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Strategically placed landscape fuel treatments decrease fire severity and promote recovery in the northern Sierra Nevada

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Abstract

Strategically placed landscape area treatments (SPLATs) are landscape fuel reduction treatments designed to reduce fire severity across an entire landscape with only a fraction of the landscape treated. Though SPLATs have gained attention in scientific and policy arenas, they have rarely been empirically tested. This study takes advantage of a strategically placed landscape fuel treatment network that was implemented and monitored before being burned by a wildfire. We evaluated treatment efficacy in terms of resistance, defined here as the capacity to withstand disturbance, and recovery, defined here as regeneration following disturbance. We found that the treated landscape experienced lower fire severity than an adjacent control landscape: in the untreated control landscape, 26% of land area was burned with >90% basal area mortality, according to the remote-sensing-derived relative differenced Normalized Burn Ratio (RdNBR), while in the treated landscape only 11% burned at the same severity. This difference was despite greater pre-treatment fire risk in the treatment landscape, as indicated by FARSITE fire behavior modeling. At a more local scale, monitoring plots within the treatments themselves saw greater regeneration of conifer seedlings two years following the fire than plots outside the treatments. Mean seedling densities for all conifer species were 7.8 seedlings m^{-2} in treated plots and only 1.4 seedlings m^{-2} in control plots. These results indicate that SPLATs achieved their objective of increasing forest resistance and recovery.

Key words: forest resilience; frequent-fire forests; regeneration; mixed-conifer forest; restoration; Sierra Nevada; landscape treatments.

1. Introduction

Many frequent-fire-adapted forests are at risk of uncharacteristically severe wildfire as a consequence of climate change and forest management legacies (Keyser and Westerling, 2017; Miller et al., 2012). Fire suppression has led to high densities of understory fuels, including small trees and shrubs, which elevate fire risk (Collins et al., 2011). Fuel treatments, such as prescribed fire and the mechanical removal of vegetation, are often implemented to reduce the spread and intensity of large wildland fires (Fulé et al., 2012). These treatments are also ecologically appropriate in frequent-fire forests (Stephens et al., 2012). Fuel treatments cannot be used everywhere, however, as they are limited by factors such as operability, funding, road access, and sensitive habitat (Collins et al., 2010, North et al., 2015).

Research on fuel treatments has examined how to maximize their benefits given constraints on geographic placement and extent (e.g. Krofcheck et al., 2017). Modeling studies have shown that the spatial configuration of treatments influences their ability to limit fire spread. If placed strategically, i.e. in areas that maximize the interruption of large "runs" by a fire, fuel treatments on only a fraction of a landscape can reduce fire spread across the entire landscape (Finney 2001, Schmidt et al., 2008). Spatially prioritized treatments based on this research, which are referred to as "strategically placed landscape area treatments," or SPLATs, have been incorporated into US Forest Service management goals. For example, in the Sierra Nevada, SPLATs are one of the primary land management strategies employed by the U.S. Forest Service. The Sierra Nevada Forest Plan Amendment Record of Decision (2004) states that the SPLATs concept "…underpins the Decision's fire and fuels strategy" (USDA Forest Service, 2004).

Despite their centrality to management, empirical tests of SPLATs, which would require experimental wildfire, are nearly impossible. Evaluations of SPLATs have occurred only in modeling exercises (e.g. Collins et al., 2011; Dow et al., 2016; Finney et al., 2007; Schmidt et al., 2008). In fact, landscape-scale treatment networks of any kind are generally only tested in modeling exercises (e.g. Ager et al., 2010), and even where treatment networks have been implemented on the ground, fire risk is assessed through fire behavior modeling rather than actual wildfire (Moghaddas et al., 2010, Collins et al., 2013).

In this study, we take advantage of a rare opportunity to quantify landscape-scale fuel treatment efficacy in a natural experiment in which a well-monitored treatment network and control “fireshed” were both burned in a large wildfire (the 2013 American Fire) shortly after treatment implementation. A fireshed is a geographic planning unit that would be expected to contain a large or “problem” wildfire (Bahro et al., 2007). This study builds on previous research that modeled the effects of the same treatment network on predicted fire behavior and found noticeable reductions in hazardous fire potential throughout the treatment fireshed (Collins et al., 2011b).

The American Fire was within the typical range of modern wildfires that escape initial attack in mixed-conifer forests of the western Sierra Nevada. Fires in this region average 2,908 ha in size (with a median of 786 ha and maximum of 104,131 ha) and 15.6% high-severity (median 6.1%) (Lydersen et al., 2017; Miller et al., 2012). The American Fire was 11,102 ha in size and 20% high-severity.

The landscape fuel treatment network in question, called the Last Chance project, was designed by local US Forest Service managers on the Tahoe National Forest, California, USA, with the aim of conforming to SPLAT principles as part of the Sierra Nevada Adaptive Management Project (SNAMP; Collins et al., 2011b). Because the SNAMP project was an experiment in adaptive management, the design and implementation of SPLATs was left entirely up to the US Forest Service. The spatial configuration of treatments at Last Chance (Fig. 1) deviates from the ideal SPLAT design proposed by fire behavior modeling research (Finney, 2001), reflecting operational limitations inherent to public land management (Collins et al., 2010). Thus, the Last Chance project is the first opportunity to test the potential for SPLATs to achieve their objectives given the constraints typical of any landscape treatment network on federal lands.

The objectives of the Last Chance project were to reduce the potential for large and destructive wildfires and to improve forest resilience. We evaluated the treatments' fulfillment of these objectives. While definitions of resilience vary, we define it here as the capacity of a system to withstand and recover from disturbance such that it retains its initial structure and function (Levine, 2017; Scheffer, 2009). We focused on two aspects of this definition: 1) withstanding disturbance, which is often termed "resistance", and 2) recovering from disturbance. With regard to wildfire, resistance can be quantified using fire severity, defined as mortality of dominant vegetation, while recovery can be measured by regeneration of dominant tree species following fire.

Assessments of fuel treatments often emphasize the ability of treatments to slow down fire spread and reduce overall tree mortality during fire, with little attention paid to indicators of the forests' post-fire recovery potential (e.g. Schmidt et al., 2008). Our study is unique not only in its empirical evaluation of fuel treatments, but also in that it recognizes the importance of recovery in addition to resistance as integral components of forest resilience. In doing so, we link two ecological processes, mortality and regeneration, that are both vital to forest restoration and

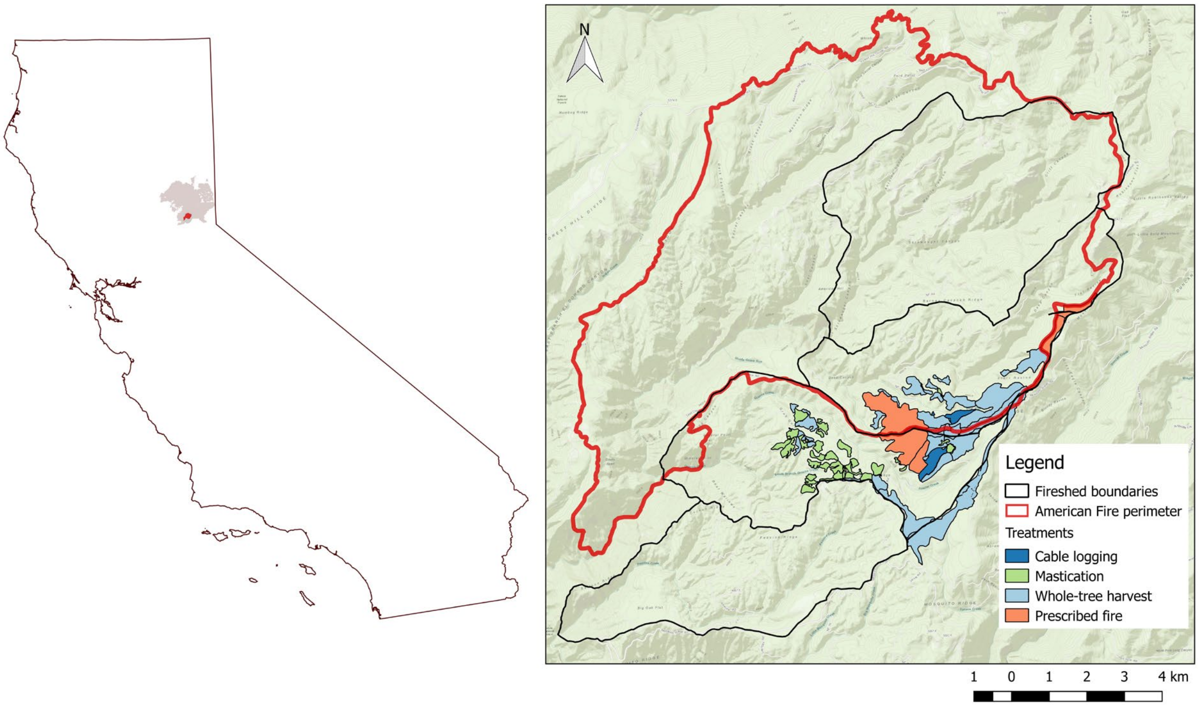

Figure 1: Perimeters of the American Fire and the original four firesheds established by the Last Chance project. The two firesheds that fall within the American Fire perimeter, one control and one treatment, were used in the present study. The overview map on the left shows the location of the American Fire (red) within the Tahoe National Forest (gray).

management but are often studied separately. We evaluated recovery potential by analyzing the spatial patterns of overstory mortality and by quantifying initial post-fire seedling densities. We were particularly concerned with large, regular-shaped patches of stand-replacing fire (>90% basal area loss) that threaten forest structure and function in the long term by making it difficult for native tree species to re-occupy burned areas, since seed dispersal limits the recovery of large stand-replacing patches in the Sierra Nevada (Welch et al., 2016). We quantified how fuel treatments affected a metric of high-severity patch size and shape that is related to recovery potential, namely core patch area, defined as the area within stand-replacing patches that is greater than 120 m from a seed source.

The objectives of this study were to a) evaluate the effects of treatments on wildfire severity, and to b) compare conifer seedling regeneration following fire between treatment and control plots. Based on modeling studies predicting that SPLATs would reduce fire severity in our study area, we expected treatments to reduce fire severity and, in moderating fire effects, facilitate higher conifer regeneration rates (Collins et al., 2011b, Shive et al., 2013, Stevens et al., 2014).

Specifically we asked:

1) How did fuel treatments affect fire severity patterns at the landscape scale?

2) What post-fire plot characteristics (cover of bare mineral soil, tree basal area, fire severity, shrub cover, and conspecific basal area) influenced conifer seedling densities?

3) Did treatments influence post-fire conifer seedling densities at the plot scale, and if so, how did these patterns compare for *Pinus* seedlings versus *Abies* and *Pseudotsuga* seedlings?

4) How did treatments influence each of the post-fire plot characteristics identified as important drivers of seedling densities?

