Title

Post-fire tree regeneration in an altered disturbance regime: community dynamics and interactions with land management

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By

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Committee in charge:

Professor John J. Battles, Co-chair
Professor Scott L. Stephens, Co-chair
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Abstract

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Doctor of Philosophy in Environmental Science, Policy, and Management

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Professors John Battles and Scott Stephens, Co-chairs

Fire has long shaped forests across the globe. Anthropogenic forces are reshaping fire regimes, leading to unprecedented forest conditions and unknown long-term consequences. Land management can help mitigate undesired effects of altered fire regimes, but effective management requires information about tree species' responses to disturbances both historical and modern. In my dissertation, I add to a body of literature examining how novel fire patterns affect tree regeneration and whether forest management strategies can mitigate any undesired effects. I focus on mixed-conifer forests of the Sierra Nevada, where logging, fire exclusion, and climate change have shifted the fire regime from frequent, heterogenous fire to infrequent fire with greater high severity. The tree species that have long comprised these forests are not well adapted to regenerate in large, homogenous fire patches. My dissertation investigates three main questions in three chapters: 1) Can forest management prevent large fire patches and promote post-fire recovery? 2) Will the novel fire regime shift overall species composition toward firs and away from pines? 3) What is the role of post-fire shrub dynamics in determining ecological succession in novel-type fire patches? In Chapter 1, I show that strategically placed fuel reduction treatments effectively reduced fire severity and promoted recovery when burned in a wildfire. In Chapter 2, I explore the idea that the shifting fire regime may lead to regional fir enrichment. I focus on plant interactions following severe wildfire and show that shrub competition affects ponderosa pine more strongly than it affects white fir. However, simulation modeling results in Chapter 3 show that, on net, shrub neighborhood dynamics do not produce an ecological filter favoring firs, though patterns are sensitive to shrub species. These three chapters together illustrate the importance of forest patch dynamics for wildfire resistance and recovery.

For my dad, who is no doubt bragging about his daughters to the worms and roots where he rests.

And for my big sister Greta, whose belief in me is so strong and loving that she sometimes convinces me I'm as great as she thinks I am.

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Introduction

Disturbances, whether wind, fire, or insect attack, have long shaped forests across the globe. Every tree species has unique characteristics that affect its ability to survive disturbances and regenerate afterwards, which may in turn affect future disturbance patterns. Anthropogenic forces are reshaping disturbance regimes, leading to unprecedented forest conditions and unknown long-term consequences. Land management can help mitigate undesired effects of altered fire regimes, but effective management requires information about tree species' responses to disturbances both historical and modern. In my dissertation, I add to a body of literature examining how novel fire patterns affect tree regeneration and whether forest management strategies can mitigate any undesired effects.

I focus on mixed-conifer forests of the Sierra Nevada, where logging, fire exclusion, and climate change have shifted the fire regime. Fire was once frequent, patchy, and heterogeneous, with a mixture of low, moderate, and high severity patches. Increasingly, forests experience either no fire at all or severe fire producing large patches of near-total overstory mortality. The tree species that have long comprised these forests are not well adapted to regenerate in large, homogenous fire patches. My dissertation investigates three main questions in three chapters: 1) Can forest management prevent large fire patches and promote post-fire recovery? 2) Will the novel fire regime shift overall species composition toward firs and away from pines? 3) What is the role of post-fire shrub dynamics in determining ecological succession in novel-type fire patches?

Chapter 1 takes advantage of a natural experiment to test the efficacy of a common land management strategy in promoting fire resistance and recovery. Strategically placed landscape treatments (SPLATs) is a term coined in the early 2000s to describe the practice of actively managing a small fraction of a landscape to achieve landscape-wide fire mitigation. SPLATs can be forest thinning, prescribed fire, or other strategies that reduce fuels. They are placed in portions of the landscape where they are expected to affect downstream fire behavior. Though the SPLATs concept underpins regional public forest plans, it has rarely been tested empirically. In the late 2000s, a treatment network was implemented in an area termed Last Chance, in the Tahoe National Forest within the northern Sierra Nevada. This treatment network was monitored closely by the Sierra Nevada Adaptive Management Project (SNAMP) to test the effects of a real-world treatment network designed to conform with SPLAT principles. In 2013, SNAMP post-treatment field surveys were abruptly halted by the American Fire, an 11,102-ha wildfire typical of modern mixed-severity fire. The American Fire produced a natural experiment, allowing us to test whether the Last Chance treatments performed as expected in an actual wildfire. In 2015, I returned to SNAMP plots within the American Fire footprint to measure post-fire tree regeneration. I also analyzed the spatial patterns of the American Fire using field data, fire behavior modeling, and a fire severity map derived from remote sensing.

I found that the treated portion of the Last Chance study area experienced lower fire severity and fewer large high-severity fire patches than the adjacent untreated portion. The success of treatments was likely due in part to their placement in the highest-risk areas of the landscape. I also found that treated plots had higher seedling densities than untreated plots, potentially due to the fact that fire moderated neighborhood fire severity, which enhanced tree regeneration. Regeneration was dominated by firs.

Chapter 2 focuses on differences between firs and pines under the altered fire regime of the Sierra Nevada. It is well known that fire exclusion advantages shade-tolerant trees (e.g. firs) over shade-intolerant trees (e.g. pines). I explore the idea that large stand-replacing fire patches, a result of fire exclusion, may also promote firs. I developed a conceptual framework describing how the novel fire regime promotes two types of fir enrichment, overstory-driven fir enrichment and patch-driven fir enrichment, with the latter caused by differences in dispersal as well as in shrub/tree interactions. Shrub interactions are particularly important in post-fire recovery because native shrubs quickly reoccupy severely burned areas. I measured fir and pine growth and survival in relation to shrub neighborhood to test whether shrub interactions provide an advantage to firs. I found that ponderosa pine growth is more sensitive to shrub competition following wildfire than fir growth, presumably due to fir's high shade tolerance. Though pines are generally considered fire-adapted, this study argues that post-fire species interactions in a novel fire regime may exacerbate the already shifting species composition toward shade-tolerant species, which are less well adapted to survive future fires and to persist in future drier, warmer climates.

In Chapter 3, I further explore the effect of shrub neighborhood dynamics on fir and pine recovery. The results of Chapter 2 provided initial evidence that post-fire shrub patches may favor firs. However, to test whether the species differences I found have long-term ramifications, it was necessary to model tree growth and survival through time under realistic post-fire conditions. To do this, I developed a data-driven statistical simulation model that builds on the equations found in Chapter 2. Additional information on shrub dynamics was required to parameterize the model, so I synthesized and analyzed data from regional field surveys. I used the model to test whether shrubs act as an ecological filter by precluding, delaying, or altering the composition of conifer recovery. I also tested differences in model results for individual shrub species and individual dimensions of shrub neighborhood dynamics. My model indicated that, contrary to the hypothesis put forth in Chapter 2, shrub competition does not impede pine recovery enough to shift relative success towards firs. In the model, pines grew slower under higher shrub competition, but because of rapid initial growth and low mortality rates they reached the overstory in equal proportions to firs. In fact, pine relative success was higher than fir's under two of the three focal shrub species: deerbrush and whitethorn ceanothus. However, the final densities of pine were far lower than fir because of large differences in initial seedling densities. Thus, a stronger ecological filter may exist during the establishment phase than the growth and survival phases.

CHAPTER 1

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

Carmen L. Tubbesing, Danny L. Fry, Gary B. Roller, Brandon M. Collins, Varvara A. Fedorova, Scott L. Stephens, and John J. Battles

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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.

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 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?

METHODS

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).

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).

Field measurements

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.

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.

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.

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).

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.

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).

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 $\alpha = 0.05$ with a Bonferroni correction for multiple comparisons.

RESULTS

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 ($P = 0.38$).

Regeneration

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).

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).

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.

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; $P = 0.054$).

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 $\alpha = 0.05$ 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).

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.

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).

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 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.

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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TABLES

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

	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 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).”

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

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 $\alpha=0.10$ for 5 comparisons
**$P < 0.01$, the Bonferroni-corrected value of $\alpha=0.05$ for 5 comparisons

FIGURES

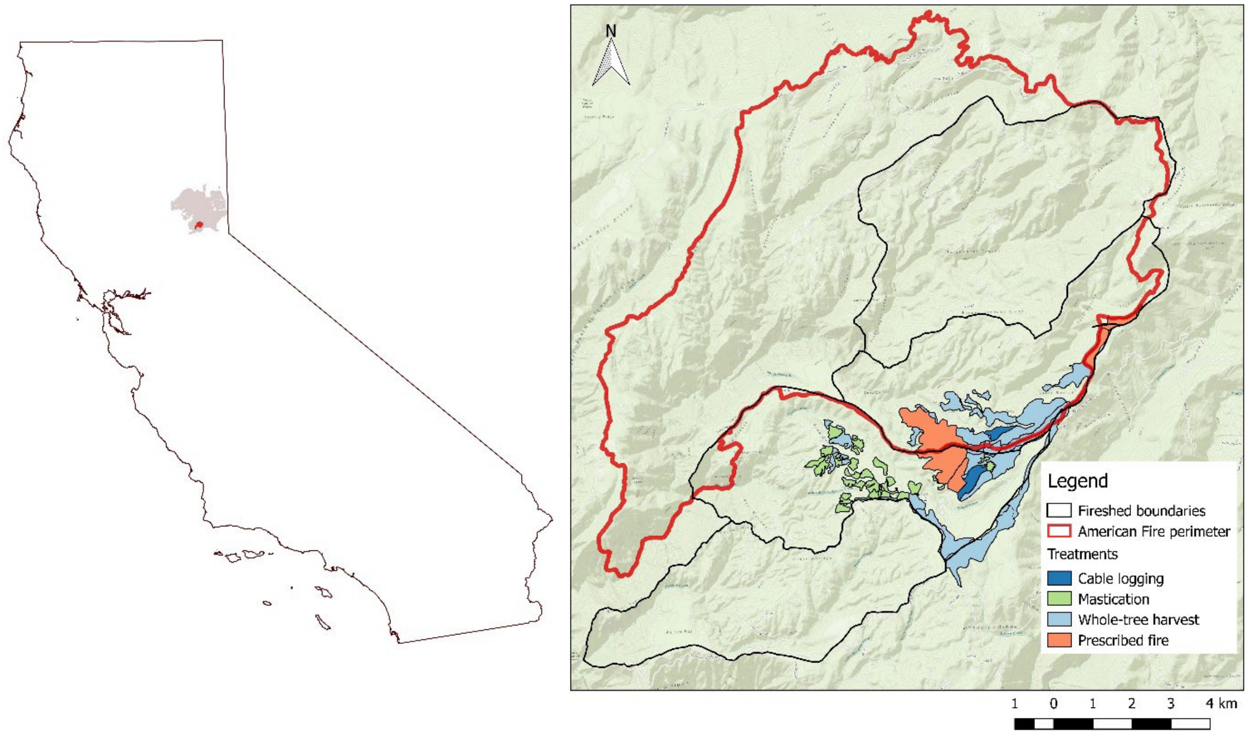

Figure 1. Perimeters of the American Fire and the original four firesheds established by the Last Chance project. The two firesheds that fall within the American Fire perimeter, one control and one treatment, were used in the present study. The overview map on the left shows the location of the American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

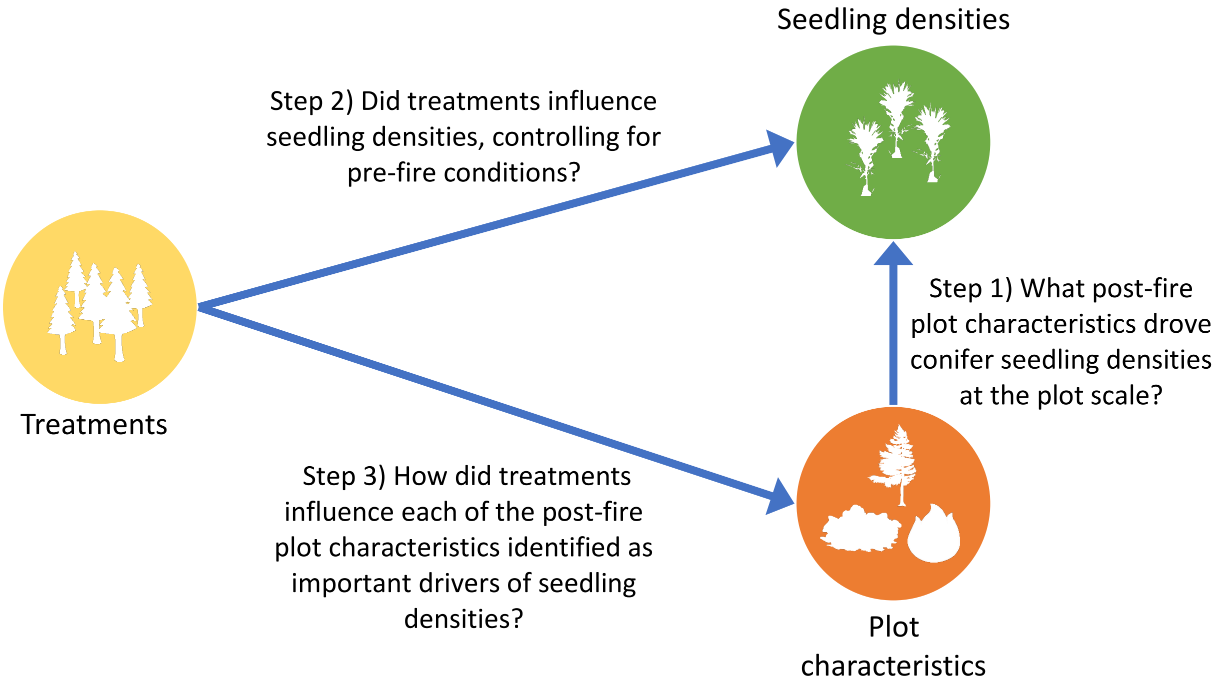

Figure 2. Analytical framework for seedling analyses. Seedling densities were analyzed in three steps, first identification of the drivers of seedling densities (Step 1), followed by analysis of the overall effect of treatments on seedling densities (Step 2), and finally the effects of treatments on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

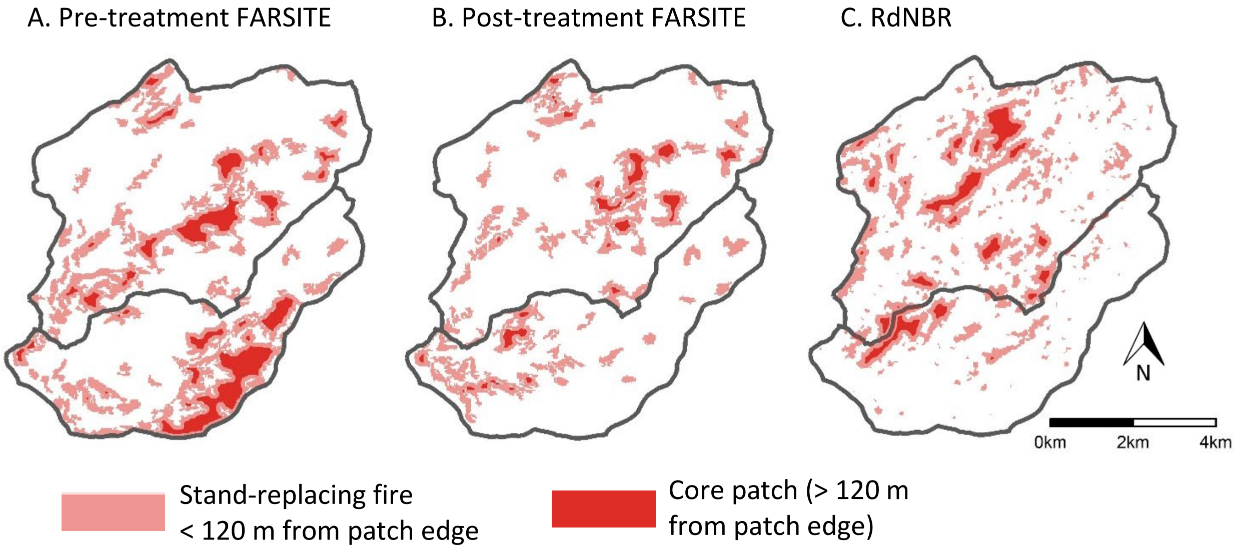

Figure 3. Stand-replacing fire patches and core patch areas based on pre-treatment FARSITE model output (A), post-treatment FARSITE model output (B) and actual RdNBR American Fire severity (C). The southern fireshed was treated while the northern fireshed was a control.

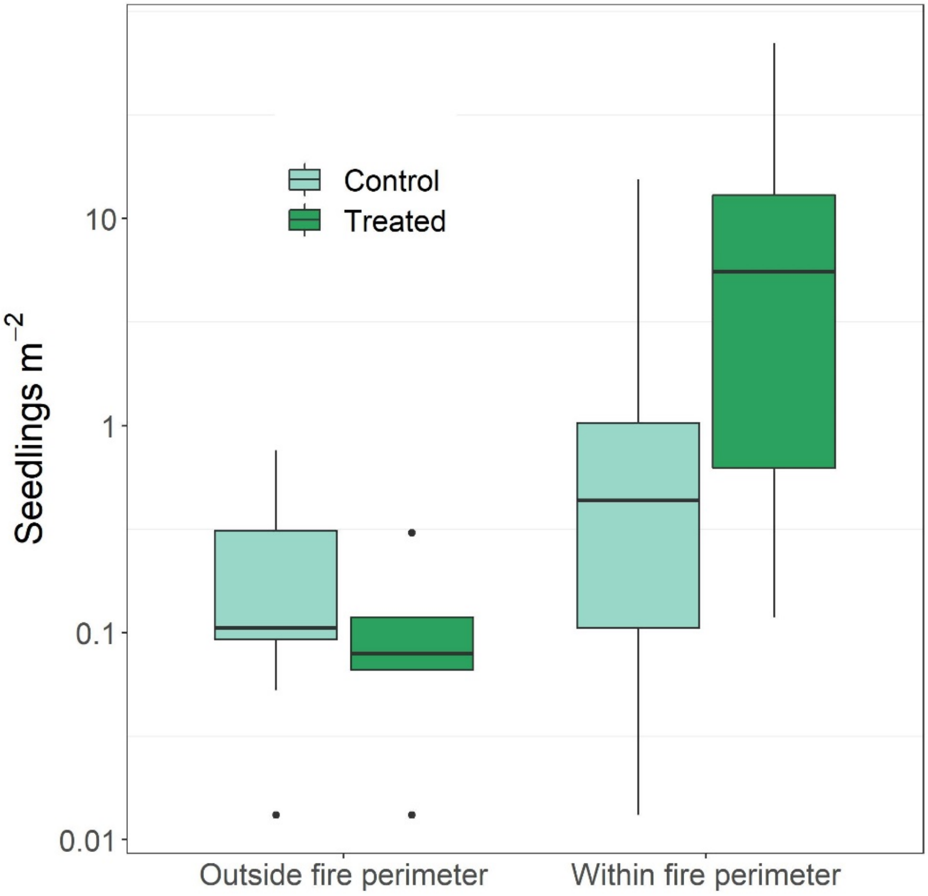

Figure 4. Seedling densities by treatment at the plot scale for all seedling species combined. Note the log scale on the y-axis. The midline of the boxplot represents the median of the data, the upper and lower limits of the box represent the third and first quartile of the data, and the whiskers represent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

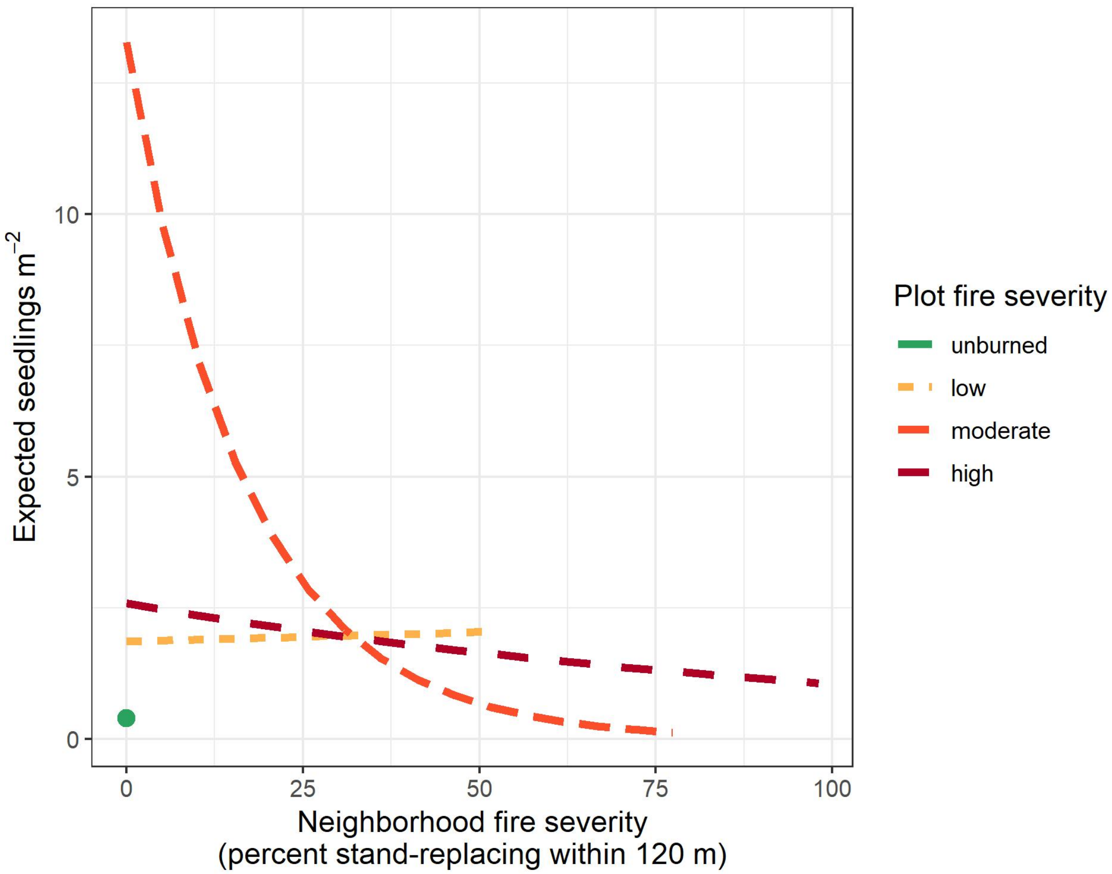

Figure 5. Predicted fir seedling densities in relation to plot-scale and neighborhood-scale fire severity for the best fir seedling driver model from Step 1. To generate these lines, the model was applied to a matrix of all variable combinations within the parameter space of the original data, and the 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.

