

FINAL REPORT

Predicting forest recovery following high-severity fire

JFSP PROJECT ID: 17-2-01-23

MAY 2020

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Key words

Disturbance, Patch dynamics, Succession, Interspecific competition, Fire regime, Chaparral, Shrubs

Acknowledgements

We thank Varvara Fedorova, Azalie Welsh, Diana Wahl, and Elliot Kuskulis for their intrepid assistance in the field. Brandon Collins and Daniel Foster provided input on data analysis and manuscript writing. Adrian Das provided input on the population-level mortality simulations. Charles Canham and Lora Murphy provided input on model development. We gratefully acknowledge funding from the Joint Fire Science Program for providing a GRIN award to C. L. Tubbesing, as well as the Garden Club of America and W.S. Rosencrans Fellowship. We also acknowledge financial support from the California Agricultural Research Station.

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 then developed a data-driven simulation model that we use to predict conifer emergence above the shrub canopy. 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. However, 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: $82\% \pm 6\%$ for pine and $83\% \pm 5\%$ for fir. These results show that, on net, 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.

Objectives

Our objective was to better understand long-term tree recovery in large high-severity fire patches.

Question 1: How do conifer seedling and sapling growth rates vary with shrub cover, shrub height, shrub species, shrub light attenuation, and conifer species?

Question 2: What demographic processes most strongly limit long-term conifer dominance in these fire footprints, and to which initial condition are outcomes most sensitive?

In addition, Our proposal aimed to produce the following information and products:

- 1) An improved understanding of shrub-seedling interactions in high-severity fire patches.
- 2) A Sierra Nevada version of the SORTIE forest growth simulation model that predicts long-term conifer recruitment using initial post-fire data.

Our study met our central objective, answered Question 1, and contributed to answering Question 2. No single study is likely to entirely answer Question 2, as fully evaluating all demographic processes related to post-fire recovery is beyond the scope of a single study. We produced the information and products we aimed to produce.

Background

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 species¹. 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 microclimate². If the recalcitrant layer affects tree species differently, it may ultimately determine the composition of the overstory canopy. The herb and shrub stratum can act as a sieve, selectively filtering out tree seeds and seedlings ill-adapted to establish, grow, and survive beneath it³. Shrub layers can offset the increased light availability created by canopy gaps, leading to low post-disturbance seedling survival⁴. Depending on the strength of the filter and how it differentially affects tree species, the understory may preclude, delay, or alter long-term forest succession¹.

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^{5,6}. In forests that historically experienced frequent, heterogenous fire, fire severity and homogeneity has increased⁷. Small patches of stand-replacing fire were characteristic of the historic fire regime⁸, but modern stand-replacing patch sizes often exceed the historical range of variability and are continuing to increase in size⁹⁻¹². 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 matrix¹³, shrubs generally occurred in the understory or in small canopy gaps¹⁴. Fire suppression has reduced small canopy gaps and increased large canopy openings^{9,15}, which native shrubs quickly revegetate, leading to the development of extensive patches of montane chaparral. These patches are likely to continue increasing and growing in size as changes in the fire regime are exacerbated by climate change^{16,17}.

In addition to maintaining small shrub patches, fires in frequent-fire forests prior to European settlement helped maintain tree species diversity¹⁸. 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 flora¹⁹. Niche differentiation varied according to species' differences in shade tolerance, drought resistance, and fire sensitivity²⁰ (Figure 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 demand²¹⁻²³, along with its thick bark and high crown base, which improve survival in low- and moderate-severity fires²⁴. On the other hand, regeneration of shade-tolerant tree species, predominately Sierra white fir (*Abies lowiana* Gord. & Glend.), prevails in unburned patches²⁵.

