

ARTICLE

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

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Abstract

Wildfires may facilitate climate tracking of forest species moving upslope or north in latitude. For subalpine tree species, for which higher elevation habitat is limited, accelerated replacement by lower elevation montane tree species following fire may hasten extinction risk. We used a dataset of postfire tree regeneration spanning a broad geographic range to ask whether the fire facilitated upslope movement of montane tree species at the montane-to-subalpine ecotone. We sampled tree seedling occurrence in 248 plots across a fire severity gradient (unburned to >90% basal area mortality) and spanning ~500 km of latitude in Mediterranean-type subalpine forest in California, USA. We used logistic regression to quantify differences in postfire regeneration between resident subalpine species and the seedling-only range (interpreted as climate-induced range extension) of montane species. We tested our assumption of increasing climatic suitability for montane species in subalpine forest using the predicted difference in habitat suitability at study plots between 1990 and 2030. We found that postfire regeneration of resident subalpine species was uncorrelated or weakly positively correlated with fire severity. Regeneration of montane species, however, was roughly four times greater in unburned relative to burned subalpine forest. Although our overall results contrast with theoretical predictions of disturbance-facilitated range shifts, we found opposing postfire regeneration responses for montane species with distinct regeneration niches. Recruitment of shade-tolerant red fir declined with fire severity and recruitment of shade-intolerant Jeffrey pine increased with fire severity. Predicted climatic suitability increased by 5% for red fir and 34% for Jeffrey pine. Differing postfire responses in newly climatically available habitats indicate that wildfire disturbance may only facilitate range extensions for species whose preferred regeneration conditions align with increased light and/or other postfire landscape characteristics.

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KEYWORDS

climate, fire severity, leading-edge range extension, regeneration niche, shade tolerance, subalpine forest

INTRODUCTION

With increasing global temperatures, many species are expected to track their current climatic niches by moving north in latitude (Parmesan et al., 1999) or upward in elevation (Konvicka et al., 2003). While upslope habitats may fulfill species' temperature and precipitation requirements (Woodward, 1987), both dispersal limitation and competition from existing vegetation may impede the colonization of newly climatically available habitats (Liang et al., 2018; Svenning et al., 2014). Such competition can limit species transition especially for long-lived and stress-tolerant species like trees. Removing pre-existing vegetation via disturbance may catalyze species range shifts into newly climatically available habitats (Chapin et al., 2004; Clark et al., 1996; Overpeck et al., 1990). However, forest ecosystems will not be equally affected by disturbance-accelerated climate tracking. Where leading-edge range extension is limited, such as in high elevation subalpine forests, competition from increased upward movement of lower elevation montane species may elevate extinction risk for subalpine tree species (Bell et al., 2014b).

Evidence for fire as a catalyst of tree species 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 (Moran & Ormond, 2015; Stralberg et al., 2018), others find only weak evidence (Campbell & Shinneman, 2017; Liang et al., 2018) or stress that the influence of disturbance may depend on its frequency (Moran & Ormond, 2015) or severity (Brice et al., 2020). Empirical studies often describe the negative impacts of fire on tree regeneration at the warmer, more arid trailing edges of species distributions (Davis et al., 2019; Renwick et al., 2016), but empirical evidence for fire-induced movement at the leading edges of species distributions is less clear perhaps due to the lack of robust datasets across species range limits (Brice et al., 2020; Hill & Field, 2021). In one study, fire increased the magnitude of range shifts toward cooler conditions for two of eight species in the western USA (Hill & Field, 2021), indicating that some species may be more likely than others to follow fire into new habitats. We know little, however, about which species life history traits might facilitate such expansion.

Where fire kills trees it 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 become established after fires (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 (Gray et al., 2005); increasing fire disturbance is thus poised to facilitate upward range shifts in early successional species (Meier et al., 2012). Similarly, fire may differentially accelerate the upslope movement of far-dispersing species, which are more likely to take advantage of large high-severity patches containing few surviving seed sources (Brodie et al., 2021; Stevens et al., 2015). For shade-tolerant and later successional species, conversely, fire may produce unfavorable regeneration conditions that could slow upslope climate tracking (Liang et al., 2018; Loehle, 2003). Although theoretical modeling studies abound, observational datasets that are far-ranging enough to document range shifts are rare.

Climate-induced upslope advance will probably increase the competition and/or extinction risk for species in high-elevation subalpine forest (Bell et al., 2014b; Thorne et al., 2018). 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 & Johnson, 2013). Colonization of such upslope habitat is not predicted to keep up with habitat loss at the 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 to increasing temperatures at their lower range limits (Hill & Field, 2021). Lower elevation montane species, conversely, 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 montane species throughout much of what is currently subalpine forest. Furthermore, while cool temperatures and high precipitation have limited fire in most subalpine ecosystems in the past, modern increases in atmospheric aridity are correlated with the rapidly increasing area

burned in subalpine forests (Alizadeh et al., 2021; Schwartz et al., 2015). If fire facilitates the upward movement of montane species, more fire may accelerate changes in species composition in subalpine forest ecosystems.