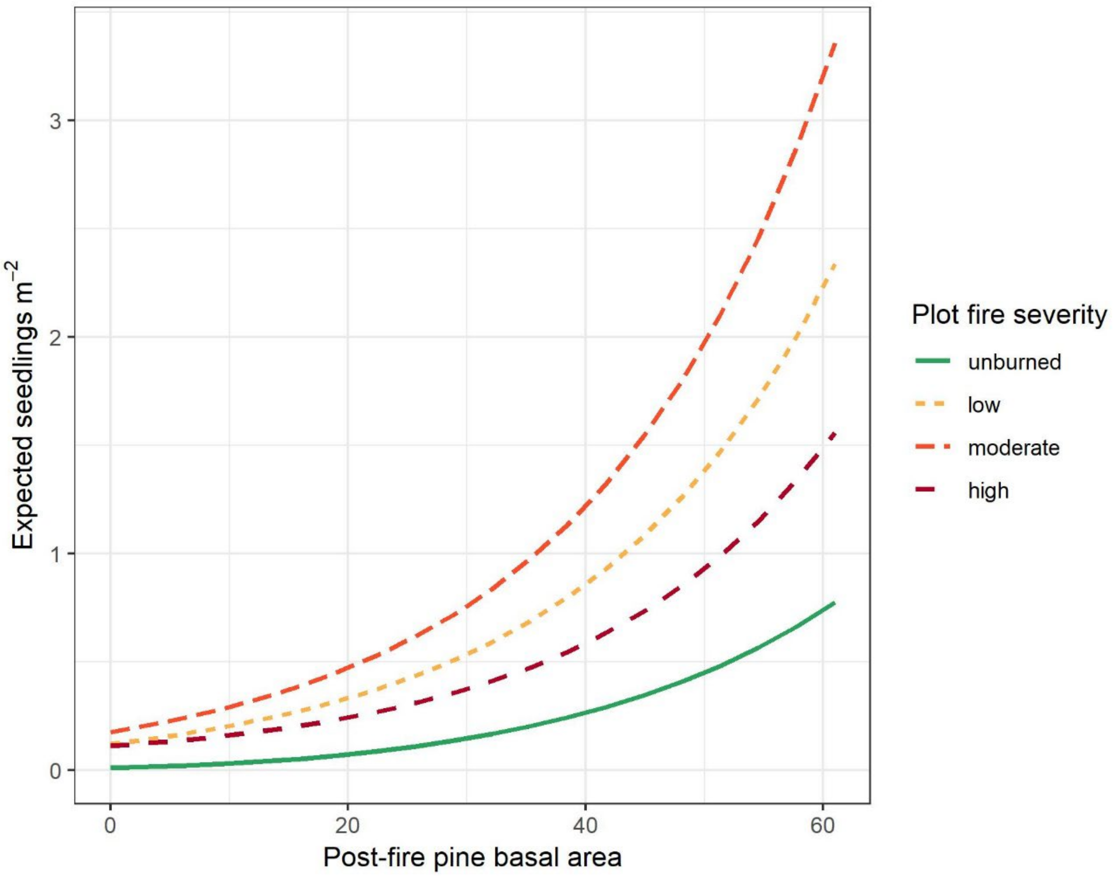

Figure 6. Predicted pine seedling densities in relation to post-fire pine basal area and plot-scale fire severity. Lines represent predictions based on the best pine seedling driver model from Step 1. To generate these lines, the same method was used as for Fig. 5.

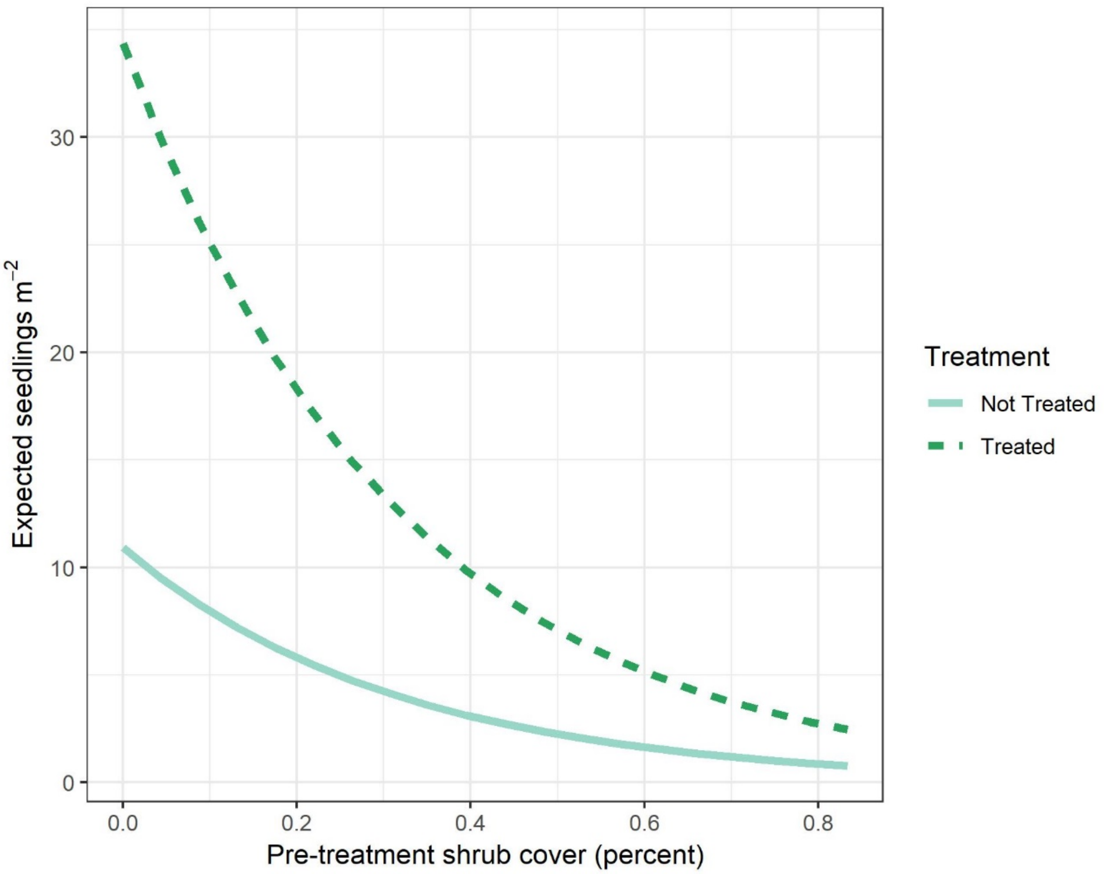

Figure 7. Predicted fir seedling densities in relation to treatment and pre-treatment shrub cover for the fir treatment model from Step 2. For ease of visualization, plots outside the fire perimeter are excluded from this figure. To generate these lines, the same method was used as for Figs. 5 and 6.

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In **Chapter 1**, I analyzed post-fire regeneration patterns and found that shade-tolerant tree species regenerated in much higher densities than shade-intolerant species. I also found that regeneration patterns were affected by neighborhood fire severity. In **Chapter 2,** I explore the idea that shifts toward shade-tolerant species may be occurring on a larger scale in response to the changing fire regime. As indicated in Chapter 1, neighborhood fire severity is likely to play a significant role in the new fire regime. Patches of high-severity fire may favor shade-tolerant firs because they foster dense, dark shrub layers that shade-intolerant pines may struggle to grow in. In Chapter 2, I present a conceptual framework illustrating how regional fir enrichment may occur. I then test a component of that framework. I ask: Does competition with shrubs in high-severity fire patches affect pines more strongly than it affects firs? Are these effects likely to alter fir and pine mortality rates?

CHAPTER 2

Rethinking fire-adapted species in an altered fire regime

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ABSTRACT

Novel combinations of fire regime and forest type are emerging in areas affected by climate change, fire exclusion, and other stressors. Species interactions following wildfire in these areas are not well understood. In Sierra Nevada mixed conifer forests, large patches of stand-replacing fire were once rare but are becoming increasingly prevalent and are quickly revegetated by native shrubs. There is uncertainty as to which tree species are best adapted to recover in the resulting post-fire environments. We introduce a conceptual framework for understanding how the altered fire regime in the Sierra Nevada may affect species composition. We investigate an understudied link in this framework: how juvenile ponderosa pine (*Pinus ponderosa*) and white fir (*Abies lowiana*) growth and mortality rates are affected by shrub competition following stand-replacing fire. We measured juvenile conifer growth in relation to shrub competition in five fire footprints ranging from 8 to 35 years old and > 400 ha in size. To test whether reductions in conifer growth may lead to increased mortality, we also evaluated how recent tree growth predicts mortality of similarly aged juvenile trees in nearby managed stands. We found that juvenile ponderosa pine growth was negatively associated with nearby shrub competition, but white fir growth was not. Both species grew slower preceding mortality, with a steeper relationship found in ponderosa pine. Across the range of shrub competition in this study, expected pine annual relative growth rate varied from 0.27 to 0.10, which corresponded to an eleven-fold difference in annual probability of mortality (0.1% to 1.1%, respectively). These results show that ponderosa pine is sensitive to shrub competition following wildfire in terms of both growth and survival while white fir is less sensitive, presumably due to its high shade tolerance. Though pines are generally considered fire-adapted, this study argues that post-fire species interactions in a novel fire regime may exacerbate the already shifting species composition toward shade tolerant species, which are less well adapted to survive through future fires and to persist in future drier, warmer climates.

INTRODUCTION

Fire regimes across the Western US are shifting in response to a warming climate and the consequences of a long-term policy of wildfire exclusion (Taylor et al. 2016, Hessburg et al. 2019). Historically, many forests in the region experienced frequent low- and mixed-severity wildfires. Today, wildfires are less frequent but are larger and more severe (Miller et al. 2009, Westerling 2016, Collins et al. 2019). This shift leads to mismatches between the fire regime and fire adaptations of endemic flora (Lytle 2001, Cavender-Bares and Reich 2012). Regeneration of dominant flora is particularly sensitive to changes in disturbance characteristics (Sousa 1984) and changes in community assembly after disturbance can have long-term effects on species composition and ecosystem function (Miller et al. 2012, Johnstone et al. 2016).

Prior to European settlement, fires in frequent-fire forests burned at variable intensities across the landscape, which helped maintain species diversity (Noss et al. 2006). In Sierra Nevada mixed conifer forests, the historic fire regime helped to generate a wide range of resource availability by creating a variety of canopy gap sizes. In turn, this resource gradient supported recruitment of a diverse woody flora (Safford and Stevens 2017). Niche differentiation varied according to species' differences in shade tolerance, drought resistance, and fire sensitivity (Parsons and DeBenedetti 1979; Fig. 1a). For example, the persistence of ponderosa pine (*Pinus ponderosa* Doug.) can be attributed to its abundant seed germination and rapid seedling growth in post-fire patches with mineral soil seedbeds, high light availability, and high evaporative demand (York et al. 2003, Bonnet et al. 2005, Annighöfer et al. 2019), along with its thick bark and high crown base, which improve survival in low- and moderate-severity fires (Schwilk and Ackerly 2001). On the other hand, regeneration of shade-tolerant tree species, predominately Sierra white fir (*Abies lowiana* Gord. & Glend.), prevails in unburned patches (Crotteau et al. 2013).

Under today's disturbance regime, defined by less frequent fire but larger stand-replacing patches (Stevens et al. 2017), the conditions that historically maintained species coexistence have changed. Not only do long fire-free periods favor shade-tolerant species (i.e., white fir) over intolerant species (i.e., ponderosa pine; Collins et al. 2011, Levine et al. 2016; Fig. 1b), but increasingly prevalent stand-replacing fire may also promote fir dominance (Fig 1c).

The goals of this paper are to a) introduce a conceptual framework for understanding how fir enrichment can result from multiple aspects of the modern fire regime in Sierra Nevada mixed-conifer forests (Fig. 1), and b) to quantify the effect of shrub competition on relative growth and mortality of dominant conifer species in stand-replacing fire patches. In severely burned patches, fir recruits at higher densities than pine (Nagel and Taylor 2005, Crotteau et al. 2013, Collins and Roller 2013, Lauvaux et al. 2016) but the drivers of this fir dominance are unknown and could be related to any of several phases of post-fire recovery – dispersal, germination, growth, or survival. The latter phases, growth and survival, are particularly understudied, as most research on post-fire recovery does not track individuals. Typically, studies on regeneration success rely on seedling counts in the decade after fire (Welch et al. 2016, Young et al. 2019), but are missing the critical demographic transition between establishment and sexual maturity.

Under a novel fire regime, competition with shrubs after fire may elevate the importance of seedling growth and survival in determining long-term species composition (Fig. 1b-c). In Sierra mixed conifer forest, shrubs typical of the montane chaparral plant community quickly revegetate severely burned patches via their ability to sprout or germinate from seed banks after fire, begin root expansion early in the growing season, outpace conifer growth, and tolerate extreme resource limitation (Kauffman and Martin 1991, McDonald and Fiddler 2010, Collins and Roller 2013). These shrub communities often form dense, continuous canopies one to two meters tall, lacking the environmental heterogeneity of smaller canopy gaps (Nagel and Taylor 2005). Heavy shrub cover is known to delay or preclude conifer recruitment in general and pine growth in particular (Zhang et al. 2006, Welch et al. 2016). This heavy competition with shrubs has been proposed as the reason for low pine densities in severely burned areas despite pine's preference for the substrate conditions and high light availability created immediately after high-severity fire (Crotteau et al. 2013, Welch et al. 2016).

While there is abundant research on shrub effects in ponderosa pine in managed plantations (e.g. McDonald and Abbott 1997, McDonald and Fiddler 2010), the nature of shrub/seedling interactions in post-high severity wildfire environments has not been closely examined. There are several aspects of plantations that make the research difficult to transfer to unmanaged wildfire footprints. Since nursery grown seedlings are larger and more vigorous than typical natural regeneration of similar age, planted seedlings in plantations bypass some shrub competition in the initial phase when competition with shrubs may be especially impactful, essentially getting a "head start" that can substantially alter the negative effects of shrub competition (McDonald and Fiddler 2010). For example, nine years after planting, nursery-grown ponderosa pine were found to exceed natural seedling size by 2.5 times under equal shrub competition and respond differently to resource limitation (McDonald et al. 2009). Importantly, planting usually follows site preparation, which can dramatically alter soil substrate, woody debris structure, shrub development, and any natural seedling regeneration that occurred prior to site preparation. Finally, traditional research on shrub effects examines single-species plantations, often of ponderosa pine (McDonald and Fiddler 2010). Both even-aged managed modern plantations and post-wildfire stands are likely to be much more diverse compared to the plantations used to develop competition control strategies in managed plantations (Van Mantgem et al. 2006). In order to understand succession in unmanaged wildfire footprints, data on mixed species stands of naturally regenerating conifers, including the effects of shrubs on shade tolerant species like white fir, are needed.

Research on post-wildfire recruitment patterns has supported competing explanations of the underlying processes driving species composition and the role of shrubs (Gray et al. 2005, Collins and Roller 2013, Tubbesing et al. 2019). Some studies indicate that montane chaparral inhibits conifer survival via moisture competition rather than shading (Conard and Radosevich 1982, Shainsky and Radosevich 1986, Royce and Barbour 2001, Plamboeck et al. 2008, McDonald and Fiddler 2010), a process that may favor more drought-resistant species like pines over firs (Niinemets and Vallardes 2006). Other studies suggest that shrubs may facilitate seedling survival by moderating harsh microclimates, particularly when seedlings are young (Gray et al. 2005, North et al. 2005).

To increase understanding of the impact of a novel fire regime on community assembly during the shrub-dominated stage of post-fire recovery, we performed in situ measurements of juvenile tree growth across a chronosequence of wildfires in the Sierra mixed conifer forest. We limited field sites to the interiors of large, stand-replacing patches characteristic of the contemporary fire regime (Stevens et al. 2017). We also evaluated the connection between growth rates and mortality for similarly aged trees to assess the influence that shrub suppression of tree growth may have on tree mortality rates. We measured live and dead trees in a nearby experimental forest where it was possible to locate a sufficiently large number of recently dead trees to analyze mortality. We used our demographic data on growth and mortality to assess the evidence for the "patch-driven" pathway outlined in our conceptual model (Fig. 1c), which stipulates that the shift toward less frequent but more severe fires has tilted post-fire recruitment dynamics in favor of the more shade-tolerant, fire-sensitive canopy tree species. Specifically, we tested two hypotheses: 1) Shrubs in wildfire footprints suppress the relative growth rates of ponderosa pine to a greater extent than white fir; 2) suppressed growth rates correlate with higher mortality rates of juvenile ponderosa pine and white fir.

METHODS

Study areas

We focused on patches of stand-replacing fire (>90% tree basal area mortality) within fire footprints in the central Sierra Nevada. Forests in our study area experience a Mediterranean-type climate with wet winters and dry summers lasting 4-6 months. Forest composition is typical of mixed-conifer forests of the Sierra Nevada, which are dominated by ponderosa pine and Sierra white fir and also contain sugar pine (*Pinus lambertiana* Dougl.), Douglas-fir (*Pseudotsuga menziesii* Mirb.), incense-cedar (*Calocedrus decurrens* Torr.), and red fir (*Abies magnifica* A. Murr). Shrub patches are dominated by greenleaf manzanita (*Arctostaphylos patula* Greene), whitethorn ceanothus (*Ceanothus cordulatus* Kellogg), deerbrush (*Ceanothus integerrimus* Hook. & Arn.), mountain misery (*Chamaebatia foliolosa* Benth.), and tanoak (*Notholithocarpus densiflorus* Hook. & Arn.), with other shrub species in lower densities.

Our site selection objective was to identify post-fire shrub fields across a range of fire footprint ages in order to capture gradients of shrub maturity, cover, and height. Because shrub-free areas are rare in stand-replacing fire patches of the Sierra Nevada (Young et al. 2019), we quantified juvenile conifer growth across a gradient of shrub competition rather than comparing high-shrub areas to shrub-free areas. To ensure that environmental conditions were similar across sites, we limited sites to fire footprints that met the following requirements: between the North and South forks of the American River; greater than 400 ha in size; 5-50 years old; within the Tahoe or Eldorado National Forests; not planted or herbicided following fire; and containing identifiable shrub fields surrounded by mixed conifer forest according to satellite imagery. We identified five fire footprints that met these criteria (Appendix S1: Table S1). At the time of first field measurements (2016) the fires ranged in age from 8 to 35 years.

Within the five fire footprints, we located shrub patches using Google satellite imagery. We visited all accessible shrub-dominated patches that were greater than 1 ha in size, approximated using Google satellite imagery analyzed in QGIS 2.18.13. Only those shrub patches that contained juvenile conifers farther than 20 m from patch edge were measured (Fig. 2). Shrub patches ranged in size from approximately 1.5-1,116 ha (median 9.8 ha).

Because it was impractical to sample a sufficiently large number of dead trees in the shrub patches described above, mortality measurements were carried out at Blodgett Forest Research Station (BFRS), located near Georgetown, California, USA (38°520N; 120°400W). BFRS has similar climate, elevation range, and species composition to the wildfire footprints described above. We focused on two study units that had high levels of shrub cover. These areas had been mechanically thinned and then prescribe burned in 2002 as part of a long-term study (Collins et al. 2014). This management history promoted high densities of shrubs and conifer seedlings and saplings. We measured recent (3-year) vertical growth of live and dead juvenile conifers to evaluate how growth rates affect mortality probability.

Field measurements

Wildfire footprints. At each shrub patch, field crews located white fir and ponderosa pine seedlings and saplings 10-300 cm in height (hereafter referred to as juvenile conifers) located at least 20 m from live adult trees. Measurements were limited to these two species because of the scarcity of other species across shrub patches and the fact that white fir and ponderosa pine exemplify distinct differences in ecological strategy (e.g., shade tolerance, drought resistance, and fire sensitivity). This targeted sampling approach allowed for a larger sample size than gridded or random plot sampling because juvenile conifers were rare in most of the shrub patches. Though all conifers meeting our criteria that we encountered were sampled, it was impractical to perform exhaustive surveys of juvenile conifers in the shrub patches, so we do not know what proportion of total conifers in the shrub patches were surveyed. We chose 20 m from patch edge as our threshold for patch interiors because previous research has shown that our study species experience minimal edge effects at distances greater than 20 m from patch edges (York et al. 2003, 2004). Juvenile trees that appeared to have been affected by herbivory or physical disturbance were ignored.

Juvenile conifers were tagged, GPS pinned, and measured for height and diameter. We then measured annual vertical growth based on distances between bud scars for the 2015, 2016, and 2017 growing seasons. We chose to measure these three years of growth because they were reliably identifiable using bud scars and because they represented a range of annual climatic conditions. The 2015 growing season concluded four years of drought in the Sierra Nevada and had record low April 1 snowpack (5% of normal), whereas the winter preceding the 2016 growing season had close to average precipitation. The following winter was exceptionally wet, with April 1 snowpack 175% of normal (https://wrcc.dri.edu/Climate/Monthly_Summaries).

Shrub cover surrounding each juvenile conifer was measured for each shrub species using the line-intercept method along three-meter transects facing each of the four cardinal directions. We chose three meters for transect lengths because it represents the distance at which two-meter-tall shrubs (the approximate maximum shrub height in our study area) would block sunlight from reaching the base of the focal tree for all sunlight <33° from horizontal. Measurements were conducted in 2016 and 2017. We were unable to analyze diameter growth of juvenile conifers because measurements occurred in different seasons, and seasonally-driven diameter variation prevented analysis of year-to-year growth.

Mortality study. To investigate how shrub suppression of juvenile conifer growth may affect survival, we estimated the relationship between vertical growth and probability of mortality for ponderosa pine and white fir. Growth declines are common predictors of gymnosperm mortality (Cailleret et al. 2017) and have been used to predict mortality for mature trees in the Sierra Nevada (e.g. Das et al. 2007) and for saplings in British Columbia (Kobe et al. 1995). We sampled from Blodgett Experimental Forest because it was impractical to sample a sufficiently large size of dead trees in the shrub patches described above. The Blodgett units we sampled from were majority Site Classes III (a measure of site productivity, Skovsgaard and Vanclay 2008) with some area in Site Class IV, making them similar to our fire footprints, which had 63% of samples in Site Class III and 22% of samples in Site Class IV.

We surveyed live and dead juvenile tree densities across 275 plots making up 864 m^2 of area and hundreds of trees, yet we found fewer than 30 dead trees of each species. To capture adequate sample sizes of dead trees, we combined this plot survey with targeted sampling of equal numbers live and dead trees for more detailed growth measurements. Thus, two types of data were gathered: 1) a survey of live and dead juvenile tree densities, and 2) growth rates of live and dead juvenile trees paired by species, proximity, and height.

