

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 yr 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 (0.1–1.1%, 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.

Key words: disturbance; fire regime; interspecific competition; patch dynamics; succession.

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INTRODUCTION

Fire regimes across the western United States 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 (1) 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 (Fig. 1), and (2) 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, Collins and Roller 2013, Crotteau et al. 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

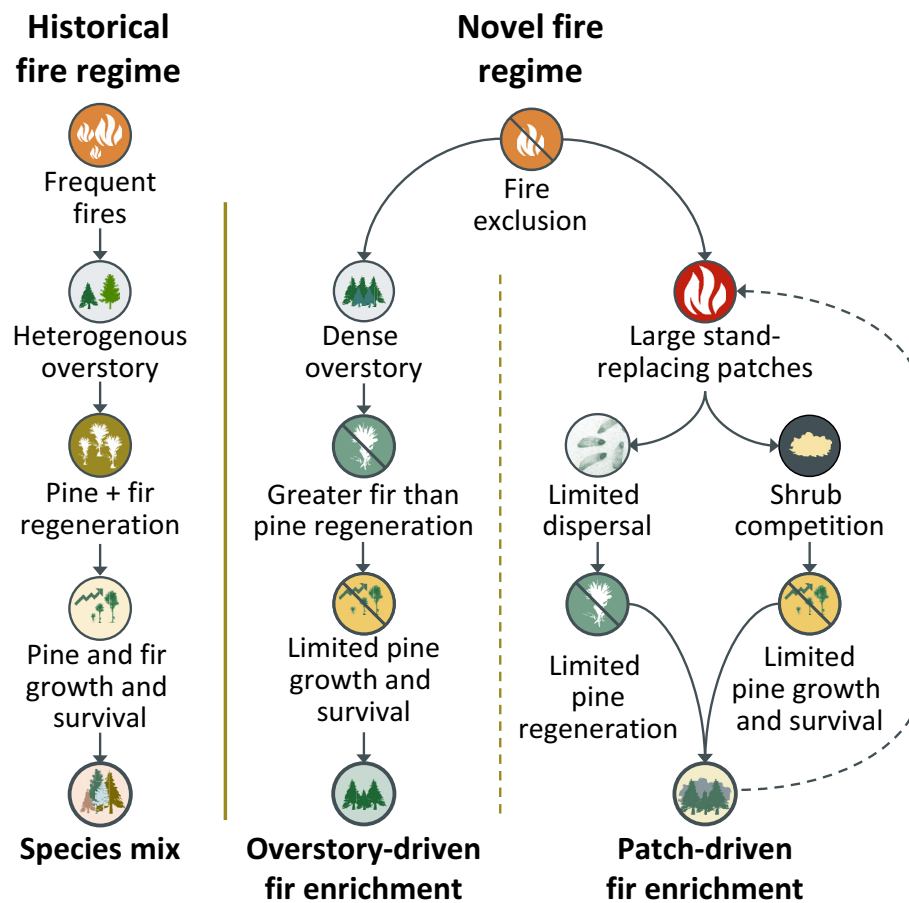


Fig. 1. Conceptual diagram of the effects of the shifting fire regime on species composition in mixed-conifer forests of the Sierra Nevada. The present study examines the right-most downward pathway, namely the potential for shrub competition following stand-replacing fire to favor understory-tolerant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

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 (Niemets and Vallades 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; >400 ha in size; 5–50 yr 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 yr.

Within the five fire footprints, we located shrub patches using Google satellite imagery. We visited all accessible shrub-dominated patches that were >1 ha in size, approximated using Google satellite imagery analyzed in QGIS 2.18.13 (Open Source Geospatial Foundation, Beaverton, Oregon, USA). 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 1.5–1116 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°520' N; 120°400' W). 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