2. Methods

2.1 Study area

The Last Chance study area is located within the Tahoe National Forest in the northern Sierra Nevada. The climate is Mediterranean, with the majority of precipitation occurring in winter as snow. Precipitation averaged 1,182 mm per year in 1990-2008, and mean monthly temperatures were 3°C in January and 21°C in July (Hell Hole Remote Automated Weather Station, 19 km from study area). Elevations range from 800 m to 2,200 m. Soils are moderately deep, well-drained Inceptisols with a gravely loam texture (NRCS, 2017). Vegetation on this landscape is typical of the western slopes of the Sierra Nevada: mixed-conifer forest dominated by white fir (*Abies concolor*; 31% by basal area according to pre-treatment field surveys), sugar pine (*Pinus lambertiana*; 22%), Douglas-fir (*Pseudotsuga menziesii*; 19%), ponderosa pine (*Pinus ponderosa*; 13%), with some incense-cedar (*Calocedrus decurrens*; 8%), red fir (*Abies magnifica*; 5%), and California black oak (*Quercus kelloggii*; 2%). Montane chaparral is interspersed throughout the area, with diverse shrub species including several species of manzanita (*Arctostaphylos)* and *Ceanothus,* chinquapin (*Chrysolepis sempervirens),* huckleberry oak (*Quercus vacciniifolia)* and the shrub growth habit of tanoak (*Notholithocarpus densiflorus).* Fire history analysis using fire scars recorded in tree rings suggests a fire regime with predominantly frequent, low- to moderate-severity fires with a median fire return interval of 15 years (Stephens and Collins 2004, Krasnow et al., 2016). The study area consists of four adjacent firesheds: two treatment and two control (Fig. 1). In this study, we focus on the two firesheds that were located inside the American Fire perimeter (Fig. 1): a control fireshed to the north (3,455 ha) and treatment fireshed to the south (2,162 ha).

2.2 Fuel treatments

Fuel treatments were implemented between 2008 and 2012 (Tempel et al., 2015). Treatment types included whole-tree harvest, cable harvest, prescribed burning, and mastication. Whole-tree harvest included commercial and biomass thinning from below followed by mechanical/hand piling and burning. For harvest treatments, the target was to retain at least 40%

of the initial tree basal area, while also keeping at least 40% canopy cover in the residual stand. This priority was achieved by removing mid-canopy and understory trees. Secondary goals of the treatments were to increase vertical and horizontal heterogeneity and to shift residual species composition toward pines. Within the treatment fireshed, 18% of the area was treated, with the majority whole-tree harvested (Table 1).

	Area (ha)	*Percent of total fireshed area*
Whole-tree harvest	226.4	10.5%
Prescribed fire	143.9	6.7%
Cable logging	13.2	0.6%
Mastication	5.6	0.3%
Total	**389.0**	**18.0%**

Table 1. Area of each treatment type applied in the treatment fireshed

2.3 Field measurements

2.3.1 Pre-fire measurements. Plots were established on a 500 x 500 m grid across both the control and treatment firesheds based on a random starting location. In some areas, sampling was intensified to 250 m spacing in order to accommodate hydrological research in the two instrumented catchments (Hopkinson and Battles, 2015) (Hopkinson and Battles 2015). Plots were circular and 0.05 ha in size. In the summers of 2007 and 2008, pre-treatment measurements were conducted, including species, height, vigor, and diameter at breast height (DBH) of all trees ≥ 19.5 cm DBH ("overstory trees"), which were tagged for long-term monitoring. The cover and average height of shrubs were measured by species using the line intercept method (total length sampled = 37.8 m). Fuels were measured on three randomly chosen transects within each plot, as described in Collins et al. (2011b).

In 2013, plots were re-measured to capture post-treatment conditions, following the pre-treatment measurement protocol. The American Fire began burning in August of 2013, cutting short field measurements, so that 369 of the 408 plots were re-measured before the fire.

2.3.2. Post-fire measurements. In 2014, we re-measured 162 plots within the American Fire perimeter, including 69 in the treatment fireshed and 93 in the control fireshed, all of which were on the main 500-m grid.

2.3.3. Regeneration measurements. In 2015, we visited 97 plots for seedling measurements. Our research goal was to evaluate the effect of treatments on seedling regeneration at the plot scale, so we measured seedling densities within treated areas and in nearby untreated areas. We adjusted the grid-based sampling regime in order to ensure a more even sample size of treatment and control plots within the fire perimeter, visiting some plots on the densified 250 m grid. We avoided plots that had been salvage logged or planted since the fire. We visited 20 unburned plots, 5 treatment and 15 control, in the neighboring fireshed south of the fire perimeter to capture regeneration differences between treatment and control plots in the absence of fire.

At each plot, we repeated the shrub measurements that had been previously performed. We also recorded ground cover type using the line-intercept method in 10-cm increments along the same transects as were used for shrub measurements. We then tallied seedlings by species on belt transects originating from the shrub and ground cover transects. Because of high variation in seedling densities, we used a variable sampling area to increase sampling efficiency: belt transects were 0.5 m, 1 m, or 2 m wide, depending on the number of seedlings counted in the first 0.5 m wide transect sampled. Thus, total seedling sampling area in a plot varied between 18.9 m^2 and 75.6 m^2. We included all seedlings that were young enough to have germinated after the fire, as determined by size and whorl counts.

2.4. Statistical Analyses

Our analytical framework combined spatial analysis of satellite data, fire modeling, and statistical analysis of field data. We used the fireshed scale to evaluate treatment effects on resistance to fire because SPLATs were explicitly designed to affect fire behavior at the landscape scale. In other words, we compared fire severity metrics across the entire treatment fireshed (18% of which was treated) to the control fireshed, rather than comparing areas within the same fireshed. On the other hand, seedling densities were analyzed at the plot scale to capture local influences on conifer regeneration (Legras et al., 2010, Welch et al., 2016). Additionally, fireshed-scale analyses of seedling densities would violate independence assumptions used in our statistical analyses due to spatial clustering of treatment plots within the treatment fireshed. Plot-scale analyses helped to alleviate this lack of independence, particularly because the factors influencing seedling regeneration generally act more locally than spacing between plots.(Legras et al., 2010; Welch et al., 2016).

2.4.1. Fire severity analysis

The effects of treatments on fire severity patterns were evaluated using analysis of remotely sensed relative differenced Normalized Burn Ratio (RdNBR), fire behavior modeling results, and direct field measurements of tree mortality.

Remote sensing fire severity analysis. To compare fire severity patterns in the American Fire between the treatment fireshed and control fireshed, we analyzed stand-replacing polygons based on Landsat-derived RdNBR calibrated to ≥90% basal area loss, available at https://www.fs.usda.gov/detail/r5/landmanagement/gis/?cid=stelprd3804878 (Miller and Quayle 2015, Stevens et al., 2017). We calculated the percent area of each fireshed that burned at stand-replacing severity as well as the mean stand-replacing patch size using a minimum patch size of 0.5 ha (*sensu* Collins and Stephens, 2010). Next, we calculated the sum of the “core patch areas” of each fireshed. Core patch area is the area within a stand-replacing patch that is farther than a certain distance from patch edge, and thus less likely to recover to forest within a few decades (Cansler and McKenzie, 2014). We used a distance of 120 m from the patch edge because it is greater than the likely dispersal distance for California mixed-conifer species (*sensu* Collins et al., 2017). Small areas of live trees are unlikely to be an equivalent seed source to external patch edge. Therefore, we filled in internal “islands” of lower severity within stand-replacing patches, considering them part of the stand-replacing patch, if the internal islands were 0.81 ha (9 pixels) or smaller (*sensu* Stevens et al., 2017). All fire severity pattern analysis was performed in R 3.4.3 (R Core Team, 2017).

Fire modeling. Our comparison of the treatment fireshed to control fireshed would be incomplete without consideration of pre-treatment fire risk, as differences in fire severity patterns could have been due to factors such as topography or vegetation types that existed before treatments. Thus, we ran the fire behavior model FARSITE using pre-treatment vegetation data to simulate how the American Fire would have burned had treatments not occurred. This study design follows the principles of a before-after control-impact (BACI) experiment (Stewart-Oaten and others 1986).

To check the validity of comparing pre-treatment modeled fire severity to actual wildfire severity, we also simulated American Fire behavior using post-treatment vegetation data and compared results to severity as measured by RdNBR. Since the post-treatment vegetation data was taken the same year the American Fire burned, we expected these model predictions to resemble actual burn patterns. However, given FARSITE's limitations in predicting large, contiguous high-severity fire (Coen et al., 2018), we did not expect the spatial patterns of fire in post-treatment FARSITE model to exactly match RdNBR burn severities (Collins et al., 2013).

We used FARSITE (v.4.1.005) for fire behavior modeling because it simulates an individual fire initiating from a single point on a landscape, which allowed us to use American Fire inputs for weather and ignition location. FARSITE is a landscape-scale, spatially explicit fire growth model requiring inputs of detailed forest structure data, fuel models, topography, and weather (Finney, 1998). While FARSITE models have been used to examine treatment effects at Last Chance in previous studies (Tempel et al., 2015), this is the first time FARSITE has been used with inputs based on the American Fire (weather and ignition location).

Our methods for developing the necessary layers for FARSITE are described in detail by Tempel et al. (2015) and Fry et al. (2015) and summarized in the Appendix. In short, we created wall-to-wall maps of vegetation structure in the study firesheds based on a combination of field measurements and LiDAR. This was completed once using pre-treatment data from field plots and LiDAR and again using post-treatment plot and LiDAR data.

We categorized flame lengths from FARSITE model output into three classes: 0-1.2 m, 1.3-2.4 m, and >2.4 m, based on likelihood of crowning and torching (NWCG, 2006). Though these flame lengths are not equivalent to RdNBR-derived fire severity classes, we compared them to low, moderate, and high fire severity classes for the purposes of examining patterns in stand-replacing area and core patch area (*sensu* Collins et al., 2013; Miller and Quayle, 2015). This resulted in maps of stand-replacing polygons similar to those derived from RdNBR, allowing comparison of severity patterns between model results and remotely sensed metrics. We quantified the percent of total fireshed area predicted to burn at high severity for both pre- and post-treatment FARSITE output severity maps. For both FARSITE-based severity maps, we calculated the sum of the “core patch areas” of each fireshed following the method used with RdNBR.

Field measurements of fire severity. We compared overstory tree mortality between firesheds from plot data by using a generalized linear mixed model (GLMM) with a binomial distribution and logit link, and with plot as a random effect. We used the package “lme4” in R (Bates et al., 2015). This comparison was made using only plots that were re-visited in 2014 because the plot sample in 2015 was selected to represent plot-scale differences in seedling densities, not fireshed-scale differences in tree mortality. Due to the spatial clustering of plots in the treatment fireshed and control fireshed the plots in this test are not strictly independent.

