THESIS

LODGEPOLE PINE RESILIENCE IN TROUBLESOME TIMES: THE INFLUENCE OF STAND-LEVEL CHARACTERISTICS ON REGENERATION FOLLOWING BARK BEETLE MORTALITY AND WILDFIRE

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ABSTRACT

LODGEPOLE PINE RESILIENCE IN TROUBLESOME TIMES: THE INFLUENCE OF STAND-LEVEL CHARACTERISTICS ON REGENERATION FOLLOWING BARK BEETLE MORTALITY AND WILDFIRE

Climate-driven increases in disturbance activity from bark beetle outbreaks and wildfire have prompted concerns for potential declines in tree regeneration. In forests of the Southern Rocky Mountains, widespread tree mortality from bark beetles over the last few decades has resulted in forest conditions that may drive alternate patterns of recovery following subsequent wildfire. As such, the extreme fire season of 2020 presents a unique opportunity to examine the patterns of forest recovery following two disturbances that are unprecedented in their severity and extent. In this study, I collected field data on lodgepole pine seedling recruitment following the East Troublesome fire, which burned through beetle-killed lodgepole pine stands (11-19 years post outbreak), to 1) assess the potential for natural forest recovery and 2) determine the primary stand-level factors that influence the abundance of post-fire lodgepole pine seedlings. In the summer of 2022, I sampled 116 plots across gradients of beetle severity, fire severity, and stand age in Rocky Mountain National Park, Colorado. In each plot, I measured variables capturing fire effects, forest structure, topography, and post-fire regeneration. General linear mixed models were used to determine the relative influence of fire effects, seed source, stand characteristics, and topography on post-fire lodgepole pine seedling density. I found that 97% of the study area had lodgepole pine seedlings established at 2 years post-fire, and 70% of the study area had seedling densities exceeding 370 t ha $^{-1}$, however, seedling densities were highly

variable across the landscape. The abundance of lodgepole pine seedlings at the plot-level was strongly associated with the density of cone-bearing trees, elevation, and tree consumption. These results highlight the mechanisms by which pre-fire forest structure and canopy consumption alter post-fire seed availability to influence post-fire lodgepole pine recruitment. My findings help inform predictions of future forest trajectories following sequential disturbance by bark beetle outbreaks and wildfire and underscore the need for tailored forest management approaches that consider both the legacy of bark beetle outbreaks as well as the variable nature of fire effects.

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1. INTRODUCTION

Large-scale disturbances by bark beetle outbreaks and wildfire are natural processes that have shaped the composition and vegetation dynamics of Rocky Mountain forests for centuries to millennia (Veblen et al. 1994; Peet 2000; Kulakowski & Veblen 2015), though climate-driven increases in the frequency and extent of these two disturbances have the potential to drive markedly different ecosystem trajectories. Recent outbreaks of multiple bark beetle species (genus *Dendroctonus*) have led to extensive tree mortality across forests of western North America since the late 1990s (Raffa et al. 2008; Meddens et al. 2012). Coincident increases in annual area burned and frequency of wildfires (Westerling et al. 2011; Higuera et al. 2015; Jolly et al. 2015; Abatzoglou et al. 2021) thus increase the likelihood for these two disturbances to overlap in time and space (Turner et al. 2013). The interactions between multiple disturbances can result in altered disturbance characteristics and/or produce synergistic effects on vegetation response (Paine et al. 1998; Turner 2010; Kane 2017). Yet, the processes leading to interactive effects between multiple disturbances and their consequences for ecosystem recovery are not well understood. Of particular interest is whether the changes to forest structure and composition resulting from a bark beetle outbreak may result in compound disturbance effects with subsequent fire to alter post-fire recovery and forest resilience. Because post-fire recruitment exerts a strong influence on long-term forest structure and composition, continued study of post-fire regeneration in forests impacted by multiple disturbance events is critical for improving our understanding of the impacts of climate-driven changes in disturbance activity across forest systems.

Forest recovery from a disturbance is strongly moderated by mechanisms influencing propagule availability and dispersal (Turner et al. 1998; Davis et al. 2018). In high-elevation forests of the Rocky Mountains that have historically experienced infrequent, stand-replacing fire events, post-fire reproductive strategies such as resprouting, seed release from aerial seedbanks, and long-distance seed dispersal (Pausas & Keeley 2014) shape the rates and patterns of initial forest recruitment (Peet 2000; Turner et al. 1999). Lodgepole pine (*Pinus contorta* var. *latifolia*) is a widespread species across Rocky Mountain subalpine forests due to its ability to regenerate quickly and prolifically following fire (Brown 1975; Romme and Knight 1981; Lotan et al. 1983; Veblen 2000). Lodgepole pine stands express variable levels of serotiny, whereby mature cones are sealed in a resinous bond until subjected to high temperatures, often through fire, that prompt cone opening and seed release (Lotan 1976). As such, serotiny is considered a disturbance-adapted trait (Buma et al. 2013), and fire plays a critical role in the regeneration of serotinous lodgepole pine stands (Lotan 1976; Tinker et al. 1994).

The mechanisms determining propagule availability and subsequent germination and establishment of serotinous species post-fire can vary from those of other, non-serotinous conifers. Moreover, disturbance characteristics further alter the demographic stages of regeneration (Davis et al. 2018), and consecutive disturbances can amplify constraints on regeneration (Johnstone et al. 2016). I present a conceptual framework, adapted from Wooten et al. (2022), to outline the demographic filters shaping post-fire regeneration of serotinous lodgepole pine forests following bark beetle outbreaks and wildfire (Fig. 1). In this framework, I separate the processes controlling seed availability, which is the first demographic filter that must be passed for regeneration, into multiple filters to account for the changes occurring with each disturbance, followed by the processes influencing seedbed conditions to shape subsequent

germination and establishment. This model helps identify which environmental variables may be most relevant to regeneration processes and elucidates the mechanisms by which they shape the patterns of forest recruitment.

First, the proportion of trees bearing serotinous cones is closely tied to post-fire lodgepole pine seedling densities (Tinker et al. 1994; Turner et al. 1997; Schoennagel et al. 2003). Serotiny levels can be highly variable at regional and landscape scales due to differences in stand age, fire return intervals, and topography (Lotan 1975; Schoennagel et al. 2003). Further, individual disturbance events may also significantly alter the persistence and availability of serotinous cones, influencing propagule availability in subsequent years. For example, lodgepole pine forests infested by mountain pine beetles (*Dendroctonus ponderosae;* hereafter, MPB) may experience reductions in the aerial seedbank over time as beetle-killed trees deteriorate. Following tree mortality in the first 1-2 years of the outbreak (known as the "red phase"), trees transition to the "grey phase", characterized by the fall of needles and progressive deterioration of snags (Hood 2020). Serotinous cones in the canopy of beetle-killed stands may be relocated to the forest floor due to branch breakage and snag fall during the grey phase (Teste et al. 2011). Additionally, the loss of canopy cover in beetle-killed stands may prompt seed release in serotinous cones due to increased temperatures, sun exposure, and weathering (Lamont et al. 1991; Teste et al. 2011). Previous studies have estimated that between 38-45% of the canopy seedbank is released within 6-9 years post-outbreak (Teste et al. 2011), though rates of seed loss following tree mortality are largely unknown and may increase with time as beetle-killed stands continue to deteriorate. Nonetheless, outbreak-driven changes to the aerial seedbank may reduce the availability of viable seed for regeneration from subsequent wildfire, especially if the fire occurs before any post-outbreak lodgepole pine recruitment is reproductively mature.

Fire effects also influence propagule availability and mechanisms of seed dispersal for post-fire recruitment (Davis et al. 2018). Severe surface fires and crown fires, which are associated with extensive tree mortality, tend to result in high post-fire lodgepole pine seedling densities as these conditions provide adequate canopy heating (45-50°C) for seed release (Crane 1972; Anderson and Romme 1991; Turner et al. 1999). However, extreme temperatures in cases of severe crown fire may lead to seed death or consumption and result in lower post-fire seedling densities (Turner et al. 1999; Rhoades et al. 2018). Bark beetle outbreaks lead to changes in fuel structure and fuel flammability that may alter fire behavior and subsequent fire effects. Fire simulation modeling suggests that increased surface fuel loading in grey stage stands may result in greater surface fire severity, while canopy fire severity may decrease (Hicke et al. 2012), though the added fuel complexity created by downed snags and post-outbreak regeneration may increase ladder fuels for crown fire (Simard et al. 2011). Field studies have shown that the desiccation of pre-fire snags heightens the potential for scorching, deep char development, and greater consumption of bark and canopy fuels (Donato et al. 2009; Talucci & Krawchuk 2019). Should the decreased moisture content of canopy fuels and cones on beetle-killed snags result in significant cone consumption, severe bark beetle outbreaks may have additive effects with subsequent fire to constrain post-fire seedling establishment.

Beyond the mechanisms influencing propagule availability and dispersal, characteristics of the post-fire environment influence post-fire recruitment via controls on seedling germination and establishment (Davis et al. 2018). Fire generally creates favorable conditions for the germination and establishment of lodgepole pine. For example, reduced canopy cover and increased availability of exposed mineral soil following fire enhance lodgepole pine germination rates (Lotan 1976). Specific fire effects at the stand level will vary with fire behavior and pre-fire

vegetation, and there remains great uncertainty whether pre-fire fuel changes from bark beetle outbreaks significantly influence post-fire conditions for germination and establishment. The accumulation of coarse woody fuels with time since outbreak (Schoennagel et al. 2012; Shapira et al. 2021) may result in increased soil heating to have negative effects on post-fire recovery (Carlson et al. 2017). However, the relationship between outbreak severity on surface fire effects varies with burning conditions and outbreak stage (Harvey et al. 2014a; Agne et al. 2016), and there is a lack of research explicitly evaluating surface fire effects on lodgepole pine regeneration in older, grey-stage MPB stands. In addition to fire effects, the influence of post-fire climate conditions on the germination, establishment, and survival of seedlings is well-established. At the landscape scale, topographic variables (i.e., elevation, aspect, slope), along with vegetation patterns, mediate broader-scale climatic conditions to drive fine-scale variability in temperature, solar radiation, and site moisture. Consequently, post-fire recruitment may vary across topographic gradients (Coop et al. 2010; Littlefield et al. 2019), and these effects may be particularly pronounced with disturbance-driven changes in microclimate via canopy loss (Hoecker et al. 2019).

Despite our awareness of the mechanisms involved in post-fire forest regeneration, the occurrence of novel disturbance characteristics and the associated difficulty in teasing apart their impacts at fine spatial scales limits our ability to anticipate post-fire forest recovery. Extreme wildfire activity across the western U.S. in 2020 provides a poignant example of the surprising and devastating impacts of climate-driven increases in wildfire activity. Multiple large wildfires that burned in high-elevation forests of the Southern Rocky Mountains in 2020 yielded fire frequencies, rates of spread, and fire extents that had not previously been observed for this region (National Interagency Coordination Center 2020; Higuera et al. 2021; Coop et al. 2022). This

includes the East Troublesome fire in northern Colorado, which is notorious for burning nearly 100,000 acres (40,469 ha) within a 24-hour period (National Interagency Coordination Center 2020). The East Troublesome burn perimeter included extensive patches of lodgepole pine-dominant forest with significant pre-fire mortality from the MPB outbreaks in the early 2000s (Rodman et al. 2022). Consequently, this fire provides a unique opportunity to evaluate post-fire regeneration in the context of increasingly extreme, overlapping bark beetle and wildfire activity that is anticipated for the 21st century.