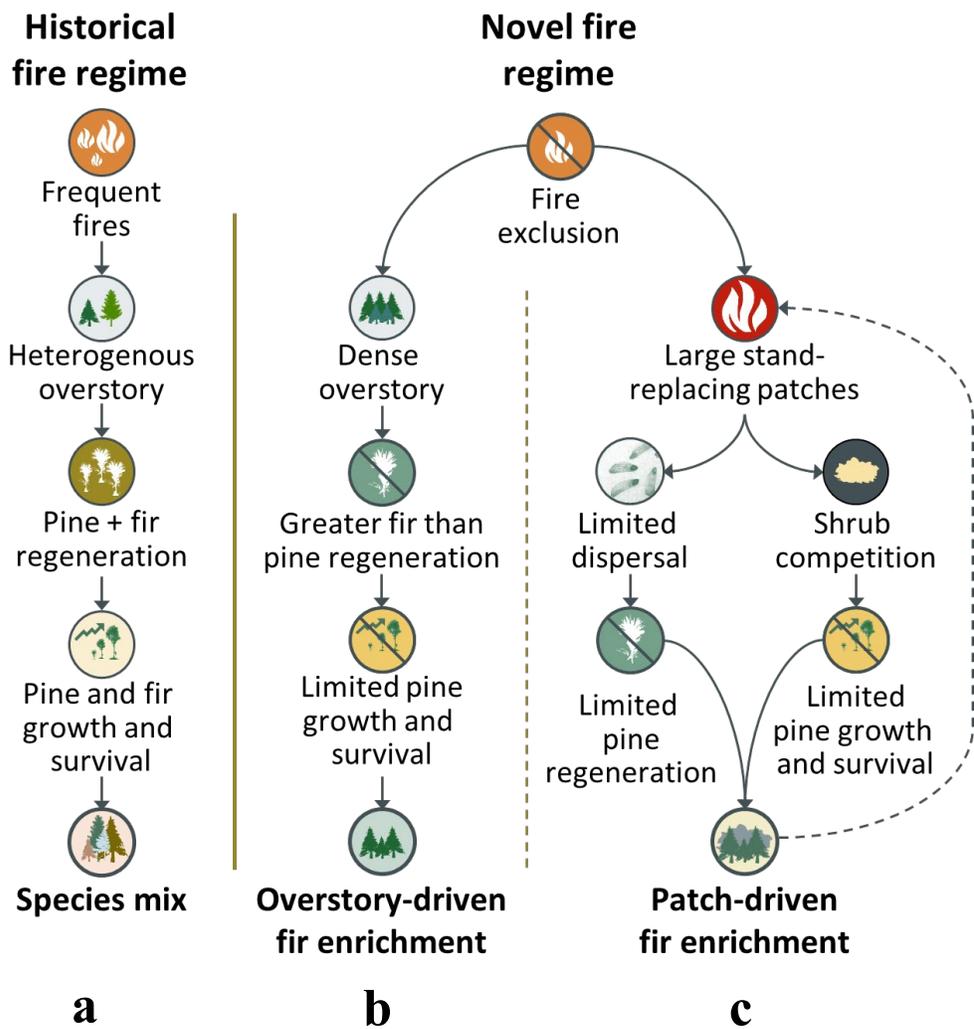


Figure 1. Conceptual diagram of the effects of the shifting fire regime on species composition in mixed-conifer forests of the Sierra Nevada. The present study examines the right-most downward pathway, namely the potential for shrub competition following stand-replacing fire to favor understory-tolerant firs over understory-intolerant pines. The dashed arrow pointing from patch-driven fire 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.

Under today's disturbance regime, defined by less frequent fire but larger stand-replacing patches⁹, 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^{26,27}) (Figure 1b), but increasingly prevalent stand-replacing fire may also promote fir dominance (Figure 1c).

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^{28,29}. In severely burned patches, fir recruits at higher

densities than pine^{25,30-33} even though pines are well-adapted to germinate and quickly grow in post-fire abiotic conditions, including mineral soil, high light availability, and high evaporative demand²¹⁻²³. Several factors may contribute to post-fire fir enrichment, including pre-fire species composition, dispersal limitation^{34,35}, and shrub effects^{30,36}. 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 state³⁷.

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^{29,31}. 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^{29,31,34,37,38}. 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 expansion³⁹. 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 seedlings⁴², site preparation, and monospecific stands, often of pine⁴⁰. In order to understand succession in unmanaged wildfire footprints, study 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^{29,31,34,37,38}. We examined whether the shrub filter at this stage precludes, delays, or alters long-term forest succession. Research on post-wildfire recruitment patterns has supported competing explanations of the underlying processes driving species composition and the role of shrubs^{31,43,44}. Some studies indicate that montane chaparral inhibits conifer survival via moisture competition rather than shading^{40,45-48}, a process that may favor more drought-resistant species like pines over firs⁴⁹. Other studies suggest that shrubs may facilitate seedling survival by moderating harsh microclimates, particularly when seedlings are young^{43,50}.

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 regime⁹. 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.

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 relationships⁵¹⁻⁵³. 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 dynamics⁵¹. 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 “shrubs neighborhood species coefficient.” The first and third of these shrub dimensions were derived from our field data. 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.

In this report, we a) introduce a conceptual framework for understanding how fire enrichment can result from multiple aspects of the modern fire regime in Sierra Nevada mixed-conifer forests (Figure 1), and b) to quantify the effect of shrub competition on relative growth and mortality of dominant conifer species in stand-replacing fire patches, and c) use data-driven simulation modeling to evaluate conifer growth and survival in shrub-dominated high-severity fire patches during the period between establishment and emergence above the shrub canopy. We used our demographic data and model results to assess the evidence for the “patch-driven” pathway outlined in our conceptual model (Figure 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.

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 Nevada³⁸, 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 (Table 1). At the time of first field measurements (2016) the fires ranged in age from 8 to 35 years.

Table 1. Fires sampled

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

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 (Figure 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 study⁵⁴. 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.

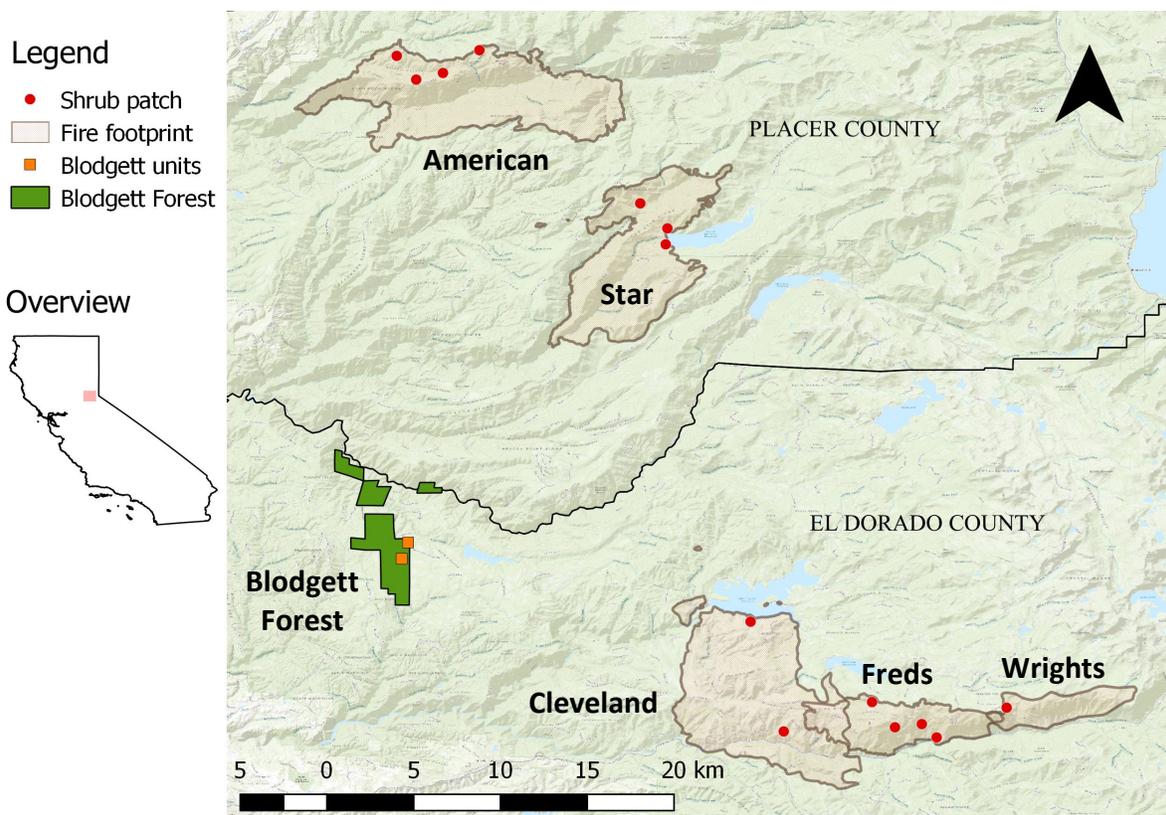


Figure 2. Study area in the northern Sierra Nevada. The overview map shows study area location within California, USA. Wildfire footprint data was gathered at shrub patches (red), while mortality data was gathered at Blodgett units (orange) within Blodgett Forest Research Station (green). Wildfire footprints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

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^{21,55}. 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 $<33^\circ$ 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 mortality⁵⁶ 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 Columbia⁵⁸. 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 m² 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.