2.4.2. Seedling density analysis.

Our analytical approach was designed to determine the effect of treatments on regeneration and to identify a potential mechanism behind that effect. Thus, we not only analyzed the relationship between treatments and seedling densities, but we also identified what specific plot characteristics drove seedling densities and how those characteristics were affected by treatments (Fig. 2)

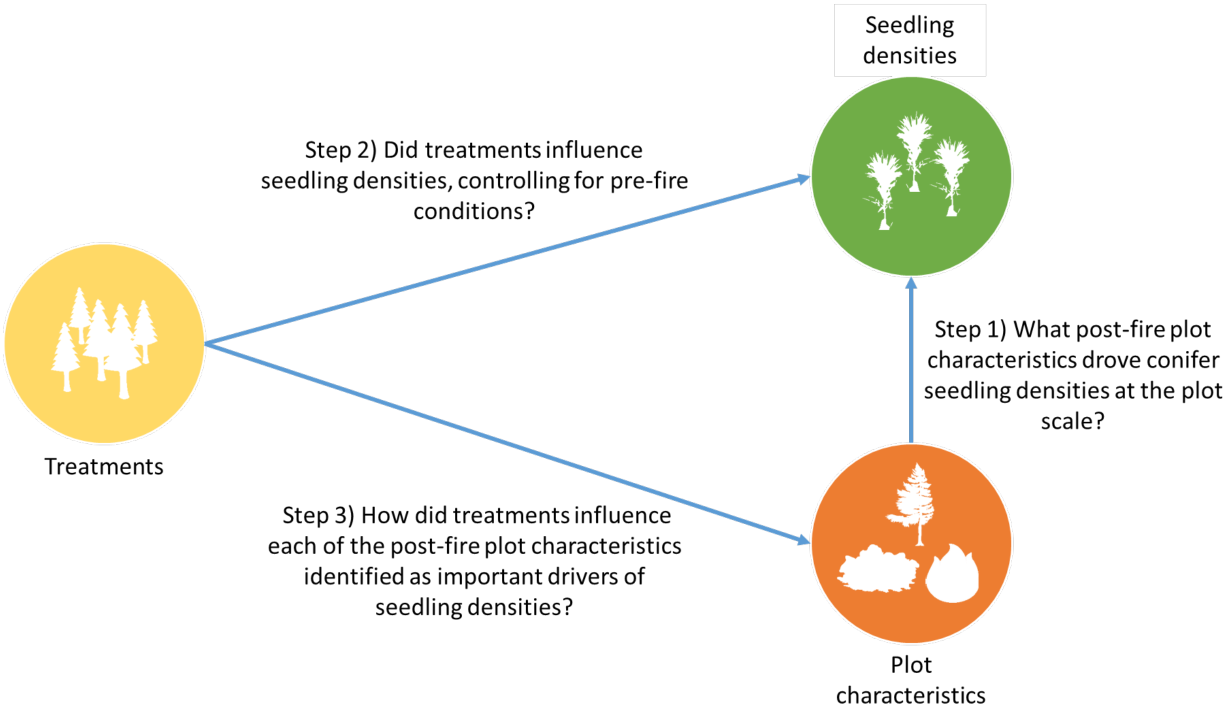

Figure 2. Analytical framework for seedling analyses. Seedling densities were analyzed in three steps, first identification of the drivers of seedling densities (Step 1), followed by analysis of the overall effect of treatments on seedling densities (Step 2), and finally the effects of treatments on drivers of seedling densities (Step 3). Results from Step 1 dictated the set of explanatory variables that were used in Steps 2 and 3.

Our analysis was also guided by our desire to avoid attributing regeneration differences to treatments if those trends were actually caused by plot characteristics that were present before treatments. For example, if control plots happened to have higher shrub cover than treatment plots before the experiment began, we did not want to erroneously attribute seedling differences to treatments if they were actually driven by shrub cover.

In order to achieve these analytical goals, we used a combination of seedling data, pre-treatment plot data, and post-fire plot data in three steps:

1. We first identified which post-fire plot characteristics (e.g. tree basal area, shrub cover, etc.) were most strongly associated with seedling densities (Fig. 2, Step 1).
2. We then tested for a treatment effect on seedling densities (Fig. 2, Step 2). We included pre-treatment plot variables to control for inherent differences (i.e., differences unrelated to the fire or the treatment) that were likely to affect seedling densities, as determined by the results of Step 1. For example, if post-fire shrub cover was identified as a driver of seedling densities by Step 1, we included pre-treatment shrub cover in the model used to test for treatment effects on seedling densities in Step 2. We included these pre-treatment plot characteristics rather than post-fire characteristics because we expected post-fire variables to be correlated with the treatment effect, and our goal was to attribute all variation in the data caused by treatments to the treatment variable alone. For example, we expected treatments to directly affect post-fire basal area through tree harvest, so including post-fire tree basal area in the model would confound the treatment effect signal.
3. Finally, we tested the effect of treatment on each plot characteristic that was identified as an important driver of seedling densities by Step 1 (Fig 2, Step 3). If any plot

characteristic that significantly affected seedling densities and was significantly affected by treatments, then we identified it as a possible mechanism behind treatments' effect on seedling densities.

These three steps are described in more detail below.

Identifying plot-scale drivers of post-fire seedling densities. To identify the most important drivers of post-fire seedling densities, we modeled seedling densities as a function of post-fire plot characteristics using generalized linear models (GLMs) with model selection based on the Akaike Information Criterion, corrected for small sample sizes (AICc). We analyzed seedling densities separately for each of two species groups: A) seedlings in the "fir functional group," which included *Abies concolor, A. magnifica,* and *Pseudotsuga menziesii* (hereafter referred to as "firs") and B) seedlings in the *Pinus* genus, including *P. ponderosa* and *P. lambertiana* (hereafter referred to as "pines"). These two species groups were used for three reasons: because it is difficult to identify 1-2 year old seedlings to the species level; because the species in each group share traits associated with tolerance of shade and microclimatic conditions (Niinemets and Vallardes, 2006); and because there were few *P. menziesii* seedlings. Of the fir functional group, 93.3% were of the *Abies* genus, while 6.7% were *P. menziesii.* We also analyzed all seedling species together, which included the addition of *C. decurrens* to the species in the above two groups, but because these results were heavily driven by firs, which were the most abundant seedling group, we report them only in the Appendix.

For the fir group, we used GLMs with negative binomial distribution and log link using the function "glm.nb" in the R package "MASS" (Venables and Ripley, 2002). For the pine species group, 21 out of the 97 plots had zero pine seedlings. To account for this zero-inflated data, we applied GLMs using the function “hurdle” in the R package “pscl”, which combine binomial and negative binomial models to account for zero-inflated data (Jackman, 2017; Zeileis et al., 2008). More details on these statistical methods can be found in the Appendix.

We chose which plot characteristics to include in the analysis by selecting variables that could be calculated from available data and that were likely to affect seedling growing conditions via their effects on light availability, moisture competition, seed bed quality, or seed source. For each of the two species groups, we calculated AICc for all combinations of the following plot variables: shrub cover; cover of bare mineral soil; basal area of overstory trees; plot-scale fire severity class; neighborhood fire severity; and conspecific overstory tree basal area, as a proxy for seed availability. Plot-scale fire severity class was based on proportion of tree basal area that died in that plot (<20% = low severity, 20-70% = moderate severity, and >70% = high severity) with an additional “unburned” class for plots outside the fire perimeter. Neighborhood fire severity was defined as the proportion of RdNBR pixels within 120 m of the plot center that experienced stand-replacing fire. We also included two interactions. The interaction between fire severity and post-fire basal area was included because fire severity is calculated relative to pre-fire tree basal area and may have different effects depending on basal area. The interaction between plot-scale fire severity and neighborhood-scale fire severity was included because we were specifically interested in the spatial aspects of fire severity and expected neighborhood fire severity to affect seedling densities differently depending on plot-scale fire severity. We then calculated the weight of evidence and evidence ratio for each model, which are reported in the Appendix (Burnham and Anderson, 2002). We calculated McFadden’s pseudo R^2 for the best fir seedling driver model, but we do not report a metric of model fit for the pine seedling analysis because the hurdle model does not lend itself to calculations of pseudo R^2.

Treatment effects on seedling densities. To evaluate the effect of fuel treatments on post-fire conifer seedling densities, we used GLMs and likelihood ratio tests for each species group with seedling count as the response variable. We grouped treatment types into “treatment” and “control” because only 2 of the 29 treatment plots were prescription burned, and the other 27 were whole-tree harvested.

We chose which pre-treatment plot characteristics to include in the treatment effects models based on the results of Step 1. If a post-fire plot variable was included in any model within 2 AICc of the best seedling driver model, and if the variable was measured pre-treatment, we included the pre-treatment version of the treatment effects model. Some post-fire variables lacked pre-treatment analogs, either because they did not exist pre-treatment (e.g. fire severity) or because they were not measured in pre-treatment surveys (e.g. cover of bare mineral soil). All pre-treatment variables were calculated from 2007 and 2008 field data. We also included a binary variable for whether or not a plot was within the fire perimeter and an interaction between fire and treatment. For each species group, likelihood ratio tests were performed between 1) the full treatment model, containing pre-treatment plot characteristics, fire, and treatment, and 2) the null model, containing pre-treatment plot characteristics and fire but no treatment. If these two models significantly differed, we determined that the effect of treatments on seedling densities was significant.

Treatment effects on drivers of seedling densities. We tested whether treatments affected each of the post-fire variables that were identified in Step 1 as potential drivers of seedling densities at the plot scale, again using the threshold of 2 AICc from the best model. For each variable, we chose between ANOVA and Wilcoxon rank-sum tests based on the distribution of data. When pre-treatment data were available for the plot variable of interest, we included pre-treatment data in the analysis in order to account for pre-existing plot conditions. We used α = 0.05 with a Bonferroni correction for multiple comparisons.

3. Results

3.1. Fire severity patterns

The control fireshed burned with 25.6% stand-replacing fire, while the treatment fireshed burned with only 11.3% stand-replacing fire, according to RdNBR (Table 2). The FARSITE simulation predicted higher pre-treatment fire severity in the treatment fireshed (37.7% stand-replacing in treatment vs. 28.0% in control), indicating that the effect size of treatments was larger than fireshed differences in actual fire severity suggests. Using the principles of the BACI study design, we estimated the treatment effect size by comparing the change in the treatment fireshed between pre- and post-treatment to the change in the control fireshed during the same time period. Treatments reduced stand-replacing area by approximately 24 percentage points (Table 2).

The treatment fireshed also had a lower percentage of core patch area than the control fireshed, with only 1% of area farther than 120 m from patch edge, compared to 2.4% in the control fireshed (Table 2; Fig. 3). The treatment fireshed had greater expected pre-treatment core patch area than the control fireshed (6.5% vs. 2.6%). Again using the BACI framework, the treatments reduced core patch area by approximately 5.3 percentage points (Table 2). These results match the pattern found in stand-replacing patch sizes; the mean stand-replacing patch size in the treated fireshed was 7.6 ha (median 1.37 ha, maximum 123 ha), whereas in the control fireshed the mean stand-replacing patch was 10.1 ha (median 1.37 ha, maximum 258 ha).

More overstory trees (i.e. trees ≥19.5 cm DBH) died in the control fireshed than in the treatment fireshed (40% vs. 32%), but this difference was not significant (*P* = 0.38).

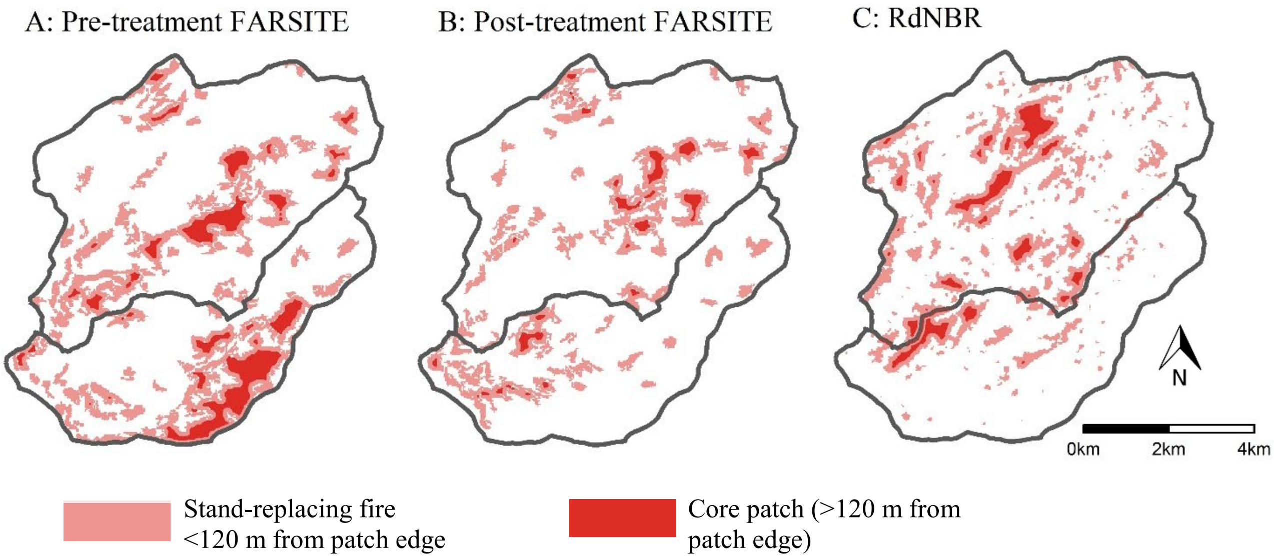

Figure 3. Stand-replacing fire patches and core patch areas based on pre-treatment FARSITE model output (A), post-treatment FARSITE model output (B) and actual RdNBR American Fire severity (C). The southern fireshed was treated while the northern fireshed was a control.

