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Patterns of conifer regeneration following high severity wildfire in ponderosa pine – dominated forests of the Colorado Front Range ☆

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ABSTRACT

Many recent wildfires in ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson) – dominated forests of the western United States have burned more severely than historical ones, generating concern about forest resilience. This concern stems from uncertainty about the ability of ponderosa pine and other co-occurring conifers to regenerate in areas where no surviving trees remain. We collected post-fire conifer regeneration and other data within and surrounding five 11–18 year-old Colorado Front Range wildfires to examine whether high severity burn areas (i.e., areas without surviving trees) are regenerating, and how regeneration density is related to abiotic and biotic factors such as distance from surviving forest, elevation, and aspect. We found that some conifer regeneration has occurred in high severity burn areas (mean and median of 118 and 0 stems ha^{-1}, respectively), but at densities that were considerably lower than those in unburned and in low to moderate severity burn areas. Generalized estimating equation analyses revealed that distance from surviving forest was the most important predictor of conifer regeneration in high severity burn areas, with regeneration declining as distance from surviving forest increased; estimates of conifer regeneration were 211 stems ha^{-1} immediately adjacent to surviving forest but only 10 stems ha^{-1} 200 m from surviving forest. These analyses also revealed that conifer regeneration densities declined as elevation decreased. Regression tree analyses likewise showed that distance from surviving forest and elevation were important predictors of conifer regeneration in high severity burn areas; within 50 m of surviving forest mean (median) regeneration was 150 (0) stems ha^{-1} at elevations ⩽2490 m and 1120 (1000) stems ha^{-1} at elevations >2490 m, but at distances ⩾50 m from surviving forest mean (median) regeneration was only 49 (0) stems ha^{-1}, regardless of elevation. Applying regression tree results spatially to the 2002 Hayman Fire, Colorado's largest and most severe known wildfire, we found that 70% of the area without surviving forest exceeded this 50 m threshold. These patterns of conifer regeneration suggest that Colorado Front Range ponderosa pine – dominated forests may not be resilient to high severity wildfire, particularly where surviving forest is not in close proximity. We recommend that land managers consider planting conifers within the interiors of large high severity burn patches, as well as implementing treatments to reduce the risk of uncharacteristic high severity wildfire in unburned forests, where maintaining a forested condition is desired.

1. Introduction

Wildfire has long been an important and complex disturbance agent in ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson) – dominated forests of the western United States. Studies conducted across the range of ponderosa pine have documented that historical fire regimes varied from frequent, low severity regimes, where high severity fire was but a minor component (Fisher et al., 1987; Baisan and Swetnam, 1990; Fulé et al., 1997; Everett et al., 2000; Scholl and Taylor, 2010; Brown et al., 2015), to mixed severity regimes, where high severity fire played a more substantial role (Brown et al., 1999, 2008; Veblen et al., 2000; Hessburg et al., 2007; Williams and Baker, 2012; Sherriff et al., 2014). However, many recent fires have burned with high severity across large, contiguous areas, resulting in vast expanses with no overstory tree survivorship, and the amount and extent of high severity burning in these fires commonly exceeds that of historical ones (Goforth and Minnich, 2008; Haire and McGarigal, 2010;

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O'Connor et al., 2014; Sherriff et al., 2014; Guiterman et al., 2015; Harris and Taylor, 2015; P.J. Fornwalt, unpublished data). This trend of more severe fire effects is thought to be the result of increased forest density and homogeneity due to fire suppression, livestock grazing, and logging activities since Euro-American settlement (Goforth and Minnich, 2008; O'Connor et al., 2014; Guiterman et al., 2015; Harris and Taylor, 2015), as well as of factors associated with changing climate (Westerling et al., 2006).

The life history traits of ponderosa pine and co-occurring conifers (e.g., Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco)) present several challenges for the regeneration of ponderosa pine - dominated forests following uncharacteristically severe burning, making the resilience of these forests to recent fires unclear. Although ponderosa pine is well-adapted to survive low severity fire, it does not sprout, it has non-serotinous cones, and it has seeds that are short-lived in the soil seed bank (Oliver and Ryker, 1990; Bai et al., 2004), meaning that post-fire regeneration following high severity fire depends on seed production from surviving trees in adjacent areas. Furthermore, its relatively heavy seeds generally do not disperse more than two tree heights away from parent trees (Barrett, 1966; McDonald, 1980; Johansen and Latta, 2003), suggesting that they may not be able to readily disseminate into the interiors of high severity burn patches, particularly those that are large. Indeed, several studies conducted in severely burned ponderosa pine - dominated forests have found little or no tree regeneration, except sometimes near surviving trees (Fig. 1; Bonnet et al., 2005; Keyser et al., 2008; Roccaforte et al., 2012; Collins and Roller, 2013). Douglas-fir also relies on seed production from surviving trees to regenerate following high severity fire, although it may be able to more effectively regenerate in the interiors of high severity burn patches because its relatively light seeds can disperse further than those of ponderosa pine (Herman and Lavender, 1990).

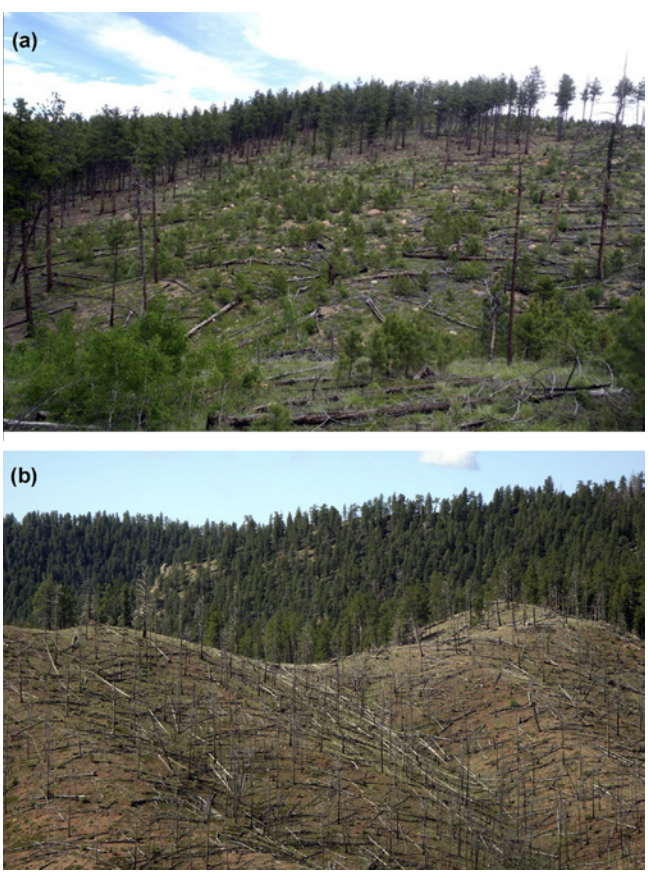

Fig. 1. Photos illustrating varying post-fire regeneration conditions in the 1996 Buffalo Creek Fire, Colorado, USA, 18 years after burning; (a) depicts high severity area in the central portion of the fire with ample conifer regeneration near surviving trees, and (b) depicts a high severity area in the eastern portion of the fire with no obvious conifer regeneration.

Other abiotic and biotic factors, such as aspect, elevation, and understory vegetation, may further limit the ability of ponderosa pine and co-occurring conifers to establish in high severity burn portions of recent fires. Ponderosa pine and Douglas-fir have been observed to have lower rates of post-fire regeneration on south-facing slopes compared to north-facing slopes (Rother, 2015). South-facing slopes receive more solar radiation than north-facing slopes during the hot afternoon hours, creating higher temperatures and higher evaporative demand. Similarly, lower elevations have also been shown to pose greater challenges for post-fire regeneration than higher elevations, owing to higher temperatures, lower precipitation, and higher evaporative demand (Dodson and Root, 2013; Rother, 2015). A warming or drying trend in future climate may further exacerbate conditions unfavorable for tree regeneration (IPCC, 2013; Lukas et al., 2014; Rother et al., 2015; Petrie et al., 2016). A dense layer of understory vegetation may also negatively impact post-fire regeneration due to competition (Bonnet et al., 2005; Collins and Roller, 2013; but see Kemp et al., 2016).

In ponderosa pine – dominated forests of the Colorado Front Range, historical fires often contained a high severity component (Brown et al., 1999; Veblen et al., 2000; Williams and Baker, 2012; Sherriff et al., 2014), yet many recent fires are thought to have more and larger high severity burn patches than historical ones (Sherriff et al., 2014; P.J. Fornwalt, unpublished data), paralleling trends observed across the west. Thus there is uncertainty about whether sufficient post-fire conifer regeneration in high severity burn patches will make these forests resilient to recent fires, or whether a lack of regeneration will cause them to convert to another vegetation type, such as grassland or shrubland. Our overall objective was to evaluate whether ponderosa pine and other conifers were regenerating in high severity burn patches of recent Colorado Front Range wildfires, and to relate regeneration density to potential abiotic and biotic drivers. Specifically, we aimed to: (1) quantify conifer regeneration in high severity burn areas and compare these values to those for unburned and low to moderate severity burn areas; (2) investigate the relationship between regeneration density in high severity burn areas and distance from surviving forest; (3) investigate how other biotic and abiotic factors relate to regeneration density in high severity burn areas; and given knowledge gained from addressing these three objectives, (4) develop a predictive map of regeneration density within high severity burn patches of the 2002 Hayman Fire, the largest and most severe wildfire known to have occurred in Colorado.