Statistical Analysis

Part 1: Juvenile conifer growth and mortality in relation to shrubs

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

$$\text{Relative growth rate} = \frac{\text{height}_{\text{time2}} - \text{height}_{\text{time1}}}{\text{height}_{\text{time1}}} \quad (1)$$

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 m² in ArcMap 10.6.1. The remainder of analyses were performed using R 3.6.1⁶⁰. We then calculated heat load and potential direct incident radiation using slope, folded aspect, and latitude⁶¹. 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^{62,63}. 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 depth⁴⁸. 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 2. Initial height and diameter of the focal tree were included to account for size-related differences in biomass allocation in plants of the same species⁶⁴.

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”⁶⁵. 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” package⁶⁶. We evaluated model fit using conditional R² (R_c²) and marginal R² (R_m²) using the “MuMIn” package. While R_c² represents the proportion of variation explained by both fixed and random effects, R_m² represents the variation explained by the fixed effects alone⁶⁷. 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_m², effect sizes, and Akaike

Information Criterion corrected for small sample sizes (AICc) with and without the interaction.

Table 2. 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

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^{58,68}.

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. 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.

Part 2: Forest recovery simulation modeling

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-ND⁵². 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 above and 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.

As described above, we used field data 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 simulation modeling, 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 results 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 3). 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 managers²⁹ and because they were prevalent in our data, allowing for robust analyses. All analyses and model development were performed in R 3.6.2⁶⁰.

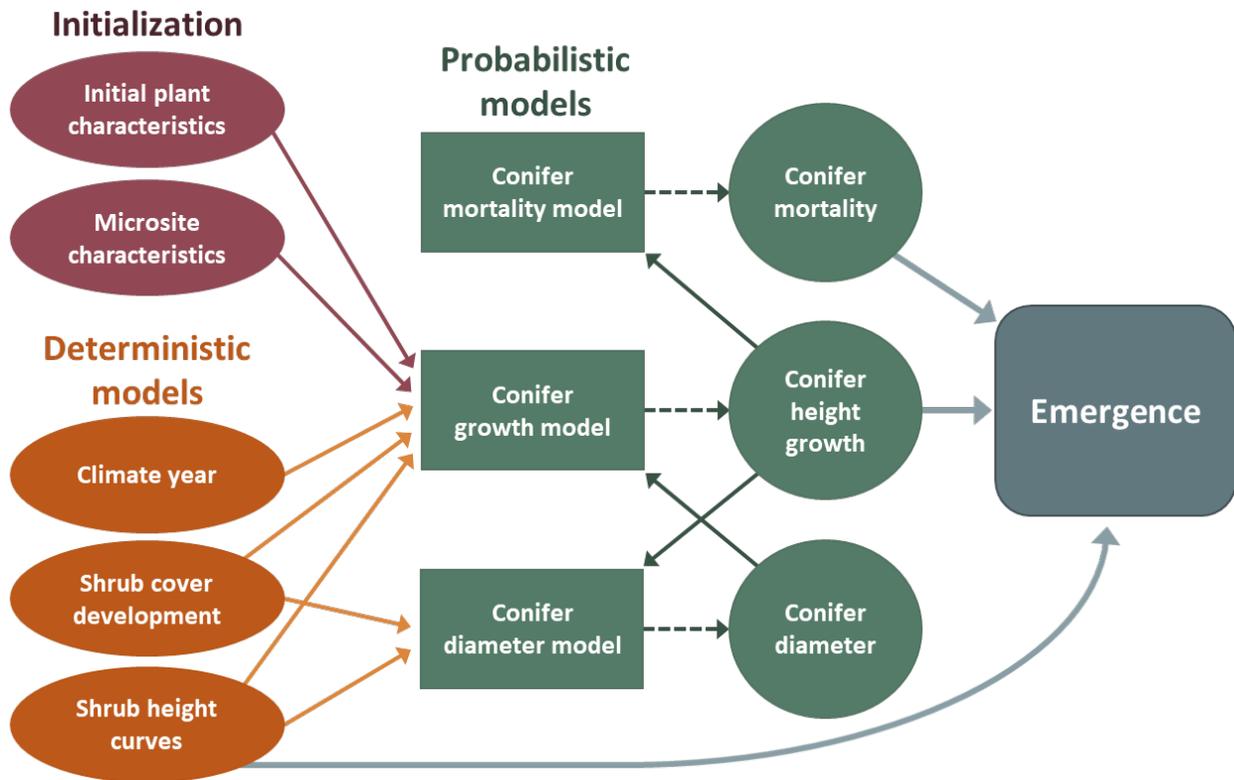


Figure 3. Diagram illustrating the data-driven simulation modeling framework. Ovals represent deterministic model parameterization, including initialization by bootstrap sampling of field data, climate year based on the historical record, and shrub height and growth curves fit to regional field survey 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).

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 our field data with data from 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 described above.

To develop shrub height growth curves over time, we separately analyzed plots dominated by each of the four common shrub species separately 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 this study because the shrub cover measurement methods varied between 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 the analysis in Part 1, which used linear mixed effects models with model selection based on random forests. However, 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. Including 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 and small effects on AIC_c: including the interaction increases AIC_c by 1.85 for white fir and reduces AIC_c by 3.8 for ponderosa pine. For model development, 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 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 etiolation⁷⁰. We used linear regression models of juvenile conifer diameter in relation to tree height and our index of shrub competition ($\sqrt{\text{shrubs height} * \text{shrubs cover}}$) for the year 2017. We used Akaike Information Criterion model selection corrected for small sample sizes (AIC_c) 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. As with conifer vertical growth models, we used bootstrapping with 1,000 resamples to evaluate uncertainty in model fits.