	Control fireshed				**Treatment fireshed**				Treatment impact (Treatment Δ - Control Δ)
	Pre-trt (model)	Post-trt (RdNBR)	Post-trt (model)	Δ (RdNBR - Pre-trt)	Pre-trt (model)	Post-trt (RdNBR)	Post-trt (model)	Δ (RdNBR - Pre-trt)	
Percent area stand-replacing	28.0	25.6	22.0	-2.4	37.7	11.3	20.6	-26.4	-24
Mean stand-replacing patch size (ha)	8.41	10.1	6.85	1.69	11.7	7.64	5.25	-4.06	-5.8
Percent core patch area	2.60	2.39	1.11	-0.21	6.50	1.02	0.47	-5.5	-5.3

Table 2. Patterns of stand-replacing fire in the treatment and control firesheds. "Pre-trt (model)" refers to stand-replacing patches derived from FARSITE model predictions using pre-treatment vegetation data, while "Post-trt (model)" refers to stand-replacing patches derived from FARSITE model predictions using post-treatment vegetation data. "Post-trt (RdNBR)" results were calculated from American Fire RdNBR. "Δ (RdNBR - Pre-trt)" is the difference between "Post-trt (RdNBR)" and "Pre-trt (model)."

3.2. Regeneration

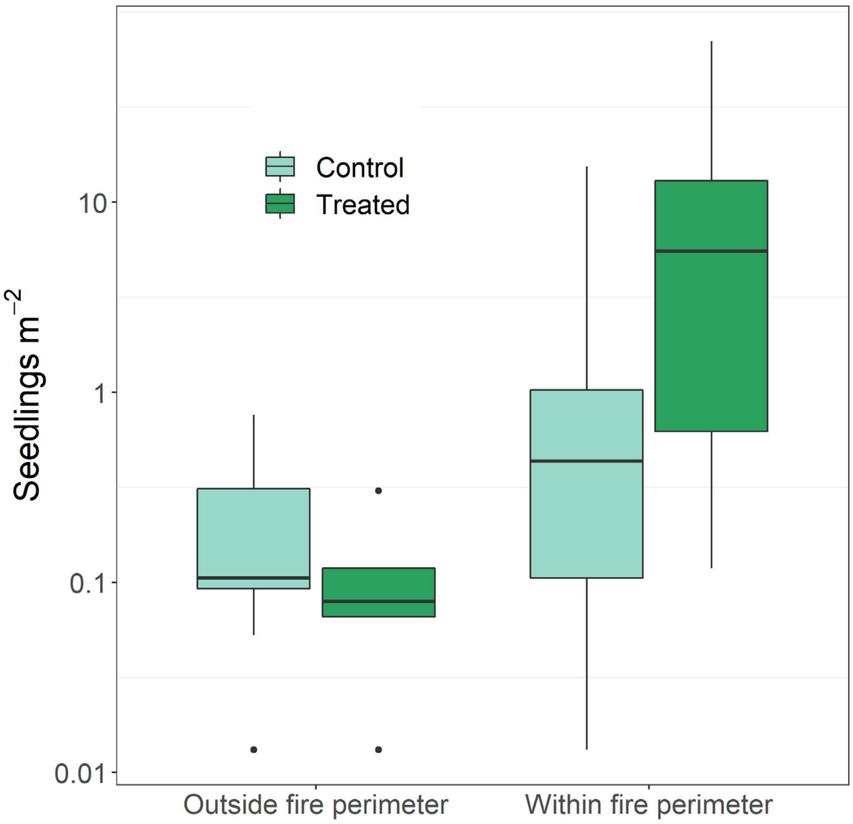

Figure 4. Seedling densities by treatment at the plot scale for all seedling species combined. Note the log scale on the y-axis. The midline of the boxplot represents the median of the data, the upper and lower limits of the box represent the third and first quartile of the data, and the whiskers represent 1.5x the interquartile range from the third and first quartile. The points represent data outside 1.5x the interquartile range from the third and first quantile.

Seedling densities were higher in treatment plots than control plots. On average there were 7.8 seedlings m^{-2} in treatment plots and 1.4 seedlings m^{-2} in control plots for all species combined. There were more seedlings inside than outside the fire perimeter, with a mean of 4.1 seedlings m^{-2} inside and 0.2 seedlings m^{-2} outside the fire (Fig. 4). The majority of seedlings were firs, which had a mean density of 3.0 seedlings m^{-2} (median 0.23) compared with a mean of 0.20 pine seedlings m^{-2} (median 0.07).

3.2.1. Drivers of post-fire seedling densities. In the fir seedling driver model with the lowest AICc (“best” model; Table A.3), fir seedling densities decreased with shrub cover and neighborhood fire severity, and increased with plot fire severity and tree basal area. The interaction between tree basal area and fire severity and the interaction between neighborhood fire severity and plot fire severity were also present in the best fir seedling driver model, which had a pseudo R^2 of 0.45. The interaction between plot and neighborhood fire severity was especially pronounced for plots with moderate plot-scale fire severity (Fig. 5; Table A.1).

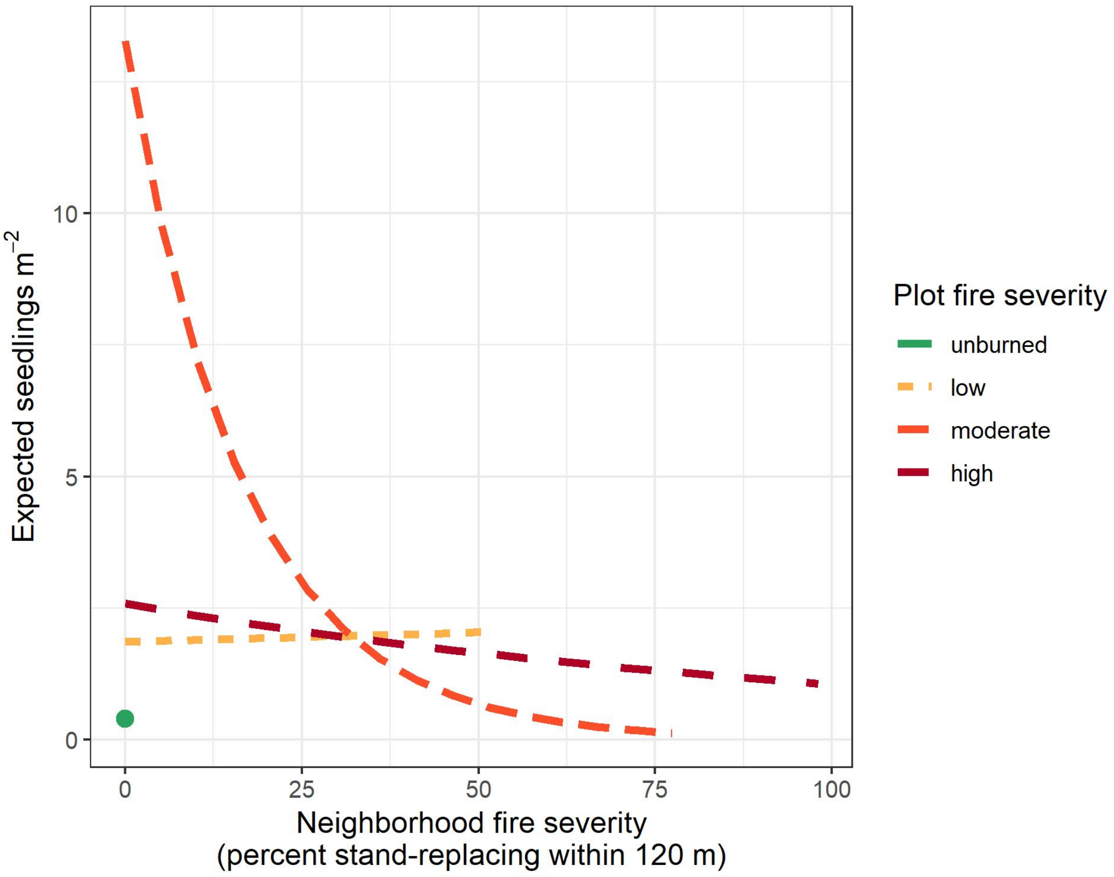

Figure 5. Predicted fir seedling densities in relation to plot-scale and neighborhood-scale fire severity for the best fir seedling driver model from Step 1. To generate these lines, the model was applied to a matrix of all variable combinations within the parameter space of the original data, and the median predicted seedling density was calculated for each combination of the two fire severity variables. All plots that were unburned at the plot scale had zero neighborhood fire severity, represented by the green point. See Table A.1 for model coefficients.

According to the best pine seedling driver model, pine seedling densities increased with pine basal area and were highest in moderate severity plots (Fig. 6).

For both pine and fir seedling driver analyses, though we used the best models for visualizing results (Figs. 5 and 6), the top three models are all within 2 AICc (Tables A.3 and A.4), indicating substantial evidence supporting their selection as the best model (Burnham and Anderson, 2002). We therefore incorporated variables from all three of these top models into Steps 2 and 3 of the analysis.

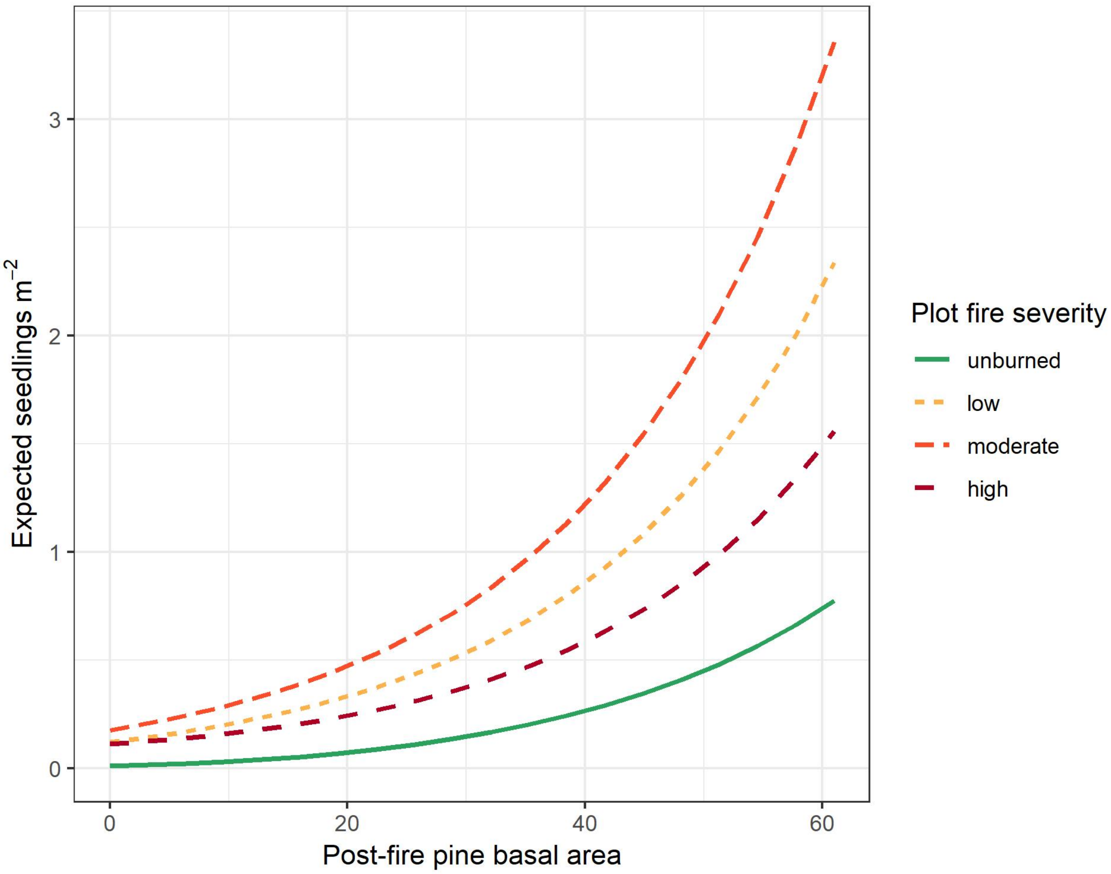

Figure 6: Predicted pine seedling densities in relation to post-fire pine basal area and plot-scale fire severity. Lines represent predictions based on the best pine seedling driver model from Step 1. To generate these lines, the same method was used as for Fig. 5.