2. Methods

2.1. Study area

This study was conducted in a ~40 km wide by ~170 km long band of montane forest in the Colorado Front Range, USA (Fig. 2). At lower elevations (~1600–2200 m), forests are generally characterized by relatively open stands of ponderosa pine on south slopes and denser stands of ponderosa pine and Douglas-fir on north slopes; some Rocky Mountain juniper (*Juniperus scopulorum* Sarg.) can also be found (Peet, 1981; Kaufmann et al., 2000). At higher elevations (~2200–2800 m), stands of ponderosa pine and Douglas-fir can also contain quaking aspen (*Populus tremuloides* Michx.), blue spruce (*Picea pungens* Engelm.), and lodgepole pine

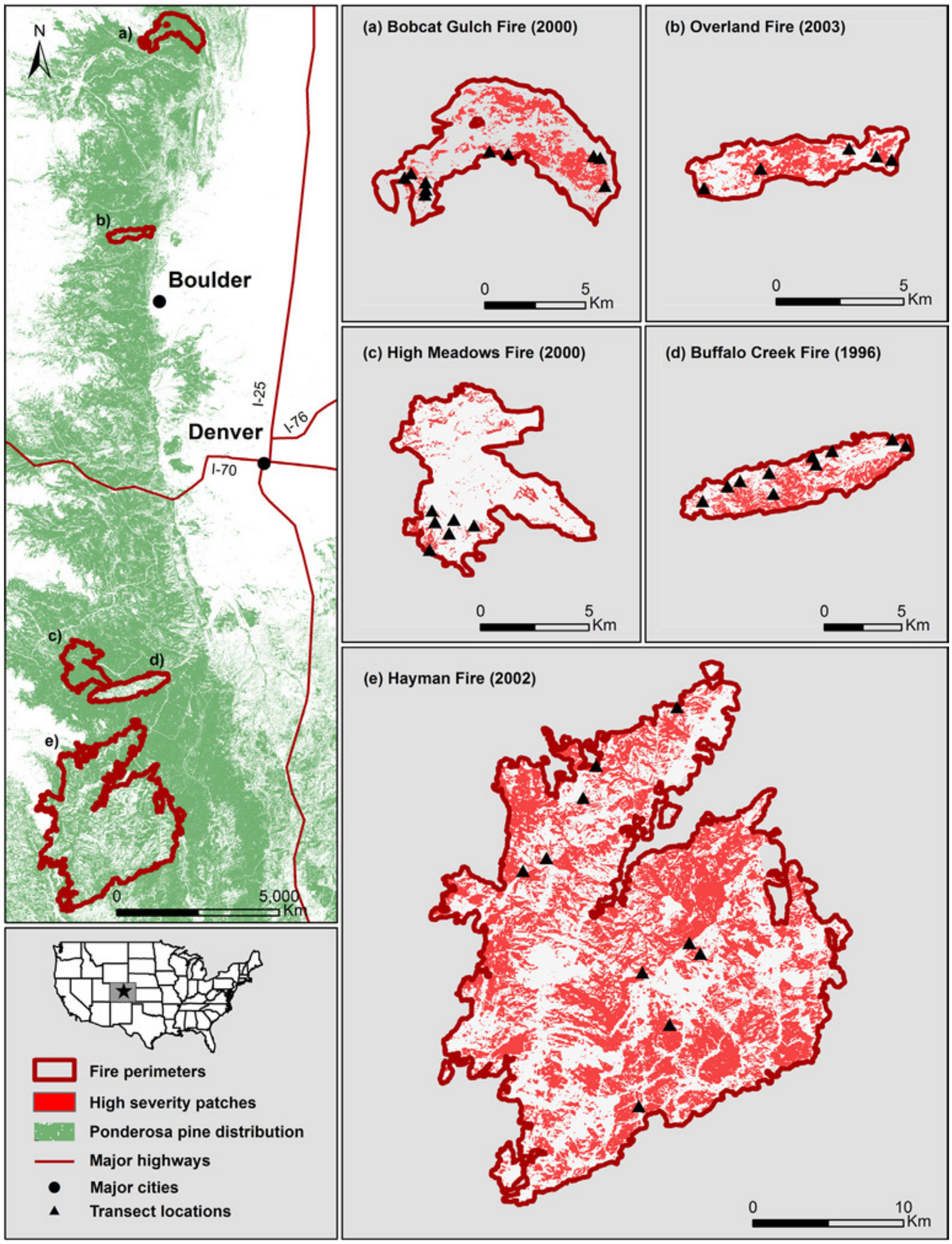

Fig. 2. Map of the five sampled wildfires in the Colorado Front Range, USA. The distribution of ponderosa pine – dominated forest was taken from LANDFIRE (2012) and fire perimeters and high severity burn patches were taken from MTBS (2014). Note that the MTBS high severity category does not necessarily represent 100% overstory tree mortality (our definition of high severity fire) and is shown for general insight only.

(*Pinus contorta* Douglas ex Loudon), with density increasing and the latter three species becoming more common as elevation increases and as aspect becomes more northerly. Understory plant communities throughout the study area tend to be diverse and dominated by graminoids and forbs (e.g., common yarrow (*Achillea millefollium* L.), white sagebrush (*Artemisia ludoviciana* Nutt.), Ross' sedge (*Carex rossii* Boott), mountain muhly (*Muhlenbergia montana* (Nutt.) Hitchc.), Peet, 1981; Fornwalt et al., 2009). Relatively short-statured shrubs are often also present (e.g., kinnikinnick (*Arctostaphylos uva-ursi* (L.) Spreng.), alderleaf mountain mahogany (*Cercocarpus montanus* Raf.)). Mean annual precipitation and temperature in representative urban areas within the study area average 44 cm yr^{-1} and 9.5 °C for Lyons (~1600 m), 51 cm yr^{-1} and 8.5 °C for Morrison (~1800 m), 44 cm yr^{-1} and 6.3 °C for Estes Park (~2300 m), and 63 cm yr^{-1} and 4.6 °C for Woodland Park (~2600 m; PRISM, 2014).

2.2. Data collection

Data collection occurred in 2014, within and surrounding five large (>1000 ha) 11–18 year-old wildfires: the 2000 Bobcat Gulch Fire, the 1996 Buffalo Creek Fire, the 2002 Hayman Fire, the 2000 High Meadows Fire, and the 2003 Overland Fire (Table 1; Fig. 2). Fires that were >10 years old were specifically chosen to allow sufficient time for tree regeneration to occur, as it can be episodic (Shepperd et al., 2006).

We established 42 transects across the five fires. Transect locations were determined by first utilizing ArcGIS 10.1 (ESRI, Redlands,

Table 1
Characteristics of the five sampled wildfires, Colorado, USA. Ownership indicates the primary public land management agencies impacted by the fires, and where sampling occurred. Fire areas and burn severity percentages are from MTBS (2014); note that the MTBS high severity category does not necessarily represent 100% overstory tree mortality (our definition of high severity fire) and is included only to provide general insight each fire's amount of high severity burning.

Fire name (year burned)	Ownership	Fire area (ha)	Elevation range (m)	Low severity (% of fire area)	Moderate severity (% of fire area)	High severity (% of fire area)	Number of transects
Bobcat Gulch (2000)	Roosevelt National Forest; City of Fort Collins	3695	1690–2550	48	22	30	10
Buffalo Creek (1996)	Pike National Forest	3964	1900–2360	42	21	37	10
Hayman (2002)	Pike National Forest	52,353	2000–3230	34	22	43	10
High Meadows (2000)	Pike National Forest	3888	2090–2630	60	31	8	7
Overland (2003)	Roosevelt National Forest; Boulder County	1308	1770–2610	40	21	34	5

California, USA), along with Monitoring Trends in Burn Severity (MTBS) layers of fire severity (MTBS, 2014), the ArcGIS aerial imagery base layer, other layers (e.g., land ownership layers, post-fire management activity layers; Pike National Forest and Roosevelt National Forest unpublished data), and our personal knowledge of the fires, to identify study sites within which to place one transect. Sites were a minimum of 10 ha in size. The number of sites per fire was dictated by the availability of locations that met the following four criteria, up to a maximum of ten sites. First, sites needed to contain both surviving forest and an adjacent high severity burn patch (or a portion of a patch) where all trees appeared to have been killed. The high severity burn patch needed to measure at least 300 m wide on all sides so that it could house a transect as described below. Second, pre-fire forests at the sites needed to have been dominated or co-dominated by ponderosa pine. Third, sites needed to exclude private land and inaccessible terrain. Fourth, sites needed to have not experienced post-fire tree planting and salvage logging activities. Post-fire tree planting was conducted in portions of the Buffalo Creek, Hayman and High Meadows Fires, and post-fire salvage logging was conducted in portions of the Hayman and High Meadows Fires. We estimate that planting and logging activities, which were largely restricted to areas near roads, impacted <10% of the high severity burn area in these fires. Next, points were generated in ArcGIS along the surviving forest edge at each site, and one point was randomly selected. Then, in the field we verified that the four site selection criteria were being met, and we established a transect through the random point. The transect originated 50 m inside the surviving forest in the low to moderate severity burn patch and extended out into the high severity burn patch 150–250 m. When placing the transect within the high severity burn patch, we were careful to ensure that the distance along it equaled the distance to the surviving forest from which it originated. We were also careful to ensure that other surviving trees (e.g., trees that had not been apparent in the aerial imagery, trees along another surviving forest edge) were at least as far away from the transect as the originating surviving forest. Distances were verified with a hand-held long-distance rangefinder as necessary.