Despite the recent trends of increased warming, competition with montane species, and fire in subalpine forests, few empirical studies document the influence of fire on regeneration and upslope movement into this remote forest type. Using an extensive 248-plot network spanning 13 fires and ~500 km of latitude, we provide empirical data on postfire regeneration patterns in Mediterranean-type, dry-summer biome subalpine forest and ask whether fire facilitates upslope movement of montane species at the montane-to-subalpine ecotone.

MATERIALS AND METHODS

Study area

We measured tree regeneration in 248 plots in burned and unburned subalpine forests following 13 wildfires in Central and Southern California. California subalpine forests are unique in North America due to their Mediterranean-type climate in which precipitation (750–1250 mm) falls primarily as snow in winter and monsoonal moisture from thunderstorms punctuates otherwise dry summers (Fites-Kaufman et al., 2007). In contrast, the large expanses of subalpine forest found in the Pacific Northwest and the Rocky Mountains experience much lower evapotranspiration and (in the Rocky Mountains) notably higher summer precipitation (Barbour & Billings, 2000). Historically, the growing season in Mediterranean-type California subalpine forest has ranged from 6 to 9 weeks (Fites-Kaufman et al., 2007), although 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 & Rundel, 2016). Wildfire was historically infrequent (57–338 years in sampled stands in the Sierra Nevada and regularly for thousands of years in foxtail pine stands) and of variable severity depending on dominant tree species, stand density, and weather conditions (Meyer & North, 2019; Rourke, 1988). We sampled within latitude-specific estimated elevation for subalpine forest (Millar & 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 (see *Species* below) (Sawyer et al., 2009; USDA, 2004).

Fire and plot selection

Sampling in subalpine forest has been limited both by the relatively small numbers of fires above 2750–2900 m (Millar & Rundel, 2016) and their remoteness. We selected fires that had occurred less than 2 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% (Stewart et al., 2021; Welch et al., 2016). We calculated the percent basal area mortality using the remotely sensed fire severity metric, relative differenced Normalized Burn Ratio (RdNBR; 30-m resolution) as in Miller et al. (2009). We sampled a total of 13 fires including all 10 fires that fitted our criteria at the time of sampling, as well as three additional fires that did not contain all fire severity classes but were easy to access (Figure 1; Table 1). Sampling all available fires resulted in a range of 2–17 years since fire at sampling.

In each fire, we aimed to sample three plots per fire severity class in burned areas and five unburned “control” plots, for a total of ~20 plots per fire and 248 plots in total (Table 1). Plot centers were located on the nodes of a 200 × 200 m spatial grid and stratified first by fire severity and second (if possible) by aspect. Control plots were selected along the same grid as close to the fire as possible while matching elevation, aspect, and dominant forest cover. Within a given fire severity class and cardinal direction, grid points were visited in a random order to establish 0.1-hectare circular plots (11.37 m radius; hereafter, “main plot”). In each plot, we visually estimated the 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 m² regeneration subplot (4.37 m radius; hereafter “regeneration plot”) at the plot center, we identified, tallied, and aged conifer seedlings using terminal bud scars (Welch et al., 2016).

Tree species

We differentiated between subalpine specialists, subalpine generalists, and montane tree species. We defined subalpine specialists as species that occurred only in subalpine forest: southern foxtail pine, whitebark pine (*P. albicaulis*), mountain hemlock (*Tsuga mertensiana*), and limber pine (*P. flexilis*). We defined subalpine generalists as species that occurred across a broader elevation

