THESIS

DRIVERS OF CONIFER REGENERATION IN SEVERELY BURNED PONDEROSA PINE – DOMINATED FORESTS OF THE COLORADO FRONT RANGE

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ABSTRACT

DRIVERS OF CONIFER REGENERATION IN SEVERELY BURNED PONDEROSA PINE – DOMINATED FORESTS OF THE COLORADO FRONT RANGE

Wildfires have increased in size and severity in ponderosa pine (*Pinus ponderosa*) – dominated forests in recent decades, and the ability of ponderosa pine and other co-occurring conifers to regenerate in severely burned portions of such fires is unclear. I collected post-fire conifer regeneration and other data within and surrounding five 11 to 18 year-old Colorado Front Range wildfires to examine whether severely burned patches are regenerating, and how regeneration density in these patches is governed by biotic and abiotic factors. Data were collected in plots distributed along transects originating within surviving forest and extending into high severity burn areas, and in plots located outside the fire perimeters. My results indicate that conifers have regenerated in severely burned areas (mean density of 118 stems ha^{-1}, 81% of which is ponderosa pine), but at densities that were more than five times lower than those in unburned and lightly to moderately burned areas. Generalized linear mixed model analyses revealed that as distance from surviving forest increased, conifer regeneration decreased; estimates of conifer regeneration were ~100 stems ha^{-1} 50 m from surviving forest but <10 stems ha^{-1} ≥200 m from surviving forest. These analyses also identified elevation as an important predictor of conifer regeneration in high severity burn patches, with densities decreasing with decreasing elevation. Regression tree analyses likewise found distance from surviving forest and elevation to be important predictors of regeneration, where within 50 m of live trees mean

regeneration was 150 stems ha^{-1} at elevations ≤2490 m and 1120 stems ha^{-1} at elevations >2490 m, but at distances ≥50 m from live trees mean regeneration was 49 stems ha^{-1}. Extrapolating my regression tree results to the 2002 Hayman Fire, 84% of the now unforested portion of this fire is predicted to have regeneration densities of 150 stems ha^{-1} or less. Taken as a whole, these findings suggest that activities such as tree planting may be warranted in high severity patches of Colorado Front Range wildfires if managers wish to return these areas to ponderosa pine – dominated forest in the foreseeable future, particularly where surviving forest is not in close proximity or where elevation is low.

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CHAPTER 1- DRIVERS OF CONIFER REGENERATION IN SEVERELY BURNED PONDEROSA PINE – DOMINATED FORESTS OF THE COLORADO FRONT RANGE

1.1. INTRODUCTION

Wildfires are important and complex ecological phenomena in forests of the western United States, but wildfires in the past two decades have increased in their size and severity (Westerling 2006; Miller et al. 2009; Litschert et al. 2012; Robichaud et al. 2014). Many of these fires burned with high severity across large, contiguous areas, resulting in vast expanses with little to no overstory tree survivorship (Graham 2003; Shoennegal et al. 2004; Lentile et al. 2005, 2007; Running et al. 2006; Haire & McGarigal 2008, 2010; Miller et al. 2009; Litschert et al. 2012; Adams 2013). This trend of larger and more severe wildfires is thought to be the result of past land management activities such as grazing, fire suppression, and timber extraction (Covington 2000; Hayes & Robeson 2011), as well as factors associated with changing climate, such as earlier snowmelt and warmer and drier growing season conditions (Running et al. 2006; Adams 2013).

In ponderosa pine (*Pinus ponderosa*) – dominated forests, fire regimes are driven by local site characteristics such as site productivity, latitude, elevation, and climate, all of which vary across this forest type's expansive range (Perry et al. 2011). Historically, fire regimes in ponderosa pine – dominated forests at lower elevations and latitudes followed patterns of high frequency, low to moderate severity burns where a majority of established trees survive (Fulé *et al.* 1997; Brown et al. 1999; Brown & Wu 2005; Brown et al. 2008; Scholl & Taylor 2010). At higher elevations and latitudes, these forests historically burned with longer intervals between fires, and with more variable severities (Brown et al. 1999; Hessburg et al. 2007; Perry et al. 2011; Sherriff & Veblen 2006, 2007; Odion et al. 2014). While high severity fires were a part of the historical fire regime throughout much of the range of ponderosa pine, high severity patches with complete overstory mortality are not thought to be >100 ha (Romme et al. 2003; Scholl & Taylor 2010; Sherriff et al. 2014; Huffman et al. 2015; see Williams & Baker 2012a, Williams & Baker 2012b for an exception). .

The life history traits of ponderosa pine present several challenges for regeneration following high severity wildfire, and thus the ability of ponderosa pine - dominated forests to reestablish within modern wildfire perimeters where high severity patch sizes differ considerably from historical ones is unclear. Ponderosa pine is a non-sprouting, non-serotinous conifer, and its seeds are not thought to persist in the soil seed bank (Stein & Kimberling 2003). Consequently post-fire regeneration of ponderosa pine depends on seed production from surviving trees. Furthermore, the relatively large seeds of ponderosa pine generally do not disperse more than two tree heights away from parent trees (Johansen & Latta 2003; Haire & McGarigal 2010; Dodson & Root 2013). Regeneration in severely burned areas is often concentrated near surviving trees (Figure 1; Barrett 1966; Bonnet et al. 2005; Donato et al. 2009), suggesting that seeds may not be able to disperse into the interiors of large stand replacing burn patches.

Other biotic and abiotic factors also likely influence the ability of ponderosa pine to establish in severely burned areas. For example, ponderosa pine has been observed to have lower rates of post-fire regeneration on south and west facing slopes, even near parent trees, compared to north and east facing slopes (Figure 1; Casady et al. 2010). South and west facing slopes receive more solar radiation during the hot afternoon hours creating high evaporative demand. Lower elevations have also been shown to provide greater challenges for seedling establishment than higher elevations, owing to higher temperatures, lower precipitation, and higher evaporative demand (Dodson & Root 2013). A warming or drying trend in climate could exacerbate conditions unfavorable for post-fire tree recruitment (IPCC 2013). Post-fire regeneration can additionally be limited by competition with existing or establishing understory vegetation (Bonnet et al. 2005; Dodson & Root 2013).

The number of wildfires in ponderosa pine – dominated forests increased dramatically in recent decades in the Colorado Front Range, paralleling trends observed across the west (Graham et al. 2012; MTBS 2015). Historical fires in this region contained a high severity component (Brown et al. 1999; Sherriff & Veblen 2007; Sherriff et al. 2014), but many recent fires may have been larger and more severe (Fornwalt et al. unpublished data; Graham et al. 2012; but see Sherriff et al. 2014 and Williams & Baker 2012b for opposing viewpoints). Several studies examining post-fire regeneration in high severity burn areas across the distribution of ponderosa pine-dominated forests have found little or no tree regeneration (Savage & Mast 2005; Keyes et al. 2007*a*; Roccaforte et al. 2012; Collins & Roller 2013). Thus there is widespread concern about the potential for large patches of severely burned forest to naturally recover, or alternatively, be converted into grasslands or shrublands in the absence of management activities such as tree planting (Bonnet et al. 2005; Strom & Fulé 2008; Collins & Roller 2013).