We established circular 100 m^2 (5.67 m radius) plots at 50 m intervals along the 42 transects, with an additional plot in the high severity burn patch at 25 m from the surviving forest edge to intensify sampling near living trees. The transects contained a total of 305 plots, with 42 in low to moderate severity burn areas and 263 in high severity burn areas. We 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, we identified sites in ArcGIS that were at least 10 ha in size and that met criteria two and three above, and we randomly located the plot within it. At least three unburned plots were established for each fire; a total of 21 unburned plots were established across all five fires.

Within each 100 m^2 plot, we recorded the height and species of all live post-fire regenerating trees $\geqslant$5 cm tall. If we were uncertain about whether a tree regenerated post-fire, we estimated its age by whorl counting (Urza and Sibold, 2013). We measured topographic attributes of the plot, including elevation, slope, and aspect. We also reconstructed pre-fire stand structure, recording live or dead status, species, and diameter at breast height (DBH) for all pre-fire trees $\geqslant$4 cm DBH. Within each 100 m^2 plot, we established four 2 m^2 subplots between 2.5 and 4.5 m from the plot center in each cardinal direction, and within these, we made ocular cover estimates of graminoids, forbs, shrubs, fine (<7.6 cm diameter) wood, coarse ($\geqslant$7.6 cm diameter) wood, and other ground cover variables. The cover of each variable was estimated to the nearest 1% if it was $\leqslant$20% or $\geqslant$80%, and to the nearest 5% otherwise.

2.3. Data analysis

We used a mixed model analysis of variance in SAS 9.4 (PROC GLIMMIX; SAS Institute Inc., Cary, North Carolina, USA) to examine tree regeneration density in high severity burn areas relative to areas that were unburned and that burned with low to moderate severity. We 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 included in these or other analyses. Models used a Poisson distribution, and incorporated transect as a random effect. Pairwise differences between severity classes were determined using least squares means with a Tukey-Kramer adjustment. Statistical significance in these and all other analyses was assessed with an $\alpha = 0.050$.

We examined the influence of a suite of biotic and abiotic explanatory variables on tree regeneration densities in areas with high severity fire effects using two complementary analytical approaches. First, we used a generalized estimating equation approach in SAS (PROC GENMOD; Liang and Zeger, 1986), modeling all explanatory variables against the regeneration densities of all conifers, ponderosa pine, and Douglas-fir. This analytical approach allowed us to examine the continuous influence of an explanatory variable on the response variable while accounting for other explanatory variables, thereby enabling us to gain nuanced ecological insights into the possible factors governing conifer regeneration following high severity fire. To account for the potential lack of independence among plots on the same transect, transect was included in the models as a repeated measures subject with a compound symmetry correlation structure. Second, we examined the influence of explanatory variables on the regeneration density of all conifers, ponderosa pine, and Douglas-fir using non-parametric regression trees. Regression tree analyses are useful because they can handle complex relationships between explanatory variables and the response variable. Regression tree analyses can also identify explanatory variable threshold values, which can be easily interpreted and utilized by managers as part of post-fire decision-making processes. Regression tree analyses were conducted in R 2.14.12 (R Core Team, 2014) using the CTREE function of the PARTY package (Breiman et al., 1984; Hothorn et al., 2006). We calculated an overall r^2 for our regression trees as 1 − (variance of the residuals/total variance).

Field-measured biotic and abiotic explanatory variables for the two analytical approaches described above included pre-fire stand basal area, understory vegetation cover (the sum of graminoid, 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 average

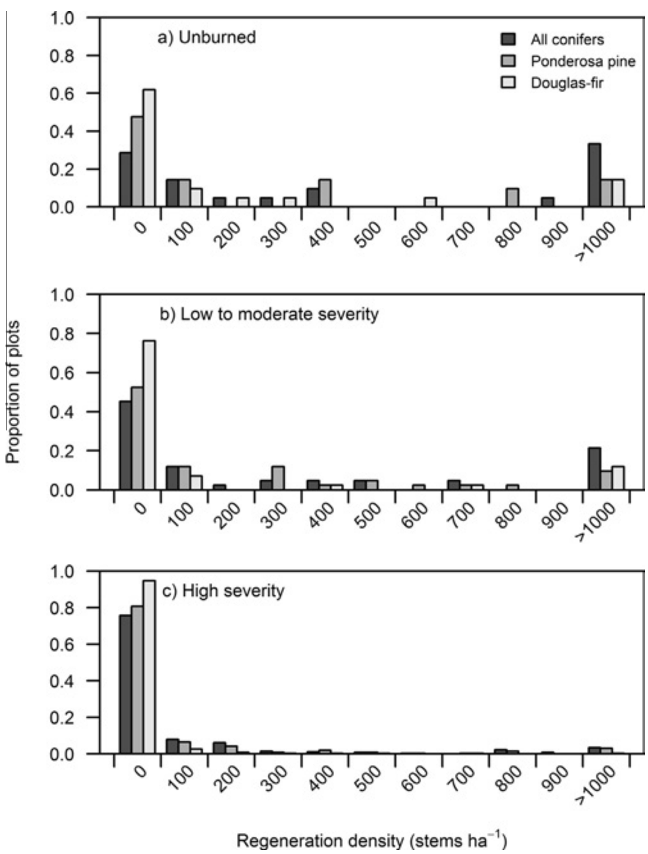

Fig. 3. Frequency distributions of post-fire tree regeneration density, by species, in (a) unburned plots, (b) low to moderate severity burn plots, and (c) high severity burn plots. Regeneration density values on the x-axis are the upper bounds of the bin.

annual precipitation (PRISM, 2014), soil productivity index (FHTET, 2015), drainage index (FHTET, 2015), topographic wetness index, and annual solar radiation. Topographic wetness index, an index of water availability that incorporates the slope of a plot and the upslope area draining to that plot (Beven and Kirkby, 1979), was calculated in ArcGIS using 10 m resolution digital elevation models and several hydrology tools (NRCS, 2015). Annual solar radiation was calculated in ArcGIS using 10 m resolution digital elevation models and the points solar radiation tool (NRCS, 2015).

We used regression tree results to develop a predictive map of conifer regeneration density in high severity burn patches within the Hayman Fire. Elevation and distance from surviving forest were the significant predictors of conifer regeneration in the regression tree analysis (described in more detail below). The Hayman Fire perimeter layer was taken from MTBS (2014). The elevation layer was derived from a 10 m resolution digital elevation model (NRCS, 2015). The distance from surviving forest layer was derived from post-fire aerial imagery (1 m resolution 2013 National Agriculture Imagery Program (NAIP) imagery; NAIP, 2015). The distance from surviving forest layer was created by first creating a layer of surviving forest. This was accomplished by performing a supervised classification of the imagery with the maximum likelihood classification tool in ArcGIS. The resulting layer was then converted to a polygon layer and all surviving forest polygons within 20 m were aggregated and any holes less than 50 m^2 were dissolved. The entire surviving forest polygon layer was edited to omit unforested areas and to contain all tree canopies. Surviving forest polygons were edited until a 90% kappa was obtained. Accuracy of the surviving forest layer was assessed on two occasions with two different validation datasets. Within each dataset we classified 1000 random points as forested or unforested based on the NAIP imagery and compared these points to the surviving forest layer; the final surviving forest layer was determined to be 95% accurate with a commission error of 4%. The high severity burn layer was also derived from the surviving forest layer, as its inverse. This layer was used to define the prediction area within the Hayman Fire, and assumes that post-fire unforested areas were previously forested and burned with high severity fire.