For the survey of live and dead tree densities, we placed evenly spaced 1-m radius circular plots on a 20x30 m grid across two study units at Blodgett Forest. In each plot, we counted live and dead white fir and ponderosa pine in each plot that were < 200 cm tall.

To sample growth rates of paired live and dead juvenile trees, we walked along pre-determined parallel lines running east-west in the two study units, each separated by 20 m. As we walked, we searched for dead white fir and ponderosa pine juvenile trees < 200 cm in height as we walked. When we located a dead juvenile tree, we measured its height, diameter, and the past three years of growth by measuring distance between bud scars.

We also photographed each tree and recorded details of its physical characteristics such as twig retention, bark status, and needle color to help estimate its year of death. We then located the nearest living conspecific tree whose height was within 10 cm of the height of the dead tree and performed the same measurements. We harvested the live and dead trees at soil level to perform dendrochronological measurements, which were used to help identify year of death (See Appendix S1).

Statistical Analysis

Wildfire footprints. We calculated relative annual vertical growth rate of juvenile conifers using the formula:

$$Relative\ growth\ rate = \frac{height_{time2} - height_{time1}}{height_{time1}} \qquad (1)$$

Because we measured the distance between bud scars for the past three growing seasons for each tree, equation (1) was applied to each tree three times, using 2015, 2016, and 2017 growth, except where mortality or other factors prevented measurement of all three years of growth. This resulted in multiple values of relative growth rate per tree. In the regression models described below, the natural log of relative growth rate was used as the response variable. We determined elevation, azimuth, and slope for each juvenile tree using a USGS digital elevation model (DEM; https://viewer.nationalmap.gov/basic/) with a cell size of 100 m^2 in ArcMap 10.6.1. The remainder of analyses were performed using R 3.6.1 (R Core Team 2019). We then calculated heat load and potential direct incident radiation using slope, folded aspect, and latitude (McCune and Keon 2002). We identified site productivity class for each seedling using a 250-m resolution site class raster produced from Forest Inventory and Analysis data (unpublished, Barry (Ty) Wilson, USFS Northern Research Station *personal communication,* 2019).

We calculated the weighted mean shrub height surrounding each seedling using shrub cover by species as weights. We calculated a shrub competition index by multiplying cover by weighted mean height, aggregating data from the four transects, and then taking the square root to maintain a linear framework. The most common shrub species surrounding each focal tree was determined using cumulative shrub cover across the four transects.

To identify predictor variables that may influence juvenile conifer growth, we performed variable selection using the R package VSURF (Genuer et al. 2010, 2015). The VSURF algorithm uses iterative random forest models, created from 2000 regression trees, to identify predictor variables that influence the response variable while minimizing redundancy between predictors and reducing model instability. Years since fire was used as a measure of maturity of reseeding shrub species, which we expected to affect shrub competition via root depth (Plamboeck et al. 2008). Before running VSURF, we normalized numeric variables by subtracting the mean and dividing by the standard deviation. Each year of growth (2015, 2016, 2017) was treated as a unique observation in VSURF. Trees that died before the conclusion of the study or that could not be located in the second year of measurements had fewer observations. All predictor variables used as VSURF inputs are listed in Table 1. Initial height and diameter of the focal tree were included to account for size-related differences in biomass allocation in plants of the same species (Coleman et al. 1994).

To quantify the influence of shrub competition on juvenile tree growth, we used the variables selected by VSURF to run a mixed effects linear regression model with natural log of relative growth rate as the response variable using the R package “nlme” (Pinheiro et al. 2019). Since there were multiple measurements of relative growth rate for different years on each tree, we used focal tree, shrub patch, and wildfire as nested random effects. Effects and confidence limits were visualized for individual predictor variables using the “effects” package (Fox and Weisberg 2018). We evaluated model fit using conditional R^2 (R_c^2) and marginal R^2 (R_m^2) using the “MuMIn” package. While R_c^2 represents the proportion of variation explained by both fixed and random effects, R_m^2 represents the variation explained by the fixed effects alone (Nakagawa and Schielzeth 2013). We predicted that there may be an interaction between the height of juvenile conifer and shrub competition. We determined whether to include this interaction in the models for each species by comparing R_m^2, effect sizes, and Akaike Information Criterion corrected for small sample sizes (AICc) with and without the interaction.

Mortality study. To investigate the relationship between juvenile tree growth rates and mortality probabilities, we first quantified the differences in growth rates between live and dead trees from our paired samples and then combined these results with the plot survey of live and dead tree densities. We compared relative growth rates between live and dead juvenile trees using generalized linear models with a logit link and analysis of deviance tests. The response variable was live/dead status and the predictor variable was the natural log of mean annual relative growth rate from the previous three years using Equation (1). Size was not included in the model of mortality probability because studies have shown that sapling mortality is not influenced directly by size, but rather indirectly through the effect of size on growth (Kobe et al. 1995, Kobe and Coates 1997).

To determine annual mortality rates from surveyed densities of live and dead trees, it was necessary to determine how long dead trees had been standing. We estimated year and season of death for each dead tree using a combination of dendrochronological data and physical characteristics (see Appendix S1). To investigate the relationship between growth rates and annual mortality probabilities, we used a resampling technique similar to the method used by Das et al. (2007). Mortality was simulated by combining survey results of live and dead juvenile tree densities and paired samples of live and dead growth rates as follows: We randomly sampled live and dead tree growth rates with replacement from the set of growth rates measured from the paired tree study. The number of dead trees sampled matched the number of dead trees whose growth rates were measured. The number of live trees sampled was determined by the ratio of live to dead trees found in the density survey, such that the simulated population mortality rate matched the empirically measured mortality rate. Finally, a logistic regression model of mortality in relation to growth was fit to these samples, and the parameter values were extracted. This process was repeated 1,000 times for each tree species. Final parameter values were calculated as the mean across all simulations and confidence intervals were determined using the 25th and 975th ranked parameter values.

RESULTS

Wildfire footprints

We analyzed growth from 123 white fir and 93 ponderosa pine individuals. Because of mortality and the difficulty re-locating trees, some trees did not have growth measurements for all three years; we analyzed 312 tree-year combinations for white fir and 251 for ponderosa pine. Shrub height weighted means ranged from 11 - 213 cm (mean 85 cm) and cover ranged from 3% -142% with a mean of 78%. Total cover exceeded 100% in some cases due to independent measurements of each shrub species, in which multiple species may overlap.

The variables that VSURF identified as predictors of juvenile tree growth are included in Table 2. The interaction between tree height and shrub competition was not included for either species (see Appendix S1). For pines, the linear mixed-effects model using these variables showed that the predictors with the strongest effect on juvenile growth were shrub competition, year of growth, years since fire, and tree height (Table 2). Increasing shrub competition was associated strongly with decreased pine growth (Table 2, Fig. 3). For white fir, tree height, slope, and elevation had the strongest effects on juvenile growth while shrub competition had a weak positive effect (Table 2, Fig. 3). Model fits were better for pine ($R_c^2 = 0.69$; $R_m^2 = 0.62$) than for fir ($R_c^2 = 0.40$; $R_m^2 = 0.17$). Years since fire, which was included as a proxy for shrub maturity, was associated with lower juvenile tree growth for both tree species (Table 2) and was not highly correlated with our index of shrub competition.

The VSURF algorithm identified dominant shrub species as an important predictor of growth for pines but not for firs. Shrub species was therefore included in the mixed effects model for pines, though the likelihood ratio test for shrub species had a *P*-value of 0.2 (Table 2). Juvenile pine relative growth rate was lowest near *N. densiflorus* and highest near the two *Ceanothus* species, *C. cordulatus* and *C. integerrimus* (Fig. 4).

Mortality Study

In our gridded survey of live and dead juvenile tree densities, we visited 275 1-m radius plots, for a total of 864 m^2 of sampled area. Across those plots, we found 1,103 juvenile white fir, 25 of which were dead (2.3%) and 530 juvenile ponderosa pine, 6 of which were dead (1.1%). We measured growth rates of 80 pairs of live and dead white fir and 79 pairs of ponderosa pine.

Live juvenile trees had significantly higher relative growth rates than dead juvenile trees for both pines and firs (analysis of deviance $P < 0.0001$ for pines and $P = 0.0003$ for firs; Appendix S1: Fig. S4). Simulations of population-level mortality using resampling showed a strong negative relationship between growth and mortality probability for both species, with a steeper curve for ponderosa pine (Fig. 5).

We applied predictions from the mortality study to results from the wildfire footprints to demonstrate how mortality may vary in response to shrub competition. We found that the ponderosa pine relative growth rate associated with maximum observed shrub cover, according to mixed-effects models predictions, was 0.10, which corresponds to a predicted annual mortality probability of 1.1%. At minimum observed shrub cover, the predicted pine growth rate was 0.27, which corresponds to a 0.1% mortality probability. For white fir, predicted relative growth rates at maximum and minimum shrub cover were 0.16 and 0.11, respectively, which correspond with annual mortality probabilities of 0.72% and 1.1%.

DISCUSSION

We have presented a conceptual model (Fig. 1) positing that fir enrichment occurs under both of the two primary modes of the contemporary disturbance regime, which has shifted to feature far fewer but more severe fire events (Miller et al. 2009, Westerling 2016, Collins et al. 2019). In areas with fire deficits, fir gains a relative advantage over pine due to its shade tolerance ("overstory-driven fir enrichment;" Fig. 1b), while in areas with large stand-replacing fire patches, fir enrichment results from both dispersal limitation and shrub competition ("patch-driven fir enrichment;" Fig. 1c). Previous research has documented overstory-driven fir enrichment and the effect that seed dispersal can have on patch-driven fir enrichment (Zald et al. 2008, Welch et al. 2016, Shive et al. 2018). Our research documented the second mechanism of patch-driven fir enrichment: shrub competition. We found meaningful differences in the responses of white fir and ponderosa pine to shrub competition in the post-fire environment, differences that confer a considerable demographic advantage to white fir (Fig. 3).

Our results on the effects of shrub competition are of increasing important across the Sierra Nevada, where changes in montane chaparral distribution have mirrored changes in the fire regime. While chaparral was historically a more common component of the mixed conifer forest matrix (Collins et al. 2017), shrubs most commonly occurred in small canopy gaps (Knapp et al. 2013). Fire suppression has reduced the abundance of small canopy gaps (Lydersen et al. 2013) and increased large canopy openings (Stevens et al. 2017). Native shrubs species have quickly revegetated these openings after severe wildfire, leading to the development of extensive patches of montane chaparral. Initiation rates of these patches are likely to continue increasing and growing in size as changes in the fire regime are exacerbated by climate change (Keyser and Westerling 2017, Hurteau et al. 2019).

We found that the dense shrub canopy characteristic of post-fire chaparral patches exerts strong competitive pressure on shade-intolerant tree species, resulting in a relative advantage for shade-tolerant firs (Fig. 3). While white fir showed only slight and variable changes in growth in response to shrub abundance, ponderosa pine consistently grew much more slowly in areas with higher shrub competition. Furthermore, decreases in ponderosa pine growth were associated with strong increases in its mortality (Fig. 5), indicating that shrub competition decreases both growth and survival of the species.

Fir enrichment in large post-fire shrub patches may lead to long-term changes in species composition that in turn could create a positive feedback in the fire regime. Firs lack traits that increase fire survival, making them more fire sensitive than pines (Schwilk and Ackerly 2001). Furthermore, fir dominance increases fine woody fuel loads, which contribute to fire risk (Lydersen et al. 2015, Cansler et al. 2019). Increased dominance of this fire-sensitive species may push the disturbance regime further toward high-intensity, high-severity fire.

The degree of fir enrichment across all high-severity fire patches in the region will depend on several factors, including the extent and density of shrub competition arising in stand-replacing patches. Under the maximum shrub competition found in this study, predictions of fir growth and survival exceeded those of pine, whereas under minimum shrub competition the reverse was true. We used a targeted sampling approach in which shrub competition was only measured near juvenile conifers. Thus, average shrub competition in the area is likely higher than what we measured because conifer densities tend to be lower under high shrub competition (Welch et al. 2016). Existing region-wide shrub data rely on coarse ocular measurements, making it difficult to compare these data to the detailed line intercept measurements taken in this study (Nagel and Taylor 2005, Welch et al. 2016, USDA Forest Service 2018). Furthermore, climatic drying and warming increases post-fire shrub abundance (Tepley et al. 2017, Young et al. 2019). Therefore, it is likely that regional shrub influences not only are stronger than measured in this study, but also may become increasingly important under future climate change. A regional investigation of shrub competition in stand-replacing fire patches would aid in understanding how forests will change under the modern fire regime and climate.

Our results show that shrub competition is a driver of community assembly in post-fire environments. The nature of this shrub competition is not uniform, however, and likely depends upon site-specific variation in shrub maturity, light, moisture, and nutrient availability. For example, juvenile tree growth decreased with time since fire for both species, with stronger effects for ponderosa pine (Table 2). Time since fire, which was used as a proxy for shrub maturity, was not highly correlated with our index of shrub competition that combined shrub cover and height. Therefore, older shrubs compete with juvenile conifers more than younger shrubs independent of their aboveground volume, likely due to their greater root depth.

The fact that shrub competition reduced growth for drought-resistant pine but not for shade-tolerant fir suggests that competition for light may be a stronger driver of post-fire species interactions than previously considered in this region. Our results may not apply to more southern portions of the Sierra Nevada, where strong moisture competition between conifer seedlings and *Arctostaphylos* shrubs has been found (McDonald and Abbott 1997, Plamboeck et al. 2008). While warm and dry conditions can increase regeneration failure in some areas of California, the Rocky Mountains, and the American Southwest (Savage et al. 2013, Stevens-Rumann et al. 2018, Young et al. 2019), other factors may also be important in determining species shifts, particularly in more mesic environments. For pines, which are less sensitive to warming and drying than other species (Moran et al. 2019), shrub effects under a novel fire regime may be more important drivers of decreasing regeneration in our study area than changes in climate, though more research is needed on climate and shrub effects on regenerating pines.

Shrub suppression of pine growth was weaker where *Ceanothus cordulatus* or *C. integerrimus* dominated compared to other shrub species, which may be due to that genus's nitrogen-fixing ability (Fig. 4). In contrast, previous research has found higher ponderosa pine growth under *Arctostaphylos* than under *Ceanothus*, but this was likely due to higher cover of *Ceanothus* whereas our evaluation of shrub species effect controlled for shrub cover and height (Zhang et al. 2018). The lack of shrub species effect for white fir was consistent with other studies (Oakley et al. 2006).

With multiple drivers of fir enrichment in post-fire environments (Fig. 1c), each affected by several interacting site factors that are in turn affected by shifts in fire regime and climate, field research alone is insufficient to predict long-term forest succession. The results from our study can be combined with existing data on post-fire dispersal and establishment patterns to develop an individual-based modeling framework. Such a framework has the advantage of allowing for parsing of individual demographic processes and species interactions, which would allow us to explore under what conditions the alternatives in Fig. 1 occur.

Though ponderosa pine is considered a fire-adapted species in frequent-fire forests, the shift toward infrequent, stand-replacing fire favors firs over pines. Species coexistence in mixed conifer forests was historically driven by differences in functional traits adapted to niches within a heterogeneous forest mosaic. As forest heterogeneity gives way to larger, more homogenous patches of either dense forest or stand-replacing fire, the traits adaptive to regeneration success are shifting to favor firs. Traits that historically allowed ponderosa pine to outcompete white fir under the endemic low/mixed-severity fire regime, such as thick bark and high crowns, are poorly suited to the dominant stressors of the novel fire regime. Our results highlight the role that shrub dominance of stand-replacing patches plays in this favoring of firs over pines.

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TABLES

Table 1. Predictor variables included as inputs to VSURF, a variable selection method based on random forests

Category	Variable
Shrub competition variables of interest	Shrub competition, $\sqrt{\text{cover (cm)} * \text{height (cm)}}$
	Dominant shrub species
	Years since fire
Growing site environmental control variables	Elevation
	Slope
	Heat load
	Potential incident radiation
	Site class
	Year of growth (2015, 2016, 2017)
Tree-level control variables	Juvenile conifer height before growth
	Juvenile conifer basal diameter in 2016

Table 2. Mixed effects model results. For each conifer species, predictor variables are listed in descending order of importance according to single-term deletion likelihood ratio tests. The last column shows P-values from those tests. Numeric variables were normalized before model runs by subtracting the mean and dividing by the standard deviation to make coefficients comparable. For factor variables, treatment contrasts were used, in which the first factor level coefficient is set to 0 and all other levels' values are relative to the first level. Random effects are not included in this table.

Variable	Factor level	Direction	Coefficient	*P*-value
Ponderosa pine				
Juvenile conifer height		(–)	-0.41	< 0.0001
Years since fire		(–)	-0.34	< 0.0001
Shrub competition, $\sqrt{cover\ (cm) * height\ (cm)}$		(–)	-0.23	< 0.0001
Year of growth	2015	0	0	< 0.0001
	2016	(+)	0.19	
	2017	(–)	-0.13	
Juvenile conifer basal diameter		(+)	0.30	0.0007
Heat load		(–)	-0.11	0.089
Dominant shrub species 0-3 m	Arctostaphylos spp.	0	0	0.205
	Ceanothus cordulatus	(+)	0.16	
	Ceanothus integerrimus	(+)	0.26	
	Chamaebatia foliolosa	(+)	0.07	
	Notholithocarpus densiflorus	(–)	-0.10	
	Other	(+)	0.26	
White fir				
Juvenile conifer height		(–)	-0.22	0.0005
Slope		(–)	-0.20	0.0005
Elevation		(+)	0.27	0.0006
Incident radiation		(–)	-0.29	0.001
Years since fire		(–)	-0.27	0.013
Shrub competition $\sqrt{cover\ (cm) * height\ (cm)}$		(+)	0.08	0.146
Heat load		(–)	-0.005	0.964

FIGURES

Figure 1. Conceptual diagram of the effects of the shifting fire regime on species composition in mixed-conifer forests of the Sierra Nevada. The present study examines the right-most downward pathway, namely the potential for shrub competition following stand-replacing fire to favor understory-tolerant firs over understory-intolerant pines. The dashed arrow pointing from path-driven fir enrichment to large stand-replacing patches is a hypothesized linkage requiring more research, though it is supported by literature on flammability of white fir compared to ponderosa pine.

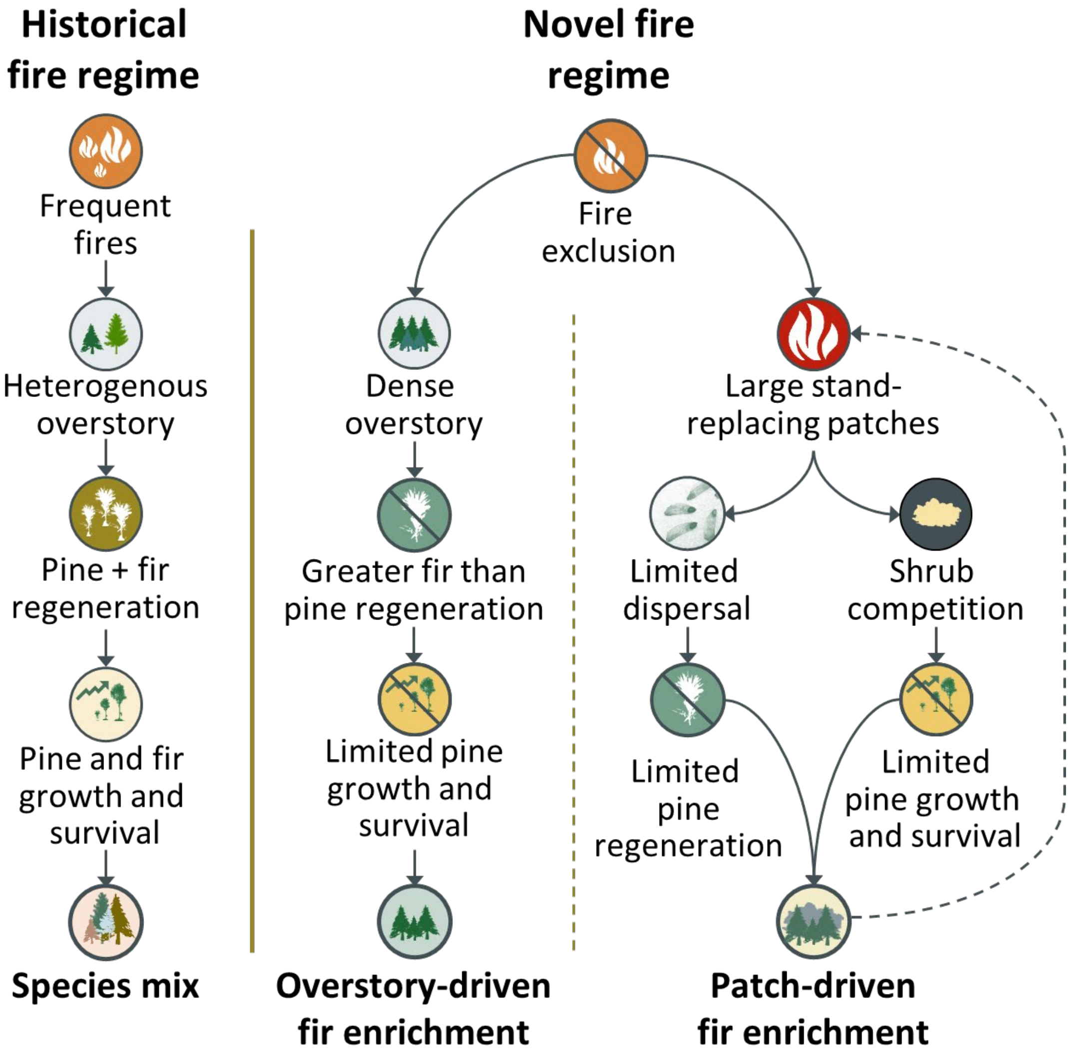


Figure 2. Study area in the northern Sierra Nevada. The overview map shows study area location within California, USA. Wildfire footprint data was gathered at shrub patches (red), while mortality data was gathered at Blodgett units (orange) within Blodgett Forest Research Station (green). Wildfire footprints are labeled in black.