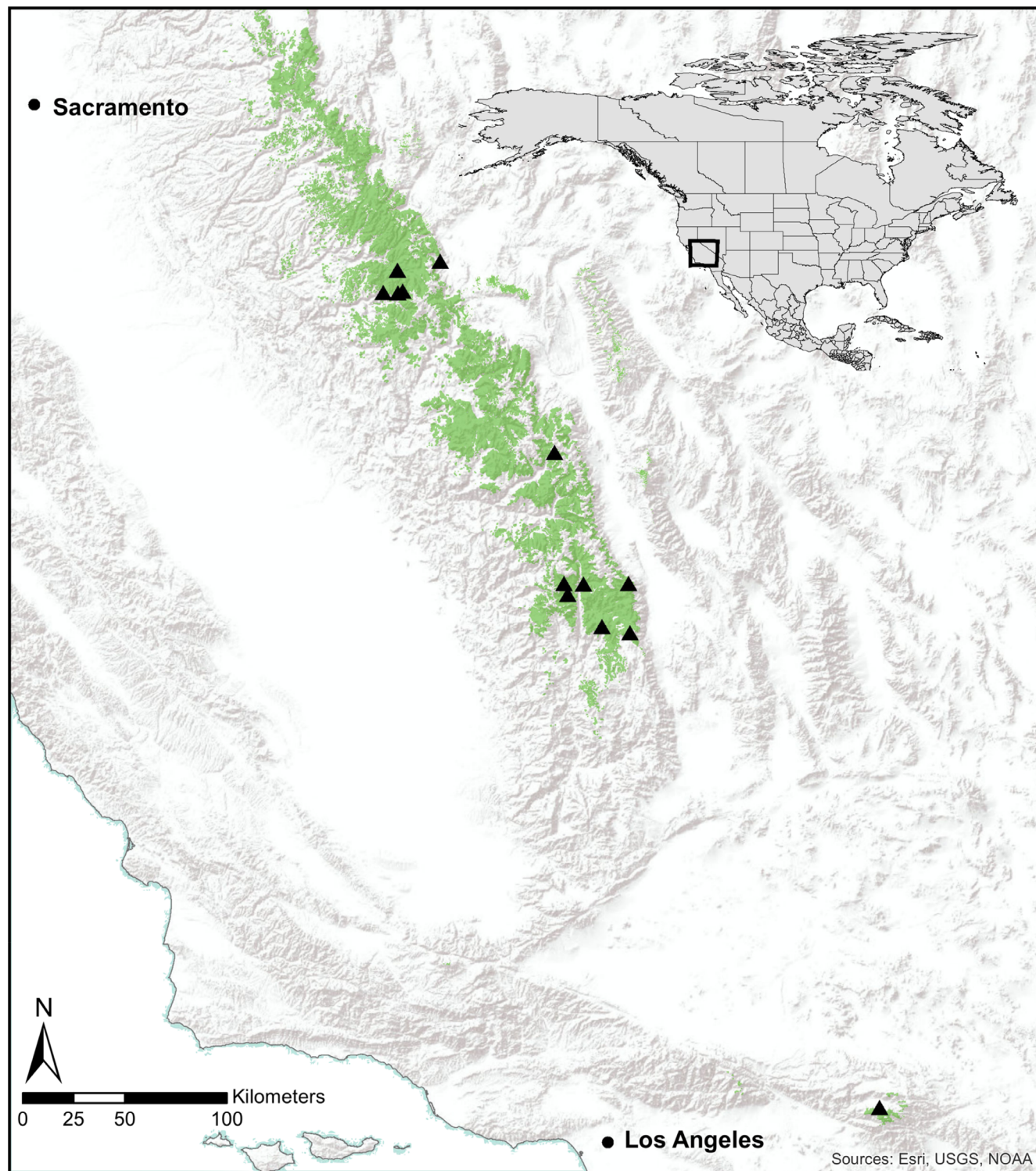


FIGURE 1 Map of the study area in Central and Southern California, USA, predominantly within the North American Mediterranean Climate Zone. Subalpine forest in the region is shown in light green and fires sampled are represented by black triangles.

range but were typically dominant or co-dominant 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 montane conifers that were not typically dominant or co-dominant in subalpine forests: red fir (*Abies magnifica*) and Jeffrey pine (*P. jeffreyi*). Homogeneous red fir forest generally borders lower subalpine forest in the Sierra Nevada (Meyer & North, 2019). In contrast

TABLE 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	12,660	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	149,475	2823–3045	5	3	3	3	3	4
Total						60	33	31	44	35	45

Note: Table modified from Brodie et al. (2021).

with 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 (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 & Stevens, 2017). Although 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), Jeffrey pine is considered a component of lower elevation (montane) mixed-conifer forests (Safford & Stevens, 2017).

With all or part of seven subalpine conifer species distributions in our study—including California endemic southern foxtail pine (Kauffmann, 2013)—we limited plots included in our 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). For the analysis of any given species or species group (e.g., montane), we only included plots from fires in which adults or seedlings of that species or species group were present within the fire perimeter (Appendix S1: Table S1). By limiting plots to those where a species or group was observed nearby, we assumed that we could attribute the presence or absence of that species or group to the study variables rather than to the plot being well in or outside their known range. Similarly, this

technique helped to ensure that fires included in analyses of shade-tolerant and later successional species were old enough to contain them.