I collected post-fire tree regeneration and other data in five 11 to 18 year-old Colorado Front Range fires to quantify regeneration density in severely burned forests, and to relate regeneration density to potential biotic and abiotic drivers. Specifically, my objectives were to: 1) quantify tree regeneration in severely burned areas, and compare these values to those for unburned and lightly to moderately burned areas; 2) investigate the pattern of regeneration as a function of distance to surviving trees; 3) investigate the role that other biotic and abiotic factors, such as aspect, elevation, and understory vegetation, have in governing regeneration in severely burned areas; and given knowledge gained from addressing these objectives, 4) develop a predictive map of regeneration density within severely burned portions of the 2002 Hayman Fire, the largest fire known to have occurred in Colorado Front Range ponderosa pine – dominated forests (Graham 2003).

1.2. METHODS

1.2.1. STUDY AREA

My study area is a band of montane forest in the Front Range of Colorado, USA, ~40 km wide by ~170 km long (Figure 2). At lower elevations (~1700 - 2200 m), these forests are primarily characterized by stands of pure ponderosa pine on south and west slopes and ponderosa pine - Douglas-fir (*Psuedotsuga menziesii*) on north and east slopes; some Rocky Mountain juniper (*Juniperus scopulorum)* can also be found (Peet 1981). At higher elevations (~2200 - 2800 m), ponderosa pine and Douglas-fir often mix with quaking aspen (*Populus tremuloides*), blue spruce (*Picea pungens*), and lodgepole pine (*Pinus contorta*), with the latter three species becoming more common as elevation increases and as aspect becomes more northerly and/or easterly (Peet 1981). Mean annual precipitation and temperature for Morrison, located 26 km west of Denver at 1757 m elevation, averages 51 cm yr^{-1} and 8.5° C, respectively, while mean annual precipitation and temperature for Woodland Park, located 89 km southwest of Denver at 2580 m elevation, averages 63 cm yr^{-1} and 4.6° C (PRISM 2015).

Dendrochronological studies indicate that historical fire regimes in the Colorado Front Range also varied with elevation. At lower elevations, low-severity, high-frequency fire regimes were most common with fire return intervals <30 years (Sherriff et al. 2014; Brown et al. 2015). At higher elevations, mixed severity fire regimes were prevalent historically. These historical fires typically burned with a heterogeneous mosaic of severities at intervals of 30 to over 100 years, and created high severity patches estimated to be up to 100 ha in size (Brown et al. 1999; Romme et al. 2003; Sherriff et al. 2014).

1.2.2. DATA COLLECTION

In 2014, I established 42 transects across five large (>1000 ha) 11 to 18 year-old fires: the 2000 Bobcat Gulch Fire, the 1996 Buffalo Creek Fire, the 2002 Hayman Fire, the 2000 Hi Meadow Fire, and the 2003 Overland Fire (Table 1). Fires that were 10 years old or older were specifically chosen to allow sufficient time for regeneration to occur. Transect locations were determined by first using Monitoring Burn Severity Trends (MTBS) maps of fire severity (MTBS 2015) and the aerial imagery base map in ArcGIS 10.1 (ESRI, Redlands, California, USA) to identify high severity patches that were at least 300 m wide on all sides (> 9 ha). High severity patches were defined as areas that experienced 100% overstory tree mortality. Any surviving trees visible on the imagery within a high severity patch, either in the interior of the patch or near the surviving forest edge, were considered in measuring patch size. I disregarded patches located predominately on private land or where post-fire tree planting or salvage logging activities had occurred. Once suitable patches were identified, points were generated in ArcGIS along the surviving forest edge, and one point was randomly selected. Live trees at forest edges were confirmed to be reproductively mature. I then established a transect at that point that originated 50 m inside the surviving forest and extended out into the high severity patch 150 to 250 m (Figure 3). Transects were carefully placed to ensure that the distance to the closest surviving tree equaled the distance along the transect within the high severity patch. Transects typically ran perpendicular to the forest edge, but sometimes the transect angle was adjusted slightly if surviving trees along the forest edge or within the high severity patch were closer than the distance along the transect.

I established circular 100 m^2 (5.67 m radius) plots at 50 m intervals along the transects, with an additional plot in the high severity patch at 25 m from the forest edge to intensify sampling near surviving trees. The transects contained a total of 305 plots. I also located circular 100 m^2 plots in unburned areas outside of each fire, as close to the transects as possible. To locate these plots, I delineated suitable areas in ArcGIS approximately 50 to 100 ha in size and randomly located the plot within it. At least three unburned plots were established for each fire; twenty-one unburned plots were established across all five fires.

I recorded the height and species of all post-fire regenerating trees greater than 5 cm tall within each 100 m^2 plot. If I was uncertain about whether a tree regenerated post-fire, I estimated its age by whorl counting (Urza & Sibold 2013). I measured topographic attributes of the plot, including elevation, slope, slope position, slope shape, and aspect. I also quantified pre-fire stand structure, recording live or dead status, species, and diameter at breast height (DBH) for all pre-fire trees ≥4 cm DBH. Four 2 m^2 subplots per plot were established between 2.5 and 4.5 m from the plot center in each cardinal direction, and within these, I estimated percent cover of grasses, forbs, shrubs, fine (<2.5 cm diameter) wood, coarse (≥2.5 cm diameter) wood, and other ground cover variables.

1.2.3. DATA ANALYSIS

I used an analysis of variance (ANOVA) in SAS 9.4 (PROC GLIMMIX; SAS Institute Inc., Cary, North Carolina, USA) to examine tree regeneration density in severely burned areas relative to areas that were unburned and that burned with low to moderate severity. I examined three regeneration categories: 1) all conifers, which included ponderosa pine, Douglas-fir, Rocky Mountain juniper, blue spruce, and lodgepole pine, 2) ponderosa pine, and 3) Douglas-fir. Other conifer species were not abundant enough to analyze individually. Aspen regeneration was also rarely encountered and was not incorporated into this or other analyses. Pairwise differences between severity classes were determined using least squares means with a Tukey-Kramer adjustment.

I examined the influence of a suite of biotic and abiotic explanatory variables on tree regeneration densities in severely burned areas using two complementary analytical approaches. First, I used generalized linear mixed models in SAS 9.4 (PROC GENMOD), modeling all biotic and abiotic variables against conifer, ponderosa pine, and Douglas-fir regeneration density. Transect was included in the model as a random effect. Second, I examined the influence of biotic and abiotic variables on conifer, ponderosa pine, and Douglas-fir regeneration densities using non-parametric regression trees. Regression tree analyses were conducted in R 2.14.12 (R Core Team 2014) using the CTREE function of the PARTY package (Hothorn et al. 2006). Field-measured biotic and abiotic explanatory variables for both these analytical approaches included pre-fire stand basal area, understory vegetation cover (the sum of grass, forb, and shrub cover), distance from surviving forest, elevation, slope, aspect (defined as degrees from southwest), and fine and coarse wood cover. Derived variables included 30 year annual average precipitation (PRISM 2015), soil productivity and drainage index (USDA Forest Service Forest

Health Protection 2014), topographic wetness index (Qin et al. 2011), and annual solar radiation; the latter two variables were calculated in ArcGIS using 10 m resolution digital elevation models.