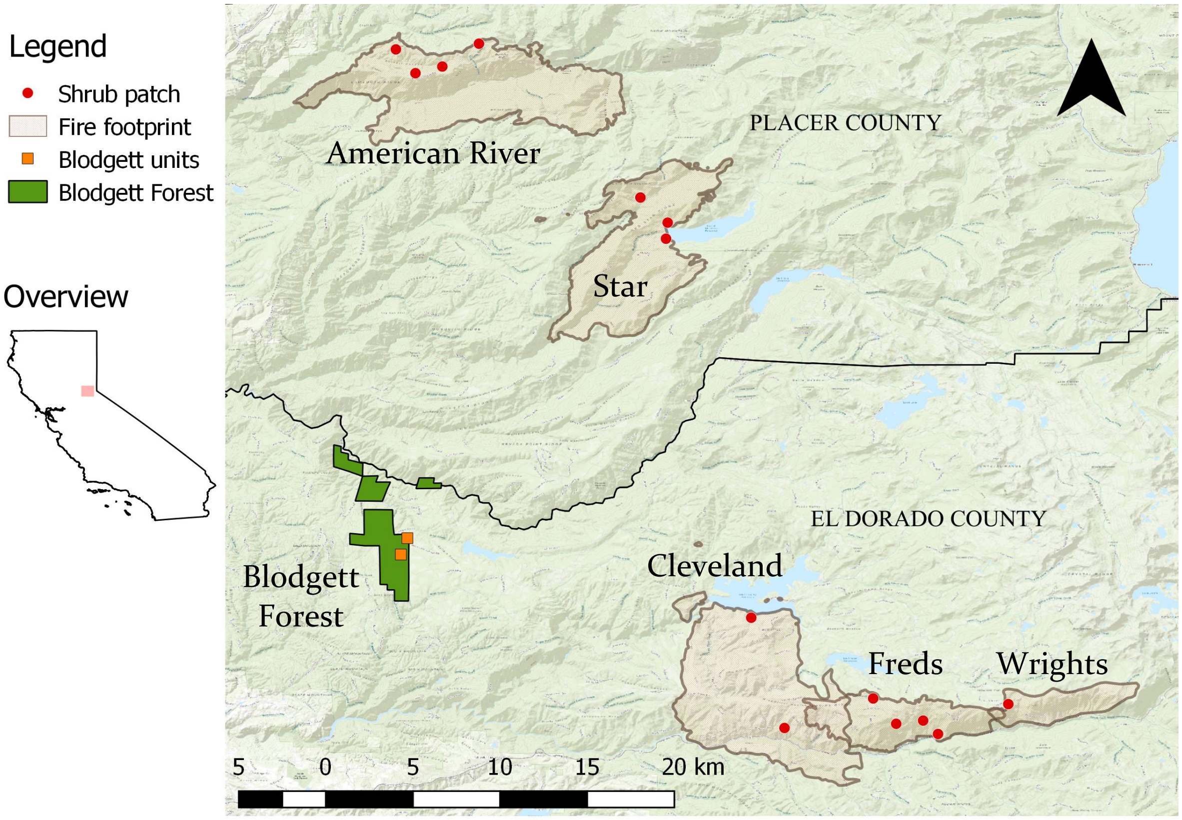


Figure 3. Predicted juvenile relative growth in relation to shrub environment for a) ponderosa pine, and b) white fir. Predicted relative growth estimates are generated across mean values of other continuous predictors and weighted averages of categorical predictors (Fox and Weisberg 2018). Shaded areas represent 95% pointwise confidence envelopes.

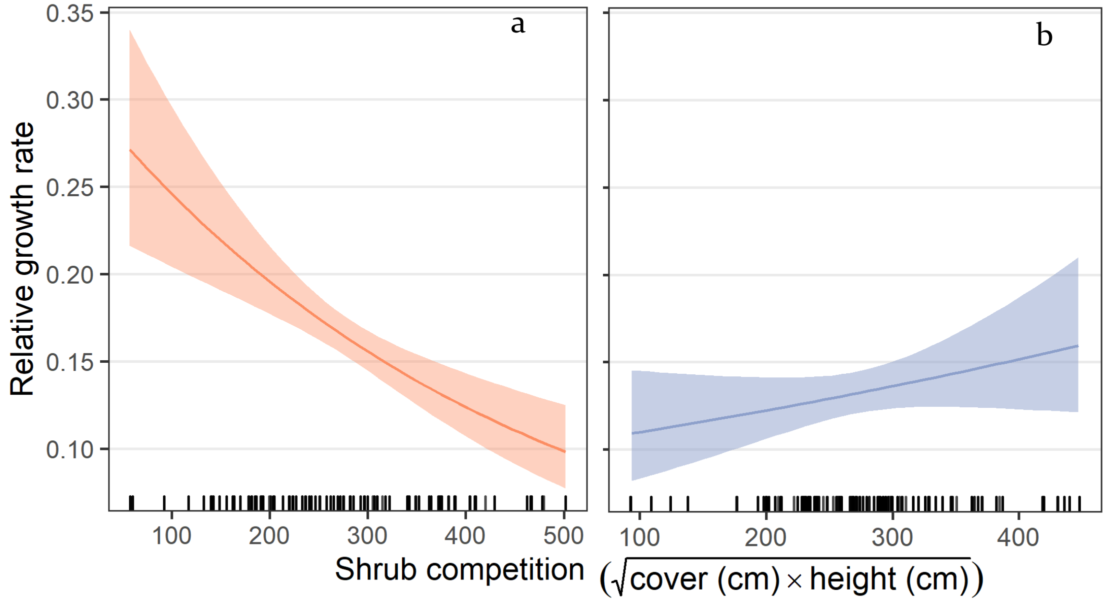


Figure 4. Relative ponderosa pine growth rate in relation to dominant shrub species within 3 m. Estimates are generated across mean values of other continuous predictors and weighted averages of categorical predictors (Fox and Weisberg 2018). Error bars represent 95% confidence intervals.

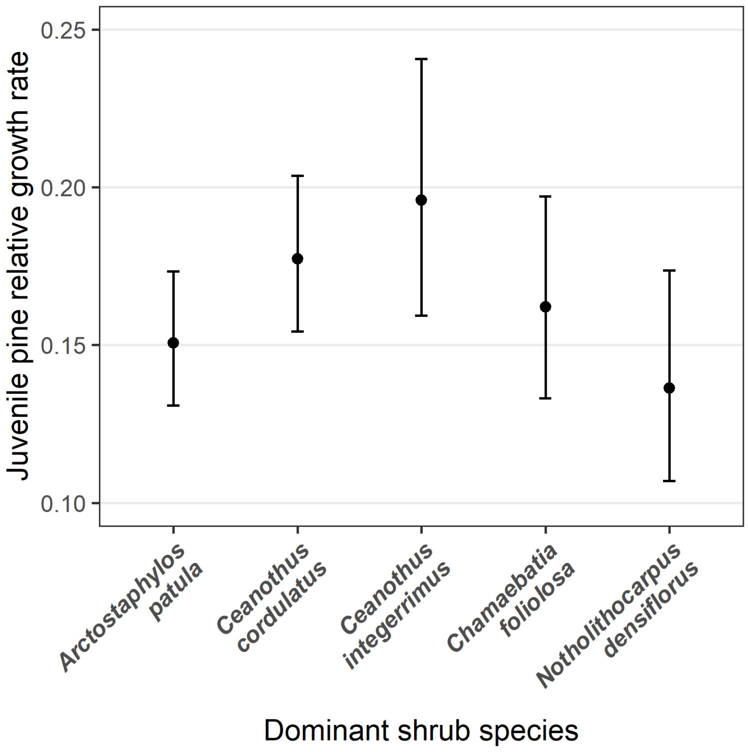
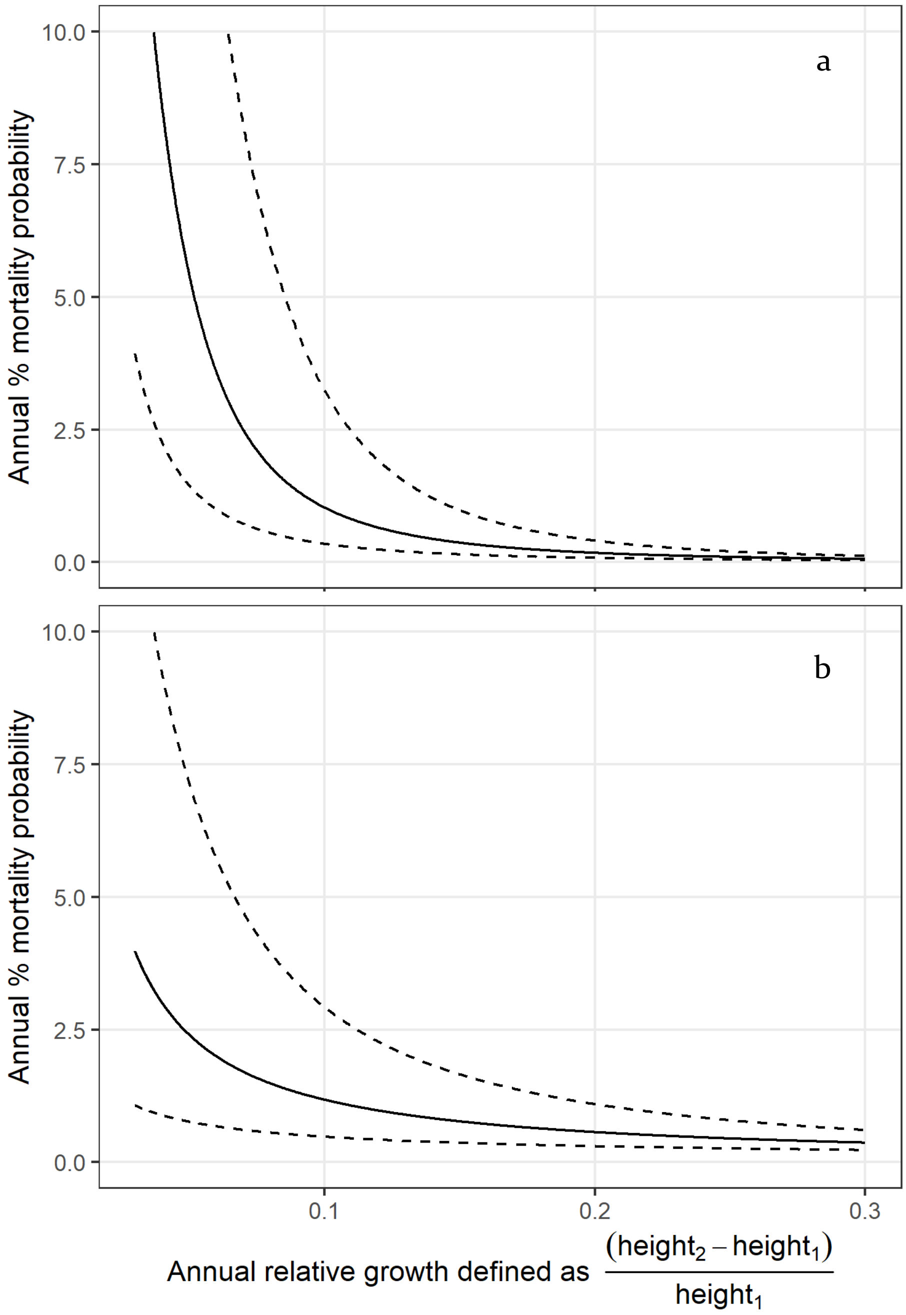


Figure 5. Simulation results showing probability of mortality in relation to relative growth rate for a) ponderosa pine and b) white fir. Dotted lines represent 95% confidence intervals.



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In **Chapter 2**, I showed that shrub competition affects pine growth and mortality more strongly than it affects firs. I hypothesized that these species differences may contribute to regional fir enrichment related to the shifting fire regime. In order to fully test my hypothesis, longer-term analyses were needed. In **Chapter 3**, I applied the findings of Chapter 2 to a forest growth simulation model. The model allowed me to test whether the differences shown in Chapter 2 led to differential outcomes between fir and pine during the period between conifer seedling establishment and emergence above the shrub canopy. My simulation model also allowed me to test how different shrub species affect the relative success of fir and pine. These analyses expand and refine upon the findings of Chapter 2.

CHAPTER 3 Forest succession in an altered fire regime: the role of shrub neighborhood dynamics

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ABSTRACT

As fire regimes shift in Western North America, patches of stand-replacing fire are becoming larger. Long-term succession in these patches is not well understood. There is concern that competition with rapidly reestablishing shrubs, combined with dispersal limitation, may delay or impede conifer recovery and potentially shift tree composition toward shade-tolerant species. However, tree-shrub interactions and shrub neighborhood dynamics have not been closely examined. To investigate the patterns and processes determining long-term forest succession after severe wildfire, we developed a data-driven simulation model that we use to predict conifer emergence above the shrub canopy. Our model results showed that ponderosa pine (*Pinus ponderosa*) emerged at a faster rate than white fir (*Abies lowiana*) under whitethorn ceanothus (*Ceanothus cordulatus*) and deerbrush (*Ceanothus integerrimus*), and at a similar rate under greenleaf manzanita (*Arctostaphylos patula*). Across all shrub species, ponderosa pine had a relative advantage over fir in the period between conifer establishment and peak shrub competition, requiring a mean of 18 ± 2 years for 50% of individuals to emerge compared to 21 ± 1 years for white fir. Fir emergence rates then surpassed those of pine, leading to similar overall emergence by the end of the simulation: 82% ± 6% for pine and 83% ± 5% for fir. These results show that, on balance, shrub neighborhood dynamics do not produce an ecological filter favoring firs, but that emergence patterns are sensitive to shrub species. Further modeling based on this data-driven simulation framework could improve understanding of other important components of post-fire succession, including the understudied process of conifer seedling establishment under shrubs.

INTRODUCTION

Forest disturbance patterns are changing worldwide due to severe fire, insect outbreaks, and other threats. Altered disturbance regimes often lead to the formation of a recalcitrant layer of shade-intolerant, rapidly regenerating understory species (Royo and Carson 2006). This layer can be thought of as an ecological filter, as it may delay the recovery of slower growing species by influencing light availability, moisture, litter structure, and/or microclimate (George and Bazzaz 1999). If the recalcitrant layer affects tree species differently, it may influence the composition of the overstory canopy. The herb and shrub stratum can act as a sieve, selectively filtering out tree seedlings ill adapted to establish, grow, and survive beneath it (Landuyt et al. 2019). Shrub layers can offset the increased light availability created by canopy gaps, leading to low post-disturbance seedling survival (Beckage et al. 2005). Depending on the strength of the filter and how it differentially affects tree species, the understory may preclude, delay, or alter long-term forest succession (Royo and Carson 2006).

The role of disturbance-induced shrub and herb layers is becoming increasingly important in western North America, where fire regimes are shifting in response to climate change and decades of wildfire exclusion (Taylor et al. 2016, Hessburg et al. 2019). In forests that historically experienced frequent, heterogenous fire, fire severity and homogeneity have increased (Miller and Safford 2012). Small patches of stand-replacing fire were characteristic of the historic fire regime (Collins and Stephens 2010), but modern stand-replacing patch sizes often exceed the historical range of variability and are continuing to increase in size with successive fire seasons (Miller et al. 2009, 2012, Stevens et al. 2017, Steel et al. 2018). In the Sierra Nevada, changes in montane chaparral distribution have mirrored changes in the fire regime. Though chaparral was historically a common component of the mixed conifer forest matrix (Collins et al. 2017), shrubs generally occurred in the understory or in small canopy gaps (Knapp et al. 2013). Fire suppression has reduced small canopy gaps and increased large canopy openings (Lydersen et al. 2013, Stevens et al. 2017), which native shrubs quickly revegetate, leading to the development of extensive patches of montane chaparral. Future fires are likely to contain increasingly large high-severity patches as changes in the fire regime are exacerbated by climate change (Keyser and Westerling 2017, Hurteau et al. 2019).

Large, continuous patches of shrubs may act as an ecological filter via their effects on regenerating conifers. Heavy shrub cover is known to delay or preclude conifer recruitment in general and pine growth in particular (Zhang et al. 2006, Welch et al. 2016). In severely burned patches, fir recruits at higher densities than pine (Nagel and Taylor 2005, Van Mantgem et al. 2006, Crotteau et al. 2013, Collins and Roller 2013, Lauvaux et al. 2016) even though pines are well adapted to germinate and quickly grow in post-fire abiotic conditions, characterized by exposed mineral soil, high light availability, and high evaporative demand (York et al. 2003, Bonnet et al. 2005, Annighöfer et al. 2019). Several factors may contribute to post-fire fir enrichment, including pre-fire species composition, dispersal limitation (Clark et al. 1999, Shive et al. 2018), and shrub effects

(Nagel and Taylor 2005, Tubbesing et al. 2020). In post-fire patches with particularly delayed forest recovery, vulnerability to severe reburn may increase due to the structure and flammability of shrubs, generating a positive feedback cycle that may shift burned areas to a non-forested alternative stable state (Coppoletta et al. 2015).

Despite increased research interest in the recovery of high severity burn patches, the successional dynamics in these patches are poorly understood. It is unknown which demographic process(es) may alter or impede long-term tree recovery. Regenerating conifers in shrub patches are difficult to study because they are generally rare, slow growing, and challenging to locate, inhibiting detailed long-term studies (Collins and Roller 2013, Welch et al. 2016). The majority of recent research on the topic relies on one-time surveys of juvenile conifers within a decade after fire followed by correlative analysis of tree densities in relation to site variables (Collins and Roller 2013, Coppoletta et al. 2015, Welch et al. 2016, Shive et al. 2018, Young et al. 2019). Information about individual processes or longer-term patterns is limited. Though competition with montane chaparral likely affects conifer growth and mortality, there is little understanding of shrub canopy development or individual species interactions. Differences in shrub height and cover may strongly influence conifer success; studies have shown that conifers establishing immediately after disturbance have greater overstory recruitment, while those that establish longer after disturbance have lower height growth, potentially due to shrub growth and expansion (Tepley et al. 2017).While there is abundant research on shrub effects in ponderosa pine in managed plantations (e.g. McDonald and Abbott 1997, McDonald and Fiddler 2010), there are several aspects of plantations that make the research difficult to transfer to unmanaged wildfire footprints, including the use of nursery-grown seedlings (McDonald et al. 2009), site preparation, and monospecific stands, often of pine (McDonald and Fiddler 2010). In order to understand succession in unmanaged wildfire footprints, research is needed on mixed species stands of naturally regenerating conifers without shrub control or site preparation.

This study specifically tests for shrub filter effects in the stage between seedling establishment and emergence of conifers above the shrub canopy, which complements previous studies of densities of established seedlings (Collins and Roller 2013, Coppoletta et al. 2015, Welch et al. 2016, Shive et al. 2018, Young et al. 2019). We examined whether the shrub filter at this stage precludes, delays, or alters long-term forest succession. Previous work on shrub effects during this stage has shown that shrubs reduce pine growth and survival but not fir growth, indicating that the shrub filter may alter, rather than preclude or delay, long-term succession (Tubbesing et al. 2020). Here we expand upon previous work to further examine the hypothesis that the shrub filter contributes to fir enrichment.

To understand the patterns and processes of forest recovery in shrub-dominated, post-fire landscapes, we developed a statistical simulation model informed by field measurements. Simulation models allow for estimations of long-term processes by synthesizing several data sources and demographic relationships (Pacala et al. 1996, Coates et al. 2003, Uriarte et al. 2009). We developed an individual-tree simulation model inspired by the principles of SORTIE-ND whereby field measurements, statistical estimators, and models were designed in tandem to optimize projections of demographic rates and patch dynamics (Pacala et al. 1996). Because we used complete data sets in parameter development, we were able to incorporate uncertainty into model runs by bootstrapping the analyses used to develop individual parameters. We were also able to initialize the model with empirically observed combinations of variables, including microsite environmental conditions. Since the field data used to develop the model was measured during three very different climate years, we incorporated realistic variability in tree growth as it relates to precipitation.

Our modeling approach also allowed us to parse the relative importance of individual processes through sensitivity analyses. We used sensitivity analyses to examine differences among tree species, shrub species, and three dimensions of shrub neighborhood: 1) initial shrub cover and height, 2) shrub growth trajectories over time, and 3) how a given cover and height of each shrub species affected conifer growth, as determined by linear modeling. This last dimension was termed the "shrub neighborhood species coefficient." The first and third of these shrub dimensions were derived from field data detailed in Tubbesing et al. (2020). To parameterize shrub growth trajectories over time, we combined data sources from regional surveys and developed height and cover curves in relation to time since fire.

The objective of this paper is to use data-driven simulation modeling to evaluate conifer growth and survival in an increasingly prevalent landscape component, namely shrub-dominated high severity fire patches, during the period between establishment and emergence above the shrub canopy. Specifically, we asked:

1) Does shrub neighborhood act as an ecological filter favoring fir emergence over that of pine?
2) How do shrub neighborhood effects on the timing and magnitude of conifer emergence vary among shrub and conifer species?
3) What dimensions of shrub neighborhood influence species differences in emergence effects?

METHODS

Study areas

We focused on patches of stand-replacing fire (> 90% tree basal area mortality) within fire footprints in the central Sierra Nevada. Forests in our study area experience a Mediterranean-type climate with wet winters and dry summers lasting 4-6 months. Forest composition is typical of mixed-conifer forests of the Sierra Nevada, which are dominated by ponderosa pine (*Pinus ponderosa* Doug.) and Sierra white fir (*Abies lowiana* Gord. & Glend.) together with lower abundances of sugar pine (*Pinus lambertiana* Dougl.), Douglas-fir (*Pseudotsuga menziesii* Mirb.), incense-cedar (*Calocedrus decurrens* Torr.), and red fir (*Abies magnifica* A. Murr). Shrub patches are dominated by greenleaf manzanita (*Arctostaphylos patula* Greene), whitethorn ceanothus (*Ceanothus cordulatus* Kellogg), deerbrush (*Ceanothus integerrimus* Hook. & Arn.), bush chinquapin (*Chrysolepis sempervirens* Kellogg), and a shrub form of tanoak (*Notholithocarpus densiflorus* Hook. & Arn.), with other shrub species in lower densities.

All data were collected on US National Forest Service land. We focused on high severity burn patches within wildfire footprints that had not experienced post-fire land management such as shrub cover reduction or tree planting. Our study region experienced frequent fire prior to fire exclusion, with low- to moderate-severity fires occurring with a median return interval of 15 years (Stephens and Collins 2004, Krasnow et al. 2016). Modern fires in the region are larger and have large contiguous areas of high severity. For example, the 2014 King Fire burned 39,545 ha, including one continuous 13,683-ha high-severity burn patch (DA says to add linear dimensions here) (Jones et al. 2016).

Modeling approach

Our simulation model of post-fire recovery trajectories combines shrub-conifer functional relationships with regional data on shrub characteristics and growth. We used an individual-tree, data-driven modeling approach inspired by SORTIE-ND (Uriarte et al. 2009). As in the SORTIE family of models, field surveys to parameterize demographic processes for our model were conducted in tandem with model development. These field surveys are described in Tubbesing et al. (2020). In summary, juvenile conifer vertical growth was measured in relation to shrub competition within a 3 m radius surrounding each tree in five fire footprints ranging from 8 to 35 years old. Additionally, recent growth of similarly aged juvenile live and dead trees was measured in a nearby managed stand to evaluate the relationship between conifer growth and mortality probability.

