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Impacts of Changing Fire Regimes on Tree Regeneration and Diversity in California Forests

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Impacts of Changing Fire Regimes on Tree Regeneration and Diversity in California Forests

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Abstract

The historical patterns of fire type, size, severity, and seasonality that have long characterized western North American forests are rapidly changing. Factors that limited fire in the past have been altered by climate change and fire suppression across many forest types. In subalpine forests where high snowpack and cool summers generally resulted in infrequent fire, warmer, drier, and longer summers are giving rise to more burning. In mixed-conifer forests where frequent fire under indigenous burning practices reduced fuel loads and limited the severity of fire, a century of fire exclusion has resulted in denser forests and extremely high fuel accumulations. In this dissertation, I focus on the influence of changing fire regimes on understory biodiversity and tree regeneration in two distinct forest types. First, I consider the influence of fire in historically infrequent-fire subalpine forests, and second, the influence of fire suppression in historically frequent-fire mixed-conifer forests.

In Chapter 1, I used an extensive subalpine forest plot network stratified across natural gradients of productivity and fire severity to investigate how the impacts of fire severity changed due to underlying forest productivity. Specifically, I sought to determine whether severe fire had a more positive effect on understory diversity in higher productivity forest where disturbance might result in greater release from competition for colonizer-type species. I found that plant species richness increased with increasing fire severity in subalpine forest and that indeed this relationship was stronger in higher productivity plots. Providing evidence for release from competition, the positive interaction between fire severity and productivity was driven by far-dispersing species, whose occurrence probability increased more than that of their near-dispersing counterparts in high productivity forest that burned at high severity.

In Chapter 2, I used tree regeneration data from the same plot network to test theoretical predictions that disturbance would facilitate species range shifts into newly climatically available upslope habitat. While predicted habitat suitability increased for the two lower elevation tree species found at subalpine study sites (red fir [*Abies magnifica*], and Jeffrey pine [*Pinus jeffreyi*]), response to disturbance still depended on species traits. I found that disturbance reduced the probability of shade-tolerant red fir regeneration in subalpine forest, while it increased the probability of shade-intolerant Jeffrey pine. These results suggest that the impact of wildfire disturbance on species range shifts may depend on whether the postfire landscape aligns with a species' regeneration niche.

In Chapter 3, I studied the timing and drivers of understory change that has led to contemporary reductions in pine (*Pinus spp.*) in mixed-conifer forest overstories. I leveraged an historical tree regeneration experiment consisting of four large forestry plots that were mapped and logged in the early 1900's and resampled in 2016. I found that the increased light availability from post-logging gaps was insufficient to promote post-logging pine regeneration and increase pine in the contemporary overstory. While the relative percentage of pine regeneration stayed low over time (9-6%), that of incense-cedar (*Calocedrus decurrens*) doubled (26-51%). Such changes in understory composition occurred despite lower relative basal area of incense-cedar in plot overstories at every time period. This persistent mismatch between overstory and understory indicates that the historical frequent-fire regime likely played an important role in advantaging pines at early demographic stages by differentially killing small cedars and firs. My results also serve to highlight that light alone is not sufficient to maintain co-dominance of pine in mixed-

conifer forests in the west, and management efforts should strive to emulate multiple ecosystem conditions associated with the historical fire regime.

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Chapter 1

Productivity modifies the effects of fire severity on understory diversity

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Abstract

High severity fire may promote or reduce plant understory diversity in forests. However, few empirical studies test long-standing theoretical predictions that productivity may help to explain observed variation in post-fire plant diversity. Support for the influence of productivity on disturbance-diversity relationships is found predominantly in experimental grasslands, while tests over large areas with natural disturbance and productivity gradients are few and have yielded inconsistent results. Here, we measured the response of post-fire understory plant diversity to natural gradients of fire severity and productivity in a large-scale observational study in California's subalpine forests. We found that plant species richness increased with increasing fire severity and that this trend was stronger at high productivity. We used plant traits to investigate whether release from competition might contribute to increasing diversity and found that short-lived and far-dispersing species benefited more from high severity fire than their long-lived and near-dispersing counterparts. For far-dispersing species only, the benefit from high severity fire was stronger in high productivity plots where unburned species richness was lowest. Our results support theoretical connections between fire severity, productivity and plant communities that are key to predicting the consequences of increasing fire severity and frequency on diversity in the coming decades.

Introduction

In fire-prone ecosystems, plant community composition, structure, and diversity are strongly influenced by patterns of fire frequency, size, seasonality, and severity collectively referred to as the ecosystem's fire regime (Johnstone et al. 2016). Fire regimes have been altered by human activities in many ecosystems, with cascading effects on plant communities (McKenzie et al. 2004). While fire severity (fire-caused mortality and vegetation consumption) is projected to increase at both local and global scales in the coming decades (Lutz et al. 2009, Flannigan et al. 2013), the effects of high severity fire on plant diversity are not consistent within or among ecosystems and the reasons for this inconsistency are poorly understood (Miller and Safford 2020). Across North American coniferous forests, for example, high severity fire can result in either higher or lower species richness than low severity fire (Miller and Safford 2020).

Variability in the relationship between disturbance and species diversity is often attributed to differences in ecosystem productivity (Huston 1979, Kondoh 2001), but empirical tests in terrestrial systems have been inconclusive. In high productivity environments, strong resource competition and high growth rates may lead to competitive exclusion and the potential for local extinction of poor competitors (Huston 1979). Disturbance in high productivity environments may enhance diversity by temporarily removing strong competitors and allowing colonizers and/or weak competitors to coexist, a phenomenon known as competitive release (Grime 1973). Conversely, in low productivity environments where competitive displacement is rare and species growth rates are low, disturbance may limit species' ability to grow and reproduce without simultaneously increasing opportunities for colonization, ultimately lowering diversity (Huston 1979). Empirical studies supporting productivity's predicted effects on disturbance-diversity relationships are largely controlled experiments with grazing or clipping disturbance (Proulx and Mazumder 1998). Observational studies to date lack continuous productivity gradients (i.e. comparing "high" vs "low" productivity, sometimes without quantifying productivity) and have produced inconsistent results, reporting increases (Safford and Harrison 2004), decreases (Burkle et al. 2015), and no change (DeSiervo et al. 2015) in post-disturbance diversity at high productivity.

Life history differences among species may help to explain patterns of diversity along disturbance severity and productivity gradients. Undisturbed sites are predicted to favor strong competitors with higher resource use efficiency and slower growth rates, while disturbed sites favor weak competitors (strong colonizers) with lower resource use efficiency and higher growth rates (Huston 1979, Tilman 1994). Empirical tests have found that some post-disturbance communities do indeed experience increased average intrinsic growth (Haddad et al. 2008) and maturation rates (Donato et al. 2009) as well as increased occurrence of wind-dispersed species (Stevens et al. 2015), suggesting that "winners" after disturbance may be colonizers that are able to exploit higher levels of light. Because light is more limiting in high productivity forest stands with denser canopies, post-fire colonizers with traits that facilitate rapid resource acquisition (such as short lifespan) may increase more after disturbance in high than low productivity stands. However, the interactions between fire severity, productivity, and plant traits have rarely been explored, particularly across large-scale natural environmental gradients.

Here, we study how productivity influences the effects of fire severity on understory species diversity in Mediterranean-type subalpine forest in California, where mountainous terrain drives local variation in productivity via steep temperature and moisture gradients (Meyer and North 2019). We sampled understory plant richness in 13 subalpine fires that spanned nearly 500 km in latitude and included both fire severity and productivity gradients (Appendix S1: Fig. S1.1). Productivity was measured via the proxy of remotely sensed pre-fire Normalized Difference Vegetation Index (NDVI), a measure of green foliage density linked to gross primary productivity (Glenn et al. 2008). We predicted that the effects of fire severity on plant communities would be contingent on productivity. Specifically, we hypothesized that due to a history of relatively high severity fire in subalpine forests (Appendix S1: Fig. S1.2), (**H1**) species richness would peak at moderate to high fire severity (Miller and Safford 2020). Further, (**H2**) because high productivity stands experience greater change in available resources after fire, we predicted that richness would increase more after high severity fire in high productivity stands. To help elucidate a possible mechanism for hypothesized diversity patterns, we tested how the probability of colonizer-type species changed across interacting fire severity and productivity gradients. Specifically, we predicted that (**H3**) the probability of occurrence of species with short lifespans and long-distance dispersal capabilities would increase with fire severity and that (**H4**) this trend would be more pronounced in high productivity stands where competitive exclusion may have reduced pre-fire colonizer richness. Together, our hypotheses test theoretical relationships between fire severity, productivity, and plant community diversity and composition that are essential to understanding where high severity fire may pose a threat to biodiversity.

Methods

Study system – We sampled recently burned subalpine forest in the southern Sierra Nevada and San Bernardino Mountains of California, found in or immediately adjacent to the North American Mediterranean climate zone (see map, photos, and additional site information in Appendix S1: Fig. S1.3, Fig. S1.4, & Section S1.1). Subalpine forests are high elevation forested communities where most of the annual precipitation falls as snow (Millar and Rundel 2016). Dominant trees in the study area were western white pine (*Pinus monticola*), foxtail pine (*P. balfouriana*), lodgepole pine (*P. contorta ssp. murrayana*), whitebark pine (*P. albicaulis*), mountain hemlock (*Tsuga mertensiana*), limber pine (*P. flexilis*), and red fir (*Abies magnifica*).

Fire and plot selection – Over the course of three summers (July – September, 2017 – 2019), we sampled 248 plots across 13 fires in subalpine forest (see Appendix S1: Table S1.1 for fire information). We identified fires that contained each of six fire severity classes (unburned, low, low-moderate, moderate, high-moderate, and high) corresponding to fire-caused basal area mortality (0%, 0-25%, 25-50%, 50-75%, 75-90%, and 90-100% respectively) using the remotely sensed relativized differenced normalized burn ratio (RdNBR; Miller and Thode 2007). Relativized fire severity measures such as RdNBR report relative change such that areas of both sparser and denser vegetation can experience the full fire severity spectrum. This helps to decouple the correlation between fire severity and productivity that can arise with absolute measures of biomass change or mortality (Pausas and Bradstock 2007). We sampled all 10 subalpine fires in the study region that contained six fire severity classes and were within two days hike of a trailhead as well as 3 smaller fires with fewer severity classes. Time since fire at the time of sampling ranged relatively evenly from 2-17 years.

We used a stratified random sampling design, placing 405 square meter circular plots at the crosshairs of a 200x200 meter grid in upland areas with no recorded history of previous fire or logging. We stratified plots across preliminary fire severity classes (from RdNBR) as well as aspect (see Appendix S1: Fig. S1.1 & Section S2) and estimated final plot-level fire severity based on fire-caused basal area mortality as described above as well as fuel consumption (see Appendix S1: Table S1.2 for fire severity class descriptions). We subsequently censused all vascular plant species in the plot by systematically searching the plot area. Species richness was low in our study area (median 10), making it easy to locate all species.

Remotely sensed environmental variables

We used NDVI, a remotely sensed measure of photosynthetic activity, to represent plot-level productivity. NDVI has strong theoretical and empirical links to Gross Primary Productivity (GPP; Glenn et al. 2008), and robust correlations have been found between NDVI and tree radial growth measurements in other energy-limited systems like boreal forest (Beck et al. 2011). NDVI derived from 30x30m Landsat imagery is commonly used to represent productivity in montane forest (Burkle et al. 2015) and a recent study in Sierra Nevada subalpine forest found that it declined with mortality in whitebark pine stands and that inter-annual variability in NDVI tracked snow accumulation throughout a 30 year study period (Potter and Dolanc 2016). Using Google Earth Engine, we removed snow and cloud pixels from Landsat V imagery and calculated the average of maximum annual NDVI for the years 1995 through 2000 (Pettorelli et al. 2005, Gorelick et al. 2017). This six-year period predates sampled fires, represents both wet and dry years in the study region, and its average correlates well with total aboveground tree biomass calculated for 37 unburned plots (Appendix S1: Fig. S1.1). We calculated Heat Load Index, a single metric accounting for slope, aspect, and some elements of slope position and shadow (essentially a measure of plot-level solar radiation), using the R package spatialEco (McCune and Keon, 2002).

Plant trait data

We compiled available information on plant life history and dispersal syndrome for species in our dataset using the University of California Jepson Herbarium (http://ucjeps.berkeley.edu), the USDA Forest Service Fire Effects Information System (feis-crs.org), JSTOR Global Plants (https://plants.jstor.org/), and our own familiarity with the species. We characterized species life history as either annual/biennial, short-lived perennial (non-woody perennial without rhizomes, stolons, bulbs or root storage organs) or long-lived perennial (woody perennials and/or perennials with rhizomes, stolons, bulbs, or other storage organs), and species dispersal syndrome as either far-dispersing (vertebrate or wind dispersal syndrome) or near-dispersing (unassisted dispersal syndrome). Species dispersal syndrome was classified as vertebrate-dispersing if the reproductive structures were fleshy or adhesive, wind-dispersing if the reproductive structure included a pappus, and unassisted if the reproductive structure had none of the previously described characteristics.

Statistical models

Local species richness – To determine the effect of fire severity on plot-level diversity (**H1**) and whether it depended on local productivity (**H2**), we regressed species richness against fire severity (represented as an ordered category as in Bürkner & Charpentier (2020)), productivity, and their interaction using a Bayesian generalized linear mixed model with a negative binomial likelihood. We further conditioned the model on time since fire and heat load index to account for other major effects on species richness and used a varying intercept for each fire to account for non-independence of plots within fires (Appendix S1: Eqn. S1 & Section S3).

Plant traits – To determine whether burned plots had more species with “colonizer” traits (**H3**), and whether this relationship was more pronounced at high productivity (**H4**), we modeled species presence-absence using a trait-by-environment multi-level model with binomial likelihood as in Miller et al. (2019) (Appendix S1: Eqn. S2 & Section S3). The terms of greatest interest in the model were the interaction between fire severity and plant trait ($\beta_{fire\_sev:trait}$) and the three-way interaction between fire severity, productivity and plant trait ($\beta_{fire\_sev:trait:NDVI}$), which dictate whether the probability of occurrence of the trait varies significantly across environmental predictors or their interaction. We constructed two different models, one for life history and another for dispersal syndrome.

All models were created in the Stan computational framework (Stan Development Team 2018) with the brms package (Bürkner 2017) in the R statistical environment version 4.0.0 (R Core Team 2020). We used brms default mildly regularizing priors to help prevent over-fitting, assessed convergence by visually inspecting traceplots and ensuring that Rhat values were less than or equal to 1.01 for all posterior estimates, and compared observed values against posterior draws to assess model fit (McElreath 2020). Parameters and contrasts were considered significant when the 95% highest posterior density interval (HPDI) did not cross zero and marginally significant when the 90% HPDI did not cross zero.

Results

Local species richness – As predicted, we found that understory species richness increased with increasing fire severity in California subalpine forest (**H1**; mean β_{fire_sev} = 0.17; 95% HPDI [0.14, 0.21]; Fig. 1.1). Species richness also increased *more* across fire severity in higher productivity forest (**H2**; $\beta_{fire\_sev:NDVI}$ = 0.04 [0.01, 0.08]; Fig. 1.1). Although fire severity and productivity can be correlated, our use of a relativized burn severity index for initial plot stratification helped to decouple these predictors for analysis (Appendix S1: Fig. S1.1). The effect of productivity alone on species richness was negative (β_{NDVI} = -0.22 [-0.36, -0.09]), while the effect of heat load index (a measure of solar radiation) was positive ($\beta_{heat\_load\_index}$ = 0.10 [0.04, 0.17]). Time since fire had a positive but non-significant effect on species richness ($\beta_{time\_since\_fire}$ = 0.27 [-0.04, 0.72]; see Appendix S1: Section S4 for further discussion of time since fire).

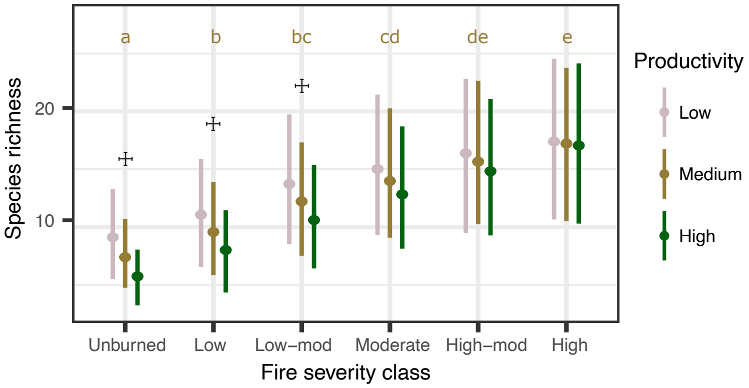

Figure 1.1. Species richness increases with increasing fire severity across productivity in 405m^2 *plots in California subalpine forest. This relationship is stronger at high productivity and weaker at low productivity. Dots and bars show model-derived means and 95% CIs at the 15*th*(low), 50*th *(medium), and 85*th *(high) productivity quantiles (measured as averaged maximum NDVI). For medium productivity only, a shared letter indicates that fire severity classes are not significantly different from one another. Crosses indicate fire severity classes in which species richness is significantly greater in low productivity plots than high productivity plots. Low-mod = Low-moderate, High-mod = High moderate.*

Plant traits – Our results supported our hypothesis that colonizer-type species (short-lived and far-dispersing species here) would increase more than other groups across the fire severity spectrum irrespective of productivity (**H3**; Appendix S1: Table S1.4 & S1.5). From low to high fire severity, annual, biennial, and short-lived species occurrence increased significantly more than long-lived species occurrence ($\beta_{fire\_sev:life\_history\_long}$ = -0.21 [-0.37, -0.06], Fig.

1.2) and far-dispersing species occurrence increased marginally more than near-dispersing species occurrence ($\beta_{fire\_sev:dispersal\_far}$= 0.09 [-0.02, 0.22], Fig. 1.3).

Higher productivity intensified the positive effect of fire severity on far-dispersing species (**H4;** $\beta_{fire\_sev:NDVI:dispersal\_far}$ = 0.09 [0.00, 0.18], Fig. 1.3), which increased by about 13 percent more in high (85th percentile) – versus low (15th percentile) – productivity stands (0.13 [0.05, 0.22], Fig. 1.3). Higher productivity had inconsistent effects on the positive relationship between short-lived species occurrence and fire severity, with short-lived perennials increasing more along the fire severity spectrum at high productivity sites (**H4;** $\beta_{fire\_sev:NDVI:perennial\_short}$ = 0.20 [0.09, 0.32], Fig. 1.2) and annual/biennials unchanging across productivity. Surprisingly, long-lived perennials also increased more across the fire severity spectrum in high than low productivity stands (**H4;** $\beta_{fire\_sev:NDVI:perennial\_long}$ = 0.14 [0.04, 0.24], Fig. 1.2).

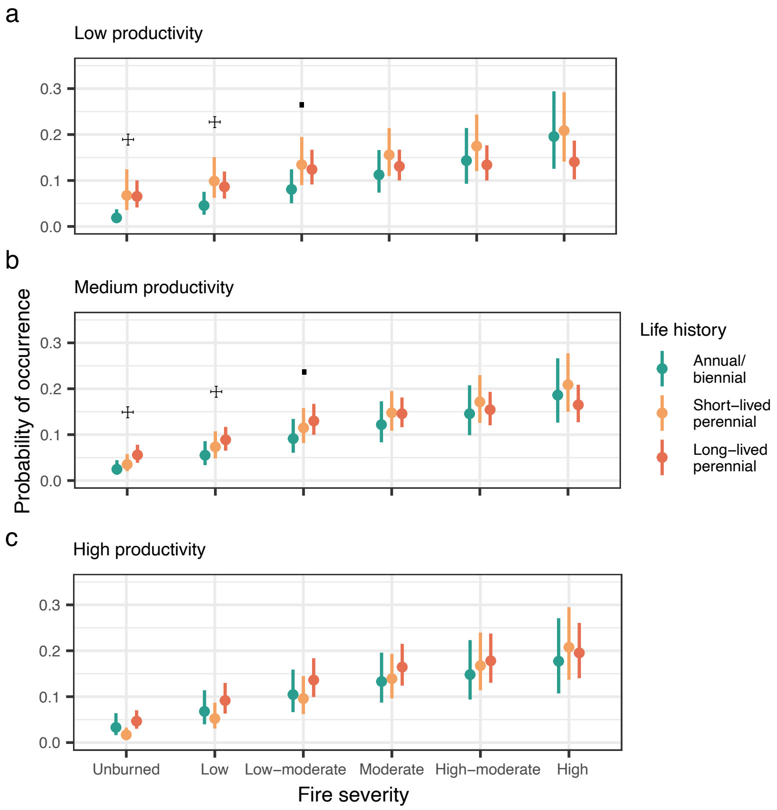

Figure 1.2. Probability of occurrence of annual/biennial and short- and long-lived perennial species across fire severity classes shown at (a) 15th, (b) 50th, and (c) 85th productivity quantiles. Annual/biennial and short-lived perennial occurrence increases more than long-lived perennial occurrence across fire severity. Productivity strengthens the species occurrence – fire severity relationship for all perennials. Error bars show 95% CIs around model estimated occurrence probability. Crosses (and dots) indicate a significant (or marginally significant) difference between annual/biennial and long-lived perennial occurrence for that fire severity class.

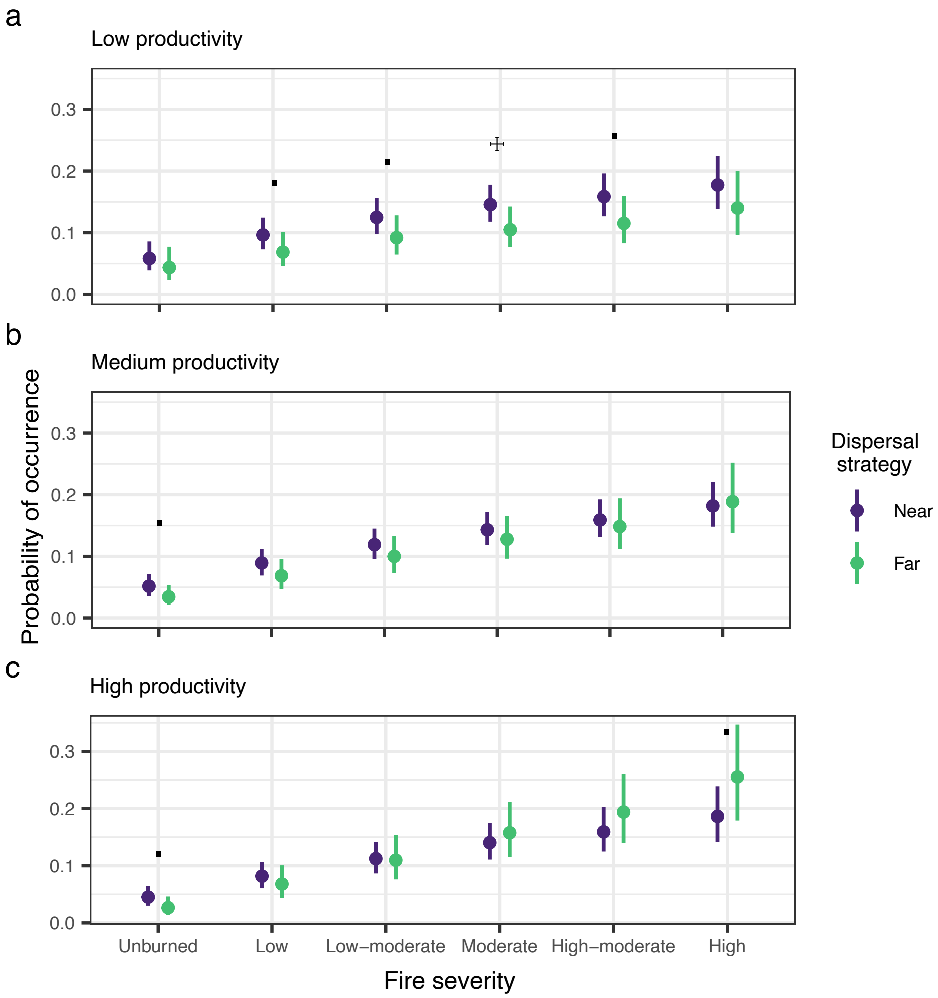

Figure 1.3. Probability of occurrence of near- and far-dispersing species across fire severity classes shown at (a) 15^th^, (b) 50^th^, and (c) 85^th^ productivity quantiles. In low productivity subalpine forest, the occurrence both near- and far-dispersing species increase with fire severity class. However, in high productivity subalpine forest, the occurrence of far-dispersing species increases significantly more than near-dispersing species across the fire severity gradient. Error bars show 95% CIs around model estimated occurrence probability. Crosses (and dots) indicate a significant (or marginally significant) difference, between near- and far-dispersing species occurrence for that fire severity class and productivity level.