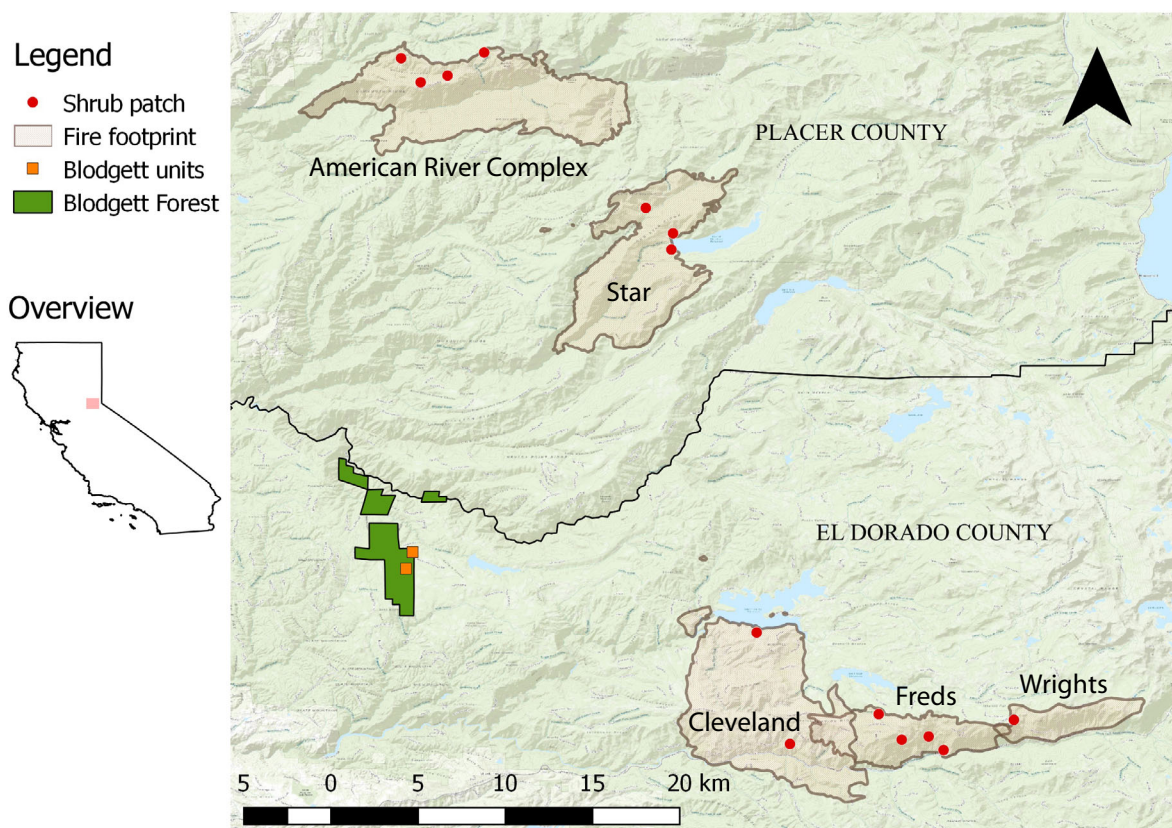


Fig. 2. Study area in the northern Sierra Nevada. The overview map shows study area location within California, USA. Wildfire footprint data were gathered at shrub patches (red), while mortality data were gathered at Blodgett units (orange) within Blodgett Forest Research Station (green). Wildfire footprints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

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-yr) 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 >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 Class 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 20 × 30 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:

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

Because we measured the distance between bud scars for the past three growing seasons for each tree, Eq. 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 (Esri, Redlands, California, USA). 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 (B. Wilson, *personal communication*).

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 (AIC_c) 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

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

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 Eq. 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 1000 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 to 213 cm (mean 85 cm), and cover ranged from 3% to 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 m² of sampled area. Across those plots, we found 1103 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.

Table 2. Mixed-effects model results.

Variable	Direction	Coefficient	P
Ponderosa pine			
Juvenile conifer height	–	–0.41	<0.0001
Years since fire	–	–0.34	<0.0001
Shrub competition†	–	–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			
<i>Arctostaphylos</i> spp.	0	0	0.205
<i>Ceanothus cordulatus</i>	+	0.16	
<i>Ceanothus integerrimus</i>	+	0.26	
<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†	+	0.08	0.146
Heat load	–	–0.005	0.964

Notes: 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.

† $\sqrt{\text{cover (cm)} \times \text{height (cm)}}$.