3. Results

We documented 734 post-fire regenerating conifers in our 326 100 m^2 plots, with ponderosa pine (69%) and Douglas-fir (28%)

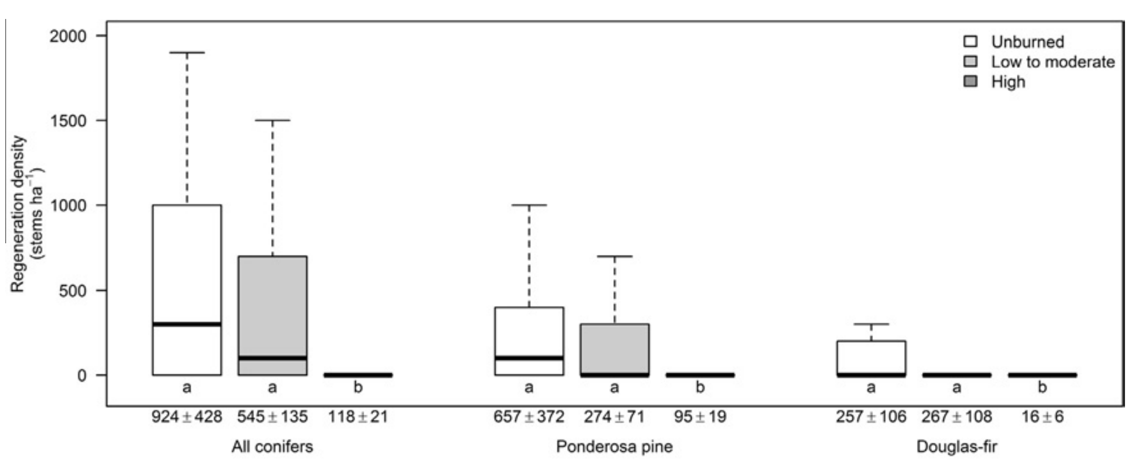

Fig. 4. Box-and-whisker diagrams depicting post-fire tree regeneration density (stems ha^{-1}) by severity class and species groups. The mean (±1 standard error of the mean) density is reported along the x-axis. For each species group, fire severity classes that share letters were not significantly different (α = 0.050).

Table 2
Generalized estimating equation results of post-fire tree regeneration density in high severity plots, by species. Significant (α = 0.050) variables are highlighted in bold. The plot-level range of observed values for each variable is also shown.

Variable	Range	All conifers	Ponderosa pine	Douglas-fir
Distance from surviving forest (m)	0–250	**<0.001**	**<0.001**	0.234
Elevation (m)	1733–2728	**<0.001**	**0.002**	**0.009**
Slope (°)	2–60	0.506	0.250	0.492
Aspect (° from southwest)	0–180	0.277	0.545	0.599
Precipitation (mm yr^{-1})	409–587	0.526	0.317	0.185
Pre-fire stand basal area (m^2 ha^{-1})	0–61	0.289	0.421	0.210
Coarse wood (% cover)	0–34	0.332	0.121	0.351
Fine wood (% cover)	0–27	0.767	0.854	0.108
Understory vegetation (% cover)	3–100	0.492	0.462	**0.031**
Productivity index	0–16	0.525	0.832	0.177
Drainage index	7–93	0.396	0.550	0.931
Topographic wetness index	3–10	0.521	0.665	0.733
Solar radiation (MJ m^{-2} yr^{-1})	3279–6378	0.655	0.974	0.427

dominating. Regeneration density across the plots was highly variable, but was nonetheless related to fire severity (Figs. 3 and 4). Some conifer regeneration was found in high severity burn areas, with a mean density of 118 stems ha^{-1} and a median density of 0 stems ha^{-1}, but unburned and low to moderate severity burn areas had considerably more. Likewise, ponderosa pine and Douglas-fir regeneration densities were also higher in both unburned and low to moderate severity burn areas compared to high severity burn areas. Conifer regeneration in high severity burn areas was concentrated in only 25% of the plots; 75% of plots had no conifer regeneration. In contrast, 40% of plots in low to moderate severity burn areas and 30% of plots in unburned areas lacked post-fire conifer regeneration.

Generalized estimating equation analyses revealed that post-fire conifer and ponderosa pine regeneration densities in areas burned by high severity fire declined as distance from surviving forest increased, but Douglas-fir density did not (Table 2, Fig. 5). Conifer and ponderosa pine regeneration densities immediately adjacent to surviving forest were estimated to be 211 and 167 stems ha^{-1}, respectively. At 50 m from surviving forest, conifer and ponderosa pine regeneration density estimates declined by more than half, to 96 and 67 stems ha^{-1}, respectively. Conifer and ponderosa pine regeneration densities were estimated to be only 10 and 5 stems ha^{-1}, respectively, in areas 200 m from surviving forest.

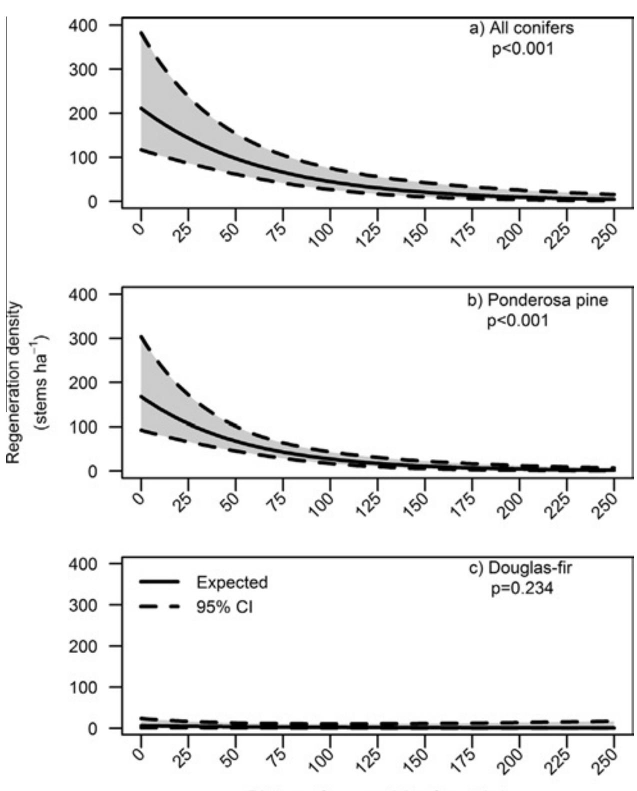

Fig. 5. Estimated (and 95% confidence interval (CI)) post-fire tree regeneration density in high severity plots as a function of distance from surviving forest, for (a) all conifers, (b) ponderosa pine, and (c) Douglas-fir.

Generalized estimating equation analyses further identified other significant predictors of post-fire conifer, ponderosa pine, and Douglas-fir regeneration densities in high severity burn areas (Table 2; Figs. 6 and 7). Elevation was correlated with regeneration density for all three species groups, with densities increasing with increasing elevation. At 2200 m elevation, regeneration densities were estimated to be 33, 21, and 1 stems ha^{-1} for all conifers, ponderosa pine, and Douglas-fir, respectively. At 2400 m elevation, estimated densities were 85, 51, and 7 stems ha^{-1} for all conifers, ponderosa pine, and Douglas-fir, respectively, and at 2600 m, estimated densities were 217, 124, and 34 stems ha^{-1}, respectively. Understory vegetation cover was also correlated with Douglas-fir regeneration density, with higher levels of cover fostering more regeneration; understory vegetation cover was not correlated with conifer or ponderosa pine regeneration density.

Regression tree analyses likewise identified distance from 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 (Fig. 8). Distance from surviving forest was the first and most significant predictor of both conifer and ponderosa pine regeneration density. At distances ⩾50 m from surviving forest, mean post-fire conifer and ponderosa pine regeneration was 49 and 34 stems ha^{-1}, respectively, while median 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, mean (median) conifer and ponderosa pine regeneration densities were 150 (0) and 132 (0) stems ha^{-1}, respectively. Where elevation was >2490 m, mean (median) conifer and ponderosa pine regeneration densities were 1120 (1000) and 930 (750) stems ha^{-1}, respectively. The conifer regression tree produced an overall r^2 of 0.35 and the ponderosa pine regression tree produced an overall r^2 of 0.30.

Applying the conifer regression tree results spatially to the high severity portions of the 52,353 ha Hayman Fire, we found that 16% of the area that burned at high severity (5922 of 36,525 ha) was predicted to have mean (median) regeneration densities of 1120 (1000) stems ha^{-1} (i.e., distance from surviving forest <50 m and

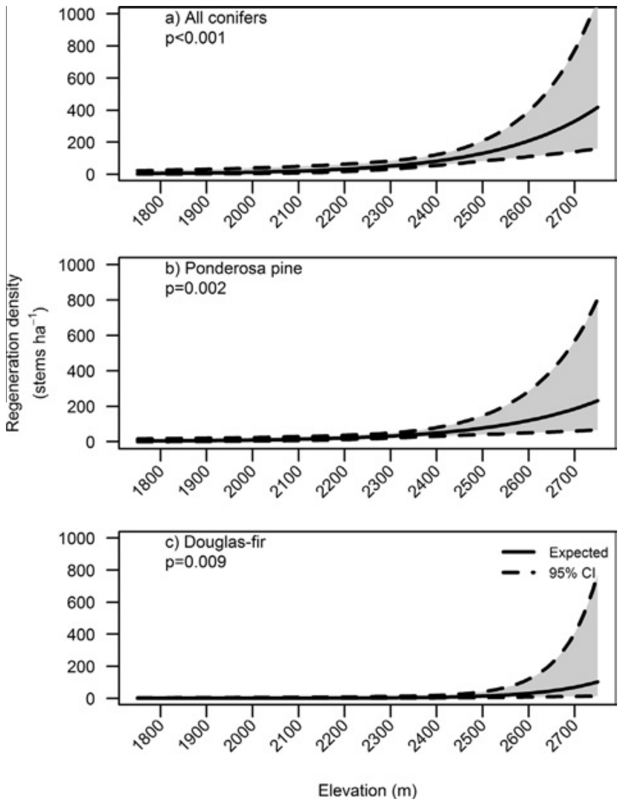

Fig. 6. Estimated (and 95% confidence interval (CI)) post-fire tree regeneration density in high severity plots as a function of elevation for (a) all conifers, (b) ponderosa pine and (c) Douglas-fir.