In this study, I examine post-fire regeneration following the East Troublesome fire that burned through grey-phase, post-outbreak lodgepole pine forests in the Southern Rocky Mountains. First, I quantify the density of post-fire lodgepole pine seedlings across the landscape to determine the extent to which the regeneration processes of serotinous lodgepole pine forests are maintained following unprecedented activity by bark beetles and wildfire. Local levels of serotiny are assumed to be relatively high across this landscape, based on serotiny data reported by prior field studies (Sibold et al. 2007; Aoki 2010). Previous studies have emphasized that serotinous lodgepole pine forests are relatively resilient following compound beetle and fire disturbance, documenting high post-fire seedling densities due to the preservation of the serotinous seedbank over both disturbances (Harvey et al. 2014a,b; Talucci et al. 2019). However, differences in fire history, land use, vegetation patterns, and recent disturbance activity may contribute to alternate regeneration patterns. For example, more extreme fire events associated with significant crown fire may consume serotinous cones, resulting in little to no post-fire lodgepole pine regeneration (Rhoades et al. 2018). Additionally, this study captures a longer interval between MPB outbreak and wildfire (11-19 years post-outbreak at the time of the fire) as compared to other recent field studies in lodgepole pine forests (e.g., 3-9 years by Harvey

et al. 2014a, 8 years by Rhoades et al. 2018, 10-12 years by Talucci et al. 2019). Differences in the timing of beetle and subsequent fire could alter post-fire recovery, as time since outbreak is associated with stand deterioration, seed loss, and decreasing seed viability (Teste et al. 2011a,b; Rhoades et al. 2022). Consequently, it remains critical to determine whether such disturbance characteristics may override lodgepole pine resilience to wildfire.

Second, I evaluate the relative influence of cone abundance, fire effects, pre-fire vegetation structure, and topography on post-fire lodgepole pine seedling densities at the stand-level to elucidate the predominant filters shaping lodgepole pine regeneration following short-interval beetle and fire disturbance. Following the proposed framework for lodgepole pine recruitment (Fig. 1), post-fire seed availability represents the availability of viable seed from serotinous cones, resulting from three primary filters: 1) processes influencing stand-level seed abundance (i.e., abundance of serotinous cones in a stand) prior to bark beetle activity and wildfire, 2) the persistence and viability of seed following the MPB outbreak, and 3) seed release and survival through subsequent fire. Should the combined effects of the variables related to these filters result in the loss of available seed, regeneration failure may result. However, if ample post-fire seed is available, then regeneration will depend on the post-fire conditions that influence germination and establishment, which I broadly evaluate through environmental factors related to seedbed quality and resource availability. Understanding how disturbance effects and other environmental variables may relate to seed availability and/or the conditions necessary for germination and establishment serves to help anticipate where fire-mediated vegetation change may occur.

2. METHODS

2.1 Study area and site selection

The East Troublesome fire ignited on October 14, 2020, near Kremmling, Colorado, and spread eastward under high winds and dry conditions. Between October 21st and October 22nd, the fire expanded rapidly at a rate of 2,428 hectares per hour, spreading into the west side of Rocky Mountain National Park (ROMO) and ultimately crossing the continental divide to ignite the park's forests near Estes Park (National Interagency Coordination Center 2020). By the time the fire was contained on November 30th, it had burned 78,433 hectares to become Colorado's second-largest wildfire on record. Remotely sensed measures of burn severity provided by the Monitoring Trends in Burn Severity Project (2022) estimate that over 59% of the East Troublesome fire area was burned at moderate to high severity.

The study area for this research encompasses 2,842 hectares of lodgepole pine forest that burned on the west side of the continental divide in ROMO, Colorado (Fig. 2). At the nearest weather station in Grand Lake, CO, mean temperature ranges from a minimum of -16.4 °C in January and a maximum of 24.6 °C in July, with an average total precipitation of 483 mm annually (Western Regional Climate Center, 2024). Lodgepole pine is the dominant forest type on the western side of ROMO, spanning elevations between 2500 and 3300 m. Varying with elevation and site moisture, these stands may also include aspen (*Populus tremuloides*), Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), and, in a small portion of the landscape, Douglas fir (*Pseudotsuga menziesii*). Recent field studies conducted in this area of the park have documented high levels of serotiny across lodgepole pine stands (Sibold et al. 2007; Aoki 2010). Specifically, Aoki (2010) reported median serotiny levels of 69% for the west

side of the park, and though serotiny decreased with elevation, overall variance in serotiny was relatively low (SD: 18%).

Historically, these forests have experienced infrequent, stand-replacing fire events that recurred at 162–216-year intervals (Sibold et al. 2006). Much of the study area is composed of dense, even-aged lodgepole pine stands that established following large stand-replacing fires in the mid-to late-1800s, with longer time-since-fire intervals observed at higher elevations (Sibold et al. 2006). Following the Park's establishment in 1915, strict fire control measures were enacted in the 1920s. Fire suppression stayed in effect until 1972 when the National Park Service shifted to fire management policies that permitted lightning-caused fires to burn. However, the dangers posed by the Ouzel fire in 1978 resulted in the re-adoption of fire suppression in the park (Hess 1993). Currently, the Park employs an adaptive fire management plan that includes fuel reduction treatments, prescribed fire, and wildfire management (National Park Service 2012). Recent fires on the west side of the park include the 2010 Onahu Creek fire (4 hectares) and the 2013 Big Meadows fire (244 hectares) (National Interagency Fire Center 2022). Both fire areas were partially reburned in the East Troublesome fire, however, they were excluded from this study.

The recent mountain pine beetle outbreak first appeared on the western side of the park in 2001 and spread extensively between 2002 and 2008 (Chapman et al. 2012; USDA Forest Service 2022). Research conducted in beetle-killed forests on the west side of ROMO reported >70% loss of lodgepole pine basal area due to the outbreak (Nelson et al. 2014; Perovich and Sibold 2016). The time between outbreak initiation and the fire for the stands in my study area ranged from 11-19 years, though given that bark beetle activity peaked in 2005, most stands were ~15 years since infestation (USDA Forest Service 2022). As such, beetle-infested stands

were well into the grey stage of the outbreak, which is characterized by the loss of needles and fine branches in the canopy as dead trees deteriorate (Hood 2020).

I selected field sites using a spatially balanced, stratified random sampling design (Theobald et al. 2007). The sampling area was delineated using geospatial data from the Vegetation Inventory Mapping project of ROMO (National Park Service 2009) to identify lodgepole pine-dominant forest within the burn perimeter. The sampling area was stratified by 30m resolution raster data representing the year of the last stand-replacing fire (Sibold et al. 2006), MPB outbreak severity (Rodman et al. 2021), and burn severity classes from Monitoring Trends in Burn Severity (MTBS 2022). Each stratification variable was classified into two categories to create 8 strata (Table 1). At each site, I established a cluster of up to three 15 m radius circular (0.07 ha) plots for data collection: one positioned at the site center and two situated randomly at distances between 60 m to 120 m along varying azimuths from the central plot. In some cases, I was unable to establish a second or third plot at a site due to a lack of lodgepole pine dominance (<50% of overstory trees). Selected site coordinates were positioned at the center of a Landsat pixel to align field data more accurately for analysis with geospatial data.

2.2 Field Sampling

Between July and August of 2022, 116 0.07 ha plots were sampled across 46 sites to collect data on post-fire regeneration, pre-disturbance stand structure, seed availability, and fire effects. To quantify seedling abundance, the species and number of all tree seedlings were recorded within each quadrant of a plot. In plots with abundant seedlings (i.e., > 300 t/plot), I subsampled the number of seedlings in one quadrant of the plot to derive a plot-level estimate. Terminal bud scar counts were used to distinguish pre-fire seedlings from post-fire seedlings

(Urza & Sibold 2013). Seedlings with three or more bud scars were considered pre-fire seedlings, while all established post-fire seedlings were classified as either 1 or 2 years old, based on the number of whorls on the stem (Kershaw et al. 2016). The sum of 1- and 2-year-old live lodgepole pine seedlings in each plot was used to quantify the total density (t ha^{-1}) of post-fire lodgepole pine recruits.

2.2.1 Fire effects

Fire effects were categorized at multiple scales within each plot. At the plot level, burn severity class, representing either surface fire or crown fire, was determined for each plot following Turner et al. (1997). Surface fire sites included characteristics representing light to severe surface burns and were differentiated from crown fire sites by the presence of needles in pre-fire live trees and/or the lack of evidence of charring in the canopies of pre-fire dead trees. At the tree level, a canopy consumption index was recorded for every tree or snag within the plot based on residual fine fuels and branches (Table 2, Fig. 3). The mean and variance of canopy consumption index values for all standing trees within the plot were used to summarize canopy consumption at the plot level.

Surface fire effects were assessed in eight one-by-one-meter quadrats within each plot. Quadrats were established at varying distances of 3, 8, or 13 m from the plot center along the central axis of each quadrant (N, E, S, W). Within each quadrat, ash depth was measured to the nearest mm, and soil burn severity and understory vegetation cover were visually assessed. The proportion of live, non-forest vegetation cover was classified into one of six categories using the Braun-Blanquet cover-abundance scale (Braun-Blanquet, 1932). Soil burn severity was assessed based on changes in surface color, structure, ground cover, and root structure in the surface soil horizon, following the methods outlined by Parsons et al. (2010). These characteristics were used

to assign soil burn severity into one of four categories: unburned/low, moderate-low, moderate-high, and high. Soil burn severity and understory vegetation cover indices from all quadrats within a plot were averaged to obtain a single, plot-level value for each measure.

2.2.2 Pre- and post-disturbance stand characteristics

To capture the disturbance-driven changes in forest structure, I recorded the species, diameter at breast height (DBH), status (live or dead), and snag fall of all trees taller than 1.4 m. I attempted to quantify pre-fire mountain pine beetle-related tree mortality by removing the bark on every lodgepole pine snag >5 cm DBH and recording the tree as MPB-killed if *Dendroctonus* galleries were present. However, in most of my plots, the cambium on dead lodgepole pine snags was consumed in the fire, and beetle galleries could not be directly observed. Consequently, I was only able to accurately assess beetle severity in 18 of my plots that burned at lower severity. Post-fire field studies have sometimes relied on other signs of pre-fire mortality in high-severity plots, such as weathered or decayed wood, bole rot, or deep charring at the bole, to identify trees that were likely beetle-killed (e.g., Agne et al. 2016; Harvey et al. 2014a). However, the exceptional burning conditions characterized by the East Troublesome fire resulted in such high consumption in most of my plots that burning characteristics in and of themselves could not be used to estimate the number of beetle-killed trees reliably.

In the 18 plots where beetle-killed trees could be identified, I found that the percent of beetle-killed lodgepole pine basal area in my plots varied considerably from the measure of total bark beetle-caused tree mortality (%) provided from the GIS data by Rodman et al. (2022) that was used for site stratification (data not shown). Remote sensing data can be effective for capturing patterns and landscape and regional scales but is limited in its ability to capture fine-scale variation at the stand level. Moreover, 30 m resolution spectral indices derived from

Landsat data cannot readily distinguish co-occurring mortality agents (Senf et al. 2015), and spatial discrepancies in geospatial forest cover data may also conflate spruce-beetle mortality and MPB mortality in mixed-species stands. Consequently, I determined that remotely sensed measures could not reliably capture the variability in MPB mortality at the plot level and proceeded without a direct measure of pre-fire tree mortality.

For all lodgepole pine stems taller than 1.4 m, I noted whether cones were present or absent in the canopy. A tree was determined to have cones present if any extant cones remained on the branches in the canopy, regardless of whether the cone was scorched or could be assumed to contain seed. As such, the number of trees with cones present serves as a necessary, but not sufficient, condition for post-fire seed availability. The absence of cones in the canopy indicates the absence of a seed crop, but the presence of remnant cones does not necessarily indicate the retention of viable seed. Post-fire field studies are often limited in their ability to determine the mechanisms impacting seed availability, given that fire partially destroys indicators of pre-fire forest conditions. For example, the majority of cones were significantly charred and/or partially consumed in my plots, rendering plot-level estimates of pre-fire serotinous cone abundance unreliable. Nonetheless, it would be reasonable to assume that serotinous trees were fairly abundant in most areas, given the levels of serotiny previously reported for the area (Sibold et al. 2007; Aoki 2011). Moreover, while my measure of cone presence does not explicitly capture the abundance of viable seed, it integrates canopy fire effects and pre-fire stand deterioration from the MPB outbreak as mechanisms influencing post-fire propagule availability (Talucci et al. 2019; Fig. 1), thus serving as a meaningful indicator of seed loss and the relative availability of seed post-fire.