Discussion

We tested relationships between fire severity, diversity, and productivity in California subalpine forests and used trends in colonizer-type species occurrence to support competitive release as a mechanism for observed changes in post-fire diversity. Species richness almost tripled between unburned and severely burned subalpine forest, increasing most in higher productivity stands where unburned species richness was lowest (**H1** & **H2**; Fig. 1.1). In keeping with the idea that low richness results from overstory competition, we found disproportionate increases in short-lived and far-dispersing species across the fire severity spectrum (**H3**; Figs. 1.2 & 1.3). While disturbance is known to favor colonizer-type species (Stevens et al. 2015), we found that for far-dispersing species (wind- or animal-dispersed), the benefits of high severity fire were strongest in higher productivity plots (**H4**; Fig. 1.3). Ours is the first study we are aware of to demonstrate the long-hypothesized interaction between fire severity, productivity, and colonizer plant traits (Grime 1973, Huston 1979) with observational field data and supports competitive release as one mechanism for increased post-fire richness.

Our finding of increased richness after high severity fire (irrespective of productivity) mirrors results from other forests characterized by relatively low-frequency, high-severity fire regimes (Miller and Safford 2020). In wet-summer biome subalpine forests (Doyle et al. 1998, Coop et al. 2010), where high severity fire is notably more prevalent than in California subalpine (Appendix S1: Fig. S1.2), species richness increases after high severity fire and stays elevated for up to 30 years. Such patterns support the working hypothesis that post-fire species richness peaks after fire severities that best correspond with an ecosystem's natural fire regime (Miller and Safford 2020) due to "ecological memory" or the long-term filtering effects of fire regime on species pools (Denslow 1980, Johnstone et al. 2016). However, the natural fire regime in dry-summer biome California subalpine forest is dominated more by moderate or mixed-severity fire (Meyer and North 2019; Appendix S1: Fig. S1.2), which alone would predict a plateau in the relationship between fire severity and species richness (Miller and Safford 2020).

The average increase in post-fire plant diversity was greatest in higher productivity forest, where unburned plots had the lowest species richness (Fig. 1.1). This pattern supports predictions that strong competitors may depress richness at higher productivity (i.e. canopy density), and that disturbance can maximize richness by allowing the coexistence of both strong and weak competitors (Grime 1973, Huston 1979). However, the coexistence of strong and weak competitors may not last long in ecosystems where succession occurs quickly or where one lifeform (e.g. shrubs) quickly outcompetes the others. Burkle et al. (2015) investigated the interaction of fire severity and productivity in lower elevation Rocky Mountain forests 6-12 years postfire and found that species richness was lowest at their highest productivity site due to near-complete cover of lodgepole pine seedlings and saplings. In lower elevation Sierra Nevada forests, fire-adapted shrubs quickly dominate after high severity fire, reducing richness (Richter et al. 2019). This strong shrub response is absent in California subalpine forest and the lack of a single or several dominant species in the initial post-fire years results in lasting understory richness especially in high productivity stands that burned at high severity.

We found moderate support for competitive release as a potential mechanism for the elevated post-fire diversity that we observed. As we expected, both short-lived (annual, biennial, and short-lived perennial) and long-dispersing species increased more along the fire severity spectrum than their long-lived and near-dispersing counterparts (Fig. 1.2b & Fig. 1.3b). For far-dispersing species, the greatest increases followed high severity fire in high productivity stands

(Fig. 1.3), suggesting a greater relative increase in resource availability in higher productivity areas. Removal of litter, duff, and canopy cover via fire increases bare mineral soil and light for understory plant establishment and growth (Grime 1977, Merrill et al. 2018). Our results indicate that wind- and animal-dispersed colonizers took advantage of increased regeneration microsites and, while all but two species in our study were native, that invasion risk is likely to increase with both fire severity *and* productivity where non-native species are present. Further, though high severity fire may increase water stress and reduce species richness in water-limited forests (Stevens et al. 2015), ours and other studies (Coop et al. 2010) show that light and heat from solar radiation may have a more consistent positive effect on diversity in energy-limited ecosystems like subalpine forests (Stephenson 1998).

Contrary to our expectations post-fire increases in annual and biennial species changed little with productivity, but both short- and long-lived perennials experienced the greatest increases after fire in high productivity stands (Fig. 1.2). In many ecosystems, consumption of litter and duff and reduction of canopy cover as a result of burning leads to germination of soil seed banks and the emergence of long-lived geophytes (Merrill et al. 2018). In Mediterranean grassland and woodland, geophyte diversity increases more in response to grazing in high than low productivity sites (Noy-Meir and Oron 2001). Though geophytes alone are not driving the response of long-lived perennials in our study system (Appendix S1: Table S1.6), it may be that high productivity stands support more fire-stimulated perennial species that emerge from underground perennating structures or persist in the soil seedbank. Several shrub species that were common in high severity stands (e.g. *Arctostaphylos patula* and *Ceanothus cordulatus*) are known to have persistent, fire-stimulated soil seed banks (Nagel and Taylor 2005), but we were unable to explicitly account for seed bankers due to limited data on seed storage and longevity in subalpine forest understories.

Overall, our findings support predictions that high severity fire within an ecosystem's natural range of variation is more likely to increase species richness in high productivity stands or forest types (Huston 1979). We found evidence of competitive release as one mechanism for increased richness, with far-dispersing colonizer occurrence increasing most after high severity fire in higher productivity stands. Taken together, our findings support theoretical connections between fire severity, productivity, and plant community diversity and composition that, along with historical fire regimes and local species pools, help to explain the inconsistent impacts of high severity fire on forest ecosystems (Miller and Safford 2020). Understanding what causes variability in ecosystem response to high severity fire is the first step to predicting changes in local diversity under future fire regimes (Lutz et al. 2009, Flannigan et al. 2013) and establishing informed conservation and management priorities.

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Supplementary information

Supplemental methods

Section S1.1: Study system

Subalpine forests and woodlands are high elevation forested communities occurring just below the alpine zone, where temperatures become too low for tree survival (Millar and Rundel 2016). They are important ecosystems in California in part because they occupy the upper watersheds of most major river drainages and influence snowpack formation and retention (Hunsaker et al. 2012). They are also predicted to act as climate refugia for species fleeing warming temperatures at lower elevations (Millar et al. 2015). Precipitation ranges from 750mm-1250mm and occurs mostly in the form of snow, with summer precipitation limited to local thunderstorm events. Soils are sandy and poorly developed, with little organic matter; rocky areas are common and can result in a very patchy distribution of forest (Fites-Kaufman et al. 2007).

For the purposes of this study, we defined subalpine forest using a combination of elevation and forest type. Plots were above 2,575 meters in the central Sierra Nevada, 2,750 meters in the southern Sierra Nevada, and 2,900 meters in the San Bernardino mountain range (Millar and Rundel 2016). Further, all plots were characterized by one of the eight "Regional Dominance Types" for subalpine forest as defined by The Classification and Assessment with Landsat of Visible Ecological Groupings or CALVEG (USDA 2004, Sawyer et al. 2009).

Our study area has a history of infrequent and relatively high severity fire compared to lower elevation forest types (see Figure S1; Steel et al. 2015). While plant diversity in lower elevation forests in the study region generally responds negatively to high severity fire due to a strong shrub response or a lack of species adapted to high severity fire (Richter et al. 2019), a more positive diversity response is predicted in subalpine forests where species pools evolved with greater exposure to high severity fire (Miller and Safford 2020). Patterns of fire activity in subalpine forest are still considered to be within their natural range of variation (Meyer and North 2019), however, larger fires are beginning to occur at higher elevations (Schwartz et al. 2015) and increases in relative area burned are greater than in any other California forest type (Mallek et al. 2013). Further, small tree density has increased by >60% in the last century, probably driven by increases in nighttime temperatures and growing season length, which have positive effects on biological productivity (Dolanc et al. 2013). Increasing productivity and fire activity in subalpine forests highlight the need to understand how simultaneous changes in these environmental variables affect biodiversity.

Section S1.2: Controlling for confounders

As is common in observational studies, we were unable to control for all factors with the potential to confound our response variables (species richness and colonizer species occurrence). While we stratified plots by fire severity and aspect, the limited number of sample locations did not allow us to ensure a balanced distribution of pre-fire productivity or slope. To verify that fire severity was unlinked to pre-fire productivity and the combined topographic influence of slope and aspect (which can be measured as heat load index), we tested the relationship between fire severity and both predictors. We found that neither pre-fire productivity (mean $\beta_{\text{fire\_sev}} = 0.00$; HPDI[-0.10, 0.00]) nor heat load index ($\beta_{\text{fire\_sev}} = 0.01$ [0.00, 0.02]) varied systematically with fire severity (Figure S1) and concluded that they were unlikely to be biasing the understory community response to fire severity that we observed.

Another important consideration is the influence of stand age and previous disturbance on our measure of pre-fire productivity (Landsat-derived 30x30m resolution NDVI), which is sensitive to beetle-induced tree mortality in the study area (Potter and Dolanc 2016). Selection of fires with significant pre-fire disturbance could bias the influence of productivity on our response variables. We selected sites that had not been logged and had no previous recorded fire in the California Fire Perimeters dataset (https://frap.fire.ca.gov/frap-projects/fire-perimeters/), which is highly accurate back to the 1940s and 50s, and reasonably accurate for federal lands to about 1908 (Miller et al. 2009). While we saw some evidence of lightning strikes in unburned areas, they rarely killed the tree that was struck and with average fire return intervals of 160 in California subalpine forest (Meyer and North 2019), the possibility of sampling a recent reburn is unlikely. In one fire (the 2015 Walker fire, 17 of 248 plots) a mountain pine beetle attack had taken place prior to the fire and many overstory trees were likely dead before they burned. Due to the influence of pre-fire mortality on pre-fire NDVI and understory plant communities, we ran our analyses again without the 17 plots from the Walker fire but found that it made no difference to the direction or significance of parameter estimates and decided to keep this fire in the dataset for final analyses. In all other fires, there was no evidence of pre-fire disturbance and we could be sure that we were sampling in old forest in which biomass (correlated with NDVI in our unburned study plots, see Figure S1) reflects net primary production accumulated over time (Clark et al. 2001).

A final source of potential bias is the non-independence of plots within the same fire. While some spatial autocorrelation is inevitable, van Mantgem and Schwilk (2009) tested for autocorrelation in species richness in plots from the same fire in Sierra Nevada mixed conifer forest and found none. Further, by placing plots 200 meters apart we ensured that many plots in the same fire would have burned on different days and under different weather conditions, increasing likelihood of independence between them. Lastly, we used mixed effects modeling to account for the similarities in burn environment and species pools at each fire (McElreath 2020).

Section S1.3: Statistical models

Local species richness

[Eqn. S1]

$$\text{species\_richness}_{i,j} \sim \text{negbinomial}(\lambda_{i,j}, \phi)$$

$$\log(\lambda_{i,j}) = \alpha + a_{fire[j]} + \beta_{fire\_sev:NDVI}\text{fire\_sev}_i * NDVI_i + \beta_{fire\_sev}\text{fire\_sev}_i + \beta_{NDVI} NDVI_i + \beta_{heat\_load\_index}\text{heat\_load\_index}_i + \beta_{time\_since\_fire}\text{time\_since\_fire}_j$$

$$a \sim \text{Gaussian}(0,\ \sigma_a^2)$$

We used an ordered categorical predictor to estimate the effects of fire severity as in Bürkner & Charpentier (2020). In this method, known as a monotonic effects model, the ordered category is forced to have a monotonic effect on the response variable. We tested for non-monotonicity by substituting a continuous fire severity measure for our fire severity classes and comparing models fit with and without a second order polynomial term using leave one out cross validation. Because adding a polynomial term did not enhance the predictive ability of the continuous fire severity model (see Table S1.3), we proceeded to use an ordered categorical variable as originally intended. By treating the fire severity factor as ordered, we take advantage of the information encoded in the ordering of the factor levels, while retaining the flexibility for the effect of each level to be different (e.g. the effect on diversity of a shift from low to moderate severity could be smaller than the effect of a shift from moderate to high severity, or the reverse).

Plant traits

[Eqn. 2]

$$\text{species\_occurence}_i \sim \text{Bernoulli}(p_i)$$

$$\begin{aligned}\text{logit}(p_i) = \; & \alpha + a_{\text{spp}[i]} + \; b_{\text{plot}[i]} + \beta_{fire\_sev:trait:NDVI} * \text{fire\_sev}_{\text{plot}[i]} * \text{trait}_{\text{spp}[i]} * NDVI_{\text{plot}[i]} \\ & + \; \beta_{fire\_sev:trait} * \text{fire\_sev}_{\text{plot}[i]} * \text{trait}_{\text{spp}[i]} + \; \beta_{fire\_sev:NDVI} * \text{fire\_sev}_{\text{plot}[i]} \\ & * \text{NDVI}_{\text{plot}[i]} + \; \beta_{trait:NDVI} * \text{trait}_{\text{spp}[i]} * \text{NDVI}_{\text{plot}[i]} \\ & + \left(\beta_{fire\_sev} + c_{spp[i]}\right)\text{fire\_sev}_{\text{plot}[i]} + \; \beta_{trait} * \text{trait}_{\text{spp}[i]} + \; \beta_{NDVI} * \text{NDVI}_{\text{plot}[i]}\end{aligned}$$

$$\begin{bmatrix} a_{spp} \\ c_{spp} \end{bmatrix} \sim \text{MVGaussian}(0, \mathbf{\Sigma})$$

$$b_{\text{plot}} \sim \text{Gaussian}(0, \; \sigma_b^2)$$

Hierarchical models of the type that we used (Eqn. 2) have good type I error control and are recommended over community-weighted mean approaches when testing functional trait composition across an environmental gradient (Jamil et al. 2013, Miller et al. 2019). Here, $\text{species\_occurrence}_i$ is the presence or absence of a species in each row of the species-by-plot data frame. Species-plot combinations were generated separately for each fire to conserve probability of occurrence values despite differing species pools. Each species-plot combination can respond differently to fire severity (again, modeled as an ordered category) due to varying intercept ($a_{spp[i]}$) and slope ($c_{spp[i]}$) terms for species. A varying intercept for plot ($b_{plot[i]}$) allows species occurrence to vary by plot independent of plot-level fire severity and results in better out-of-sample accuracy than models without it (Jamil et al. 2013).

Supplemental results

Section S1.4: Time since fire

We sampled all California subalpine fires that met study criteria during planning in 2017, which resulted a wide range of time since fire (2-17 years) in our final dataset. While we accounted for time since fire as a linear predictor in the species richness model, its positive effect was not significant, and more fires would be needed to test its interaction with fire severity. To explore the influence of using a wide range of time since fire on our results, we ran the species richness model separately for the six fires under five years time since fire ("young" fires) and the seven fires with over ten years time since fire ("old" fires). Parameter estimates for old and young fires where of the same direction and significance as the combined model except that productivity was no longer significant in either model and the interaction between fire severity and productivity was no longer significant in the young fire model (which had fewer observations at 115 of the original 248 plots). With less data, it is logical that several terms (especially the interaction term) were no longer significant, and we do not believe that our dataset contains strong evidence of an interaction between fire severity and time since fire. We note that we did not sample any fires the year of or one year after fire, at which time species richness is may have been depressed in high severity areas.

Section S1.5: Understory communities

We found a total of 268 understory species in our study area, with species pools varying substantially between the central Sierra Nevada and the San Bernardino Mountains in southern California. We found trace amounts (less than one percent of plot area) of two non-native species in the dataset, *Lactuca serriola* and *Bromus tectorum*, both of which are annual species designated as "naturalized" in the Jepson Manual of California (Jepson Flora Project 2021). Species were generally long-lived, with only 37 characterized as annual or biennial and 61 as short-lived perennials. 77 species were characterized as far-dispersing. Common species included graminoids (*Stipa occidentalis*, *Carex rossii*, and *Elymus multisetus*), forbs (*Boechera platysperma*, *Gayophytum diffusum*, and *Penstemon davidsonii*), and shrubs (*Chrysolepis sempervirens*, *Arctostaphylos patula*, *and Ribes cereum*) (See associated Dryad repository for full species list with associated traits). Though shrubs were common, appearing in 187 of 248 plots, they averaged only 11.2 percent (median 2.8 percent) cover when present and had an average modal height (most common height of shrub lifeform in the plot) of 1.2 meters (median 0.4 meters). In the field, we saw no evidence of a vigorous post-fire shrub response in subalpine forest as is often seen at lower elevations, particularly in the genera *Ceanothus* and *Arctostaphylos* (Richter et al. 2019). While we do not have reliable data on forb cover as many forb species were designated as "trace", we compared the contributions of different lifeforms to overall species richness and observed that forbs have higher species richness than other lifeform categories and increase the most across the fire severity spectrum in our dataset (Figure S5).

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Supplemental tables

Table S1.1. Information about all 13 fires in the study including burn year, year of sampling, total fire size, elevation range of sampling, and plots sampled per fire severity class.

Fire Name	Burn year	Sample year	Years since fire	Size (ha)	Elevation range (m)	Plots per fire severity class					
						0	1	2	3	4	5
Horseshoe	2016	2018	2	151	2902-3170	6	4	3	4	2	6
Walker	2015	2017	2	1544	2828-3077	5	0	1	4	2	5
Big Five	2015	2018	3	107	2978-3179	5	3	2	4	3	2
Cathedral	2014	2017	3	8	2775-2830	2	1	0	2	1	0
Lake	2015	2019	4	12660	2986-3214	6	4	3	4	3	4
Meadow	2014	2018	4	1932	2760-2949	5	3	3	5	3	4
Willow	2007	2018	11	75	2974-3293	5	3	2	4	3	3
Babcock	2007	2019	12	107	2762-3013	5	3	2	3	5	5
Crystal	2005	2019	14	42	2761-2961	2	0	2	1	1	1
Hotsprings	2004	2019	15	134	2891-3087	5	3	3	4	3	4
Palisade	2002	2018	16	606	2641-2906	4	3	3	3	3	3
Summit	2003	2019	16	1929	2845-3096	5	3	4	3	3	4
McNally	2002	2019	17	149475	2823-3045	5	3	3	3	3	4
					Total	60	33	31	44	35	45

Table S1.2. Description of fire severity classes estimated on the ground at each plot. Table is adapted from Welch et al (2016).

Fire severity class	Fire severity label	Percentage basal area mortality	Description
0	Unburned	0	Unburned
1	Low	0-25	Lightly burned, no significant overstory mortality, patchy spatial burn pattern, groups of surviving shrubs/saplings
2	Low-moderate	25-50	Lightly burned, isolated overstory mortality, most saplings/shrubs dead
3	Moderate	50-75	Moderately burned, mixed overstory mortality, understory mostly burned to ground
4	High-moderate	75-90	High-moderate intensity, significant overstory mortality, dead needles remaining on trees 1 year later
5	High	>90	High intensity burn, total/near total mortality of overstory, most needles consumed in fire

Table S1.3. Fixed effects model summaries and differences in expected log predictive density (or elpd) for models testing the effect of fire severity, productivity, and their interaction on species richness (see Eqn. S1) with a continuous fire severity measure (integer) instead of the ordered categorical variable used in final analysis. The "Integer" model only includes fire severity as an integer from 1 to 6, while the "Integer + integer^2" model includes fire severity as an integer as well as a squared integer term. The models are not significantly different in predictive ability as the difference in elpd (estimated by leave one out cross validation) is less than twice the standard error of the difference in elpd.

Model	Parameter	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS
Integer	Intercept	1.79	0.21	1.36	2.22	1.00	1424
	Fire severity	0.17	0.02	0.14	0.21	1.00	4689
	Productivity	-0.26	0.07	-0.41	-0.12	1.00	2807
	Time since fire	0.27	0.21	-0.06	0.73	1.01	1222
	Heat load index	0.11	0.03	0.05	0.18	1.00	4224
	Fire severity:Productivity	0.04	0.02	0.01	0.08	1.00	2932

Integer + integer^2	Intercept	1.53	0.24	1.07	2.03	1.00	1748
	Fire severity	0.38	0.08	0.2	0.54	1.00	3541
	Productivity	-0.23	0.07	-0.38	-0.09	1.00	3017
	Fire severity^2	-0.03	0.01	-0.05	0	1.00	3578
	Time since fire	0.27	0.19	-0.07	0.7	1.00	1460
	Heat load index	0.1	0.03	0.04	0.17	1.00	4333
	Fire severity:Productivity	0.04	0.02	0.01	0.07	1.00	3237

Model comparisons

	Difference elpd	SE difference
Integer	0	0
Integer + integer^2	-2.2	2.5

Table S1.4. Model summary for Bayesian generalized linear mixed model testing whether annual/biennial and short-lived perennial species occurrence changes across fire severity and the interaction of fire severity and productivity (see Eqn. S2).