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 (Appendix S1: Table S2) (Stevens-Rumann & Morgan, 2019). We used bilinear interpolation to extract candidate predictor variables from raster surfaces describing fire severity (as basal area mortality; see *Fire and plot selection* above), topography, seed availability, and both long-term and short-term climate variables. We obtained slope and aspect from a 30-m resolution digital elevation model and long-term 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 that a seedling receives (Welch et al., 2016). We used the *spatialEco* package in R (Evans, 2021) to calculate the

TABLE 2 Tree species sampled in study area with relevant reproductive and fire-related traits (Abrahamson, 2003; Sawyer et al., 2009).

Tree species	Elevation range	Study designation	Seed dispersal	Shade tolerance	Reproductive age	Fire resistance
Red fir	1200–2800 m	Montane	Wind	Moderate	30–600 years	Fire hardy; thick epidermis; low flammability
Jeffrey pine	450–3100 m	Montane	Animal; wind	None	8–500 years	Fire hardy; thick epidermis
Mountain juniper	100–3100 m	Subalpine generalist	Animal; gravity; water	Moderate	20+ years	Fire sensitive; thin epidermis; high flammability; canopy architecture susceptible
Whitebark pine	2000–3700 m	Subalpine specialist	Animal	None	20–700 years	Fire sensitive; thin epidermis; high flammability
Southern foxtail pine	2700–3700 m	Subalpine specialist	Animal; gravity; wind	None	20–1500 + years	Fire hardy; thick epidermis; canopy architecture resistant
Lodgepole pine	1000–3500 m	Subalpine generalist	Animal; wind	Moderate	4–600+ years	Fire sensitive; thin epidermis
Limber pine	1830–3700 m	Subalpine specialist	Animal	None	20–1000 years	Fire sensitive; thin epidermis
Western white pine	150–3400 m	Subalpine generalist	Wind	Moderate	2–400+ years	Fire hardy; thick epidermis; canopy architecture resistant
Mountain hemlock	1200–3500 m	Subalpine specialist	Wind	High	20–250 years	Fire sensitive; high flammability; canopy architecture susceptible

heat load index at each plot, a measure of incident radiation scaled with the 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 predicted conifer species basal area that incorporated disturbances from before 2017 (Ohmann et al., 2011). From species basal area, we calculated species-specific seed production (Greene & Johnson, 1994: equations 2 and 5) and finally seed density (in seeds/m²) using a half-Gaussian dispersal kernel and a 75-m dispersal parameter (σ ; Stewart et al., 2021). Our selected dispersal parameter corresponded 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 represented a midrange value compared with 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 the seed source could be more precise, our seed density estimates allowed 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 the plot center.

At each plot, we extracted climate variables from gridded datasets and calculated the 30-year normal (between 1981 and 2010) and postfire (ranging from

2–17 years) averages. While averaging across only the first 3–5 postfire years is common where an immediate postfire pulse in regeneration drives longer-term trends (Harvey et al., 2016; Urza & Sibold, 2017), we observed consistent regeneration rates across time at many of our fires (Appendix S1: Figure S1). We calculated precipitation and climatic water deficit (CWD; a measure of potential evapotranspiration minus actual evapotranspiration that is often used to capture drought; Stephenson, 1990) 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 & 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 & Sibold, 2017).

In addition to average climate and postfire weather, we calculated the anomaly of postfire weather and extreme postfire weather compared with long-term climate as *z*-scores (Young et al., 2019). Postfire weather anomaly is calculated relative to long-term averages and variability at each plot, which aids in comparing the influence of postfire weather across a wide geographic range. One extreme postfire 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” postfire weather anomaly using

the postfire year with minimum precipitation, maximum CWD, and maximum GDD.

Model selection

To understand if montane species regenerated with greater success than resident subalpine species after high-severity fires, we tested whether the interaction of fire severity and tree species “typical elevation” (montane vs. subalpine [both generalist and specialist]; Table 2) influenced the presence or absence of postfire 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 montane and subalpine tree species in the general area ($n = 157$; see *Tree species* above). To evaluate species-specific differences in regeneration patterns and influences, we fitted separate models for those species with more than 20 observations of postfire seedlings in the regeneration subplot (i.e., positive trials, see Appendix S1: Table S1): western white pine (total trials or $n = 179$), southern fox-tail pine ($n = 129$), lodgepole pine ($n = 248$), and red fir ($n = 157$). There were only eight postfire observations of Jeffrey pine in regeneration subplots, but there were 22 observations in the main plots. While observations from the main plot were not aged and therefore could not be separated into prefire and postfire categories, we 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 conducted 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 (see Appendix S1: Section S1).

In addition to elpd, we used k -fold predictions to calculate the area under the receiver operating curve (AUC), an absolute measure of model fit that ranges from 0 to 1 with 0.5 indicating random prediction and 1 indicating perfect prediction (Fielding & 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).