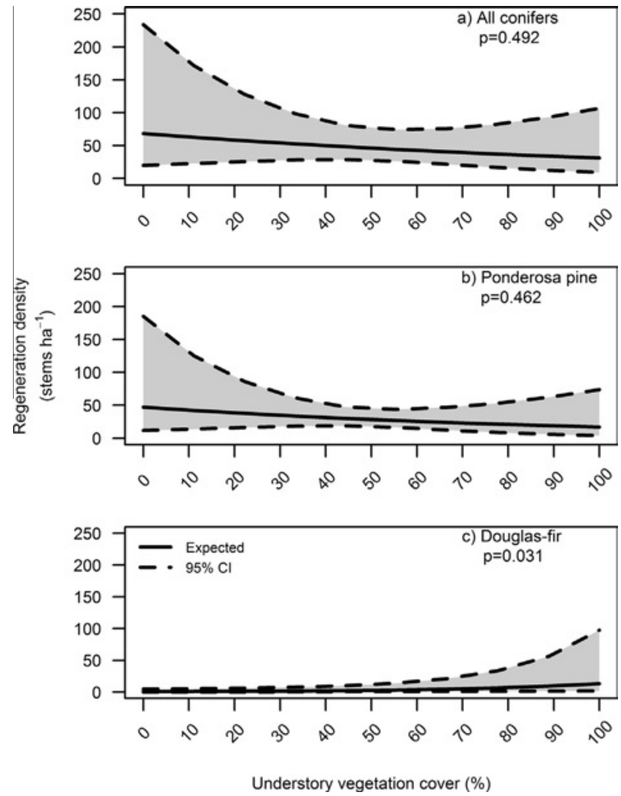

Fig. 7. Estimated (and 95% confidence interval (CI)) post-fire tree regeneration density in high severity plots as a function of understory vegetation cover for (a) all conifers, (b) ponderosa pine and (c) Douglas-fir.

elevation >2490 m; Fig. 9). Meanwhile, 14% of the high severity area (5095 ha) was predicted to have mean (median) conifer regeneration densities of 150 (0) stems ha^{-1} (distance <50 m and elevation $\leqslant$2490 m), and 70% (25,508 ha) was predicted to have mean (median) regeneration densities of 49 (0) stems ha^{-1} (distance $\geqslant$50 m). Contiguous areas predicted to have mean (median) regeneration densities of 49 (0) stems ha^{-1} averaged 14 ha in size, with 23 areas (representing 60% of the total high severity burn area) >100 ha.

4. Discussion

The resilience of ponderosa pine – dominated forests in high severity burn areas of recent wildfires is predicated on sufficient post-fire tree regeneration, as no surviving trees remain. Our examination of regeneration in high severity burn areas of five Colorado Front Range fires illustrates that ponderosa pine and other conifers such as Douglas-fir have naturally regenerated in the 11–18 years since the fires occurred, but at very low densities relative to areas that were unburned or that burned with lesser severity (Figs. 3 and 4). Similar studies conducted in ponderosa pine – dominated forests have likewise found a dearth of regeneration in high severity burn areas (Bonnet et al., 2005; Savage and Mast, 2005; Keyser et al., 2008; Roccaforte et al., 2012; Collins and Roller, 2013). Ponderosa pine and Douglas-fir's reliance on live trees as seed sources likely limits their regeneration in high severity burn areas as a whole (Barrett, 1966; McDonald, 1980; Herman and Lavender, 1990; Oliver and Ryker, 1990; Johansen and Latta, 2003; Bai et al., 2004). Unfavorable climate may further limit regeneration in high severity burn areas. High temperatures, wind speeds, and solar radiation due to a lack of overstory trees can result in unfavorable germination conditions, or, if germination occurs, in desiccation of establishing and established seedlings (Stein and Kimberling, 2003; Feddema et al., 2013; Petrie et al., 2016).

In this study, two complementary analytical approaches indicated that, within high severity burn areas, distance from surviving forest was the most important predictor of both all conifer and ponderosa pine regeneration (Table 2; Figs. 5 and 8). Generalized estimating equation analyses revealed that all conifer and ponderosa pine regeneration declined as distance from surviving forest increased. Similarly, regression tree analyses identified 50 m as a threshold, with regeneration more abundant at distances below than above this distance. Our findings are consistent with those from similar studies conducted not only in the Colorado Front Range (Rother, 2015), but also in South Dakota (Bonnet et al., 2005), in Idaho and Montana (Kemp et al., 2016), and in New Mexico and Arizona (Haire and McGarigal, 2010; Haffey, 2014). Our findings are also in line with the general rule that ponderosa pine seeds disperse distances of only one or two times the parent tree height (Barrett, 1966; McDonald, 1980; Oliver and Ryker, 1990; Johansen and Latta, 2003). In contrast, the relationship between distance from surviving forest and Douglas-fir regeneration was not significant in any of our analyses. This may be because Douglas-fir seeds are smaller and are more readily wind-dispersed than those of ponderosa pine (Herman and Lavender, 1990). In the Klamath-Siskiyou region, Oregon, Donato et al. (2009) found that median Douglas-fir – dominated regeneration densities were in excess of 1000 stems ha^{-1} until distance exceeded 400 m, at which point they declined.

Elevation was also an important predictor of where regeneration occurred in high severity burn areas. The results of our

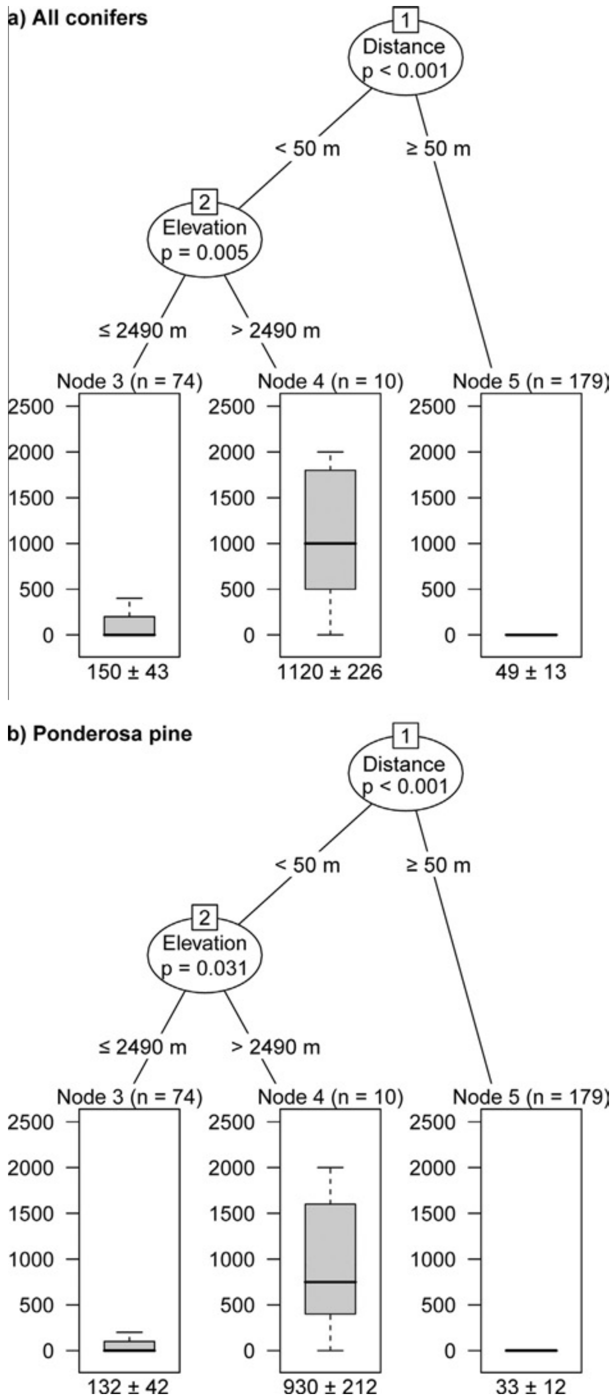

Fig. 8. Regression trees of post-fire tree regeneration density (stems ha^{-1}) in high severity burn plots for (a) all conifers and (b) ponderosa pine. Distance is distance from surviving forest (m). Box-and-whisker diagrams are shown for each division, along with the mean (±1 standard error of the mean).

generalized estimating equation analyses showed that elevation was highly positively correlated with regeneration density for all conifers, ponderosa pine, and Douglas-fir (Table 2; Fig. 6), while regression tree analyses indicated that elevations >2490 m were associated with increased regeneration densities for all conifers and ponderosa pine relative to elevations ⩽2490 m, at least near surviving forest (Fig. 8). While only 10 plots were located at elevations >2490 m, they were distributed across three of the five sampled fires (Bobcat, High Meadows, and Hayman Fires), and thus we believe that the latter results are likely generalizable across our study area. Elevational gradients are marked by gradients of temperature, precipitation, and evapotranspiration, with areas at lower elevations typically experiencing higher temperatures, lower precipitation, and higher evapotranspiration rates than their higher elevation counterparts (Peet, 1981). Our results suggest that the harsher environmental conditions typically associated with lower elevations may pose challenges for successful regeneration, even when surviving forest is in close proximity. Other studies in ponderosa pine – dominated forests have likewise found that lower elevations were associated with decreased regeneration densities (Dodson and Root, 2013; Rother, 2015).