In Tubbesing et al. (2020), these field data were used to develop two demographic linear models: 1) vertical conifer growth in relation to shrub neighborhood, site characteristics, and tree size, 2) mortality probability in relation to recent growth. For the present study, we added a third linear model: conifer diameter in relation to conifer height and shrub neighborhood. This diameter model was required because conifer diameter was a predictor of vertical growth in the simulation, in accordance with variable selection results to develop the vertical conifer growth model. We also incorporated uncertainty into the analyses by bootstrapping each of the three linear models 1,000 times. Parameter estimates from a single bootstrap sample were used for each simulation run. We ran the simulation model 1,000 times to generate output distributions that reflected uncertainty in the empirical demographic relationships.

To parameterize shrub development over time in the simulations, we developed two types of deterministic models from regional field survey data: 1) generalized additive models (GAMs) of shrub height over time for individual shrub species, and 2) a linear model of shrub cover over time across all shrub species of interest.

Our simulation calculated each tree's growth and mortality at each year based on its unique characteristics such as size, species, and shrub neighborhood (Figure 1). During the initialization stage, plant characteristics and microsite characteristics were randomly selected with replacement from field data gathered at eight years post-fire. Then, at each yearly time step, shrub cover and shrub height were estimated based on deterministic models derived from regional field data. Climate year was assigned based on a historical climate record. Conifer vertical growth was then estimated from a bootstrap sample of the vertical conifer growth linear model. Next, conifer diameter was estimated from the conifer diameter linear model, again using one bootstrap sample. Conifer mortality was assigned based on the probability of mortality estimated from a bootstrapped mortality model using height growth as the predictor. Finally, the tree was determined to have emerged if it was alive and half or more of its crown exceeded its neighborhood shrub height. Trees that had emerged or died were removed from the analysis before the calculations were repeated for the next yearly time step. Emergence was summarized across years for 1,000 simulation runs and the entire process was repeated for several shrub neighborhood scenarios. We focused shrub-species-specific analyses on deerbrush, manzanita, and whitethorn ceanothus because they are common shrub species often encountered by forest managers (Welch et al. 2016) and because they were prevalent in our data, allowing for robust analyses. All analyses and model development were performed in R 3.6.2 (R Core Team 2019).

Parameter development

Shrub dynamics. We synthesized data on shrub cover and height in Sierra Nevada fire footprints to develop growth curves by shrub species. We combined data from Tubbesing et al. (2020), Welch et al. (2016), Young et al. (2019), Shive et al. (2018) and unpublished data collected by the Andrew Latimer lab at the University of California, Davis. We limited analysis to plots that met the following criteria: no shrub release treatments (e.g. mastication) following fire according to the Forest Activity Tracking System (FACTS) database, no remnant overstory trees < 20 m from plot center, high fire severity (> 75% basal area mortality), and containing shrub species found during conifer growth measurements in Tubbesing et al. (2020) (Appendix S1: Figure S1).

To develop shrub height growth curves over time, we separately analyzed plots dominated by each of the four common shrub species as well as an "other" category. We lumped *Arctostaphylos patula* and *A. viscida* because of their similar growth forms and low density of *A. viscida.* For each shrub species category, we developed generalized additive models using natural cubic regression spline with four knots using plot-level shrub height as the response variable and years since fire as the predictor (GAMs; Zuur et al. 2009).

To evaluate shrub cover change over time, we analyzed only data collected for Tubbesing et al. (2020) because the shrub cover measurement methods varied among studies. Preliminary analysis showed that trends in shrub cover were more linear and more similar across shrub species than for shrub height. Thus, we lumped all shrub species and used linear regression rather than GAMs. We included shrub height in the linear regression model and used a square root transformation to ensure the normality of residuals.

Conifer vertical growth. Our methods for developing relationships between shrub competition and conifer growth were based on Tubbesing et al. (2020), which used linear mixed effects models with model selection based on random forests. However, unlike in that study, we included interactions between shrub competition and juvenile conifer height in our mixed effects modeling to account for different competition effects as trees emerge from the shrub canopy. This interaction was not included in the previous study because it did not strongly alter the results, having the smallest effect size of all covariates for both tree species (Appendix S1: Figure S3) and small effects on the Akaike Information Criterion corrected for small sample sizes (AICc): including the interaction increases AICc by 1.85 for white fir and reduces AICc by 3.8 for ponderosa pine. For the present study, we included the interaction because we were specifically interested in changes in shrub neighborhood effects as trees emerge from the shrub layer. We performed bootstrapping of mixed effects model fits for each conifer species by randomly sampling observations with replacement and rerunning the models, repeating this process 1,000 times. These bootstrap results were used in the simulation to evaluate model uncertainty.

Conifer diameter. Since conifer diameter was a predictor of vertical growth in the simulation, a method of predicting conifer diameter throughout the simulation was required. We used the fire footprint data gathered in Tubbesing et al. (2020) to parameterize conifer diameter estimations. We predicted that tree height as well as shrub competition may influence diameter: taller trees will have larger diameters, but under higher shrub competition a given height may be associated with a smaller diameter due to etiolation (Weber et al. 2017). We used linear regression models of juvenile conifer diameter in relation to tree height and our index of shrub competition ($\sqrt{shrub\ height * shrub\ cover}$) for the year 2017. We used AIC_c model selection to determine whether to include shrub competition and the interaction between height and shrub competition. For both fir and pine, the best model included height, shrub competition, and their interaction (Appendix S1: Table S1). As with conifer vertical growth models, we used bootstrapping with 1,000 resamples to evaluate uncertainty in model fits (Appendix S1: Figure S5).

Conifer mortality. Our methods for predicting conifer mortality probability are detailed in Tubbesing et al. (2020) and summarized here. Mortality was analyzed by combining a) survey results of a gridded plot network of live and dead juvenile tree densities with b) 3-year vertical growth rates from paired live and dead juvenile trees found during targeted sampling. We created 1,000 bootstrapped realizations by randomly sampling live and dead tree growth rates with replacement to match the live/dead ratio found in population surveys, and then fit a logistic regression model to each bootstrapped population.

Climate years. Though we did not directly incorporate climate variables into our analysis, annual variation in climate was accounted for by way of the mixed effects model predicting juvenile ponderosa pine growth, which included a term for measurement year

(2015, 2016, 2017). The effect of year was likely due to widely differing climate conditions: The 2015 growing season had record low April 1 snowpack (5% of normal), whereas the winter preceding the 2016 growing season had close to average precipitation, and the following winter was exceptionally wet, with April 1 snowpack 175% of normal (https://wrcc.dri.edu/Climate/Monthly_Summaries). To incorporate realistic climate variability into the simulations, we grouped historical years 1970-2014 into one of three categories depending on which of our three measurement years most closely matched its total September-August precipitation (PRISM Climate Group 2020). We used coefficients from our three measurement years in proportion to their frequency in the historical record, as described below.

Base model

We initialized the base model by randomly selecting 200 juvenile trees from the fire footprint data of the American River Complex Fire. Because our field sampling was not fully randomized, we weighted the sampling probabilities by the frequency of conifer and shrub species combinations found in regional surveys (Welch et al. 2016), limiting survey data to plots measured 5-8 years following fire and meeting study specifications as described above for shrub height growth. Each tree retained its original data for height, diameter, shrub neighborhood, and environmental control variables (i.e. elevation, slope, heat load, and incident radiation). In other words, the simulation was initialized with empirically observed combinations of each variable. While the regional field survey data included areas with dominant deerbrush ceanothus, deerbrush was never the dominant shrub for trees sampled in American River Complex Fire footprint. To accommodate this gap in our base model, we initialized deerbrush height by randomly selecting deerbrush height values from the same subset of Welch et al. (2016) as was used for weighting initialization sampling. To initialize deerbrush cover and the traits of conifers co-located with deerbrush, we sampled from our whitethorn data. We chose whitethorn because deerbrush is congeneric with whitethorn and the two species had similar cover in the Welch database (Appendix S1: Figure S3). Though deerbrush was not dominant in any of our American River Complex Fire observations, it was dominant in many of our observations at older fires, which allowed us to parameterize deerbrush neighborhood coefficients. Aside from the deerbrush adjustments made for the initialization stage, we used empirically derived, species-specific simulation parameters for growth and competition coefficients for all shrub species, as described above.

At each yearly time step of the simulation, individual trees were assigned vertical growth values. To incorporate uncertainty into our conifer growth parameterization, for each simulation we randomly selected one bootstrapped sample of each conifer species and used the coefficients from that sample's mixed effects model. The growth model inputs included the focal tree's local shrub and environmental conditions and "climate year." We populated climate years in the simulation using historical data starting at 1970 in chronological order. At each yearly time step, the climate year effect was assigned to either 2015, 2016, or 2017 based on which of those three years best matched the precipitation of the historical year. The tree was then assigned a diameter using a randomly selected linear model chosen from the bootstrap results for conifer diameter.

Each tree was next assigned to either survive or die. We randomly selected one bootstrapped mortality population and used the coefficients from that population's logistic regression model for each iteration of the simulation. After each tree was assigned a mortality probability, it was also assigned a random number from 0-1 drawn from a uniform distribution. If that random number was below the mortality probability, the tree "died" and was removed from the simulation.

Over the course of each simulation, shrub cover and height surrounding each tree changed according to the shrub cover linear model and species-specific vertical growth GAM models. We adjusted shrub cover and height predictions relative to the starting shrub cover and height measured at that tree, such that the shapes of growth curves matched model predictions, but the intercepts differed based on empirical starting conditions.

Finally, for each yearly time step we calculated whether each tree had emerged above its local shrub canopy. Emergence was defined as half or more of the tree crown exceeding the average shrub height at location i:

$$emerged = 1 \text{ if } \quad height_{tree_i} - 0.5 * crown\ length_{tree_i} > height_{shrubs_i} \qquad (1)$$

Crown length was determined by multiplying height by live crown ratio. This ratio was calculated from Forest Inventory and Analysis (FIA) data for California (1994-2017). Specifically, we estimated live crown ratio for white fir (N = 685) and ponderosa pine (N = 196) as the mean of small trees (3 m > height > 1.5 m) in the database derived from FIA data. If a tree was determined to have emerged, it was recorded and removed from the simulation.

We repeated the simulation 1,000 times, running each iteration until all trees had either died or emerged above the shrub canopy. The sample of initial trees, growth parameters, diameter model, and mortality parameters differed slightly for each iteration. We calculated average cumulative proportion of initial trees that had emerged by year and the standard deviation of this value. As trees died, we did not adjust the denominator for the emergence calculation. Thus, by the conclusion of the simulation, when all trees had either emerged or died, the proportion of trees that died was equal to one minus proportion emerged. We compared the number of years required to reach 50% emergence ("Q50") between ponderosa pine and white fir, as well as the final proportion emerged. We then converted proportion emerged to density of trees per square meter based on juvenile tree densities by species found in our subset of the Welch et al. (2016) database.

Shrub species effects on conifer emergence

To evaluate shrub species effects, we ran simulation scenarios in which only conifers found under a single shrub species were used to initialize the model, implementing the same adjustments for deerbrush as described above. We repeated the simulation 1,000 times each for manzanita, deerbrush, and whitethorn, starting with 200 conifers in each simulation. We calculated Q50 and the average cumulative proportion of initial trees that had emerged by year, as we did for the base model.

We then investigated how individual dimensions of shrub species differences affected long-term recovery. To do this, we first ran a model similar to the base model but with all trees assigned the shrub species competition coefficient of one shrub species. The competition coefficient is the effect of shrub competition on conifer growth for a given shrub cover and height and is determined from linear regression modeling, as shown in Appendix S1: Figure S3. For the "Competition coefficient" scenarios, initial shrub cover and height and shrub growth over time were based on observed shrub species, but the competition coefficient was assigned to only one shrub species. We then ran scenarios in which competition coefficients were returned to their values in the base model, but initial shrub cover and height were assigned to an individual species. This allowed us to evaluate how starting shrub conditions affect long-term recovery trajectories. Finally, we evaluated how species-specific shrub development patterns affected recovery. To do so, we modified the base model by assigning all shrubs the GAM-based growth patterns of a single shrub species and allowed the other components of shrub species competition to vary by species.

RESULTS

Shrub development over time

For all focal shrub species, height increased after fire before leveling off and beginning to decrease within 10-25 years after fire (Figure 2). The GAM models predict an earlier and higher peak shrub height for deerbrush (*Ceanothus integerrimus*) than for any other shrub species. Maximum height was second highest for manzanita (*Arctostaphylos patula* and *A. viscida*). For shrub cover, we found a significant positive relationship between years since fire and shrub cover (Appendix S1: Figure S2).

Base model

In the base model, ponderosa pine emergence rates exceeded those of white fir until ~15 years after fire, at which point pine emergence flattened and fir emergence accelerated (Figure 3). Pine required an average of 18 years to reach 50% emergence (Q50), while Q50 for fir was 21 years (116% greater; Table 1). Both species showed decreasing relative growth rates over time, with variation by climate year for ponderosa pine (Figure S7). Ending proportions of pine and fir emergence were similar (82 ± 6% and 83 ± 5%, respectively; Table 1). In other words, since simulations ended only after all trees had either emerged or died, 18% ± 6% of pines died and 17% ± 5% of firs died. Pine and fir simulation lengths were also similar, with pines reaching complete mortality or emergence at 37.1 ± 2.8 years and fir taking 35 ± 3.2 years (Table 1).

Despite the similar proportional success of pine and fir, densities of emerged white fir exceeded those of pine for the majority of the simulation period. Fir had higher maximum density (0.11 ± 0.006 tree/m^2 for fir, 0.07 ± 0.005 tree/m^2 for pine; Figure 3b). The difference between proportional results and density results is due to higher initial seedling densities of fir than pine.

Shrub species effects on conifer emergence

Single-shrub species models showed strong differences between emergence rates for the three shrub species of interest. Emergence occurred fastest and with highest maximum values for whitethorn, followed by deerbrush (Figure 4). Ponderosa pine's advantage over white fir was evident in final emergence results in the whitethorn and deerbrush models (whitethorn: 98 ± 3% for pine, 85 ± 5% for fir; deerbrush: 85 ± 7% for pine, 75 ± 7% for fir) but in the manzanita model final emergence of pine was nearly equal that of fir (62 ± 12% for pine, 64 ± 10% for fir). Other shrub species beyond these three were included in the base model but not modeled individually due to lower data availability per species, which is why the base model resulted in similar emergence for pine and fir. For all three shrub species, pine emergence was faster than fir during the first 5-15 years of the simulation, after which fir emergence rates reached or exceeded those of pine. Because of this early pine advantage, Q50 values were lower for pine than for fir across all three species (Figure 4). With the exception of pine under whitethorn, simulation duration was similar across species combinations: pine reached complete emerged or mortality in 26.4 ± 2.7, 37.9 ± 2.0, and 35.6 ± 3.9 years for whitethorn, manzanita, and deerbrush, respectively, while fir duration was 32.7 ± 3.9, 36.0 ± 2.9, and 37.0 ± 3.2 years under the same species.

The simulations that parse individual dimensions of shrub neighborhood dynamics showed that shrub cover, height, and growth influenced emergence more strongly than shrub species competition coefficients (Figure 5). When all trees were assigned initial shrub cover and height values of deerbrush, both fir and pine emergence was severely dampened and nearly 50% of pines died (Figure 5c-d). The model adjusting only shrub development trajectory parameters showed the strong effect of manzanita growth on emergence in years 10-30 after fire, particularly for white fir (Figure 5e-f). Adjusting only the shrub competition coefficients resulted in more similar patterns across shrub species (Figure 5a-b).

DISCUSSION

Our model results indicated that shrub filter effects on regenerating conifers depend on shrub species. We sought to determine whether the shrub layer acts as an ecological filter by precluding, delaying, or altering conifer recovery. We found that manzanita delays recovery while whitethorn and deerbrush alter it by favoring ponderosa pine over white fir, though not dramatically (Figure 4). Interestingly, when all shrub species were combined (including more than the three mentioned above), rates of emergence above the shrub canopy were similar for white fir and ponderosa pine. This indicates that shrubs overall delay, rather than alter, conifer emergence. However, pine and fir experienced peak emergence rates at different points throughout the simulation (Figure 3). The shrub layer may act as a stronger filter at other stages in post-fire succession, such as establishment. Though the proportions of pine and fir that emerged were similar, densities of emerged pine fell far below those of fir due to differences in established seedling densities at the start of the simulation (Figure 3b).

By decomposing three dimensions of shrub competition and performing sensitivity tests on each one, we showed that shrub growth patterns are important drivers of post-fire succession. While shrub neighborhood species coefficients – i.e. the degree a species reduces conifer growth for a given shrub height and cover – affected conifer emergence (Figure 5b), shrub height and cover development were also critical (Figure 5 c-f). Shrub growth trajectory sensitivity tests showed that manzanita had the strongest growth trajectory effect (Figure 5c,d). Though deerbrush reached greater maximum heights than manzanita (Figure 2), most deerbrush height growth occurred before the start of the simulation. Thus, initializing the simulation with deerbrush cover and height resulted in large reductions in emergence (Figure 5e,f).

This study's findings contradict the hypothesis that shrub competition produces an overall advantage for fir over pine during post-fire emergence. Though ponderosa pine growth is more strongly affected by shrub competition than fir growth (Tubbesing et al. 2020), these differences do not appear to translate to decreased emergence rates for pine. Pine growth rates rarely fell low enough for mortality probability to sharply rise. Our mortality model predicted that pine mortality rate exceeds 2% per year only after pine relative annual growth falls below 7.7%. In our simulations, mean pine growth fell below this threshold at 21 years after fire (Figure S7). By this time, nearly 60% of pines had escaped shrub competition by emerging above the shrub canopy. Rapid emergence was particularly evident under whitethorn, where 76% of pines had emerged by 15 years post-fire (Figure 4b).

We examined important stages within the complex process of post-fire succession. To reach maturity, regenerating conifers must overcome several potential bottlenecks, including dispersal, establishment, survival, emergence, and reproductive maturation. Emergence can be broken down into two substages: emergence during shrub layer development and under a mature shrub layer. We found that ponderosa pine has a relative advantage over white fir during shrub layer development, while the reverse is true under the mature shrub layer, and the degree of relative advantage depends upon shrub species at each substage (Figure 6).

The fact that the relative advantage of pine and fir reversed throughout shrub development is consistent with the life history strategies of those two species. While ponderosa pine exemplifies a shade-intolerant strategy, including rapid growth under high light, white fir growth is less affected by shading and exceeds pine growth rates at low light (Niinemets and Vallardes 2006, Zald et al. 2008, Tubbesing et al. 2020). The gap between pine and fir emergence was highest at earlier stages in the model (~ years 10-20) and narrowed by the conclusion of the simulations (Figure 4). This timing corresponded with peak shrub height, which occurred between 10 and 25 years, depending on species (Figure 2). As shrub heights peaked, pine emergence flattened and was exceeded by fir emergence rates, likely due to increased shading.

Early pine emergence was particularly rapid under whitethorn (Figure 4), which had the lowest heights among the three shrub species of interest (Figure 2). Low shrub heights likely led to rapid early pine emergence in two ways: 1) lower heights produced weaker competition with conifers, and 2) lower heights reduced the threshold at which a juvenile pine was considered emerged. Sensitivity analyses showed that manzanita shrub growth trajectories decreased emergence for both fir and pine. Deerbrush initial shrub height and cover did the same. Whitethorn displayed neither of these effects. These results suggest that whitethorn's lower heights did contribute to rapid conifer emergence.

Differences in shrub neighborhood species coefficients, which measure shrub effects on conifer emergence for a given height and cover, may be due to differences in leaf area density or may reflect differences in belowground interactions. The neighborhood coefficients for the two *Ceanothus* species reduced pine emergence less than that of manzanita, which may be due in part to nitrogen-fixing abilities in the *Ceanothus* genus. Previous allometric research has indicated that, for a given crown area, leaf biomass and total biomass are highest for manzanita, low for whitethorn, and lowest for deerbrush (Huff et al. 2018). These allometric differences match the pattern we found in shrub neighborhood species coefficients (Figure 5b). However, the results of previous shrub allometry studies are difficult to compare to our findings because they analyze shrubs as individuals (McGinnis et al. 2010, Huff et al. 2017, 2018), whereas we measured shrubs as a continuous layer because shrub crowns often overlapped and interlocked. Huff et al. (2018) also ignore shrub height as a predictor of biomass, relying only on crown area, despite height being a significant predictor of shrub biomass (McGinnis et al. 2010). More detailed analyses of the predictors of competitive ability for individual shrub species would help improve our model.

Our sensitivity test results show that understanding shrub development trajectories is critical to understanding post-fire conifer recovery. Our data syntheses showed that, for all species, shrub height declined after peaking. Previous research has found similar patterns of shrub growth followed by decline in the second decade and have attributed the decline to increased competition from overstory trees (Tepley et al. 2017). However, very little overstory shading was observed in our study sites. Shrub declines may also be related to age-related stand decline or senescence (Hilbert and Larigauderie 1990). Since most data on shrub height after 15 years comes from only a few fire footprints (Figure S1), more research on shrub recovery trajectories will be an important step toward a better understanding of post-fire succession in the Sierra Nevada.

Improved understanding of climate effects on post-fire succession would also help contextualize our results. We parameterized climate year effect using historical precipitation records rather than expected future conditions because of uncertainty in how climate change will affect precipitation patterns. We hope that future applications of our simulation model will add complexity to the climate component in order to better predict future climate change impacts, as climate may influence height dominance of our study species (Young et al. 2019). Furthermore, the three measurement years used to build our linear models predicting conifer growth overlapped with the end of a multi-year severe drought. Though we captured growth during an average and a wet year following the drought, growth may still have been affected by drought lag effects.

We found that in the base model, which used weighted averages of all shrub species, ponderosa pine and white fir emerged in approximately the same ratio in which they existed at eight years post-fire, when the simulation began. Given previous findings of higher post-fire fir than pine recruitment (Nagel and Taylor 2005, Crotteau et al. 2013, Collins and Roller 2013, Lauvaux et al. 2016), fir enrichment is likely driven by a different stage of post-fire succession (Figure 6). Unfortunately, the effects of shrub competition on conifer seedling establishment are difficult to study and poorly understood. We found ponderosa pine juveniles under significantly lower shrub competition than white fir, but because of our targeted sampling design it is difficult to make inferences based on this observation. Experimental work has shown that shrubs suppress post-fire seedling recruitment under normal weather conditions but has found no significant differences in shrub effects between ponderosa pine and white fir (Werner et al. 2019). Future detailed measurement of seedling establishment in the early years after fire would help identify whether establishment alters long-term conifer species composition.