3.2.2. Treatment effects on seedling densities. Treatment plots had more seedlings than control plots (Fig. 4). This difference was particularly pronounced for firs, which had mean densities of 7.1 seedlings m^{-2} in treatment plots and 1.2 seedlings m^{-2} in control plots.

For analyses of treatment effects on seedling densities, we chose which pre-treatment plot variables to include based on the results of Step 1. For firs, we included pre-treatment shrub cover and pre-treatment tree basal area because the post-fire analogs of those two variables were in at least one of the top three models with < 2 AICc and were possible to calculate from pre-treatment data. For pines, we included pre-treatment shrub cover, pre-treatment tree basal area, and pre-treatment pine basal area for the same reasons.

Treatment was strongly associated with greater seedling densities for firs (likelihood ratio test; P < 0.001; Fig. 7). Pine seedling densities were higher in treatment plots, though the difference was not significant (means 0.27 seedlings m^{-2} vs. 0.17 seedlings m^{-2}; likelihood ratio test; P = 0.054).

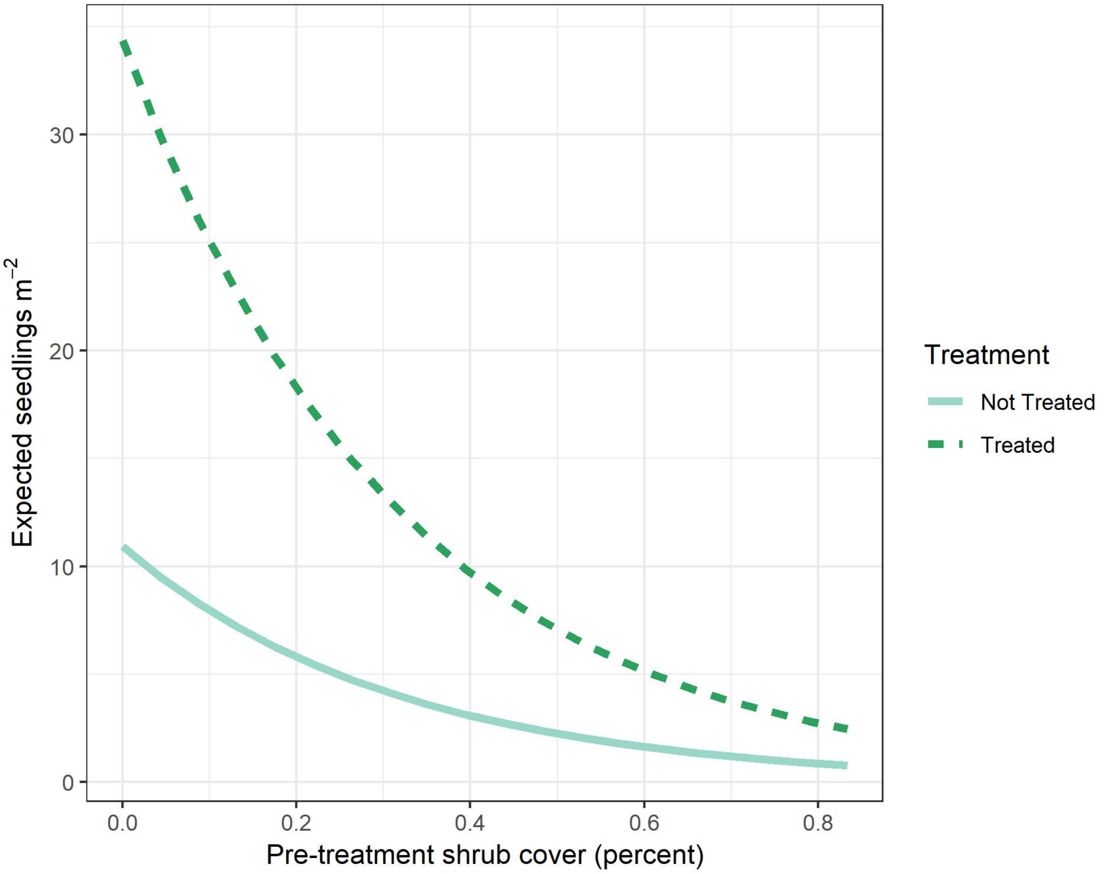

Figure 7. Predicted fir seedling densities in relation to treatment and pre-treatment shrub cover for the fir treatment model from Step 2. For ease of visualization, plots outside the fire perimeter are excluded from this figure. To generate these lines, the same method was used as for Figs. 5 and 6.

3.2.3. Treatment effects on drivers of seedling densities. Treatments reduced tree basal area (ANOVA; *P* = 0.003) and decreased neighborhood fire severity, though the latter was not significant at α = 0.05 with a Bonferroni correction for 5 comparisons (Wilcoxon rank-sum; *P* = 0.017; Table 3). Neighborhood fire severity data were heavily zero-inflated, with medians of zero for both treatment and control plots, but there were more and larger non-zero values in control plots (31.3% of observations, with a median of 17) than treatment plots (13.8% of observations, with a median of 4). The other variables tested were not affected by treatments (Table 3).

Response variable	Transformation of response variable	Pre-treatment data included?	Test	Treatment effect	*P*
Tree basal area	Square root	Yes	ANOVA	(-)	0.003**
Shrub cover	None	Yes	ANOVA	(-)	0.034
Pine basal area	None	Yes	ANOVA	(-)	0.44
Neighborhood fire severity	None	No	Wilcoxon rank-sum	(-)	0.017*
Local fire severity	None	No	Wilcoxon rank-sum	(+)	0.45

*P < 0.02, the Bonferroni-corrected value of α=0.10 for 5 comparisons

**P < 0.01, the Bonferroni-corrected value of α=0.05 for 5 comparisons

Table 3.Tests for treatment effects on the drivers of seedling densities.

4. Discussion

SPLATs moderated landscape-level fire severity, resulted in post-fire vegetation patterns that will likely improve long-term ecological integrity of the studied forest, and promoted conifer seedling regeneration in the two years following fire.

4.1 Fire Resistance

The Last Chance fuel treatments not only decreased the area that experienced stand-replacing fire, but also reduced the core patch area. In the treatment fireshed, the stand-replacing burn area was half that of the control, while the core patch area was less than half that of the control, despite the treatment fireshed having greater modeled fire hazard before treatments. Thus, the SPLAT network achieved the objective of increasing resistance to fire at the landscape scale, as predicted by modeling studies conducted before the implementation of treatments at Last Chance (Collins et al., 2011b).

These treatment effects were achieved with only 18% of the fireshed treated. This proportion of area treated is comparable to other studies of landscape-scale treatment effects on fire behavior. For example, in one field study on the Rim Fire, 10-40% of the area needed to be treated to see an effect on fire severity at the scale of 2,000 ha (the treatment fireshed at Last Chance was 2,162 ha; Lydersen et al., 2017). Modeling studies suggest that for strategically placed treatments there may be diminishing returns for increasing area treated beyond 40% (Finney et al., 2007). Ager et al. (2010) found, however, that the marginal decrease in hazardous fire potential began diminishing beyond 10-20% of the landscape treated. Similarly, in the Lake Tahoe Basin, increasing area treated from 13% to 30% did not substantially decrease landscape-level fire hazard (Stevens et al., 2016).

The large landscape-scale effect of treatments may have been due in part to the overlap between treatments and the highest fire risk areas of the fireshed. The treatments were largely located in the southern and southeastern portions of the fireshed, which were also predicted to have the highest risk of stand-replacing fire before treatments (Figs. 1 and 3). Previous studies have shown that prioritizing treatments in highest fire risk areas achieves greater hazard reduction (Krofcheck et al., 2017).

Treatments brought fire severity patterns closer to historical norms. The high-severity fire patterns observed in the treatment fireshed were more consistent with the natural range of variation for mixed-conifer forests of the Sierra Nevada than either the control fireshed or the expected pre-treatment patterns in the treatment fireshed. Historically, fires in the area averaged 5-10% high severity (Mallek et al., 2013, Meyer 2015), and high-severity patches were only a few ha in size (Collins and Stephens 2010, Stephens et al., 2015, Safford and Stevens 2017).

Our BACI analytical framework relies on FARSITE simulations to provide the pre-treatment controls. Thus the treatment impacts in Table 2 that compare pre-treatment model results to post-treatment empirical results (i.e., RdNBR results) do not follow a BACI design in the strictest sense. Empirical measures of pre-treatment differences in fire behavior would be preferable but were logistically impossible. Although fire behavior models like FARSITE are simplified simulations of complex fire events and therefore inherently limited in their predictive ability, they provided the best available means to account for pre-treatment differences in fire hazard between the firesheds. The large treatment impact suggests that the treatment effect we detected was real. Moreover, our FARSITE predictions of post-treatment fire behavior match empirical measurements better than the pre-treatment FARSITE predictions do (Table 2; Fig. 3). This matching indicates that the pre-treatment model at least partially captures differences in fire effects had treatments not occurred. FARSITE results using post-treatment vegetation data resembled actual burn patterns in terms of severity but did not replicate the exact spatial pattern of fire severity (Fig. 3). Even with detailed vegetation and weather data to parameterize the model, FARSITE simulates a dynamic biophysical process.

Moreover, the actual fire was influenced by suppression efforts. For example, fire fighters burned areas in advance of the main fire front along the southern boundary of the treatment fireshed. The effect of suppression on fire severity was likely smaller than the effect of treatments because FARSITE model runs did not include suppression efforts yet yielded a strong effect of treatments. Furthermore, whatever influence suppression may have had on fire severity was in part a consequence of treatments, as fire crews were able to safely burn-out in areas where it may not have been possible otherwise (Larry Peabody, personal communication, 2017). Part of the goal of SPLATs is to reduce fire severity indirectly by facilitating suppression efforts, and this effect can be significant (Finney, 2001; Moghaddas and Craggs, 2007), though it is very difficult to quantify, and as such it is rarely captured in simulation studies.

Our remote-sensing-based analyses of fire severity showed stronger treatment effects than did field-based measurements of tree mortality. The fact that field measurements of tree mortality were not significantly different between the two firesheds may be due to study design. Tree mortality was measured in plots and thus our analysis needed to include a random effect for plots. As a consequence, the model results were disproportionately affected by trees in sparse plots, which were more likely to experience lower fire severity, while trees in dense, severely burned plots contributed proportionally less to the model results. We do not interpret the weaker effect detected by field data as contradictory to satellite fire severity results, especially considering the relative scarcity of plot data compared to RdNBR.