I developed a predictive map of conifer regeneration for portions of the 2002 Hayman Fire without surviving forest using results from the conifer regression tree analysis. Elevation and distance to surviving forest were the significant predictors of conifer regeneration in this analysis (described below). The Hayman Fire perimeter was defined using the MTBS map of fire extent (MTBS 2015), and the elevation map was derived from a 10 m resolution digital elevation model (NRCS-GDG 2015). The distance to surviving forest map was derived from a 1 m resolution map of surviving forest produced from post-fire National Agriculture Imagery Program (NAIP) aerial imagery (NAIP 2015; Malone et al. unpublished data). The surviving forest map was created using a supervised classification 2013 NAIP imagery of forested areas within and around the perimeter of the Hayman Fire, and was manually checked for quality assurance. The elevation and distance to surviving forest maps were queried per the divisions identified in the regression tree analysis and the mean conifer regeneration values for each division were assigned to unforested areas within the fire perimeter.

1.3. RESULTS

A total of 734 post-fire regenerating conifers were found in my 326 100 m^2 plots, with ponderosa pine (69%) and Douglas-fir (28%) dominating. The distribution of these trees across the plots was highly variable, but was nonetheless related to fire severity (Table 2; Figure 4). Conifer regeneration was present in severely burned areas, averaging 118 stems ha^{-1}, but lightly to moderately burned areas had five times more regeneration and unburned areas had eight times more. Ponderosa pine regeneration in severely burned areas averaged 95 stems ha^{-1} and accounted for 81% of the conifers in severely burned areas; fire severity trends for this species were similar to those observed for all conifers. Douglas-fir regeneration density, which averaged 16 stems ha^{-1} in severely burned areas, was 16 times greater in both unburned and lightly to moderately burned areas. Conifer regeneration in severely burned areas was concentrated in only 25% of my plots; 75% of plots had no conifer regeneration. In contrast, only 40% of plots in lightly to moderately burned areas and 30% of plots in unburned areas lacked conifer regeneration.

Post-fire conifer and ponderosa pine regeneration densities in severely burned areas declined strongly with distance from the surviving forest, but Douglas-fir density did not (Table 3; Figure 5). Conifer and ponderosa pine regeneration densities immediately adjacent to the surviving forest averaged 211 and 167 stems ha^{-1}, respectively. At 50 m from the surviving forest, regeneration densities declined by about half, to 96 and 67 stems ha^{-1}, respectively. Plots within 50 m of the surviving forest contained 88% of all regenerating conifers and 92% of regenerating ponderosa pine observed in severely burned areas. Only 10% of plots ≥ 200 m from the surviving forest contained regenerating conifers, and generalized linear mixed model analyses estimated conifer and ponderosa pine regeneration densities to be <10 and <5 stems ha^{-1} in these areas, respectively.

Generalized linear mixed modeling analyses further identified other significant predictors of conifer, ponderosa pine, and Douglas-fir regeneration density in high severity burn areas (Table 3; Figures 6, 7). Elevation was correlated with regeneration density for all three species groups, with densities increasing with increasing elevation. For example, regeneration densities were estimated to be <30 stems ha^{-1} for all species groups when elevation was <2200 m, but when elevation was 2600 m, estimated densities were 207, 119, and 31 stems ha^{-1}, for all conifers, ponderosa pine, and Douglas-fir, respectively. Understory vegetation cover was also correlated with Douglas-fir regeneration density, with higher levels of understory vegetation cover fostering more regeneration.

Regression tree analyses likewise identified distance from the surviving forest and elevation as significant predictors of conifer and ponderosa pine regeneration density in high severity burn areas, while no significant predictors were identified for Douglas-fir (Figure 8). Distance from the surviving forest was the first and most significant predictor for both conifer and ponderosa pine regeneration density. At distances ≥50 m from the surviving forest, mean predicted post-fire conifer and ponderosa pine regeneration was 49 and 34 stems ha^{-1}, respectively, while median predicted densities were 0 stems ha^{-1}. At distances <50 m from the surviving forest, a second division based on elevation was identified. Where elevation was ≤2490 m, predicted mean (median) conifer and ponderosa pine regeneration densities were 150 (0) and 132 (0) stems ha^{-1}, respectively; where elevation was >2490 m, predicted mean (median) conifer and ponderosa pine regeneration densities were 1120 (1000) and 930 (750) stems ha^{-1}, respectively. The conifer regression tree produced an r^2 of 0.35 and the ponderosa pine regression tree produced an r^2 of 0.30.

According to my predictive map of post-fire conifer regeneration densities for the 2002 Hayman Fire, 16% of this fire's area without surviving forest can be expected to have mean regeneration densities of 1120 stems ha^{-1} (Figure 9). In contrast, 14% of the fire's currently unforested area can be expected to have mean conifer regeneration densities of 150 stems ha^{-1}, and 70% can be expected to have mean regeneration densities of 49 stems ha^{-1}. Contiguous areas that are predicted to have mean regeneration densities ≤150 stems ha^{-1} averaged 1 ha in size, with 22 areas (representing 93% of the total unforested area) >50 ha.

1.4. DISCUSSION

My examination of tree regeneration in severely burned patches of five Colorado Front Range fires illustrates that natural conifer regeneration is occurring, but at low densities. Conifer regeneration averaged 118 stems ha^{-1} across the high severity plots, values that were far lower than those in adjacent areas that burned at low to moderate severity or in unburned areas (Table 2). Similar studies in the ponderosa pine – dominated forests have likewise found a dearth of conifer regeneration in severely burned areas (Lentile et al. 2005; Savage & Mast 2005; Roccaforte et al. 2012, Collins & Roller 2013; Rother 2015). The evolutionary adaptations of ponderosa pine to low and moderate severity fire may limit regeneration in larger stand replacing patches (Covington & Moore 1994). Ponderosa pine seeds do not persist in seed banks following wildfire, due to high rates of predation by insects, small mammals, and birds (Stein & Kimberling 2003; Bai et al. 2004; Krannitz & Duralia 2004; Shepperd et al. 2006; Zwolak et al. 2010). Unfavorable climate within high severity burn patches may also limit germination and establishment success. Increased maximum temperatures, wind speeds, and solar radiation (Feddema et al. 2013) due to a lack of overstory trees can result in decreased soil moisture availability and may result in failure to germinate, or, if germination occurs, desiccation of establishing seedlings (Stein & Kimberling 2003). Furthermore, the majority of seedlings that do become established often die in the first few years due to herbivory and moisture stress (Heidmann et al. 1982; Stein & Kimberling 2003).