Fixed effects		Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS
	Intercept	-3.73	0.34	-4.42	-3.11	1.00	1121
	long_perennial	0.89	0.36	0.22	1.61	1.00	1028
	short_perennial	0.40	0.36	-0.27	1.16	1.00	1213
	Productivity	0.28	0.17	-0.05	0.64	1.00	1170
	long_perennial: Productivity	-0.44	0.21	-0.87	-0.05	1.00	1151
	short_perennial:Productivity	-0.95	0.26	-1.49	-0.48	1.00	1381
	Fire severity	0.45	0.08	0.31	0.61	1.00	1114
	Fire severity: long_perennial	-0.21	0.08	-0.37	-0.06	1.00	1039
	Fire severity: short_perennial	-0.05	0.08	-0.22	0.09	1.00	1237

	Fire severity: productivity	-0.07	0.05	-0.17	0.03	1.00	1128
	Fire severity: long_perennial: Productivity	0.14	0.05	0.04	0.24	1.00	1136
	Fire severity: short_perennial: Productivity	0.20	0.06	0.09	0.32	1.00	1408

Random effects		Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS
Plot	sd(Intercept)	0.76	0.10	0.59	0.97	1.01	748
	sd(long_perennial)	0.39	0.14	0.07	0.66	1.03	180
	sd(short_perennial)	0.19	0.13	0.01	0.48	1.01	617
Species	cor(Intercept, long_perennial)	-0.46	0.23	-0.80	0.11	1.01	1059
	cor(Intercept, short_perennial)	-0.42	0.42	-0.95	0.63	1.00	1778
	cor(long_perennial, short_perennial)	0.28	0.47	-0.75	0.93	1.01	994
	sd(Intercept)1	1.32	0.13	1.09	1.58	1.00	1138
	sd(Fire severity)	0.25	0.03	0.19	0.31	1.00	806
	cor(Intercept, Fire severity)	-0.67	0.08	-0.80	-0.50	1.00	1156

Table S1.5. Model summary for Bayesian generalized linear mixed model testing whether far-dispersing species occurrence changes across fire severity and the interaction of fire severity and productivity (see Eqn. S2).

Fixed effects		Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS
	Intercept	-2.92	0.19	-3.30	-2.56	1.00	2974
	Far-dispersers	-0.43	0.26	-0.96	0.05	1.00	2974
	Productivity	-0.13	0.10	-0.35	0.06	1.00	2889
	Far-dispersers:Productivity	-0.11	0.19	-0.52	0.22	1.00	4378
	Fire severity	0.28	0.04	0.20	0.37	1.00	2950
	Fire severity:Far-dispersers	0.09	0.06	-0.02	0.22	1.00	2990
	Fire severity:Productivity	0.03	0.03	-0.03	0.10	1.00	2540

	Fire severity:Productivity:Far-dispersers	0.09	0.05	0.00	0.18	1.00	4217
Random effects		Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS
Plot	sd(Intercept)	0.65	0.05	0.56	0.75	1.00	3355
	sd(Far-dispersers)	0.43	0.12	0.17	0.64	1.00	975
	cor(Intercept, Far-dispersers)	-0.13	0.20	-0.49	0.29	1.00	4443
Species	sd(Intercept)	1.32	0.13	1.08	1.58	1.00	1978
	sd(Fire severity)	0.25	0.03	0.20	0.32	1.00	1377
	cor(Intercept, Fire severity)	-0.68	0.07	-0.80	-0.52	1.00	1807

Table S1.6. Model summary for Bayesian generalized linear mixed model testing whether geophyte occurrence changes across fire severity and the interaction of fire severity and productivity (see Eqn. S2).

Fixed effects		Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS
	Intercept	-3.01	0.17	-3.36	-2.68	1.00	3266
	Geophyte	-1.22	0.83	-2.96	0.30	1.00	5333
	Productivity	-0.14	0.10	-0.35	0.05	1.00	3758
	Geophyte:Productivity	-0.34	0.61	-1.81	0.62	1.00	5804
	Fire severity	0.31	0.04	0.23	0.39	1.00	3577
	Fire severity:Geophyte	0.17	0.19	-0.21	0.54	1.00	5200
	Fire severity:Productivity	0.05	0.03	0.00	0.11	1.00	3341
	Fire severity:Productivity:Geophyte	0.02	0.16	-0.26	0.38	1.00	6199
Random effects							
Plot	sd(Intercept)	0.64	0.04	0.55	0.73	1.00	2667
	sd(Geophyte)	0.55	0.41	0.02	1.49	1.00	1464
	cor(Intercept, Geophyte)	-0.02	0.44	-0.88	0.86	1.00	7375

Species	sd(Intercept)	1.33	0.13	1.10	1.61	1.00	1958
	sd(Fire severity)	0.26	0.03	0.20	0.32	1.00	1418
	cor(Intercept, Fire severity)	-0.70	0.07	-0.81	-0.54	1.00	2045

Supplemental figures

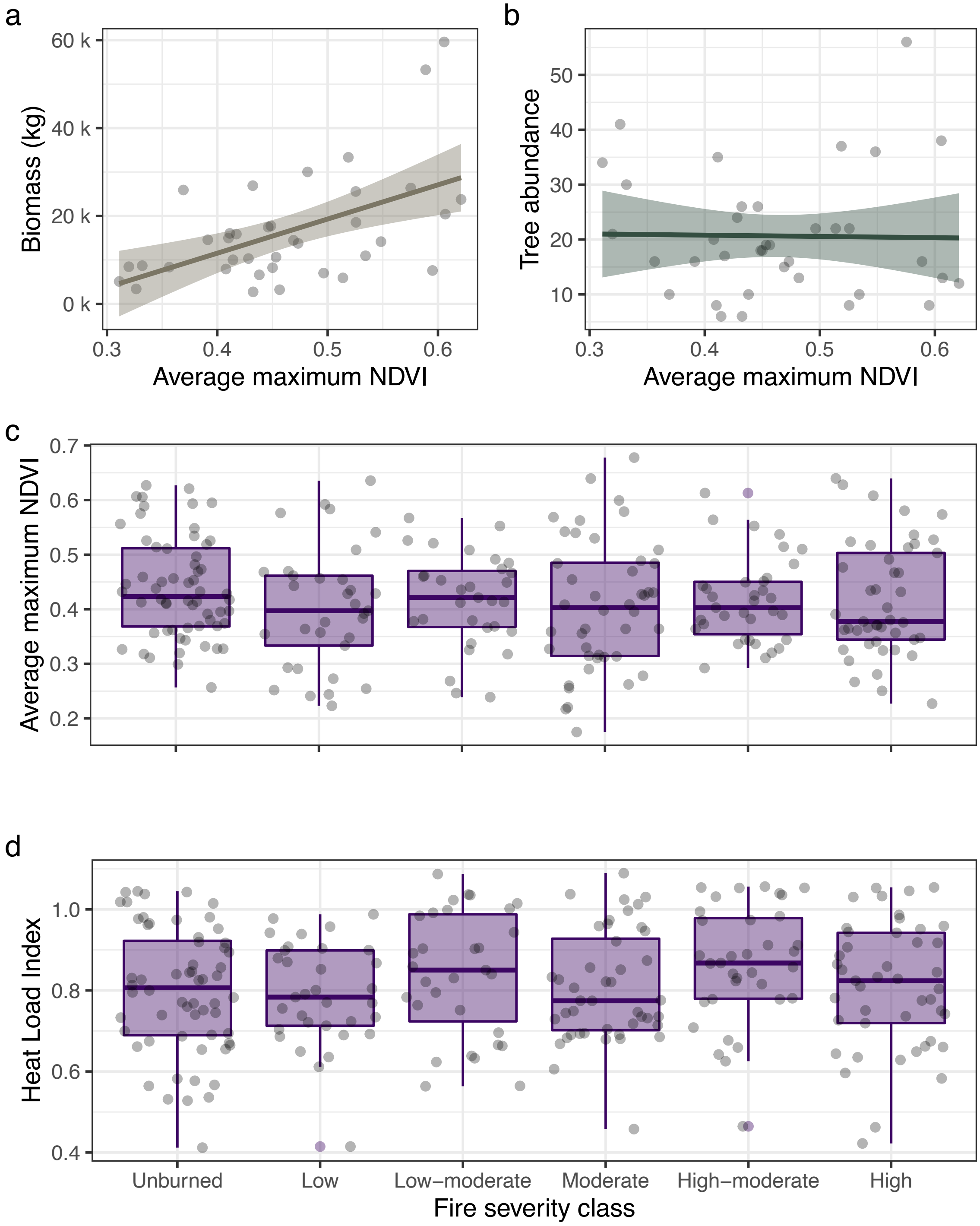

Figure S1.1. Scatterplot and best fit linear model with 95% CI for the relationship between maximum plot-level NDVI averaged across six pre-fire years and both biomass (a) and tree abundance (b) in 37 unburned study plots (Pearson's correlation coefficient = 0.53 [p < 0.0001] *and 0.017 [p = 0.92], respectively). Biomass was calculated using tree height, diameter at breast height, and allometric equations from the National Biomass Estimator Library* (Wang 2019). *The positive relationship between aboveground biomass and Normalized Differenced Vegetation Index (NDVI) supports our use of NDVI to represent aboveground primary productivity at the plot level because (in undisturbed sites dominated by species that can live several thousand years such as these control plots) biomass represents the accumulation of net primary production over time (Clark et al. 2001). The range and distribution of averaged maximum NDVI sampled is shown across fire severity classes (c), demonstrating that NDVI is relatively evenly distributed across fire severity classes and does not have an upward or downward trend across fire severity classes (from regression of NDVI on fire severity: mean* β_{fire_sev} *= 0.00 HPDI[-0.10, 0.00]). The full range of NDVI is zero to one and a large portion of this range (0.18 – 0.68) is captured in the sampled plots. Maximum NDVI does not saturate near the top of its range, a problem that can occur when using NDVI to compare heavily forested locations (Pettorelli et al. 2005). Lastly, the range and distribution of heat load index (HLI) is shown across fire severity classes (d), demonstrating that HLI is relatively evenly distributed across fire severity classes and does not have an upward or downward trend across fire severity classes (From regression of HLI on fire severity:* β_{fire_sev} *= 0.01 [0.00, 0.02]).*

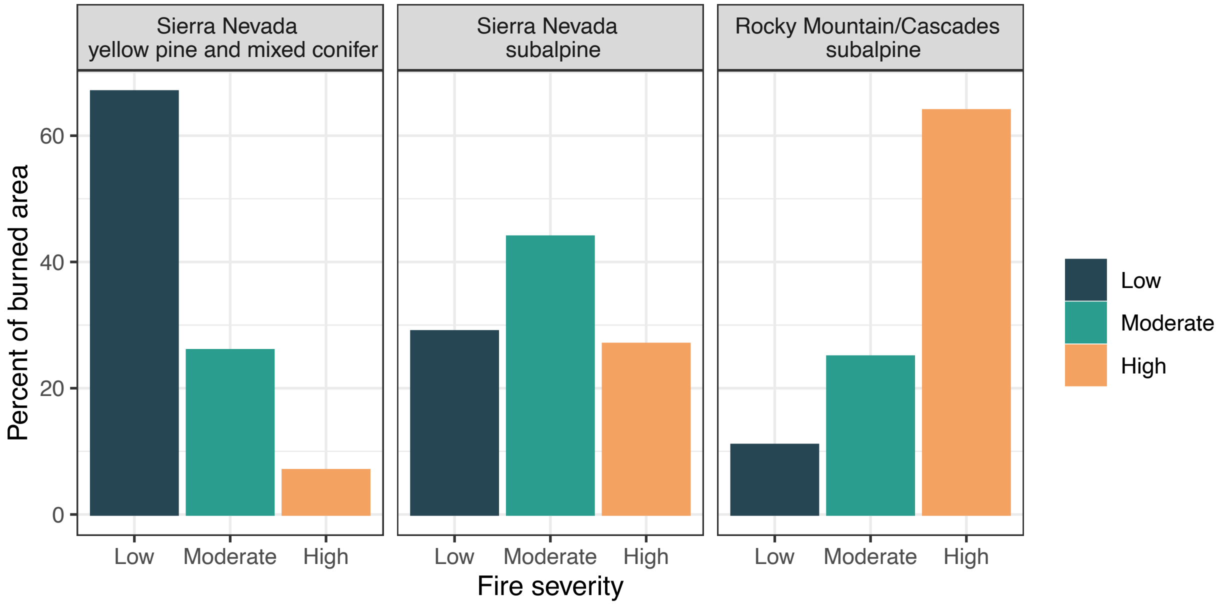

Figure S1.2. Simulated characteristic fire severity patterns under the natural range of variation for Sierra Nevada yellow pine and mixed conifer forest, Sierra Nevada subalpine forest and woodland, and subalpine forests and woodlands in the northern and central Rocky Mountains and Cascade Range. Percent of area burned shown at different severities (Low = tree mortality < 25%, Medium = tree mortality >25% and <75%, High = tree mortality >75%). Data derived by averaging LANDFIRE Biophysical Settings state and transition model outputs for each forest type (Sierra Nevada yellow pine and mixed conifer = 7 models, Sierra Nevada subalpine = 8 models, Rocky Mountain/Cascade subalpine = 35 models) from August 2020 update (https://landfire.gov/bps-models.php). For Sierra Nevada subalpine, values provided in Meyer and North (2019; Table 19) were averaged with LANDFIRE model outputs to increase sample size (Sierra Nevada subalpine = 10 averaged values) with summaries of more recent science and only changed final estimates by three to eight percent.

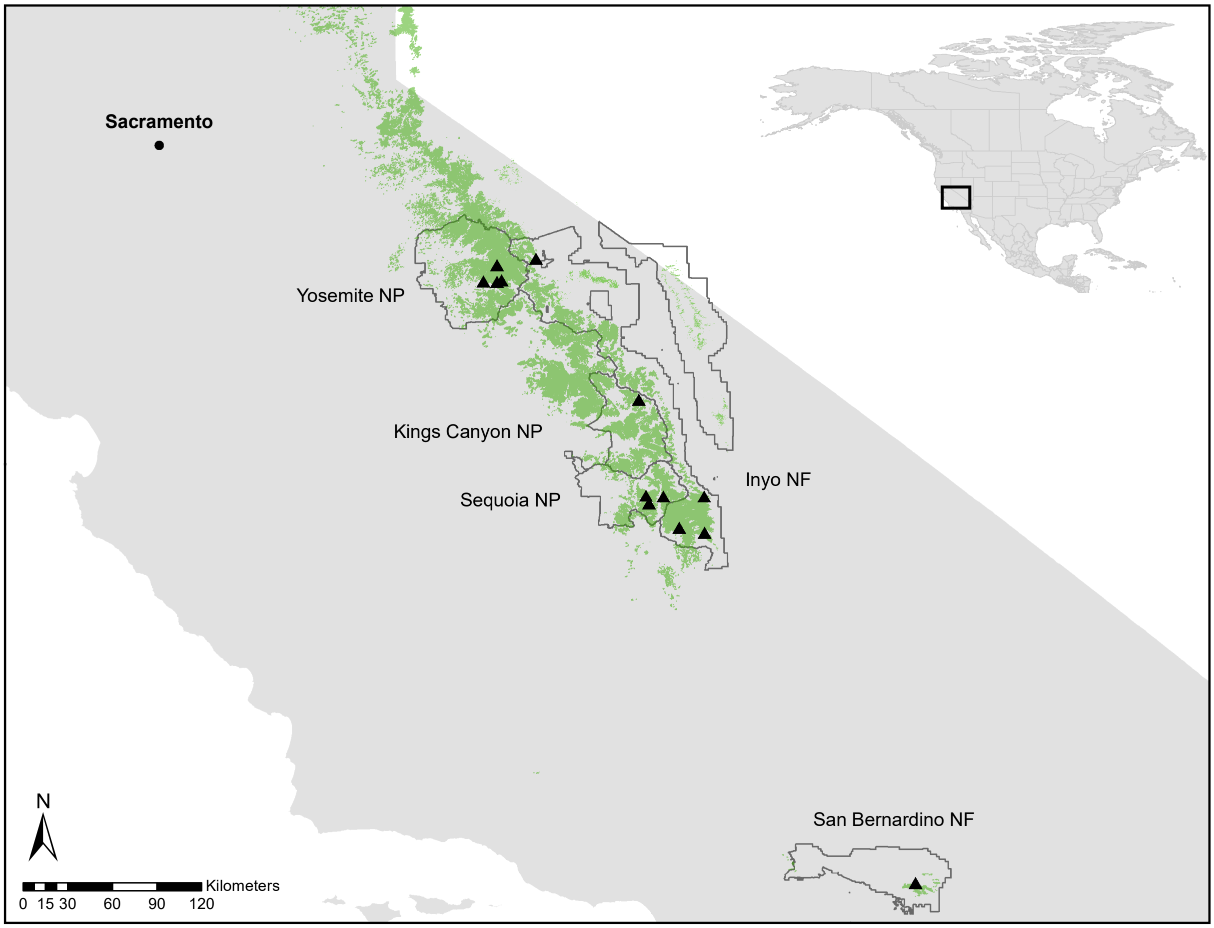

Figure S1.3. Map of the study area in central and southern California, USA. Subalpine forest in the region is shown in light green and fires sampled are represented by black triangles. National parks and forests containing target fires are labeled and outlined in grey.

Figure S1.4. Foxtail pine forest in (a) unburned and (b) severely burned condition, and lodgepole pine forest in (a) unburned and (b) severely burned condition.

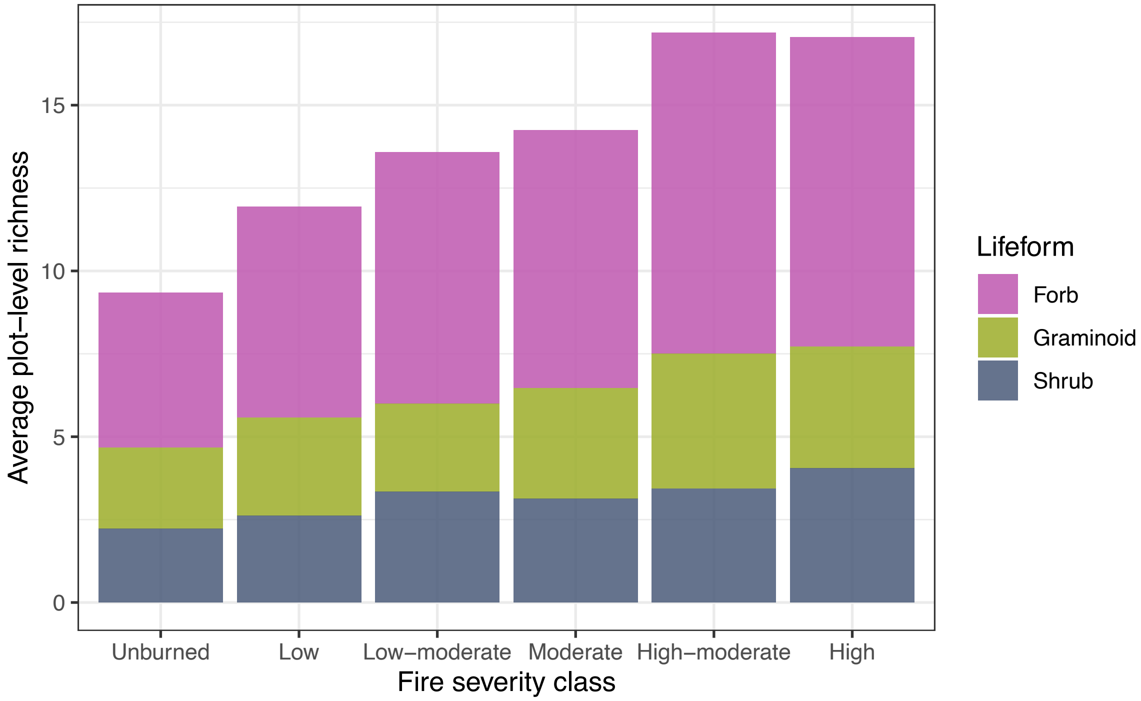

Figure S1.5. A summary of average plot-level richness broken down by lifeform category and shown across fire severity classes. Forbs have higher richness than other lifeform groups in subalpine forest understories in our sample and increase the most after high severity fire.

Chapter 2

Wildfire facilitates upslope advance in a shade-intolerant but not a shade-tolerant conifer

Submitted as:

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Abstract

Wildfire may facilitate climate tracking for forest species moving upslope or north in latitude by eliminating competition from long-lived resident trees. However, while empirical evidence supports wildfire facilitating trailing edge range contractions, it is mixed for wildfire-facilitated leading edge range extensions. Leading edge extensions are especially important in high elevation subalpine forests, which have little available upslope habitat and are expected to be colonized by lower elevation montane species. To understand the impact of wildfire on species range shifts at the montane-to-subalpine ecotone, we used seedling presence-absence data from 248 plots across a gradient of canopy loss from wildfire (fire severity) and spanning 500 km of latitude in subalpine forest. First, we asked whether climatic suitability improved for lower elevation species at our subalpine study sites. Second, we asked whether postfire regeneration of lower elevation species was positively associated with fire severity relative to resident subalpine tree species. Third, we explored how individual tree species contributed to overall recruitment patterns. We found that between 1990 and 2030 predicted climatic suitability grew for the two lower elevation species at our subalpine study sites: 34% for Jeffrey pine (*Pinus jeffreyi*) and 5% for red fir (*Abies magnifica*). In contrast to our expectation, leading edge range expansion (i.e. regeneration of low elevation species at higher elevation) was roughly four times higher in unburned plots relative to burned plots. While high-elevation recruitment of the more common and shade-tolerant red fir seedlings decreased with fire severity, recruitment of the less common and shade-intolerant Jeffrey pine seedlings increased. Fire severity was uncorrelated or weakly positively correlated with postfire regeneration of resident subalpine species. Our results highlight how the impact of wildfire disturbance on species range expansion depends on whether the postfire landscape aligns with each species' regeneration niche.

Introduction

With increasing global temperatures, many species are expected to track their current climatic niches by moving north in latitude (Parmesan et al. 1999, Hickling et al. 2005) or upwards in elevation (Konvicka et al. 2003, Moritz et al. 2008). While upslope habitats may fulfil species' temperature and precipitation requirements (Woodward 1987, Rehfeldt 2006), both dispersal limitation and competition from existing vegetation may impede colonization of newly climatically available habitats (Svenning et al. 2014, Liang et al. 2018). Such competition can limit species transition especially for long-lived and stress tolerant species like trees. It follows that disturbance that removes preexisting vegetation may catalyze species range shifts into newly climatically available habitats (Overpeck et al. 1990, Clark et al. 1996, Chapin et al. 2004). With large-scale disturbance from wildfire increasing in montane forests (Barbero et al. 2015, Williams et al. 2019), we asked whether tree mortality from fire facilitated the upslope movement of lower elevation montane tree species into high elevation subalpine forests.

Evidence for fire as a catalyst of tree range shifts is mixed. Simulation modeling is the most common approach to obtaining such evidence and while some models support disturbance as a facilitator of climate-induced range expansion (Caplat et al. 2008, Moran and Ormond 2015, Stralberg et al. 2018), others do not (Campbell and Shinneman 2017, Liang et al. 2018) or stress that the influence of disturbance may depend its frequency (Moran and Ormond 2015) or severity (Brice et al. 2020). Empirical studies often describe negative impacts of fire on tree regeneration at the warmer, more arid trailing edges of species distributions (Renwick et al.

2016, Davis et al. 2019), but empirical evidence for fire-induced movement at the leading edges of species distributions is less clear (Brice et al. 2020, Hill and Field 2021). In one study, fire increased the magnitude of range shifts towards cooler conditions for two of eight species in the western United States (Hill and Field 2021), indicating that some species may be more likely than others to follow fire into new habitat. We know little, however, about which traits might facilitate such expansion.