Pre-disturbance stand structure variables (i.e., pre-fire and pre-outbreak) were estimated from our post-fire tree measures and summarized at the plot level with calculations of the following: lodgepole pine quadratic mean diameter (QMD), stem density and basal area of all species, and lodgepole pine dominance (proportion of stems). Potential seed source was represented by the total basal area of all cone-bearing lodgepole pine.

2.3 Topography

A 30-meter digital elevation model in ArcGIS Pro 3.0 (ESRI 2022) was used to derive elevation (m), slope (degrees), aspect (degrees), and heat load index (HLI) for each plot. Aspect was converted to a linear scale between 0.00 and 2.00, with greater values approaching 45° using the equation from Beers et al. (1966): $A' = \cos(45 - A) + 1$, where A is the aspect of the slope measured in degrees clockwise from north and A' is the transformed aspect. Heat load index is a measure of direct incident solar radiation as a function of latitude, aspect, and slope (McCune & Keon 2002) and was used to account for the temperature differences between plots.

2.4 Statistical analysis

To summarize the patterns of post-fire lodgepole pine regeneration across the landscape, I calculated summary statistics from seedling counts and the proportion of plots meeting specific regeneration thresholds (Table 3). All statistics of regeneration were calculated using weighted measures to account for the stratified sampling design. The mean and median post-fire lodgepole pine seedling densities for each of the eight strata were weighted by the total area represented by each stratum to estimate the overall weighted mean and median of seedling density across the burned lodgepole pine forests in the study area. Additionally, I calculated three stratum-weighted measures to estimate: 1) the percent of the landscape that is regenerating (i.e., presence of post-fire seedlings), 2) the percent of the study area with lodgepole pine seedling densities exceeding

pre-disturbance stem densities, and 3) the percent of the study area that has lodgepole pine seedling densities exceeding 370 t ha^{-1}. The latter threshold is based on the stocking value used by the US Forest Service as the minimum number of seedlings required for successful regeneration of lodgepole pine stands following forest treatments (USDA 1997). Importantly, this threshold does not necessarily match the pre-fire stocking densities of the forests in this study area and, therefore, is not meant to imply that areas reaching this threshold are expected to recover to pre-disturbance stocking levels. Nonetheless, the 370 t ha^{-1} threshold serves as a standardized stocking measure by which to compare to other studies and may indicate which areas are regenerating with enough seedlings to recover to a lodgepole pine stand, should the majority of seedlings survive in subsequent years. Meanwhile, the estimate for the area in which post-fire regeneration exceeds the pre-disturbance (pre-outbreak and pre-fire) lodgepole pine stem density may be used to more directly evaluate the levels of regeneration with respect to pre-disturbance conditions. Weighted variances were used to calculate a 95% confidence interval for each estimate.

I assessed the influence of plot-level variables on post-fire lodgepole pine regeneration using a combination of univariate statistical tests, ordination techniques, and general linear mixed effects models. All statistical analyses were conducted in R Statistical Software (version 4.2.2; R Core Team 2022). A Wilcoxon Rank Sum test was used to determine whether post-fire lodgepole pine seedling densities differed between crown fire plots and surface fire plots. As many of my plot-level explanatory variables were significantly correlated, I used a principal components analysis (PCA) to visualize the multivariate associations between field measures sampled at all 116 plots. The PCA was performed using ‘prcomp’ function in R. Highly skewed variables were transformed as needed to meet assumptions of linearity, and all variables were

standardized prior to building the PCA. The first and second principal component axes were used to visualize the associations between variables in a biplot. Points on the biplot were classified by a) burn severity (i.e., crown or surface fire) and b) post-fire lodgepole pine seedling density to interpret the variation in regeneration as a function of the environmental gradients captured by the PCA.

I used general linear mixed effects models (GLMMs) to model post-fire lodgepole pine seedling density as a function of fire effects, cone presence, topography, and pre-fire forest structure. I created separate models for seedling regeneration in crown fire plots and surface fire plots. This approach allowed me to more precisely account for the distinct post-disturbance environments associated with each burn severity class and explore whether the influence of specific variables on regeneration varies with burn severity. A third model of regeneration across all 116 sites, with burn severity as a predictor variable, was fit to summarize the variables consistently influencing regeneration and support the results of the two sub-models (Appendix 1).

For all GLMMs, seedling density was modeled with a negative binomial distribution with a log-link using the 'spaMM' package in R (Rousset & Ferdy 2014). Due to the spatial autocorrelation of plots clustered within sites, a Matérn covariance structure using plot x-y coordinates was included as a spatial random effect in each model. Spearman rank correlation tests were used to identify potential relationships between plot-level variables and post-fire seedling densities. Covariate pairs with Spearman correlation coefficients (r_s) greater than 0.6 were not included in the same model to avoid issues of multicollinearity. All fixed effect covariates were standardized to allow for the inclusion of interactive effects and aid in the interpretation of parameter estimates. I proceeded with stepwise variable selection based on the

Akaike Information Criterion (AIC; Akaike 1974) for model selection. Final models were selected from the combination of fixed effect terms that optimized the conditional AIC (AICc). Terms that did not significantly improve model fit (ΔAICc < 2) were excluded unless they provided ecologically meaningful interpretations. For example, the variance in canopy consumption was included in the model for surface fire plots to compare the role of canopy consumption between crown and surface fire plots despite only marginally improving model fit (ΔAICc = 1). Fixed effect predictors in final models included cone-bearing lodgepole pine basal area, lodgepole pine QMD, live lodgepole pine basal area, elevation, slope, soil burn severity, and variance in canopy consumption (for variable descriptions, see Table 4). Across all models, interaction terms and quadratic terms did not significantly improve model fit and were not included in the final models.

Model fit was further evaluated with the conditional and marginal pseudo-R^2 for final models: the former estimates the variance explained by both fixed and random effects, while the latter estimates the variance explained by fixed effects only. I calculated 95% confidence intervals for all parameter estimates. Model residuals were visually assessed using the 'DHARMa' package (Hartig 2022) to confirm that there were no significant violations of model assumptions. Additionally, correlograms of model residuals were calculated using Moran's I in the 'pgirmess' package (Giraudoux 2022) to ensure that spatial autocorrelation was accounted for with the inclusion of the spatial random effect.

3. RESULTS

3.1 Post-fire seedling presence and abundance

I observed high levels of post-fire lodgepole pine regeneration across the study area, with a mean seedling density of 8,510 t ha^{-1} (median: 1,030 t ha^{-1}; Table 3). Post-fire lodgepole pine seedlings were present in 113 out of 116 plots, though seedling densities varied widely, ranging from 0 to 121,000 t ha^{-1} (Fig. 4, Table 5). Based on whorl counts, 68% of lodgepole pine seedlings had established in the first year following the fire, with the remaining seedlings established in the second year. Post-fire aspen recruits were present in 71 of 116 plots with a mean of 325 t ha^{-1} (Table 5). Aspen recruits outnumbered lodgepole pine recruits in 11 plots, however, lodgepole pine was the most abundant post-fire species overall, comprising 97% of post-fire recruits. Post-fire seedlings of other species, such as subalpine fir or Engelmann spruce, were rarely observed.

Based on my seedling counts, and accounting for the stratification scheme, I estimate 97% (95% CI: 94–100%) of the burned lodgepole pine forests in this area are regenerating with at least some lodgepole pine seedlings established at two years post-fire. Additionally, I estimate that 70% (95% CI: 61–78%) of this area has seedling densities exceeding the 370 t ha^{-1} stocking threshold established by the US Forest Service (USDA 1997), indicating areas capable of recovering to lodgepole pine stands. While the mean density of post-fire seedlings far exceeded the mean of pre-disturbance (pre-outbreak and pre-fire) lodgepole pine stem density (8,510 seedlings per hectare and 1,780 stems per hectare, respectively; Table 5), regeneration is not consistently higher than the pre-disturbance density of trees at the stand level. Based on the comparison of pre-disturbance stem densities to post-fire seedling densities within plots, I

estimate that post-fire regeneration is greater than pre-disturbance lodgepole pine stocking density in 41% (95% CI: 32–50%) of the study area. As these estimates capture the patterns of initial seedling establishment, whether these regeneration trends are indicative of future lodgepole pine stand development will depend on the survival of seedlings and rates of additional tree recruitment in subsequent years.

3.2 Variables influencing post-fire regeneration

Despite my attempts to sample equally in areas that burned at lower severity and areas that burned at higher severity via stratified site selection, discrepancies between geospatial data and what was observed in the field limited my ability to locate lodgepole pine dominant sites that burned at lower severity. As a result, I sampled substantially more plots that were classified as crown fire (n=95) compared to surface fire (n=21). Nonetheless, both crown and surface fire plots encompassed a wide range of variability across metrics representing pre-disturbance forest structure and composition, topography, fire effects, and post-fire regeneration. I found no significant difference in mean seedling density between crown fire plots and surface fire plots ($t = -0.54$, $P = 0.59$).

The PCA reduced the plot-level explanatory variables into two components, summarizing the primary environmental gradients through which I was able to evaluate post-fire regeneration (Fig. 5). The first principal component (PC1) accounted for 32.5% of variance across sites and was strongly influenced by metrics capturing fire effects, with the highest variable loadings associated with average canopy consumption, the percent of snags with complete canopy consumption, live lodgepole pine basal area, and cone-bearing lodgepole pine basal area. The second principal component accounted for 19.6% of the variance and was associated with topography (elevation and slope) and pre-disturbance stand structure variables (lodgepole pine

QMD, lodgepole pine basal area, and non-lodgepole pine basal area). Notably, cone-bearing lodgepole pine basal area showed meaningful relationships with several plot-level variables. The basal area of cone-bearing trees was most strongly correlated with fire effects; it was negatively correlated with plot-level canopy consumption and positively correlated with the variance in canopy consumption. The basal area of cone-bearing trees was also positively correlated to pre-fire lodgepole pine stem density and total lodgepole pine basal area.

The distribution of field sites between the two axes allowed for meaningful interpretations of the relationships between post-fire lodgepole pine regeneration and different combinations of explanatory variables (Fig. 5). Plots with little to no post-fire regeneration were largely clustered with negative values of PC2, and were associated with greater canopy consumption, higher elevations, steeper slopes, and larger QMD of pre-fire lodgepole pine trees. Plots with abundant post-fire seedlings, on the other hand, showed positive associations with pre-fire lodgepole pine stem densities, variance in canopy consumption, the basal area of cone-bearing trees, and live lodgepole pine basal area.

3.2.1 Drivers of seedling density in crown and surface fire plots

All crown fire plots showed 100% tree mortality following MPB and wildfire, however, the degree of stand deterioration and fire effects varied widely between plots. Many plots represented extreme burning conditions; the proportion of trees classified as crown plus (i.e., complete canopy consumption) exceeded 50% in 27 plots. The best-fit model for seedling regeneration in crown fire sites included cone-bearing lodgepole pine basal area, elevation, variance in canopy consumption, soil burn severity, and lodgepole pine QMD as fixed effects. The presence of cones and elevation had the greatest influence on estimated lodgepole pine seedling densities (Fig. 6). Regeneration density was positively related to cone-bearing lodgepole

pine basal area and variance in canopy consumption and negatively related to elevation and lodgepole pine QMD (Fig. 6, Table 6). Soil burn severity did not show a significant relationship with seedling density in crown fire plots.

