THESIS

LODGEPOLE PINE REGENERATION AFTER MOUNTAIN PINE BEETLE AND WILDFIRE: A CASE STUDY IN THE HIGH PARK FIRE, CO

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ABSTRACT

LODGEPOLE PINE REGENERATION AFTER MOUNTAIN PINE BEETLE AND WILDFIRE: A CASE STUDY IN THE HIGH PARK FIRE, CO

The 2012 High Park Fire burned over 35,000 hectares, including 5,000 hectares of lodgepole pine (*Pinus contorta*) forest that had recently been attacked by mountain pine beetle (MPB, *Dendroctonus ponderosae*). This sequence of events provided an excellent opportunity to investigate the effects of combined disturbance on lodgepole pine regeneration trajectories. I examined the influence of MPB mortality, high canopy fire severity, site characteristics, and post fire mulching treatments on lodgepole pine recovery at both landscape (∼hectare) and fine (∼cm) spatial scales.

At the landscape scale, lodgepole pine seedling densities varied from 240 to 470,000 stems/ha. Seedling densities decreased as MPB mortality and high canopy fire severity increased. At the fine scale, lodgepole pine seedling establishment was positively related to local cone abundance and negatively related to high canopy fire severity. Topographic variables such as aspect and elevation did not have a strong influence on seedling density or establishment at either scale, nor did competition from recovering vegetation have an influence at the fine scale where it was considered. In areas with high canopy fire severity, post-fire straw mulching treatments were positively related to seedling establishment, indicating that mulching treatments may have additional benefits beyond erosion control. My research demonstrates that combinations of pre-fire mountain pine beetle mortality and high canopy fire severity can affect lodgepole pine regeneration, and may drive heterogeneity in the post-fire landscape.

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1 Introduction

Fire and bark beetle outbreaks are common natural disturbances in coniferous forests throughout the American West. Both disturbances can cause tree mortality, thereby shaping forest structure, composition, and productivity (Romme et al., 1986; Veblen et al., 1994; Turner, 2010; Romme et al., 2011). However, as higher temperatures and drought become more prevalent (Dale et al., 2001; Wuebbles et al., 2014), the frequency, severity, and extent of both wildfire (Westerling et al., 2011; Liu et al., 2013) and bark beetle outbreaks (Kaufmann et al., 2008; Raffa et al., 2008; Safranyik et al., 2010) are expected to increase. Such alterations to disturbance regimes have already been observed (Westerling et al., 2006; Safranyik et al., 2010; Dennison et al., 2014; Rocca et al., 2014). These trends increase the likelihood that these disturbances will interact, which highlights the need for a greater understanding of compound disturbance interactions and their impacts on ecosystem resilience (Paine et al., 1998; Turner, 2010; Buma and Wessman, 2011; Buma, 2015). In this study, I describe the effects of combined mountain pine beetle (*Dendroctonus ponderosae*, hereafter MPB) and fire on lodgepole pine (*Pinus contorta*) regeneration in the northern Front Range of Colorado. I also investigate how the post-fire seedbed environment affects lodgepole pine regeneration, including the influence of post-fire mulching treatments, a frequently used erosion mitigation technique (Robichaud et al., 2010).

The 2012 High Park Fire burned through approximately 5,000 hectares of mature lodgepole pine forest that had recently experienced a MPB outbreak, at least 25% of which was in the latter stages of attack (Figure 1, Stone 2015). Additionally, about 35% of the area occupied by lodgepole pine forest within the High Park Fire was treated with mulch as an erosion control measure. This series of events provided a unique opportunity to study the effects of disturbance interactions and management response on the regeneration success of a key serotinous species. I was able to utilize recently developed high resolution remote sensing data products, including MPB and burn severity classification rasters created by Stone

(2015). These data were instrumental in characterizing the level of disturbance interaction at the landscape scale, and for projecting my findings back onto the landscape.

I addressed four main questions:

(1) How do MPB and fire severity interact to affect lodgepole pine regeneration at the landscape scale?

I investigated the stand-scale drivers of lodgepole pine seedling densities across a 5,000 hectare landscape. I hypothesized that, in the absence of MPB mortality, post-fire seedling densities would decrease with increasing canopy fire severity because high severity fire would kill and/or consume portions of the serotinous canopy seed bank (Anderson and Romme, 1991; Turner et al., 1999; Harvey et al., 2014a,b). I also hypothesized that MPB mortality would lead to reduced post-fire seedling densities regardless of canopy fire severity, as MPB mortality causes a portion of the serotinous canopy seed bank to release prior to the fire event (Teste et al., 2011). Furthermore, I reasoned that MPB mortality would result in increased canopy flammability (Page et al., 2012; Jolly et al., 2012) which in turn can lead to greater seed mortality as flame residence times and fire line intensity increase (Johnson and Gutsell, 1993; Alexander and Cruz, 2012).

(2) Do MPB and high canopy fire severity interact to affect variation in lodgepole pine's canopy seed bank?

In this question, I attempt to identify the mechanisms that drive post-fire patterns of seedling density that are identified in question 1. MPB mortality and fire will likely influence lodgepole pine regeneration via mechanisms that alter the canopy seed bank. For example, fire may destroy cones (Anderson and Romme, 1991), or, where burning is particularly intense or long-lived, kill the seeds in the cones that remain (Knapp and Anderson, 1980; Johnson and Gutsell, 1993; Alexander and Cruz, 2012). Even in the absence of fire, MPB mortality can result in loss of the canopy seed bank through cone fall or reduced serotiny as cones open with increasing time since mortality (Teste et al., 2011). I hypothesized that when MPB mortality and fire are combined, the lower fuel moistures in trees killed by MPB would cause more cones to be destroyed than by either disturbance alone, especially when high canopy fire severity combines with severe MPB mortality (Harvey et al., 2014b).

(3) To what extent is fine-scale lodgepole pine seedling establishment controlled by local seed source, seedbed factors, the presence and severity of MPB mortality, and the canopy fire severity?

Individual lodgepole pine seedling establishment likely varies with local microsite characteristics, such as the availability of mineral soil and the presence of unburned forest floor materials (Lotan and Critchfield, 1990; Page-Dumroese et al., 2002; Edwards et al., 2015). However, I hypothesized that the availability of a viable canopy seed bank is likely to be the strongest driver of post-fire lodgepole pine regeneration, as seedlings are more likely to establish in areas with more abundant viable seed (Lotan et al., 1985; Turner et al., 1997; Schoennagel et al., 2003; Harvey et al., 2014a,b). I expected fire and MPB mortality to primarily influence regeneration through their effect on the canopy seed bank, as outlined in question 2. Beyond its influence on canopy seed availability, I hypothesized that high canopy fire severity would influence seedling establishment through alteration of the seedbed environment, including by increasing the exposure of mineral soil, reducing understory vegetation cover, and reducing the abundance of post fire litter (Turner et al., 1999).

(4) Do variations in post-fire mulching treatments influence the establishment of lodgepole pine at the fine scale?

I hypothesized that post-fire mulching applications would benefit seedling establishment, largely through improvements to the micro-environment, such as increased soil moisture retention (McDonald et al., 1990; Amaranthus et al., 1993; Dodson and Peterson, 2010). Alternatively, post fire mulching may inhibit seedling establishment through a variety of mechanisms, including the formation of a physical barrier that would impact either dispersing seeds or emerging seedlings (Kruse et al., 2004).

2 Methods

2.1 Study Area

The High Park Fire area is located just west of Fort Collins in Larimer County, in the northern Front Range of Colorado (Figure 1). The fire was ignited by lightning on the 7th of June, 2012, and spread rapidly under dry conditions and high winds (Coen and Schroeder, 2015). Prior to its containment on July 1st, the fire destroyed 259 homes and burned over 35,000 hectares (InciWeb, 2012). At the time, it was the largest and most destructive fire in Colorado (BAER, 2012; Coen and Schroeder, 2015).

The study area has a continental climate, characterized by cold winters and unstable summer weather typical of the Front Range (Peet, 1981). Mean monthly temperatures in the fire area range from 26.8°C in July to -7.4°C in January; annual precipitation for the area averages 54.6 cm, with a monthly peak of 8 cm in May (Western Regional Climate Center, Buckhorn Mountain Station http://www.wrcc.dri.edu/). The fire area is characterized by a strong east-west elevation gradient, ranging from approximately 1585m on the eastern portions of the fire to 3140m in the west, with a corresponding gradient in forest type (Peet, 1981; BAER, 2012). Stands of ponderosa pine and juniper were found at lower elevations, transitioning to mixed conifer forests, while lodgepole pine dominated much of the higher elevation areas (LANDFIRE, 2010; BAER, 2012).

Following the fire, erosion control was identified as a top priority in the Burned Area Emergency Response Report (BAER, 2012). Based on these recommendations, over 4,300 hectares of the fire were mulched by a variety of agencies between 2012 and 2014. A majority (90%) of the mulch treatments that were applied in the lodgepole zone between 2012 and 2013 used straw mulch, but ∼168 hectares were mulched with of wood chips, primarily on ridge tops and other areas where mulch would be vulnerable to wind transport (BAER, 2012).

2.2 Data Collection

To determine if the density of regenerating lodgepole pine seedlings varies with MPB mortality and canopy fire severity, I implemented a random stratified sampling design. Stratifications were based on the presence or absence of pre-fire MPB mortality and high or low/moderate canopy fire severity, for a total of four strata. All strata were sampled in both years (Table 1). Canopy fire severity and MPB mortality classifications were estimated using 25m data products taken from Stone (2015). Stone (2015) classified both canopy fire severity and MPB mortality using a two-tiered approach. In the first tier, Stone (2015) classified 15m plots using photo interpretation; the spectral values for each class were used as training data to create a 5m raster. For the second tier, Stone (2015) trained a model on both the photo interpretation classification and the fraction of individual plots occupied by each class of the 5m raster from tier 1; a final 25m classification map was created using the same class-fraction approach. Stone (2015) classified a plot as containing MPB mortality if 25% or more of the pre-fire data indicated canopy mortality, which was assumed to be due to MPB. Stone (2015) defined high canopy fire severity as complete consumption of canopy and understory fuels, while moderate severity was defined by scorching, but not consumption, of canopy fuels. Stone (2015) characterized areas of ground fire that did not scorch the canopy as low severity. This methodology does not rely on image comparison, limiting the potential bias that can occur using other methods, such as when creating differenced burn severity ratios in MPB infested stands (Stone, 2015). Using these data, I estimated 72% of the lodgepole pine in the High Park Fire burned at high severity, and 64% was classified as MPB mortality (Stone, 2015).

Low and moderate severity classes were combined into a single classification, as these classes both represented surface fire behavior, where tree canopies were not consumed (Stone, 2015). I therefore refer to "canopy fire severity" as the variable that distinguishes whether or not a tree's canopy was consumed during the fire. "High canopy fire severity" refers to the more or less total consumption of needles in the area of interest, while I use "low canopy fire severity" to refer to situations in which at least some of the needles remain.

The potential sampling area was limited to a distance of 2km uphill and 1km downhill from drivable access roads. Candidate sites were located in the field with a GPS. Sites were approved for sampling if lodgepole pine made up 50% or more of the stand basal area, measured from the central point with a standard factor 10 wedge prism.

2.2.1 Landscape-scale data collection

If a site met the suitability criteria, I established a 0.49 hectare "grid" consisting of eight parallel 70m belt transects, separated by 10m (Figure 2). I tallied lodgepole pine seedling abundance in each belt transect. Transect width was determined using a visual estimation of seedling density, with .5, 1, and 2m transect widths for dense, moderate, and sparse seedling densities, respectively. Transect widths were held constant within grids. During the 2015 field season, I also classified seedlings in the transects by growth stage—seedlings that had not developed fascicles or bud scars were classified as being in their first year of growth (William Romme, personal communication; Urza and Sibold, 2013). Five grids, one of each classification including one extra, were re-sampled in the second year to look for changes in seedling density between years.

Raster data (25m resolution) created by Stone (2015) were chosen to assess MPB mortality and canopy fire severity for the landscape scale analysis. The % cover classifications for MPB and canopy fire severity for each grid were estimated by calculating the percentage of the grid area that was classified as high canopy fire severity or MPB mortality. These percentages were typically near 0 or 100 due to the stratified sampling design.

I derived landscape-scale topographic variables from a 25m DEM. These included elevation, slope, aspect, and a compound topographic index (CTI), a proxy for site wetness that incorporates catchment area and slope angle (Moore et al., 1993; Gessler et al., 1995).

Elevation, slope, and CTI were averaged over the grid area, while aspect (to 45°, Beers et al., 1966) was estimated from the grid center.

2.2.2 Fine-scale data collection

Every 10 meters along each seedling transect, I systematically placed a 25×25cm quadrat, which was rotated on center to align with local slope direction. I recorded the location of each quadrat placement using a Trimble Juno. I took a minimum of 200 positions at each quadrat, which were then corrected in post processing (mean horizontal accuracy approximately 3.72 meters). These positions were used to relate extract the remote sensing data for both the landscape and fine scale analyses. I characterized fine scale post fire regeneration success by tallying all tree seedlings at each quadrat location.

I estimated fine scale variability in canopy fire severity by classifying each quadrat with a binary variable based on the needle retention ratio of the tree crowns surrounding the quadrat. If fewer than 50% of the trees that were tallied with a standard factor 10 wedge prism still retained needles at the time of sampling, that site was classified as high canopy fire severity; similarly, if the needle retention ratio exceeded 50%, then the site was classified as low canopy fire severity (Figure 3). This distinction was unambiguous; typically, needle retention ratios were close to 0 or 1, even in the second year of sampling. The fine-scale canopy fire severity values generally corresponded well with the landscape-scale remote sensing classification, with a Spearman's rho of 0.89 to aggregated field values (Figure 4). One grid was misclassified by the 25m data, it was removed from the analysis.

At each quadrat, I estimated the basal area for lodgepole pine that were dead at the time of the fire by tallying trees with deep charring around the bole (Figure 5), as live trees do not char in this fashion (Turner et al., 1999). Typically, charring was located either along the entire stem or localized near the base. Where this metric was ambiguous, I used a 50% circumference threshold for the final determination, though often the entire bole was charred, especially in areas that had experienced high canopy fire severity. I estimated prefire MPB outbreak severity by converting the basal area for trees dead at the time of the fire to a percentage of total lodgepole pine basal area, which was also estimated using the wedge prism. I assumed that all tree mortality was beetle related, as MPB mortality was very extensive across the lodgepole zone (Stone, 2015). I was unable to base the MPB characterization on physical evidence of beetles such as galleries or pitch tubes, as charring in stands that burned at high severity was often so extensive that all evidence was erased. This classification also corresponded well with the remote sensing data, with a Spearman's rho of 0.67 between aggregated field values and the remote sensing (Figure 6).