Climatic suitability for montane species in subalpine forest

Our assumption that montane species' seedling-only ranges constituted leading-edge range extension hinged on the assumption that climatic suitability had increased for these species at our subalpine study sites. To test this assumption, 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) (Coffield et al., 2021; Kattsov et al., 2013), and the RCPs represent 4.5 (moderate) and 8.5 (high) watts/m² 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.

RESULTS

Regeneration of montane versus subalpine species

We found that fire severity had no influence on the probability of postfire seedling presence (effect size: -0.01 ; 95% confidence interval (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 (subalpine vs. montane) was negative (-0.75 ; 95% CI: $[-1.38, -0.13]$), indicating that postfire seedling presence generally declined with increasing fire severity for montane species, but did not

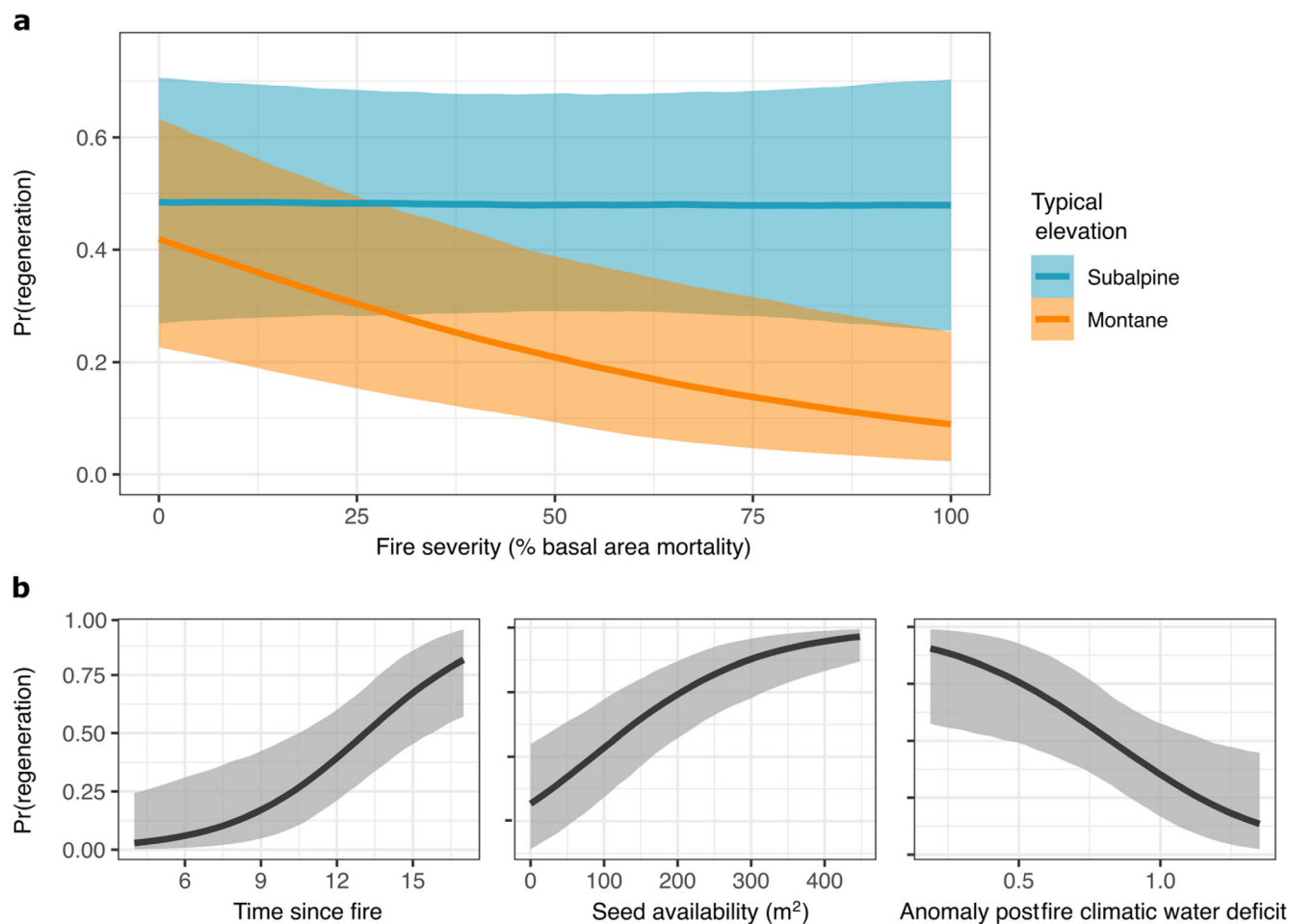


FIGURE 2 Pr(regeneration)—the probability that a 60 m² plot contains at least one postfire seedling—changes little with fire severity for subalpine species and decreases with fire severity for montane species (here combined red fir and yellow pine) (a). Regardless of species typical elevation, Pr(regeneration) is positively correlated with time since fire and seed availability and negatively correlated with anomaly of postfire climatic water deficit (b). Lines and shading show model-estimated means and 95% confidence intervals.

change for subalpine species (Figure 2; Appendix S1: Table S3). Overall, we found fewer montane species than subalpine 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 postfire seedling presence, and anomaly of postfire CWD (−1.18; 95% CI: [−2.20, −0.24]) decreased the probability of postfire seedling presence (Figure 2).