Total tree mortality following MPB and wildfire ranged from 14% to 100% in surface fire plots (mean: 83%). Most of these plots (15 out of 21) burned as severe surface fire, characterized by moderate-high or high soil burn severity and significant char development on pre-fire downed trees and boles of standing trees. Seedling density in surface fire plots was best explained by cone-bearing lodgepole pine basal area, slope, live lodgepole pine basal area, soil burn severity, and variance in canopy consumption as fixed effects. Estimated seedling density had a positive relationship with the basal area of cone-bearing lodgepole pine and was negatively related to the basal area of live lodgepole pine and slope (Fig. 6; Table 7). In contrast to crown fire plots, soil burn severity had a significant positive relationship with seedling density, while canopy consumption variance did not show a significant relationship (Fig. 6, Table 7). Despite the greater uncertainty in the surface fire model due to the small sample size, the covariate-response relationships were consistent with the results of the model of seedling density across all plots (see Appendix; Table A1, Fig. A1), providing support for model results.

4. DISCUSSION

My results highlight the resilience of serotinous lodgepole pine forests in the face of unprecedented disturbance activity from bark beetle outbreaks and wildfire. Post-fire lodgepole regeneration is abundant across the landscape despite widespread pre-fire tree mortality from the mountain pine beetle outbreak (Nelson et al. 2014; Perovich & Sibold 2016) and the exceptional burning conditions characterizing the East Troublesome fire. These results indicate that pre-fire tree mortality from the outbreak, and the associated changes in stand structure, did not produce significant, compounded effects to constrain post-fire regeneration at the landscape scale. Rather, I found further support for the role of stand-replacing fire in initiating lodgepole pine regeneration in stands heavily impacted by bark beetle mortality (Harvey et al. 2014a,b; Edwards et al. 2015; Talucci et al. 2019).

4.1 Stand-level influences on post-fire recovery

At the stand level, the abundance of post-fire lodgepole pine seedlings varied across gradients of fire severity, topography, and pre-disturbance forest structure. Dense post-fire regeneration is present in areas that experienced moderate to high, but not extreme, fire severity, generally characterized by significant consumption at the surface level and moderate levels of canopy consumption, with an abundance of trees retaining remnant cones in the canopy. Additionally, areas successfully regenerating are associated with dense pre-disturbance stands of even-aged lodgepole pine that tend to occur on low- to mid-elevations in the landscape. Meanwhile, areas with low levels of post-fire recruitment generally meet at least one of three conditions: 1) stands that experienced very light surface fire, 2) severe crown fire areas that had near complete canopy consumption, and/or 3) high-elevation stands on steep slopes. These

patterns reveal important influences of disturbance effects and biophysical site conditions on post-fire seed availability and seedling germination and establishment to ultimately shape post-fire regeneration (Fig. 1).

4.1.1 Influences on post-fire seed availability

My findings suggest that post-fire lodgepole pine regeneration was largely driven by variables influencing post-fire seed availability. Previous studies have emphasized the predominant influence of pre-fire serotiny levels on post-fire lodgepole pine seedling densities (Tinker & Romme 1994; Turner et al. 1997, 1999; Schoennagel et al. 2003), including forests impacted by prior bark beetle outbreaks (Harvey et al. 2014a,b). While I was not able to measure stand-level serotiny, the abundance of seedlings that had established at 1-year post-fire at most plots implies that a local serotinous seed source was widely available, as seed dispersal from live, non-serotinous individuals is associated with significantly lower rates of immediate establishment (Tinker et al. 1994; Turner et al. 1997). Though I have reason to believe that serotiny levels were fairly high across the study area (Sibold et al. 2007; Aoki 2010), differences in the abundance of serotinous cones between plots could have contributed to variable rates of post-fire recruitment. I found that post-fire seedling densities decreased with elevation, which may be partially due to the lower levels of serotiny associated with high-elevation stands (Tinker & Romme 1994; Schoennagel et al. 2003; Aoki 2010). Additionally, lower recruitment observed in low-density stands, coinciding with larger diameter lodgepole pine and/or a higher proportion of spruce or fir species, may be a consequence of fewer serotinous cones in the aerial seedbank. In contrast, high seedling densities coincided with dense, even-aged stands of pure lodgepole pine, which characterize relatively young stands that had established

after stand-replacing fires in the last 150 years (Sibold et al. 2006) and are likely to have a greater abundance of serotinous trees (Schoennagel et al. 2003; Aoki 2010).

The degree to which pre-outbreak and pre-fire abundance of serotinous cones reflects post-fire seed availability depends on seed persistence and viability through subsequent disturbances. In the forests studied here, actual post-fire seed availability is moderated by the MPB outbreak, fire effects, and their interactions. My results show that seedling densities were strongly associated with the abundance of cones remaining in the canopy and fire effects, which, as demonstrated in Figure 1, reflect the cumulative impacts of bark beetles and wildfire on seed persistence, viability, survival, and release. I discuss each of these potential mechanisms in turn.

Tree mortality resulting from the MPB outbreak likely reduced the canopy seedbank prior to the fire. Snag fall, branch breakage, seed predation, and pre-fire cone opening on beetle-killed snags result in reductions in the aerial seedbank with time since outbreak (Teste et al. 2011a). In nearby high-elevation forests of Colorado, a study by Rhoades et al. (2020) estimated that roughly half of beetle-killed snags will fall by 15-20 years following peak infestation, aligning with the timeline of the post-outbreak forests in this study. Previous studies have suggested that these processes may contribute to lower post-fire recruitment in grey-phase forests when compared to forests that burned in the red phase of the outbreak (Harvey et al. 2014a; Rhoades et al. 2018). I anticipate that these changes to the pre-fire seedbank may be even more pronounced in the forests studied here, given the protracted interval between the MPB outbreak and wildfire. Thus far, it remains unclear whether these patterns of pre-fire seed loss significantly alter post-fire recruitment independent from fire-driven seed loss (e.g., Talucci et al. 2019), and these relationships are likely to vary with fire severity, as discussed below. Whether serotinous cones remaining in the canopy on dead snags retain viable seed is also a significant source of

uncertainty. Prior studies have found that most beetle-killed trees will retain similar levels of seed viability to live trees in the first 3-10 years following tree mortality (Aoki et al. 2011; Teste et al. 2011b). However, a recent study by Rhoades et al. (2022) found that the amount of viable seed in the aerial seedbank was significantly reduced at ~15 years post-outbreak in unburned lodgepole pine forests adjacent to four wildfires in 2020, including the East Troublesome fire. As cone age increases on beetle-killed snags, lower moisture content of cones and reduced seed viability could significantly limit germination in long-dead beetle-killed stands (Rhoades et al. 2022). Though many of my plots had reasonable levels of recruitment, it is quite possible that pre-fire cone and seed losses on beetle-killed snags, combined with the reduced density of live cone-bearing trees at the time of the fire, resulted in reduced post-fire seedling densities in stands with significant beetle mortality.

Moreover, fire effects on recruitment may partially reflect the underlying influence of the MPB outbreak on tree-level consumption and seed loss. Though I was not able to directly evaluate this relationship due to a lack of accurate, fine-scale data representing pre-fire forest conditions, previously observed associations between MPB severity and subsequent fire severity aid in the interpretation of my results. Pre-fire dead trees are more likely to experience significant combustion, deep char development, and branch consumption than pre-fire live trees (Turner et al. 1999; Campbell et al. 2007; Donato et al. 2016a), even under extreme burning conditions (Talucci & Krawchuk 2019). Thus, cone consumption by fire is likely to be greater on beetle-killed snags, especially as the desiccation of canopy fuels and cones may promote ignition and combustion (Rhoades et al. 2018, 2022). Furthermore, I anticipate that stands with a mix of pre-fire live and pre-fire dead trees are likely to exhibit more variability in tree-level consumption. This was especially apparent in surface fire plots; while overall canopy

consumption was low, a notable proportion of trees would show disproportionately greater consumption via bole scorch, deep char, and canopy loss, indicating these snags were likely to be dead pre-fire (and, indeed, this proved to be the case for the surface fire plots in which I was able to identify beetle-galleries). The variance in canopy consumption may thus be a partial proxy for pre-fire tree mortality. Among crown fire plots, low variance in canopy fuels was indicative of plots exhibiting complete canopy consumption on most snags, which is most likely to represent stands with high pre-fire tree mortality (Talucci & Krawchuk 2019).

Canopy consumption influences lodgepole pine recruitment via effects on seed availability. In this study, the abundance of trees with remnant cones in the canopy, which had the greatest influence on post-fire seedling densities across all plots, is the closest index of the cumulative effects of MPB and fire on seed availability. Indeed, the basal area of cone-bearing trees was most strongly correlated with plot-level canopy consumption and was negatively related to the proportion of completely consumed trees (Fig. 5). In stands experiencing severe crown fire, higher fire temperatures and fuel consumption may result in seed death or cone consumption to constrain regeneration (Anderson & Romme 1991; Turner et al. 1999; Rhoades et al. 2018; Littlefield et al. 2019; Talucci et al. 2019). In contrast, greater fire intensity in surface fire plots may augment seed release from serotinous cones to enhance regeneration (Turner et al. 1997). This may explain why I found a negative influence of live lodgepole pine basal area on seedling abundance in surface fire sites; areas with greater numbers of post-fire live trees may reflect low-severity, light surface burns that did not produce the necessary temperatures or residence times to release seed. Additionally, I found that seedlings were more abundant in plots exhibiting greater variance in canopy consumption. Overall, my results suggest that fire severity has a nonlinear relationship with post-fire recruitment of lodgepole pine, reinforcing the idea that

lodgepole pine regenerates best under moderate to moderate-high fire severity and is limited at the extremes (e.g., homogenous areas of either extreme crown fire severity or light surface fire severity) (Turner et al. 1997, 1999; Harvey et al. 2014a). Variation in canopy fuels may be even more consequential in more severely burned areas, as even a small proportion of trees with less severely consumed canopies may be able to supply enough seed for reasonable levels of regeneration.

Altogether, the patterns observed in the data are consistent with my presumption that seed availability is the primary filter structuring lodgepole pine recruitment following repeated disturbance from MPB outbreaks and wildfire, emphasizing the cumulative impacts of MPB-induced tree mortality and fire effects on post-fire seed viability and survival. Further, these findings indicate that increasing fire severity and/or longer intervals between beetle and fire approach the limits of lodgepole pine resilience, similar to the patterns of reduced lodgepole pine regeneration following compound disturbances by blowdown and fire (Buma & Wessman 2011) or short interval reburns (Turner et al. 2019; Braziunas et al. 2023).

4.1.2 Post-fire conditions shaping seedling germination and establishment

Fire effects may also influence the germination of tree seedlings via changes to seedbed conditions (Fig. 1). My study finds that in areas burning as surface fire, lodgepole pine seedlings were more abundant under moderate to moderate-high soil burn severity. This may partially reflect increased seed release and seed heating associated with severe surface fire temperatures to enhance germination (Johnstone & Chapin 2006). However, increasing burn severity also lends to greater availability of exposed mineral soil and reduced competition from understory vegetation to support lodgepole pine germination and establishment (Lotan 1983). Understory vegetation cover was not directly evaluated in GLMMs due to its strong correlation with soil

burn severity, however, I did observe that plots with >50% cover of understory vegetation had relatively low post-fire seedling densities. In crown fire stands, soil burn severity did not strongly affect germination, as these plots were consistently characterized by moderate to moderate-high soil burn severity. Despite the fire's extreme behavior, there were very few plots characterized by severe surface consumption- i.e., complete consumption of roots and organic matter, deep ash layer, and oxidized soil (Parsons et al. 2010)- and the decreased regeneration observed in more severely burned plots is likely the result of seed consumption rather than inhospitable seedbed conditions, per se.