In this study, two complementary analytical approaches indicated that distance to seed source was the most important predictor of both conifer and ponderosa pine regeneration density in severely burned areas (Table 3; Figures 5 & 8). I found that 88% of the conifer regeneration and 92% of the ponderosa pine regeneration I observed in severely burned areas was within 50 m of live trees, and that little to no regeneration occurred at distances ≥200 m. My findings of conifer and ponderosa pine densities that declined with increasing distance from live trees are consistent with findings from similar studies conducted not only in the Colorado Front Range (Rother 2015), but also in the Black Hills, South Dakota (Bonnet et al. 2005), in Idaho and Montana (Kemp et al. 2015), and in New Mexico and Arizona (Haffey 2014). My findings are also consistent with the rule of thumb that ponderosa pine seeds generally disperse distances of only one or two times the parent tree height due to their large size (Barrett 1966; McDonald 1980; Keyes & Maguire 2007*b*). Douglas-fir seeds are smaller and are more readily dispersed on the wind (Burns & Honkala 1990), which may explain why the relationship between distance to seed source and Douglas-fir regeneration was not significant in any of my analyses. In the Klamath-Siskiyou region, Oregon, Donato et al. (2009) found that Douglas-fir dominated regeneration densities were consistent up to 400 m from live trees before declining.

Elevation was also an important predictor of where natural conifer regeneration occurred in severely burned landscapes**.** The results of my generalized linear mixed models showed that elevation was highly positively correlated with regeneration density for all conifers, ponderosa-pine, and Douglas-fir (Table 3), while regression tree analyses indicated that higher elevations (>2490 m) were associated with increased regeneration densities for all conifers and ponderosa-pine (Figure 8). At elevations >2490 m, conifer regeneration accounted for 46% of the regeneration found across all high severity plots, yet only 12% of my plots were located at these elevations. Other studies in ponderosa-pine dominated forests found that higher elevations were associated with increased regeneration densities across all burn severity types in the Colorado Front Range (Rother 2015), the 2002 Rodeo-Chedeski Fire in northern Arizona (Casady et al. 2010), and in stand replacing burn areas in the Cascade Range, Oregon (Dodson & Root 2013). Elevations are marked by gradients of temperature, precipitation, and evapotranspiration rates. Lower elevations are commonly associated with higher temperatures, lower precipitation, and higher evapotranspiration rates, while higher elevations typically experience diminished maximum temperatures and evapotranspiration rates, while receiving increased rates of precipitation (Casady et al. 2010). Adequate soil moisture is thought to be a key factor in the success of germination and establishment for naturally regenerating conifers (Stein & Kimberling 2003; Puhlick et al. 2012). Decreased precipitation and soil moisture availability typically associated with lower elevations may pose challenges for successful forest regeneration (Dodson & Root 2013), particularly in light of projected changes in temperature and precipitation regimes in the coming decades (IPCC 2013).

I found that understory vegetation cover did not influence conifer or ponderosa pine regeneration densities in high severity burn areas, although it did have a positive influence on Douglas-fir regeneration (Table 3). These findings for ponderosa pine are surprising considering that understory vegetation has been repeatedly found to inhibit regeneration in burned environments (Bonnet et al. 2005; Dodson & Root 2013; Collins & Roller 2013). The light requirements of ponderosa pine and Douglas-fir may explain their contrasting relationship to understory vegetation cover. Ponderosa requires abundant light for successful recruitment (Stein & Kimberling 2003). Douglas-fir, on the other hand, is sensitive to high light levels, and understory vegetation may provide small Douglas-firs protection from the high light levels encountered in severely burned areas (Shatford 2007).

Several variables not measured here may further drive post-fire tree regeneration in severely burned areas. Soil moisture is thought to be one of the most important factors influencing post-fire regeneration of ponderosa-dominated forests (Casady et al. 2010; Dodson & Root 2013; Puhlick et al. 2012). While I suspect soil moisture is correlated with some of the variables I did quantify, such as elevation and understory vegetation cover, I did not explicitly quantify it. However, soil moisture is most important within the first year of growth (Stein & Kimberling 2003), and therefore it is perhaps not informative to quantify it 10+ years post fire. The topographic position and direction of the surviving forest relative to high severity burn patches may also influence post-fire regeneration patterns. Surviving forest that is uphill of severely burned areas, and/or in the direction of the prevailing winds, may be more effective at dispersing seeds longer distances than forest that is not (Barrett 1966, McDonald 1980).

The results of my predictive map suggest that most of the 2002 Hayman Fire's currently unforested areas likely have very low densities of regenerating conifers. I found that 16% of unforested areas within the Hayman Fire were predicted to have 1120 regenerating conifers ha^{-1}, while 84% of unforested areas were predicted to have $\leq$150 regenerating conifers ha^{-1} (Figure 9). While not all fires in the Colorado Front Range are as large as the Hayman Fire, or burned as severely, this fire is representative of mega-fires that are predicted to increase in occurrence with changing climate (Covington 2000; Adams 2013). One limitation of this map is that unforested areas were derived solely from post-fire NAIP imagery, and consequently some post-fire unforested areas were likely also unforested prior to the fire. An examination of vegetation maps suggests that grasslands, shrublands, and other unforested vegetation types accounted for <10%

of the Hayman's area prior to the fire (Pike National Forest, unpublished data). Despite this limitation, my predictive map will likely be valuable for post-fire restoration and management efforts.

1.5. CONCLUSIONS AND MANAGEMENT IMPLICATIONS

Post-fire regeneration is occurring within high severity patches of recent Colorado Front Range fires, but regeneration densities are very low, and it is uncertain whether this regeneration is sufficient for forest recovery. The regeneration densities that are occurring in these patches, particularly in areas where surviving forest is not in close proximity and where elevation is low, are generally lower than both National Forest Management Act (NFMA) and historical benchmarks. The NFMA dictates that regeneration values of 370 stems ha^{-1} or more are necessary for ponderosa-pine dominated forests of this region to be considered minimally stocked (PSICC 1984; ARP 1997). Across the distribution of ponderosa pine, historical stand densities averaged ~100 stems ha^{-1} in one lower elevation study area of the Colorado Front Range and ~140 stems ha^{-1} in the broader Front Range region (Brown et al. 2015; Battaglia et al. unpublished data), ~150 stems ha^{-1} in the South Dakota Black Hills (Brown & Cook 2006), and ~140 – 250 stems ha^{-1} in the Southwest (Fulé et al. 2002). Thus a long-term conversion to a non-forested vegetation community may occur in considerable portions of severely burned areas in the absence of tree planting (Savage & Mast 2005; Strom & Fulé 2008; Haire & McGarigal 2010; Collins & Roller 2013; Abella & Fornwalt 2015). This may especially be true in light of projections of increased temperatures and decreased rates of precipitation in the Colorado Front Range and the west, creating drought conditions unfavorable for post-fire seedling establishment yet favorable for the occurrence of subsequent fires that may destroy the little regeneration that has occurred in these severely burned areas (Feddema et al. 2013; IPCC 2013; Savage et al. 2013). Post-fire planting within high severity burn patches should be aimed at areas more than approximately 50 m from live trees, and at all distances from live trees at elevations lower than approximately 2500 m**.**

Figure 1: Photos illustrating varying regeneration conditions in the Pike National Forest, Colorado, USA. Top: Area in the north central Buffalo Creek Fire illustrating regeneration occuring within ~50 m of forest edge. Bottom: Area in the eastern portion of the Buffalo Creek Fire illustrating no obvious conifer regeneration.