Conifer mortality. Our methods for predicting conifer mortality probability are detailed in Methods Part 1 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 precipitation⁷¹. 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 surveys²⁹, limiting survey data to plots measured 5-8 years following fire and that met 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. However, the regional field survey data included areas with dominant deerbrush ceanothus, but 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. 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 GLM 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 :

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

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 (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 for each of 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. 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

Part 1: Juvenile conifer growth and mortality in relation to shrubs

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 3. The interaction between tree height and shrub competition was not included for either species. 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. Increasing shrub competition was associated strongly with decreased pine growth (Table 3, Figure 4). For white fir, tree height, slope, and elevation had the strongest effects on juvenile growth while shrub competition had a weak positive effect (Table 3, Figure 4). 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 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 1). Juvenile pine relative growth rate was lowest near *N. densiflorus* and highest near the two *Ceanothus* species, *C. cordulatus* and *C. integerrimus* (Figure 5).

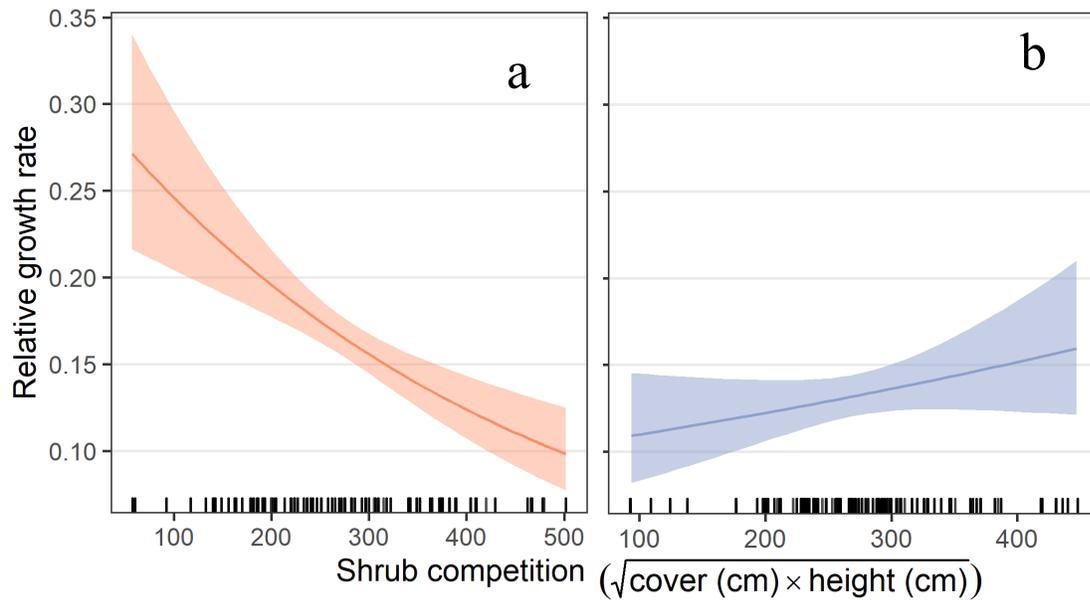


Figure 4. Predicted juvenile relative growth in relation to shrub environment for a) ponderosa pine, and b) white fir. Predicted relative growth estimates are generated across mean values of other continuous predictors and weighted averages of categorical predictors (Fox and Weisberg 2018). Shaded areas represent 95% pointwise confidence envelopes.

Table 3. 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	<i>P</i> -value
Ponderosa pine	Juvenile conifer height		(-)	-0.41	< 0.0001
	Years since fire		(-)	-0.34	< 0.0001
	Shrub competition, $\sqrt{\text{cover (cm)} * \text{height (cm)}}$		(-)	-0.23	< 0.0001
	Year of growth	2015	0	0	
		2016	(+)	0.19	< 0.0001
		2017	(-)	-0.13	
	Juvenile conifer basal diameter		(+)	0.30	0.0007
	Heat load		(-)	-0.11	0.089
	Dominant shrub species 0-3 m	<i>Arctostaphylos spp.</i>	0	0	
		<i>Ceanothus cordulatus</i>	(+)	0.16	
<i>Ceanothus integerrimus</i>		(+)	0.26	0.205	
<i>Chamaebatia foliolosa</i>		(+)	0.07		
<i>Notholithocarpus densiflorus</i>		(-)	-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 $\sqrt{\text{cover (cm)} * \text{height (cm)}}$		(+)	0.08	0.146
	Heat load		(-)	-0.005	0.964

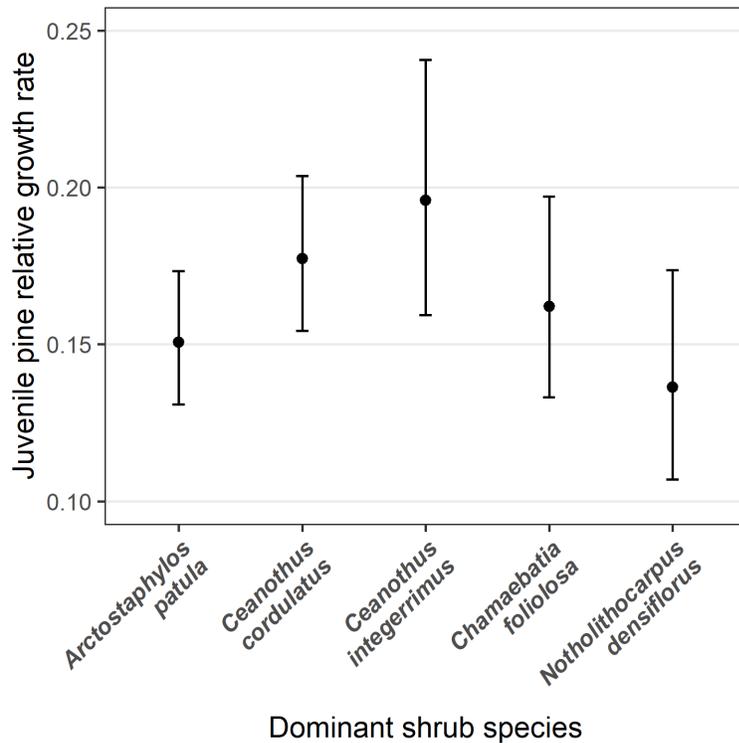


Figure 5. Relative ponderosa pine growth rate in relation to dominant shrub species within 3 m. Estimates are generated across mean values of other continuous predictors and weighted averages of categorical predictors (Fox and Weisberg 2018). Error bars represent 95% confidence intervals.