Changes to fuel structures resulting from both fire and the recent MPB outbreak can alter the microsite conditions controlling seedling establishment. Reductions in canopy cover due to pre-fire stand breakdown and the consumption of live and dead trees in the fire result in increased light availability, which is generally favorable for lodgepole pine establishment (Lotan 1983). I did not directly measure canopy openness or light availability, though differences in light availability may have also contributed to the pattern of higher seedling densities in plots with the consumption of fine and moderate canopy fuels than in plots containing trees with unburned or scorched canopies. Significant reductions in canopy cover can, however, constrain regeneration due to reduced microclimate buffering provided by remaining fuel structures (Turner et al. 2019; Hoecker et al. 2020). The shade provided by post-fire snags retaining fuels in the canopy serves to moderate surface temperatures and soil moisture (Donato et al. 2006; Wooten et al. 2022) and can substantially influence the opportunities for post-fire tree recruitment (Davis et al. 2019; Clark-Wolf et al. 2021). Again, I believe that severely burned plots were largely limited by seed availability, however, the loss of canopy

fuels and greater proportion of downed snags may have further constrained subsequent seedling establishment and survival in these areas.

In addition, I found that seedling densities varied considerably with topography; low levels of regeneration coincided with steeper slopes and high elevations. The significant positive relationship between slope and elevation makes it difficult to tease apart their individual contributions to post-fire recruitment, especially given that they were evaluated in separate models. However, both elevation and slope retained strong negative correlations with post-fire seedling densities when evaluated across all plots, and I do not believe that this relationship is fundamentally different between crown fire plots and surface fire plots. The negative relationship between slope and post-fire lodgepole pine seedling densities has been reported elsewhere (e.g., Schoennagel et al. 2003; Coop et al. 2010) and may indicate the negative impacts of post-fire erosion and deposition on recruitment. Steep slopes are more likely to experience seed loss (Han et al. 2011) and/or seedling burial and mortality via deposition in extreme runoff events. Informal observations at my plots support this mechanism, as plots situated on steep slopes frequently exhibited erosional rills and the accumulation of sediment near downed snags. Occasionally, I noted post-fire seedlings buried under deposited sediment and coarse woody debris. As low-elevation plots tended to coincide with toeslope positions and valley bottoms and greater accumulation of cones on the ground, the high seedling densities in these areas may be partially attributed to reduced rates of seed relocation off-site and increased seed delivery from stands upslope.

Notably, differences in temperature and moisture availability across elevational gradients exert relevant controls on post-fire establishment. Slower snowpack melt-out rates at higher elevations can result in shorter growing seasons, limiting the germination and establishment of

lodgepole pine seedlings (Turner et al. 2004). This may have further constrained recruitment, in addition to reduced seed availability, to limit regeneration at my high-elevation plots. Aspect and heat load index can also be relevant metrics for evaluating the influence of topoclimatic buffering on post-fire recruitment, and warmer and drier conditions on south-facing aspects have been associated with decreased lodgepole pine recruitment following severe crown fire (Hansen & Turner 2019; Hoecker et al. 2020). However, neither heat load index nor aspect had an appreciable relationship with post-fire seedling densities in this study. Nonetheless, as I did not directly measure post-fire climatic conditions, such as ambient air and soil temperatures and moisture levels, I cannot preclude the possibility that climatic factors may have contributed to the variation in post-fire seedling densities. Future studies should continue to explore the influence of microclimatic factors on regeneration, particularly under changing climate conditions (Stevens-Rumann et al. 2018; Davis et al. 2019)

4.2 Implications for forest recovery and resilience

My findings indicate that the areas of ROMO dominated by lodgepole pine before the MPB outbreak and the East Troublesome fire were largely able to regenerate. Previous studies have demonstrated lower levels of recruitment in unburned beetle-killed forests relative to post-fire recruitment (Edwards et al. 2015; Talucci et al. 2019). While I was not able to directly compare the post-fire seedling densities to the advanced regeneration that occurred in the years between the MPB outbreak and the fire, I found average post-fire seedling densities are an order of magnitude higher than the average post-outbreak seedling densities reported in the west side of ROMO by Perovich and Sibold (2016). In this context, greater rates of lodgepole recruitment following the fire suggest a shift in forest development towards dense, even-aged lodgepole pine stands across the study area. Meanwhile, surrounding, unburned lodgepole pine forests are more

likely to result in uneven-aged cohorts of lodgepole pine forest and/or a reduction in lodgepole pine dominance with a higher prevalence of non-host forest species regenerating in beetle-killed stands (Sibold et al. 2007; Diskin et al. 2011, Nelson et al. 2014, Perovich and Sibold 2016; Shapira et al. 2021). Relative to the pre-disturbance lodgepole pine densities in these stands, my results show that a considerable portion of the study area is regenerating with enough seedlings at two years post-fire to be capable of recovering close to pre-outbreak forest conditions. However, given that a little over half of the study area was estimated to have fewer seedlings than pre-disturbance stem densities, I expect that initial forest recovery will result in a somewhat reduced density of lodgepole pine compared to the mature forests that were present before the onset of the MPB outbreak in the 2000s. Nonetheless, I emphasize that overall, the fire likely enhanced the rate of lodgepole pine recovery relative to post-outbreak, pre-fire recruitment.

Of course, the variability in seedling densities indicates that some areas with little to no post-fire lodgepole pine recruitment may experience different trajectories of recovery, whereby other forest species may be able to establish in subsequent years. For example, I found significant aspen recruitment in many of my plots, particularly in low- to mid-elevation areas. Aspen can regenerate prolifically following fire due to vegetative resprouting (Peet 2000), as well as long-distance seed dispersal (Nigro et al. 2021), which may lead to higher dominance of aspen in forests experiencing compound disturbances (Kulakowski et al. 2013; Andrus et al. 2021). The resulting variability in post-fire species composition and stand densities contribute to forest heterogeneity within the burn perimeter and across the broader landscape, which may enhance forest resilience to future disturbance and changing climate conditions (Turner 1994; Turner et al. 2013).

In general, lodgepole pine establishment in the first few years following stand-replacing fires is highly predictive of stand development over subsequent decades, particularly when recruitment is dense (Lyon 1976; Nyland 1998). However, ultimate stand development may vary considerably from the initial establishment of seedlings reported here. In stands with lower levels of initial recruitment following compound disturbances, longer-term regeneration patterns can be highly variable (Gill et al. 2017). Additionally, tree seedlings and juveniles are particularly vulnerable to extreme climatic conditions (Johnstone et al. 2010; Dobrowski et al. 2015), and warmer, drier conditions anticipated with climate change may result in seedling mortality and regeneration failure in subsequent years (Donato et al. 2016b; Conlisk et al. 2017). Consequently, continued monitoring for potential declines in forest regeneration may be warranted for recently burned stands, particularly those with initially low levels of recruitment.

The patterns and processes of post-fire forest recovery, as explored in this study, have implications for forests experiencing compounded disturbance by bark beetle outbreaks and wildfire across the western U.S. Current and projected increases in fire activity in the 21st century are associated with regeneration declines for many conifer species (Stevens-Rumann et al. 2018), though lodgepole pine forests are often predicted to regenerate well following large, high-severity fires (Davis et al. 2022; Rodman et al. 2022). The lodgepole pine regeneration densities I observed in the East Troublesome burn perimeter at 2 years post-fire align with these predictions, yet I underscore the potential for more extreme fire activity and influences from prior disturbances to override resilience and produce differential outcomes. I find evidence for lodgepole pine recruitment failure in areas experiencing severe crown fire due to complete canopy and cone consumption. Thus, larger extents of high-severity burn patches, particularly in areas with significant pre-fire tree mortality, may inhibit lodgepole pine regeneration in other

areas (Rhoades et al. 2018). Even in stands with high levels of serotiny, these areas should be prioritized for post-fire management activities (Rodman et al. 2022). Meanwhile, intact canopy fuels in post-fire lodgepole stands may help identify areas that are able to naturally recover, where post-fire reforestation efforts (e.g., active seeding) are not needed. Additionally, site topography can also be used to anticipate which areas are likely to experience more limited or unpredictable rates of post-fire recovery. Stands occurring near the upper elevational range or on steep slopes may be particularly vulnerable to recruitment failure following stand-replacing fires (Stevens-Rumann et al. 2018; Hoecker et al. 2020). Management activities aimed at reducing erosion potential may be beneficial for post-fire seedling establishment in severely burned areas (Wright & Rocca 2017; Jonas et al. 2019).

This study also highlights relevant considerations for management in unburned, beetle-killed lodgepole pine forests. Stand-replacing fires promote seed release and forest regeneration in beetle-killed lodgepole pine forests (Harvey et al. 2014a,b; Talucci et al. 2019). Management interventions in post-outbreak stands, such as fuel reduction treatments to reduce subsequent fire severity, are likely unnecessary for the persistence of lodgepole pine forests where serotinous trees are abundant. In fact, my results suggest that the cones retained on beetle-killed snags continue to support post-fire recovery for 15 or more years following the outbreak. As such, the removal of standing snags following bark beetle outbreaks may negatively impact lodgepole pine resilience to subsequent fire. However, at longer intervals between bark beetle outbreaks and fire, decreasing cone viability will likely render other beetle-killed forests less resilient to future fire activity (Harvey et al. 2014a; Rhoades et al. 2022). Additional studies in beetle-killed, serotinous lodgepole pine forests are needed to better understand the rates of seed loss and changes to seed viability following MPB outbreaks, particularly over longer intervals since tree

mortality. Furthermore, continued monitoring of post-fire recovery in subsequent years remains critical for anticipating future scenarios in which the serotinous seedbank can no longer support forest recovery.

Ultimately, differences in the timing, severity, and spatial patterns of disturbances can result in substantially different forest trajectories, and as such, remain hard to predict (Turner 2010). Nonetheless, I find that the mechanisms by which lodgepole pine forests regenerate following wildfire continue to support the persistence of this species even after exceptionally severe and extensive disturbance from MPB outbreaks and fire. Where fire continues to initiate the regeneration and development of lodgepole pine forests, the increasing dominance of serotinous lodgepole pine stands in forested landscapes may facilitate forest adaptation to changing environmental conditions, as they may be better equipped to withstand changing climate conditions and subsequent fires. Further evaluation of long-term forest successional trajectories is needed to anticipate and respond to future forest dynamics as disturbance and climate regimes continue to change.

TABLES

Table 1. Classification of strata for field site locations, their representation across the landscape, and sample size. Strata were classified from 30 m resolution raster data representing each variable of interest. MTBS burn severity classes derived from a dNBR image were used to identify areas that burned at high severity and either low or moderate burn severity. Beetle-caused tree mortality, calculated from Landsat time series products by Rodman et al. (2021), was used to identify high outbreak severity areas (80-100% mortality) and moderate outbreak severity areas (41-79% mortality). Reconstructed fire history data from Sibold et al. 2006 was used to stratify areas by the last stand-replacing fire year, distinguishing between longer (pre-1850) and shorter (post-1850) fire return intervals.

Stratum	Fire severity	Outbreak severity	Last stand-replacing fire year	Proportion of study area	# Plots sampled
1	High	Moderate	Pre-1850	0.16	10
2	High	High	Pre-1850	0.05	11
3	High	Moderate	Post-1850	0.11	13
4	High	High	Post-1850	0.11	25
5	Low-Moderate	Moderate	Pre-1850	0.05	9
6	Low-Moderate	High	Pre-1850	0.10	15
7	Low-Moderate	Moderate	Post-1850	0.09	12
8	Low-Moderate	High	Post-1850	0.32	21

Table 2. Description of canopy consumption criteria used to classify all standing adult trees (DBH > 5 cm) with a categorical value between 0 and 4 representing the degree of fire-caused change or loss in canopy structure. A total of 8,264 canopy trees were sampled across all plots. See Figure 3 for photos of trees.