Species-specific models

For foxtail pine (Figure 3; Appendix S1: 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 postfire 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% CIs did not cross zero). Time since fire (0.49; 95% CI: [−0.92, 2.00]) had no detectable effect.

For western white pine (Figure 3; Appendix S1: Table S5; 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 postfire CWD (−0.67; 95% CI: [−1.99, 1.06]) were undetectable.

For lodgepole pine (Figure 3; Appendix S1: Table S6; 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 on postfire seedling occurrence (0.34; 95% CI: [−0.14, 0.82])

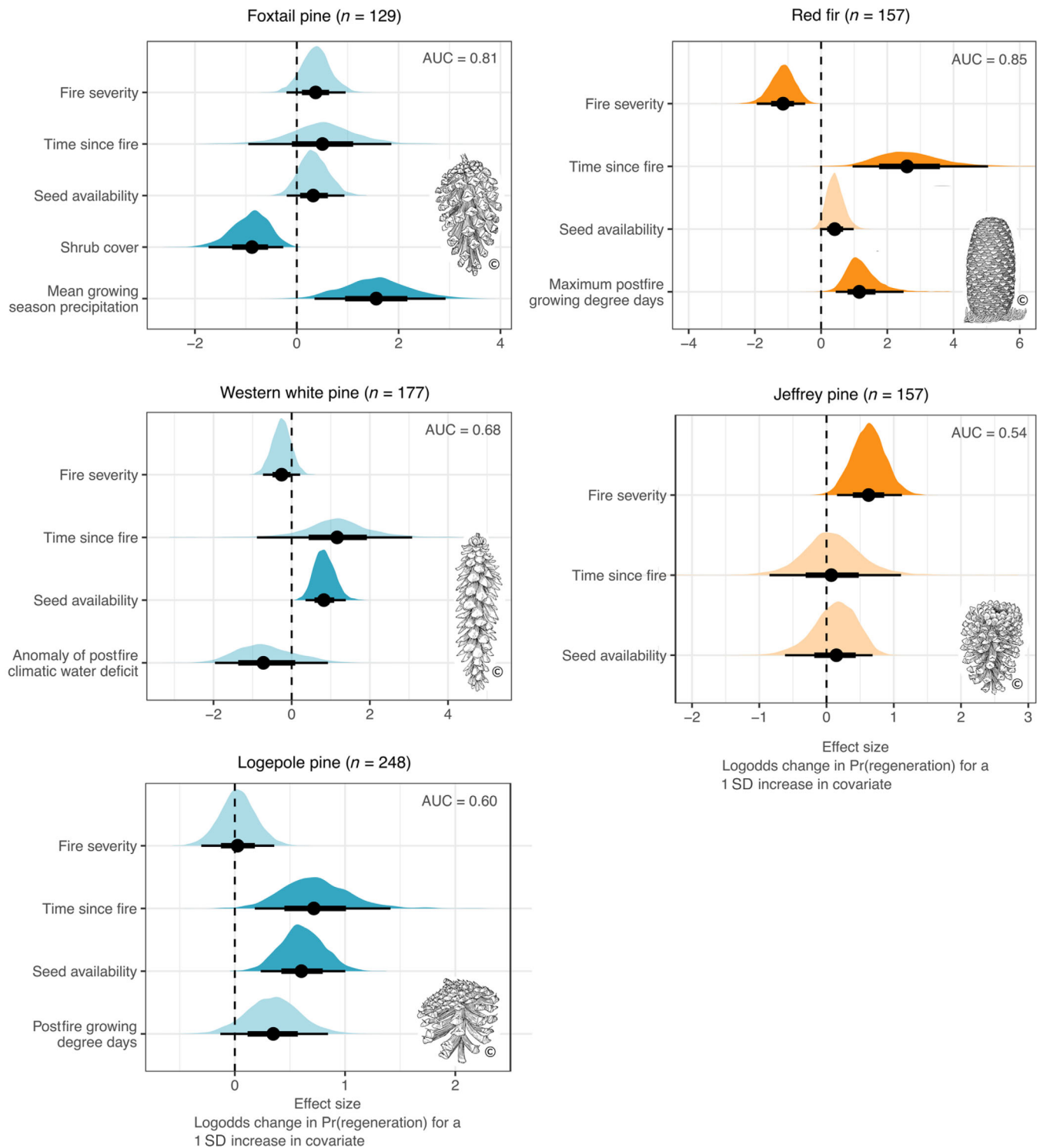


FIGURE 3 Plots showing the effect size of predictors on $\Pr(\text{regeneration})$ for foxtail pine, western white pine, lodgepole pine, red fir, and Jeffrey pine in subalpine forest. $\Pr(\text{regeneration})$ is the probability that a 60 m² plot (405 m² for Jeffrey pine) contains at least one postfire seedling (seedling of any age for Jeffrey pine). Black dots and bars show model-estimated means with 80% and 95% confidence interval (CI), respectively. Shading shows distribution of the mean, with darker shading indicating that the 95% CI does not cross zero. Blue shading represents subalpine species, and orange shading represents montane 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.

and fire severity had no detectable effect (0.03; 95% CI: [−0.31, 0.36]).

For red fir (Figure 3; Appendix S1: Table S7; 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 the 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]), decreasing the probability of occurrence in regeneration plots from 0.34 in unburned forest to 0.03 in severely burned forest.

Our model of Jeffrey pine seedling occurrence produced poor predictions (Figure 3; Appendix S1: Table S8; 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]). Predicted seedling occurrence increased by almost four times, from 0.07 to 0.27. 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 discernible effect on Jeffrey pine seedling occurrence.