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 m² 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; Fig. A4). 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%.

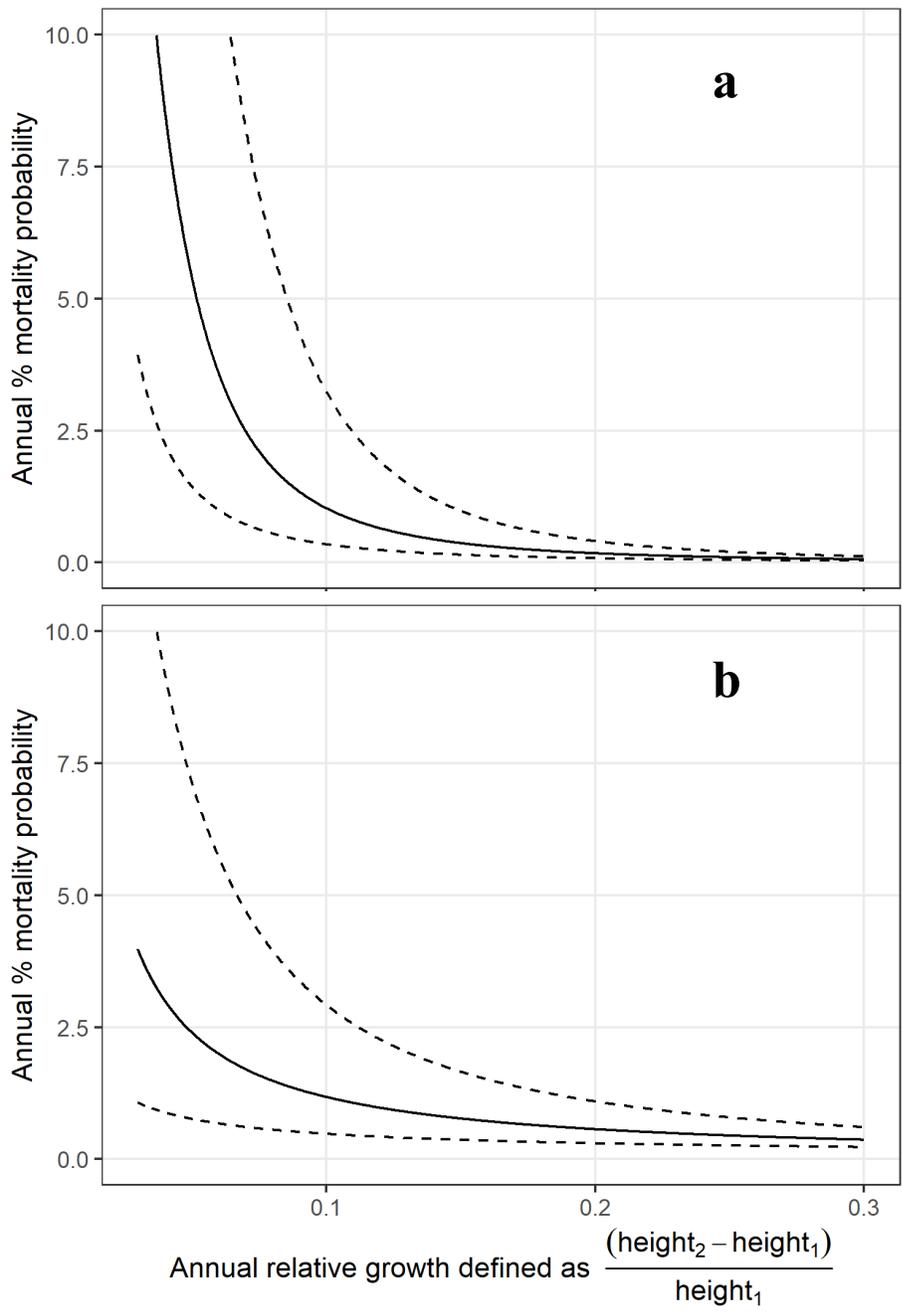


Figure 6. Simulation results showing probability of mortality in relation to relative growth rate for a) ponderosa pine and b) white fir. Dotted lines represent 95% confidence intervals.

Part 2: Forest recovery simulation modeling

Shrub development over time

For all four shrub species, height increased after fire before leveling off and beginning to decrease within 10-25 years after fire (Figure 7). 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 (Figure 8).