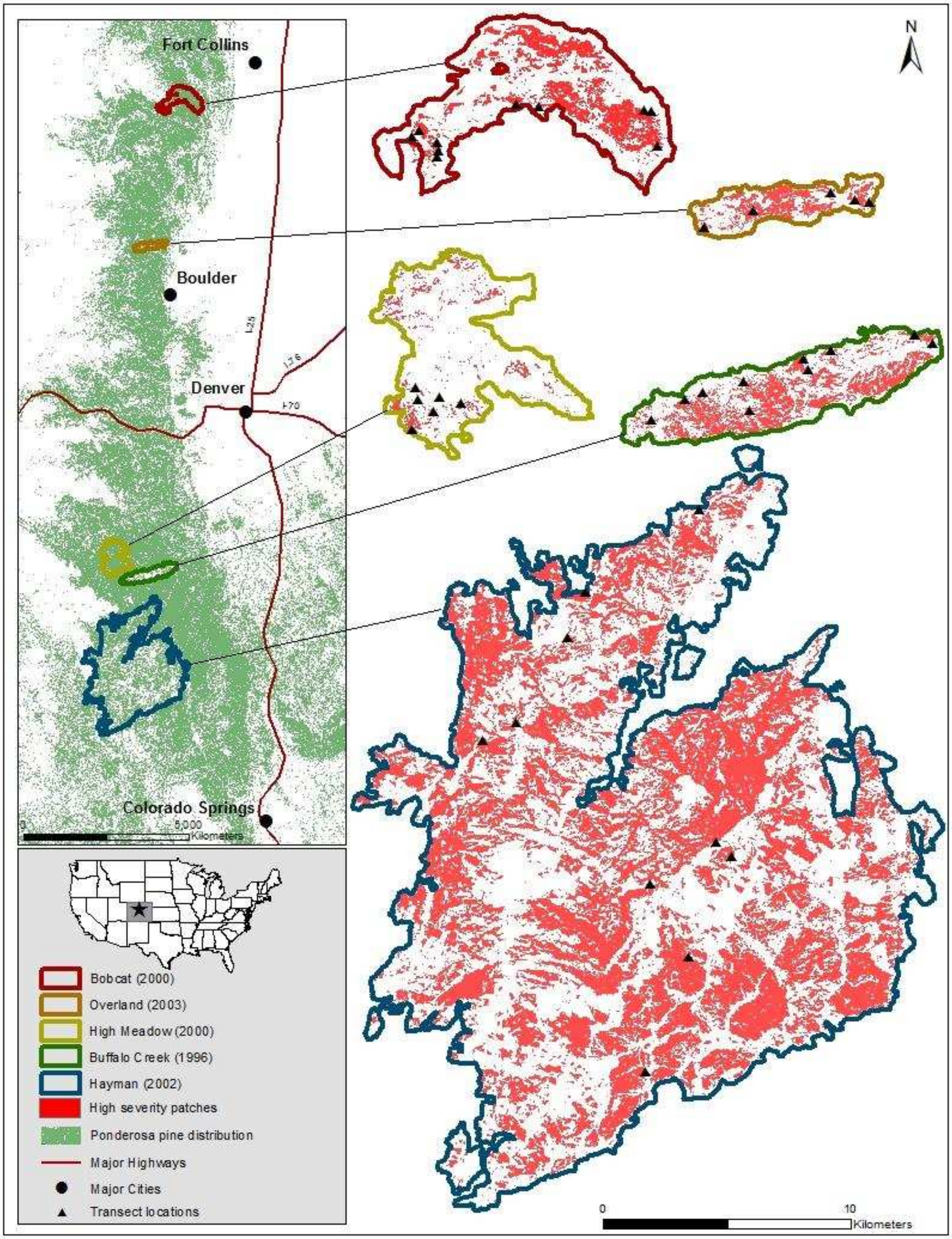

Figure 2: Map of sampled fires. Fire perimeters, high severity patches (MTBS 2015), and transect locations for the five sampled fires in the Colorado Front Range, USA. The distribution of ponderosa pine – dominated forest is derived from LANDFIRE (LANDFIRE 2013).

Table 1: Characteristics of the five sampled fires. Ownership indicates the primary public land management agencies impacted by the fire, and where sampling occurred. Burn areas and high, moderate, and low severity percentages are taken from MTBS (2015).

Fire name	Year burned	Ownership	Fire area (ha)	High Severity (% of fire area)	Moderate Severity (% of fire area)	Low Severity (% of fire area)	Number of transects
Bobcat Gulch	2000	Arapaho-Roosevelt National Forest; City of Fort Collins	3,695	30	22	48	10
Buffalo Creek	1996	Pike National Forest	3,963	37	21	42	10
Hayman	2002	Pike National Forest	53,216	44	22	34	10
Hi Meadow	2000	Pike National Forest	3,889	9	31	60	7
Overland	2003	Arapaho-Roosevelt National Forest; Boulder County	1,308	36	22	42	5