CONCLUSION

We synthesized several data sources into a Monte Carlo simulation model predicting post-fire recovery. By strongly grounding each model step in empirical data, we represented realistic distributions of long-term outcomes. We found that some shrub species favor the emergence of ponderosa pine relative to white fir, but across all shrub species pine and fir experienced similar success rates. Since white fir began at much higher seedling densities than ponderosa pine, fir outnumbered pine by the simulations' end (Figure 3b). If higher pine than fir densities are desired, active management may be required. Management could include planting pine seedlings and/or controlling shrubs surrounding juvenile pines, particularly manzanita because it most strongly suppresses pine growth.

More research is needed on the factors leading to fir enrichment after fire. Legacy effects of logging and fire suppression may be partly responsible for higher initial fir seedling densities, as there are higher densities of firs than pines in nearby surviving forests to serve as parent trees. Firs also distribute seed farther than pines (Clark et al. 1999). Establishment rates of fir and pine under shrubs remain an important missing piece. The simulation model presented here could be expanded by adding dispersal, establishment, adult tree competition, and/or sexual maturation to create a spatially explicit model that captures additional potential post-fire succession bottlenecks.

ACKNOWLEDGEMENTS

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TABLES

Table 1. Emergence rates for ponderosa pine and white fir according to the base model. Q50 is defined as the number of years required for 50% of trees to emerge above the shrub layer. Lower and upper bounds are derived from emergence curves ±1 standard deviation from the mean.

	Ponderosa pine	White fir
Q50 (years)	18 ± 2	21 ± 1
Total emergence (%)	82 ± 6	83 ± 5
Simulation duration (years)	37.1 ± 2.8	35 ± 3.2

FIGURES

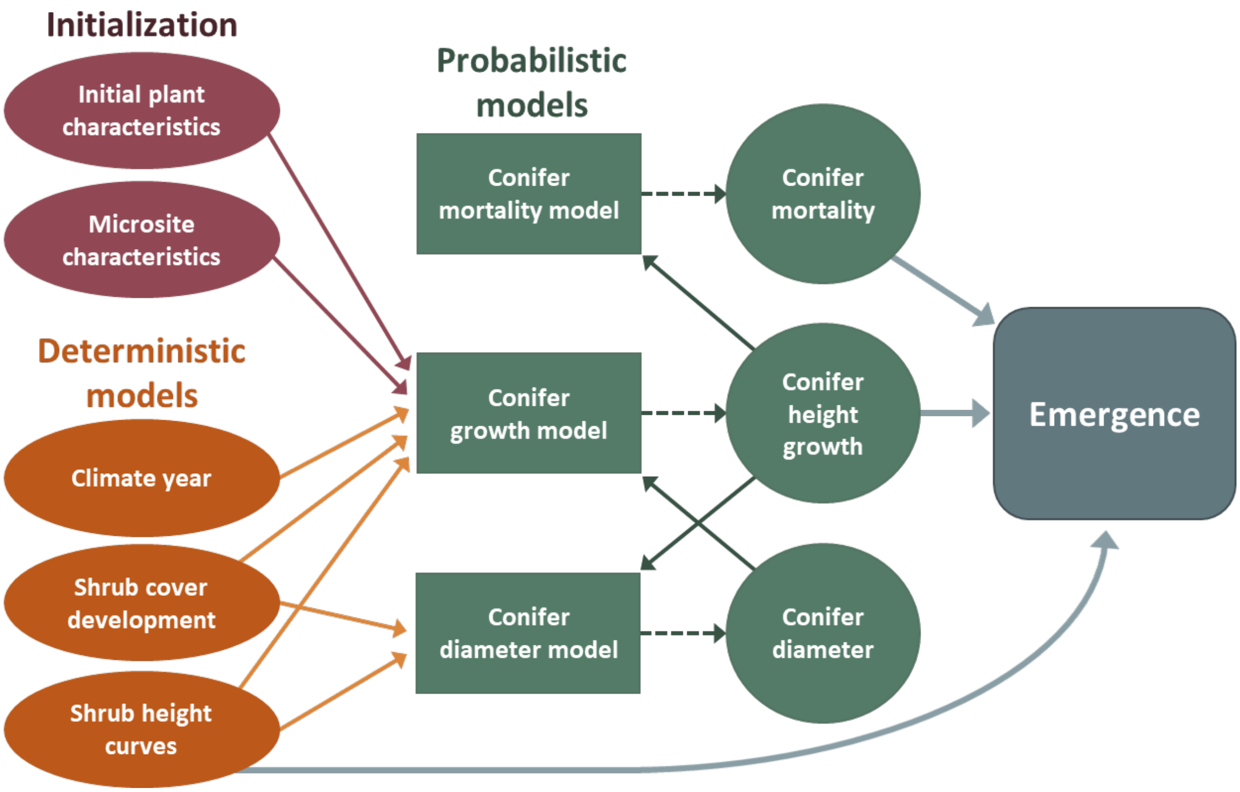


Figure 1. Diagram illustrating the data-driven simulation modeling framework. Ovals represent deterministic model parameterization, including initialization by bootstrap sampling of field data, climate year based on the historical record, and shrub height and growth curves fit to regional field survey data. Green boxes represent linear models derived from field data. Orange, purple, and green solid arrows represent linear model inputs while dashed green arrows represent outputs. Teal circles represent the conifer dynamics predicted by the linear models. Conifer height and diameter measurements come directly from field data for the first year of the simulation, represented in the purple arrow originating at “Initial plant characteristics,” and come from modeled results for subsequent years, represented by the green arrows. Neighborhood shrub height, derived from deterministic shrub height curves, is combined with conifer mortality and height to determine emergence at each year in the simulation (thick blue-grey arrows).

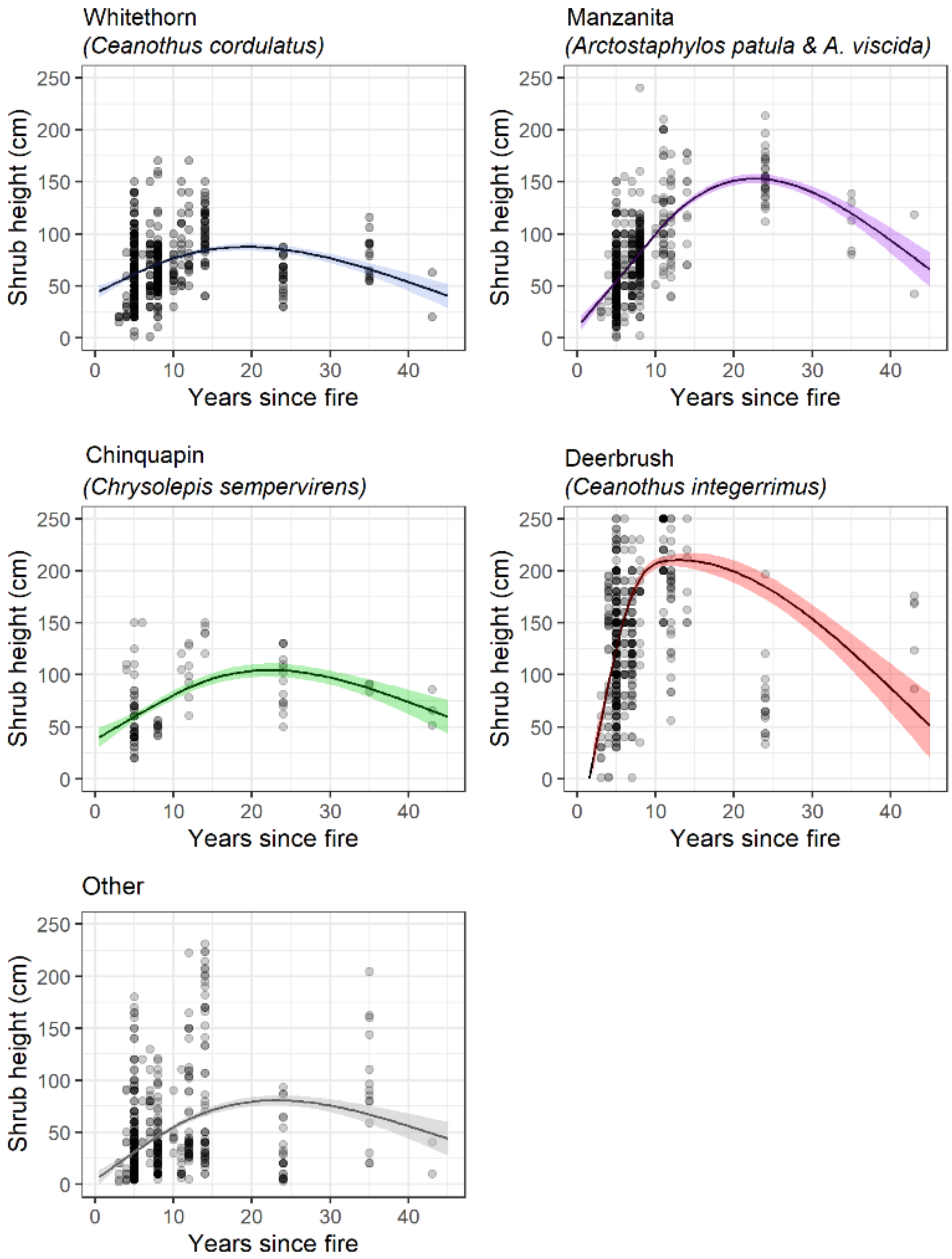


Figure 2. Shrub height GAMs. Shaded areas show standard error estimates.

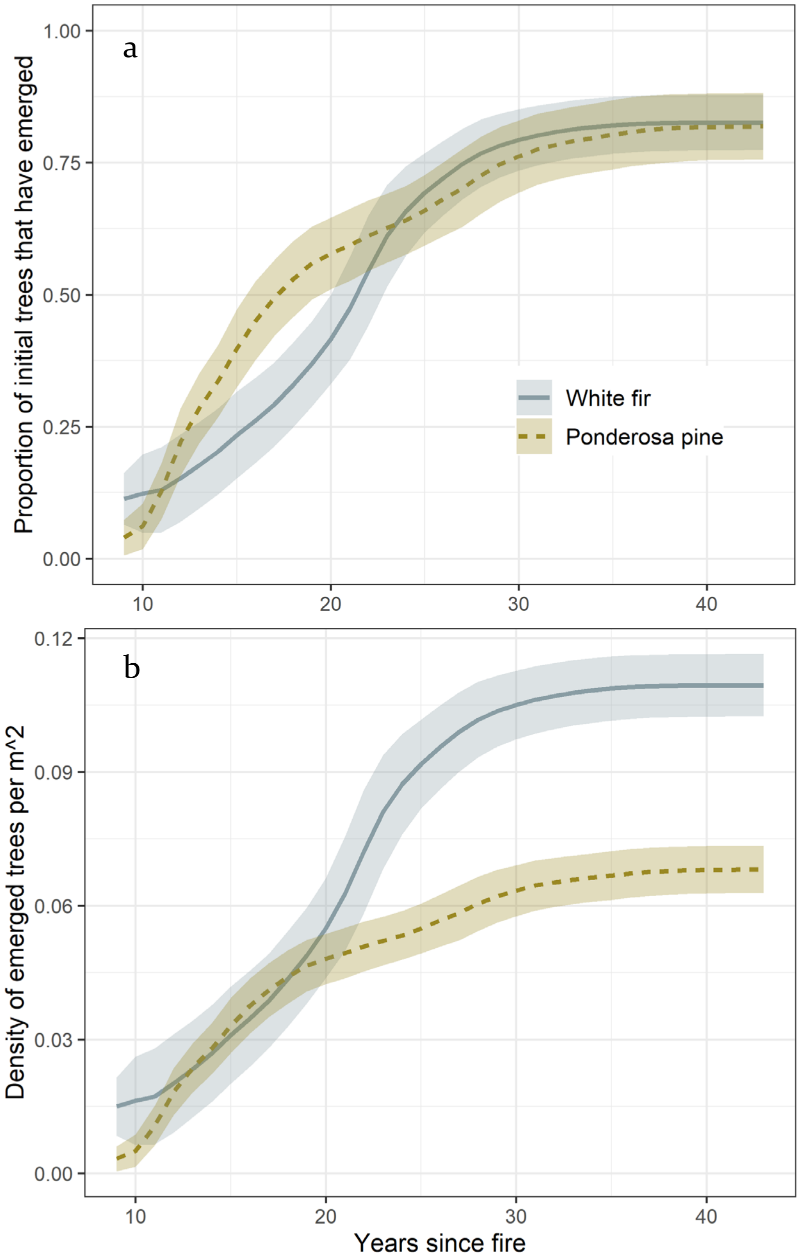


Figure 3. Base model predictions of juvenile ponderosa pine and white fir emergence above the shrub canopy over time, shown as a) proportion of initial juvenile trees that emerged above the shrub canopy, and b) density of trees that emerge above the shrub canopy. Shading shows time ±1 standard deviation.

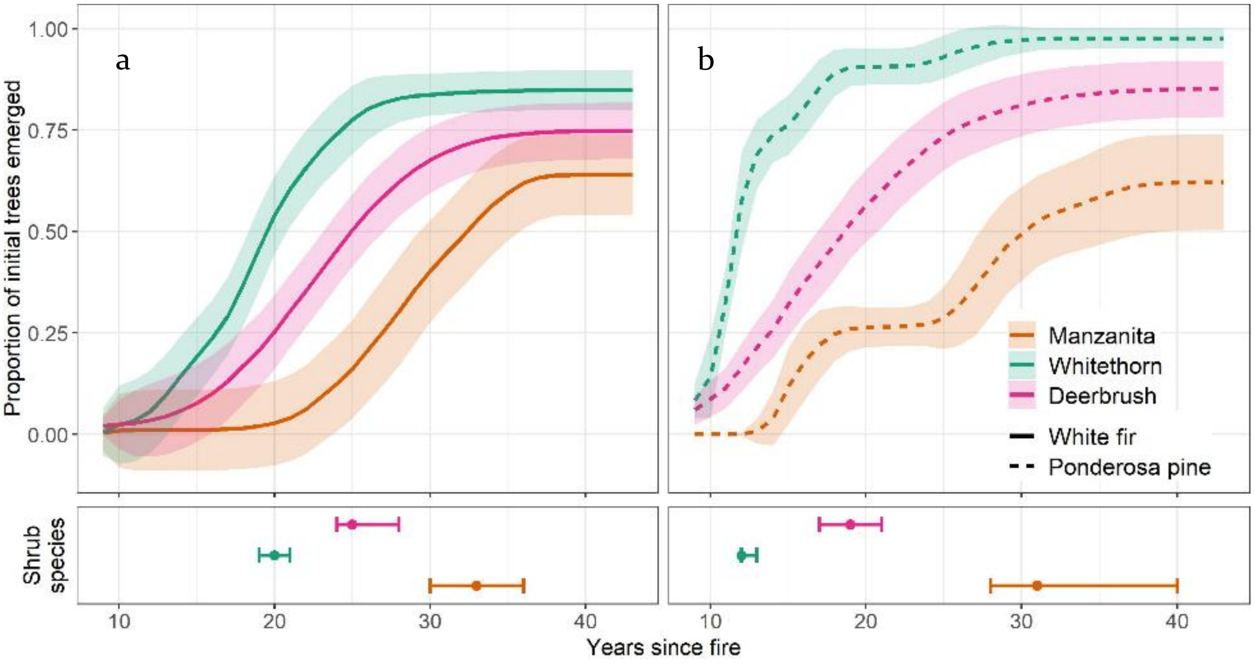
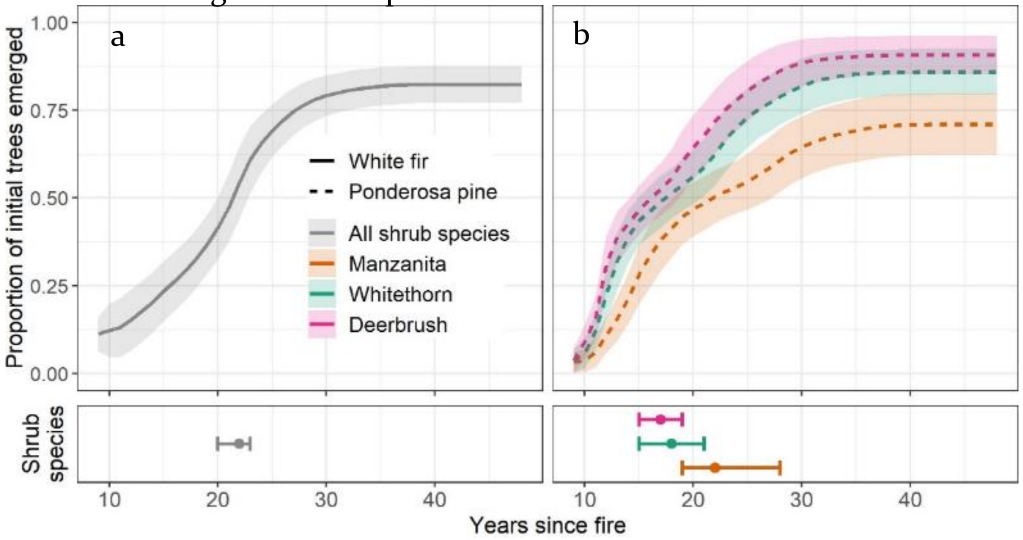
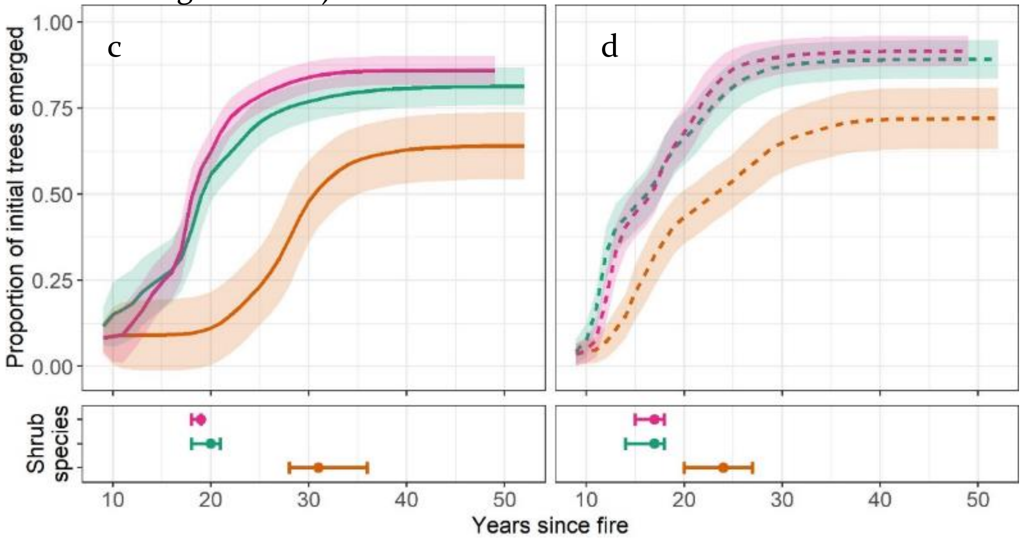


Figure 4. Conifer emergence above the shrub canopy for single-shrub species models, shown as the proportion of initial juvenile trees that emerge over time ±1 standard deviation for (a) white fir and (b) ponderosa pine. Points and error bars show the number of years required for 50% of initial trees to emerge, termed Q50.

Shrub neighborhood species coefficient



Shrub growth trajectories



Initial shrub cover and height

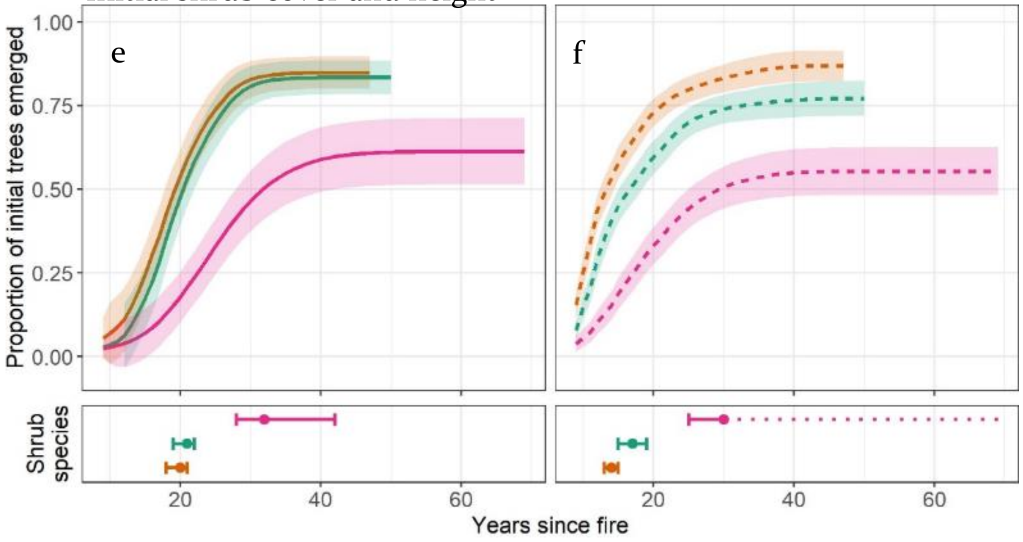


Figure 5. Simulation results for shrub species sensitivity tests. Lines and shading show mean emergence above the shrub canopy over time ±1 standard deviation. Points and error bars show Q50, defined as the number of years before 50% of initial trees emerge above the shrub canopy. In panel (a), all white fir results are shown together in gray because there was no difference in shrub neighborhood species coefficients for white fir. The dotted line in (f) illustrates that the lower bound of emergence never reaches 50%.