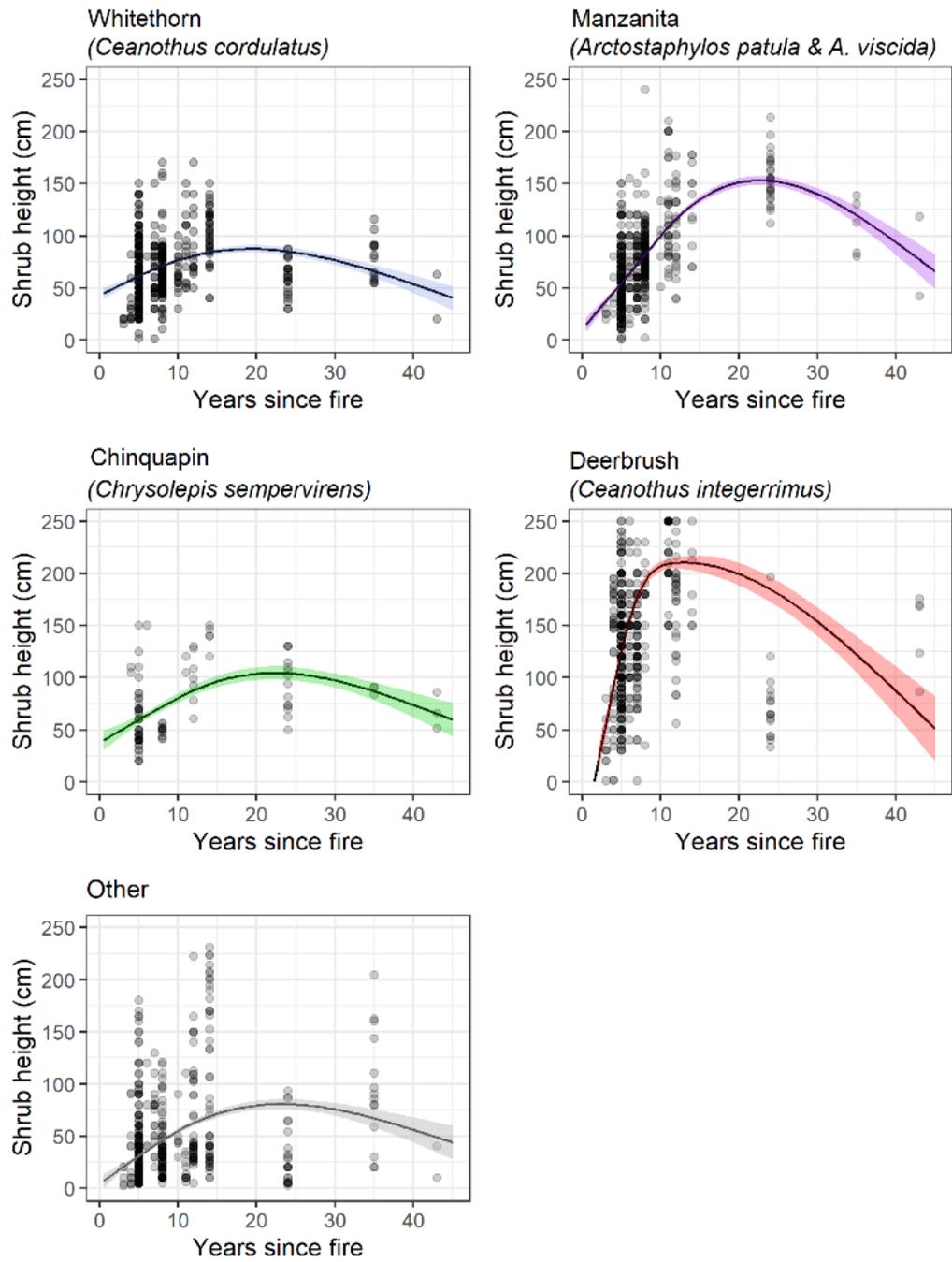


Figure 7. Shrub height GAMs. Shaded areas show standard error estimates.

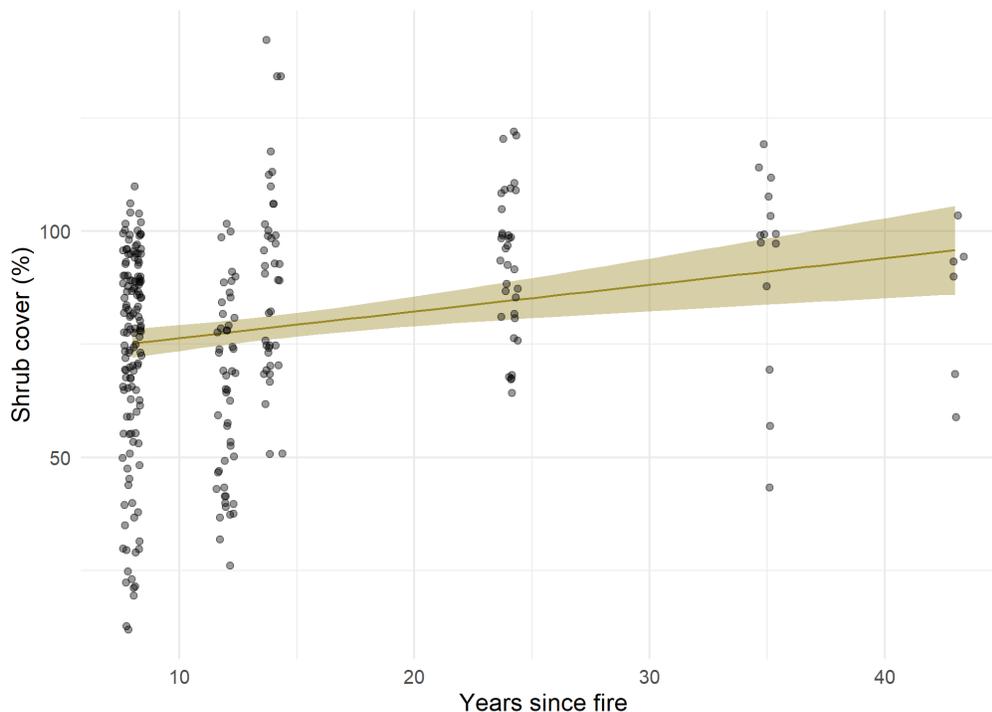


Figure 8. Shrub cover over time. The tan line shows the effect of time fire on shrub cover according to the linear model that was used in simulations. Shaded areas represent 95% confidence intervals. Points represent observations, jittered to improve visibility.

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 9). Pine required an average of 18 years to reach 50% emergence (Q50), while Q50 for fir was 21 years (116% greater; Table 4). Both species showed decreasing relative growth rates over time, with variation by climate year for ponderosa pine. Ending proportions of pine and fir emergence were similar ($82 \pm 6\%$ and $83 \pm 5\%$, respectively; Table 4). In other words, since simulations ended only after all trees had either emerged or died, $18\% \pm 6\%$ of pines died and $17\% \pm 5\%$ 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.

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/m² for fir, 0.07 ± 0.005 tree/m² for pine; Figure 9b). The difference between proportional results and density results is due to higher initial densities of fir than pine.