Climatic suitability for montane species in subalpine forest

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 decrease (−5%) under the RCP4.5 (moderate) emissions scenario (Figure 4). All climate model and emissions scenarios predicted increased suitability (23%–46%, mean 34%) for Jeffrey pine in subalpine forest by 2030.

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 montane tree species in our study area (Figure 4), regeneration of montane species was more than four times as likely to occur in unburned than severely burned subalpine forest (Figure 2). Greater regeneration of montane species in unburned areas suggests that competition may not currently be a major force preventing climate tracking in California subalpine forests (Liang et al., 2018; Svenning et al., 2014). However, the establishment of individual montane species diverged across a fire severity gradient. Regeneration of red fir, which contributed most to montane species trends in the combined model, was 11 times lower in severely burned forest than unburned forest (Figure 3). Red fir seedlings and saplings are moderately shade tolerant (Sawyer et al.,

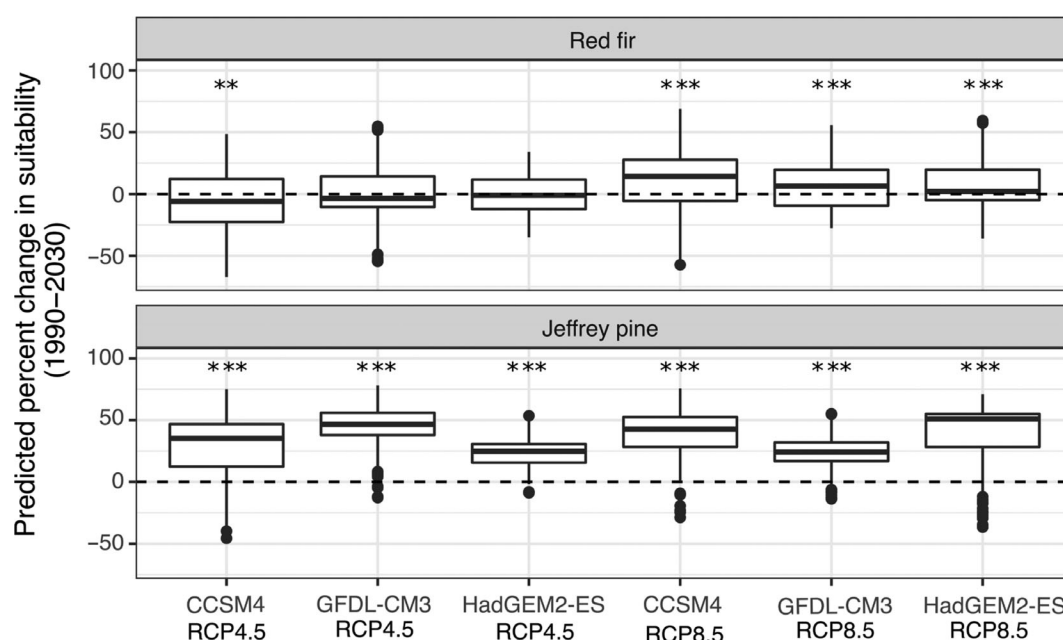


FIGURE 4 Box plots show the change in suitability between 1990 and 2030 for red fir and Jeffrey pine—montane species—in the study plots in subalpine forest under six climate model and emissions scenarios. RCP4.5 and RCP8.5 are moderate and high emissions, respectively, and CCSM4, GFDL-CM3, HadGEM2-ES are General Circulation Models that span a range of possible future precipitation. Asterisks indicate a nonzero difference (** $p < 0.01$, *** $p < 0.001$) in suitability based on a two-sided t -test with Bonferroni correction for six tests.