I estimated the potential lodgepole pine seed source at each quadrat by tallying the basal area of cone-bearing lodgepole pine with a standard factor 10 wedge prism. For the majority of individual lodgepole pine trees, cones were either abundant or absent; however, the presence of even a single cone was sufficient for a tree to be classified as cone-bearing. While this metric does not precisely describe the abundance of cones or viable seed at each site, it provided a rapid way for us to assess whether a seed source was present at a location and how abundant, relatively speaking, potential seed sources might have been (Turner et al., 2007).

I estimated micro-site topography using quadrat slope measurements, which were determined by laying a inclinometer along the quadrat frame. Additionally, aspect and elevation values were extracted from a 1m DEM using the GPS-derived quadrat point locations. Aspects were transformed to values between 0 and 2, with higher values given to northeastern aspects (45°, Beers et al., 1966).

For each quadrat, I performed a visual cover estimations for vegetation, mineral soil, litter, coarse wood, rock, and mulch. No distinction was made between live or dead vegetation cover. All cover estimates were rounded to the nearest 5%. I calculated % "growable area" as the proportion of each quadrat not occupied by rock or coarse wood. I assumed that growable area was representative of the mineral soil seedbed available immediately after the fire, as unburned material was rare throughout the study area. Quadrats with growable area values

<10 were removed from the analysis. The major source for litter in my study area was post-fire needle cast and fine branches. Litter cover had a strong inverse relationship with canopy fire severity (Spearman's rho=-0.76, Figure 7); surface fires may kill surrounding trees, but do not consume the needles and fine branches in the canopy (Anderson and Romme, 1991; Turner et al., 1999).

2.3 Statistical analysis

I used an information theoretic approach, which compares the level of support for a model to other candidate models, each model reflects a different hypothesis about the question at hand (Anderson et al., 2000; Burnham et al., 2011). Candidate models are ranked by the likelihood that they are the best model given the available data, with the "best" model defined as the model where Akaike Information Criterion (AIC) is minimized (Anderson et al., 2000). Differenced AIC values (ΔAIC, calculated using the formula $\Delta\text{AIC} = \text{AIC}_i - \text{AIC}_{min}$) quantify the strength of evidence for each candidate model as compared to the best model in the set (AIC_{min}); models with ΔAIC values <2 have strong relative support from the data, though models with ΔAIC up to 7 may contain information that should also be considered (Burnham and Anderson, 2004; Burnham et al., 2011). Akaike weights (w_i), the likelihood that the model is "best" given the data, can also be used to characterize variable importance by summing w_i for each model where that variable appears (Anderson et al., 2000). I report the regression estimates for all models with $\Delta\text{AIC} \leq 7$, and AIC, ΔAIC, and w_i, for all models (for an example of the latter, see Borgmann and Rodewald, 2005), as I could not use model averaging due to collinearity between key predictor variables included in separate models (Freckleton, 2010)—for example, the basal area of cone bearing trees and MPB mortality (Spearman's rho=-0.71). All statistical analyses were performed using R statistical computing software (R version 3.2.2, R Core Team, 2015). I calculated AIC corrected for small sample size (AICc) when the model sample to parameter ratio was less than 40 (Symonds and Moussalli, 2011). Model fit for generalized linear models was evaluated using graphical techniques and chi-square goodness of fit tests. Model fit for logistic mixed models was assessed using area under the receiver-operating curve (AUC) and Hosmer-Lemeshow goodness of fit tests from the "ROCR" (Sing et al., 2005) and "ResourceSelection" (Lele and Keim, 2006) packages, respectively. AUC values of >0.70 indicate an "acceptable" level of model prediction error, while AUC >0.80 is considered to be an "excellent" level of prediction error (Hosmer and Lemeshow, 2013, p. 177). With the exception of MPB mortality and canopy fire severity in the canopy seed bank analysis, I did not include variables whose correlations exceeded 0.50 in the same model—this can lead to model redundancy and biased regression estimates (Freckleton, 2010; Burnham et al., 2011). I tested for multicollinearity for all models under consideration using variance inflation functions from the "car" package (Fox and Weisberg, 2011) and mixed model function (authored by Austin Frank, accessed from https://hlplab.wordpress.com/2011/02/24/diagnosing-collinearity-in-lme4/). I tested for spatial autocorrelation of residuals for models with spatial data using Moran's I with an inverse distance weights matrix using the "APE" package (Paradis et al., 2004; Assal et al., 2015). Continuous variables were standardized where appropriate to ease model interpretation and to ensure convergence. I estimated variance explained with marginal and conditional r^2 using the piecewiseSEM package (Lefcheck, 2015), which report variance explained by fixed effects and both fixed and random effects (mixed models only), respectively (Nakagawa and Schielzeth, 2013). Spearman's rank correlation coefficient was used to test for dependence between variables.

2.3.1 Landscape-scale seedling densities

To determine if MPB and canopy fire severity interact to affect lodgepole pine regeneration at the landscape scale, I used general linearized models with negative binomial errors and a log link function (MASS package, Venables and Ripley, 2002). Variables were not standardized in this analysis. A Kruskal-Wallis rank sum test indicated no significant difference in seedling densities between sample years for the re-sampled grids (p-value=0.41), so data from grids sampled in either year were included in this analysis. In total, data from 51 grids were included in this analysis. I fit the following models: 1) a intercept only model that would indicate that MPB, canopy fire severity, and topographic variables are not influencing seedling density in the High Park Fire area, 2 through 5) models with and without both topographic variables and an interaction term between canopy fire severity and MPB—these models would determine whether or not topographic variables influenced lodgepole pine regeneration, and would indicate the how interactions between MPB and fire influence lodgepole pine seedling densities, and 6 and 7) simple models that included either MPB or canopy fire severity alone—these models would indicate that either MPB or fire had a majority of the influence on lodgepole pine seedling densities. Models and hypotheses are listed in Table 2.

The model with the lowest AIC was used to predict a raster surface for seedling density using the "raster" package in R (Hijmans et al., 2015). MPB mortality and high canopy fire severity values in the models listed in Table 2 are the percentage of each grid classified by the 25m raster as either MPB mortality or high canopy fire severity, so I aggregated 5m MPB and burn severity rasters that were also created by Stone (2015) into a 25m raster, assigning each 25m pixel a value for the % occupied by 5m MPB mortality or high canopy fire severity classifications. The resulting prediction surface was masked to the lodgepole pine zone using a species map created by Aniruddha Gosh and Steven Filippelli, which was classified using random forests (Breiman, 2001) with spectral and topographic input variables. I grouped the projected densities into five subjectively selected classes: below 10,000 stems/ha, 10,000-20,000 stems/ha, 20,000-50,000 stems/ha, 50,000-100,000 stems/ha, and over 100,000 stems/ha. I increased the density range with each class to better describe the spatial distribution of densities in the lower classes while minimizing the overall number of classes. I calculated maximum and mean patch size for each density class. Patch size was defined as connected area of the same classification.

2.3.2 Seed bank

I modeled the potential lodgepole pine seed source as a function of MPB mortality and canopy fire severity. I included topographic variables as covariates in this analysis. Spatial correlation of model errors was present in these models, so I created a series of linear mixed effects models with exponential error structures using the "nlme" package (Pinheiro et al., 2009, 2015), with grid as a random effect. All other variables were considered fixed effects. The binary variable for canopy fire severity was used in these models. I fit the following models: 1) a intercept only model that would indicate no effects from the measured variables on potential seed source, 2 and 3) canopy fire severity, MPB, and topographic variables, both with and without interaction terms between MPB and fire—these models would suggest that MPB, fire, and topography all influence potential seed source, with additive effects 4 and 5) canopy fire severity and MPB, with and without an interaction term— these models would describe the effects from combined MPB and fire, and would indicate that topography does not influence potential seed source 6 and 7) models with main effects from MPB or canopy fire severity alone—these models suggest that either MPB or fire influences potential seed source, but not the other. Models and hypotheses are listed in Table 3.

2.3.3 Fine-scale controls on seedling establishment

The importance of potential seed source, seedbed factors, MPB, and canopy fire severity for fine scale lodgepole pine seedling establishment was analyzed using data that were sampled in 2015, because the field metric for MPB mortality was measured during that year. Ultimately, I was unable to fit a model to the seedling abundance data—it was highly skewed with abundant zeros—so seedling abundance was converted to a presence-absence variable. The data were analyzed using a series of binomial mixed effects models with logit link functions (package lme4, Bates et al., 2015). Grid was treated as a random effect, all other variables were considered fixed effects. I elected to use litter cover as the indicator of canopy fire severity in these models to avoid any potential collinearity, as the correlation between the binary canopy fire severity variable and MPB exceeded my 0.50 threshold (Spearman's rho= 0.55) and using the binary variable for canopy fire severity instead of litter cover increased AIC by 4.3 points in the best model (model not shown). The models under consideration included the following: 1) a intercept only model that would indicate that MPB, canopy fire severity, and ground cover are not influencing seedling establishment in the High Park Fire area, 2 through 5) models including litter and either MPB or potential seed source, both with and without topographic variables—these models would indicate whether or not potential seed source was more important for seedling establishment than MPB, and whether or not seedling establishment varied with micro-topography 6 and 7) models with an interaction term between MPB and litter cover, both with and without topographic variables—these models would indicate the how combinations of MPB and fire influence fine-scale seedling establishment, and whether or not micro-topography influenced these dynamics 8) a model with additive effects from potential seed source, litter cover, topographic variables, available seedbed, and vegetation cover—this model would indicate that MPB does not effect the odds of seedling establishment, but that potential seed source, micro-topography, and ground cover variables do 9) a model with potential seed source, litter cover, available seedbed, and vegetation cover—this model would indicate that potential seed source, micro-topography, and ground cover variables affect seedling establishment, but MPB and micro-topography do not. Models and hypotheses are listed in Table 4.

2.3.4 Mulch effects

This analysis was limited to quadrats with high canopy fire severity that were located within grids that contained at least one mulched quadrat, and to the grids sampled in 2014 so that I could assume that mulch application occurred following seed release, but prior to seedling establishment. Treatments were completed during April 2013, less than a year from the fires' containment, and prior to the second year seedling germination pulse that has been observed in lodgepole pine ecosystems (Turner et al., 1999).

I created a series of binomial mixed effects models with logit link functions. Grid was treated as a random effect, all other variables were considered fixed effects. Lodgepole pine seedling abundance data was converted to a presence-absence variable. I used % litter cover as the canopy fire severity indicator in these models, as described above in section 2.3.3. The following models were included in the analysis: 1) an intercept only model, which would indicate that none of the selected variables are important for lodgepole pine seedling establishment 2 and 3) models with mulch cover, quadrat slope, potential seed source, litter, available seedbed, both with and without vegetation cover—these models would indicate the influence of mulch, and whether or not vegetation cover was important for these relationships 4 and 5) models with potential seed source, litter cover, available seedbed, vegetation cover, and mulch cover, both with and without interactions between mulch and quadrat slope—these models would indicate that mulch was benefiting lodgepole pine regeneration through soil and seed retention. Models and hypotheses are listed in Table 5.

3 Results

3.1 How do MPB and canopy fire severity interact to affect lodgepole pine regeneration at the landscape scale?

Grid elevations spanned most of the range occupied by lodgepole pine in the High Park Fire area, extending from 2,440m to almost 3,000m (Table 6). Grid slope and aspect were fairly consistent throughout the area studied—80% of the grids sampled had generally northern aspects (Transformed aspect 1∼2), and mean grid slope was 15°(+/−10°). Lodgepole pine seedling densities were highly variable at the landscape scale, ranging from 240 to over 470,000 stems per hectare, with a mean and standard error of 44,000 and 11,000 stems per hectare, respectively (Table 6). The density of lodgepole pine regeneration was negatively affected by both high canopy fire severity and MPB mortality—seedling densities decreased as % cover of these classifications increased (Figure 8). Conversely, grids which were classified as not having experienced MPB mortality or high canopy fire severity (11% of the grids sampled) had the highest seedling densities (>100,000 for all grids meeting these criteria, Figure 8). The model that included a statistical interaction between these variables received modest support (ΔAICc 2.4 and w_i of 0.23, Table 7), though the coefficient estimate and 95% confidence interval for this interaction indicated that most of this support comes from the main effects of MPB mortality and canopy fire severity (Figure 9). These results suggest that MPB mortality and high canopy fire severity interact in an additive fashion. Models that included topographic variables had very little support in the data, with ΔAICc of >8 or more for all models where these variables were included. The model with the most support (lowest AIC) explained about 49% of the variance in the data (Table 7).

The pattern of predicted seedling densities reflected the underlying heterogeneity in MPB mortality and canopy fire severity (Figure 10). Mean patch size across all classes was 0.318 hectares, roughly the size of my sample grids. Of the seedling density classes, the 10,000-20,000 stems/ha and 20,000-50,000 stems/ha classifications were most common, covering approximately 35% and 39% of the lodgepole pine burned in the fire, respectively (Table 8). Maximum patch size followed these trends, with the 20,000-50,000 class having the largest patch size of 138 hectares. Mean patch size was largest for the 10,000-20,000 stems/ha class at 0.43 hectares, though the most common size for all classes was a single pixel (0.0625 hectares).

3.2 Do MPB and canopy fire severity interact to affect fine scale variation in lodgepole pine's canopy seed bank?

There was strong evidence that combinations of MPB and high canopy fire severity created synergistic negative effects on the potential seed source for lodgepole pine. These compound effects are readily apparent when examining the data graphically—the basal area of cone-bearing lodgepole pine was lower in areas that had greater MPB mortality before the fire—this relationship was intensified when these stands burned at high severity (Figure 11). The candidate models that included this interaction term had summed w_i near one, and ΔAIC for the next best model was >10, indicating almost no support for models that did not include this interaction term (Table 9). Marginal r^2, the variance explained by the fixed effects alone, ranged between 0.30 and 0.38 for the supported models, while conditional r^2 was 0.63 (Table 9).