Table 4. 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 \pm 2	21 \pm 1
Total emergence (%)	82 \pm 6	83 \pm 5
Simulation duration (years)	37.1 \pm 2.8	35 \pm 3.2

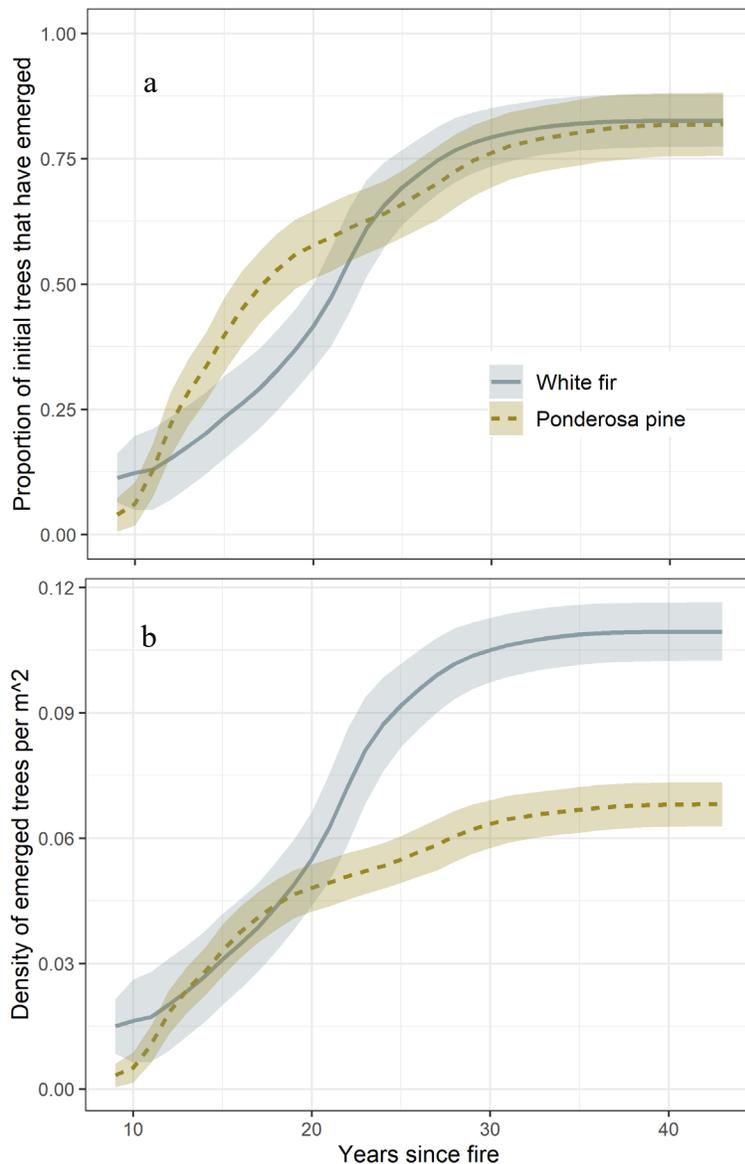


Figure 9. Base model predictions of juvenile ponderosa pine and white fir emergence above the shrub canopy over time, shown as a) proportion of initial juvenile trees that emerged above the shrub canopy, and b) density of trees that emerge above the shrub canopy. Shading shows time ± 1 standard deviation.

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 10). Ponderosa pine's advantage over white fir was evident final emergence in the whitethorn and deerbrush models but in the manzanita model final emergence of pine was nearly equal that of 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 10). With the exception of pine under whitethorn, which emerged quickly, simulation duration was similar across species combinations.

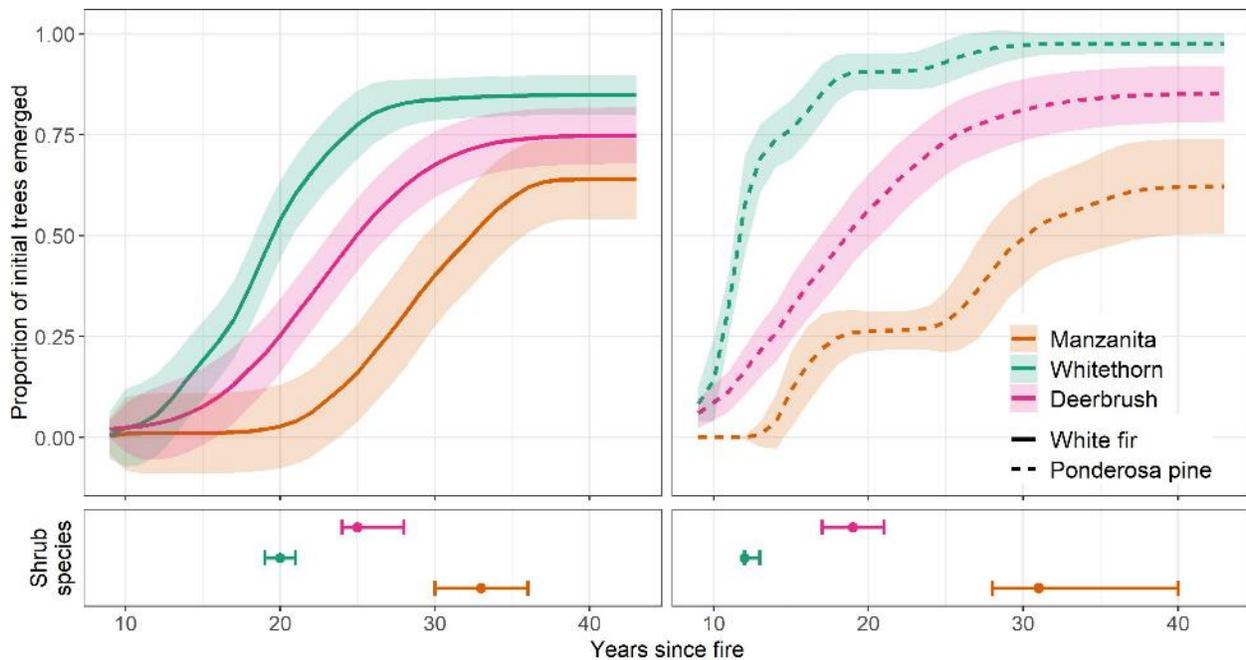


Figure 10. Conifer emergence above the shrub canopy for single-shrub species models, shown as the proportion of initial juvenile trees that emerge over time ± 1 standard deviation for (a) white fir and (b) ponderosa pine. Points and error bars show the number of years required for 50% of initial trees to emerge, termed Q50.

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. 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. 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. Adjusting only the shrub competition coefficients resulted in more similar patterns across shrub species.