Fire generally causes tree mortality and creates open patches for new tree establishment while changing the environment in many other ways that affect colonizing species. Accordingly, species' disturbance-related traits such as regeneration niche and dispersal mechanism are likely to interact with changing climatic suitability to determine which species establish after fire (Loehle 2003). Early successional or pioneer tree species such as pines are more successful after canopy loss from fire than shade-tolerant and later successional trees such as firs or hemlocks (Selter et al. 1986, Gray et al. 2005a); increasing fire disturbance is thus poised to facilitate upward range shifts in early successional species (Meier et al. 2012). In shade-tolerant and later successional species, on the other hand, unfavorable regeneration conditions could slow upslope climate tracking (Loehle 2003, Liang et al. 2018). Similarly, far-dispersing species are more likely to take advantage of severely burned areas (Stevens et al. 2015, Brodie et al. 2021), which may accelerate their response to increasing wildfire upslope. Though theoretical modeling studies abound, observational datasets far-ranging enough to document range shifts are rare.

Climate-induced upslope advance poses a unique risk to high elevation subalpine forests (Bell et al. 2014b). Because they grow on or near mountaintops, subalpine tree species have less available upslope habitat than other tree species and this habitat can be too steep or too geologically young to be suitable (Macias-Fauria and Johnson 2013). Colonization of such upslope habitat is not predicted to keep up with habitat loss at trailing edges (Conlisk et al. 2017), contributing to predictions of substantial reductions in subalpine forests in the near future (Bell et al. 2014b, Thorne et al. 2018). Nonetheless, reproduction has increased for some subalpine species in response to longer growing seasons (Dolanc et al. 2013) and increasing temperatures at their lower range limits (Hill and Field 2021). Lower elevation montane species, on the other hand, are likely to track steep elevational and climatic gradients upslope (Bell et al. 2014b), and trailing edge contractions appear to be common (Bell et al. 2014a, Davis et al. 2019). Such trends will put subalpine species in direct competition with lower-elevation species throughout much of what is currently subalpine forest. Furthermore, while cool temperatures and high precipitation limited fire in most subalpine ecosystems in the past, modern increases in atmospheric aridity correlate with rapidly increasing area burned in subalpine forests (Schwartz et al. 2015, Alizadeh et al. 2021). If fire facilitates the upward movement of migrants from lower elevations, more fire may accelerate changes in species composition in subalpine forest.

Despite the recent trends of increased warming, competition with lower elevation species, and fire in subalpine forests, few empirical studies document the influence of fire on upslope movement into this remote forest type. We provide some of the first empirical data on postfire regeneration patterns in Mediterranean-type, dry-summer biome subalpine forest using an extensive 248-plot network spanning 13 fires and about 500 km of latitude. We ask:

1. Is climatic suitability increasing at our subalpine study sites for the lower elevation tree species poised to potentially migrate upslope?
2. Does seedling occurrence of lower elevation species increase more after wildfire than seedling occurrence of resident subalpine species?
3. How do individual tree species contribute to overall recruitment patterns?

Methods

Study area

We measured tree regeneration in 248 plots following 13 wildfires in subalpine forests in central and southern California. California subalpine forests are unique in North America due to their Mediterranean-type climate where precipitation (750mm-1250mm) falls primarily as snow in winter and monsoonal moisture from thunderstorms punctuates otherwise dry summers (Fites-Kaufman et al. 2007). Historically, the growing season ranged from six to nine weeks (Fites-Kaufman et al. 2007), though earlier snowmelt timing with climate change may have already extended the season to 11+ weeks (Westerling et al. 2006). Subalpine forests grow primarily on rocky, poorly developed soils or talus, which contribute to a heterogeneous distribution of forest cover, with sparse trees and bare rock interspersed with patches of denser tree cover (Millar and Rundel 2016). Wildfire was historically infrequent (57-338 years in sampled stands in the Sierra Nevada and regularly thousands of years in foxtail pine stands) and of variable severity depending on dominant tree species, stand density, and weather conditions (Rourke 1988, Meyer and North 2019). The California subalpine fire regime contrasts with wet-summer biome subalpine forests such as those in the Rocky or Cascade mountain ranges where historical fires were also infrequent, but generally of high severity (Veblen et al. 1991).

We sampled within latitude-specific estimated elevation for subalpine forest (Millar and Rundel 2016) and where dominant tree species were characteristic of subalpine forest according to the Classification and Assessment with Landsat of Visible Ecological Groupings or CALVEG (USDA 2004, Sawyer et al. 2009). Within the CALVEG subalpine tree species, we differentiate between high elevation specialists (species that occur only in subalpine forest: southern foxtail pine, whitebark pine [*P. albicaulis*], mountain hemlock [*Tsuga mertensiana*], and limber pine [*P. flexilis*]) and high elevation generalists (species that occur across a broader elevation range but typically form stands in California subalpine forest: lodgepole pine [*P. contorta ssp. murrayana*], western white pine [*P. monticola*], and Sierra juniper [*Juniperus grandis*]). We also observed seedlings, saplings, and occasional adults of two lower elevation conifers that do not typically form stands in subalpine forest: Red fir (*Abies magnifica*) and Jeffrey pine (*P. jeffreyi*). Homogeneous red fir forest generally borders lower subalpine forest in the Sierra Nevada (Meyer and North 2019). In contrast to the open canopies and generally shade-intolerant species of subalpine forests and woodlands, red fir forests are characterized by denser canopy cover and red fir seedlings are relatively shade-tolerant (Table 2.1; Safford et al. 2021). Jeffrey pine produces shade-intolerant seedlings and generally occurs in dry and open, single-species, or mixed conifer stands in more stressful environments below the red fir zone (Safford and Stevens 2017). Though individual Jeffrey pine are occasionally found at subalpine elevations on the east side of the southern Sierra Nevada on dry slopes (see elevation range in Table 2.1), it is generally a component of lower elevation (montane) mixed conifer forests (Safford and Stevens 2017).

Fire and plot selection

We selected fires in subalpine forest that were less than two days hiking from trailheads and that contained the full range of fire severity across the following six classes of basal area mortality (which were also used for stratification of gridded plot locations): 0, <25%, 25-50%, 50-75%, 75-90%, and >90% (Welch et al. 2016, Stewart et al. 2021). We calculated percent basal area mortality using the remotely sensed fire severity metric, relative differenced Normalized Burn Ratio (RdNBR; 30-m resolution; J. D. Miller & Thode, 2007) as in Miller et al. (2009). We sampled all ten fires that fit our criteria at the time of sampling as well as another three that did not contain all fire severity classes but were easy to access (Fig. 2.1). Fires sampled ranged from 2-17 years post-fire at the time of sampling (for more information about fires sampled see Table S2.1).

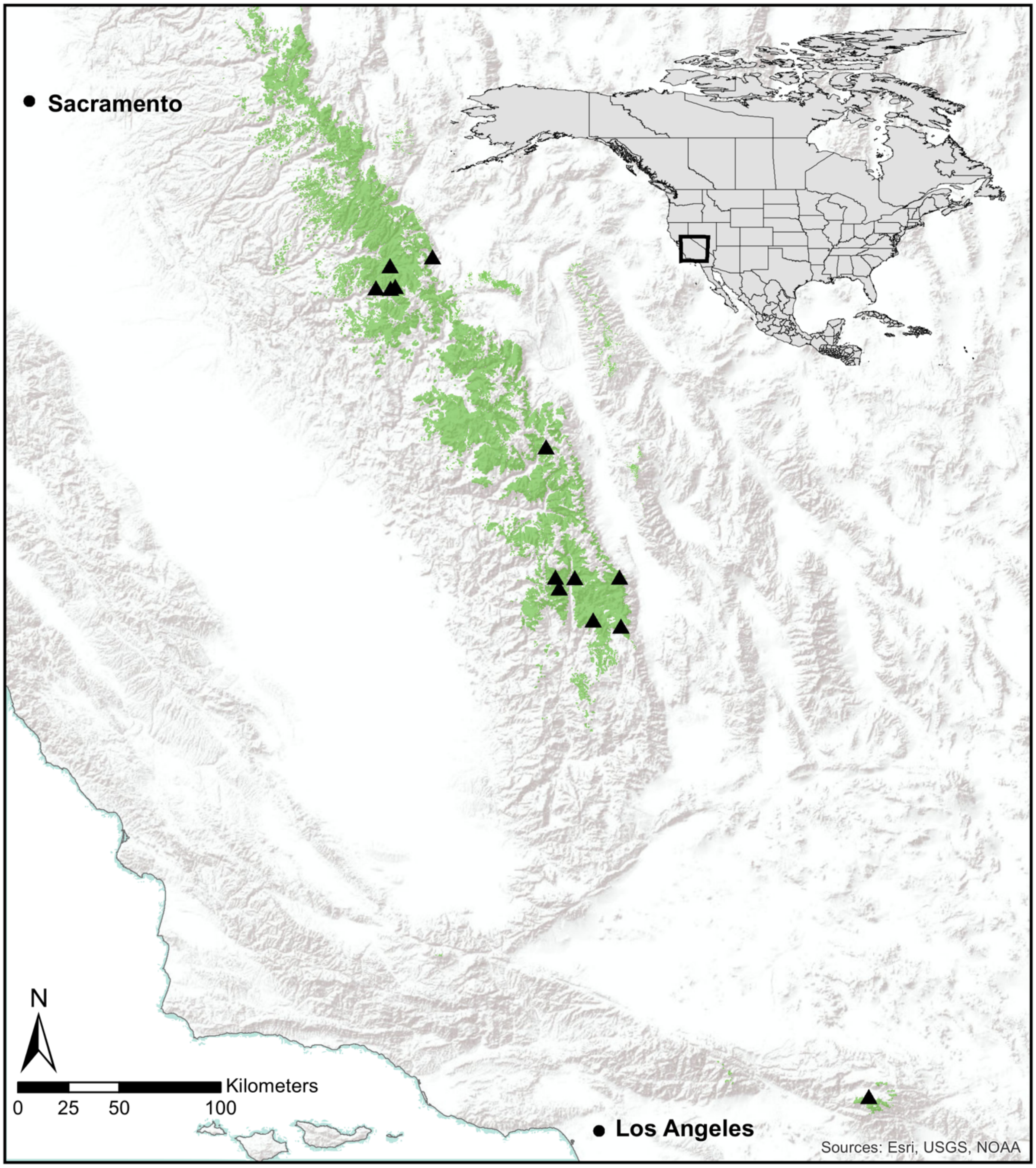

Figure 2.1. Map of the study area in central and southern California, USA. Subalpine forest in the region is shown in light green and fires sampled are represented by black triangles.

Siting plot centers at the nodes of a 200x200 m spatial grid overlaying a digital elevation model and fire severity map, we established 0.1-hectare circular plots (11.37 m radius; hereafter, "main plot") stratified across the fire-caused basal area mortality classes and aspect. Within each plot, we visually estimated percent shrub cover and identified any seedlings (<1.37 m tall) or saplings (<7.6 cm diameter at breast height) to species. In a 60 m^2 regeneration subplot (4.37 m radius; hereafter "regeneration plot") at plot center, we performed an exhaustive search for conifer seedlings, which we identified to species, tallied, and aged using terminal bud scars (Welch et al. 2016). Due to the open nature of subalpine forest understories, regeneration subplots were mostly clear of obstructions (i.e. shrub cover) and it was relatively easy to locate seedlings.

Characterizing recent changes in climatic suitability for lower elevation species

To determine whether climate suitability was increasing for lower elevation species in our study area, we calculated the change in suitability for red fir and Jeffrey pine at study plot locations between 1990 and 2030 using suitability maps from the USDA Forest Service Rocky Mountain Research Station (accessed November 2021: https://www.fs.usda.gov/ccrc/tool/plant-species-and-climate-profile-predictions). Maps are derived from random forest models that fit species occurrence records to 35 historical climate variables derived from gridded climate surfaces (Crookston et al. 2010). Future climate estimates were calculated from three general circulation climate models (Canadian Center for Climate Modeling and Analysis [CCSM4], Geophysical Fluid Dynamics Laboratory [GFDL-CM3], and Hadley Center/World Data Center [HadGEM2-ES]) and two emissions scenarios (Representative Concentration Pathways [RCPs] 4.5 and 8.5), for a total of six possible scenarios. The climate models represent a range of predictions for precipitation in California, from drier (GFDL-CM3) to wetter (HadGEM2-ES) (Kattsov et al.

2013, Coffield et al. 2021), and the RCPs represent 4.5 (moderate) and 8.5 (high) watts/m^2 additional radiative forcing by 2100 respectively. We used two-sided t-tests with Bonferroni correction for six tests to determine whether changes in suitability were different from zero.

Characterizing fire severity and high severity patch size in the study area

Regeneration failure often occurs in large patches of high severity wildfire due to lack of seed dispersal from distant patch edges (Welch et al. 2016, Shive et al. 2018). We quantified the amount of high severity patch area far from patch edges by calculating a stand-replacement decay coefficient using the PatchMorph tool in R (Girvetz and Greco 2007, Collins et al. 2017). We also compared the proportion of fire in different severity classes to historical estimates of fire severity for California subalpine forests (Meyer and North 2019). We used RdNBR values from within fire perimeters for the seven fires that burned solely within subalpine forest and from within perimeters clipped to patches sampled in subalpine forest for the six fires that burned up from lower elevations. Because clipping necessarily reduces the size of high severity patches near edges, we performed separate analyses for (a) fires that burned entirely in subalpine forest and (b) all fires.

Linear models

Candidate predictor variables

To unconfound the influence of fire and fire severity on regeneration and produce more realistic model effect sizes, we performed model selection with a variety of candidate predictors that have been found to be important for conifer regeneration in western North American forests (Table 2.2; reviewed in Stevens-Rumann and Morgan 2019). We used bilinear interpolation to extract candidate predictor variables from raster surfaces describing fire severity (as basal area mortality – see *Plot and fire selection* above), topography, seed availability, and both long- and short-term climate variables. We obtained slope and aspect from a 30-m resolution digital elevation model (U.S./Japan ASTER Science Team 2019) and long- and short-term climate and weather data from the 270-m resolution Basin Characterization Model version 8 (Flint et al. 2013).

Topographic elements such as slope and aspect are important fine-scale indicators of regeneration conditions because they influence the amount of light and heat a seedling receives (Welch et al. 2016). We used the `spatialEco` package in R (Evans 2021) to calculate heat load index at each plot, a measure of incident radiation scaled with aspect so that radiation is stronger on warmer (i.e. southwesterly) slopes (McCune 2007).

We estimated plot-level seed availability using 30-m resolution maps of 2017 predicted conifer species basal area that incorporate disturbances from before 2017 (Ohmann et al. 2011). From species basal area, we calculated species specific seed production (Greene and Johnson 1994: Eqs 2 and 5) and finally seed density (in seeds/m^2) using a half-Gaussian dispersal kernel and a 75-m dispersal parameter (σ; Stewart et al. 2021). Our selected dispersal parameter corresponds to a mean dispersal distance of 60 m with 95% of seeds falling within 147 m of seed trees. Due to a lack of empirical knowledge regarding mean taxon-specific dispersal distances and in an effort to reduce over-fitting, our dispersal parameter represents a mid-range value compared to dispersal parameters calculated via model fit in a recent study of mixed-conifer regeneration in California (Stewart et al. 2021). While an on-the-ground measure of distance to seed source could be more precise, our seed density estimates allow us to account for the influence of all nearby trees (including their size and density)—not just the nearest tree of each species visible from plot center.

At each plot, we extracted climate variables from gridded datasets and calculated 30-year normal (between 1981 and 2010) and post-fire (ranging from 2-17 years) averages. While averaging across only the first 3-5 post-fire years is common where an immediate post-fire pulse in regeneration drives longer-term trends (Harvey et al. 2016, Urza and Sibold 2017), we observed consistent regeneration rates across time at many of our fires (Fig. S2.1). We calculated precipitation and climatic water deficit (CWD; a measure of potential evapotranspiration minus actual evapotranspiration that is often used to capture droughtiness (Stephenson 1990, 1998)) across the snow-free growing season (July-September) because seedling establishment and growth are more sensitive to summer monsoonal moisture than to snowpack in the harsh high elevations of the study system (Smithers and North 2020). We calculated growing degree days (GDD; a measure of growing season length) using daily temperatures with a base temperature of 0°C (Urza and Sibold 2017).

In addition to average climate and post-fire weather, we calculated the anomaly of post-fire weather and extreme post-fire weather compared to long-term climate as z-scores (as in Young et al. 2019). Post-fire weather anomaly is calculated relative to long-term averages and variability at each plot, which aids in comparing the influence of post-fire weather across a wide geographic range. One extreme post-fire weather year could also be influential for seedling presence-absence (Young et al. 2019). To account for the possibility of outsized influence, we calculated "extreme" post-fire weather anomaly using the post-fire year with minimum precipitation, maximum CWD, and maximum GDD.

Table 2.1. Tree species sampled in study area with relevant reproductive and fire-related traits (Abrahamson 2003, Sawyer et al. 2009).

	Elevation range	Study designation	Seed dispersal	Shade tolerance	Reproductive age	Fire resistance
red fir	1200-2800 m	Low elevation	Wind	Moderate	30–600 years	Fire-hardy; thick epidermis; low flammability
Jeffrey pine	450-3100 m	Low elevation	Animal; wind	None	8–500 years	Fire-hardy; thick epidermis
mountain juniper	100-3100 m	High elevation	Animal; gravity; water	Moderate	20+ years	Fire-sensitive; thin epidermis; high flammability; no/low sprouter; canopy architecture susceptible
whitebark pine	2000-3700 m	High elevation specialist	Animal	None	20–700 years	Fire-sensitive; thin epidermis; high flammability; no/low sprouter

southern foxtail pine	2700-3700 m	High elevation specialist	Animal; gravity; wind	None	20–1500 + years	Fire-hardy; thick epidermis; canopy architecture resistant
lodgepole pine	1000-3500 m	High elevation	Animal; wind	Moderate	4–600+ years	Fire-sensitive; thin epidermis; no/low sprouter
limber pine	1830-3700 m	High elevation specialist	Animal	None	20–1000 years	Fire-sensitive; thin epidermis; no/low sprouter
western white pine	150-3400 m	High elevation	Wind	Moderate	2–400+ years	Fire-hardy; thick epidermis; canopy architecture resistant
mountain hemlock	1200-3500 m	High elevation specialist	Wind	High	20–250 years	Fire-sensitive; high flammability; no/low sprouter; canopy architecture susceptible

Table 2.2. Candidate predictor variables used in model selection broken into core and climate variable categories. An asterisk indicates that the variable is included in every model.

Type	Candidate predictor variable	Description

Core	Fire	Fire severity or Burned/unburned*	Fire severity as percent basal area mortality calculated from the relativized normalized delta burn ratio (RDNBR), 30-m resolution (Miller and Thode, 2007)
		Time since fire*	Time since fire at sampling
	Biological	Seed availability*	Number of seeds per square meter, calculated using 30-m resolution maps of conifer basal area (Ohmann et al. 2011) and half-gaussian dispersal kernel as in Stewart et al. (2021)
		Shrub cover	Ocular estimate of percent shrub cover in 405 square meter main plot
	Topographic	Heat load index	A measure of incident solar radiation that combines latitude, slope, and folded aspect such that radiation is stronger on warmer (i.e. southwesterly) slopes (Mccune and Keon 2002)
Climate	Long-term	30-yr average climatic water deficit	Average growing season (July-Sept) climatic water deficit 1981-2010
		30-yr average precipitation	Average growing season (July-Sept) precipitation 1981-2010
		30-yr average growing degree days	Average annual number of days with mean temperature greater than 0 °C 1981-2010
	Short-term (post-fire)	Post-fire climatic water deficit	Average growing season (July-Sept) climatic water deficit for post-fire period (range: 2-15 years)
		Anomaly post-fire climatic water deficit	Departure (z-score) of post-fire climatic water deficit from 30-yr average
		Anomaly maximum post-fire climatic water deficit	Departure (z-score) of maximum post-fire climatic water deficit from 30-yr average
		Post-fire precipitation	Average growing season (July-Sept) precipitation for post-fire period (range: 2-15 years)
		Anomaly post-fire precipitation	Departure (z-score) of post-fire precipitation from 30-yr average
		Anomaly minimum post-fire precipitation	Departure (z-score) of minimum post-fire precipitation from 30-yr average

Post-fire growing degree days	Average annual growing degree days for postfire period (range: 2-15 years)
Anomaly post-fire growing degree days	Departure (z-score) of postfire growing degree days from 30-yr average growing degree days
Anomaly maximum post-fire growing degree days	Departure (z-score) of maximum postfire growing degree days from 30-yr average growing degree days

Data preparation

Because our study included part or all of seven high elevation conifer distributions—including California endemic southern foxtail pine (Kauffmann 2013)—we limited plots included in species-specific analyses to those where the species was present nearby or within the fire perimeter (which can also be viewed as number of trials in the Bernoulli model). We marked a species as absent from the plot only when adults or seedlings of that species were present within the fire perimeter. We assumed that the presence of the same species close by meant that the absence of that species in the regeneration plot was not because the plot was too far outside the species' current range.

Model selection

To understand if lower elevation species regenerated with greater success than resident subalpine species after high severity fire, we tested whether the interaction of fire severity and tree species "typical elevation" (low versus high and high elevation specialist; Table 2.1) influenced the presence or absence of post-fire seedlings. We chose to model seedling presence-absence rather than abundance both because several "jackpots" (very high abundance values) in our dataset hindered model fit and because presence-absence is more sensitive at species range limits (Pironon et al. 2017). We used a Bayesian generalized linear model with a Bernoulli likelihood (Bürkner 2017) and constrained the dataset to plots with evidence of reproductive adults from both typically high- and low-elevation tree species in the general area (n = 157; see *Data preparation* above). To evaluate species-specific differences in regeneration patterns and influences, we fit separate models for those species with more than 20 observations of post-fire seedlings in the regeneration subplot (i.e. positive trials; Table S2.2): western white pine (total trials or n = 179), southern foxtail pine (n = 129), lodgepole pine (n = 248), and red fir (n = 157). There were only eight post-fire observations of Jeffrey pine in regeneration subplots, but there were 22 observations in main plots. While observations from the main plot were not aged and therefore could not be separated into pre- and post-fire categories, we still chose to use main plot observations to model Jeffrey pine seedling and sapling occurrence (n = 157). All other species had too few observations for species specific modeling. All models contained a random intercept for fire to account for un-modeled differences between fires.

We employed a robust two-step model selection procedure using clustered (or leave-one-fire-out) cross validation. Clustered cross validation curbs over-fitting by repeatedly testing the model on groups—in this case, fires—that are withheld from the training dataset (Roberts et al. 2017). We used the sum of the expected log pointwise predictive density (elpd) for all withheld fires (k-fold elpd) to select models. We included fire severity, time since fire, and seed availability in each model and first found the combination of heat load index and shrub cover that maximized k-fold elpd (the "Core" predictors from Table 2.2). We subsequently tested each climate and weather variable (Table 2.2) to determine whether it further increased k-fold elpd. For the best model (highest k-fold elpd) only, we tested whether any of the remaining and uncorrelated ($\rho < 0.65$) climate variables further increased model predictive capacity. If model performance increased with an additional weather or climate variable, we also tested their interaction.

In addition to elpd, we used k-fold predictions to calculate area under the receiver operating curve (AUC), an absolute measure of model fit that ranges from 0-1 with 0.5 indicating random prediction and 1 perfect prediction (Fielding and Bell 1997). Finally, we calculated Moran's I using a k-Nearest Neighbors distance matrix (k=15) and examined semivariograms to determine whether model residuals within fires were spatially autocorrelated. All analyses were performed in R Version 4.0.0 (R Core Team 2020).