Model results also indicated that topographic variables may be important factors influencing the basal area of cone-bearing lodgepole pine. The model with the most support indicated that elevation and aspect both had positive relationships with cone-bearing lodgepole pine basal area; suggesting that cone bearing basal area should be higher on northeastern aspects and higher elevations (Figure 12). Of the two, elevation had the strongest effect, with an effect size estimate nearly matching that of high canopy fire severity, and exceeding that for the fire-MPB interaction term (Figure 12).

3.3 To what extent is lodgepole pine establishment controlled by potential seed source, seedbed factors, MPB, and canopy fire severity at the fine scale?

Lodgepole pine seedlings were present in at least one quadrat in 25 of the 27 grids sampled, with a mean capture rate of 10% (Table 10). Cone-bearing lodgepole pine trees were well-distributed throughout the study area (Table 10): I tallied at least one tree with an intact cone near 98% of the more than 1,600 quadrats I sampled. Overall, more than 1,000 (62%) of the quadrats included in this analysis were classified as high canopy fire severity based on needle retention ratios, while MPB values at each quadrat ranged between 0 and 100%, with a mean of 27% (Table 10).

Lodgepole pine was by far the dominant species of seedling in all of the sampled grids. Other than lodgepole pine, aspen was the most frequently encountered regenerating species. Aspen sprouts were present in 3% of the quadrats sampled, while lodgepole pine was present in 15% of the quadrats. Though I recorded the presence of spruce and fir seedlings, fewer than 1% of quadrats contained either of these species.

Fine-scale lodgepole pine seedling establishment was primarily driven by variations in potential seed source; the mean basal area of cone-bearing lodgepole pine near quadrats where seedlings were captured was $39\text{m}^2/\text{ha}$, compared to $27\text{m}^2/\text{ha}$ for quadrats where seedlings were absent. Seedlings were also more common in quadrats that contained more post-fire litter cover and growable area.

Effect size estimates were positive for potential seed source, litter, and growable area (Figure 13). Both potential seed source and litter cover were included in all the models with summed w_i approaching one, indicating strong support for these effects (Table 11). The effects from post-fire vegetation cover and available growable area were not as strong as those relating to potential seed source and litter. While two of the supported models included vegetation cover (Table 11), the effect size for this variable was essentially zero (Figure 13), suggesting that vegetation cover had little effect on lodgepole pine seedling establishment. Area under the curve for the best model was 0.81, indicating good model fit

(Hosmer and Lemeshow, 2013). Model fixed effects explained between 11 and 13% of the variance in the data, while both random and fixed effects combined had an r^2 of 33% for all supported models (Table 11).

Topographic variables, including slope, aspect, and elevation were included in two of the supported models (Table 11). While the effects from these variables trended toward the positive, the sign and strength of these relationships is uncertain as the confidence intervals overlap 0 (Figure 13). Furthermore, summed w_i for the models that included topographic variables was 0.26, while summed w_i for models including cone-bearing basal area and litter cover approached 1, indicating that topographic variability is not as important for the establishment of lodgepole pine as the availability of seed.

Models that included MPB mortality received essentially no support. All models including MPB had w_i of less than 0.001, with marginal r^2 values about half that of the potential seed source models (Table 11).

3.4 Do variations in post-fire mulching treatments influence the post-fire establishment of lodgepole pine at the fine scale?

Overall, the mulch cover was low throughout the sampled area: mean mulch cover was 15%, with the mean cover for straw mulch and wood chips 15% and 13%, respectively (Table 12). Straw mulch was present in 14 grids, and wood chip mulch was applied within 3 grids, all of the latter were located on ridge tops where mulch redistribution was a concern (BAER, 2012). Sites with different treatment types varied in their potential seed source; areas treated with wood chips had significantly lower basal areas of cone bearing trees than areas treated with straw mulch (Kruskal Wallis p-value = <0.001, Figure 14). Ninety percent of the mulched quadrats were located in areas where high canopy fire severity had occurred, consistent with the BAER team's guideline for mulch application (BAER, 2012). Total mulch cover was unrelated to quadrat slope (Spearman's rho=0.05, p-value=0.18), though when separated by mulch type, straw mulch showed a weak positive correlation with quadrat slope (Spearman's rho=0.11, p-value=0.01), while wood chips were unrelated (Spearman's rho=-0.09 , p-value=0.29).

Straw mulch had a positive relationship with lodgepole pine seedling establishment, with an effect size rivaled only by available potential seed source (Figure 15). Though an interaction term between mulch cover and quadrat slope was included in a model with moderate support (ΔAIC 3.2), this term had an effect size near zero, and including it in the model increased ΔAIC by 1.4 from the next most parsimonious model (Table 13). These results suggest that the beneficial effect of mulch cover on seedling establishment is not influenced by steeper quadrat slopes. As expected, potential seed source was positively related to the establishment of lodgepole pine. Other variables, including vegetation cover, wood chip treatments, quadrat slope, litter cover, and growable area did not seem to have meaningful effects on lodgepole pine seedling establishment under the sampled conditions (Figure 15). All models had an AUC of 0.78, and marginal and conditional r^2 values of 01.0 and 0.28-0.29, respectively (Table 13). All models under consideration had ΔAIC values <7.

4 Discussion

This research demonstrates that MPB mortality can reduce post-fire lodgepole pine seedling densities, independent of the effects of canopy fire severity. Indeed, MPB mortality may be a driver of future stand structure heterogeneity, as seedling densities were lower where fire followed MPB mortality than where trees were alive when the fire occurred. The fine-scale analysis revealed that the likely mechanism driving the relationship between MPB, fire, and seedling establishment is via the effects on the locally available canopy seed bank. In areas with higher MPB mortality, the potential seed source was reduced, possibly due to the pre-fire release of cones and/or seeds to the forest floor (Teste et al., 2011). If the released seeds established as advanced regeneration, these were apparently killed in the fire, as seedlings that predated the fire were essentially absent from the study area. Additionally, the remaining canopy seed bank may have been more susceptible to destruction by subsequent fire due to reduced fuel moistures (Jolly et al., 2012; Page et al., 2012), so when fire burned through the crowns of trees that were already dead, the remaining cones were more likely to be destroyed.

While I did not explicitly investigate the effects of elapsed time between MPB mortality and fire on lodgepole pine regeneration, time since attack almost certainly accounted for some variation in post-fire seedling density; the latter stages of attack were likely associated with lower seedling densities overall (Harvey et al., 2014a). Most of the trees killed by MPB in the High Park Fire were attacked in 2010, two years before the fire, though a portion of the affected trees had been dead for at least an additional year by the time the fire occurred (Stone, 2015). As lag times between MPB induced mortality and fire increase, more seeds are lost from the canopy seed bank (Teste et al., 2011), which leads to reduced post-fire regeneration (Harvey et al., 2014a). In a subset of my grids where I had good information on the timing of beetle-kill, the grids with the oldest MPB mortality had the lowest seedling densities (data not shown).

Canopy fire severity was also an important driver of lodgepole pine regeneration in the High Park Fire. Seedling densities were lower in areas where the crowns were consumed than in areas where the crowns were either scorched or unburned. Higher fire temperatures and more complete fuel consumption can lead to greater seed mortality (Knapp and Anderson, 1980; Johnson and Gutsell, 1993; Despain et al., 1996), whether or not the cones are destroyed (Anderson and Romme, 1991). Indeed, high canopy fire severity was strongly associated with reduced potential seed source throughout the study area. Conversely, the greatest seedling densities were found in areas with low canopy fire severity, which likely produced sufficient heat to release, but not destroy, the canopy seed-bank while also exposing the mineral soil seed bed (Johnson and Gutsell, 1993; Turner et al., 1999; Edwards et al., 2015).

An alternate explanation for my findings might be that lodgepole pine densities reflect variability in cone serotiny rather than variation in cone abundance *per se* (Anderson and Romme, 1991; Tinker et al., 1994; Turner et al., 1997; Schoennagel et al., 2003; Harvey et al., 2014a,b). While I was unable to characterize serotiny within the burned area due to the destructive nature of the fire, I sampled serotiny throughout lodgepole forests near the study area but outside the burn perimeter, and I found serotiny percentages to be uniformly high (mean=87%) with low variability (SE=13%, see Appendix for a full discussion). While I cannot rule out variation in serotiny as a possibility, I believe it is unlikely that serotiny in the burned area would vary more than it does on the surrounding landscape, nor did I observe any stand structure changes or stand age boundaries that might suggest serotiny values vary inside the burn perimeter relative to surrounding areas.

The influence of topographic variables on lodgepole pine regeneration was largely indirect. Generally, topography seems to affect regeneration by regulating the potential canopy seed bank through tree size and density. The positive relationship between cone-bearing basal area, aspect, and elevation likely stems from the relationship these variables have on basal area in general, not necessarily cone abundance (Turner et al., 2007). Additionally, above average precipitation levels in the study area during the two years following the fire (Schmeer, 2014) may have eliminated the moisture limitations that might have led to topographic controls on regeneration in a drier year.

With the exception of available growable area and mulch cover, most ground cover and microsite variables did not have a major influence lodgepole pine regeneration. Competition from understory vegetation does not appear to have a major effect on the abundance of post fire lodgepole pine seedlings, consistent with studies from other Rocky Mountain regions (Anderson and Romme, 1991). Perhaps the most surprising result was the lack of influence from micro-topography. Seed redistribution via erosion and deposition has been observed on loess soils under extreme runoff events (Han et al., 2011). Based on my personal observations, I expected that topographic variables would reflect the erosional micro-environment, and that they therefore would explain some of the variability in seedling establishment. However, it is possible that my observations of seedling clustering in depositional environments were highly localized, and therefore not representative of the broader landscape, or the erosional/depositional processes were simply operating at a different scale than my topographic measurements.

The beneficial effects of straw mulch that I observed may be due to increased soil moisture retention, lower soil surface temperatures (Amaranthus et al., 1993; Dodson and Peterson, 2010), or from limiting the establishment of potential competitors (Amaranthus et al., 1993) in treated areas. The lack of similar effect in areas treated with wood chips may either be due to true differences in effects between the treatment types, such as different moisture retention capabilities or variation in the ability to physically obstruct emerging seedlings. Alternatively, the difference in effect may be an artifact of coincidental differences in the potential seed source between treatment areas. All of the grids treated with wood chips were classified as MPB mortality, and the potential seed source was much lower in these grids. These factors, combined with the fact that we limited this analysis to quadrats with high canopy fire severity, suggests that lodgepole pine regeneration these areas was going to be limited regardless of the mulching treatment applied.

Moving forward, areas with the lowest seedling densities within the High Park Fire, where MPB mortality and high canopy fire severity were combined, may have greater resistance to future disturbances such as drought and beetle attack. Thinned conifer stands are less susceptible to drought induced mortality, at least early in the life of the stand (D'Amato et al., 2013). Low stand densities could bolster lodgepole pine's already robust drought tolerance mechanisms, including enhanced stomatal control to prevent water loss (Knapp and Smith, 1981). Though susceptibility to MPB attack is determined by many variables (Shore et al., 2000; Björklund and Lindgren, 2009), trees in areas with lower stand densities may be less susceptible to future beetle outbreaks (Shore et al., 2000). The increased resilience that lower stand densities infer may help lodgepole pine persist within its current range, which is projected to shrink under climate change (Coops and Waring, 2011; Renwick et al., 2016).

Overall, seedling densities are highly variable as a consequence of heterogeneity in both pre-fire MPB mortality and fire effects. This heterogeneity may have a long lasting influence on forest structure and function (Turner, 1989), though lodgepole pine seems to be regenerating throughout the areas it occupied before the fire, regardless of disturbance effects. For example, only one of the grids I sampled did not meet the minimum stocking guideline of 370 stems/ha for post-harvest lodgepole pine regeneration set by the Arapaho Roosevelt National Forest (US Forest Service, 1997), and most were well above. Additionally, all but six of the grids I sampled had seedling densities exceeding the typical 20 year stocking levels for lodgepole pine given by Lotan and Critchfield (1990), though stem densities are likely to change over time due to processes like self-thinning and infilling, and will likely approach more typical stand densities as time advances (Kashian et al., 2005).

5 Conclusions

Despite the reduction in seedling densities due to the effects of MPB and high canopy fire severity, areas that were dominated by lodgepole pine before the fire will likely remain so into the future. Even though seedling densities varied dramatically, lodgepole pine was by far the most common recovering conifer, especially in the high canopy fire severity areas. Fire can reset the successional trajectory for lodgepole pine forests, counteracting any compositional shifts towards spruce and fir that may be underway following MPB infestations (Diskin et al., 2011; Edwards et al., 2015; Perovich and Sibold, 2016). This "reset" may give these stands increased resilience to future drought, fire, and bark beetle outbreaks.

Table 1: Sampling stratifications, with sample size by year. Stratifications were based on 25m raster data created by Stone (2015). CFS- canopy fire severity, MPB- mountain pine beetle mortality.

Stratification	2014	2015
High CFS, MPB Present	6	11
High CFS, No MPB	6	4
Low CFS, MPB Present	6	8
Low CFS, No MPB	7	4

Table 2: Model suite with constituent variables and hypotheses for the landscape scale seedling density analysis. Variables: CSEV- High canopy fire severity, MPB- mountain pine beetle mortality, SLP- mean grid slope, ELV- mean grid elevation, ASP- aspect from grid center, CTI- mean compound terrain index. ":" indicates an interaction term, all others are main effects.

Predictor variables	Hypothesis
Intercept only	No important predictors selected for analysis
CSEV,MPB,SLP,ELV,ASP,CTI	MPB, fire, and topographic variables drive seedling density
CSEV:MPB,SLP,ELV,ASP,CTI	Synergistic relationship between MPB & fire, topography is important
CSEV:MPB	Synergistic relationship between MPB & fire
CSEV,MPB	MPB and fire alone
MPB	MPB alone
CSEV	Fire alone

Table 3: Model suite with constituent variables and hypotheses for the Canopy seed bank analysis. Variables: CSEV- High canopy fire severity, MPB- Mountain pine beetle, ELV- elevation, ASP- aspect, QS- quadrat slope. ":" indicates an interaction term, all others are main effects.