Understory vegetation cover has been implicated by some as inhibiting tree regeneration in burned ponderosa pine – dominated forests (Bonnet et al., 2005; Collins and Roller, 2013; but see Kemp et al., 2016). Surprisingly, we found that it did not influence conifer or ponderosa pine regeneration densities in high severity burn areas, and that it positively influenced Douglas-fir regeneration (Table 2, Fig. 7). The light requirements of ponderosa pine and Douglas-fir may explain their contrasting relationship to understory vegetation cover. Ponderosa pine requires abundant light for successful recruitment (Oliver and Ryker, 1990; Stein and Kimberling, 2003), whereas Douglas-firs are sensitive to high light levels (Herman and Lavender, 1990). Thus, it is plausible that understory vegetation may provide small Douglas-firs protection from the high light levels encountered in high severity burn areas.

Several variables not examined in this study may further drive patterns of post-fire tree regeneration in high severity burn areas. Soil moisture is thought to be one of the most important factors influencing post-fire regeneration in ponderosa pine – dominated forests (Stein and Kimberling, 2003; Puhlick et al., 2012; Dodson and Root, 2013). While we suspect soil moisture is correlated with some of the variables we did quantify, such as elevation and understory vegetation cover, we did not explicitly quantify it. Field studies that monitor seed germination and seedling establishment in combination with soil moisture are limited (Petrie et al., 2016), and such studies in the context of wildfire are lacking, and would undoubtedly advance our understanding of this potential driving variable. 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 high severity burn areas, and/or in the direction of the prevailing winds, may be more effective at dispersing seeds than forest that is not (Barrett, 1966; McDonald, 1980; but see Donato et al., 2009).

Our predictive map of post-fire conifer regeneration for the 2002 Hayman Fire illustrates how the size, shape, and distribution of high severity burn patches can influence spatial patterns of forest resilience. Approximately 70% of this fire's high severity burn area was ⩾50 m from surviving forest, and was predicted to have very low densities of regenerating conifers (mean and median of 49 and 0 stems ha^{-1}, respectively). This map does come with a few limitations. First, high severity burn areas were identified as any area in the 2013 NAIP imagery that did not contain surviving trees, and thus pre-fire unforested areas likely caused us to overestimate them. An examination of pre-fire vegetation maps for the Pike National Forest suggests that unforested areas accounted for around 7% of the Hayman's area prior to the fire, and were predominately roads, followed by water bodies, grasslands, shrublands, and barren rock (Pike National Forest unpublished data). Additionally, in this study we sampled conifer regeneration in plots up to 250 m from surviving forest, but we extrapolated our regression tree results to areas >250 m from surviving forest in the predictive map. The exponential decline in conifer regeneration density with distance from surviving forest that is apparent in Fig. 5 suggests that sampling these areas could have resulted in an additional division (or more) on the regression

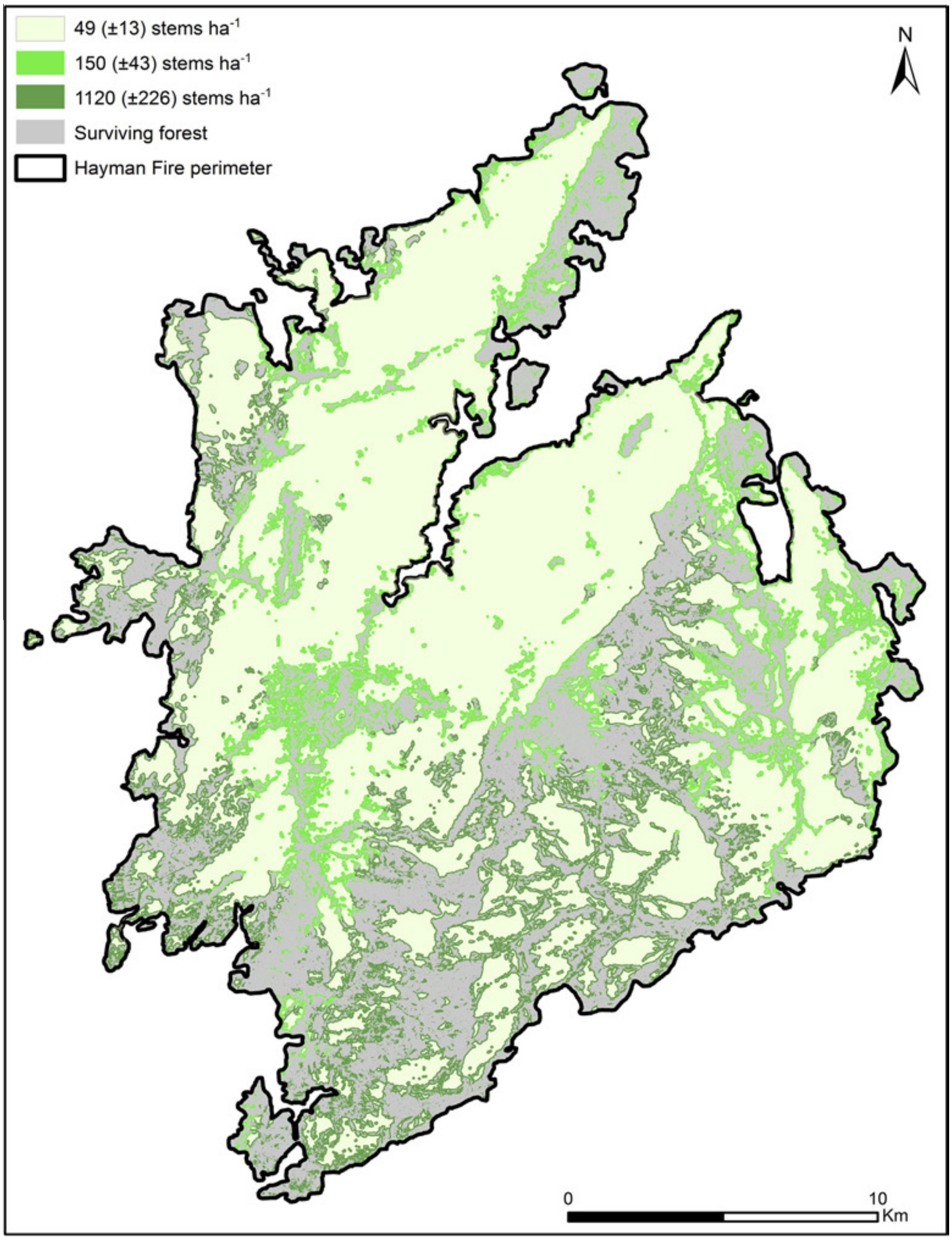

Fig. 9. Predicted mean (±1 standard error of the mean) post-fire conifer regeneration densities within unforested portions of the Hayman Fire, per the results of the all conifer regression tree analysis. Areas in pale green are ⩾50 m from surviving forest, while areas in bright green are <50 m from surviving forest and ⩽2490 m in elevation, and areas in dark green are <50 m from surviving forest and >2490 m in elevation.

tree, with mean value(s) < 49 stems ha^{-1}. Furthermore, the regression tree used to derive the predictive map had an overall r^2 of only 0.35, suggesting that the map is most appropriately used to gain general insight into the spatial distribution of regeneration in the Hayman Fire, rather than to extract precise predictions for specific locales. Nonetheless, we believe that our predictive map or similarly derived maps for other Front Range fires will be valuable tools to managers planning post-fire restoration activities in high severity burn patches.

5. Conclusions and management implications

Information on post-fire conifer regeneration is critical for the effective management of burned landscapes formerly occupied by ponderosa pine – dominated forests. The post-fire regeneration densities we found, particularly in areas where surviving forest was not in close proximity, were well below several benchmarks that might be used by Colorado Front Range land managers to assess post-fire regeneration sufficiency. The National Forest Management Act mandates that minimum regeneration values of 370 stems ha^{-1} are necessary for burned ponderosa pine – dominated forests in this area to remain in the timber base (PSICC, 1984; ARP, 1997). Our reconstruction of pre-fire stand structure indicated that densities averaged ~650 stems ha^{-1} prior to burning, similar to densities reported elsewhere in the Colorado Front Range (Kaufmann et al., 2000; Brown et al., 2015). Historical forest densities, which may provide a more appropriate benchmark than pre-fire densities because most ponderosa pine - dominated forests are widely believed to be overstocked, averaged ~100 stems ha^{-1} in one low elevation study area of the Front Range (Brown et al., 2015) and ~140 stems ha^{-1} in the broader Front Range region (M.A. Battaglia unpublished data).