Results

Characterizing recent changes in climatic suitability for lower elevation species

Between 1990 and 2030, mean red fir suitability at study plot locations increased by 5% across all climate model and emissions scenarios. Red fir suitability increased more under the RCP8.5 (high) emissions scenario (8-13%) and did not change ($p<0.5$) or decreased (-5%) under the RCP4.5 (moderate) emissions scenario (Fig. 2.2). All climate model and emissions scenarios predicted increased suitability (23-46%, mean 34%) for Jeffrey pine in subalpine forest by 2030.

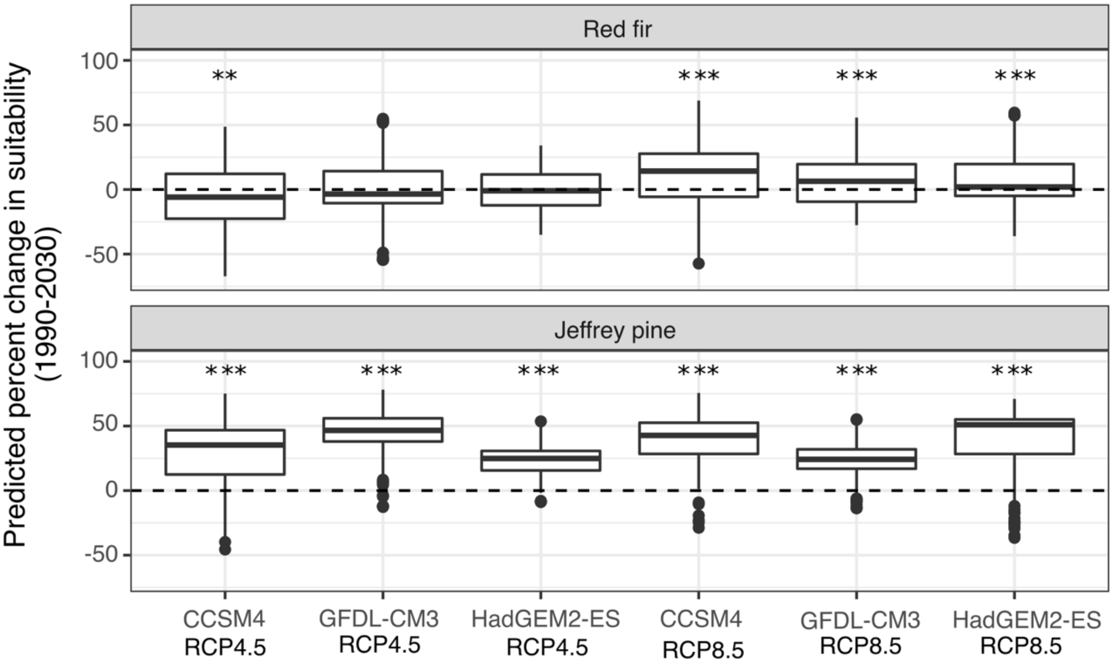

*Figure 2.2. Box plots show the change in suitability between 1990 and 2030 for red fir and Jeffrey pine—typically lower elevation species—in the subalpine plots that we sampled under six climate model and emissions scenarios. Asterix indicates a non-zero difference (*p < 0.05, **p < 0.01, ***p < 0.001) in suitability based on a two-sided t-test with Bonferroni correction for six tests.*

Characterizing fire severity and high severity patch size in the study area

Across all study fires (both those that burned entirely in subalpine forest and the clipped portions of those that burned into subalpine forest from below), 18% of fire area was high severity, 33% moderate severity, 32% low severity, and 17% unchanged (Fig. S2.2). The percentage of unchanged area was less and the percentage of high severity area more for fires that burned entirely in subalpine forest, with 27% high severity, 32% moderate severity, 36% low severity, and 6% unchanged (Fig. S2.2).

High severity patches were relatively small in study fires, with all high severity patch area within 200 m of patch edges. When more high severity patch area is further from the patch edge — as is true of more circular patches with simpler edges — the stand-replacing decay coefficient is smaller (Collins et al. 2017). The stand-replacing decay coefficient was 0.00905 for all fires combined and 0.005818 for fires that burned only within subalpine forest, indicating that subalpine-only fires not only had more high severity fire but that it was contained in larger and/or simpler patches (Fig. S2.2).

Typically "high" versus "low" elevation species

We found that fire severity had no influence on the probability of post-fire seedling presence (effect size: -0.01; 95% CI: [-0.40, 0.36]) in subalpine forest when species differences were not accounted for. However, the interaction between fire severity and species typical elevation (high versus low) was negative (-0.75; 95% CI: [-1.38, -0.13]), indicating that post-fire seedling presence generally declined with increasing fire severity for typically low elevation species but did not change for typically high elevation species (Fig. 2.3; Table S2.3). Overall, we found fewer typically low elevation species than typically high elevation species in subalpine forest (-0.99; 95% CI: [-1.82, -0.15]). For all species combined, time since fire (2.19; 95% CI: [0.82, 3.74]) and seed availability (1.03; 95% CI: 0.55, 1.58]) increased the probability of post-fire seedling presence, and anomaly of post-fire climatic water deficit (-1.18; 95% CI: [-2.20, -0.24]) decreased the probability of post-fire seedling presence (Fig. 2.3).

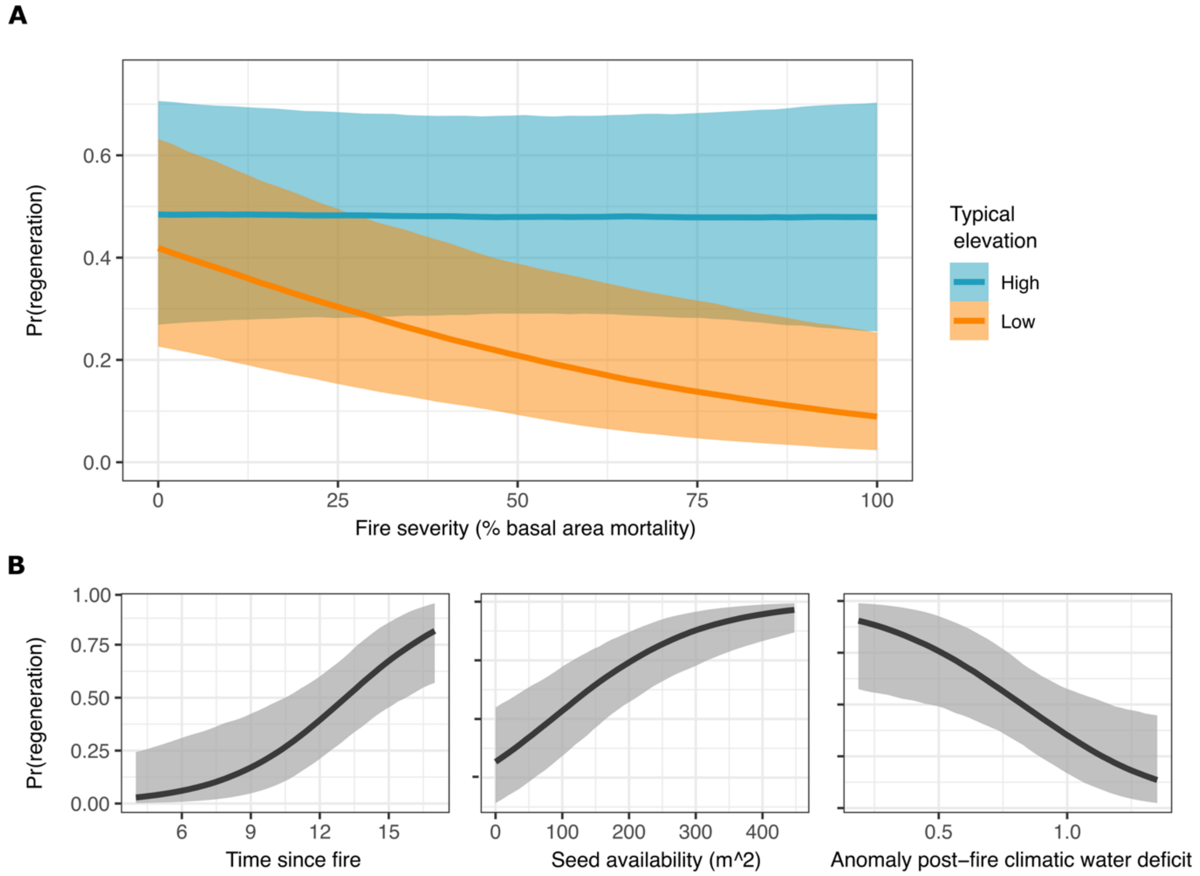

Figure 2.3. Pr(regeneration)—the probability that a 60 square meter plot contains at least one post-fire seedling—changes little with fire severity for typically high elevation species and

decreases with fire severity for typically low elevation species (here combined red fir and yellow pine) (A). Regardless of species typical elevation, Pr(regeneration) is positively correlated with time since fire and seed availability and negatively correlated with anomaly of post-fire climatic water deficit (B). Lines and shading show model-estimated mean and 95% CI.

Species specific models

For foxtail pine (Fig. 2.4; Table S4; AUC = 0.81), normal growing season precipitation had the greatest positive effect on the probability of postfire seedling occurrence (1.58; 95% CI: [0.39, 2.88]), while shrub cover negatively affected the probability of post-fire seedling occurrence (-0.92; 95% CI: [-1.73, -0.25]). Both fire severity (0.36; 95% CI: [-0.18, 0.91]) and seed availability (0.34; 95% CI: [-0.19, 0.93]) had weak positive effects on postfire seedling occurrence (their 80% CI's did not cross zero). Time since fire (0.49; 95% CI: [-0.92, 2.00]) had no detectable effect.

For western white pine (Fig. 2.4; Table S2.5; AUC = 0.68), the greatest positive predictor of postfire seedling occurrence was seed availability (0.84; 95% CI: [0.34, 1.41]), with time since fire also having a weak effect (1.21; 95% CI: [-0.67, 3.23]). The influence of fire severity (-0.25; 95% CI: [-0.74, 0.21]), and anomaly of post-fire climatic water deficit (-0.67; 95% CI: [-1.99, 1.06]) were undetectable.

For lodgepole pine (Fig. 2.4; Table S2.6; AUC = 0.60), time since fire (0.73; 95% CI: [0.14, 1.38]) and seed availability (0.62; 95% CI: [0.23, 1.02]) had positive effects on the probability of postfire seedling occurrence. Postfire growing degree days had a weak positive effect (0.34; 95% CI: [-0.14, 0.82]), while we found no effect of fire severity (0.03; 95% CI: [-0.31, 0.36]).

For red fir (Fig. 2.4; Table S2.7; AUC = 0.85), the strongest positive predictor of postfire seedling occurrence in subalpine forest was time since fire (2.69; 95% CI: 0.95, 5.04]), followed by anomaly of maximum postfire growing degree days (1.23; 95% CI: 0.44, 2.49]), and seed availability (0.43; 95% CI: -0.03, 0.98]). Fire severity had a negative influence on postfire red fir seedling occurrence (-1.17; 95% CI: [-1.94, -0.48]).

Our model of Jeffrey pine seedling occurrence produced poor predictions (Fig. 2.4; Table S2.8; AUC = 0.54), but still provided significant inference that Jeffrey pine seedling occurrence increased with fire severity in subalpine forest (0.63; 95% CI: 0.16, 1.12]). Neither time since fire (0.09; 95% CI: [-0.85, 1.11]) nor seed availability (0.12; 95% CI: [-0.62, 0.69]) had a discernable effect on Jeffrey pine seedling occurrence.

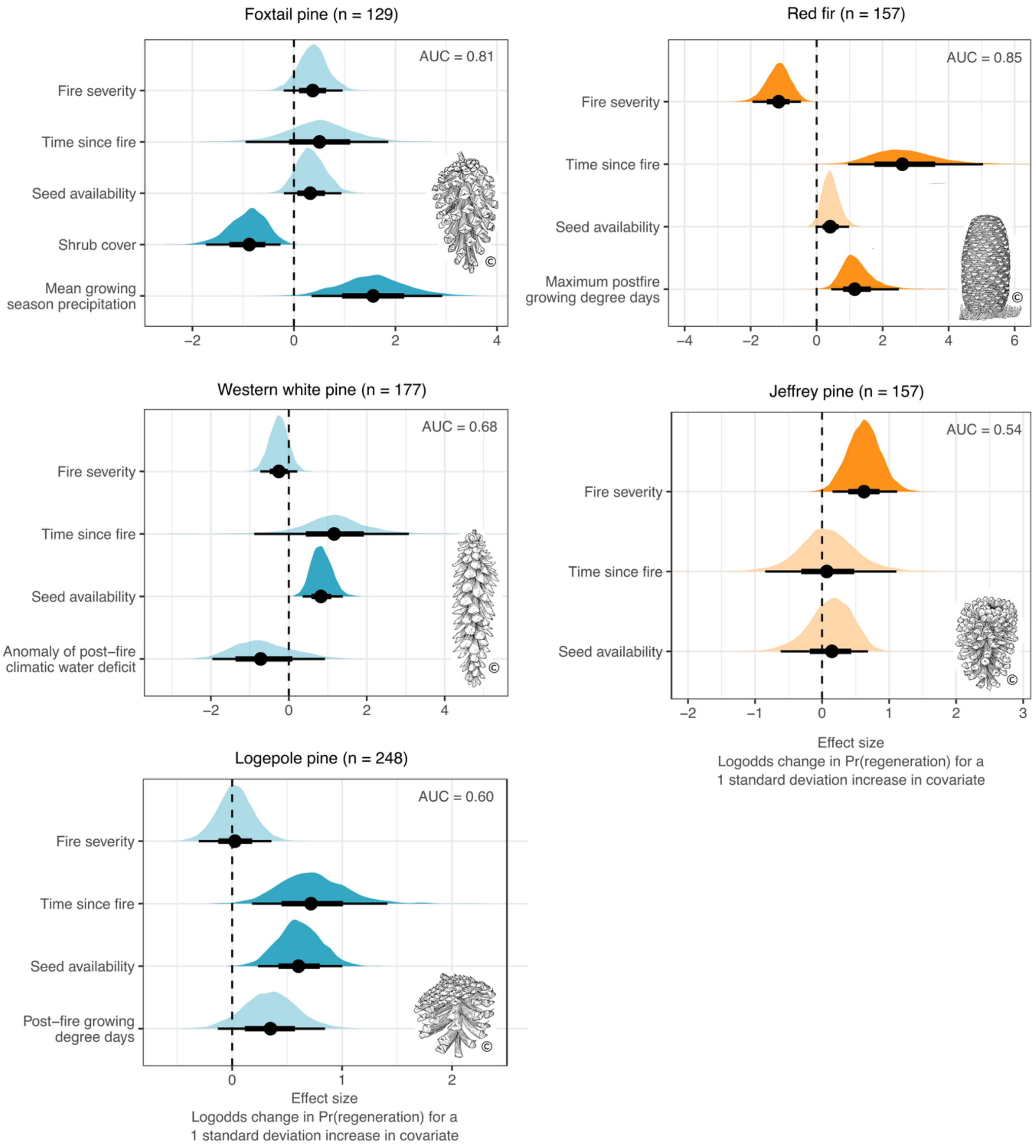

Figure 2.4. Plots showing the effect size of predictors on Pr(regeneration) for foxtail pine, western white pine, lodgepole pine, red fir, and Jeffrey pine in subalpine forest. Pr(regeneration) is the probability that a 60 square meter plot (405 square meters for Jeffrey pine) contains at least one post-fire seedling (seedling of any age for Jeffrey pine). Black dots and bars show

model estimated means with 80 and 95% CI. Shading shows distribution of the mean, with darker shading indicating that the 95% CI does not cross zero. Blue shading represents typically higher elevation species, and orange shading represents typically lower elevation species. AUC = Area Under the receiver operating Curve, a measure of model classification accuracy (range 0-1). Drawings from the Jepson eFlora (Jepson Flora Project eds., 2021, [https://ucjeps.berkeley.edu/eflora/] - © Regents of the University of California), used with permission.

Figure 2.5. Jeffrey pine seedling in high severity patch of burned foxtail pine forest with no Jeffrey pine adults in sight; a phenomenon that continually surprised us in the field!

Discussion

Our results contrast with the theoretical prediction that disturbance facilitates climate tracking by reducing competition from existing vegetation (Clark et al. 1996, Svenning et al. 2014). Despite predicted increases in climatic suitability for lower elevation tree species in our study area (Fig. 2.2), lower elevation regeneration was more than four times as likely to occur in unburned than severely burned subalpine forest (Fig. 2.3). Greater regeneration of lower elevation species in unburned areas suggests that, overall, competition may not currently be a major force preventing climate tracking in California subalpine forests (Svenning et al. 2014, Liang et al. 2018). However, individual species regeneration occurrence differed greatly along a fire severity gradient. Regeneration of red fir, which contributed most to trends for lower elevation species in the combined model, decreased steeply with increasing fire severity (Fig. 2.4). Red fir seedlings and saplings are moderately shade tolerant (Sawyer et al. 2009) and require partially shaded microsites for regeneration (Ustin et al. 1984, Selter et al. 1986, Chappell and Agee 1996). The prevalence of shade in unburned subalpine forest may allow red fir to colonize new habitat in unburned—though relatively open—subalpine forest, but not after fire-caused canopy mortality reduces tree cover. It follows that where fire produces newly available habitat *and* appropriate regeneration conditions, species should be more likely to move into that new habitat.

Indeed, we found that shade-intolerant (Gray et al. 2005b) Jeffrey pine seedlings and saplings were more likely to pioneer subalpine forest with increasing fire severity (Fig. 2.4; Fig. 2.5). Alongside an average predicted 34% increase in climatic suitability at our study sites by 2030 (compared to 5% for red fir), our results suggest that Jeffrey pine may be the most likely species to colonize future subalpine forests under predicted increases in fire and temperature (Thorne et al. 2018, Alizadeh et al. 2021, Remy et al. 2021). Our findings align with recent modeling studies, which found that Ponderosa pine (*Pinus ponderosa*)—an ecologically close and more widespread relative of Jeffrey pine (McCune 1988)—was one of only two species that expanded to higher elevations under future climate and disturbance scenarios (Remy et al. 2021) or was the most likely to do so (Campbell and Shinneman 2017). Compared to the high elevation species it replaced in simulation, ponderosa pine was adapted to warmer and drier conditions (Remy et al. 2021). Jeffrey pine, on the other hand, shares many traits with high elevation specialist pines such as primarily animal-dispersed seeds (Vander Wall 2008), shade intolerance, and the ability to withstand stressful xeric conditions and high UV exposure (Gray et al. 2005b, Staszak et al. 2007, Legras et al. 2010). Jeffrey pine's relatively high growth rate and short lifespan compared to the high elevation specialist pines (McCune 1988) may present its greatest advantage in areas where the two grow together.

The contrasting postfire responses of a shade-tolerant (red fir) and a shade-intolerant (Jeffrey pine) species are consistent with an interaction between climate-induced range shift and regeneration niche. Our results align with simulation models showing that early successional species are more likely to undergo range shifts than later successional species (Meier et al. 2012) and that disturbance slows the invasion rate of shade-tolerant species due to lower growth rates under high light conditions (Loehle 2003). While empirical studies are few, Landhäusser et al. (2010) found that mechanical disturbance increased the upslope movement of highly shade-intolerant (Sawyer et al. 2009) aspen seedlings (*Populus tremuloides*). In addition to the high light environment, seedlings responded positively to exposed mineral soil and in concave microtopographic positions (Landhäusser et al. 2010), indicating that disturbance enhanced regeneration conditions in a variety of ways. However, not all empirical examples of disturbance-mediated range shifts feature shade-intolerant species. Hill and Field (2021) found that fire enhanced seedling-only movement into cooler areas for Douglas fir (*Pseudotsuga menziesii*) and canyon live oak (*Quercus chrysolepis*), whose seedlings and saplings are moderately shade-tolerant and shade-tolerant, respectively (Sawyer et al. 2009). It may be that fire increases the quality of regeneration conditions in some other way for Douglas fir and canyon live oak such as clearing litter and duff to expose bare mineral soil (as with aspen [Landhäusser et al. 2010]) or increasing nutrient availability (Busse et al. 2014).

We found that regeneration was greater after fire for southern foxtail pine, which is phylogenetically and ecologically closely related to the other high elevation specialist pines in the region (e.g. whitebark and limber pine; McCune 1988). With their high-calorie seeds, high elevation specialist pines are often keystone species (Tomback et al. 2001), and their forests maintain snowpack for water provisioning to humans and animals at lower elevations (Messerli et al. 2004). Our work demonstrates that fires burning within their historical range of variation for severity (Meyer and North 2019) and with moderately sized high severity patches can stimulate regeneration in large populations of foxtail pine. Our results align with evidence for increased regeneration of whitebark pine after fire (Slaton et al. 2019) and beetle disturbances

(Meyer et al. 2016) as well as with the designation of white pines as both an early successional and a climax species (Arno 2001). Based on our finding that red fir encroachment into the subalpine zone was most common in unburned areas (Fig. 2.4), we suggest that fire may advantage foxtail pine over red fir. However, the opposite is likely true for Jeffrey pine. While our Jeffrey pine model predicts regeneration at a much larger scale—that of the 405m^2 main plot rather than the 60m^2 regeneration subplot—it indicates that high severity fire increases the unlikely event of Jeffrey pine regeneration in subalpine forest (Fig. 2.4; Fig. 2.5).

Beyond the influence of fire, we found that summer monsoonal moisture was important for foxtail pine regeneration. Our results again mirror findings for a closely related high elevation specialist pine that occupies xeric, dry-summer environments (Smithers and North 2020). Temperature rather than precipitation is thought to play the primary role in limiting the upper elevation of timberline tree species (Salzer et al. 2009), but seedlings often have narrower tolerances (Dobrowski et al. 2015) and may require moisture at the soil surface (presumably from more recent precipitation) to survive (Smithers and North 2020). Lastly, while fire-stimulated shrub cover is much-reduced in subalpine forests in comparison to lower elevation forests in the Sierra Nevada (Brodie et al. 2021), our finding that shrub cover negatively impacts regeneration for a shade-intolerant species is in alignment with results from lower elevation forests in the region (Tubbesing et al. 2020).

We found that regeneration probability for pines that were not high elevation specialists (lodgepole and western white pines) did not change with fire severity and increased with seed availability and time since fire (Fig. 2.4). Both species are moderately shade tolerant (Table 2.1), reducing the likelihood that they would respond positively either to shadier unburned stands or high light in burned areas. That both species were positively influenced by seed availability (based on the modeled presence of conspecific adults) and time since fire aligns with our current understanding of conifer regeneration in the western United States (Stevens-Rumann and Morgan 2019).

Conclusions

Our results highlight the importance of the interaction between climatic suitability and species traits when predicting future plant communities under increasing disturbance and climate change. We show that simply reducing competition from existing vegetation may not be enough to facilitate species range tracking, but that the postfire environment must also provide suitable regeneration conditions. Thus, removal of canopy cover through moderate to severe disturbance may disadvantage shade-tolerant species like red fir, perhaps impeding rather than facilitating their upslope movement. Conversely, shade-intolerant species with wind and animal dispersed seed like Jeffrey pine may be more likely to move upslope into small (<200m radius) high severity patches. Such patterns suggest that fire within the natural range of variation for California subalpine forests may advantage high elevation specialist white pines over encroaching red fir while simultaneously providing establishment opportunities for Jeffrey pine in newly climatically available habitat.