Predictor variables	Hypothesis
Random effects only	No important predictors selected
CSEV,MPB,ASP,QS,ELV	MPB, fire, and topographic variables regulate post fire cone availability
CSEV:MPB,ASP,QS,ELV	Synergistic MPB & fire, and topographic variables
CSEV,MPB	MPB and fire
CSEV:MPB	Synergistic relationship between MPB & fire
CSEV	Fire alone
MPB	MPB alone

Table 4: Model suite with constituent variables and hypotheses for the fine scale seedling establishment analysis. Variables: BA- Basal area of cone-bearing lodgepole pine, LIT- litter cover, VEG- Vegetation cover, GA- Growable area, MPB- mountain pine beetle mortality, QS- quadrat slope, ASP- aspect, ELV- elevation. ":" indicates an interaction term, all others are main effects. In this model suite, litter is analogous to low canopy fire severity.

Predictor variables	Hypothesis
Random effects only	No important predictors selected for analysis
BA,LIT,ASP,QS,ELV	Seed source, fire, and topographic variables drive seedling establishment
BA,LIT	Seed source and fire alone
LIT,MPB,ASP,QS,ELV	MPB, fire, and topographic variables
LIT,MPB	MPB and fire alone
LIT:MPB	Synergistic relationship between MPB & fire
LIT:MPB,ASP,QS,ELV	Synergistic relationship between MPB & fire, topography is important
BA,LIT,VEG,GA,ASP,QS,ELV	Seed source, fire, vegetation, available seedbed, and topographic variables
BA,LIT,VEG,GA	Seed source and ground cover variables alone

Table 5: Model suite with constituent variables and hypotheses for the fine mulch analysis. Variables: BA- Basal area of cone-bearing lodgepole pine, LIT- litter cover, QS- quadrat slope, VEG- Vegetation cover, GA- Growable area, STRW- Straw mulch cover, WD- Wood chip cover. ":" indicates an interaction term, all others are main effects. In this model suite, litter is analogous to low canopy fire severity.

Predictor variables	Hypothesis
Random effects only	No important predictors selected
BA,LIT,QS,GA,STRW,WD	Seed source, fire, micro-topography, and mulch drive seedling establishment
BA,LIT,QS,VEG,GA,STRW,WD	Seed source, fire, all cover variables, and mulch
BA,LIT,VEG,GA,QS:STRW,WD	Straw mulch reduces effect of slope
BA,LIT,VEG,GA,QS:WD,STRW	Wood chips reduces effect of slope

Table 6: Summary statistics for landscape scale lodgepole pine seedling density analysis. Seedling densities are lodgepole pine only. All other variables derived from 25m data, ‡ indicates % classification values, data from Stone (2015). †Aspect values were transformed to range from 0-2. Values approaching 2 are closer to 45°(Beers et al., 1966). CTI- compound terrain index. Elevation, CTI, and slope were averaged for each grid. Aspect was taken from grid center.

Variable	Range	Mean(SE)
Seedling density (lodgepole pine stems/ha)	240-470,000	44,400 (11,000)
MPB mortality (%)‡	0-100	57 (7)
High canopy fire severity (%)‡	0-100	56 (7)
Elevation (m)	2400-3000	2700 (20)
CTI	6-11	8 (0.2)
Slope (°)	4-25	15 (0.7)
Aspect (center)†	0-2	1.5 (0.1)

Table 7: Competing models for the landscape seedling density analysis, ranked by ΔAICc. AICc- Akaike Information Criterion, corrected for small sample size, ΔAICc- Differenced AICc ($AICc_i$-$AICc_{min}$), K- model parameters, w_i- Akaike weights, Mar r^2- Marginal r^2 (variance explained by fixed effects). Variables: CSEV- high canopy fire severity, MPB- mountain pine beetle mortality, SLP- mean grid slope, ELV- mean grid elevation, ASP- aspect, CTI- compound terrain index. The coefficient estimates from the supported models (ΔAICc<7, indicated in **BOLD**) are given in Figure 9. ":" indicates an interaction term, all others are main effects.

Candidate Variables	AICc	ΔAICc	K	w_i	Mar r^2
MPB,CSEV	1146.1	0.0	4	0.76	0.49
MPB:CSEV	1148.5	2.4	5	0.23	0.49
MPB,CSEV,SLP,ELV,ASP,CTI	1154.8	8.7	8	0.01	0.50
MPB:CSEV,SLP,ELV,ASP,CTI	1157.7	11.6	9	0.00	0.50
CSEV	1162.1	16.0	3	0.00	0.30
MPB	1166.3	20.2	3	0.00	0.25
Intercept only	1182.3	36.2	2	0.00	-

Table 8: Spatial extent of model prediction classes. Classes are listed in stems per hectare. Total mean= mean patch size for all classes. Pixels= number of 25m pixels/classification. Hectares= total number of hectares/class. Max= maximum patch size by class, in hectares. Mean= mean patch size by class, in hectares.

Total mean (ha)	0.32		
Class (stems/ha)	Pixels (% total)	Hectares	Max (Mean)
<10,000	8236 (10)	510	23 (0.2)
10,000-20,000	27852 (35)	1740	86 (0.4)
20,000-50,000	31430 (39)	1960	138 (0.4)
50,000-100,000	8999 (11)	560	7 (0.2)
>100,000	3966 (5)	250	17 (0.3)

Table 9: Competing models for the seed bank analysis, ranked by ΔAIC. AIC- Akaike Information Criterion, ΔAIC- Differenced AIC (AIC_i-AIC_{min}), K- model parameters, w_i- Akaike weights, Mar r^2- Marginal r^2 (variance explained by fixed effects), Cond r^2- Conditional r^2 (variance explained by fixed and random effects). Due to spatial autocorrelation of residuals, models were run with exponential correlation structures, which was selected using AIC (Pinheiro et al., 2009, 2015). The binary variable for canopy fire severity was centered to reduce variance inflation, all continuous variables were standardized. The response variable was square root transformed to meet model assumptions. Variables: MPB- mountain pine beetle mortality, CSEV- High canopy fire severity, ASP- aspect, ELV- elevation, QS- quadrat slope. The effect size estimates from models with ΔAIC<7 (indicated in **BOLD**) are reported in Figure 12. ":" indicates an interaction term, all others are main effects.

Candidate Variables	AIC	ΔAIC	K	w_i	Mar r^2	Cond r^2
CSEV:MPB,ASP,ELV,QS	4277.7	0.0	11	0.79	0.38	0.63
CSEV:MPB	4280.4	2.7	8	0.21	0.30	0.64
CSEV,MPB,ASP,ELV,QS	4290.1	12.4	10	0.00	0.38	0.63
CSEV,MPB	4292.8	15.1	7	0.00	0.31	0.64
MPB	4296.7	19.0	6	0.00	0.26	0.62
CSEV	4800.1	522.4	6	0.00	0.09	0.56
Random effects only	4840.0	562.3	5	0.00	0	0.53

Table 10: Summary statistics, quadrat data. Litter cover and growable area are percentage values of a 25cm^2 quadrat. High canopy fire severity was assumed if <50% of the basal area of standing trees retained needles. *indicates variables derived from 1m DEM. †Aspect values were transformed to range from 0-2; Values approaching 2 are closer to 45°(Beers et al., 1966). ‡ Basal area of cone-bearing lodgepole pine was both a response and predictor variable.

Variable	Range	Mean (SE)
Seedling captures per grid (lodgepole pine)	0-40	10 (2)
Cone bearing basal area (m^2/ha)‡	0-90	29 (0.5)
MPB mortality (% lodgepole pine basal area dead pre-fire)	0-100	30 (1)
Growable area (%)	10-100	80 (1)
Litter cover (%)	0-100	20 (1)
Quadrat slope (°)	0-60	15 (0.2)
Aspect*†	0-2	1 (0.01)
Elevation (m)*	2400-3000	2600 (3)

Fire Severity Classification	Number of quadrats	% of total
High canopy fire severity	1035	62
Surface fire	623	38

Table 11: Competing models for the fine scale seedling establishment analysis, ranked by ΔAIC. AIC- Akaike Information Criterion, ΔAIC- Differenced AIC (AIC_i-AIC_{min}), K- model parameters, w_i- Akaike weights, AUC- Area under the receiver operating curve, Mar r^2- Marginal r^2 (variance explained by fixed effects), Cond r^2- Conditional r^2 (variance explained by fixed and random effects). Variables: BA- Basal area of cone-bearing lodgepole pine, LIT- litter cover, VEG- Vegetation cover, GA- Growable area, MPB- mountain pine beetle mortality, QS- quadrat slope, ASP- aspect, ELV- elevation. This analysis used binomial mixed effects model with logit link functions, all continuous variables were standardized. The effect size estimates from the models with ΔAIC<7 (indicated in **BOLD**) are reported in Figure 13. ":" indicates an interaction term, all others are main effects. Litter is analogous to low canopy fire severity.

Candidate Variables	AIC	ΔAIC	K	w_i	AUC	Mar r^2	Cond r^2
BA,LIT,VEG,GA	1243.9	0.0	6	0.52	0.81	0.11	0.33
BA,LIT	1245.6	1.7	4	0.22	0.81	0.10	0.33
BA,LIT,VEG,GA,ASP,QS,ELV	1245.6	1.7	9	0.22	0.81	0.13	0.33
BA,LIT,ASP, QS,ELV	1249.1	5.3	7	0.04	0.81	0.11	0.32
LIT,MPB	1258.0	14.2	4	0.00	0.81	0.05	0.34
LIT:MPB	1259.6	15.7	5	0.00	0.80	0.05	0.34
LIT,MPB,ASP,QS,ELV	1260.5	16.6	7	0.00	0.81	0.06	0.34
LIT:MPB,ASP,QS,ELV	1261.9	18.1	8	0.00	0.81	0.07	0.33
Random effects only	1277.0	33.2	2	0.00	0.79	0	0.35

Table 12: Summary statistics, mulch data. The data set was limited to quadrats with high canopy fire severity located within mulched grids. Cover variables and growable area are the % cover values for a 25cm^2 quadrat. ‡ Basal area of cone-bearing lodgepole pine.

Variable	Range	Mean (SE)
Seedling captures per grid (lodgepole pine)	0-20	8 (2)
Cone bearing basal area (m^2/ha)‡	0-80	30 (1)
Growable area (%)	10-100	70 (1)
Litter cover (%)	0-100	6 (1)
Total mulch cover (%)	0-100	15 (1)
Straw mulch cover (%)	0-100	15 (1)
Wood chips cover (%)	0-100	13 (2)
Vegetation cover (%)	0-100	7 (1)
Quadrat slope (°)	0-52	16 (30)

Table 13: Competing models for the mulch cover analysis, ranked by ΔAIC. AIC- Akaike Information Criterion, ΔAIC- Differenced AIC (AIC_i-AIC_{min}), K- model parameters, w_i- Akaike weights, Mar r^2- Marginal r^2 (variance explained by fixed effects), Cond r^2- Conditional r^2 (variance explained by fixed and random effects), AUC- Area under the receiver operating curve. Variables: BA- Basal area of cone-bearing lodgepole pine, LIT- litter cover, QS- quadrat slope, VEG- Vegetation cover, GA- Growable area, STRW- Straw mulch cover, WD- Wood chip cover. This analysis used binomial mixed effects model with logit link functions, all continuous variables were standardized. ΔAIC for all models was <7, they are displayed in Figure 15. ":" indicates an interaction term, all others are main effects. Litter is analogous to low canopy fire severity.

Candidate Variables	AIC	ΔAIC	K	w_i	AUC	Mar r^2	Cond r^2
BA,LIT,GA,QS,STRW,WD	538.8	0.0	8	0.56	0.78	0.10	0.28
BA,LIT,GA,QS,STRW,WD,VEG	540.6	1.8	9	0.22	0.78	0.10	0.28
BA,LIT,GA,WD,VEG,QS:STRW	542.0	3.2	10	0.11	0.78	0.10	0.29
BA,LIT,GA,STRW,VEG,QS:WD	542.4	3.6	10	0.09	0.78	0.10	0.29
Random effects only	545.5	6.8	2	0.02	-	-	-

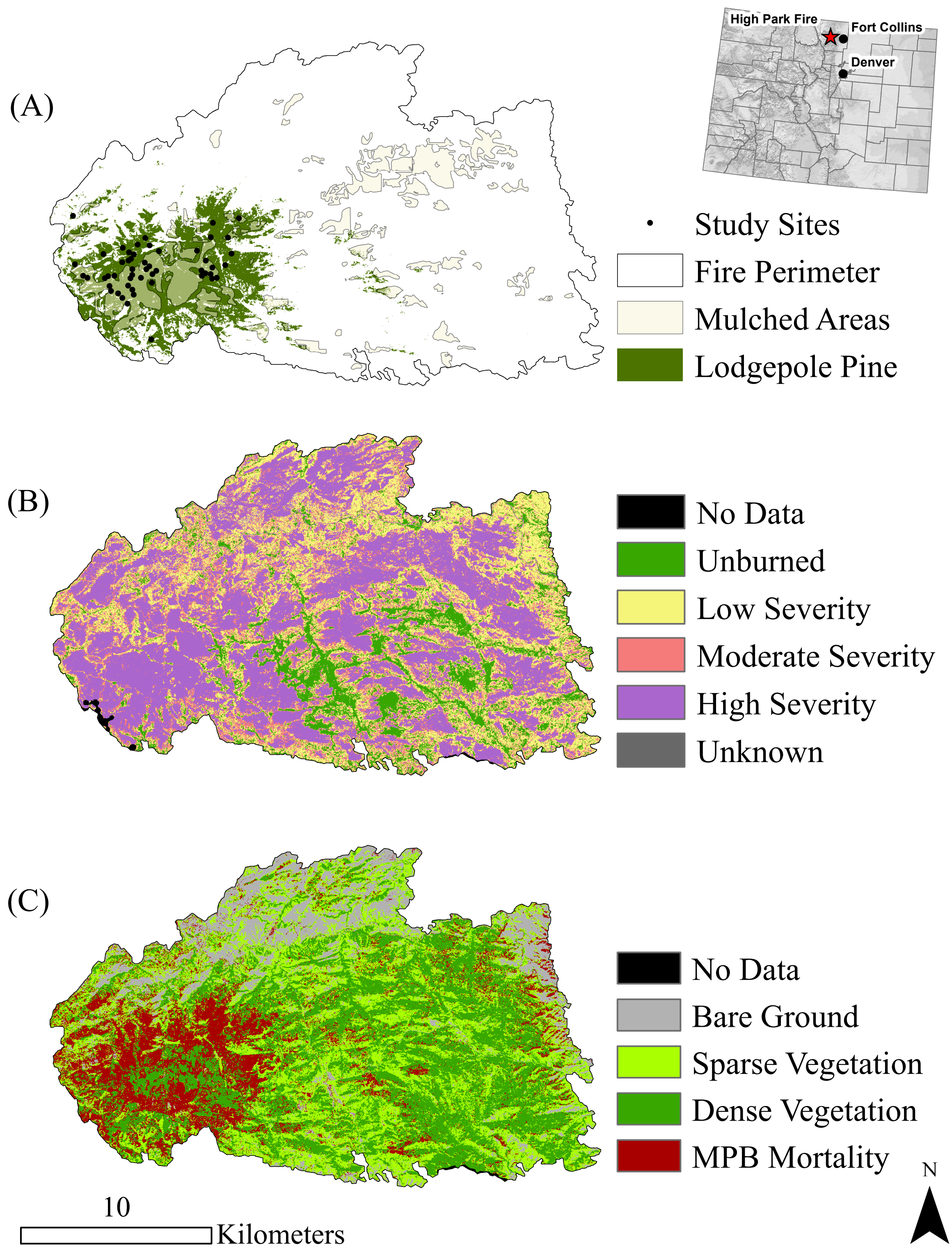

Figure 1: Maps of A) lodgepole pine and post-fire mulching treatments, B) burn severity, and C) MPB mortality. MPB, burn , and fire perimeter data from Stone (2015), lodgepole pine extent data in (A) created by Aniruddha Ghosh and Steven Filipelli. Mulch polygons are combined data from US Forest Service, Natural Resources Conservation Service, and Larimer County.