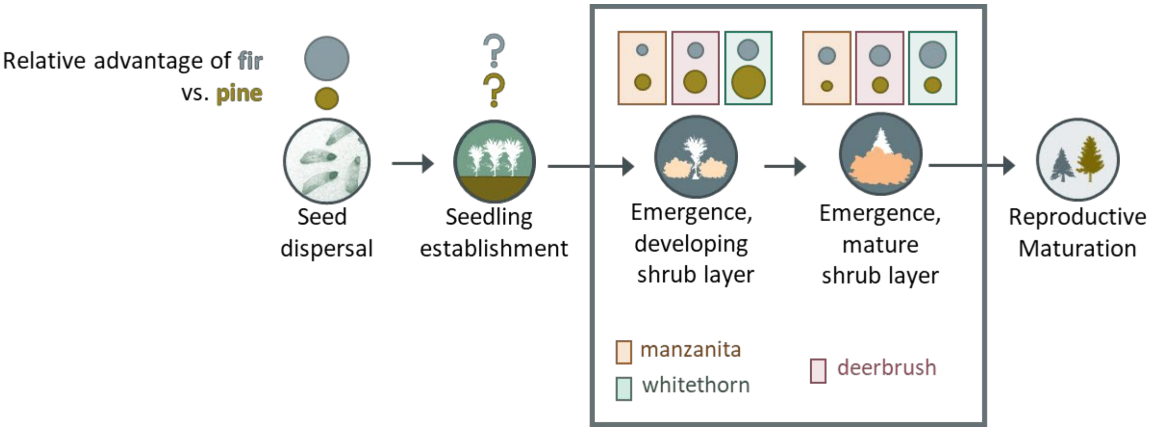


Figure 6. Conceptual diagram illustrating the relative advantage of ponderosa pine (brown) versus white fir (blue-grey) at stages throughout post-fire forest development. The size of each circle represents the approximate relative effect of each process on that species. The large box delineates patterns found in this study. The colored boxes illustrate how patterns vary under each of the three dominant shrub species. The question marks above "Seedling establishment" illustrate that species differences in germination and establishment rates in post-fire shrub fields are understudied.

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Conclusion

In this dissertation, I explored how forest regeneration is affected by a changing disturbance regime and the management strategies used to mitigate it. I showed how forest heterogeneity is important in predicting regeneration patterns. As forests and forest fires become more homogenous in the Sierra Nevada, management strategies that help foster patchy forests will be critical in ensuring future post-fire regeneration.

In the case of post-fire recovery at Last Chance, as described in Chapter 1, pre-fire fuel reduction treatments increased post-fire seedling regeneration, likely via their effects on neighborhood fire severity. Fir seedling densities were highest in patchy burned areas, where bare mineral soil was located near extant adult trees that could serve as seed sources. Forest treatments were important not just in their ability to *reduce* fire severity, but in their ability to make fire effects more *heterogeneous*.

This finding is important in informing forest management. 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. 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. More widespread use of strategically placed treatment networks could help bring wildfire effects closer to historical norms, facilitate long-term recovery from fire, and restore heterogeneous, resilient forest structures.

Chapter 1 showed encouraging results highlighting the effects of fuel treatments on seedling regeneration. However, I found much stronger regeneration of firs than pines. In Chapter 2, I explored how the novel, more homogenous fire regime affects the balance between firs and pines. I hypothesized that fir enrichment occurs in both unburned areas and severely burned areas, both of which are increasing in prevalence under the novel fire regime. Abundant research has documented fir enrichment in unburned forests due to fire exclusion and historical logging practices. Fir enrichment following severe wildfire is more difficult to document. Several processes must be studied in order to determine whether long-term fir enrichment may occur. In Chapter 2, I studied two important processes affecting fir enrichment: shrub effects on fir and pine growth rates, and the relationship between growth and mortality for fir and pine. My results supported the hypothesis of fir enrichment in severely burned areas.

To further examine the fir enrichment hypothesis, in Chapter 3 I combined my field results from Chapter 2 with other data sources to develop a Monte Carlo simulation model predicting post-fire recovery. By strongly grounding each model step in empirical data, I represented realistic distributions of long-term outcomes. I found that some shrub species favor the emergence of ponderosa pine relative to white fir, but across all shrub species pine and fir experienced similar success rates. Since white fir began at much higher seedling densities than ponderosa pine, fir outnumbered pine by the simulations' end. Thus, shrubs could be filtering out pines, but the dynamics included in my simulation model do not contain the root cause of the pine filter.

The results of Chapter 3 highlight a different type of forest heterogeneity: differences in shrub species. Individual shrub species had unique effects on long-term success of pines versus firs. When all shrub species were included in the model, pines and firs experienced similar emergence above the shrub canopy. When only a single shrub species was included, pine and fir emergence was less equal. This highlights the importance of heterogeneous species mixtures. It appears that maintaining shrub species diversity will improve forest resilience under the novel fire regime and ensure survival of multiple tree functional types.

More research is needed on the factors determining post-fire regeneration and potentially leading to fir enrichment after fire. Legacy effects of logging and fire suppression may be partly responsible for higher initial fir seedling densities, as there are higher densities of firs than pines in nearby surviving forests to serve as parent trees. Firs also distribute seed farther than pines. Establishment rates of fir and pine under shrubs remain an important missing piece. As is common in research, my dissertation opened more questions than it answered, but the themes introduced in this body of work will help guide my research for years to come.

CHAPTER 1 Appendix

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

1Shrub 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

CHAPTER 2 Appendix

A. Fires sampled

Table S1. Fires sampled

Fire	Year	Years since fire (from 2016)	Wildfire size (ha)	Patches	Patch elevation (m)
American River Complex	2008	8	4,452	4	1605 - 1929
Freds	2004	12	3,116	4	1334 - 1815
Star	2001	15	6,783	3	1583 - 1723
Cleveland	1992	24	9,947	2	1388 - 1580
Wrights	1981	35	1,619	1	2080 - 2107

B. Estimating juvenile conifer time of death for mortality study

In order to simulate juvenile conifer survival rates at the population level, it was necessary to match calendar years between vertical growth segments of live and dead trees. This matching required us to estimate the timing of juvenile conifer death.

We used ring width measurements to assist in the aging of dead trees. For each tree, a “cookie” was cut at 10 cm height. If fewer than 3 rings were visible in this cookie, a replacement cookie was taken from the base of the seedling where it was cut at ground level. Annual radial increments were measured along 3 radial transects of the cookie to the nearest 0.01 mm using a dissecting microscope and a sliding stage micrometer. We averaged yearly growth increments across the three transects to create a series for each tree and then detrended these series using the horizontal-line method, which subtracts the mean of each series from each ring width (Speer 2009). More complex detrending methods (e.g. negative exponential curves; Speer 2009) were inappropriate for these data because of the short length of the series and absence of age-related growth declines.

We plotted average growth indices for live trees of each species (Fig. S1). We then compared each dead white fir detrended series to this growth pattern. We began with white fir because it displayed distinct patterns in radial increments across years, which ponderosa pine did not, as shown in Fig. S1. For individual dead white fir that showed clear alignment with the species-specific growth pattern shown in Fig. S1B, we assigned a year of death. However, not all dead trees could unambiguously be assigned a year of death by matching patterns in growth. As an alternative, we aggregated physical characteristics such as the extent of needle and bark retention as well as needle color for individuals with a known date of death. We used these

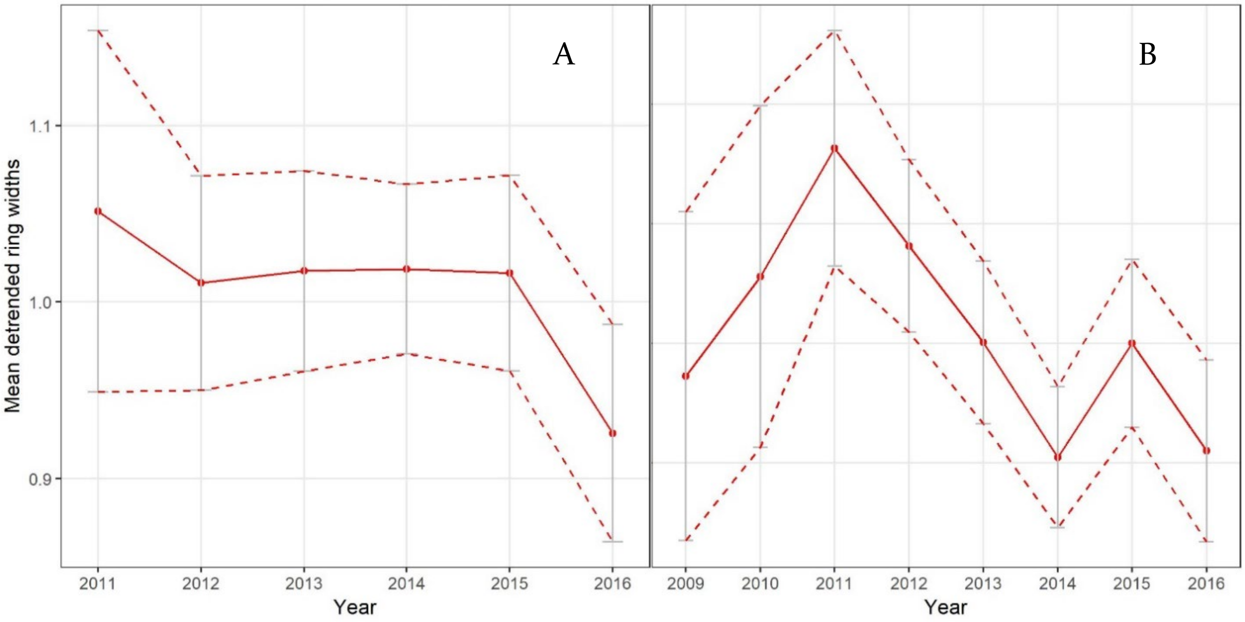


Figure S1. Mean detrended annual radial increments for live tree a) ponderosa pine and b) white fir. Dotted lines represent ± 2 standard errors.

physical characteristics along with the stage of apical bud development at time of death to assign the calendar year that corresponded with the last vertical growth segment of each tree. Using these estimates, we averaged yearly growth indices for all dead white fir to verify that their patterns matched the patterns obtained from the live trees (i.e., comparing Fig S1B to Fig. S2B).

Finally, we estimated year of death for each ponderosa pine using the criteria established for white fir and again compared yearly trends to those of live trees (i.e., Fig S1A vs. Fig S2A). The similarity in species-specific annual growth patterns between live trees and dead trees supports the contention that our age of death assignments were reasonably accurate.

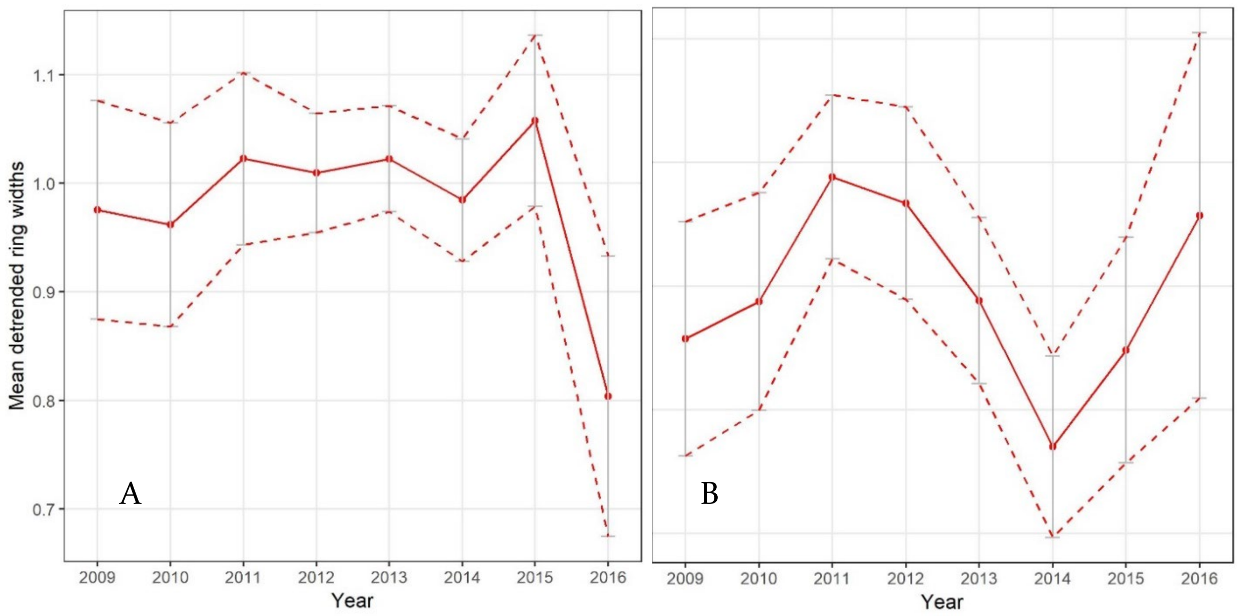


Figure S2. Mean detrended annual radial increments for dead tree a) ponderosa pine and b) white fir based on estimate time of death. Dotted lines represent ± 2 standard errors.

C. Mortality simulation sensitivity analysis

To verify that any potential error in the year of death estimates described above did not bias our results, we tested the sensitivity of the mortality simulations to variation in year of death. We repeated the simulations described in the paper, but with the following modifications to seedling ages before the logistic regression step: each tree's year of death was randomly re-assigned to within one year of its estimated death year, limited to the most recent 3 years. In other words, a tree estimated to have died in 2016 was randomly assigned to have died in 2015, 2016, or 2017, while a tree estimated to have died in 2015 was randomly assigned to either 2015 or 2016 and a tree assigned to 2017 was randomly assigned to either 2016 or 2017. These random assignments were repeated for each iteration of the simulation, which we ran 1000 times as in the main analysis. Results closely matched results from the main analysis (Fig. S3), showing that simulation results were robust to variation in year of death estimations.

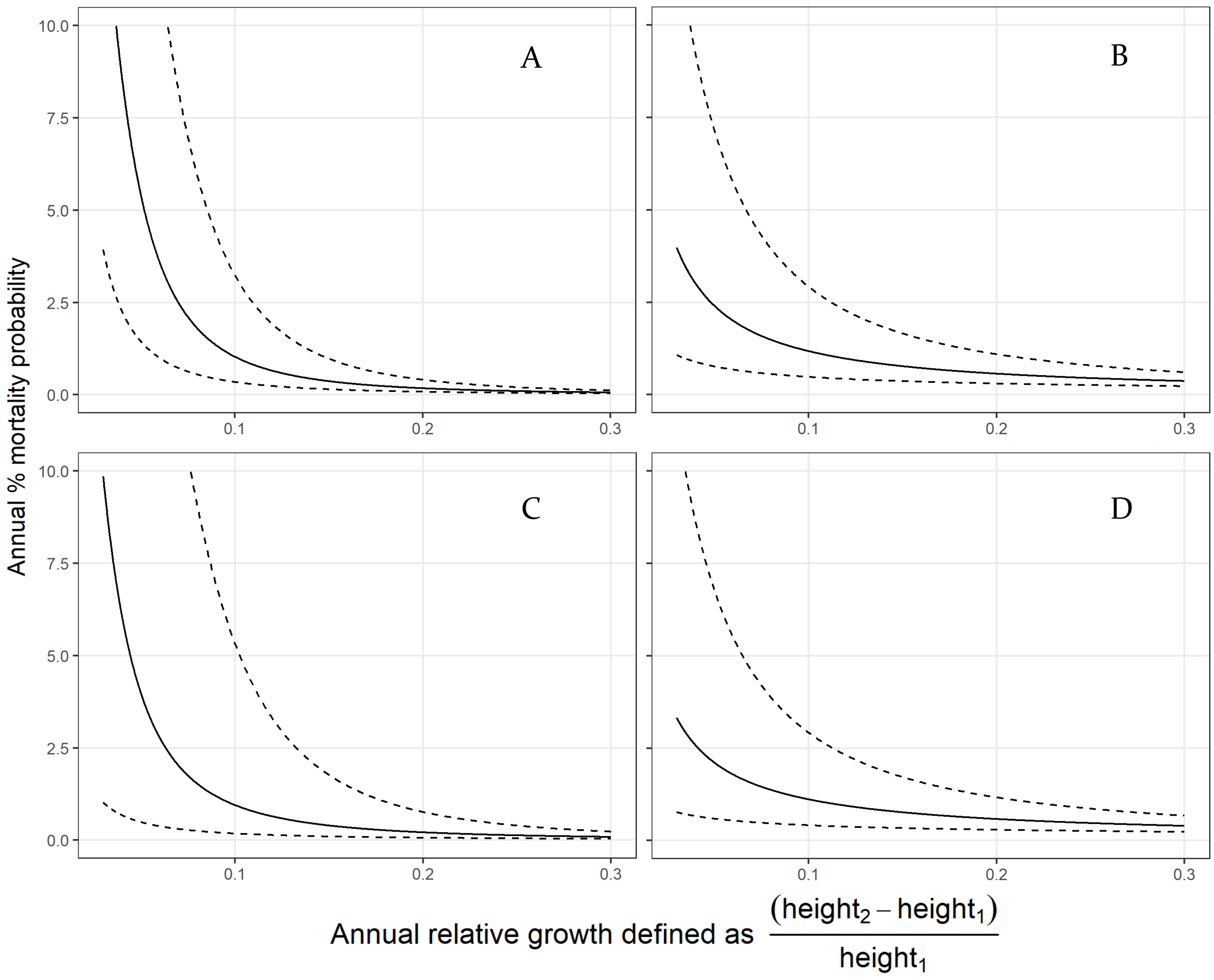


Figure S3. Results of mortality simulation sensitivity analysis. Panels (A) and (B) show simulation results using static death year assignments for pine and fir, respectively, and are identical to the figures shown in the results section of the paper. Panels (C) and (D) show simulation results using randomized death year assignments as described above for pine and fir, respectively. The similarities between the top and bottom panels show that results were not sensitive to errors in year of death assignments.

D. Evaluation of interactions in wildfire footprint growth models

The interaction between tree height and shrub competition was not included in the pine mixed effects model because it had a small effect on R_m^2 (0.63 vs. 0.62), a smaller effect size than the other predictors, and caused a relatively small decrease in AIC_c (362.9 to 359.1).

The same interaction was not included in the fir mixed effects model because it increased AIC_c (from 641.0 to 642.9) and barely increased R_m^2 (from 17.1 to 17.2).

E. Filling in missing height values

For 19 of the 563 growth measurements, height before growth was not measured but was instead estimated using other height data for those trees and a linear regression model. When the 19 measurements were taken – in June 2016 – 2016 vertical growth was not measured because trees had not yet completed that season's growth. Instead, we measured 2015 vertical growth and the overall height of the seedling. But, for those 19 trees, we failed to measure height at the start of 2015 vertical growth.

We estimated 2016 growth in order to subtract it from total growth and calculate initial height. We created a linear regression model of 2016 growth using the predictor variables: tree species, 2015 growth, the interaction of those two variables, and date of measurement. When applied to trees with 2016 growth measurements taken during the same time period, the adjusted R^2 of this model was 0.71.

F. Supplemental figures

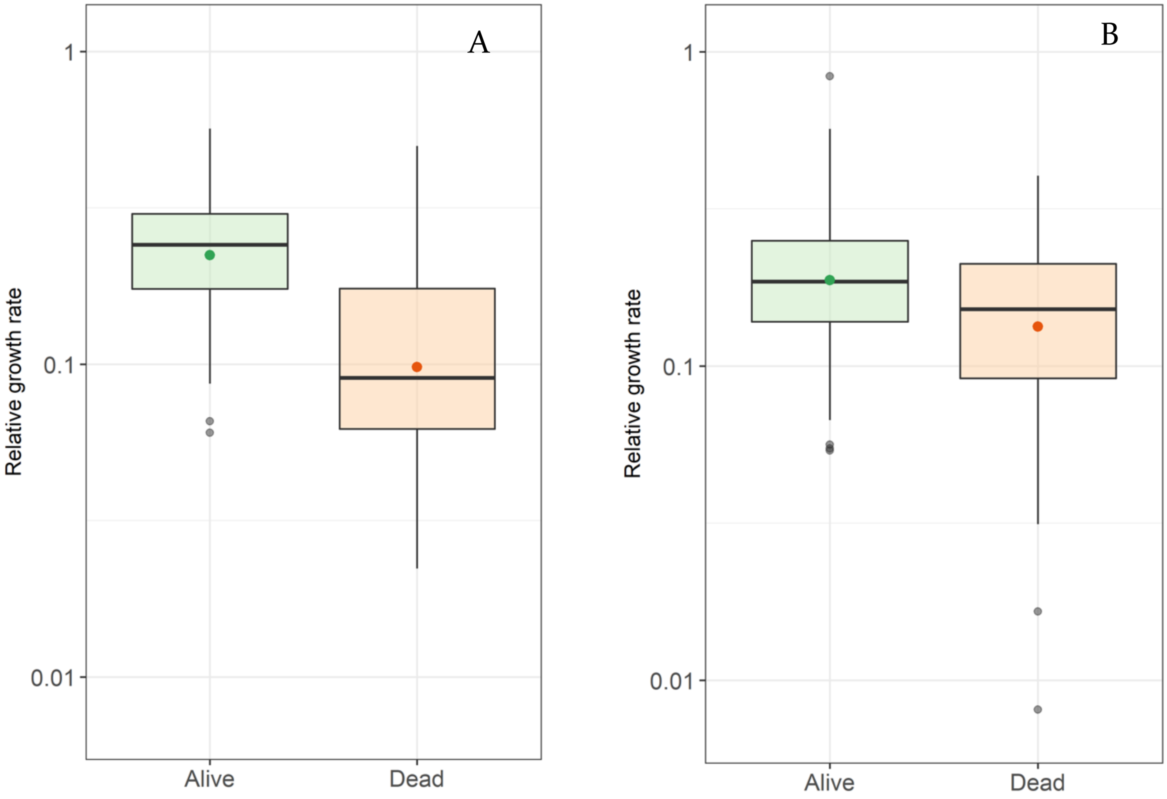


Figure S4. Relative growth rates for live and dead juvenile A) ponderosa pine and B) white fir

G. Literature Cited

Speer, J. H. 2009. Fundamentals of Tree-Ring Research.