This study does not address the longevity of treatment effects in cases where there is a time lag between treatments and wildfire, since the American Fire burned only one year after treatments were completed (five years after treatments began). Collins et. al. (2011b) showed that treatments at Last Chance were likely to affect conditional burn probabilities for 20 years. This longevity is consistent with similar treatment networks in other locations (Finney et al., 2007), though treatments may last longer if maintenance treatments are incorporated (Collins et al., 2013). Fire severity may actually have been lower in the American Fire if it had burned a few years later because activity fuels (in cable logged areas) would have decayed and compressed over time (Collins et al., 2014).

4.2. Forest Recovery

There were nearly six times more seedlings in treatment plots than in control plots, and this difference was largely driven by firs. Of the plot characteristics that our analysis identified as important drivers of seedling densities, treatments affected only two of them: tree basal area and neighborhood fire severity. Though the Wilcoxon rank-sum test showed a *P*-value of 0.017 for neighborhood fire severity, which equates to $P = 0.085$ after the Bonferroni correction for 5 comparisons (Table 3), an ecologically meaningful relationship may exist based on the large difference in their proportion and magnitude of non-zero values. Neither tree basal area nor neighborhood fire severity were associated with pine seedling densities, meaning that we did not identify a mechanism for treatment effects on pine regeneration. Since post-fire tree basal area was positively associated with fir seedling densities and negatively associated with treatments, it is unlikely that changes in basal area are the mechanism by which treatments affected regeneration. Thus, the only potential mechanism we identified for treatments’ effects on fir seedling densities was neighborhood fire severity, which was negatively associated with both treatments and fir seedling densities. Neighborhood fire severity was consistently present in the top-ranked 21 models identifying drivers of post-fire seedling densities (Table A.3).

Our findings are consistent with previous evaluations of treatment effects on seedling densities. For example, in ponderosa pine forests of the American Southwest, treatments increased regeneration densities independent of plot-scale fire severity, and this effect was likely due to moderation of neighborhood fire severity (Shive et al., 2013). Neighborhood fire severity likely influences plot-scale seedling densities by affecting the available seed source. The strong interaction we identified between plot-scale fire severity and neighborhood-scale fire severity in predicting fir seedling densities adds to a body of literature showing that fire at the plot scale promotes seedling regeneration by increasing resource availability and improving seed bed quality, but that these benefits are contingent upon there being sufficient nearby seed source (Shive et al., 2013, Welch et al., 2016).

The effect of neighborhood fire severity on seedling densities was strongest for moderately burned plots. Plots that burned at low severity may have experienced smaller increases in resource availability, causing lower fir seedling densities than moderately burned plots. Furthermore, low severity plots likely had greater post-fire tree basal area and therefore did not need additional seed sources from the surrounding neighborhood. Plots that burned at high severity also had lower fir seedling densities than moderately burned plots, which could be due to harsher microclimates not conducive to fir regeneration (Irvine et al., 2009). Moderately burned plots with low neighborhood fire severity, and thus abundant nearby seed source, appear to have the optimal conditions for fir regeneration, consistent with previous findings (Crotteau et al., 2013, Welch et al., 2016).

Within the treatment fireshed, we did not detect an effect of treatments on plot-scale fire severity (Table 3). This contrasts with our findings of strong effects of treatments on landscape-scale fire severity patterns. This difference is likely due to strong spatial autocorrelation in fire behavior at the plot scale. Because our aim was to compare seedling regeneration in treatment and nearby control plots, we measured seedlings only in the treatment fireshed. Fire behavior at each plot may be more influenced by the behavior of the fire before it reached the plot than plot-scale treatments (Kennedy and Johnson, 2014).

In contrast to fir seedlings, we did not detect a neighborhood fire severity effect on pine seedling densities. Overall, pines were rarer on the landscape with less than half of plots containing any overstory pines after the fire. Thus, neighborhood fire severity may have been less correlated with seed availability for pines than for firs. Because pines prefer more open growing conditions (York et al., 2004), nearby low severity areas could actually hinder, rather than aid, pine regeneration.

We found much higher seedling densities of firs than pines, highlighting the importance of management to facilitate pine regeneration. Shade-intolerant tree species like pines are underrepresented in many Western U.S. forests relative to historical conditions, due to logging legacies and fire suppression (Churchill et al., 2013, Stephens et al., 2015, Levine et al., 2016). Pines are critical components of mixed-conifer forests, as they are more fire resistant than other species and contribute to structural and compositional heterogeneity. Therefore, shifting species composition toward pines is a common goal of thinning treatments, including the treatments at Last Chance. We found that despite the disproportionate retention of pines in the overstory following treatment, post-fire seedling densities were much higher for firs than for pines even in treatment plots, and treatment effects on seedling densities were stronger for firs than for pines. If shifting regeneration toward pines is a management goal, more aggressive management, such as planting, may be needed.

5. Conclusion

Given the widespread incorporation of the SPLATs concept into land management planning for frequent-fire forests, empirical testing of landscape treatment networks is critical. The natural experiment created when the American Fire burned through half of the Last Chance study site allowed us to quantify treatments’ effects on wildfire resistance and forest recovery given real-world constraints on treatment placement. As noted in a recent review (Chung, 2015), there is a pressing need for "more reliable and field-verified data" to develop more efficient fire models appropriate for use by fire managers. Our results meet this need.

More importantly, this natural experiment confirmed the value of landscape fuel treatments. We found that treatments on 18% of the fireshed noticeably decreased landscape-level fire severity, and that treatments locally increased fir seedling densities. The combination of high initial post-fire seedling densities and small stand-replacing patches in the treatment fireshed bodes well for long-term integrity of the mixed-conifer forests within the American Fire, though regenerating conifers will likely be dominated by firs. More widespread use of strategically placed treatment networks could help bring wildfire effects closer to historical norms and facilitate long-term recovery from fire.

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Appendix A. Supplementary material

Additional methods details

FARSITE input layer development

To develop vegetation layers for FARSITE, we first divided the study area into 1363 polygons defined by similarities in forest structural and terrain features derived from multispectral aerial imagery and LiDAR (Su et al., 2016b). We then assigned each polygon vegetation data from field plots, using the gradient-nearest-neighbor method (Ohmann and Gregory, 2002). The gradient space was defined by multivariate analysis of field-measured plot variables including treatment type, vegetation type, canopy cover, relative density of big trees, and a suite of topographic metrics. To recreate the fine-scale heterogeneity observed in the field, we identified all plots ranked in the 95th percentile in terms of similarity to each polygon and then randomly assigned three of those plots to the polygon. Stand structure layers, including canopy cover, canopy base height, canopy height, and canopy bulk density were derived from FVS outputs for each polygon. The fuel model for each polygon was selected using multiple regression tree analyses of field-measured surface fuels and forest structure, as described in Collins et al. (2011) (Fry et al., 2015).

Topographic FARSITE model inputs were derived from LiDAR data. Ignition location and hourly weather data from the actual American Fire were used (Duncan Remote Automated Weather Station, located 11 km from study area). Crown fire using the Scott and Reinhardt (2001) method was enabled, as well as spot-fire growth with an ignition frequency of 2% and a two-minute ignition delay.

Identifying drivers of post-fire seedling densities.

To determine what plot-scale biophysical characteristics influenced post-fire seedling densities, we used AICc model selection. For all models, belt transect area was used as an offset variable because we counted seedlings over differently sized belt transects for different plots depending on seedling densities.

We used hurdle models to analyze pine seedling densities because the data were zero-inflated. We used "hurdle" in the R package "pscl," which performs a binomial GLM on the zero-only observations and a negative binomial GLM on the non-zero observations (Jackman, 2017; Zeileis et al., 2008). We used the same set of predictor variables for both the binomial and negative binomial portions of the hurdle model for all pine model runs.

Shrub cover, bare mineral soil, and tree basal area were square root transformed to approximate normality in the residuals. We then standardized all continuous variables by subtracting the mean and dividing by the standard deviation for easier comparison of coefficients. We lumped unburned and low plot fire severity for the interaction between plot fire severity and neighborhood fire severity to avoid errors due to zero variance in neighborhood fire severity at zero plot-scale fire severity. One plot was left out of the analysis because of field measurement error resulting in missing post-fire shrub cover data.

Treatment effects on seedling densities.

We identified what treatment each plot had experienced using a combination of data sources. First, field observers noted treatment type during 2013 measurements. Second, we considered treatment polygons supplied by the US Forest Service American River Ranger District (Fig. 1).

Where these two data sources differed (12 plots) we closely examined field data for changes in tree densities, shrub cover, ground fuels, and litter between pre-treatment and post-treatment measurements. Lastly, we confirmed our treatment assignments using remotely sensed change detection maps, produced by determining areas where differences between pre-treatment and post-treatment maps surpassed threshold values denoting structural change (e.g., > 10% reduction in canopy cover or mean tree height), identifying areas that were potentially thinned (Su et al., 2016a). Post-treatment sampling indicated that several plots within the prescribed fire polygons lacked evidence of fire.

We used GLMs with likelihood ratio tests to evaluate treatment effects on seedling densities. We again standardized all continuous variables by subtracting the mean and dividing by the standard deviation. We again used GLMs with a negative binomial distribution and logarithmic link function for the fir analysis and hurdle models for pines, with an offset for sample area for all models.

We chose which pre-treatment variables to include in these analyses based on the results of Step 1. For firs, we included pre-treatment shrub cover and pre-treatment tree basal area because the post-fire analogs of those two variables were in at least one of the top three models with < 2 AICc and were possible to calculate from pre-treatment data. For pines, we included pre-treatment shrub cover, pre-treatment tree basal area, and pre-treatment pine basal area for the same reasons. In other words, the effect of treatment on seedling densities was tested by performing a likelihood ratio test between the following treatment and null models for each species group:

Fir treatment model:

Seedling density ~ Pre-treatment shrub cover + Pre-treatment tree basal area + Fire*Treatment

Fir null model:

Seedling density ~ Pre-treatment shrub cover + Pre-treatment tree basal area + Fire

Pine treatment model:

Seedling density ~ Pre-treatment shrub cover + Pre-treatment pine basal area + Pre-treatment tree basal area + Fire*Treatment

Pine null model:

Seedling density ~ Pre-treatment shrub cover + Pre-treatment pine basal area + Pre-treatment tree basal area + Fire

Treatment effects on drivers of seedling densities.

We separately tested the effects of treatment on each plot characteristic that was included in either the best fir or best pine model from Step 1. We used transformations where necessary to increase normality of the residuals, as indicated in Table 3. For tree basal area, shrub cover, and pine parent potential, we included a binary variable for whether the plot was inside the fire perimeter and an interaction between that variable and treatment. For neighborhood fire severity and local fire severity, we excluded plots outside the fire perimeter.

Supplementary results

Results of seedling density analysis for all seedling species combined. Seedling densities for all species combined were best explained by the seedling driver model (Step 1) with shrub cover, basal area, plot-scale fire severity, neighborhood fire severity, the interaction between plot-scale and neighborhood-scale fire severity, and the interaction between fire severity and basal area. Pseudo R^2 for this model was 0.59. Treatments had a positive effect on seedling densities according to the likelihood ratio test performed in Step 2 ($P < 0.001$). Pre-treatment shrub cover and pre-treatment basal area were included in the treatment and null models when testing for treatment effects.

Table A.1. Coefficients for the effects of standardized post-fire plot biophysical characteristics on seedling densities for firs, for the best fir seedling driver model from Step 1. For the factor variables (plot fire severity, parent potential, and interactions), the coefficients for each group are listed using the sum-to-zero constraint.