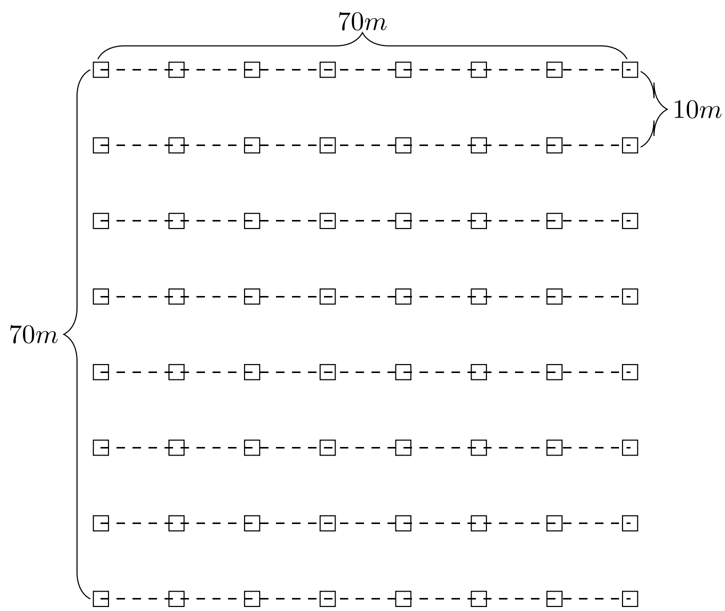

Figure 2: Grid sampling layout. Dashed lines indicate 70m seedling density transects, squares represent 25×25cm quadrat locations.

(A) High canopy fire severity.

(B) Low canopy fire severity.

Figure 3: Photos for the two canopy fire severity classifications. (A) High canopy fire severity, $<50\%$ of all trees tallied with a factor 10 basal area prism retained needles at the time of sampling. (B) Low canopy fire severity, $\geq 50\%$ of all trees tallied with a factor 10 basal area prism retained needles at the time of sampling. In (B), some canopies are scorched and have suffered partial needle loss, which has contributed to the abundance of post-fire needle cast (litter).

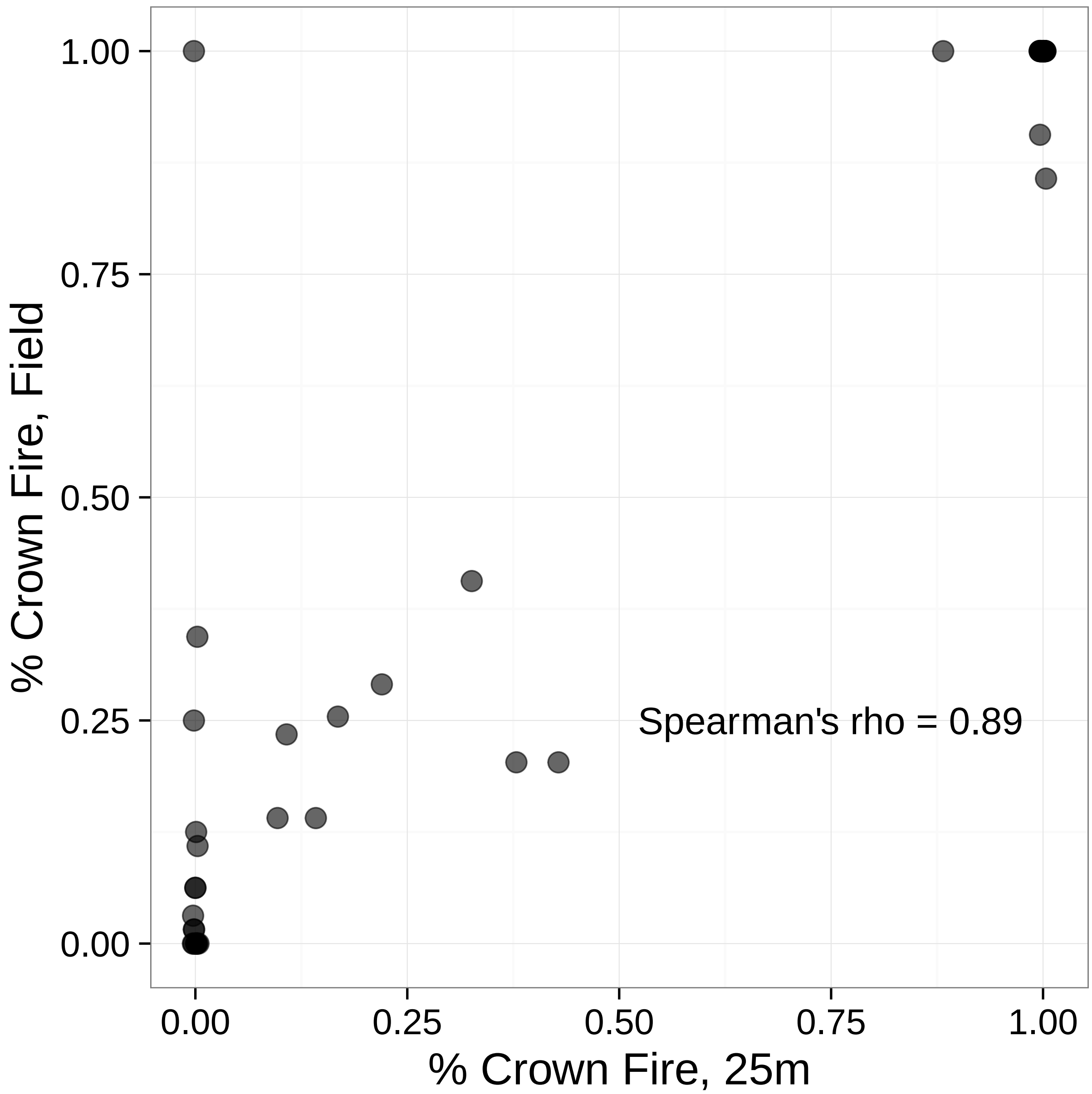

Figure 4: Relationship between remote sensing and field canopy fire severity classifications. Field canopy fire severity is the % of each grid's quadrat locations that were classified as high canopy fire severity, high canopy fire severity was assumed if <50% of the basal area of standing trees retained needles. Remote sensing canopy fire severity is the % of each grid classified as high high canopy fire severity using the 25m data (Stone, 2015). One grid was misclassified as low severity in the 25m data, this was removed from the landscape scale analysis.

(A) Extensive charring.   (B) Basal charring.

Figure 5: Deeply charred lodgepole pine (heavily charred), mixed in with trees that lack deep charring. The charred trees were most likely dead at the time of the fire. In (A), charring is extensive; any beetle damage has been removed. In (B), deep charring is concentrated around the base of the stem.

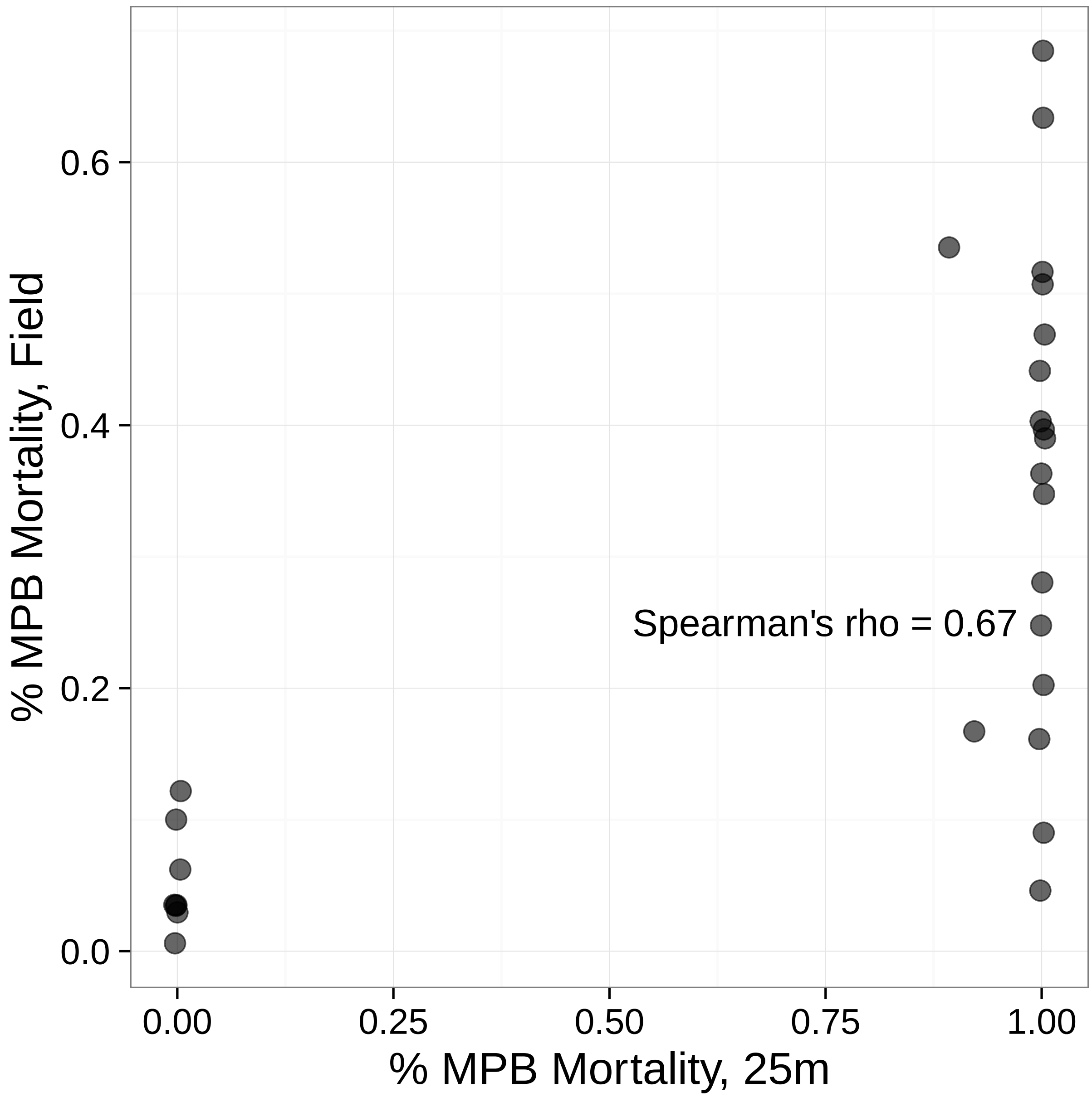

Figure 6: Relationship between remote sensing and field MPB mortality classifications. Field MPB mortality is the mean value (by grid) for the % of total lodgepole basal area that was dead at the time of the fire. Trees were assumed to have been dead at the time of the fire if they had 50% or more deep charring around the bole. The remote sensing MPB classification is the % of each grid classified as MPB mortality using the 25m data (Stone, 2015).

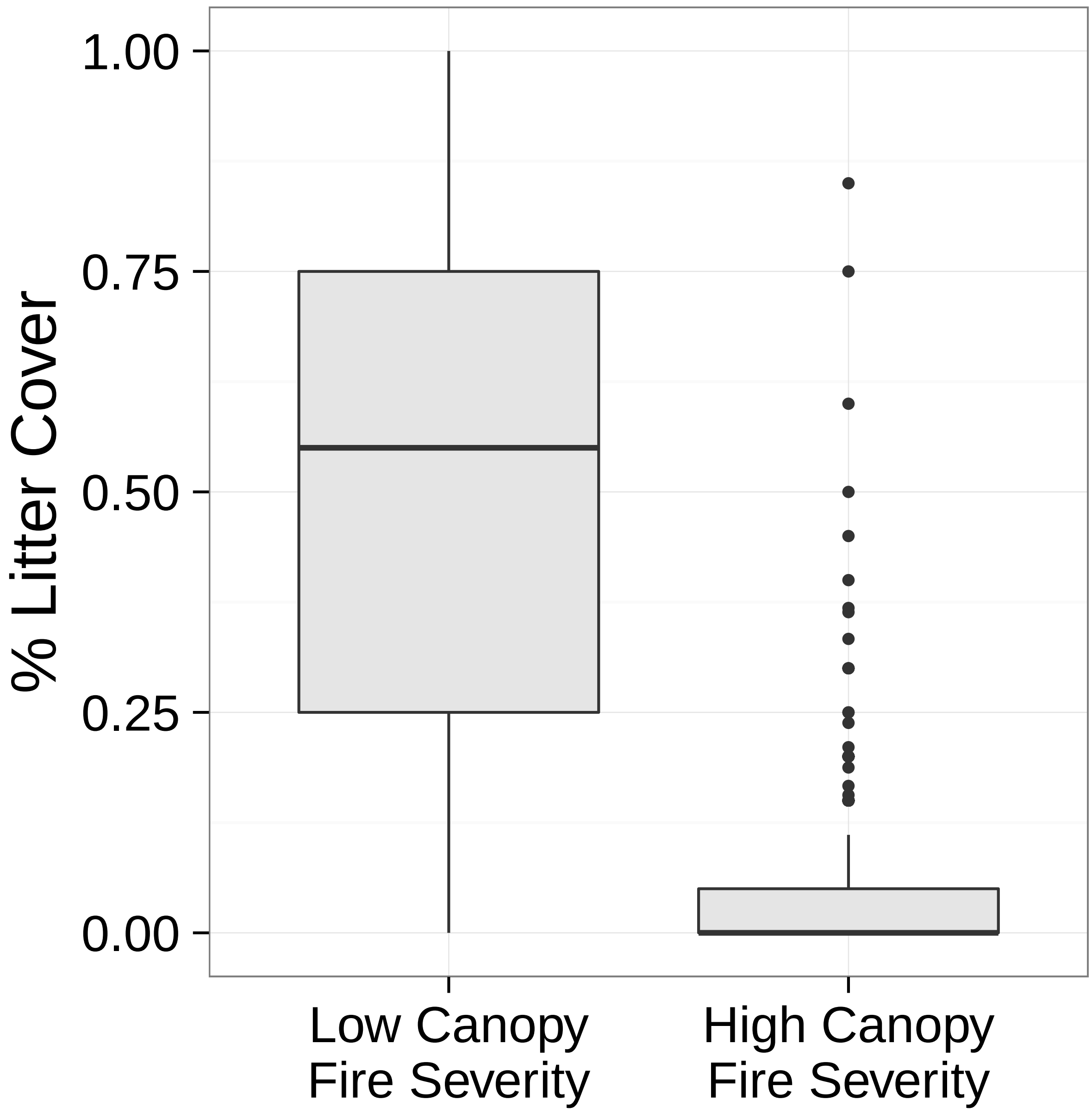

Figure 7: Litter cover as a function of canopy fire severity. Litter is the % cover of 25×25cm quadrats. Canopy fire severity was estimated based on the needle retention ratio of trees surrounding the quadrat using a 50% threshold. This inverse relationship is likely due to the absence of needles in areas of high canopy fire severity, as post fire needle cast made up a majority of the litter throughout the study area.