Discussion

We explored the idea that fir enrichment may occur under both of the two primary modes of the contemporary disturbance regime (Figure 1), which has shifted to feature far fewer but more severe fire events^{10,72,73}. In areas with fire deficits, fir gains a relative advantage over pine due to its shade tolerance (“overstory-driven fir enrichment;” Figure 1), while in areas with large stand-replacing fire patches, fir enrichment may result from both dispersal limitation and, potentially, shrub competition, (“patch-driven fir enrichment;” Figure 1c). Previous research has documented overstory-driven fir enrichment and the effect that seed dispersal can have on patch-driven fir enrichment^{29,34,74}. Our research explored a second potential mechanism of patch-driven fir enrichment: shrub competition.

Our field results showed that shrub competition affected pine growth and survival more strongly than that of fir. However, our modeling results 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 (Figure 4), 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. 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 10b).

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 10). 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 (Figure 9). 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. 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 9b).

Shrub neighborhood effects depend 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^{41,48}. While warm and dry conditions can

increase regeneration failure in some areas of California, the Rocky Mountains, and the American Southwest^{38,75,76}, 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 species⁷⁷, 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.

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, shrub height and cover development were also critical. Shrub growth trajectory sensitivity tests showed that manzanita had the strongest growth trajectory effect. Though deerbrush reached greater maximum heights than manzanita (Figure 7), 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.

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 11).

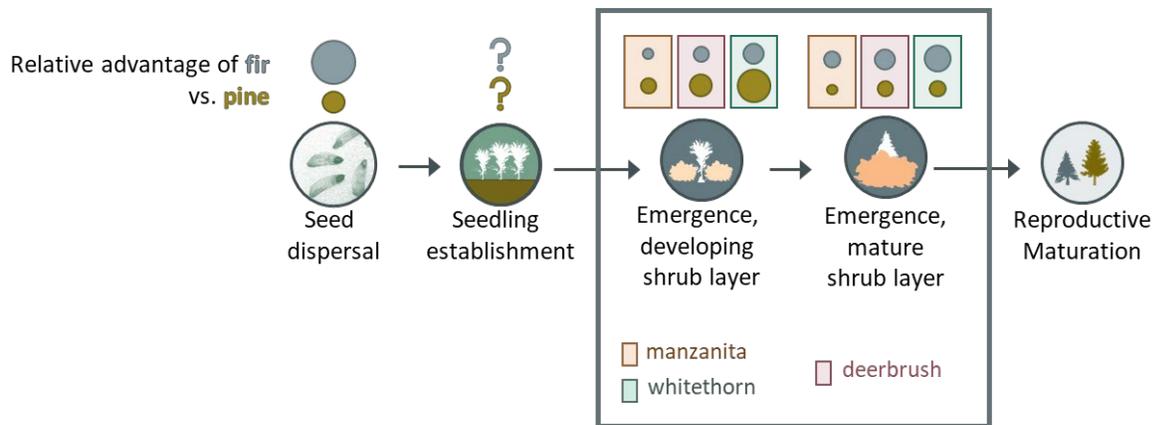


Figure 11. Conceptual diagram illustrating the relative advantage of ponderosa pine (brown) versus white fir (blue-grey) at stages throughout post-fire forest development. The size of each circle represents the approximate relative effect of each process on that species. The large box delineates patterns 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.

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^{36,49,74}. 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 9). This timing corresponded with peak shrub height, which occurred between 10 and 25 years, depending on species (Figure 7). 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 10), which had the lowest heights among the three shrub species of interest (Figure 7). 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 (Figure 5). 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 height⁷⁸. The lack of shrub species effect for white fir was consistent with other studies⁷⁹.

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 deerbrush⁸⁰. These allometric differences match the pattern we found in shrub neighborhood species coefficients. However, the results of previous shrub allometry studies are difficult to compare to our findings because they analyze shrubs as individuals⁸⁰⁻⁸², 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 biomass⁸². 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 trees³⁹. However, very little overstory shading was observed in our study sites. Shrub declines may also be related to age-related stand decline or senescence⁸³. Since most data on shrub height after 15 years comes from only a few fire footprints, more research on shrub recovery trajectories will be an important step towards 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 species³⁸. 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 8 years post-fire, when the simulation began. Given previous findings of higher post-fire fir than pine recruitment^{25,30-32}, fir enrichment is likely driven by a different stage of post-fire succession. 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 found no significant differences in shrub effects between ponderosa pine and white fir⁸⁴. Future detailed measurement of seedling establishment in the early years after fire would help identify whether establishment alters long-term conifer species composition.

Conclusions, Implications for Management/Policy, and Future Research

We combined our own field results with other data sources to develop 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 9b). 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 pines³⁵. 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.

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Appendix A: Contact Information for Key Project Personnel

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Appendix B: List of Completed/Planned Scientific/Technical Publications/Science Delivery Products

Doctoral Dissertation Chapters, Carmen Tubbesing:

- “Rethinking fire-adapted species in an altered fire regime”
- “Forest succession in an altered fire regime: the role of shrub neighborhood dynamics”

Published peer-reviewed manuscript addressing Question 1:

- Tubbesing, C. L., R. A. York, S. L. Stephens, and J. J. Battles. 2020. Rethinking fire-adapted species in an altered fire regime. *Ecosphere* 11:e03091. (open access journal)

Completed manuscript addressing Question 2 for submission to peer-reviewed journal:

- Tubbesing, C. L., Derek J. Young, R. A. York, S. L. Stephens, and J. J. Battles. 2020. Forest succession in an altered fire regime: the role of shrub neighborhood dynamics. Target journal: *Ecosystems*

Presentation:

- Tubbesing, C.L., R.A. York, S.L. Stephens, J.J. Battles. 18th International Fire Ecology and Management Congress, Oral Presentation. “Rethinking fire-adapted species in an altered fire regime,” 2019, Tucson, AZ.

Poster presentation:

- Tubbesing, C. L., R. A. York, S. L. Stephens, J. J. Battles. 17th International Fire Ecology and Management Congress, Poster Presentation. “Shrubs vs. conifer seedlings: the battle for post-fire recovery in the Sierra Nevada,” 2017, Orlando, FL.

Appendix C: Metadata

Data and metadata will be made publicly available at the Forest Service Research Data Archive (www.fs.usda.gov/rds/archive) following publication of the manuscript detailing model results.