Shrub cover	Basal area	Neighborhood fire severity	Plot fire severity (unburned, low, moderate, high)	Basal area/plot fire severity interaction (unburned, low, moderate, high)	Neighborhood/plot fire severity interaction (unburned+low, moderate, high)
-0.72	0.76	-0.47	-1.8, -1.4, 0.10, 3.1	1.72, -1.56, -0.03, -0.12	0.51, -0.79, 0.28

Table A.2. Coefficients for the effects of standardized post-fire plot biophysical characteristics on seedling densities for pines, for the best pine seedling driver hurdle model from Step 1.

	Plot fire severity (unburned, low, moderate, high)	Post-fire pine basal area
non-zeros	-0.13, -0.87, 0.31, 0.69	0.05
zeros	13.5, -6.56, -3.7, -3.27	0.08

Table A.3. Model rankings for fir post-fire plot biophysical characteristics. Evidence ratio is the Akaike weight divided by the maximum Akaike weight.

Model	AICc	ΔAICc	Akaike weight	Evidence ratio
Shrub cover + Basal area*Plot fire severity + Neighborhood fire severity*Plot fire severity	**961.74**	**0**	**0.21**	**1**
Shrub cover + Bare mineral soil + Basal area*Plot fire severity + Neighborhood fire severity*Plot fire severity	**962.95**	**1.21**	**0.11**	**0.55**
Shrub cover + Basal area + Plot fire severity + Neighborhood fire severity*Plot fire severity	**963.72**	**1.98**	**0.08**	**0.37**
Shrub cover + Basal area*Plot fire severity + Neighborhood fire severity	964.03	2.29	0.07	0.32
Shrub cover + Basal area*Plot fire severity + Fir basal area + Neighborhood fire severity*Plot fire severity	964.13	2.39	0.06	0.3
Shrub cover + Plot fire severity + Neighborhood fire severity*Plot fire severity	964.98	3.25	0.04	0.2
Shrub cover + Plot fire severity + Fir basal area + Neighborhood fire severity*Plot fire severity	965.16	3.42	0.04	0.18
Shrub cover + Basal area + Plot fire severity + Bare mineral soil + Neighborhood fire severity*Plot fire severity	965.42	3.68	0.03	0.16
Shrub cover + Bare mineral soil + Basal area*Plot fire severity + Fir basal area + Neighborhood fire severity*Plot fire severity	965.45	3.71	0.03	0.16
Shrub cover + Bare mineral soil + Basal area*Plot fire severity + Neighborhood fire severity	965.52	3.78	0.03	0.15
Shrub cover + Plot fire severity + Bare mineral soil + Neighborhood fire severity*Plot fire severity	965.61	3.87	0.03	0.14
Shrub cover + Basal area + Plot fire severity + Fir basal area + Neighborhood fire severity*Plot fire severity	966.17	4.44	0.02	0.11
Shrub cover + Plot fire severity + Bare mineral soil + Fir basal area + Neighborhood fire severity*Plot fire severity	966.32	4.58	0.02	0.1
Shrub cover + Basal area*Plot fire severity + Fir basal area	966.37	4.64	0.02	0.1
Basal area + Plot fire severity + Neighborhood fire severity*Plot fire severity	966.49	4.76	0.02	0.09
Shrub cover + Basal area*Plot fire severity + Fir basal area + Neighborhood fire severity	966.51	4.77	0.02	0.09
Shrub cover + Basal area + Plot fire severity + Neighborhood fire severity	967.15	5.41	0.01	0.07
Shrub cover + Bare mineral soil + Basal area*Plot fire severity + Fir basal area	967.6	5.86	0.01	0.05
Shrub cover + Plot fire severity + Neighborhood fire severity	967.86	6.13	0.01	0.05
Shrub cover + Basal area + Plot fire severity + Bare mineral soil + Fir basal area + Neighborhood fire severity*Plot fire severity	967.93	6.19	0.01	0.05
Basal area*Plot fire severity + Neighborhood fire severity*Plot fire severity	967.98	6.24	0.01	0.04

Shrub cover + Bare mineral soil + Basal area*Plot fire severity + Fir basal area + Neighborhood fire severity	968.07	6.33	0.01	0.04
Basal area*Plot fire severity	968.35	6.61	0.01	0.04
Basal area + Plot fire severity + Fir basal area + Neighborhood fire severity*Plot fire severity	968.66	6.92	0.01	0.03
Shrub cover + Basal area + Plot fire severity + Bare mineral soil + Neighborhood fire severity	968.74	7.01	0.01	0.03
Shrub cover + Plot fire severity + Fir basal area + Neighborhood fire severity	968.75	7.01	0.01	0.03
Shrub cover + Plot fire severity + Bare mineral soil + Neighborhood fire severity	968.81	7.07	0.01	0.03
Basal area + Plot fire severity + Bare mineral soil + Neighborhood fire severity*Plot fire severity	968.84	7.1	0.01	0.03
Shrub cover + Basal area + Plot fire severity	969.39	7.65	0	0.02
Shrub cover + Basal area + Plot fire severity + Fir basal area + Neighborhood fire severity	969.58	7.84	0	0.02
Basal area*Plot fire severity + Fir basal area + Neighborhood fire severity*Plot fire severity	969.73	8	0	0.02
Basal area*Plot fire severity + Neighborhood fire severity	969.77	8.03	0	0.02
Shrub cover + Plot fire severity + Bare mineral soil + Fir basal area + Neighborhood fire severity	969.93	8.19	0	0.02
Plot fire severity + Fir basal area + Neighborhood fire severity*Plot fire severity	969.94	8.2	0	0.02
Basal area*Plot fire severity + Fir basal area	970.26	8.52	0	0.01
Bare mineral soil + Basal area*Plot fire severity + Neighborhood fire severity*Plot fire severity	970.45	8.72	0	0.01
Bare mineral soil + Basal area*Plot fire severity	970.67	8.93	0	0.01
Shrub cover + Basal area + Plot fire severity + Bare mineral soil	970.85	9.11	0	0.01
Basal area + Plot fire severity + Bare mineral soil + Fir basal area + Neighborhood fire severity*Plot fire severity	971.06	9.32	0	0.01
Shrub cover + Basal area + Plot fire severity + Bare mineral soil + Fir basal area + Neighborhood fire severity	971.23	9.49	0	0.01
Shrub cover + Basal area + Plot fire severity + Fir basal area	971.76	10.02	0	0.01
Plot fire severity + Bare mineral soil + Fir basal area + Neighborhood fire severity*Plot fire severity	971.79	10.05	0	0.01
Basal area*Plot fire severity + Fir basal area + Neighborhood fire severity	971.85	10.11	0	0.01
Bare mineral soil + Basal area*Plot fire severity + Neighborhood fire severity	972.21	10.47	0	0.01
Shrub cover + Plot fire severity + Fir basal area	972.28	10.54	0	0.01
Bare mineral soil + Basal area*Plot fire severity + Fir basal area + Neighborhood fire severity*Plot fire severity	972.29	10.55	0	0.01
Basal area + Plot fire severity + Neighborhood fire severity	972.63	10.89	0	0
Bare mineral soil + Basal area*Plot fire severity + Fir basal area	972.63	10.89	0	0
Shrub cover + Plot fire severity	972.7	10.96	0	0
Basal area + Plot fire severity	972.73	10.99	0	0

Shrub cover + Plot fire severity + Bare mineral soil + Fir basal area	973.24	11.5	0	0
Shrub cover + Basal area + Plot fire severity + Bare mineral soil + Fir basal area	973.28	11.54	0	0
Shrub cover + Neighborhood fire severity	973.74	12	0	0
Bare mineral soil + Basal area*Plot fire severity + Fir basal area + Neighborhood fire severity	974.34	12.6	0	0
Basal area + Plot fire severity + Bare mineral soil	974.85	13.12	0	0
Basal area + Plot fire severity + Bare mineral soil + Neighborhood fire severity	974.87	13.14	0	0
Basal area + Plot fire severity + Fir basal area	974.92	13.18	0	0
Basal area + Plot fire severity + Fir basal area + Neighborhood fire severity	974.93	13.19	0	0
Shrub cover + Fir basal area + Neighborhood fire severity	975.5	13.76	0	0
Shrub cover + Basal area + Neighborhood fire severity	975.59	13.85	0	0
Plot fire severity + Neighborhood fire severity*Plot fire severity	975.68	13.95	0	0
Shrub cover + Bare mineral soil + Neighborhood fire severity	975.88	14.14	0	0
Shrub cover + Basal area + Fir basal area + Neighborhood fire severity	975.88	14.14	0	0
Plot fire severity + Bare mineral soil + Neighborhood fire severity*Plot fire severity	976.89	15.15	0	0
Basal area + Plot fire severity + Bare mineral soil + Fir basal area	977.1	15.36	0	0
Plot fire severity + Fir basal area + Neighborhood fire severity	977.16	15.42	0	0
Basal area + Plot fire severity + Bare mineral soil + Fir basal area + Neighborhood fire severity	977.22	15.48	0	0
Shrub cover + Bare mineral soil + Fir basal area + Neighborhood fire severity	977.6	15.87	0	0
Shrub cover	977.79	16.05	0	0
Shrub cover + Basal area + Bare mineral soil + Neighborhood fire severity	977.86	16.12	0	0
Plot fire severity + Fir basal area	978	16.26	0	0
Shrub cover + Basal area + Bare mineral soil + Fir basal area + Neighborhood fire severity	978.21	16.47	0	0
Shrub cover + Fir basal area	978.69	16.95	0	0
Plot fire severity + Bare mineral soil + Fir basal area + Neighborhood fire severity	978.97	17.23	0	0
Plot fire severity + Bare mineral soil + Fir basal area	979.69	17.95	0	0
Shrub cover + Basal area	979.88	18.14	0	0
Shrub cover + Bare mineral soil	979.89	18.15	0	0
Shrub cover + Basal area + Fir basal area	980.54	18.81	0	0
Shrub cover + Bare mineral soil + Fir basal area	980.91	19.17	0	0
Shrub cover + Basal area + Bare mineral soil	982.07	20.33	0	0

Shrub cover + Basal area + Bare mineral soil + Fir basal area	982.8	21.06	0	0
Plot fire severity	984.32	22.58	0	0
Plot fire severity + Bare mineral soil	985.51	23.77	0	0
Fir basal area + Neighborhood fire severity	1003.06	41.32	0	0
Fir basal area	1003.29	41.55	0	0
Bare mineral soil + Fir basal area + Neighborhood fire severity	1003.78	42.05	0	0
Bare mineral soil + Fir basal area	1004.31	42.57	0	0
Basal area + Fir basal area + Neighborhood fire severity	1005.28	43.54	0	0
Basal area + Fir basal area	1005.41	43.67	0	0
Neighborhood fire severity	1005.76	44.02	0	0
Basal area + Bare mineral soil + Fir basal area + Neighborhood fire severity	1005.98	44.24	0	0
Basal area + Neighborhood fire severity	1006.15	44.41	0	0
Basal area + Bare mineral soil + Fir basal area	1006.31	44.57	0	0
Basal area	1006.36	44.62	0	0
Basal area + Bare mineral soil + Neighborhood fire severity	1006.61	44.87	0	0
Bare mineral soil + Neighborhood fire severity	1007.05	45.31	0	0
Basal area + Bare mineral soil	1007.52	45.79	0	0
Bare mineral soil	1009.62	47.88	0	0
Shrub cover + Basal area*Plot fire severity	NA	NA	NA	NA
Plot fire severity + Neighborhood fire severity	NA	NA	NA	NA
Shrub cover + Plot fire severity + Bare mineral soil	NA	NA	NA	NA
Shrub cover + Bare mineral soil + Basal area*Plot fire severity	NA	NA	NA	NA
Plot fire severity + Bare mineral soil + Neighborhood fire severity	NA	NA	NA	NA

Table A.4. Model rankings for pine post-fire plot characteristics. Evidence ratio is the Akaike weight divided by the maximum Akaike weight.