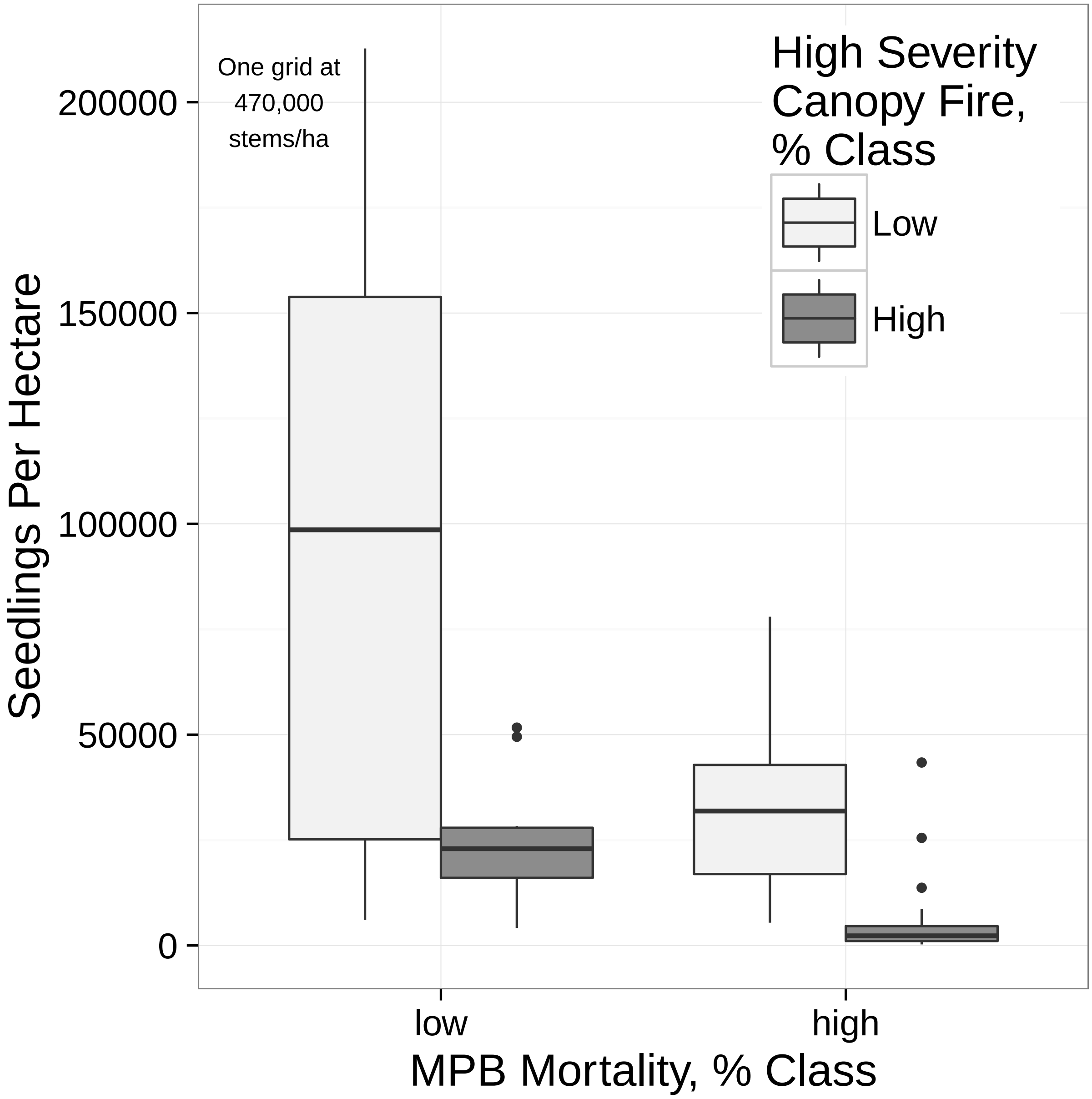

Figure 8: Seedlings per hectare as a function of MPB and burn severity class. Continuous burn severity and MPB classifications (% cover for each grid) were converted to categorical variables based on a 50% threshold, this was done for plotting only. Outlier grid with 470,000 stems/ha was removed for plotting. Middle bar indicates the median value, upper and lower boxes are 75th and 25th percentiles, respectively. Whiskers extend to data points up to 1.5 times the interquartile range, data beyond this threshold are plotted as points (Wickham, 2009).

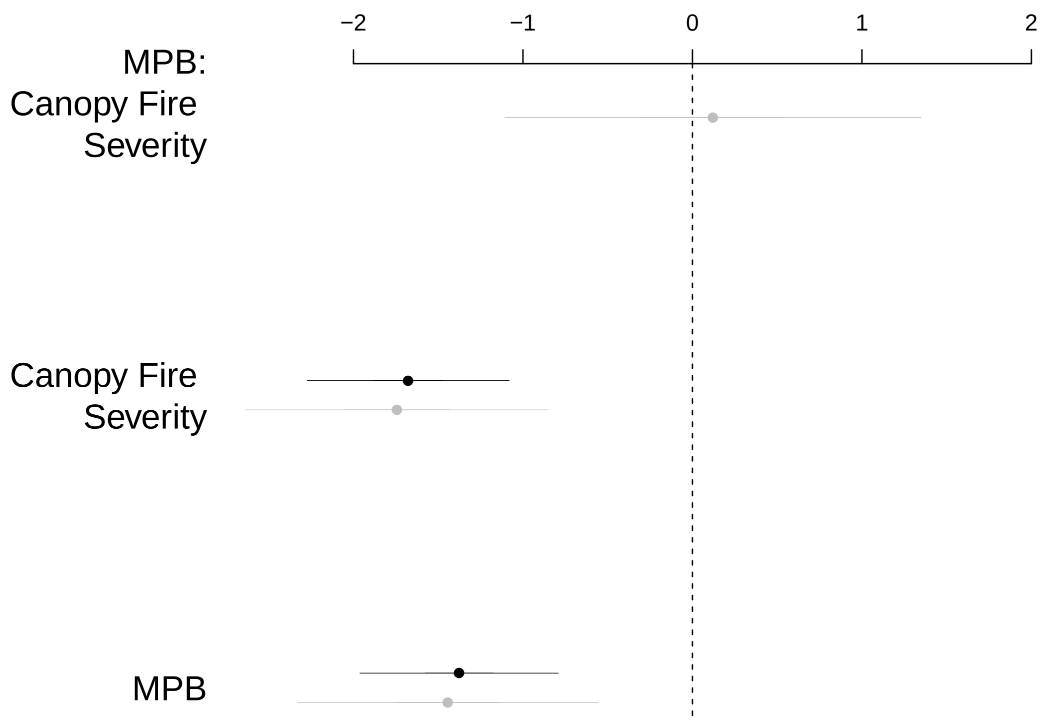

Figure 9: Regression estimates for models with ΔAIC<7 for the landscape scale seedling density analysis. Seedling density (stems/ha) was the response. The model with the lowest AIC is displayed in black. All other models are grey. Points are estimates with 95% confidence intervals. ":" indicates an interaction term, all others are main effects.

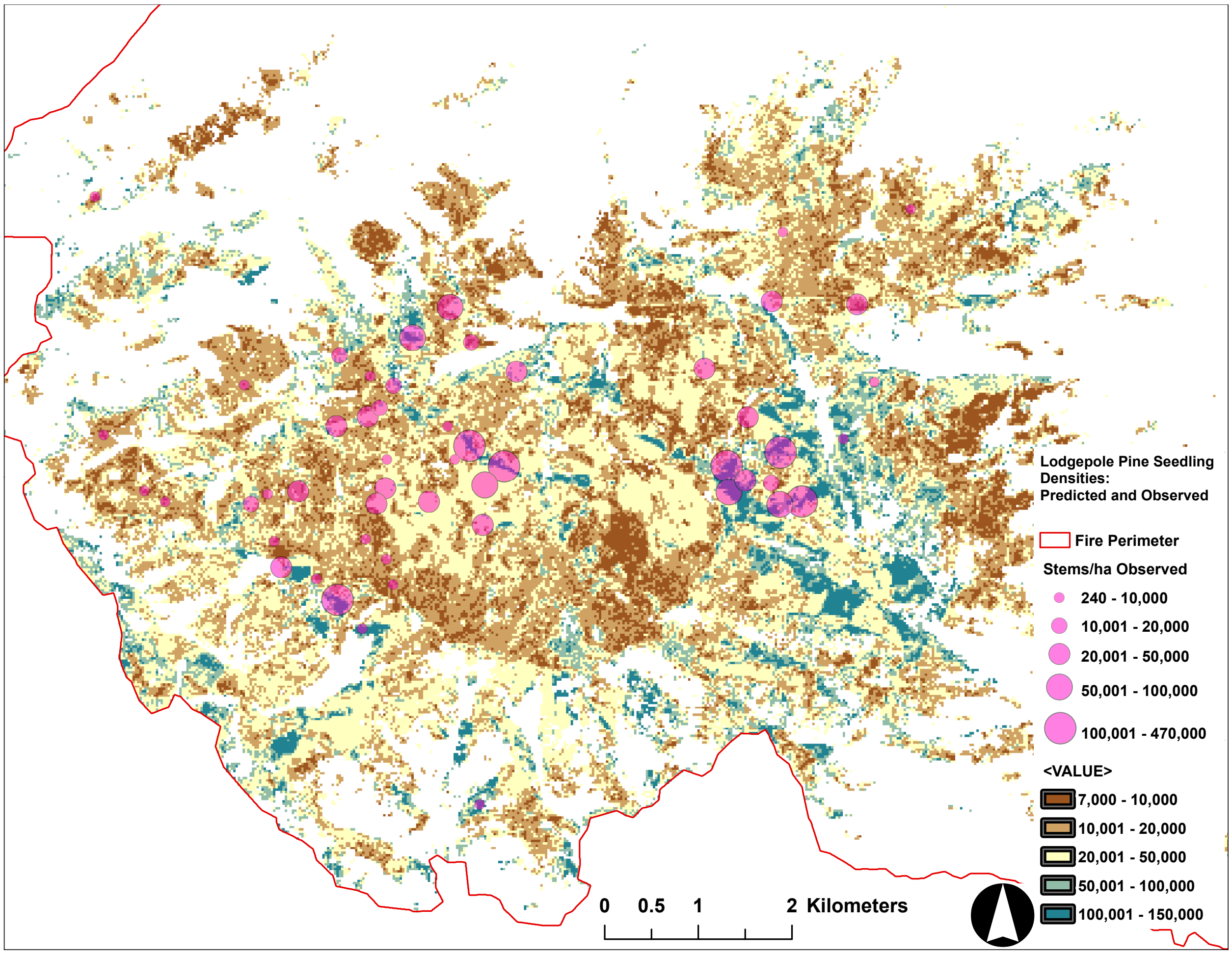

Figure 10: Lodgepole pine seedling densities, predicted and observed. Seedling densities were predicted using the model with the most support from the landscape scale MPB and burn severity analysis (Table 7). Both predicted and observed densities were subjectively binned for display and analysis in order to highlight areas with lower predicted seedling densities. The prediction raster was masked to the lodgepole pine zone with a species classification map (Aniruddha Ghosh and Steven Filippelli, personal communication).