Rating	Description	Trees Sampled
0	Unburned; live tree with green needles or pre-fire dead tree with no char in canopy	3.9%
1	Scorched; needles and fine branches remain, but needles may be brown or black	5.6%
2	Moderate consumption; Needles and most fine fuels/branches are consumed, but medium fuels and branches remain	19.9%
3	Significant consumption; fine fuels completely consumed, and only some large branches remain	20.3%
4	Crown fire plus; Entire canopy is consumed, no branches remain on snag	50.3%

Table 3. Stratum-level summary statistics used to derive estimates of post-fire lodgepole pine seedling regeneration at 2 years post-fire for the burned lodgepole pine forests in the study area. Plot-level measures of post-fire regeneration were summarized within each stratum and weighted by the proportional area of strata to estimate mean and median seedling density across the study area. The percentage of plots sampled within each stratum that had 1) seedlings present, 2) seedling densities >370 t ha^{-1}, and 3) seedling densities exceeding pre-disturbance lodgepole pine stem densities were similarly weighted by each stratum to estimate the percentage of the study area represented by each measure. Bolded values represent the final estimates and 95% confidence intervals of each regeneration metric across the study area.

					Regeneration thresholds		
Stratum	Stratum weight[1]	Plots sampled (no.)	Mean seedling density (t ha^{-1})	Median seedling density (t ha^{-1})	Seedlings present[2] (%)	Stocked[3] (%)	Exceeds pre-fire density[4] (%)
1	0.16	10	1,520	57	90	30	10
2	0.05	11	2,150	438	100	55	36
3	0.11	13	19,100	7,930	100	92	69
4	0.11	25	11,200	2,870	100	100	76
5	0.05	9	3,770	367	89	44	33
6	0.10	15	1,170	198	93	47	27
7	0.09	12	5,850	1,830	100	100	50
8	0.32	21	12,300	990	100	76	38
Estimate (95% CI)	-	-	**8,500 (4,120-12,900)**	**1,030 (622-1,580)**	**97 (94-100)**	**70 (61-78)**	**41 (32-50)**

[1]Represents the proportion represented by each stratum within the study area; total number of sampling units in the stratum divided by the total number of sampling units in the study area

[2]Represents percentage of plots sampled within each stratum that had post-fire lodgepole pine seedlings present

[3]Represents percentage of plots sampled within each stratum that had seedling densities exceeding 370 t ha^{-1} for adequate lodgepole pine stocking (USDA 1997)

[4]Represents percentage of plots sampled within each stratum where the density of post-fire seedlings exceeded the pre-disturbance (pre-MPB outbreak and pre-fire) lodgepole pine stem density

Table 4. Description of plot-level covariates considered for general linear mixed effects models of post-fire lodgepole pine seedling regeneration. Variables are grouped into broad categories representing fire effects, seed source, pre-fire and post-fire stand structure, and topography, though some variables may represent more than one category.

Category	Variable Name	Description
Fire Effects	Mean canopy consumption	Plot mean of canopy consumption ratings (integer value between 0 and 4) for all standing adult trees
	Canopy consumption variance	Plot variance of canopy consumption ratings (integer value between 0 and 4) for all standing adult trees
	Soil burn severity	Plot mean of soil burn severity ratings (integer value between 1 and 4) from quadrat measurements
Seed availability	Cone-bearing PICO BA	Basal area of all post-fire standing lodgepole pine trees with extant cones in the canopy ($m^2\ ha^{-1}$)
Pre-disturbance stand structure	QMD	Quadratic mean diameter of all lodgepole pine adults (cm)
	Total non-PICO BA	Combined basal area of all pre-disturbance spruce, fir, and/or aspen stems ($m^2\ ha^{-1}$)
	Total PICO BA	Basal area of all pre-disturbance lodgepole pine stems ($m^2\ ha^{-1}$)
	PICO stem density	Density of pre-disturbance adult lodgepole pine stems (no. ha^{-1})
Post-fire stand structure	Live PICO BA	Basal area of all post-fire living lodgepole pine ($m^2\ ha^{-1}$)
Topography	Elevation	Plot elevation, in meters, derived from 30m DEM
	Slope	Plot slope, in degrees, derived from 30m DEM
	HLI	Heat load index, derived from 30m DEM (McCune and Keon 2002)

Table 5. Summary statistics for pre- and post-disturbance stand structure characteristics across all plots. Pre-disturbance variables represent estimates of forest structure and composition prior to the recent bark beetle outbreak and the fire, as I was not able to quantify pre-fire tree mortality from the outbreak. Summary statistics are calculated from field data measured in each 15m radius circular plot.

Stand Structure Variable	Mean	SE	Range
Pre-disturbance			
Total basal area (m^2 ha^{-1})	20.9	0.94	1.26 – 60.07
Total stem density (t ha^{-1})	1,820	69	651 – 4,343
Lodgepole pine stem density (t ha^{-1})	1,780	70	580 – 4,244
Lodgepole pine QMD (cm)	15.7	0.36	6.85 – 22.59
Lodgepole pine (% stems)	97.6	0.42	71.43 – 100
Post-fire			
Live basal area (m^2 ha^{-1})	0.70	0.25	0 – 21.54
Live stem density (t ha^{-1})	52	19	0 – 1,556
Dead stem density (t ha^{-1})	1,330	53	226 – 3,791
Dead stems (%)	96.9	1.29	24.24 – 100
Snag fall (%)	29.0	1.36	3.03 – 57.81
Live pre-fire lodgepole pine seedlings (t ha^{-1})	8	4	0 – 244
Post-fire regeneration			
Post-fire lodgepole pine seedling density (t ha^{-1})	8,510	2,220	0 – 120,753
Post-fire aspen stem density (t ha^{-1})	325	101	0 – 8,205

Table 6. Generalized linear mixed effects model results for post-fire lodgepole pine seedling regeneration in plots that burned as crown fire (n=95). Shown are model estimates of beta (β) regression coefficients, conditional standard errors, t-values, and 95% significance level (p) for all fixed-effects. Beta estimates of standardized predictor variables represent the influence of 1 SD change in the predictor. The marginal and conditional pseudo r^2 values from the final model are 0.34 and 0.81, respectively.

Parameter	β	Cond. SE	t	p
Intercept	7.30	0.37	19.68	<0.01
Elevation	-0.71	0.28	-2.55	0.01
Cone-bearing PICO basal area	0.76	0.16	4.91	<0.01
Quadratic mean diameter	-0.28	0.13	-2.20	0.03
Plot variance in canopy consumption	0.50	0.15	3.41	<0.01
Plot mean soil burn severity	0.11	0.12	0.94	0.35

Table 7. Generalized linear mixed effects model results for post-fire lodgepole pine seedling regeneration in plots that burned as surface fire (n=21). Shown are model estimates of beta (β) regression coefficients, conditional standard error, t-values, and 95% significance level (p) for all fixed-effects. Beta estimates of standardized predictor variables represent the influence of 1 SD change in the predictor. The marginal and conditional pseudo r^2 values from the final model are 0.63 and 0.69, respectively.

Parameter	β	Cond. SE	t	p
Intercept	8.16	0.66	12.37	<0.01
Slope	-1.31	0.40	-3.29	0.01
Cone-bearing PICO basal area	1.56	0.29	5.29	<0.01
Live PICO basal area	-0.60	0.17	-3.52	<0.01
Plot variance in canopy consumption	0.46	0.30	1.50	0.16
Plot mean soil burn severity	1.14	0.36	3.18	0.01

FIGURES

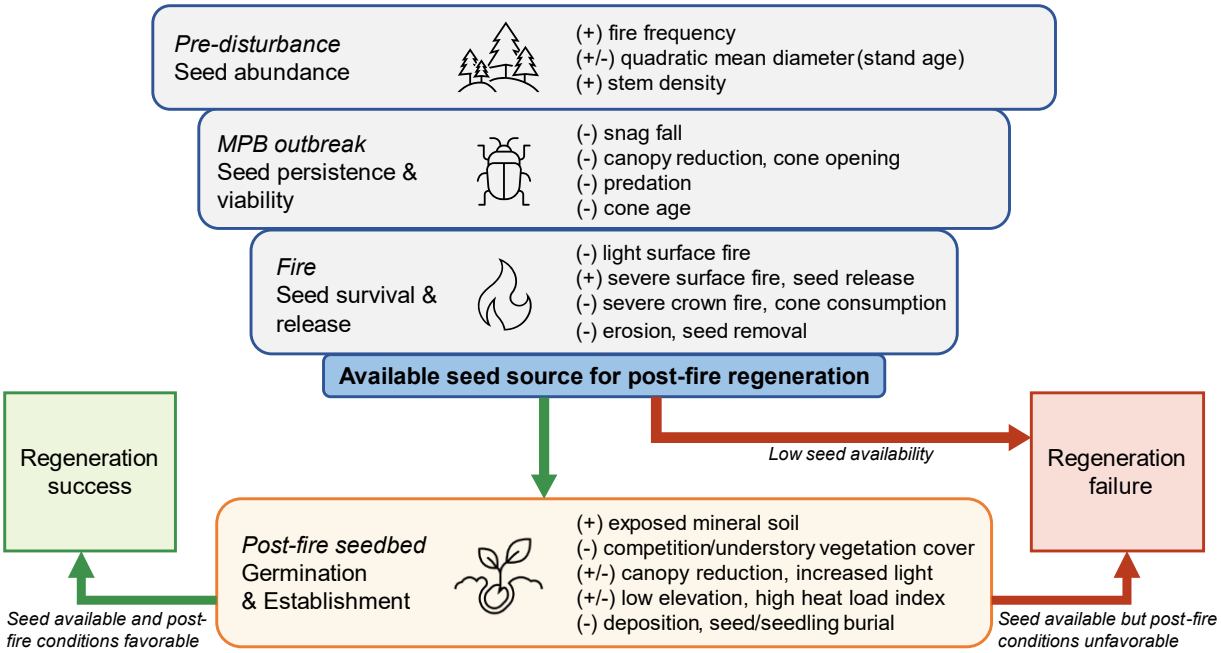

Figure 1. Proposed model of the stand-level environmental filters that influence the regeneration of serotinous lodgepole pine forests following compound disturbance by MPB outbreaks and wildfire (adapted from Wooten et al. 2022). Following fire, lodgepole pine regeneration depends on post-fire seed availability and suitable seedbed conditions for seedling germination and establishment. In a multi-disturbance system, post-fire availability of seed from serotinous cones depends on three primary environmental filters (blue boxes), characterized by the following: The pre-disturbance abundance of serotinous cones within a stand, the persistence and viability of seed following tree mortality from the mountain pine beetle (MPB) outbreak, and the survival and release of seed through fire. Seed available for post-fire regeneration must then meet suitable conditions for germination and establishment (orange box) to result in successful regeneration. Disturbance effects, stand-structure attributes, and abiotic characteristics influence the strength of each filter to have positive (+), negative (-), and/or neutral effects on regeneration.