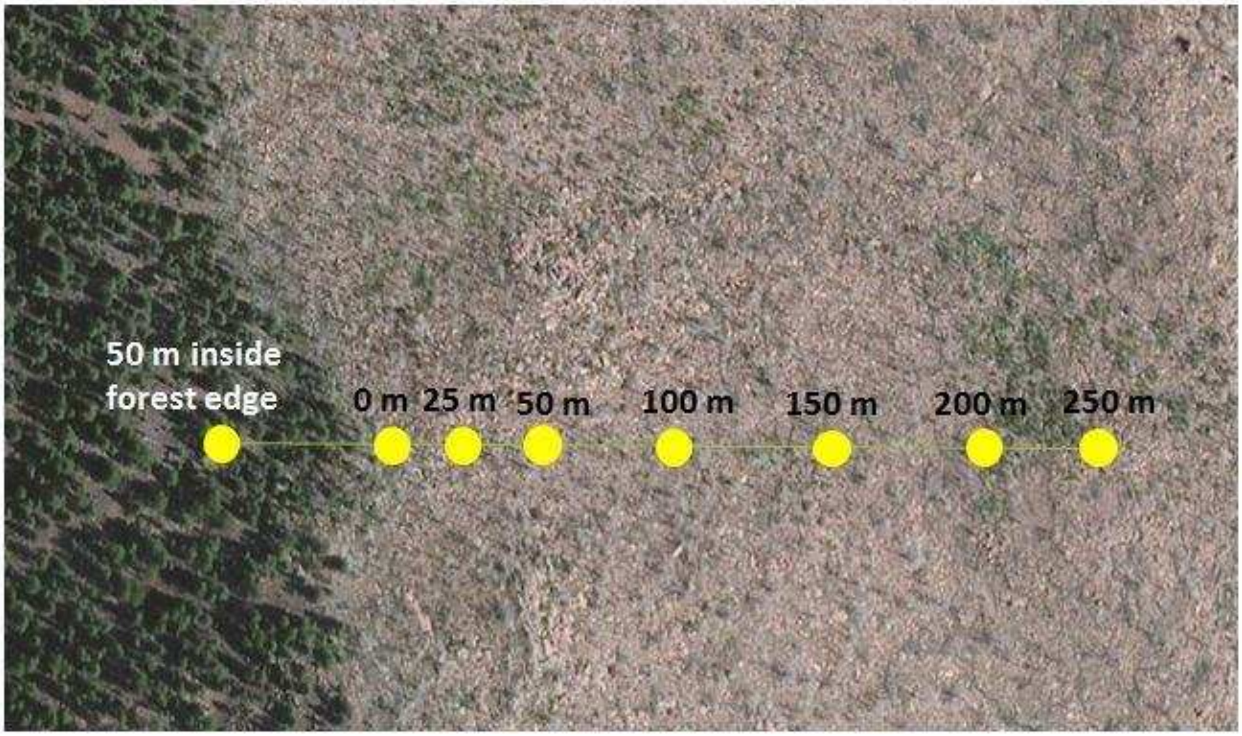

Figure 3: Transect layout. Transects were anchored 50 m inside the surviving forest, and extended into high severity patches for 150 to 250 m. 100 m^2 circular plots were established along the transects every 25 to 50 m.

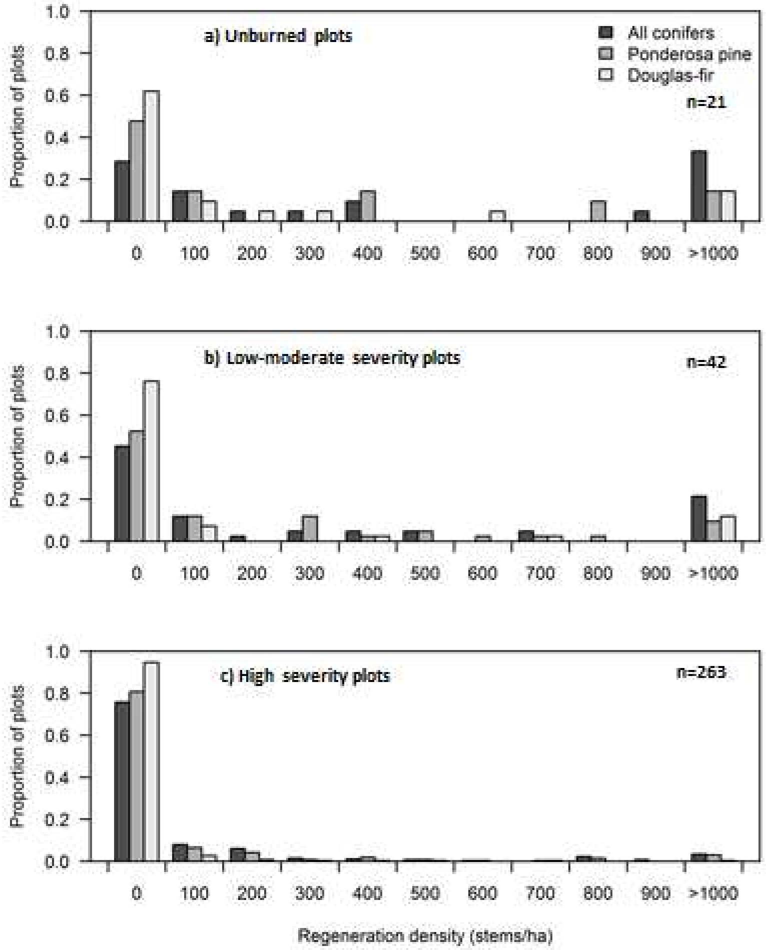

Figure 4: Frequency distributions of tree regeneration density, by species, in a) unburned plots, b) low-moderate severity plots, and c) high severity plots. Regeneration density values on the x-axis are the upper bounds of the bin.

Table 2: Mean (± 1 standard error) tree regeneration densities, by species and fire severity class. Fire severity classes that share letters were not significantly different for that species.

Fire severity	**All conifers (stems ha^{-1})**	**Ponderosa pine (stems ha^{-1})**	**Douglas-fir (stems ha^{-1})**
Unburned	924 ± 428 [a]	675 ± 372 [a]	257 ± 106 [a]
Low-moderate	545 ± 135 [a]	274 ± 71 [b]	267 ± 108 [a]
High	118 ± 21 [b]	95 ± 19 [c]	16 ± 6 [b]

Table 3- Generalized linear modelling results of tree regeneration density in high severity plots, by species. Significant variables are highlighted in bold. Precipitation is derived from 30 year annual normal conditions; productivity and drainage indices are derived from USDA-Forest Service Forest Health Protection Soils data (USDA Forest Service, 2015); topographic wetness index is derived from ArcGIS hydrology tools; solar radiation is derived from ArcGIS solar radiation tool. All other variables were collected in the field.

Variable	All conifers	Ponderosa pine	Douglas-fir
Distance from surviving forest (m)	**<0.001**	**<0.001**	0.234
Elevation (m)	**<0.001**	**0.002**	**0.009**
Slope (degrees)	0.507	0.250	0.492
Aspect (degrees from southwest)	0.277	0.545	0.599
Precipitation (mm yr^{-1})	0.526	0.317	0.185
Pre-fire stand basal area (m^2 ha^{-1})	0.289	0.421	0.210
Coarse wood (% cover)	0.332	0.121	0.351
Fine wood (% cover)	0.767	0.854	0.108
Understory vegetation (% cover)	0.492	0.462	**0.031**
Productivity index	0.525	0.832	0.177
Drainage index	0.396	0.550	0.931
Topographic wetness index	0.521	0.665	0.733
Solar radiation (MJ m^{-2} yr^{-1})	0.655	0.974	0.427

