common subalpine species in plots dominated by *P. engelmannii* before the fire (n=41). Figures f-j show mean seedling abundance in plots where *P. engelmannii* was present in the canopy before the fire. Error bars show standard error of the mean.

Table 3. Calculated parameters from each species' seedling abundance model. All variables listed were included based on model selection. Model parameters β mean, β standard deviation, and the derived parameter e^β were calculated with an MCMC algorithm.

Model Variables	β	SD	e^{β}	90% CI for e^{β}
<i>P. contorta</i>				
Intercept	2.23	0.10	9.30	7.98, 10.71
Mountain pine beetle	1.13	0.08	3.11	2.73, 3.53
Spruce beetle	-1.37	0.30	0.27	0.15, 0.39
High severity	.06	0.06	1.06	0.98, 1.14
Distance to seed (scaled)	-1.10	0.14	0.34	0.27, 0.41
Spruce beetle \times 1646 fire	0.72	0.30	2.16	1.27, 3.58
<i>P. engelmannii</i>				
Intercept	0.70	0.32	2.12	1.15, 3.31
Spruce beetle	0.82	0.41	2.48	1.18, 4.81
Slope (scaled)	-0.46	0.10	0.64	0.54, 0.74
Northness (scaled)	-0.13	0.10	0.88	0.73, 1.04
High severity	-1.42	0.45	0.27	0.12, 0.51
Distance to seed (scaled)	-1.80	0.37	0.18	0.09, 0.28
Medium-low severity \times 1646 fire	-1.03	0.17	0.37	0.28, 0.45
High severity \times 1646 fire	-0.39	0.51	0.77	0.31, 1.61
Spruce beetle \times 1646 fire	0.68	0.42	2.16	1.03, 4.69
Medium-high severity \times Mountain pine beetle	-1.15	0.29	0.33	0.20, 0.50
<i>A. lasiocarpa</i>				
Intercept	1.22	0.30	3.56	2.09, 5.54
Elevation (scaled)	-0.63	0.36	0.57	0.30, 0.99
Distance to seed (scaled)	0.18	0.23	1.22	0.81, 1.74
Low severity \times 1646 fire	2.69	0.27	15.35	9.55, 22.76
Medium-high severity \times 1646 fire	1.20	0.43	3.65	1.61, 6.75
Medium-high severity \times 1861 fire	0.66	0.77	2.64	0.55, 7.45
Low severity \times Elevation (scaled)	-0.22	0.36	0.86	0.44, 1.45
Medium-low severity \times Elevation (scaled)	0.31	0.35	1.45	0.76, 2.38
Medium-high Severity \times Mountain Pine Beetle	-1.93	0.34	0.16	0.09, 0.24
Medium-low severity \times Spruce beetle	2.23	0.23	9.5	6.39, 13.58
Medium-high severity \times Spruce beetle	1.87	0.44	7.12	3.10, 13.10
<i>P. tremuloides</i>				
Intercept	1.62	0.09	5.06	4.46, 5.69
Mountain pine beetle	1.23	0.08	3.43	3.03, 3.87
1861 fire	-0.58	0.13	0.56	0.51, 0.60
Slope (scaled)	-0.20	0.07	0.82	0.79, 0.84
Distance to root (scaled)	-2.43	0.23	0.09	0.08, 0.10
Medium-high severity \times 1861 fire	2.56	0.10	12.94	12.01, 13.94
Low severity \times Elevation (scaled)	3.68	0.25	40.35	34.43, 48.03
Medium-high severity \times Elevation (scaled)	0.88	0.05	2.41	2.25, 2.59
<i>P. flexilis</i>				
Intercept	-0.06	0.422	1.03	0.48, 1.93
Distance to seed (scaled)	-1.12	0.446	0.36	0.16, 0.69
Mountain pine beetle \times 1861 fire	0.86	0.307	2.48	1.43, 3.91

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