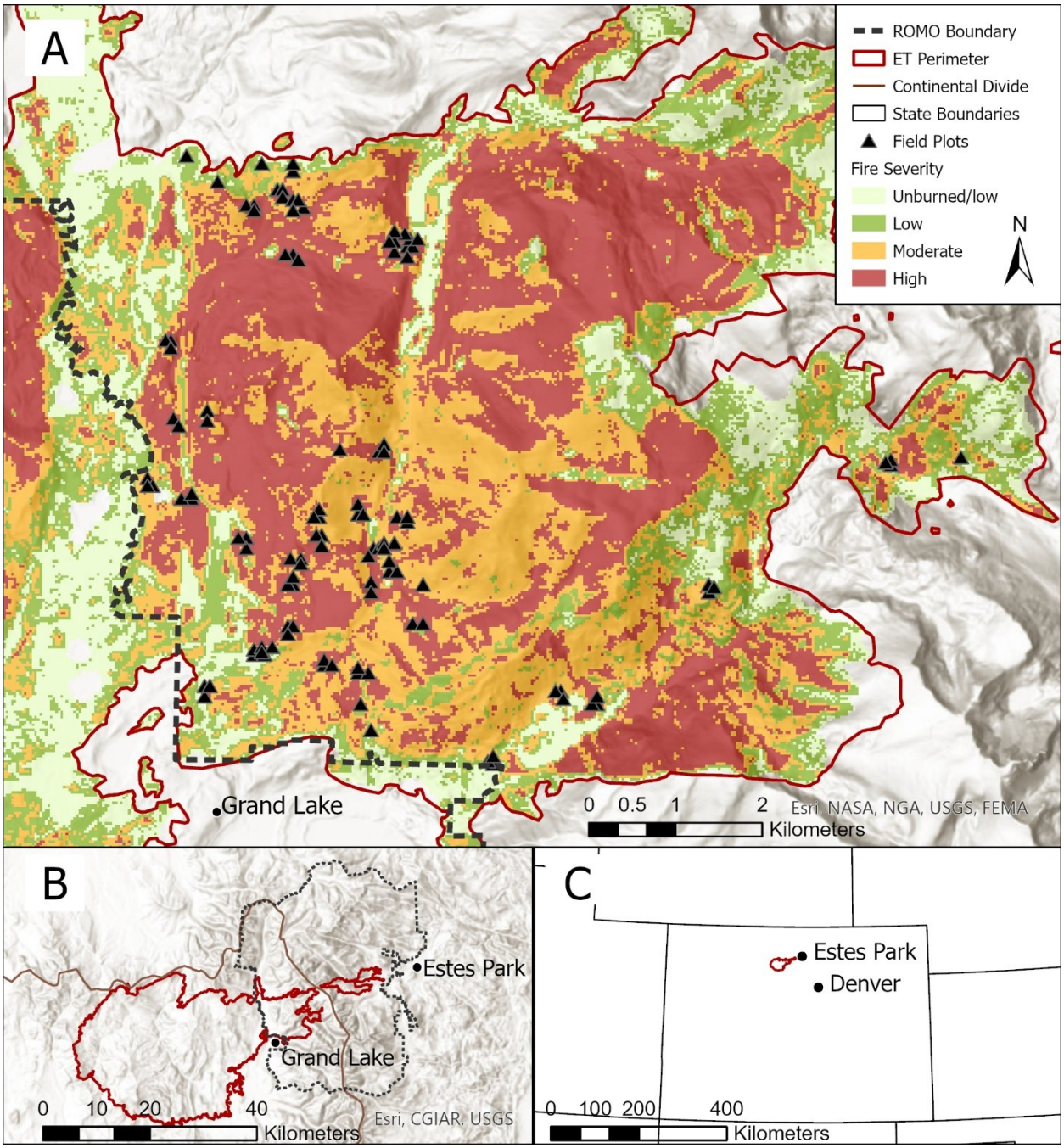

Figure 2. Study area and plot locations on the west side of Rocky Mountain National Park (ROMO), Colorado. (A) The study area comprises lodgepole pine forests that burned in the 2020 East Troublesome fire. A dNBR image and fire perimeter from the Monitoring Trends in Burn Severity project (2022) was used to stratify field sites between areas that burned at high severity (red) and areas that burned at low or moderate severity (green and orange). Site locations were additionally stratified by outbreak severity (Rodman et al. 2021) and time since last stand-replacing fire (Sibold et al. 2006). Points (black triangles) represent locations of 15m radius plots clustered within spatially balanced stratified sampling sites. The full East Troublesome fire perimeter and park boundary (B) and location of the fire perimeter within the state of Colorado (C) are shown for reference.

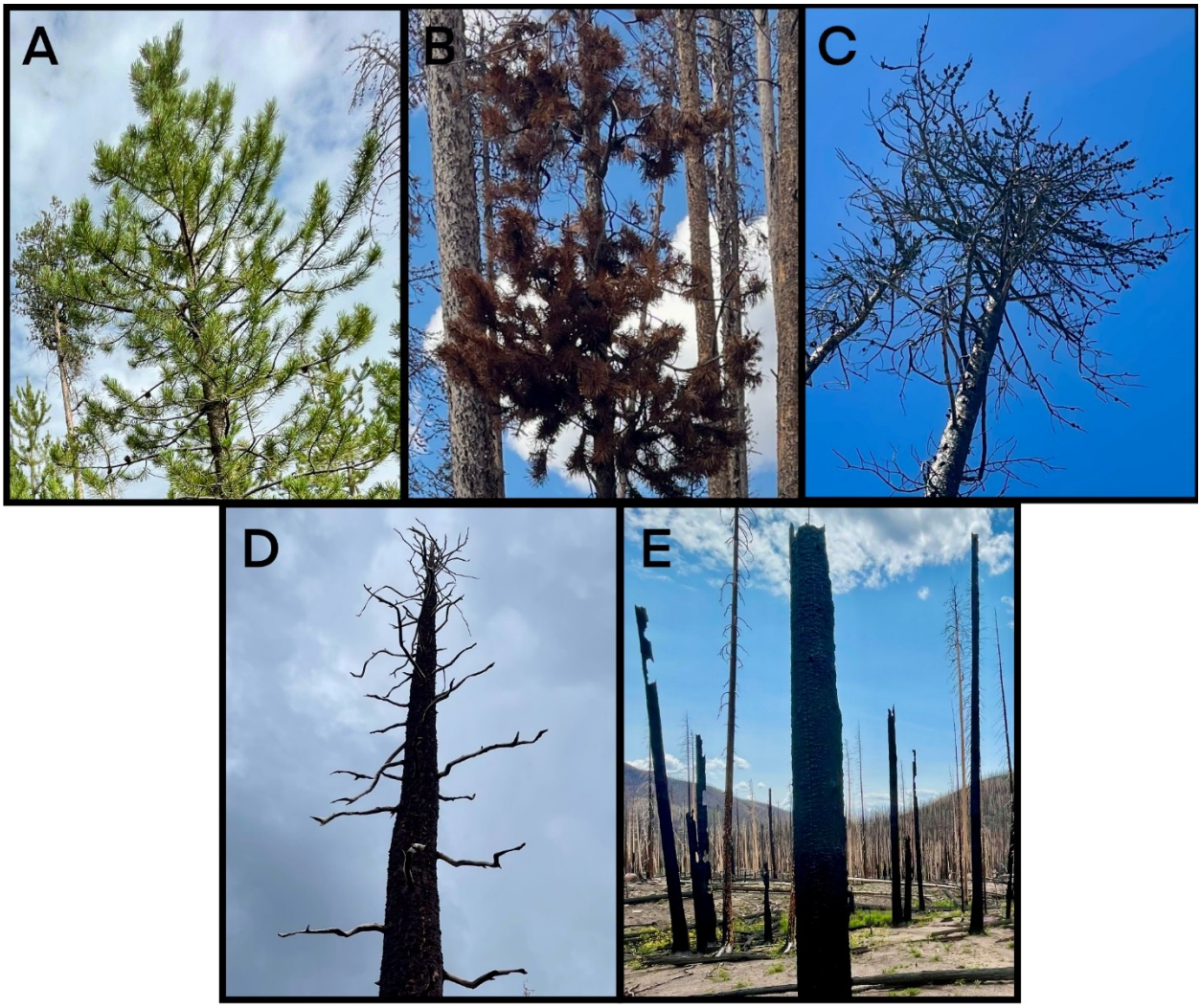

Figure 3. Photographs of post-fire canopy conditions on individual trees representing categories of canopy fire severity described in Table 2. Trees classified as unburned had green needles remaining in the canopy if live pre-fire (A). Scorched trees impacted by the fire's heat but not experiencing active crown fire were identified by red or brown needles remaining in the canopy (B). Moderately consumed trees showed needle loss but retained small- and moderate-sized branches (C), while significantly consumed trees had only large branches remaining close to the trunk (D). Snags that experienced complete consumption of the canopy with deep char along the entire stem (E) were classified ‘crown fire plus’ (Turner et al. 2019).

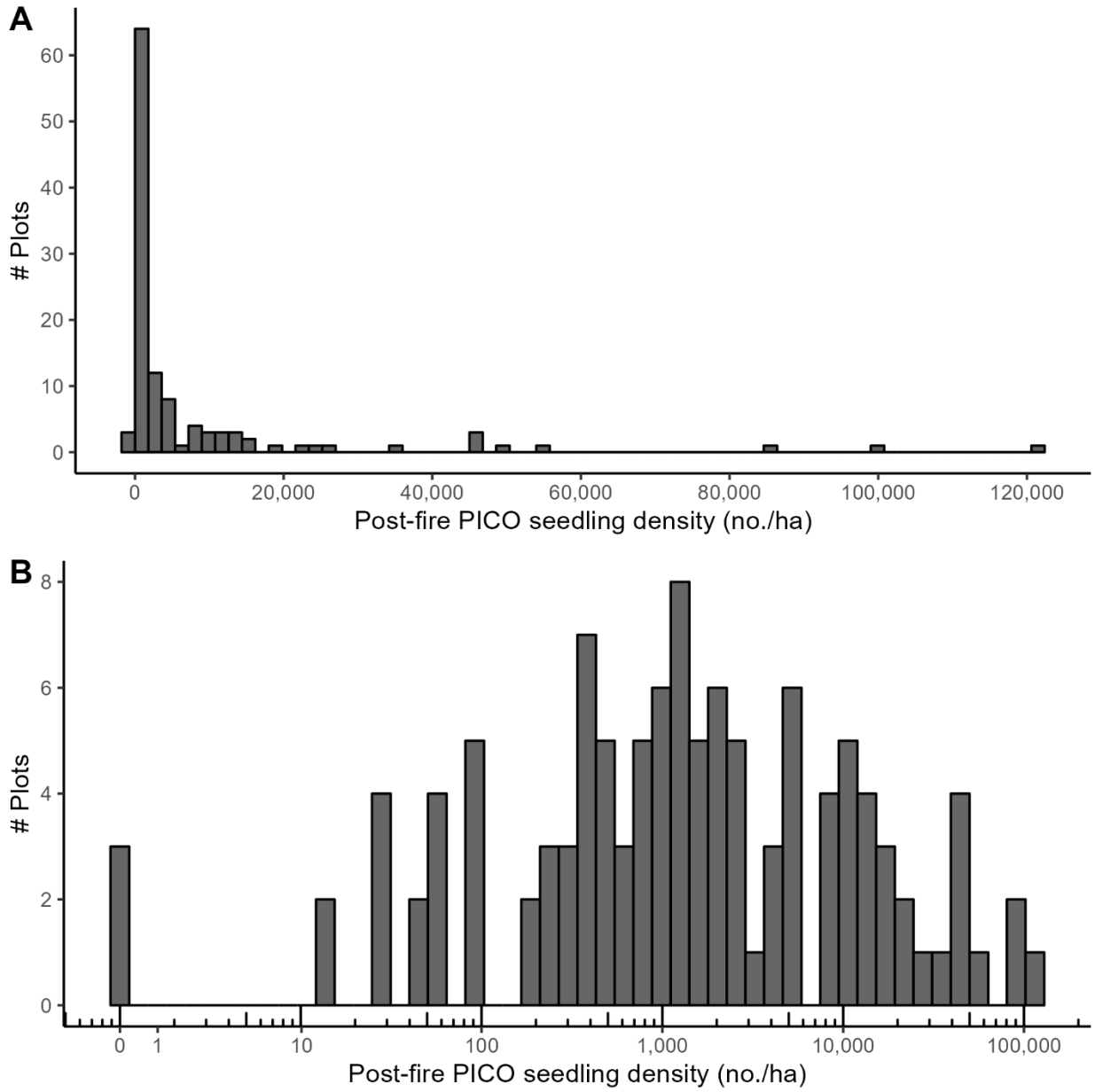

Figure 4. Histograms of post-fire lodgepole pine regeneration measured across all 116 field plots. The regeneration data presented in these plots is based on the raw data collected from each field plot and does not account for the stratified sampling design. Plot (A) shows the distribution of seedling density measurements along a linear x-axis. The same data are represented in plot (B) with a logarithmic (base 10) scale on the x-axis to better visualize the distribution.