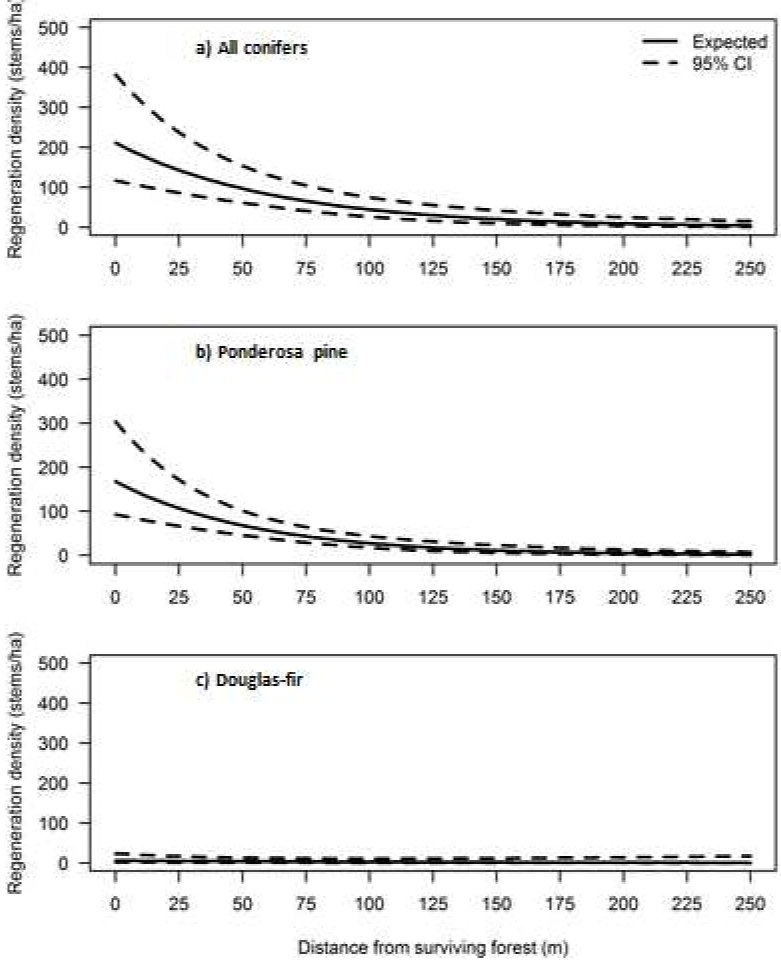

Figure 5: Expected (and 95% confidence interval (CI)) tree regeneration density in high severity plots as a function of distance from surviving forest, for a) all conifers, b) ponderosa pine, and c) Douglas-fir.

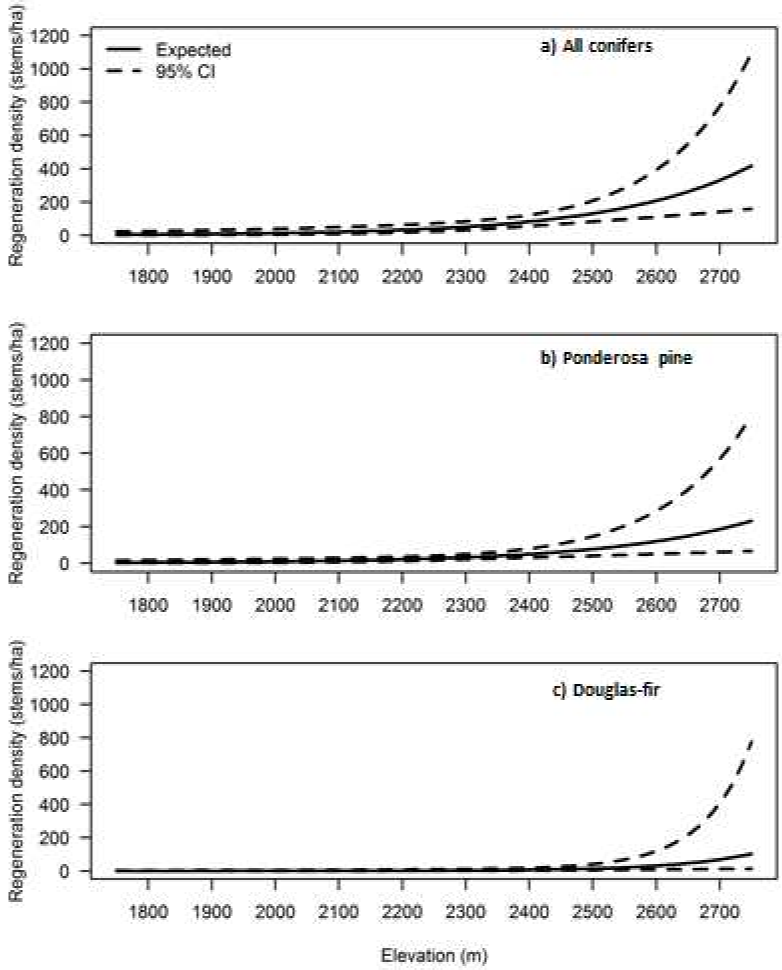

Figure 6: Expected (and 95% confidence interval (CI)) tree regeneration density in high severity plots as a function of elevation for a) all conifers, b) ponderosa pine, and c) Douglas-fir.

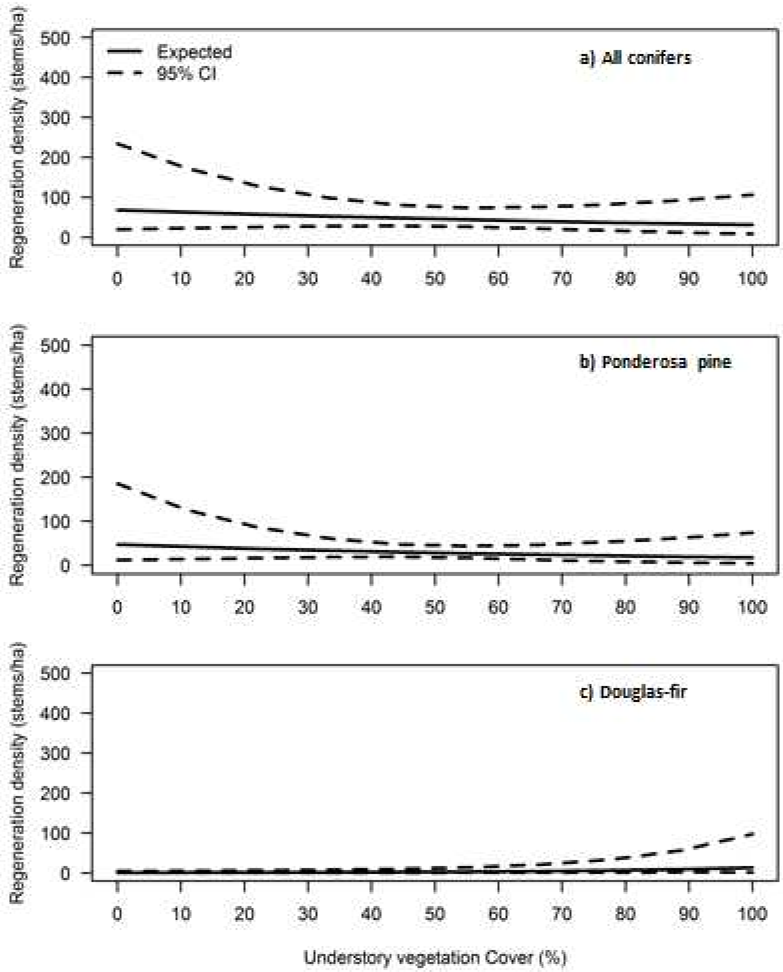

Figure 7: Expected (and 95% confidence interval (CI)) tree regeneration density in high severity plots as a function of understory vegetation cover for a) all conifers, b) ponderosa pine, and c) Douglas-fir.