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Supplementary information

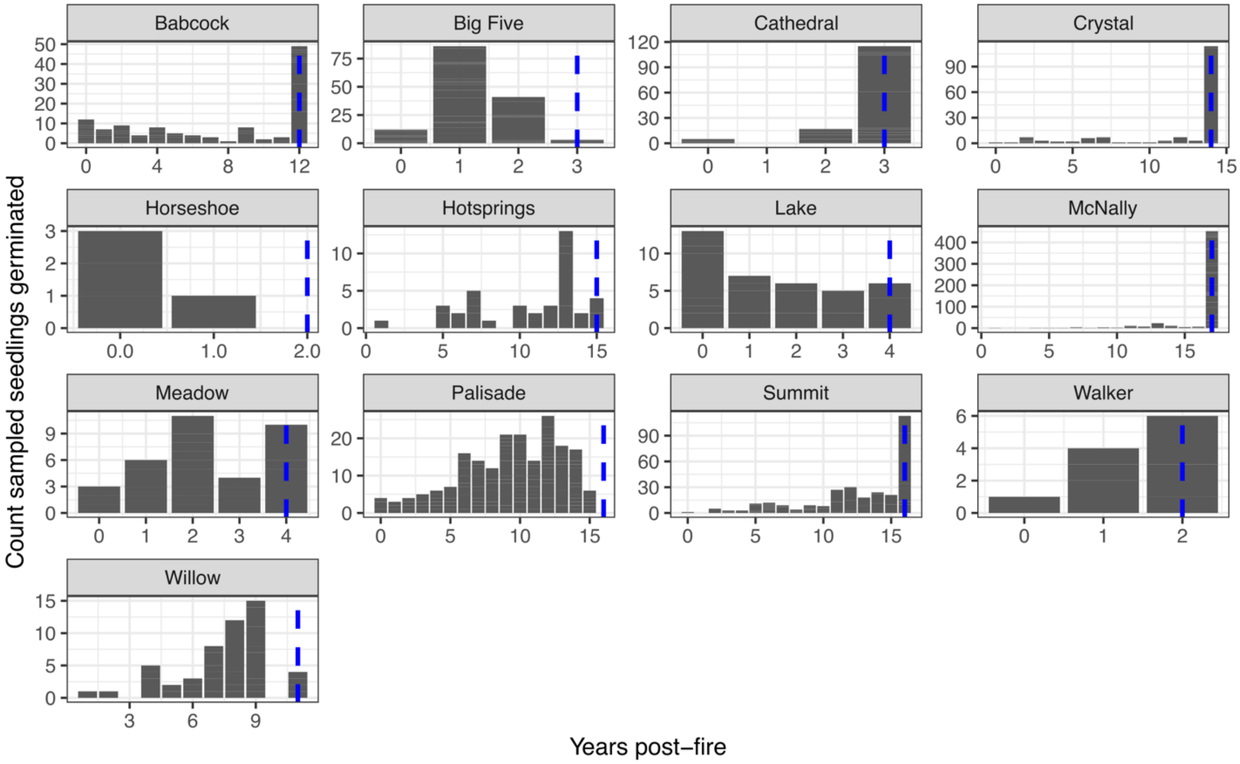

Figure S2.1. Post-fire tree regeneration across time at each fire sampled. Zero indicates that the seedling germinated the year of the fire. The blue checked line indicates the year of sampling.

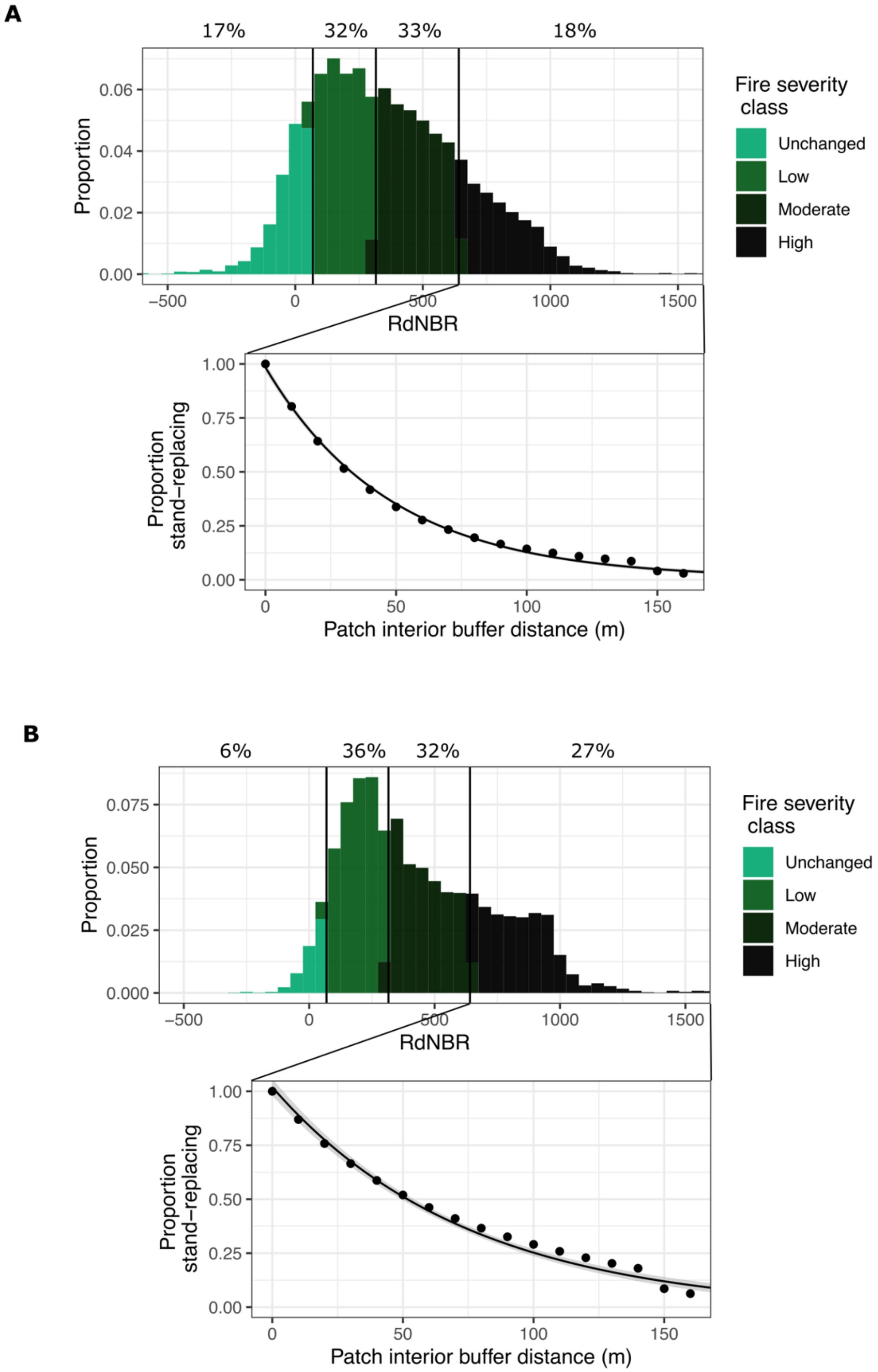
A
17%
32%
33%
18%
Proportion
0.00
0.02
0.04
0.06
RdNBR
−500
0
500
1000
1500
Fire severity class
Unchanged
Low
Moderate
High
Proportion stand−replacing
1.00
0.75
0.50
0.25
0.00
Patch interior buffer distance (m)
0
50
100
150
B
6%
36%
32%
27%
Proportion
0.000
0.025
0.050
0.075
RdNBR
−500
0
500
1000
1500
Fire severity class
Unchanged
Low
Moderate
High
Proportion stand−replacing
1.00
0.75
0.50
0.25
0.00
Patch interior buffer distance (m)
0
50
100
150

Figure S2.2. Histogram of fire severity (as RdNBR) across all study fires (a) and study fires that burned only in subalpine forest (b). Points on curve indicate proportion of high severity patch area within a given distance of the patch edge. Curve is fitted to points as in Collins et al. (2017), see main text Methods section.

Table S2.1. Information about all 13 fires in the study including forest type, year of ignition, year of sampling, total fire size, elevation range of sampling, and plots sampled per fire severity class.

Fire Name	Burn year	Sample year	Years since fire	Size (ha)	Elevation range (m)	Plots per fire severity class					
						0	1	2	3	4	5
Horseshoe	2016	2018	2	151	2902-3170	6	4	3	4	2	6
Walker	2015	2017	2	1544	2828-3077	5	0	1	4	2	5
Big Five	2015	2018	3	107	2978-3179	5	3	2	4	3	2
Cathedral	2014	2017	3	8	2775-2830	2	1	0	2	1	0
Lake	2015	2019	4	12660	2986-3214	6	4	3	4	3	4
Meadow	2014	2018	4	1932	2760-2949	5	3	3	5	3	4
Willow	2007	2018	11	75	2974-3293	5	3	2	4	3	3
Babcock	2007	2019	12	107	2762-3013	5	3	2	3	5	5
Cyrstal	2005	2019	14	42	2761-2961	2	0	2	1	1	1
Hotsprings	2004	2019	15	134	2891-3087	5	3	3	4	3	4
Palisade	2002	2018	16	606	2641-2906	4	3	3	3	3	3
Summit	2003	2019	16	1929	2845-3096	5	3	4	3	3	4
McNally	2002	2019	17	149475	2823-3045	5	3	3	3	3	4
					Total	60	33	31	44	35	45

*Table S2.2. The number of 60 m^2 regeneration plots where finding regeneration was possible for a species based on its range and presence nearby (i.e., n, or # of trials) and the number of plots where regeneration was ultimately observed for that species (i.e., positive trials). Species specific models were run for those species with >20 observations. *For Jeffrey pine, model was run on observations from the 405 m^2 main plot where it was observed 22 times.*

Species scientific name	Species common name	# plots possible (n)	# plots observed
Abies magnifica	red fir	157	28
Pinus jeffreyi	Jeffrey pine	157	8*
Juniperus grandis	mountain juniper	84	1
Pinus albicaulis	whitebark pine	23	0
Pinus balfouriana ssp. balfouriana	southern foxtail pine	129	43
Pinus contorta var. murrayana	lodgepole pine	248	61
Pinus flexilis	limber pine	71	1
Pinus monticola	western white pine	179	46
Tsuga mertensiana	mountain hemlock	95	17

Table S2.3. Model summary for Bayesian generalized linear mixed model testing whether the influence of fire severity on the presence or absence of regenerating tree species depends on tree species typical elevation (low versus high).

Fixed effects	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS
Intercept	-0.63	0.48	-1.63	0.31	1.00	2187
Fire severity	-0.01	0.19	-0.40	0.36	1.00	3454
Typical elevation (low)	-0.99	0.43	-1.82	-0.15	1.00	3086
Time since fire	2.19	0.72	0.82	3.74	1.00	2021
Seed availability	1.03	0.26	0.55	1.58	1.00	3176
Anomaly post-fire climatic water deficit	-1.18	0.50	-2.20	-0.24	1.00	2222
Fire severity:Typical elevation (low)	-0.75	0.32	-1.38	-0.13	1.00	3411
Random effects						

sd(Intercept)	0.85	0.42	0.25	1.87	1.00	1131

Table S2.4. Model summary for Bayesian generalized linear mixed model testing the influence of a variety of predictor variables on the presence or absence of ***foxtail pine*** *regeneration.*

Fixed effects	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS
Intercept	-1.31	0.61	-2.55	0.03	1.00	2885
Fire severity	0.36	0.28	-0.18	0.91	1.00	8538
Time since fire	0.49	0.69	-0.92	2.00	1.00	1901
Seed availability	0.34	0.29	-0.19	0.93	1.00	6111
Normal precipitation	1.58	0.63	0.39	2.88	1.00	4354
Shrub cover	-0.92	0.37	-1.73	-0.25	1.00	7556
Random effects						
sd(Intercept)	1.13	0.78	0.07	3.10	1.00	1556

Table S2.5. Model summary for Bayesian generalized linear mixed model testing the influence of a variety of predictor variables on the presence or absence of ***western white pine*** *regeneration.*

Fixed effects	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS
Intercept	-2.10	0.84	-4.02	-0.56	1.00	2155
Fire severity	-0.25	0.24	-0.74	0.21	1.00	7102
Time since fire	1.21	0.95	-0.67	3.23	1.00	1885
Seed availability	0.84	0.27	0.34	1.41	1.00	5806

Anomaly post-fire climatic water deficit	-0.67	0.78	-1.99	1.06	1.00	2240
Random effects						
sd(Intercept)	2.15	1.22	0.41	5.15	1.00	1324

Table S2.6. Model summary for Bayesian generalized linear mixed model testing the influence of a variety of predictor variables on the presence or absence of ***lodgepole pine*** *regeneration.*

Fixed effects	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS
Intercept	-1.36	0.30	-1.99	-0.80	1.00	4301
Fire severity	0.03	0.17	-0.31	0.36	1.00	10879
Time since fire	0.73	0.32	0.14	1.38	1.00	4550
Seed availability	0.62	0.20	0.23	1.02	1.00	7060
Post-fire growing degree days	0.34	0.25	-0.14	0.82	1.00	6120
Random effects						
sd(Intercept)	0.75	0.35	0.16	1.55	1.00	2059

Table S2.7. Model summary for Bayesian generalized linear mixed model testing the influence of a variety of predictor variables on the presence or absence of ***red fir*** *regeneration.*

Fixed effects	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS
Intercept	-3.14	0.72	-4.76	-1.87	1.00	4225
Fire severity	-1.17	0.37	-1.94	-0.48	1.00	11600
Time since fire	2.69	1.05	0.95	5.04	1.00	5234
Seed availability	0.43	0.26	-0.03	0.98	1.00	10006

Anomaly max post-fire growing degree days	1.23	0.52	0.44	2.49	1.00	2677
Random effects						
sd(Intercept)	0.89	0.77	0.03	3.95	1	2720

Table S2.8. Model summary for Bayesian generalized linear mixed model testing the influence of a variety of predictor variables on the presence or absence of ***Jeffrey pine*** *regeneration.*

Fixed effects	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS
Intercept	-2.10	0.42	-2.99	-1.30	1.00	3871
Fire severity	0.63	0.25	0.16	1.12	1.00	6697
Time since fire	0.09	0.50	-0.85	1.11	1.00	2089
Seed availability	0.12	0.33	-0.62	0.69	1.00	3698
Random effects						
sd(Intercept)	0.77	0.56	0.04	2.18	1.00	1986

Chapter 3

Long-term forest sampling reveals early and lasting effect of fire suppression on understory and overstory composition

Submitted as:

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Abstract

The proportion of pine in mixed-conifer forests in the western United States has declined over more than a century of fire suppression and logging. Yet early foresters did not intend to reduce the amount of valuable pine timber. Many believed that opening forest canopy via logging would aid in regeneration of light-loving pines in forests undergoing a “natural progression” towards more shade-tolerant white fir and incense-cedar. Here, we used a historical dataset to track tree regeneration over nearly a century: tree regeneration was measured in 440 2x2 m^2 quadrats before logging in 1928/1929, five years post-logging, and then resampled in 2016. We use these longitudinal data to investigate the timing and drivers of understory change leading to reductions in pine. We asked how the regeneration layer changed over time and how well tree seedling and sapling light environment, seed availability, and microsite conditions could predict future forest composition. We found that, while post-fire light environment, seed availability, and microsite conditions could not directly predict which quadrats contained trees in 2016, these small-scale environmental factors were important predictors of seedling abundances, which in turn predicted contemporary tree presence. The influence of seedling environment on seedling abundances differed by species and time period. “Natural” gaps in the pre-logging and contemporary periods were positively associated with pine regeneration. However, post-logging gaps—many created at the expense of large pines—were negatively associated with pine regeneration. For all species (pine, white fir, and incense-cedar), post-logging skid trails were positively associated with regeneration and woody debris was negatively associated with regeneration in at least one time period. We found that advance regeneration (already established at the time of logging) was a good predictor of which quadrats would contain trees in 2016 for all species, and that new post-logging regeneration was also important for the more shade-tolerant white fir and incense-cedar.

Incense-cedar increased in relative abundance over time (from 26 to 51%) despite limited seed sources. Conversely, the percentage of pine in the understory remained low over time (from 9 to 6%), especially when compared to nearby seed source trees. We conclude that fire acted as a selective pressure on pines at early demographic stages, and that fire suppression resulted in a mismatch between overstory and understory composition. Further, our work contributes to growing evidence that increasing light availability alone is not enough to promote pine regeneration. Other ecosystem conditions associated with the historical fire regime—including availability of disturbed substrate, lower density of woody debris, the presence of large-diameter pines as seed sources, and disproportionate mortality of shade-tolerant species—are essential for promoting pine co-dominance in mixed-conifer systems.

Introduction

Over a century and a half of fire suppression and logging have systematically reduced the proportion of pine (*Pinus spp.*) in mixed-conifer type forests in the western United States (Dolanc et al. 2014, York 2015, Collins et al. 2017). Fire suppression disadvantages pines directly by decreasing light availability via stand densification, and indirectly by increasing the probability of uncharacteristically severe fire resulting in a vigorous shrub response that competes with pine regeneration (Tubbesing et al. 2020). By cutting many of the largest trees, historical logging practices disproportionately reduced pine basal area, decreasing seed availability while increasing the proportion of shade-tolerant species such as fir (*Abies spp.*; York 2015, Collins et al. 2017). Yet the resulting reduction in pine was largely unintentional.

Many early foresters, trained in European and eastern North American forestry practices, did not understand the role of fire in mixed-conifer forests and believed that the increasing light and disturbed substrate after logging would be beneficial to pine reproduction (Dunning 1923, 1930, Hasel et al. 1934).

The expectation that pines would respond positively to logging has a reasonable basis: high-light microsites, such as those created by opening the canopy via logging or wildfire are essential to pine reproduction. Pines generally grow faster than shade-tolerant firs and cedars under high light conditions, but slower under low light conditions (Bigelow et al. 2011, Levine et al. 2016, Safford and Stevens 2017). The crossover point for relative growth rates of pines versus shade tolerant species occurs at about 30-40% full sun in the Sierra Nevada, and the probability of such microsites increases from ~15% with thinning treatments to almost 90% in gaps of ~0.7 ha (Bigelow et al. 2011). High light requirements designate pines as early successional species (expected to naturally transition to more shade-tolerant species) in most forests that do not experience frequent disturbance (Kobe et al. 1995). In California mixed-conifer, however, a history of frequent low severity fire resulted in overstories in which pines comprised a high proportion of basal area (Safford and Stevens 2017)—a surprise to early Euro-American explorers and colonists. The exclusion of Native American cultural burning and suppression of fire in these forests by the federal government and state of California has dramatically altered the fire regime since pre Euro-American settlement (Stephens et al. 2007, Van De Water and Safford 2011, Keeley and Safford 2016). Increasing the proportion of pine in contemporary forests under this altered fire regime is an area of active interest in western US forestry (York et al. 2007).

While logging creates high-light microsites that can favor pine regeneration, many of its other outcomes are unfavorable. Historical logging practices targeted large trees, which were more likely to be pines (York 2015) and are disproportionately important for seed production of yellow and sugar pines (Fowells and Schubert 1956, Collins et al. 2017). Woody debris like slash, trash, and decaying tree boles obstruct germination sites and do not provide good rooting substrate for seedlings due to their low moisture levels in summer months (Gray et al. 2005). Further, low severity fires may discriminate with respect to seedling and sapling mortality—killing mostly shade-tolerant firs and cedars and favoring the more fire-resistant and shade-intolerant pines (Zald et al. 2008). In contrast, logging disturbance indiscriminately removes advance regeneration from the stand.

Changes in the regeneration layer are the first indication of changes in the future forest (Van Mantgem et al. 2004). It is common to extrapolate future forest conditions using regeneration from the only the first five years after fire disturbance (Harvey et al. 2016, Urza and Sibold 2017, Stewart et al. 2021). The establishment of seedlings during the early post-disturbance years may saturate appropriate microsites given dispersal limitations, or seedlings that establish earlier may obtain a competitive advantage through priority effects (Welch et al. 2016, Tepley et al. 2017). Both mechanisms may also be important for advance regeneration (pre-disturbance regeneration), which plays an important role in post-logging understory composition (Dunning 1923). Few opportunities exist, however, to check assumptions about the importance of advance and post-disturbance regeneration by resampling historical datasets.

Here, we take advantage of an extensive historical dataset tracking regeneration before and after logging in 1928/1929 to learn about the influence of silvicultural treatments and microsite conditions on the forest in 2016. Duncan Dunning and other early 20th century foresters sought to release and encourage advance and new pine regeneration in California's productive white fir and sugar pine forests (Dunning 1930, Hasel et al. 1934). Despite their intentions, a 2008 re-sampling in the same stand showed that overstory pine composition had declined from 37% to 21% (Knapp 2015), mirroring results from unlogged stands in the same region (Levine et al. 2016). Logging unambiguously did not increase the proportion of pine. In this paper, we investigate why. Specifically, we investigate what a detailed record of pre- and post-logging understory conditions and tree seedling/sapling composition can reveal about the future forest by asking:

1. Do post-logging light environment, seed availability, and microsite conditions influence where individual trees develop in the future stand?
2. How do light environment, seed availability, and microsite conditions influence regeneration in the pre-logging, post-logging, and contemporary periods and how does this differ between shade-tolerant and shade-intolerant species?
3. How did composition of tree regeneration change from before logging in 1928 to after logging in 1933 and over the subsequent 83 years to resampling in 2016? In particular, was current stand composition shaped more by presence of seedlings that established prior to the logging disturbance (advance regeneration) or seedlings that established after the logging disturbance?

Methods

Study area

This study was conducted in the Stanislaus-Tuolumne Experimental Forest on the western slope of the Sierra Nevada, California. Elevations in the study area range from 1676 to 1789 m, and slopes range between 21 and 39 percent. Soils are well-drained and highly productive loam to gravelly-loam of the Wintoner and Inville families (Soil Survey Staff, 2017). The region is characterized by a winter-rainfall Mediterranean climate with a mean annual temperature of 9.02°C and mean annual precipitation of 962 mm, only ~9% of which falls during the May-September growing season (Strawberry Lake Weather Station 1922-1934; Hasel et al. 1934).

The forest type in the study area is Sierra Nevada mixed-conifer composed of four dominant tree species: white fir (*A. concolor* [Gordon & Glend.] Lindl. Ex Hildebr.), incense-cedar (*Calocedrus decurrens* [Torr.] Florin), sugar pine (*P. lambertiana* Douglas), and ponderosa pine (*P. ponderosa* Douglas ex Lawson & C. Lawson). The median historical fire return interval at the study site was six years (minimum 1, maximum 40), but due to over a century of fire suppression in the region the last recorded fire at the study site was in 1889 (Knapp et al. 2013).