Model	**AICc**	**ΔAICc**	**Akaike weight**	**Evidence ratio**
Plot fire severity + Pine basal area	**578.46**	**0**	**0.24**	**1**
Shrub cover + Basal area + Pine basal area	**578.88**	**0.43**	**0.2**	**0.81**
Shrub cover + Basal area + Plot fire severity + Pine basal area	**580.09**	**1.64**	**0.11**	**0.44**
Shrub cover + Plot fire severity + Pine basal area	580.5	2.05	0.09	0.36
Basal area + Plot fire severity + Pine basal area	580.97	2.51	0.07	0.28
Shrub cover + Basal area + Pine basal area + Neighborhood fire severity	581.3	2.84	0.06	0.24
Plot fire severity + Bare mineral soil + Pine basal area	582.48	4.02	0.03	0.13
Shrub cover + Basal area + Bare mineral soil + Pine basal area	582.58	4.12	0.03	0.13
Shrub cover + Basal area + Plot fire severity + Bare mineral soil + Pine basal area	582.79	4.34	0.03	0.11
Shrub cover + Basal area*Plot fire severity + Pine basal area	583.08	4.63	0.02	0.1
Plot fire severity + Pine basal area + Neighborhood fire severity	583.21	4.76	0.02	0.09
Basal area + Plot fire severity + Bare mineral soil + Pine basal area	583.5	5.04	0.02	0.08
Shrub cover + Basal area + Plot fire severity + Pine basal area + Neighborhood fire severity	584.12	5.66	0.01	0.06
Shrub cover + Bare mineral soil + Basal area*Plot fire severity + Pine basal area	584.71	6.25	0.01	0.04
Shrub cover + Basal area + Bare mineral soil + Pine basal area + Neighborhood fire severity	585.07	6.61	0.01	0.04
Shrub cover + Plot fire severity + Bare mineral soil + Pine basal area	585.12	6.66	0.01	0.04
Shrub cover + Plot fire severity + Pine basal area + Neighborhood fire severity	585.22	6.76	0.01	0.03
Basal area + Plot fire severity + Pine basal area + Neighborhood fire severity	585.69	7.23	0.01	0.03
Basal area*Plot fire severity + Pine basal area	586.58	8.12	0	0.02
Shrub cover + Basal area + Plot fire severity + Bare mineral soil + Pine basal area + Neighborhood fire severity	586.92	8.46	0	0.01
Plot fire severity + Bare mineral soil + Pine basal area + Neighborhood fire severity	587.47	9.01	0	0.01
Basal area + Plot fire severity + Bare mineral soil + Pine basal area + Neighborhood fire severity	588.45	10	0	0.01
Shrub cover + Basal area*Plot fire severity + Pine basal area + Neighborhood fire severity	588.65	10.19	0	0.01

Bare mineral soil + Basal area*Plot fire severity + Pine basal area	589.41	10.95	0	0
Shrub cover + Pine basal area + Neighborhood fire severity	589.51	11.05	0	0
Shrub cover + Pine basal area	589.72	11.27	0	0
Shrub cover + Bare mineral soil + Pine basal area	589.98	11.52	0	0
Plot fire severity + Pine basal area + Neighborhood fire severity:Plot fire severity + Neighborhood fire severity	590	11.55	0	0
Shrub cover + Plot fire severity	590.01	11.55	0	0
Shrub cover + Plot fire severity + Bare mineral soil + Pine basal area + Neighborhood fire severity	590.06	11.61	0	0
Shrub cover + Bare mineral soil + Basal area*Plot fire severity + Pine basal area + Neighborhood fire severity	590.21	11.75	0	0
Plot fire severity	590.98	12.53	0	0
Shrub cover + Bare mineral soil + Pine basal area + Neighborhood fire severity	591.4	12.95	0	0
Plot fire severity + Bare mineral soil	591.94	13.49	0	0
Basal area*Plot fire severity + Pine basal area + Neighborhood fire severity	592.43	13.97	0	0
Basal area + Plot fire severity + Pine basal area + Neighborhood fire severity:Plot fire severity + Neighborhood fire severity	592.51	14.05	0	0
Shrub cover + Plot fire severity + Bare mineral soil	592.61	14.15	0	0
Basal area + Pine basal area	593.61	15.15	0	0
Shrub cover + Plot fire severity + Neighborhood fire severity	594.13	15.67	0	0
Shrub cover + Basal area + Plot fire severity + Pine basal area + Neighborhood fire severity:Plot fire severity + Neighborhood fire severity	594.2	15.74	0	0
Plot fire severity + Bare mineral soil + Pine basal area + Neighborhood fire severity:Plot fire severity + Neighborhood fire severity	594.24	15.78	0	0
Shrub cover + Plot fire severity + Pine basal area + Neighborhood fire severity:Plot fire severity + Neighborhood fire severity	594.46	16	0	0
Shrub cover + Basal area	594.47	16.01	0	0
Basal area + Plot fire severity + Bare mineral soil + Pine basal area + Neighborhood fire severity:Plot fire severity + Neighborhood fire severity	594.51	16.06	0	0
Bare mineral soil + Pine basal area	594.73	16.27	0	0
Basal area + Plot fire severity	594.95	16.49	0	0
Shrub cover + Basal area + Plot fire severity	595.07	16.62	0	0
Plot fire severity + Neighborhood fire severity	595.25	16.79	0	0
Basal area + Bare mineral soil + Pine basal area	595.28	16.82	0	0

Bare mineral soil + Basal area*Plot fire severity + Pine basal area + Neighborhood fire severity	595.33	16.87	0	0
Pine basal area + Neighborhood fire severity	595.49	17.04	0	0
Bare mineral soil + Pine basal area + Neighborhood fire severity	595.65	17.19	0	0
Basal area + Pine basal area + Neighborhood fire severity	595.73	17.28	0	0
Plot fire severity + Bare mineral soil + Neighborhood fire severity	596.45	17.99	0	0
Pine basal area	596.69	18.23	0	0
Shrub cover + Basal area + Plot fire severity + Bare mineral soil + Pine basal area + Neighborhood fire severity:Plot fire severity + Neighborhood fire severity	596.81	18.35	0	0
Basal area + Plot fire severity + Bare mineral soil	596.89	18.43	0	0
Shrub cover + Plot fire severity + Bare mineral soil + Neighborhood fire severity	596.94	18.48	0	0
Shrub cover + Neighborhood fire severity	596.95	18.5	0	0
Shrub cover + Basal area + Plot fire severity + Bare mineral soil	597.13	18.67	0	0
Shrub cover + Basal area + Neighborhood fire severity	597.4	18.94	0	0
Basal area + Bare mineral soil + Pine basal area + Neighborhood fire severity	597.66	19.2	0	0
Shrub cover	598.08	19.63	0	0
Shrub cover + Bare mineral soil	598.29	19.84	0	0
Shrub cover + Basal area + Bare mineral soil	598.78	20.32	0	0
Shrub cover + Bare mineral soil + Neighborhood fire severity	599.02	20.57	0	0
Shrub cover + Plot fire severity + Bare mineral soil + Pine basal area + Neighborhood fire severity:Plot fire severity + Neighborhood fire severity	599.43	20.97	0	0
Shrub cover + Basal area + Plot fire severity + Neighborhood fire severity	599.61	21.16	0	0
Basal area + Plot fire severity + Neighborhood fire severity	599.65	21.19	0	0
Shrub cover + Basal area*Plot fire severity + Pine basal area + Neighborhood fire severity:Plot fire severity + Neighborhood fire severity	601.73	23.28	0	0
Shrub cover + Basal area + Bare mineral soil + Neighborhood fire severity	601.85	23.39	0	0
Basal area + Plot fire severity + Bare mineral soil + Neighborhood fire severity	601.85	23.39	0	0
Shrub cover + Basal area + Plot fire severity + Bare mineral soil + Neighborhood fire severity	601.9	23.44	0	0
Basal area*Plot fire severity + Pine basal area + Neighborhood fire severity:Plot fire severity + Neighborhood fire severity	602.08	23.62	0	0
Plot fire severity + Neighborhood fire severity:Plot fire severity + Neighborhood fire severity	602.25	23.8	0	0
Shrub cover + Plot fire severity + Neighborhood fire severity:Plot fire severity + Neighborhood fire severity	603.09	24.64	0	0

Plot fire severity + Bare mineral soil + Neighborhood fire severity:Plot fire severity + Neighborhood fire severity	603.29	24.83	0	0
Shrub cover + Bare mineral soil + Basal area*Plot fire severity + Pine basal area + Neighborhood fire severity:Plot fire severity + Neighborhood fire severity	603.52	25.07	0	0
Bare mineral soil + Basal area*Plot fire severity + Pine basal area + Neighborhood fire severity:Plot fire severity + Neighborhood fire severity	604.74	26.28	0	0
Basal area	605.33	26.88	0	0
Bare mineral soil	606.02	27.56	0	0
Shrub cover + Plot fire severity + Bare mineral soil + Neighborhood fire severity:Plot fire severity + Neighborhood fire severity	606.16	27.71	0	0
Shrub cover + Basal area*Plot fire severity	606.18	27.72	0	0
Bare mineral soil + Neighborhood fire severity	606.55	28.1	0	0
Basal area*Plot fire severity	606.81	28.35	0	0
Basal area + Neighborhood fire severity	607.09	28.63	0	0
Neighborhood fire severity	607.22	28.77	0	0
Basal area + Plot fire severity + Neighborhood fire severity:Plot fire severity + Neighborhood fire severity	607.22	28.77	0	0
Basal area + Bare mineral soil	607.7	29.25	0	0
Shrub cover + Bare mineral soil + Basal area*Plot fire severity	608.43	29.98	0	0
Shrub cover + Basal area + Plot fire severity + Neighborhood fire severity:Plot fire severity + Neighborhood fire severity	609.13	30.68	0	0
Basal area + Plot fire severity + Bare mineral soil + Neighborhood fire severity:Plot fire severity + Neighborhood fire severity	609.21	30.76	0	0
Bare mineral soil + Basal area*Plot fire severity	609.53	31.08	0	0
Basal area + Bare mineral soil + Neighborhood fire severity	609.72	31.27	0	0
Shrub cover + Basal area*Plot fire severity + Neighborhood fire severity	611.37	32.91	0	0
Shrub cover + Basal area + Plot fire severity + Bare mineral soil + Neighborhood fire severity:Plot fire severity + Neighborhood fire severity	611.62	33.16	0	0
Basal area*Plot fire severity + Neighborhood fire severity	612.22	33.76	0	0
Shrub cover + Bare mineral soil + Basal area*Plot fire severity + Neighborhood fire severity	613.69	35.23	0	0
Bare mineral soil + Basal area*Plot fire severity + Neighborhood fire severity	615.13	36.68	0	0
Basal area*Plot fire severity + Neighborhood fire severity:Plot fire severity + Neighborhood fire severity	621.43	42.97	0	0
Shrub cover + Basal area*Plot fire severity + Neighborhood fire severity:Plot fire severity + Neighborhood fire severity	623.08	44.62	0	0

Bare mineral soil + Basal area*Plot fire severity + Neighborhood fire severity:Plot fire severity + Neighborhood fire severity	624.16	45.71	0	0
Shrub cover + Bare mineral soil + Basal area*Plot fire severity + Neighborhood fire severity:Plot fire severity + Neighborhood fire severity	625.69	47.24	0	0