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 importance 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

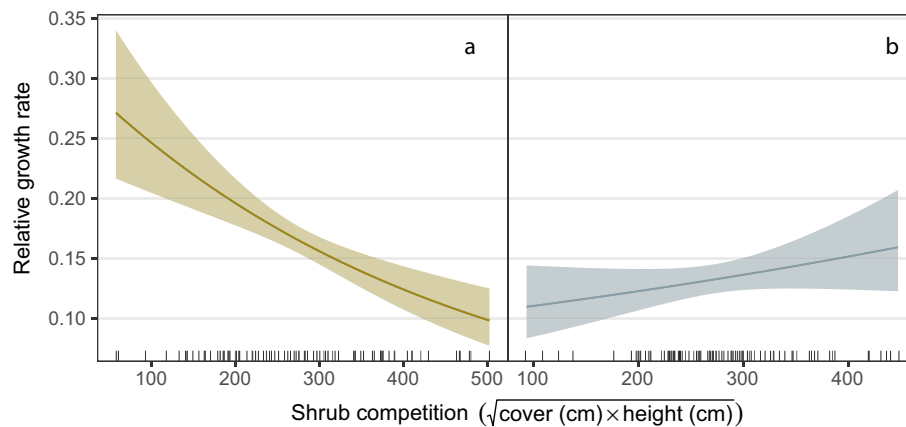


Fig. 3. Predicted juvenile relative growth in relation to shrub environment for (a) ponderosa pine and (b) white fir. Predicted relative growth estimates are generated across mean values of other continuous predictors and weighted averages of categorical predictors (Fox and Weisberg 2018). Shaded areas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

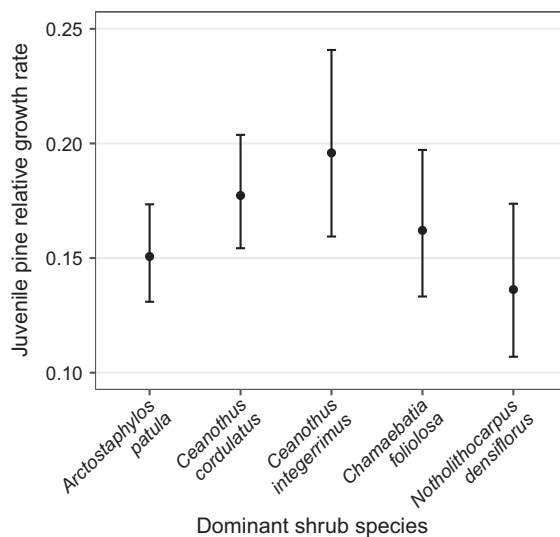


Fig. 4. Relative ponderosa pine growth rate in relation to dominant shrub species within 3 m. Estimates are generated across mean values of other continuous predictors and weighted averages of categorical predictors (Fox and Weisberg 2018). Error bars represent 95% confidence intervals.

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).

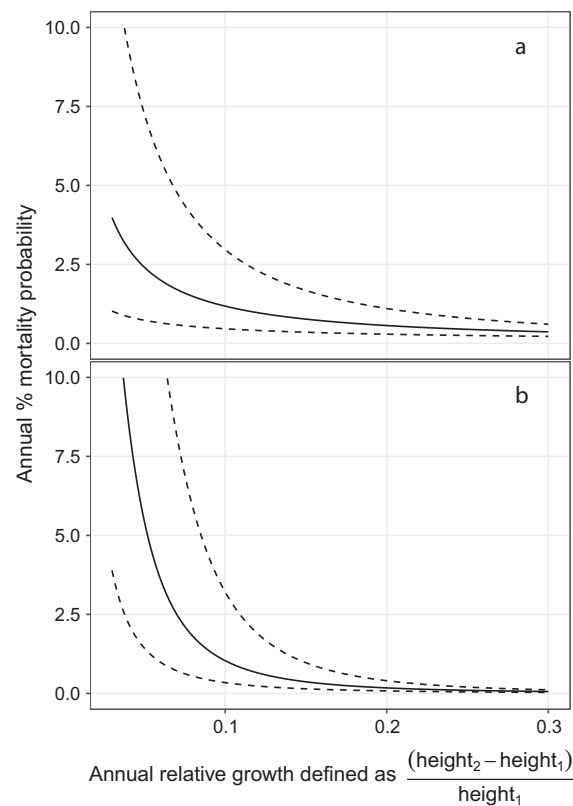


Fig. 5. Simulation results showing probability of mortality in relation to relative growth rate for (a) ponderosa pine and (b) white fir. Dotted lines represent 95% confidence intervals.

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. integriramus* 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 *Arc-tostaphylos* 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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