Historical dataset

The Methods of Cutting study was established by the USDA Forest Service in the early 1900s to track changes in forest composition and structure under varying intensity silvicultural treatments, including differences in amount of basal area removed and species favored in harvest. In 1928 (plot MC8) and 1929 (plots MC9, MC10, and MC11), four 3.5-4 ha plots were established in the Stanislaus-Tuolumne Experimental Forest (Figure 3.1), with one of the "special object[ives]…to determine whether the proportion of sugar pine [could] be increased in a stand where the natural replacement by white fir [was] in progress" (Dunning 1930). Once established, trees > 9.1 cm dbh (diameter at breast height; 1.37 m) in each plot were stem-mapped and inventoried by species, dbh, and height. Seedlings, saplings (<1.37 m), and groundcover (percent bare ground, skid trail, pile burned, shrub cover, and woody debris) were also mapped within 440, 4 m^2 quadrats arranged in transects across the width of each plot (Figure 3.1). Transects were longer than plot widths for MC9-11, and only 380 of the 440 mapped quadrats were inside plot boundaries.

After inventory, each plot was treated according to a different silvicultural prescription (see Figure 3.4; Table S3.1). MC8 and MC9 removed larger overstory trees following typical USFS practice at the time (Dunning 1930, Hasel et al. 1934). MC10 was the lightest cut, marked to give the highest short-term profit by cutting only the largest and best ponderosa and sugar pines. MC11 was the heaviest cut, and replicated the sort of harvest that would provide the highest return to the landowner before abandoning the land (Hasel et al. 1934). After harvest, the overstory and regeneration quadrats were re-mapped. Most of the regeneration quadrats were re-mapped annually through 1938 and then periodically through 1947.

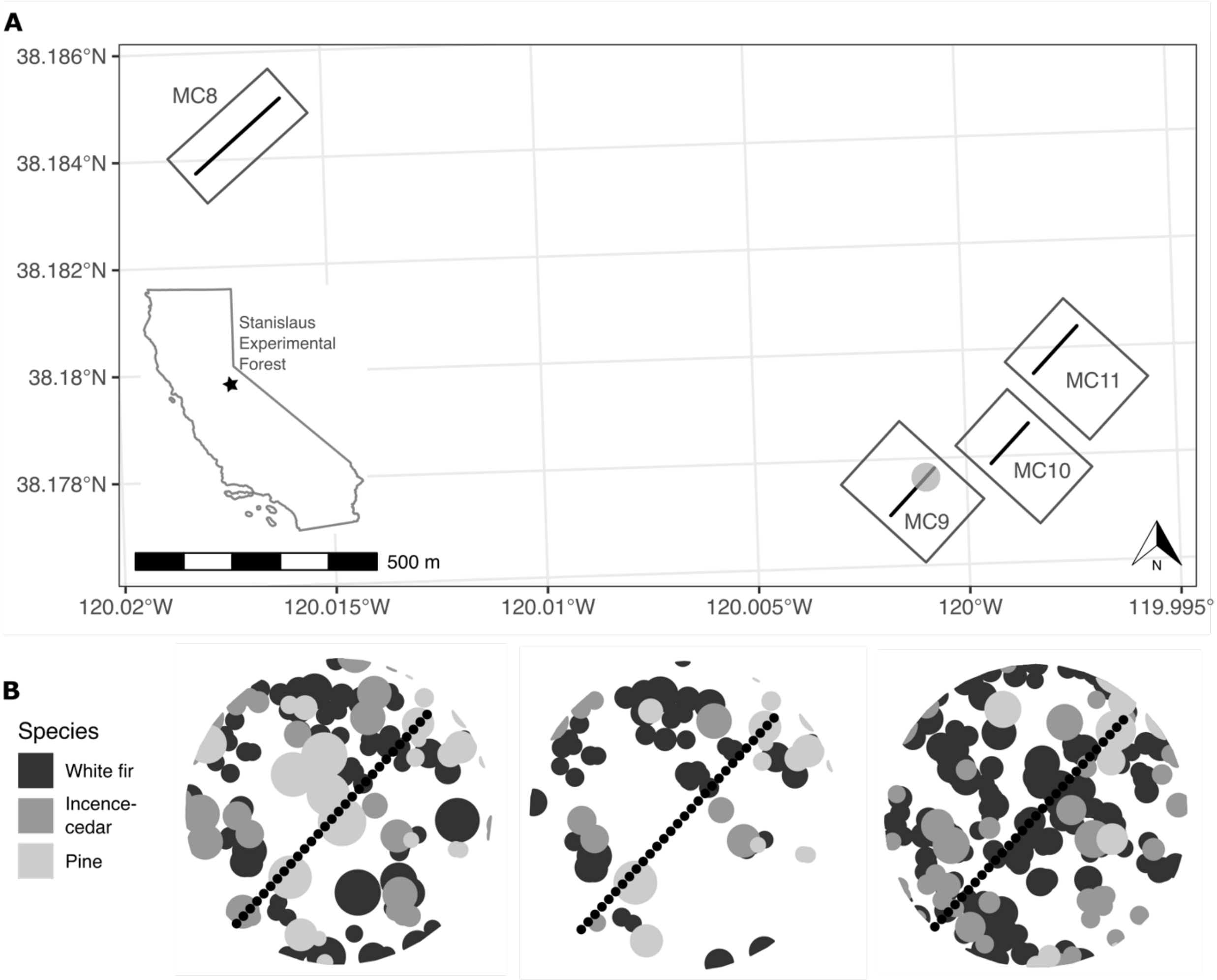

Figure 3.*1. Map of study area showing plots and transect length within 30 m of plot edge (a). Blowup of the 30 m radius circle shown in plot MC9 (b). Mapped trees shown with canopy diameter calculated from diameter at breast height using species-specific equations from* Gill et al. (2000)

Plot re-measurement

Plots were rediscovered in 2006, with no significant disturbance occurring in the intervening years. Data were digitized and overstory trees re-mapped in 2007 (MC11), 2008 (MC9, MC10), or 2016 (MC8; see Knapp et al. 2013). Re-mapping followed the historical protocol except all trees >10 cm dbh (rather than 9.1 cm dbh) were individually tagged and measured. Because mapping of overstory trees in the contemporary period occurred up to 9 years apart, we tested whether significant changes in overstory biomass occurred between 2007/2008 and 2016. In 2016, we randomly selected and sampled 30 15-m radius plots in MC9-11 initially sampled in 2007/2008. We calculated total live biomass (kg) using genera-specific allometric equations (Jenkins et al 2003) and compared it to live biomass of the same plots in 2007/2008 using a paired Wilcoxon rank sum test. All 440 understory quadrats were re-measured in 2016 using the historical methods described above.

Overstory predictors

Maps of tree locations were used to generate estimates of canopy gap area and species-specific basal area at three time periods: pre-logging (1928 or 1929), post-logging (1928 or 1929), and contemporary (2007, 2008, or 2016). To calculate canopy gap area, we first used species specific equations from Gill et al. (2000) to calculate crown radius for each mapped tree. We buffered each tree by its crown radius and used the Patch and Gap Metrics Toolbox in ArcMap (Dilts 2018) to delineate gaps with >6 m radius (>0.01 ha) as in Lydersen et al. (2013). While our minimum gap size was below the size that has been shown to have an effect on ponderosa pine growth rates (York et al. 2007), sugar pine is known take advantage of smaller gaps (Oliver and Leroy Dolph 1992). A 6 m radius also mimics the influence of all but the largest diameter trees in the study area meaning that it represents heterogeneity in light environment at the scale of the stand. After delineating canopy gap area in plots, we measured how much gap area was within a 22 m radius of each quadrat. A 22 m radius was chosen to represent the average area of light availability for seedlings around each quadrat and was calculated based on average tree height and angle of the sun at the experimental forest throughout the summer. Using dbh of mapped trees, we also calculated species-specific basal area within 30 m (~1.5 chains) of each quadrat. We chose 30 m because sugar pine and Jeffrey pine generally disperse within 30 m of the parent tree (Fowells and Schubert 1956, Kinloch and Scheuner 1990, Vander Wall 1992). By leaving at least one 46-cm pine within 30 m of 76% of quadrats, and at least one 76-cm tree within 50 m of 67% of quadrats, early foresters hoped seed rain would be sufficient to stock most quadrats with pine (Fowells and Schubert 1951).

Table 3*.1. Descriptions of the variables used to model regeneration counts and the conditions that those variables represent.*

Condition	Variable	Description
Light	Canopy gap area	Area of gaps larger than 6 m radius within 22 m radius of quadrat
Seed availability	Species specific basal area	Basal area within 30 m radius of quadrat

Regeneration microsite	Shrub cover	Cover of shrubs in 2x2 m^2 quadrat
Regeneration microsite	Woody debris cover	Cover of woody debris in 2x2 m^2 quadrat
Regeneration microsite	Bare ground/ skid trail cover	Cover of bare ground (and/or skid trails for post-logging period) in 2x2 m^2 quadrat

Changes in regeneration composition over time

We compared counts and relative abundances of species across pre-logging, post-logging, and contemporary time periods (Q3). Due to the non-random plot selection methods used by early foresters, we did not conduct statistical tests at the plot scale. To understand changes in the understory relative to changes in the overstory, we also compared the ratio of regeneration abundance to seed tree basal area at each time period as in Van Mantgem et al. (2006). We defined seed trees as trees within 30 m of quadrats to be consistent with our seed availability variable.

Statistical models

Impact of post-logging light, seed, and microsite conditions on contemporary trees

To understand whether post-logging light, seed, and microsite conditions directly influenced future stocking independent of regeneration (Q1), we used post-logging conditions in and around quadrats to predict which quadrats would contain new trees in the contemporary period. We fit Bayesian generalized linear models with Bernoulli likelihoods separately for white fir, incense-cedar, and pine. While sugar pine is more shade-tolerant and less drought tolerant than yellow pine (Minore 1979, Oliver and Leroy Dolph 1992) and the two would ideally be treated separately, we modeled them together as there were not sufficient regeneration and new trees to consider each species separately. New trees were defined as any live or recently dead (needles and/or small branches still present at the time of survey) tree >10 cm dbh. We included recently dead trees because many young trees were recently dead in the 2016 resurvey—likely due to the 2012-2016 drought—and our primary interest was where seedlings became trees and not which of those trees survived drought conditions.

To determine which variables had important influences on contemporary tree presence, we used a forward model selection approach. For our goodness of fit measure, we used the sum of the expected log pointwise predictive density (ELPD) as an approximate measure of leave-one-out cross validation. Models with higher ELPD have better fit to data both in and outside of the sample and ELPD is a more robust selection criteria than WAIC (Vehtari et al. 2017). We did not include seedling abundances as predictors of contemporary trees because the effect of microsite on future tree presence occurs indirectly via seedlings and saplings. To include them in the model would obscure the influence of microsite, which was our primary interest (see directed acyclic diagram Figure S3.1). First, we ran models with each variable separately (Table 3.1). Starting with the significant predictor with the highest ELPD, we added uncorrelated and significant predictors to the model in order of ELPD to determine whether they significantly increased the ELPD of the resulting model. We defined a significant increase in ELPD as at least twice its standard deviation.

Impact of changing light, seed, and microsite conditions on regeneration

To understand how post-logging microsite conditions influenced seedling abundances and how this changed across time (Q2), we modeled seedling abundance using a series of Bayesian generalized linear models with negative binomial likelihoods. We fit separate models for abundance of white fir, incense-cedar, and pine regeneration as well as for the pre-logging, post-logging, and contemporary time periods for a total of nine models. Pre-logging regeneration included seedlings and saplings (<10cm dbh), post-logging regeneration included only seedlings from the first five years post-logging, and contemporary regeneration again included all seedlings and saplings. We included a variety of predictors in each model, including those representing light, seed availability, and microsite (see Table 3.1). We did not include the area burned for slash disposal or bare ground for the pre-logging period because fewer than five plots contained these cover types.

Impact of regeneration timing on contemporary trees

To test whether current stand composition was shaped more by the presence of seedlings that established prior to logging disturbance or seedlings that established after logging disturbance (Q3), we modeled the presence of new trees in the contemporary period (see 2.5.1) using seedling abundances from the pre- and post-logging time periods. We fit three Bayesian generalized linear models with Bernoulli likelihoods, one each for pines, white fir, and incense-cedar. Each model contained a predictor for the number of seedlings that regenerated in the pre-logging period ("advance regeneration") as well as a predictor for the number of seedlings that regenerated in the post-logging period. We compared the effect of post-logging regeneration from within 5 years of logging ("5-year regeneration") and from within 10 years of logging ("10-year regeneration"), but did not include these two predictors in the same model as they contained many of the same seedlings. Instead, if both post-logging predictors had an important effect on contemporary tree presence, we compared delta ELPD between models.

Model fitting

Statistical models were fit in the brms and rstan packages (Bürkner 2017, Stan Development Team 2018) in the R statistical software (R Core Team 2020). We centered and scaled all continuous predictors for ease of model fit and prior selection. We chose mildly regularizing priors and used four chains with 2000 iterations each. We assessed chain convergence and mixing by visually assessing traceplots and R-hat values and model fit using model-specific posterior predictive checking as described in detail below. We considered there was strong evidence that an effect was non-zero if its 90% Highest Posterior Density Intervals (HPDI) did not cross zero (Goodrich et al. 2020, McElreath 2020).

To confirm that models were responding correctly to predictors and that the distribution of the data matched that of the posterior predictive distribution, we performed three types of posterior predictive checks. First, we compared 100 draws from the posterior predictive distribution to the data and visually assessed similarity in the distribution. Second, we ensured that models were accurately representing the large quantity of zeros in the data by making sure that the number of zeros in the data was near the center of a distribution of the number of zeros in 100 draws from the posterior predictive distribution. Third, we obtained draws from the posterior predictive distribution, sorted and binned observations into ten deciles, and compared mean and standard deviation of the posterior predictive with same deciles of the observed data and ensured that standard deviations were overlapping.

All models included a spline or “smooth” term to account for the spatial structure of quadrats along the four transects (Hedley and Buckland 2004). Smooths modeled seedling abundance response to distance from beginning of transect. Each plot (synonymous with transect) was also included in every model to account for differences in silvicultural treatments among plots.

Results

Impact of post-logging light, seed, and microsite conditions on contemporary trees

We did not detect an effect of the post-logging light, seed, or microsite conditions measured here on the presence of contemporary trees independent of regeneration conditions.

Impact of changing light, seed, and microsite conditions on regeneration

The influence of canopy gap area changed sign between time periods (Figure 3.2). While canopy gap area was marginally positively correlated with pine seedling/sapling count prior to logging (mean 90% HPDI = 0.29 [-0.01, 0.60], the large gaps generated by logging were negatively correlated with 5-year post-logging seedling count for both pine (-0.78 [-1.53, -0.10]) and white fir (-1.48 [-2.49, -0.58]). In the contemporary period, canopy gap area was again marginally positively correlated with pine (0.33 [-0.06, 0.75]), and was positively correlated with white fir (0.29 [0.00, 0.58]) and incense-cedar (0.37 [0.00, 0.71).

Skid trails and bare ground from logging were positively correlated with 5-year post-logging seedling count for all species (Figure 3.2; pine, 0.86 [0.40, 1.35]; white fir 0.84 [0.50, 1.20]; incense-cedar 0.82 [0.35, 1.31]). However, bare ground in the contemporary period was negatively correlated with seedling/sapling count for pine (Figure 3.2; -0.93 [-1.89, -0.16]).

The influence of woody debris on seedling and sapling count was generally negative or neutral (Figure 3.2). Model coefficients for woody debris were negative for incense-cedar (-0.30 [-0.56, -0.04]) and pines (-0.54 [-1.08, -0.10]) in the pre-logging period and for white fir (-0.58 [-0.81, -0.35]) and pines (-0.94 [-0.41, -0.50]) in the contemporary period. In all other time periods and for all other species coefficients were indistinguishable from zero.

We found little evidence of the influence of shrub cover and seed availability (as measured by species basal area in a 30 m radius) on seedling and sapling count. Shrub cover was positively correlated with 5-year post-logging seedling count for incense-cedar (1.08 [0.44, 1.74]), but did not have a detectable effect for all other species and time periods (Figure 3.2). While we did not detect the effect of seed availability in the pre- or post-logging periods, it was negatively correlated with white fir regeneration (-0.50 [-0.80, -0.21]) in the contemporary period.

The average number of seedlings of each species changed between plots and over time (Figure 3.3; Figure 3.4). There were fewer 5-year post-logging pine seedlings than pre-logging in plots MC9, MC11, and marginally in MC10 but similar numbers in MC8. This reduction in pine seedlings compared to pre-logging persisted through to the contemporary period in MC9 and marginally in MC11. There were fewer 5-year post-logging incense-cedar seedlings in MC9 than in the pre-logging understory. By the contemporary period, the number of incense-cedar seedlings in MC9 was again indistinguishable from the pre-logging period and there were significantly more incense-cedar seedlings in MC8 than pre-logging. Incense-cedar was the only species for which regeneration increased from pre-logging to any other period. White fir seedling abundances, on the other hand, were the most reduced compared to their pre-logging numbers. Every plot (MC8-11) contained fewer seedlings in the post-logging—versus the pre-logging—period and these reductions persisted into the contemporary period in three plots (MC9-11).

Impact of regeneration timing on contemporary trees

Advance regeneration was positively related to contemporary tree presence for all species (pine, 1.04 [0.25, 1.76]; white fir 0.50 [0.36, 0.65], and incense-cedar 0.37 [0.20, 0.55]). For pine, advance regeneration was the only detectable influence on contemporary tree presence. Five-year regeneration was marginally positively correlated with contemporary incense-cedar presence (0.45 [-0.05, 0.97]) and positively correlated with contemporary white fir presence (1.38 [0.62, 2.12]). For white fir only, 10-year regeneration also had a positive relationship with contemporary tree presence (0.60 [0.19, 1.10)—though about half as large—indicating that seedlings that regenerated up to ten years post-logging may form part of the contemporary canopy. In this case, the 10-year regeneration model was indistinguishable from the 5-year regeneration model (Δ ELPD = -1.4, SE_{Δ} = 4.5).

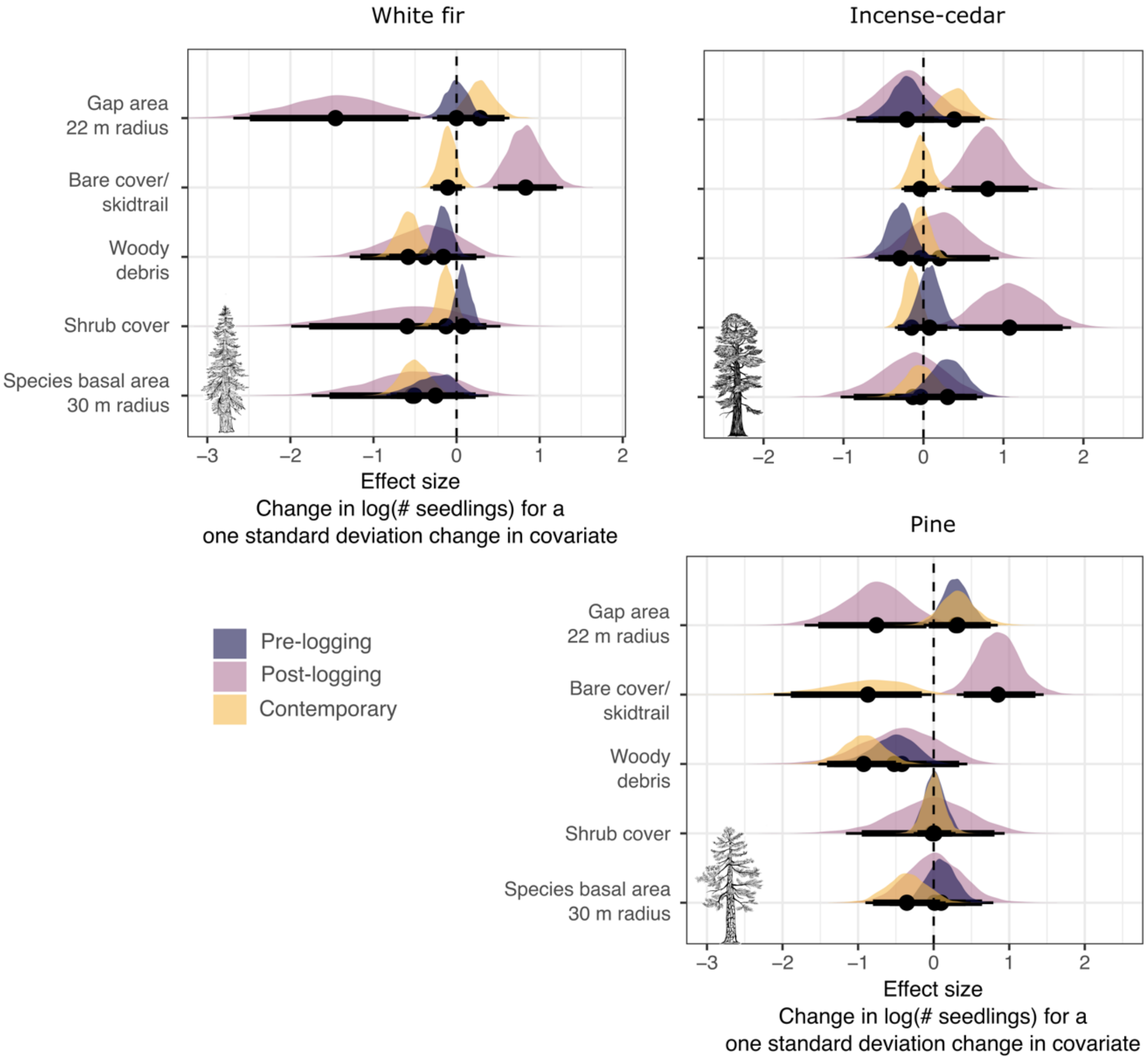

Figure 3.2. Plots showing the effect size of predictors on number of seedlings and saplings in 2x2 m^2 quadrats in the pre-logging and contemporary periods as well as the number of seedlings that regenerated in the first five years post-logging (i.e., no advance regeneration). Dots and bars indicate model estimated means and 90 and 95% CIs. Colored shading shows distribution of the mean and colors indicate time period.