CHAPTER 3 Appendix

A. Parameter development

Shrub growth

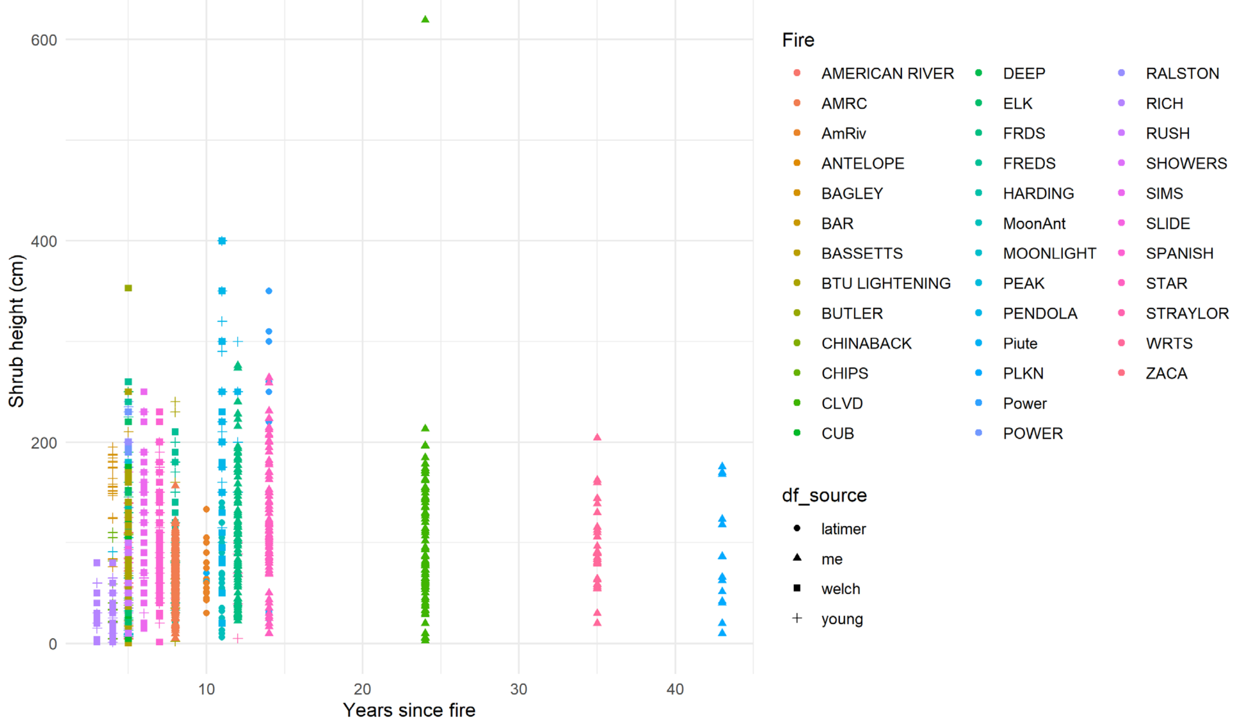


Figure S1. Shrub data sources by fire

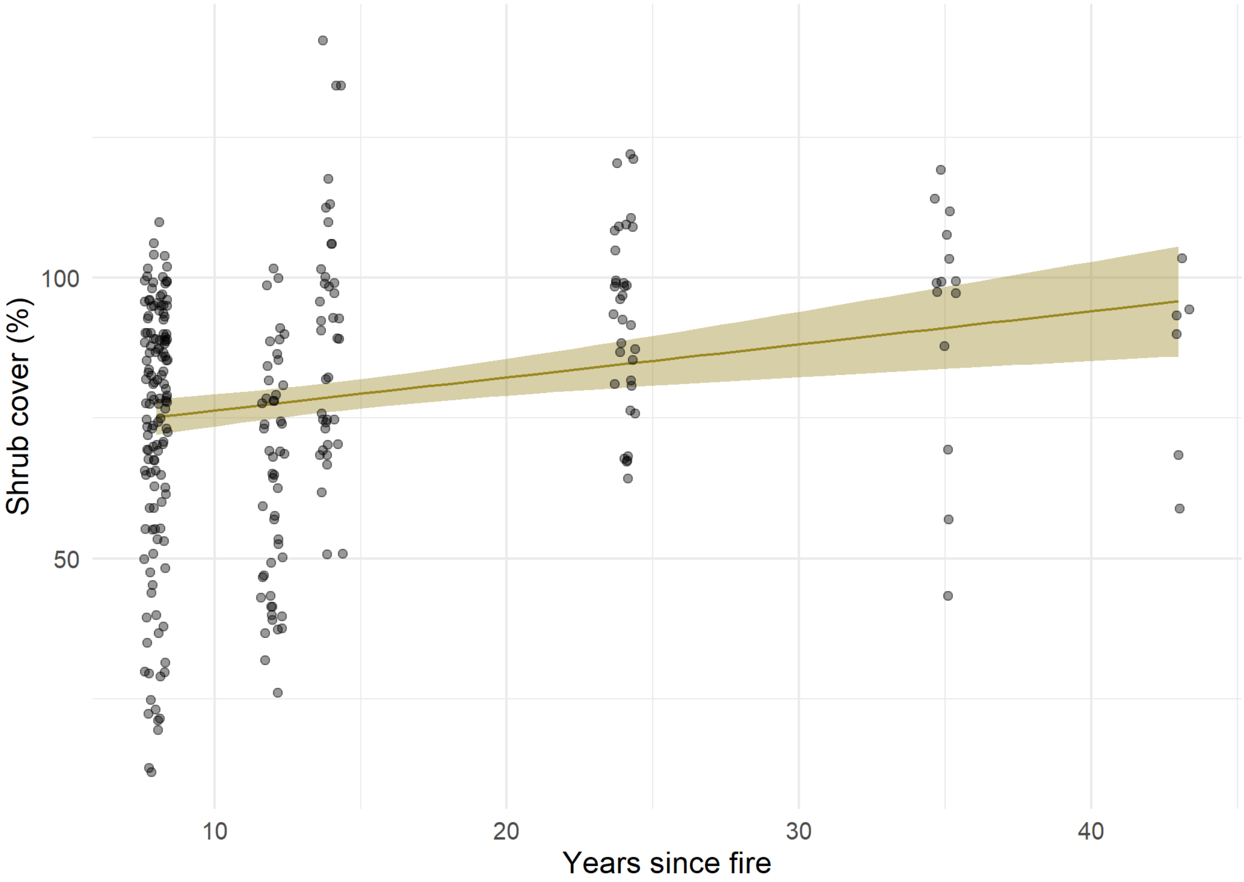


Figure S2. Shrub cover over time. The tan line shows the effect of time since fire on shrub cover according to the linear model that was used in simulations. Shaded areas represent 95% confidence intervals. Points represent observations, jittered to improve visibility.

Conifer vertical growth

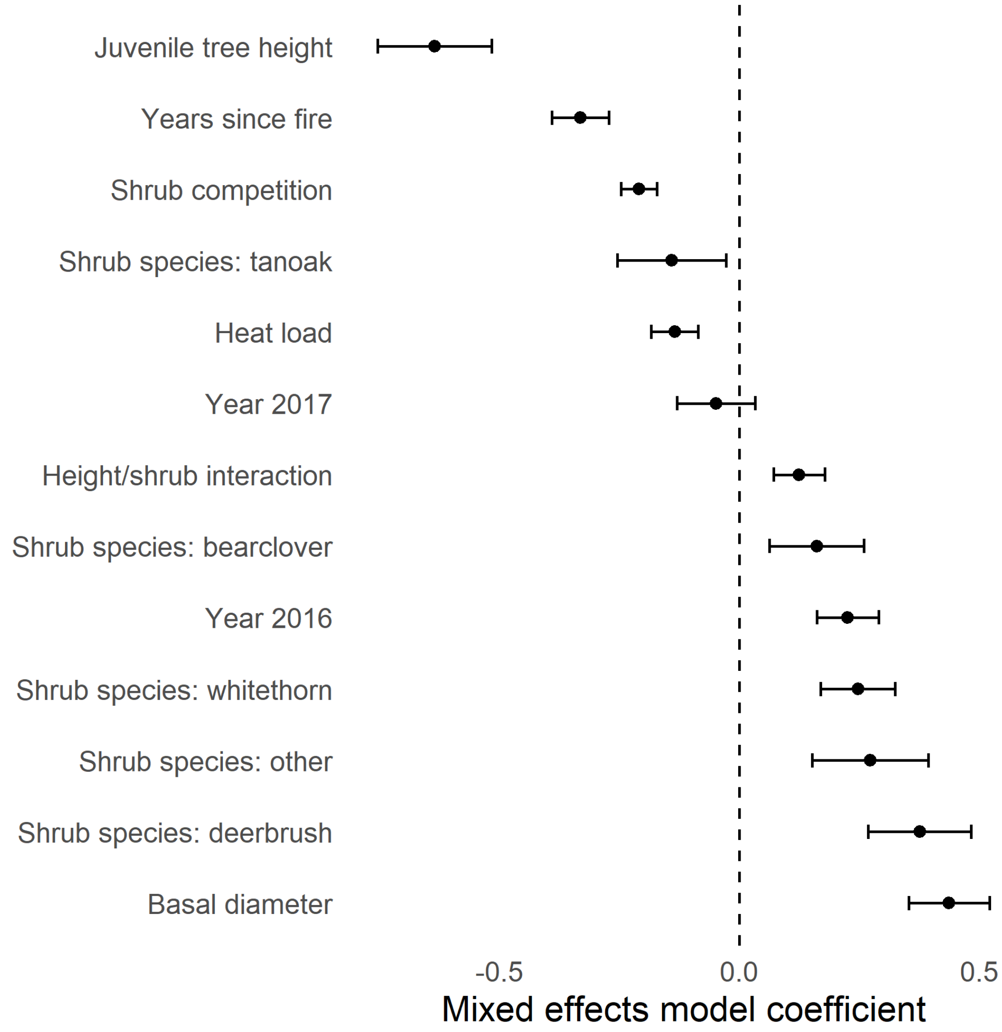


Figure S3. Mixed effects model coefficients from bootstrap sampling of ponderosa pine growth. Points represent means across 1,000 samples and error bars represent standard deviations. Numeric variables were normalized before model runs by subtracting the mean and dividing by the standard deviation to make coefficients comparable. For factor variables, treatment contrasts were used, in which the first factor level coefficient is set to 0 and all other levels' values are relative to the first level. Random effects are not included in this table.

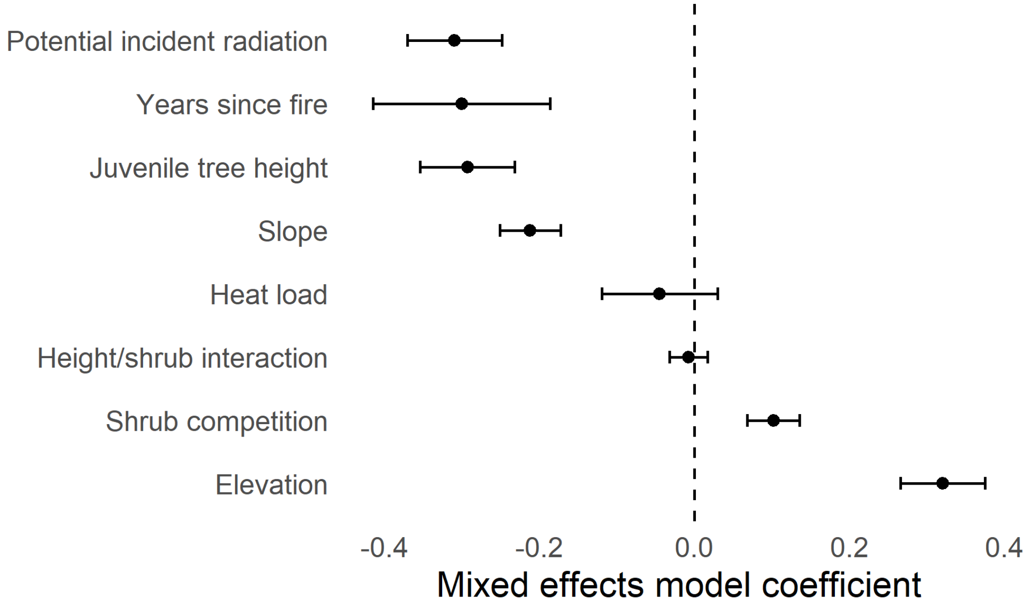


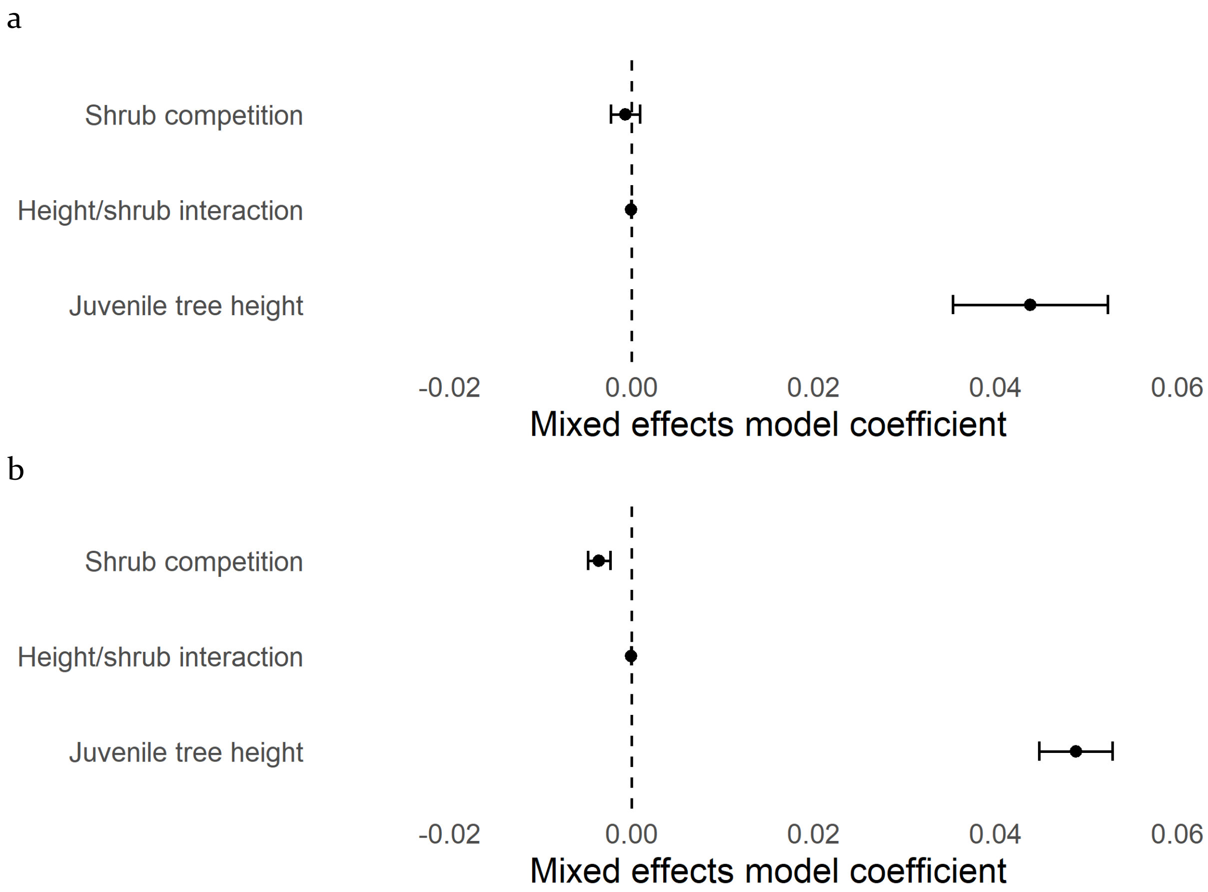
Figure S4. Mixed effects model coefficients from bootstrap sampling of white fir growth. Points represent means across 1,000 samples and error bars represent standard deviations. Numeric variables were normalized before model runs by subtracting the mean and dividing by the standard deviation to make coefficients comparable. For factor variables, treatment contrasts were used, in which the first factor level coefficient is set to 0 and all other levels' values are relative to the first level. Random effects are not included in this table.

Conifer diameter

Table S1. AICc results for model selection of conifer diameter

Species	Model	AICc	ΔAICc
White fir	Height * shrub competition	138.31	0
White fir	Height + shrub competition	140.07	1.76
White fir	Height	154.25	15.94
White fir	Shrub competition	326.3	187.99
Ponderosa pine	Height * shrub competition	164.35	0
Ponderosa pine	Height + shrub competition	167.93	3.58
Ponderosa pine	Height	199.55	35.2
Ponderosa pine	Shrub competition	344.66	180.31

Figure S5. Linear effects model coefficients from bootstrap sampling of diameter for a) white fir and b) ponderosa pine. Points represent means across 1,000 samples and error bars represent standard deviations. Numeric variables were normalized before model runs by subtracting the mean and dividing by the standard deviation to make coefficients comparable.



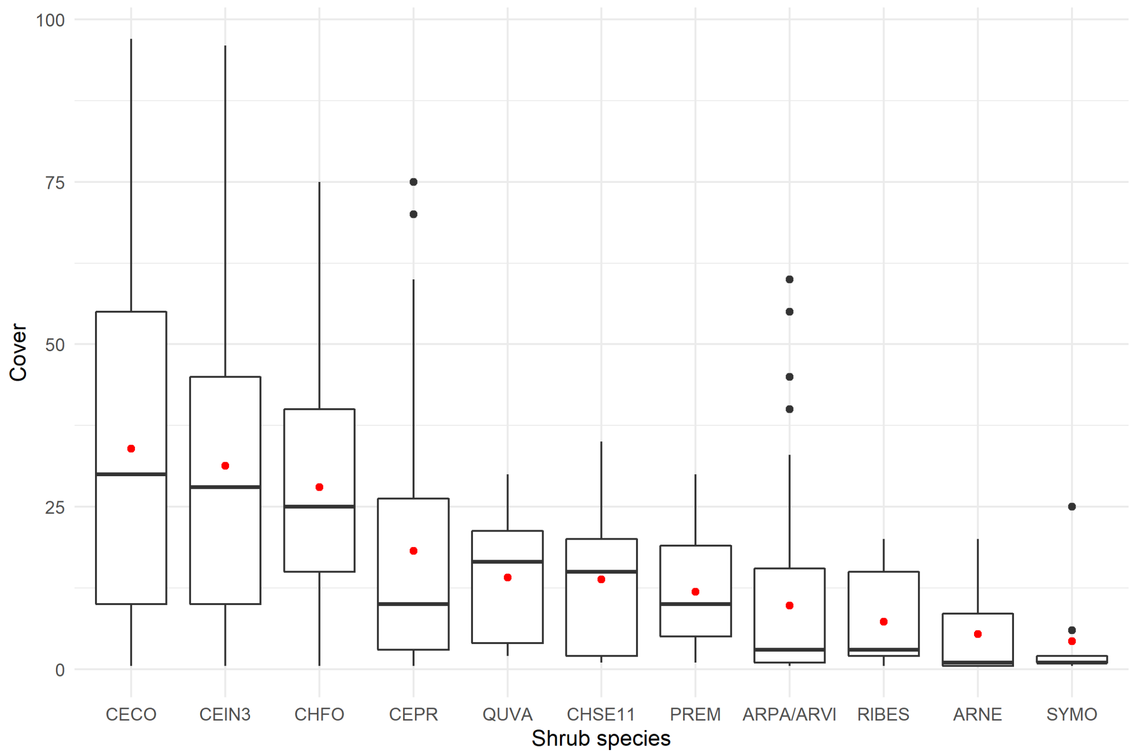


Figure S6. Shrub cover (%) results from Welch et al. 2016, filtered to areas measured 5-8 years following fire, severely burned areas, and those > 20 m from the nearest surviving adult tree. CEIN3 is deerbrush ceanothus and CECO is whitethorn ceanothus. Red dots show mean values. Based on these results, we initialized the deerbrush areas of the simulation model using cover from whitethorn samples.

C. Results

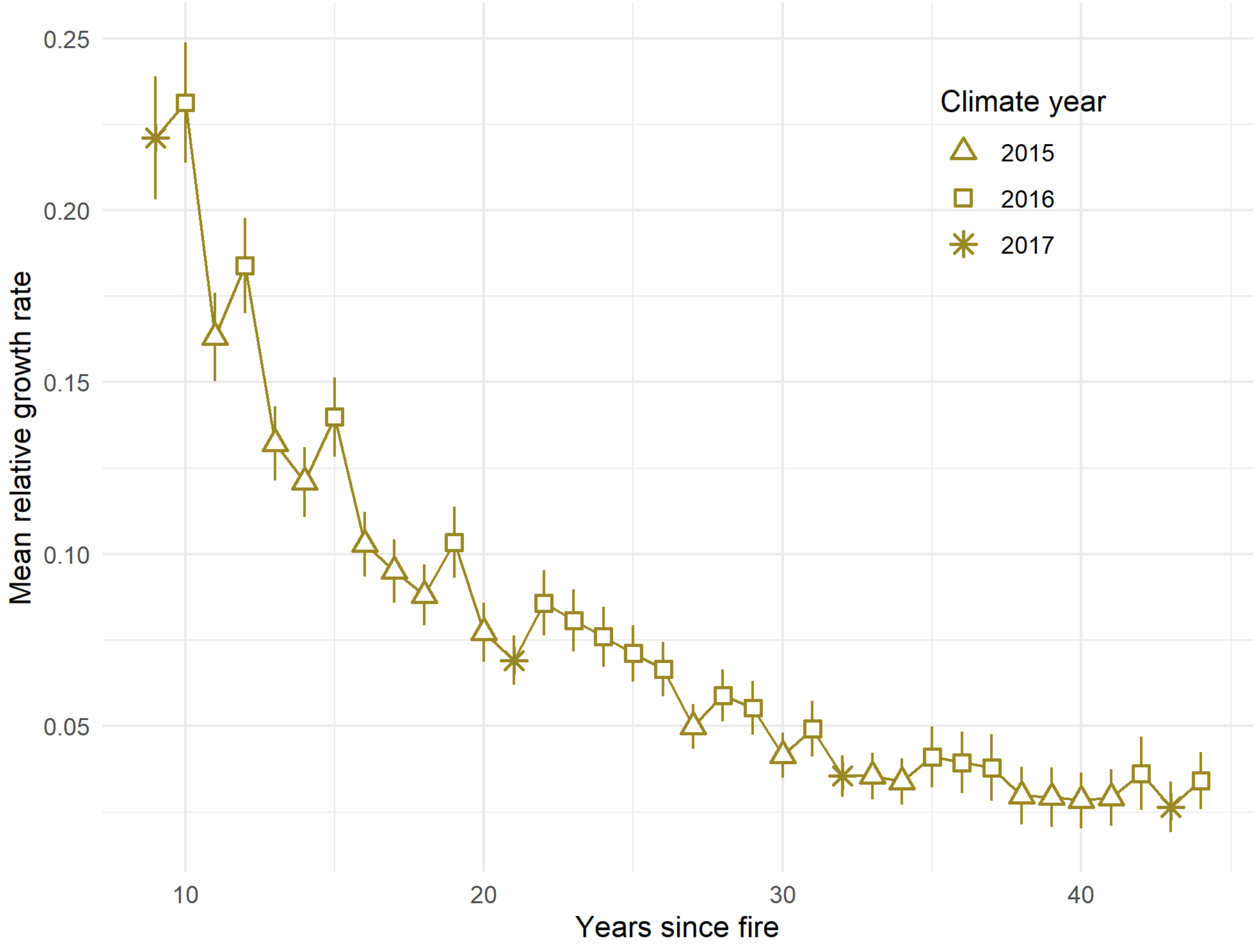


Figure S7. Ponderosa pine relative growth rate in relation to years since fire. Error bars represent the standard deviation of simulation means.