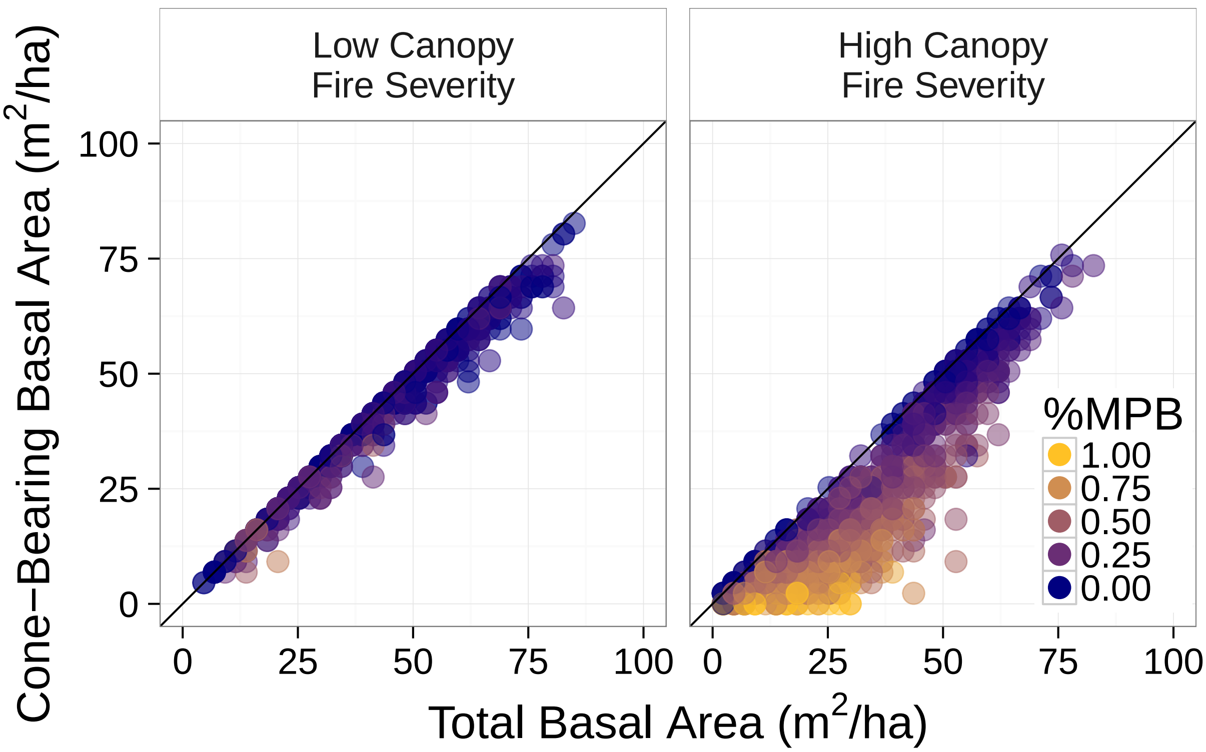

Figure 11: The proportion of total lodgepole pine basal area (m^2/ha) bearing cones as a function of MPB mortality (% of lodgepole pine basal area that was deeply charred) and high or low canopy fire severity. MPB mortality intensity (proportion of total basal area) is indicated by color gradient; yellow points indicate greater MPB mortality. Plots are split by high or low canopy fire severity. High canopy fire severity was assumed if <50% of the basal area of standing trees retained needles. Plot diagonals are 1:1 lines, departures indicate a change in the proportion of the basal area of lodgepole pine with cones.

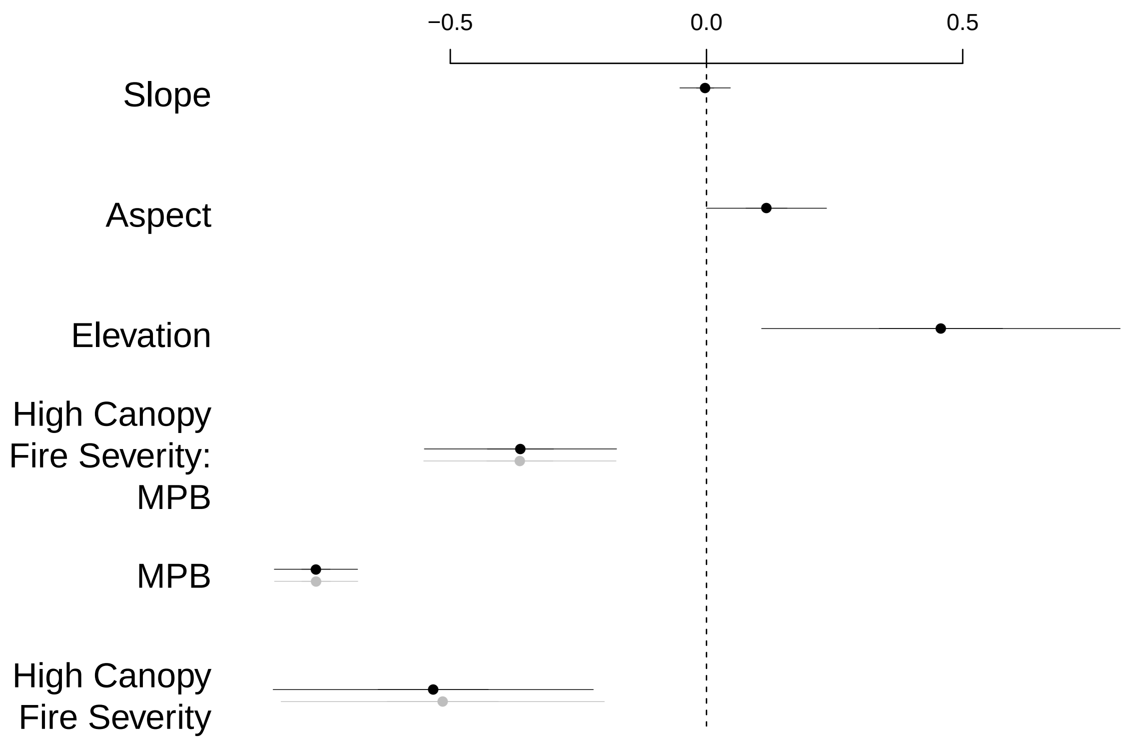

Figure 12: Effect size estimates for models with ΔAIC<7 from the canopy seed bank analysis. The model with the most support (lowest AIC) is desplayed in black. All other models are grey. Points are estimates with 95% confidence intervals. The basal area of cone bearing lodgepole pine (m^2/ha) is the response variable. Predictor variables were standardized prior to analysis. ":" indicates an interaction term, all others are main effects.

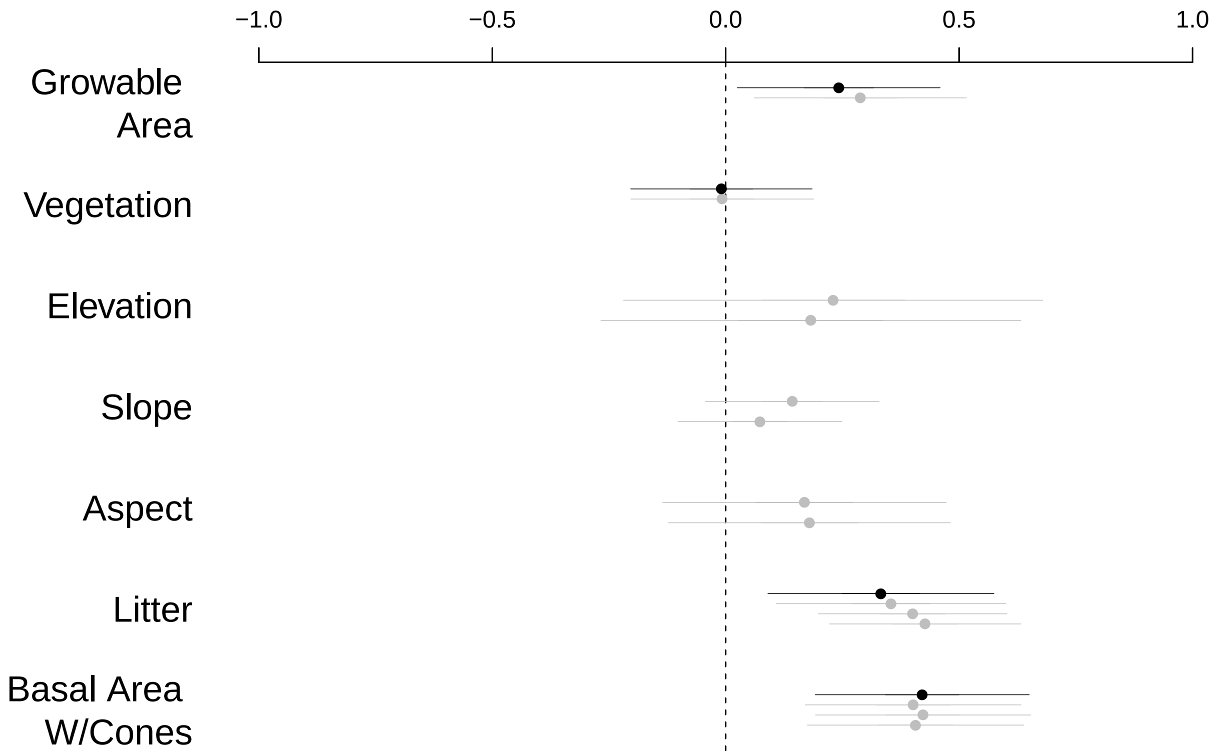

Figure 13: Effect size estimates for models with ΔAIC<7 from the fine scale seedling establishment analysis. The response variable was lodgepole pine seedling presence/absence. The model with the most support (lowest AIC) is displayed in black. All other models are grey. Points are estimates with 95% confidence intervals. Continuous variables were standardized prior to analysis. Aspect values were transformed to range from 0-2; Values approaching 2 are closer to 45°(Beers et al., 1966). Grow area is the area of the quadrat that was not occupied by rock or coarse wood.

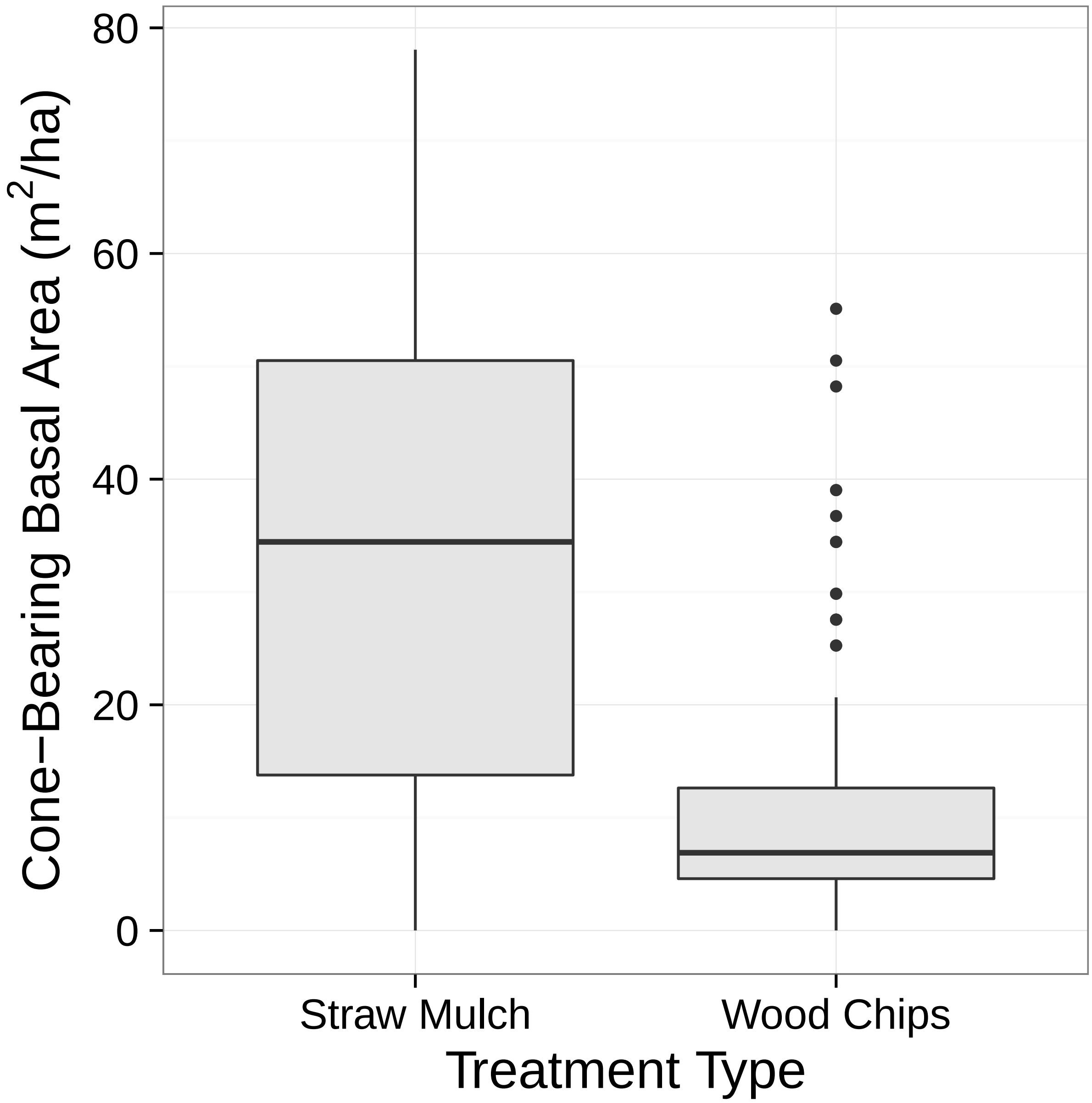

Figure 14: The difference in potential seed source, described with the basal area (m^2/ha) of lodgepole pine bearing cones, between areas with different mulch treatment types. This coincidental difference likely explains the difference in effect between straw mulch and wood chips on lodgepole pine seedling establishment. Only areas with high canopy fire severity were included in the analysis.

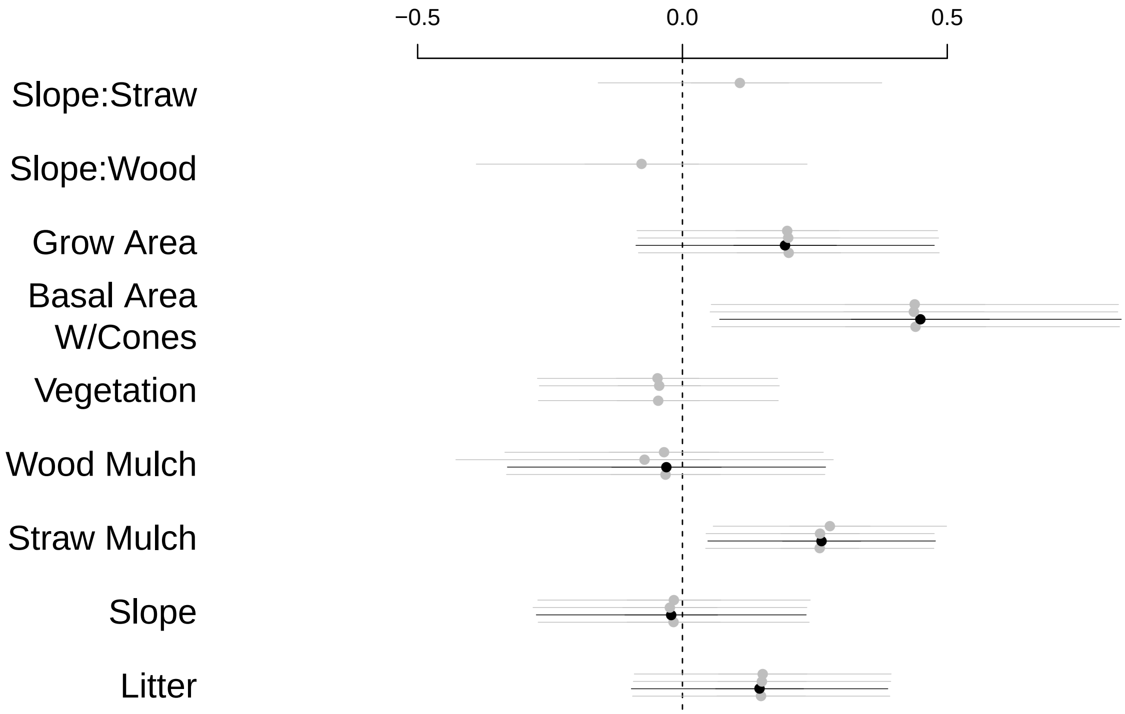

Figure 15: Coefficient plot for models with ΔAIC<7 from mulch cover analysis. The model with the most support (lowest AIC) is displayed in black. All other models are grey. Points are estimates with 95% confidence intervals. Lodgepole pine seedling presence/absence was the response. All predictor variables were standardized prior to analysis. ":" indicates an interaction term, all others are main effects.