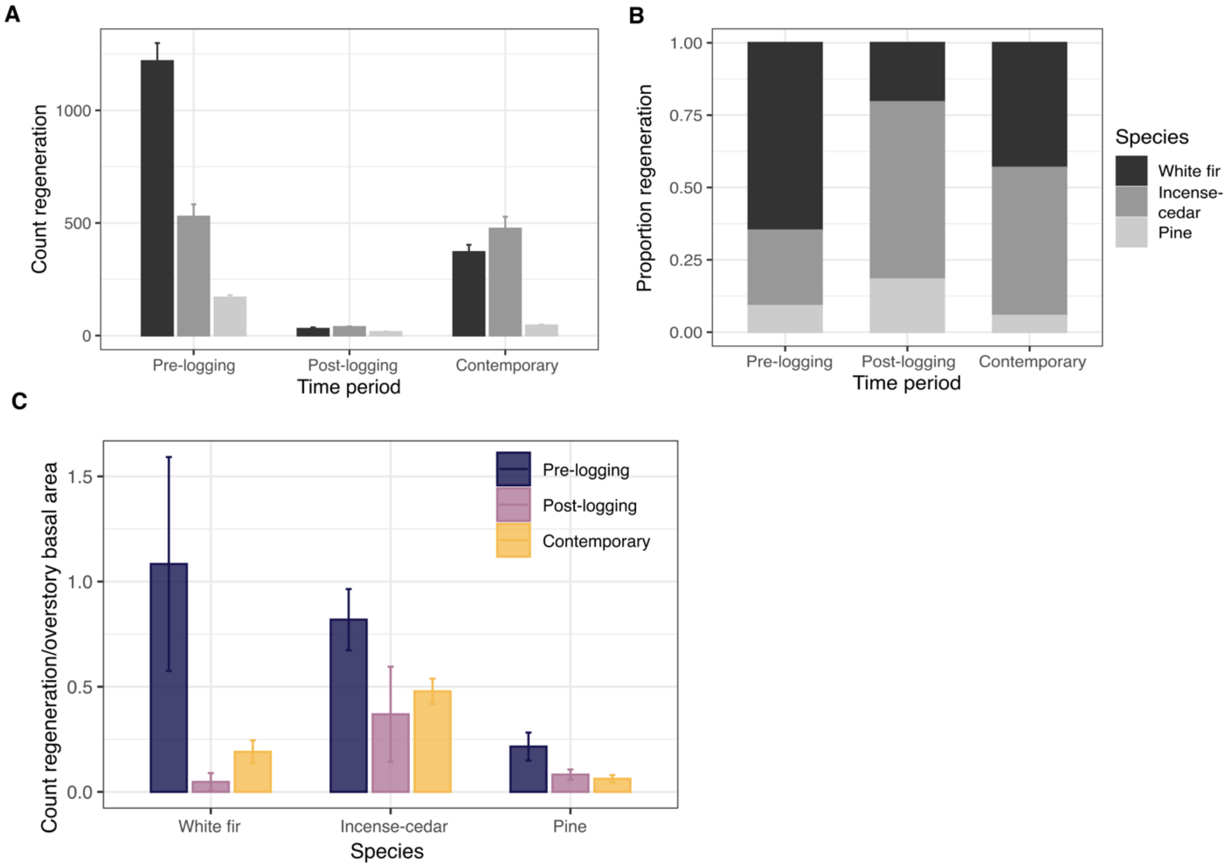

Figure 3.3. *Regeneration count at three different time periods (a). Error bars represent standard errors based on n = 4 plots. Relative abundances of seedlings at different time periods (b). Ratio of number of seedlings and saplings in 2x2 m*^{2} *quadrats to basal area of overstory trees within 30 m of quadrats (c). Note that the post-logging period only includes seedlings that regenerated in the first five years post-logging and does not include advance regeneration.*

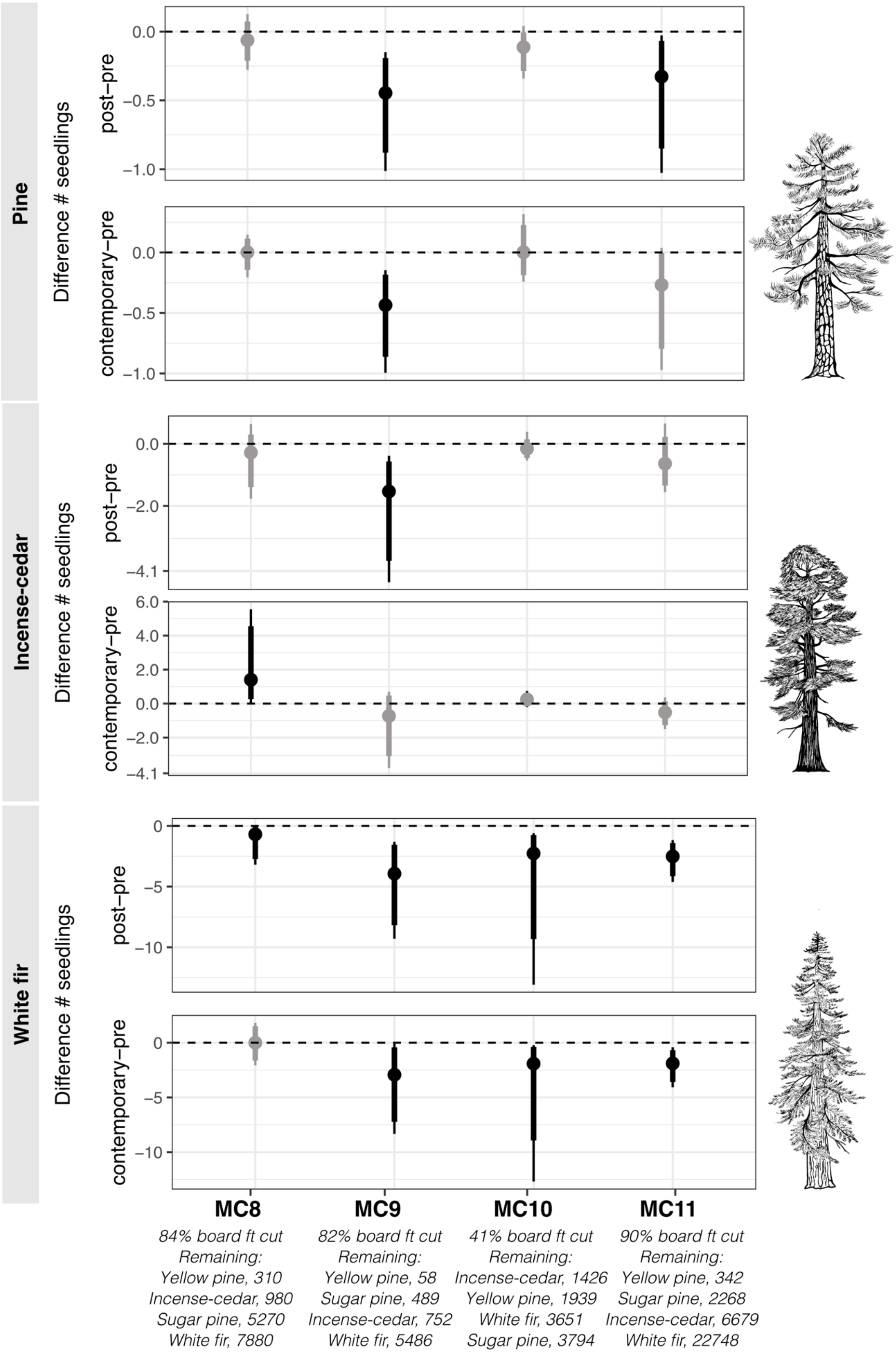
Pine
Incense-cedar
White fir
Difference # seedlings
post−pre
contemporary−pre
0.0
−0.5
−1.0
−2.0
−4.1
6.0
4.0
2.0
0
−5
−10
MC8
MC9
MC10
MC11
84% board ft cut
Remaining:
Yellow pine, 310
Incense-cedar, 980
Sugar pine, 5270
White fir, 7880
82% board ft cut
Remaining:
Yellow pine, 58
Sugar pine, 489
Incense-cedar, 752
White fir, 5486
41% board ft cut
Remaining:
Incense-cedar, 1426
Yellow pine, 1939
White fir, 3651
Sugar pine, 3794
90% board ft cut
Remaining:
Yellow pine, 342
Sugar pine, 2268
Incense-cedar, 6679
White fir, 22748

Figure 3.4. Differences in model-estimated seedling abundances between the pre-logging and post-logging periods (post-pre) and between the pre-logging and contemporary periods (contemporary-pre) shown with 90 and 95% CIs and separated by species and plot. Note that the post-logging period only includes seedlings that regenerated in the first five years post-logging and does not include advance regeneration. Negative values indicate a decrease in seedlings over time and positive values indicate an increase in seedlings over time. Differences with 90% CIs that do not cross zero are in black and differences with 90% CIs that cross zero are in grey. Plot silvicultural treatments are noted below plot name in percent of board feet removed from stand overall and amount of board feet remaining post-logging by species.

Discussion

We found that regeneration data from the historical Methods of Cutting experiment foreshadowed species re-ordering that has become widespread in contemporary forests. While pre-logging overstories contained 37% pine by basal area (Knapp et al. 2013), pine seedlings comprised only 9% of the regeneration layer (Figure 3.3). This compositional mismatch was not reversed by the creation of high light microsites after logging (Figure 3.3). In fact, gap area was negatively associated with pine in the post-logging period (Figure 3.2). In the first five years post-logging, the relative abundance of pine regeneration increased, though absolute seedling numbers were low and post-logging regeneration was not correlated with new overstory pine in the contemporary period. Incense-cedar, on the other hand, flourished in the post-logging environment, preferentially regenerating under shrubs and in skid trails and becoming the most abundant species in the contemporary understory (Figure 3.2; Figure 3.3). Overall, our results clarify that high light microsites alone do not guarantee successful pine regeneration (York et al.

2012) and suggest that fire likely exerted positive selective pressures on pines even at early demographic stages.

We could not link the effects of post-logging light environment, seed availability, and microsite directly to the locations of individual trees in the contemporary forest. However, we found that these conditions affected seedling abundances and that seedling abundances in turn affected future tree presence. Most notably, while naturally occurring gaps were positively associated with pine regeneration in the pre-logging period, gaps in the post-logging period were negatively associated with new pine and fir regeneration (Figure 3.2). Unlike naturally occurring gaps—which likely resulted from removal of shade-tolerant and fire-intolerant species via fire—post-logging gaps resulted primarily from the removal of the large pines especially important for pine seed production (Fowells and Schubert 1956). Our results align with previous findings of poor establishment after overstory thinning without burning compared to overstory thinning with burning, which authors attributed to a combination of quick-drying litter and direct sunlight (Zald et al. 2008). Though high solar radiation in gaps generally has a positive effect on yellow pine (York et al. 2007), it can reduce regeneration of white fir, incense-cedar, and even sugar pine due to desiccation of germinants (Fowells and Stark 1965, Gray et al. 2005).

Low pine recruitment in post-logging gaps may also be due to mismatch between climatic suitability and seed availability in masting species such as pines. At our study site, “heavy pine seed crops” occurred in the fourth and fifth years following logging (Fowells and Schubert 1951). Masting is important in large-seeded sugar and yellow pines because seed predation can reduce seed abundance by up to 99% (Vander Wall 1992) and high seed abundance increases the probability of uncached seed or forgotten caches. In the event that seedlings establish, unseasonably hot or dry conditions in gaps may select for drought-tolerant incense-cedar over white fir and even pines (Minore 1979). In the contemporary period, on the other hand, regeneration for all species was positively associated with gaps. A positive association between shade-tolerant species and gaps likely reflects the extreme lack of understory light after a more than two-fold increase in forest density from the pre- to post-logging period (Knapp et al. 2013). Denser forests and low light also help to explain why our measure of seed availability (species specific basal area in a 30 m radius) was negatively associated with white fir regeneration in the contemporary period (Figure 3.2).

Post-logging bare ground and skid trails increased regeneration for all species and all species were negatively associated with woody debris in at least one time period (Figure 3.2). While the disturbed soil on skid trails has been shown to stimulate germination of some conifers (Harvey and Brais 2002), long-lasting compaction along skid trails can also reduce seedling establishment and growth of existing trees (Froehlich 1979, Lucas-Borja et al. 2020). Such diverging impacts may be partially explained by differences in duration of skid trail use and soil texture (Gomez et al. 2002, Dearmond et al. 2021). In contrast, we found that bare ground was negatively associated with pine regeneration in the contemporary period. We suggest that bare ground not associated with disturbance after 100+ years of fire suppression may indicate poor or rocky soils unfit for tree regeneration. Across time periods, our finding of a negative association between woody debris and seedling abundance aligns with that of other studies from dry-summer biomes in which decomposition is slow and woody debris are too dry to provide suitable rooting substrate (Gray et al. 2005).

We found incense-cedar to be the clear "winner" over almost 90 years of change in the regeneration layer. Pine and white fir regeneration abundance never recovered to pre-logging levels. In contrast, incense-cedar increased across time in at least one plot (MC8; Figure 3.4) and made up a larger percent of the contemporary understory overall despite less basal area of adult trees within 30 m (Figure 3.3). Characteristics such as prolific (5-26 times that of pine) and far-dispersing seeds (Powers and Oliver 1990, Zald et al. 2008), early maturity (Sawyer et al. 2009), intermediate shade-tolerance, and relative drought tolerance compared to white fir and sugar pine (Minore 1979) likely contributed to incense-cedar's success. Our findings align with changes in the overstory, where incense-cedar increased ~30% more than white fir between the pre-logging and contemporary periods (Knapp et al. 2013). Similarly, a California-wide resampling of 1930's forest structure data found that the density of small (10-30 cm dbh) incense-cedar increased by about twice as much as that of small white fir (Dolanc et al. 2014). While white fir is known for higher rates of recruitment and growth in fire suppressed mixed conifer forest (Levine et al. 2016), it is more vulnerable than incense-cedar to drought and insect damage (Powers and Oliver 1990). Incense-cedar's rare ability to tolerate both drought and shade are likely linked to projections that it will be one of few species to experience increases in seedling densities under future climate and forest structure (Dobrowski et al. 2015). Post-logging incense-cedar was also the only species and time period to have a positive association with shrub cover. Shrubs can compete with seedlings for soil moisture drawdown, but may have reduced temperature stress and moisture loss in gaps (Plamboeck et al. 2008).

Advance regeneration was an important predictor of contemporary tree presence for all species and post-logging regeneration was also important for white fir and incense-cedar (Table S3.2-S3.4). Seedlings and saplings that survive logging are already established and can take advantage of new light and water resources that may be available post-logging. While silvicultural treatments in MC8 and MC10 left more mature sugar pine and succeeded in promoting more pine germinants and seedlings in the first five years (Figure 3.4), absolute seedling numbers were still low and early post-logging regeneration did not result in new pines in the overstory 83 years later. Five-year post-logging regeneration was important, however, for predicting contemporary tree presence for white fir and incense-cedar. Our results indicate that surveying regeneration 5 years post-disturbance (including both advance and early regeneration) is useful for predicting future stand composition (Welch et al. 2016, Tepley et al. 2017). We found that early five- and 10-year regeneration had similar predictive accuracy for shade-tolerant white fir, which may indicate that fir continued to successfully establish and grow as the stand became more shaded (Levine et al. 2016).

While some advance regeneration of pine reached the contemporary canopy, we believe that pre-logging understory composition was already altered by fire suppression. Based on an estimated median historical fire return interval of six years at the study site (Knapp et al. 2013), the Methods of Cutting experiment had already missed an estimated six fires before it was first sampled in 1928. By 1928, then, fire suppression had likely already substantially reduced pine regeneration compared to that of white fir and cedar (Figure 3.3). Our conjecture aligns with the observations of early silviculturist Clinton Walker, who advocated for the use of fire in silviculture as early as 1910, writing: "*It has occurred to me that perhaps the fir being more subject to thicket growths have thereby in nature been more subject to fires which have thus been thinned out leaving a better chance for the pine to mature*" (Walker 1910). Indeed, such observations are borne out in contemporary experiments finding that thin-burn treatments resulted in greater reductions of white fir and incense-cedar regeneration and increases in pine regeneration compared to burn or thin alone (Zald et al. 2008). We conclude that frequent fire likely altered the competitive balance among species at the seedling/sapling stage historically. Thus, fire suppression as early as the late 1800's probably played an important role in reducing the proportion of pine in historical forest understories, forecasting and contributing to the decline of pine in today's overstories.

Management implications

Our work contributes to growing evidence that western pine forests require many factors to persist, any one of which alone may be unsuccessful. First, large trees are required for seed production (Fowells and Schubert 1956). However, work from unlogged stands (Ansley and Battles 1998, Levine et al. 2016) as well as study plots MC8-9—which retained more pine by volume—demonstrate that large trees alone do not assure pine in the future overstory. Second, while plenty of light is required to promote germination and quick growth (York et al. 2007, Bigelow et al. 2011, Safford and Stevens 2017), our work provides additional evidence that light alone is not enough (York et al. 2012) as large post-logging gaps were negatively associated with pine regeneration. Most importantly, fire is required to remove competing regeneration, create gaps, and prepare the germination substrate (Sugihara et al. 2018, Safford et al. 2021). Nevertheless, fire without large trees and light gaps from previous fire or mechanical treatment may be less successful in promoting pine regeneration and persistence (Zald et al. 2008).

An understanding of the complex requirements for pine regeneration may help managers justify allocation of sufficient resources to pine restoration. For example, thin and burn treatments may be effective for restoring light and germination substrate, but planting or seeding should be considered if sufficient numbers or basal area of mature pines do not exist nearby. Group selection cuts may be effective for creating high light microsites, but broadcast and/or pile burning may be required to reduce woody debris and competing advance regeneration prior to seeding or planting.

Conclusions

Ultimately, pine has declined in both logged and unlogged stands of California mixed-conifer forest because conditions for its persistence are not being met in either case. We show that while pine regeneration was stimulated by skid trails in the post-logging period, the overall impacts of logging were detrimental. Gaps created in the absence of fire and at the expense of large pine trees did not promote pine regeneration as expected. Today, most pines entering the overstory already existed in the pre-logging understory (in our site, perhaps even from regeneration after the last fire in 1889) and woody debris built up via logging and fire suppression continue to limit pine regeneration. Meanwhile, understory composition has come to be dominated by the intermediate shade-tolerant and drought-tolerant incense-cedar over pines and even white fir. Our results suggest that maintaining pine as a dominant in mixed-conifer forests in the west will require management efforts that meet all—rather than some—of the requirements for pine establishment and growth. We echo other authors (North et al. 2021, Prichard et al. 2021, Stephens et al. 2021) in identifying fire as a key tool for pine restoration.

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Supplementary information

Figure S3.1. Directed Acyclic Diagram (DAG) showing hypothesized influence of post-logging predictor (here, gap area) on seedling abundance and subsequently future tree presence. Because the hypothesized influence of predictors occurs via seedling germination and growth, conditioning on seedling abundance would eliminate the influence of the predictor. For this reason, we do not include seedling abundances in models predicting future tree presence with predictor variables of interest and instead examine each predicted influence (arrow) with a different model as well as the direct influence of gap area on contemporary tree presence.

Table S3.1. Information on the four study plots including location, elevation, aspect, soil type, and silvicultural treatment.

Plot	# quadrats	# quadrats in plot	# quadrats in plot (30 m buffer)	Average slope	Elevation (m)	Soil type	Silvicultural treatment

MC8	140	140	110	38	1676	Wintoner family; loam	"USFS cut" - removed large overstory trees of all species and "two large yellow pine with an eye towards converting the stand to white fir and sugar pine"
MC9	100	80	50	21	1780	Wintoner family; gravelly loam	"USFS cut" - removed large overstory trees of all species
MC10	100	80	50	24	1789	Wintoner-Inville family; gravelly loam	"light economic selection" - only largest and best pines removed
MC11	100	80	50	39	1759	Wintoner-Inville family; gravelly loam	"heavy cut" - all merchantable timber removed before abandoning land

Table S3.2. Summary of model effects estimates from Bayesian generalized linear mixed model testing influence of advance and early regeneration of pines on contemporary pine tree presence.

Population-level effects	Estimate	Est.Error	l-90% CI	u-90% CI	Rhat	Bulk_ESS
Intercept	-5.84	0.88	-7.38	-4.54	1.00	2419
advance_pine	1.04	0.46	0.25	1.76	1.00	3443
early_5yr_pine	-0.14	0.89	-1.66	1.27	1.00	4768
Plot9	-0.59	0.88	-2.02	0.83	1.00	3728
Plot10	0.16	0.85	-1.26	1.60	1.00	3382
Plot11	1.05	0.83	-0.35	2.41	1.00	2948
stransect_dist_m:Plot8_1	-0.01	0.97	-1.59	1.62	1.00	4990
stransect_dist_m:Plot9_1	0.04	0.99	-1.55	1.70	1.00	3162
stransect_dist_m:Plot10_1	0.06	0.99	-1.56	1.69	1.00	4793
stransect_dist_m:Plot11_1	0.23	1.01	-1.44	1.87	1.00	4575
Smooth terms						
sds(stransect_dist_mPlot8_1)	0.90	0.84	0.06	2.49	1.00	2731
sds(stransect_dist_mPlot9_1)	0.97	0.92	0.06	2.73	1.00	2754

sds(stransect_dist_mPlot10_1)	1.03	1.02	0.07	2.86	1.00	3214
sds(stransect_dist_mPlot11_1)	3.14	2.32	0.34	7.57	1.00	1278

Table S3.3. Summary of model effects estimates from Bayesian generalized linear mixed model testing influence of advance and early regeneration of incense-cedar on contemporary incense-cedar tree presence.

Population-level effects	Estimate	Est.Error	l-90% CI	u-90% CI	Rhat	Bulk_ESS
Intercept	-2.13	0.29	-2.62	-1.67	1.00	3705
advance_CADE	0.37	0.10	0.20	0.55	1.00	3756
early_5yr_CADE	0.45	0.31	-0.05	0.97	1.00	4248
Plot9	-1.43	0.61	-2.48	-0.44	1.00	3014
Plot10	-1.38	0.60	-2.37	-0.41	1.00	3173
Plot11	-0.29	0.45	-1.05	0.46	1.00	3464
stransect_dist_m:Plot8_1	2.75	1.98	-0.80	5.77	1.00	2579
stransect_dist_m:Plot9_1	0.00	2.22	-3.62	3.58	1.00	4353
stransect_dist_m:Plot10_1	0.74	2.27	-3.10	4.39	1.00	4020
stransect_dist_m:Plot11_1	0.78	2.19	-2.79	4.38	1.00	3297
Smooth terms						
sds(stransect_dist_mPlot8_1)	0.85	0.70	0.06	2.20	1.00	1705
sds(stransect_dist_mPlot9_1)	0.88	0.89	0.06	2.42	1.00	2825
sds(stransect_dist_mPlot10_1)	1.09	1.14	0.07	3.22	1.00	2950
sds(stransect_dist_mPlot11_1)	0.97	0.91	0.07	2.68	1.00	2495

Table S3.4. Summary of model effects estimates from Bayesian generalized linear mixed model testing influence of advance and early regeneration of white fir on contemporary white fir tree presence.

Population-level effects	Estimate	Est.Error	l-90% CI	u-90% CI	Rhat	Bulk_ESS
Intercept	-3.12	0.40	-3.81	-2.48	1.00	2228

advance_ABCO	0.50	0.09	0.36	0.65	1.00	4555
early_5yr_ABCO	1.38	0.45	0.62	2.12	1.00	3010
Plot9	0.46	0.52	-0.38	1.33	1.00	2672
Plot10	0.60	0.50	-0.23	1.44	1.00	2620
Plot11	0.81	0.49	0.00	1.62	1.00	2618
stransect_dist_m:Plot8_1	0.27	1.94	-2.95	3.46	1.00	3964
stransect_dist_m:Plot9_1	-0.02	2.06	-3.39	3.35	1.00	5203
stransect_dist_m:Plot10_1	-0.30	2.03	-3.60	3.08	1.00	4881
stransect_dist_m:Plot11_1	0.74	2.05	-2.70	4.08	1.00	4237
Smooth terms						
sds(stransect_dist_mPlot8_1)	0.92	0.81	0.07	2.42	1.00	2216
sds(stransect_dist_mPlot9_1)	0.73	0.67	0.05	1.92	1.00	2970
sds(stransect_dist_mPlot10_1)	0.75	0.70	0.05	2.07	1.00	2852
sds(stransect_dist_mPlot11_1)	0.77	0.71	0.06	2.12	1.00	3352