Regenerating trees will continue to establish – and die – in high severity burn areas of these and other recent Colorado Front Range wildfires, making it difficult to provide managers with predictions of longer-term recovery trajectories in the absence of continued research. Nonetheless, we suspect that regeneration in high severity burn areas not in close proximity to surviving trees will be insufficient to return them to a forested condition (as evaluated by the aforementioned benchmarks) for many decades, if not centuries. Post-fire regeneration that has already established will take decades to reach reproductive maturity and in turn become a seed source (Oliver and Ryker, 1990), which is critical for the reforestation of areas where surviving forests are especially distant. Future post-fire regeneration, from seeds of either surviving or post-fire trees, may face competition from well-established understory graminoids, forbs, and shrubs (Bonnet et al., 2005; Collins and Roller, 2013). Additionally, projections of increased temperatures and decreased rates of precipitation may create conditions unfavorable for tree establishment and favorable for mortality due to drought and subsequent wildfires (Spracklen et al., 2009; Brekke et al., 2013; Feddema et al., 2013; IPCC, 2013; Savage et al., 2013; Yue et al., 2013; Lukas et al., 2014; Rother et al., 2015; Petrie et al., 2016). We suggest that managers consider reforestation activities such as tree planting in high severity burn areas where maintaining a forested condition is an objective, particularly where surviving forest is not in close proximity.

Furthermore, we recommend that managers continue to implement ecologically appropriate restoration treatments in ponderosa pine – dominated forests that are at increased risk of uncharacteristic high severity wildfire. Restoration treatments should aim to create more open and heterogeneous forest conditions by reducing canopy density while creating stands that are a diverse mixture of openings, individual trees, and tree groups (Underhill et al., 2014). Such treatments have been shown to moderate fire behavior, even under extreme weather conditions (Finney et al., 2005; Lentile et al., 2006; Fulé et al., 2012; Waltz et al., 2014), and will likely increase the probability that surviving trees remain within the footprints of future fires. Restoration treatments are especially important because future fires are predicted to become even more severe and more frequent in ponderosa pine forests of the Colorado Front Range due to climate change (Spracklen et al., 2009; Litschert et al., 2012; Liu et al., 2013; Yue et al., 2013; Rocca et al., 2014), and larger high severity burn patches coupled with shorter fire return intervals and a warmer and drier climate will provide even more challenges to the resilience of severely burned ponderosa pine – dominated forests.

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References

ARP [Arapaho and Roosevelt National Forest and Pawnee National Grassland], 1997. Revision of the Land and Resource Management Plan. US Department of Agriculture, Forest Service, Arapaho and Roosevelt National Forest and Pawnee National Grassland, Fort Collins, Colorado, USA.

Bai, Y., Thompson, D., Broersma, K., 2004. Douglas fir and ponderosa pine seed dormancy as regulated by grassland seedbed conditions. Rangeland Ecol. Manage. 57, 661–667.

Baisan, C.H., Swetnam, T.W., 1990. Fire history on a desert mountain range: Rincon Mountain Wilderness, Arizona, USA. Can. J. For. Res. 20, 1559–1569.

Barrett, J.W., 1966. A Record of Ponderosa Pine Seed Flight. Research Note PNW-38. US Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station, Portland, Oregon, USA.

Beven, K.J., Kirkby, M.J., 1979. A physically based variable contributing area model of basin hydrology. Hydrol. Sci. Bull. 24, 43–69.

Bonnet, V.H., Schoettle, A.W., Shepperd, W.D., 2005. Postfire environmental conditions influence the spatial pattern of regeneration for *Pinus ponderosa*. Can. J. For. Res. 35, 37–47.

Breiman, L., Friedman, J., Stone, C.J., Olshen, R.A., 1984. Classification and Regression Trees. CRC Press.

Brekke, L., Thrasher, B.L., Maurer, E.P., Pruitt, T., 2013. Downscaled CMIP3 and CMIP5 Climate Projections: Release of Downscaled CMIP5 Climate Projections, Comparison with Preceding Information, and Summary of User Needs. US Department of the Interior, Bureau of Reclamation, Technical Services Center, Denver, Colorado.

Brown, P.M., Kaufmann, M.R., Shepperd, W.D., 1999. Long-term, landscape patterns of past fire events in a montane ponderosa pine forest of central Colorado. Landscape Ecol. 14, 513–532.

Brown, P.M., Wienk, C.L., Symstad, A.J., 2008. Fire and forest history at Mount Rushmore. Ecol. Appl. 18, 1984–1999.

Brown, P.M., Battaglia, M.A., Fornwalt, P.J., Gannon, B., Huckaby, L.S., Julian, C., Cheng, A.S., 2015. Historical (1860) forest structure in ponderosa pine forests of the northern Front Range, Colorado. Can. J. For. Res. 45, 1462–1473.

Collins, B.M., Roller, G.B., 2013. Early forest dynamics in stand-replacing fire patches in the northern Sierra Nevada, California, USA. Landscape Ecol. 28, 1801–1813.

Dodson, E.K., Root, H.T., 2013. Conifer regeneration following stand-replacing wildfire varies along an elevation gradient in a ponderosa pine forest, Oregon, USA. For. Ecol. Manage. 302, 163–170.

Donato, D.C., Fontaine, J.B., Campbell, J.L., Robinson, W.D., Kauffman, J.B., Law, B.E., 2009. Conifer regeneration in stand-replacement portions of a large mixed-severity wildfire in the Klamath-Siskiyou Mountains. Can. J. For. Res. 39, 823–838.

Everett, R.L., Schellhaas, R., Keenum, D., Spurbeck, D., Ohlson, P., 2000. Fire history in the ponderosa pine/Douglas-fir forests on the east slope of the Washington Cascades. For. Ecol. Manage. 129, 207–225.

Feddema, J.J., Mast, J.N., Savage, M., 2013. Modeling high-severity fire, drought and climate change impacts on ponderosa pine regeneration. Ecol. Model. 253, 56–69.

FHTET [Forest Health Technology Enterprise Team], 2015. Soil Drainage Index and Productivity Index. US Department of Agriculture, Forest Service and Michigan State University (accessed 20.04.15) <http://foresthealth.fs.usda.gov/soils>.

Finney, M.A., McHugh, C.W., Grenfell, I.C., 2005. Stand-and landscape-level effects of prescribed burning on two Arizona wildfires. Can. J. For. Res. 35, 1714–1722.

Fisher, R.F., Jenkins, M.J., Fisher, W.F., 1987. Fire and the prairie-forest mosaic of Devils Tower National Monument. Am. Midl. Nat., 250–257.

Fornwalt, P.J., Kaufmann, M.R., Huckaby, L.S., Stohlgren, T.J., 2009. Effects of past logging and grazing on understory plant communities in a montane Colorado forest. Plant Ecol. 203, 99–109.

Fulé, P.Z., Covington, W.W., Moore, M.M., 1997. Determining reference conditions for ecosystem management of southwestern ponderosa pine forests. Ecol. Appl. 7, 895–908.

Fulé, P.Z., Crouse, J.E., Roccaforte, J.P., Kalies, E.L., 2012. Do thinning and/or burning treatments in western USA ponderosa or Jeffrey pine-dominated forests help restore natural fire behavior? For. Ecol. Manage. 269, 68–81.

Goforth, B.R., Minnich, R.A., 2008. Densification, stand replacement wildfire, and extirpation of mixed conifer forest in Cuyamaca Rancho State Park, southern California. For. Ecol. Manage. 256, 36–45.

Guiterman, C.H., Margolis, E.Q., Swetnam, T.W., 2015. Dendroecological methods for reconstructing high-severity fire in pine-oak forests. Tree-Ring Res. 71, 67–77.

Haffey, C.M., 2014. Patterns and Predictors of Crown Fire Induced Type Conversion in Dry Conifer Forests Thesis. Northern Arizona University, Flagstaff, Arizona, USA.

Haire, S.L., McGarigal, K., 2010. Effects of landscape patterns of fire severity on regenerating ponderosa pine forests (*Pinus ponderosa*) in New Mexico and Arizona, USA. Landscape Ecol. 25, 1055–1069.

Harris, L., Taylor, A.H., 2015. Topography, fuels, and fire exclusion drive fire severity of the Rim Fire in an old-growth mixed-conifer forest, Yosemite National Park, USA. Ecosystems 18, 1192–1208.

Herman, R.K., Lavender, D.P., 1990. Pseudotsuga menziesii (Mirb.) Franco. In: Douglas fir. Silvics of North America. Agriculture Handbook 654. US Department of Agriculture, Forest Service, Washington, DC, USA, pp. 527–540.

Hessburg, P.F., Salter, R.B., James, K.M., 2007. Re-examining fire severity relations in pre-management era mixed conifer forests: inferences from landscape patterns of forest structure. Landscape Ecol. 22, 5–24.

Hothorn, T., Hornick, K., Zeileis, A., 2006. Unbiased recursive partitioning: a conditional inference framework. J. Comput. Graph. Stat. 15, 651–674.