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APPENDIX

A1 Serotiny

A1.1 Sampling design

I was unable to estimate serotiny in the burned area, as the destructive nature of the fire made cone morphology and angle of attachment (Tinker et al., 1994) hard to discern. Instead, I estimated the variability in landscape-scale serotiny for the High Park Fire area by replicating my 70×70m grid sampling design outside the fire. Grid locations were restricted to publicly owned land within the lodgepole pine zone, as classified by the 2010 LANDFIRE dataset (LANDFIRE, 2010). Over 200 grid locations, separated by 50m and within 500m from access roads, were randomly generated in ARC GIS 10.2. I objectively selected widely dispersed points from the set in order to sample a range of lodgepole pine stands—I did not attempt to separate points during the generation in case candidate points proved unsuitable, i.e. not lodgepole pine. Grids were located with a GPS—locations were considered suitable if lodgepole pine made up 50% or more of the basal area at the central point. I sampled a total of seven grids, all of which were located between 0.5 and 7 kilometers from the fire edge, and had elevations ranging from 2,400m to 2,800m. (Figure A1). At each grid, I established a series of eight transects running parallel to the slope direction. Every 10m along these transects, I used a standard factor 10 wedge prism to select lodgepole pine at least 1.4m in height, for a total of 64 prism sites per grid. One grid partially overlapped a harvested unit, which limited the number of prism sites to 40 in that grid. Each selected tree was examined with binoculars and classified as serotinous or non-serotinous. Living trees were considered serotinous if $\geq$10% of cones >3 years old were closed; dead trees were considered serotinous if the open cones were opening asymmetrically from the tip, and many cones were located near the stem (Figure A2).

A1.2 Analysis

Serotiny in Rocky Mountain lodgepole pine is most variable at scales between 1 and 10 kilometers (Tinker et al., 1994), suggesting that most of the variability in serotiny should be between sample grids, not within them. Percent serotiny was estimated for each prism site by dividing the number of trees classified as serotinous by the total lodgepole pine count at each site. In some grids, there was overlap between prism counts; abnormally large trees could be counted twice in two adjacent prism sites. While including all data did not meaningfully change the results, I eliminated the potential bias by only analyzing data from non-adjacent prism sites.

I tested for differences in serotiny using Kruskal-Wallis rank sum tests. I used Spearman's rank correlations to look for relationships between percent serotiny, mean basal area, and mean grid elevation.

A1.3 Results

Overall serotiny was high, with a total mean of 87%. Mean serotiny by grid ranged from 75% to 92%. Kruskal-Wallis rank sum tests indicated that mean serotiny levels were different between grids ($p<0.001$), though the greatest difference between means was only 17% (Table A1). I found weak (<0.60) negative Spearman's rank correlations between percent serotiny and mean basal area, mean elevation, and aspect (Table A2, Figure A3). Elevation had a weak positive correlation to basal area, and a weak negative correlation with aspect.

Though the serotiny grids did not replicate the full range of elevation of the regeneration grids located in the burn area, these data seem indicate that serotiny in the High Park fire was likely quite high, with relatively low variability. Even though I found that serotiny in lodgepole pine outside the fire was variable between grids, serotiny levels were rarely less than 70%; only 18 (<9%) prism sites had serotiny levels lower than this threshold. Additionally, I did not notice any major differences, such as variation in stand structure, that would indicate serotiny is more variable inside the fire than out. These results suggest that while variation in serotiny almost certainly played a role in the regeneration of lodgepole pine within the High Park Fire, it is unlikely to have confounded the effects of other important variables.

Table A1: Percent serotiny and basal area for each grid in the unburned forest surrounding the High Park Fire. The number of prism sites is lower for Grid 2, as part of the grid was located in a harvested unit. Due to some overlap in basal area counts, I limited the analysis to non-adjacent prism sites.

Grid	Sites	% Serotiny (SE)	Basal Area (m^2/ha)	Elevation (m)	Aspect
1	31	92 (2)	22	2520	2.0
2	18	75 (7)	20	2710	2.0
3	32	97 (1)	30	2640	0.7
4	32	87 (1)	52	2780	1.2
5	32	89 (2)	37	2450	2.0
6	32	83 (2)	35	2730	1.5
7	32	83 (2)	63	2740	1.0

Table A2: Spearman's rank correlations for mean serotiny, mean basal area (m^2/ha), and mean elevation.

	Serotiny(%)	Basal Area (m^2/ha)	Elevation (m)	Aspect
Serotiny(%)	1.00	−0.11	−0.54	−0.02
Basal Area (m^2/ha)	–	1.00	0.50	−0.38
Elevation (m)	–	–	1.00	−0.59
Aspect	–	–	–	1.00

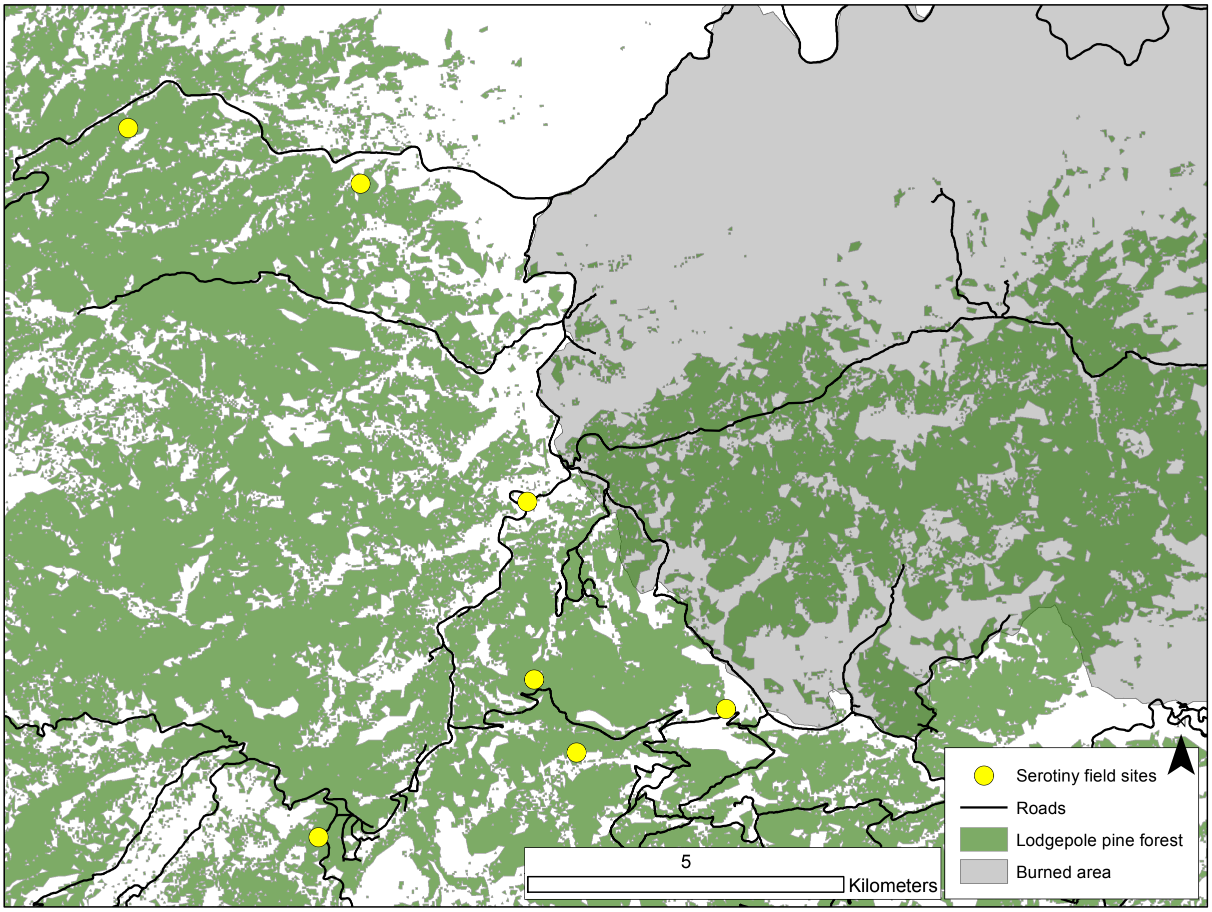


Figure A1: Map of serotiny field sites. Sites were chosen from 200 randomly generated locations if lodgepole pine made up >50% of the basal area from the central point. Lodgepole pine data from LANDFIRE (2010), fire perimeter created by (Stone, 2015), road data created by Larimer County.

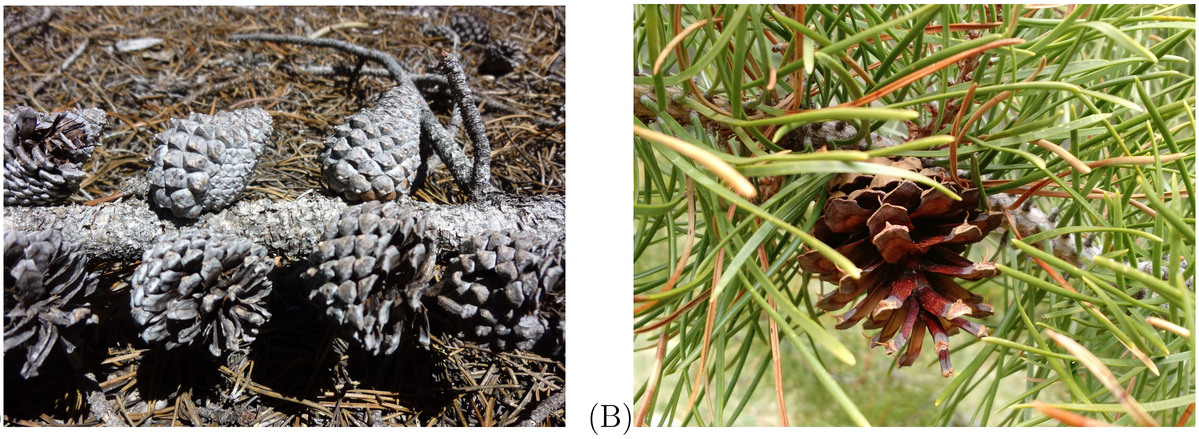
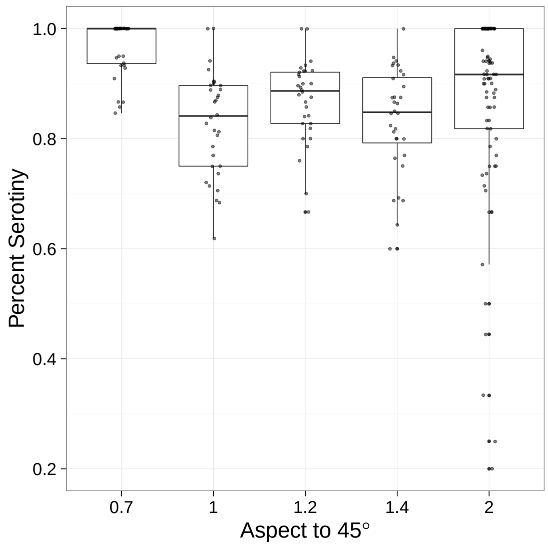
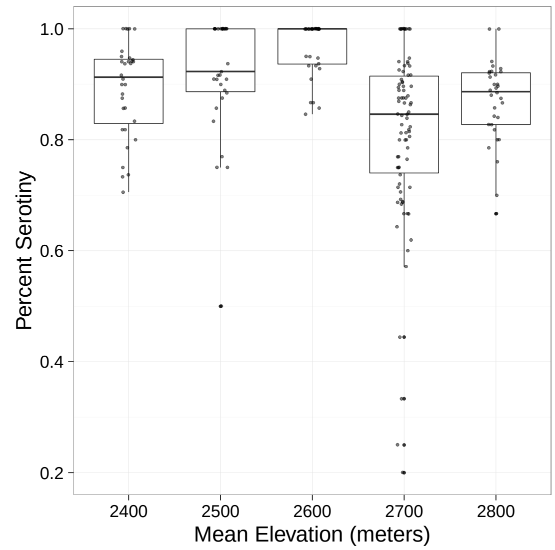
(A) (B)


Figure A2: A) Serotinous cones, some releasing seed. Cones found near Pennock Pass, approximately two kilometers southwest of the fire. B) Non-serotinous cone near Cameron Pass, located approximately 25 kilometers west of the fire. Living trees were considered serotinous if ≥10% of cones >3 years old were closed; dead trees were considered serotinous if the open cones were opening asymmetrically from the tip, and many cones were located near the stem.



(A)



(B)

Figure A3: A) Serotiny (%) in the unburned as a function of aspect, and B) serotiny (%) in the unburned as a function of elevation. Serotiny values are the % of lodgepole pine trees surrounding each prism site that were categorized as serotinous in the unburned area surrounding the High Park Fire. Elevation was averaged across each grid, aspect was taken from grid center. Aspect and elevation values were rounded for plotting only, points were added to the plots for clarity. The middle bar indicates the median value, the upper and lower boxes are 75th and 25th percentiles, respectively. The whiskers extend to data points up to 1.5 times the interquartile range, data beyond this threshold are plotted as points (Wickham, 2009).