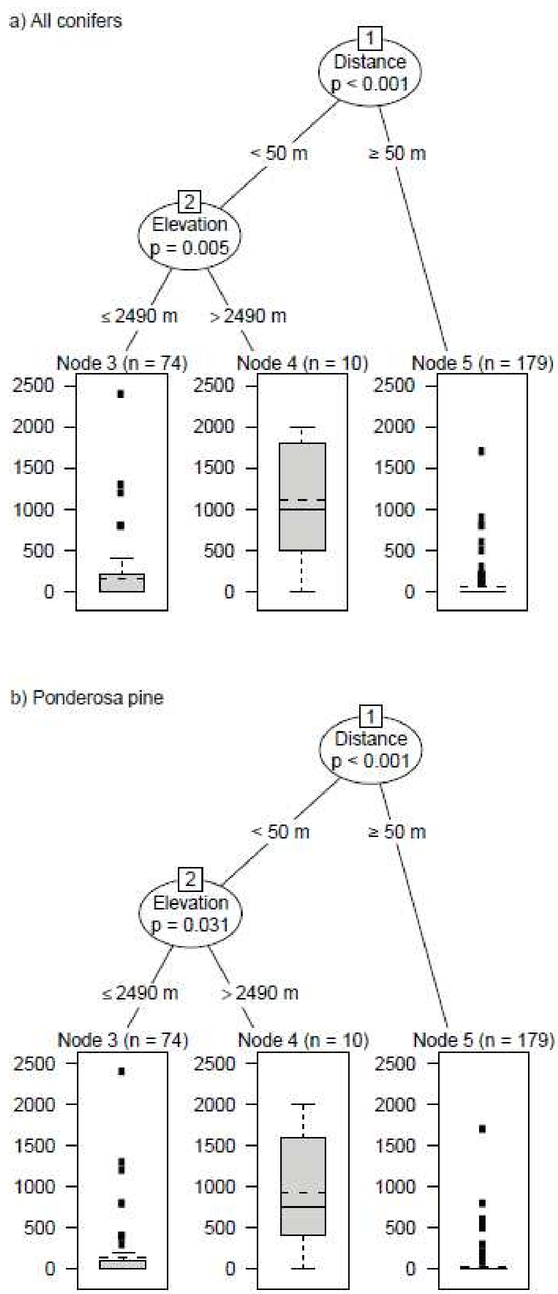

Figure 8: Regression trees of regeneration density for a) all conifers and b) ponderosa pine. Distance (m) is distance from surviving forest and elevation (m) is height above mean sea level. Box-and-whisker diagrams at the terminal nodes depict median (bold line) and mean (dotted line) regeneration densities per ha for that division.

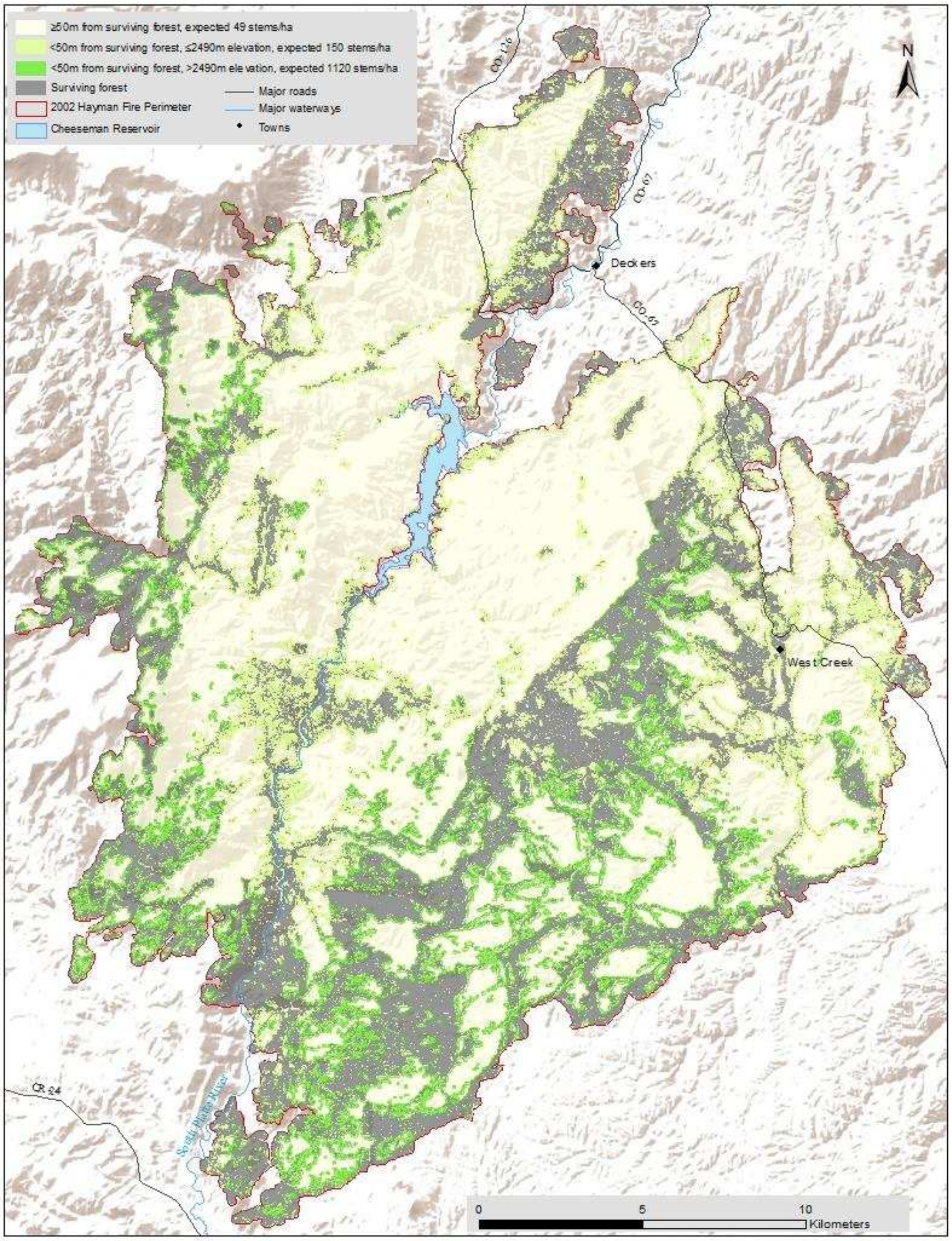

Figure 9: Map of predicted regeneration areas within the 2002 Hayman Fire. Areas in light yellow are ≥50 m from surviving forest and are expected to have regeneration densities of 49 stems ha^{-1}. Areas shown in light green, where distance from surviving forest is <50 m and elevation is ≤2490 m, are expected to have regeneration densities of 150 stems ha^{-1}. Areas shown in green, where distance from surviving forest is <50 m and elevation is >2490 m, are expected to have regeneration densities of 1120 stems ha^{-1}. Surviving forest is depicted in grey.

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