IPCC [Intergovernmental Panel on Climate Change], 2013. Summary for policymakers. In: Stocker, T.F., Qin, D., Plattner, G.K., Tignor, M., Allen, S.K., Boschung, J., Nauels, A., Xia, Y., Bex, V., Midgley, P.M. (Eds.), Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom and New York, New York, USA.
Johansen, A.D., Latta, R.G., 2003. Mitochondrial haplotype distribution, seed dispersal and patterns of postglacial expansion of ponderosa pine. Mol. Ecol. 12, 293–298.
Kaufmann, M.R., Regan, C.M., Brown, P.M., 2000. Heterogeneity in ponderosa pine/Douglas-fir forests: age and size structure in unlogged and logged landscapes of central Colorado. Can. J. For. Res. 30, 698–711.
Kemp, K.B., Higuera, P.E., Morgan, P., 2016. Fire legacies impact conifer regeneration across environmental gradients in the US northern Rockies. Landscape Ecol. 31, 619–636.
Keyser, T.L., Lentile, L.B., Smith, F.W., Shepperd, W.D., 2008. Changes in forest structure after a large, mixed-severity wildfire in ponderosa pine forests of the Black Hills, South Dakota, USA. For. Sci. 54, 328–338.
LANDFIRE, 2012. Existing Vegetation Type Layer. US Department of Interior, Geological Survey (accessed 18.09.15) <http://landfire.cr.usgs.gov/viewer/>.
Lentile, L.B., Smith, F.W., Shepperd, W.D., 2006. Influence of topography and forest structure on patterns of mixed severity fire in ponderosa pine forests of the South Dakota Black Hills, USA. Int. J. Wildl. Fire 15, 557–566.
Liang, K.Y., Zeger, S.L., 1986. Longitudinal data analysis using generalized linear models. Biometrika 73, 13–22.
Litschert, S.E., Brown, T.C., Theobald, D.M., 2012. Historic and future extent of wildfires in the Southern Rockies Ecoregion, USA. For. Ecol. Manage. 269, 124–133.
Liu, Y., Goodrick, S.L., Stanturf, J.A., 2013. Future US wildfire potential trends projected using a dynamically downscaled climate change scenario. For. Ecol. Manage. 294, 120–135.
Lukas, J., Barsugli, J., Doesken, N., Rangwala, I., Wolter, K., 2014. Climate Change in Colorado: A Synthesis to Support Water Resources Management and Adaptation. University of Colorado, Boulder, Colorado.
McDonald, P.M., 1980. Seed Dissemination in Small Clearcuttings in North-Central California, General Technical Report PSW-150. US Department of Agriculture, Forest Service, Pacific Southwest Forest and Range Experiment Station, Berkeley, California, USA.
MTBS [Monitoring Trends in Burn Severity], 2014. Monitoring Trends in Burn Severity (MTBS). US Department of Agriculture, Geological Survey and US Department of Agriculture, Forest Service (accessed 11.02.14) <http://www.mtbs.gov>.
NAIP [National Agriculture Imagery Program], 2015. USDA National Agriculture Imagery Program (NAIP). US Department of Agriculture, Farm Service Agency (accessed 10.03.15) <http://www.fsa.usda.gov/programs-and-services/aerial-photography/imagery-programs/naip-imagery/index>.
NRCS [Natural Resource Conservation Service], 2015. Geospatial Data Gateway. US Department of Agriculture, Natural Resource Conservation Service (accessed 07.02.15) <https://gdg.sc.egov.usda.gov/>.
O'Connor, C.D., Falk, D.A., Lynch, A.M., Swetnam, T.W., 2014. Fire severity, size, and climate associations diverge from historical precedent along an ecological gradient in the Pinaleño Mountains, Arizona, USA. For. Ecol. Manage. 329, 264–278.
Oliver, W.W., Ryker, R.A., 1990. Pinus ponderosa Dougl. ex Laws. Ponderosa pine. In: Silvics of North America. Agriculture Handbook 654. US Department of Agriculture, Forest Service, Washington, DC, USA, pp. 413–424.
Peet, R.K., 1981. Forest vegetation of the Colorado front range. Vegetation 45, 3–75.
Petrie, M.D., Wildeman, A.M., Bradford, J.B., Hubbard, R.M., Lauenroth, W.K., 2016. A review of precipitation and temperature control on seedling emergence and establishment for ponderosa and lodgepole pine forest regeneration. For. Ecol. Manage. 361, 328–338.
PRISM [PRISM Climate Group], 2014. PRISM Climate Data. Oregon State University (accessed 03.12.14) <http://prism.oregonstate.edu>.
PSICC [Pike and San Isabel National Forests and Comanche and Cimarron National Grasslands], 1984. Land and Resource Management Plan. US Department of Agriculture, Forest Service, Pike and San Isabel National Forests and Comanche and Cimarron National Grasslands, Pueblo, Colorado, USA.
Puhlick, J.J., Laughlin, D.C., Moore, M.M., 2012. Factors influencing ponderosa pine regeneration in the southwestern USA. For. Ecol. Manage. 264, 10–19.
R Core Team, 2014. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
Rocca, M.E., Brown, P.M., MacDonald, L.H., Carrico, C.M., 2014. Climate change impacts on fire regimes and key ecosystem services in Rocky Mountain forests. For. Ecol. Manage. 327, 290–305.
Roccaforte, J.P., Fulé, P.Z., Chancellor, W.W., Laughlin, D.C., 2012. Woody debris and tree regeneration dynamics following severe wildfires in Arizona ponderosa pine forests. Can. J. For. Res. 42, 593–604.
Rother, M., 2015. Conifer Regeneration after Wildfire in Low-elevation Forests of the Colorado Front Range: Implications of a Warmer, Drier Climate Dissertation. University of Colorado, Boulder, Colorado, USA.
Rother, M.T., Veblen, T.T., Furman, L.G., 2015. A field experiment informs expected patterns of conifer regeneration after disturbance under changing climate conditions. Can. J. For. Res. 45, 1607–1616.
Savage, M., Mast, J.N., 2005. How resilient are southwestern ponderosa pine forests after crown fires? Can. J. For. Res. 35, 967–977.
Savage, M., Mast, J.N., Feddema, J.J., 2013. Double whammy: high-severity fire and drought in ponderosa pine forests of the Southwest. Can. J. For. Res. 43, 570–583.
Scholl, A.E., Taylor, A.H., 2010. Fire regimes, forest change, and self-organization in an old-growth mixed-conifer forest, Yosemite National Park, USA. Ecol. Appl. 20, 362–380.
Shepperd, W.D., Edminster, S.B., Mata, S.A., 2006. Long-term seedfall, establishment, survival, and growth of natural and planted ponderosa pine in the Colorado Front Range. West. J. Appl. Forest. 21, 19–26.
Sherriff, R.L., Platt, R.V., Veblen, T.T., Schoennagel, T.L., Gartner, M.H., 2014. Historical, observed, and modeled wildfire severity in montane forests of the Colorado Front Range. PLoS One 9, e106971.
Spracklen, D.V., Mickley, L.J., Logan, J.A., Hudman, R.C., Yevich, R., Flannigan, M.D., Westerling, A.L., 2009. Impacts of climate change from 2000 to 2050 on wildfire activity and carbonaceous aerosol concentrations in the western United States. J. Geophys. Res.: Atmos. 114.
Stein, S.J., Kimberling, D.N., 2003. Germination, establishment, and mortality of naturally seeded southwestern ponderosa pine. West. J. Appl. Forest. 18, 109–114.
Urza, A.K., Sibold, J.S., 2013. Nondestructive aging of postfire seedlings for four conifer species in Northwestern Montana. West. J. Appl. Forest. 28, 22–29.
Underhill, J.L., Dickinson, Y., Rudney, A., Thinnes, J., 2014. Silviculture of the Colorado Front Range landscape restoration initiative. J. For. 112 (5), 484–493.
Veblen, T.T., Kitzberger, T., Donnegan, J., 2000. Climatic and human influences on fire regimes in ponderosa pine forests in the Colorado Front Range. Ecol. Appl. 10, 1178–1195.
Waltz, A.E., Stoddard, M.T., Kalies, E.L., Springer, J.D., Huffman, D.W., Meador, A.S., 2014. Effectiveness of fuel reduction treatments: assessing metrics of forest resiliency and wildfire severity after the Wallow Fire, AZ. For. Ecol. Manage. 334, 43–52.
Westerling, A.L., Hidalgo, H.G., Cayan, D.R., Swetnam, T.W., 2006. Warming and earlier spring increase western US forest wildfire activity. Science 313, 940–943.
Williams, M.A., Baker, W.L., 2012. Spatially extensive reconstructions show variable-severity fire and heterogeneous structure in historical western United States dry forests. Glob. Ecol. Biogeogr. 21, 1042–1052.
Yue, X., Mickley, L.J., Logan, J.A., Kaplan, J.O., 2013. Ensemble projections of wildfire activity and carbonaceous aerosol concentrations over the western United States in the mid-21st century. Atmos. Environ. 77, 767–780.