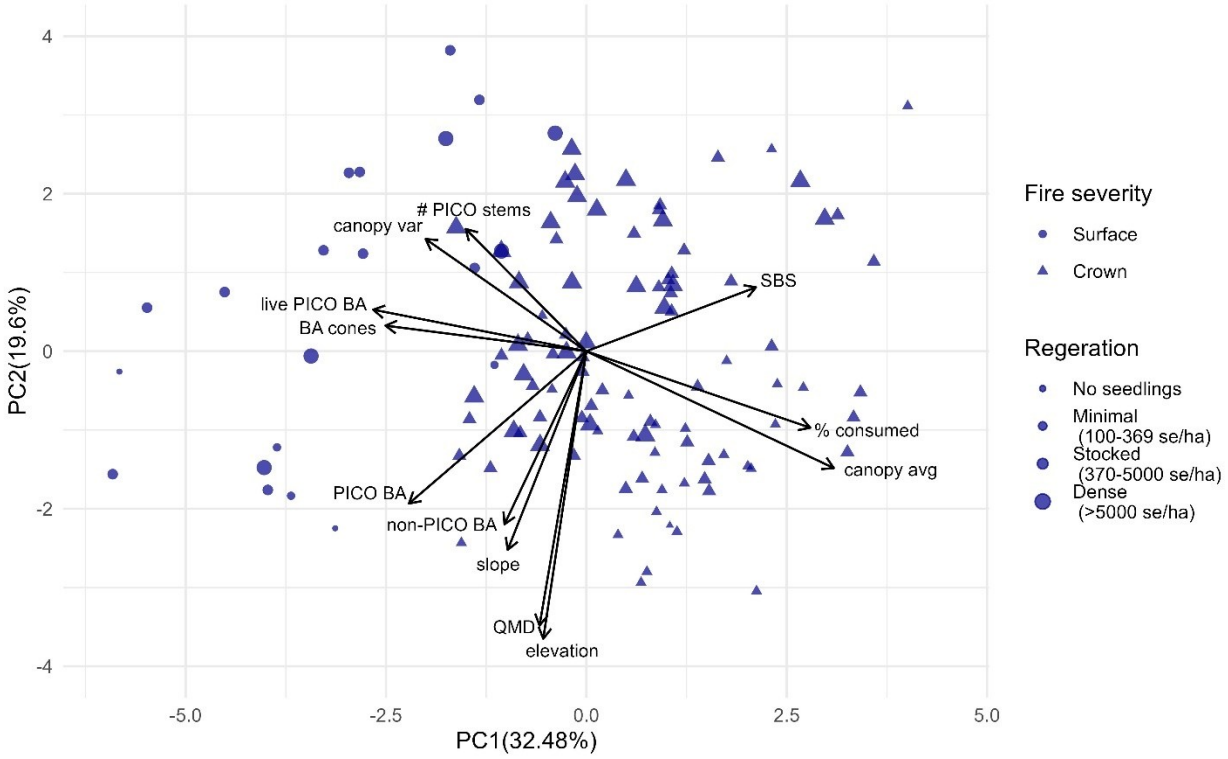

Figure 5. Biplot of principal components analysis (PCA) for variables representing fire effects, forest structure, and topography measured at all 116 field plots. The first principal component axis (PC1) captures variables representing fire effects and accounts for 32.48% of the variance in the data. An additional 19.6% of the variance is captured by topographic and pre-disturbance forest structure variables in the second axis (PC2). Variable loadings (arrows) show the contribution of each variable to the two axes and the angle between two arrows indicates the correlation between variables. Crown fire plots (triangles) are clustered with increasing fire severity metrics, in contrast to surface fire plots (circles). Point sizes correspond to binned classes of post-fire lodgepole pine seedling density to visualize relationships between plot-level variables and post-fire regeneration. Variables are coded as follows: SBS= soil burn severity; canopy avg= plot average of canopy consumption ratings; canopy var= plot variance of canopy consumption ratings within a plot; # PICO stems= density of pre-disturbance lodgepole pine stems; % consumed= percent of trees with complete canopy consumption (ie., “crown plus”); live PICO BA= post-fire live PICO basal area; BA Cones= cone-bearing lodgepole pine basal area; PICO BA= total pre-disturbance PICO basal area; non-PICO BA= total pre-disturbance basal area of spruce, fir, or aspen species; QMD= pre-fire lodgepole pine quadratic mean diameter.

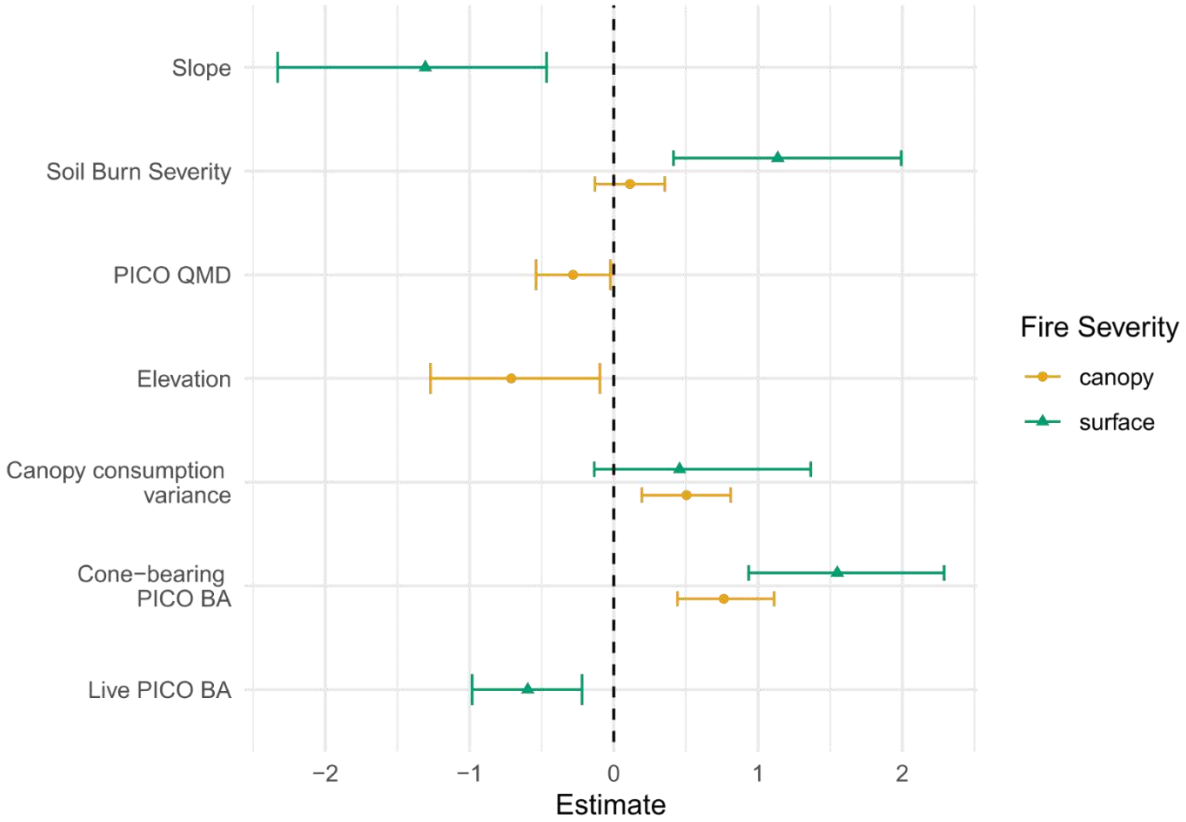

Figure 6. Regression estimates and confidence intervals from the best-fit models of lodgepole pine seedling abundance in crown fire plots (orange; n=95) and surface fire plots (green; n=21). Points are estimates of each fixed effect parameter with a 95% confidence interval. Fixed effect parameters were standardized to show the relative influence of each parameter on regeneration. Confidence intervals that do not overlap 0 indicate parameters with a significant influence on regeneration. BA= basal area (m^2 ha^{-1}). QMD= quadratic mean diameter (cm).

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APPENDIX

Table A1. Generalized linear mixed effects model results for post-fire lodgepole pine seedling regeneration across all 116 plots in the study area (crown and surface fire plots combined). Shown are model estimates beta (β) regression coefficients, conditional standard error, t-values, and 95% significance level (p) for all fixed-effects. Beta estimates of standardized predictor variables represent the influence of 1 SD change in the predictor. The marginal and conditional pseudo r^2 values are 0.36 and 0.75, respectively.

Parameter	β	Cond. SE	t	p
Intercept	6.38	0.48	13.41	<0.001
Elevation	-0.94	0.26	-3.55	<0.001
Cone-bearing PICO basal area	0.87	0.15	5.99	<0.001
Burn severity	0.70	0.42	1.67	0.098
Plot variance in canopy consumption	0.38	0.12	3.06	0.003
Quadratic mean diameter	-0.38	0.14	-2.80	0.006
Live PICO basal area	-0.64	0.16	-3.91	<0.001

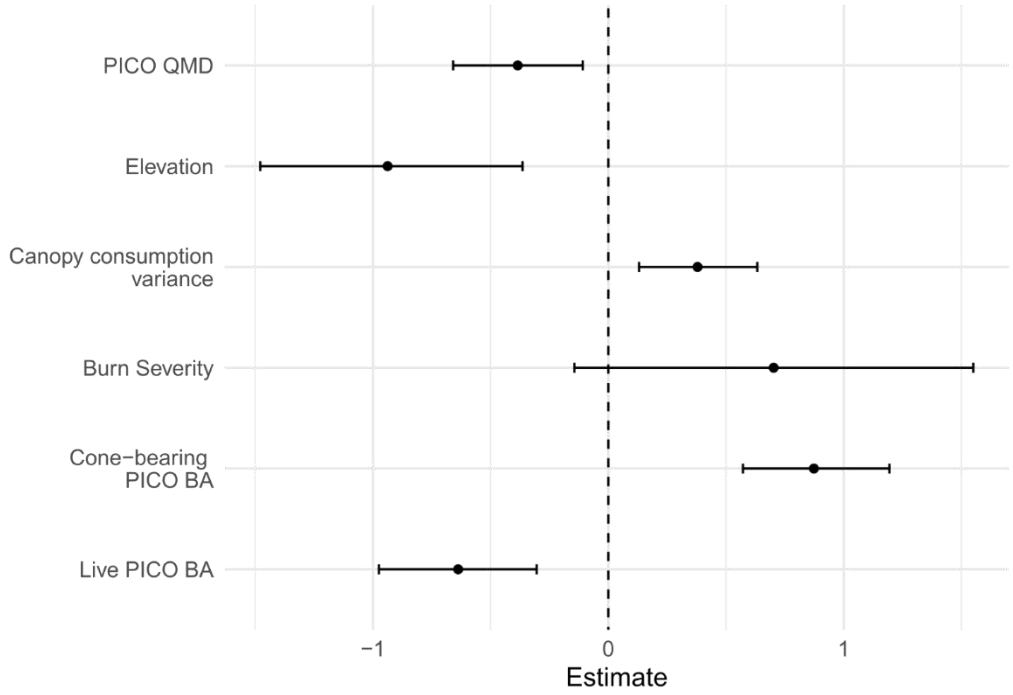

Figure A1. Regression estimates and confidence intervals from the best-fit model of lodgepole pine seedling abundance across all plots (crown and surface fire plots combined, n=116). Points are estimates of each fixed effect parameter with a 95% confidence interval. Burn severity represents a binary variable indicating plots that burned as crown fire. Fixed effect parameters of continuous variables were standardized to show the relative influence of each parameter on regeneration. Confidence intervals that do not overlap 0 indicate parameters with a significant influence on regeneration.