2009) and require partially shaded microsites for regeneration (Selter et al., 1986; Ustin et al., 1984). The prevalence of shade in unburned subalpine forest may allow shade-tolerant species to colonize new habitats in unburned—although relatively open—subalpine forest, but not after fire-caused canopy mortality reduces tree cover. Where fire produces newly available habitat and appropriate regeneration conditions, species may be more likely to move into new habitats.

Indeed, we found that shade-intolerant (Gray et al., 2005) Jeffrey pine seedlings and saplings were four times more likely to pioneer severely burned subalpine forest than unburned subalpine forest (Figures 3 and 5). Alongside an average predicted 34% increase in climatic suitability at our study sites by 2030 (compared with 5% for red fir), our results suggest that Jeffrey pine may be the species most likely to colonize future subalpine forests under predicted increases in fire and temperature (Alizadeh et al., 2021; Remy et al., 2021; Thorne et al., 2018). Our findings align with recent modeling studies from across the western USA showing that Ponderosa pine (*Pinus ponderosa*)—an ecologically close relative of Jeffrey pine in the “yellow pine” group (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 (Bell et al., 2014b; Campbell & Shinneman, 2017). Ponderosa pine was adapted to warmer and drier conditions than the subalpine fir and spruce that it replaced in the simulation (Remy et al., 2021). Yellow pines, conversely, share many traits with the subalpine specialist pines common in our dataset such as primarily animal-dispersed seeds (Vander Wall, 2008), shade intolerance, and some tolerance for drought and UV light exposure (Gray et al., 2005; Legras et al., 2010; Staszak et al., 2007). Where the two grow together in subalpine forest, yellow pines’ relatively high growth rates compared with subalpine specialist pines (McCune, 1988) may present their greatest advantage (Campbell & Joseph, 2003).

The contrasting postfire responses of a shade-tolerant (red fir) and a shade-intolerant (Jeffrey pine) species highlight that regeneration niche may determine how and where species expand their ranges under a changing climate. For example, simulation modeling shows 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 the Rocky Mountains. In a study encompassing the entire western USA, Hill and Field (2021) found that fire enhanced seedling-only movement into cooler areas for one moderately shade-tolerant and one shade-tolerant species. It may be that fire increases the quality of regeneration conditions for shade-tolerant species in other ways such as clearing litter and duff to expose bare mineral soil (Landhäusser et al., 2010) or increasing nutrient availability (Busse et al., 2014).

Overall, we did not find strong evidence that fire-facilitated range shifts would hasten the decline of subalpine forests at the montane-to-subalpine ecotone. Regeneration for resident subalpine species was stable across a fire severity gradient, with weak evidence for the increased regeneration of southern foxtail pine in high-severity burn areas. In contrast, high-severity fire virtually eliminated the regeneration of shade-tolerant montane species in the subalpine zone. Our results suggest that subalpine forests dominated by specialist five-needle pines such as foxtail, whitebark, and limber pine (McCune, 1988) may be advantaged under increasing incidence of fire by early seral characteristics like increased growth and recruitment post-disturbance



FIGURE 5 Jeffrey pine seedling in a high-severity patch of burned foxtail pine forest at 3100 m. No Jeffrey pine adults were visible within the fire perimeter or in the surrounding forest. Photograph credit: Emily G. Brodie.

(Coop & Schoettle, 2009; Perkins, 2015; Slaton et al., 2019). Such results bode well for a group that includes federally protected and keystone tree species in North American subalpine forests (Government of Canada, 2012; Tomback et al., 2001; US Fish and Wildlife Service, 2022). However, fires in this study were still within the natural range of variation for fire severity and frequency (see Appendix S1: Section S2 and Figure S2). Larger high-severity patches may reduce postfire regeneration even of early successional pines (Coop & Schoettle, 2009; Harvey et al., 2016; Moser et al., 2010), and increasing fire frequency in historically infrequent-fire ecosystems is already compromising the resilience of wet-summer biome subalpine forests such as those in the Rocky Mountains (Turner et al., 2019).

Wet-summer biome subalpine forests may be further impacted by the increasing incidence of subalpine fire (Alizadeh et al., 2021) due to differences in species life history traits across elevational bands. Wetter subalpine regions are more likely to contain shade-tolerant subalpine specialists such as subalpine fir or mountain hemlock (Barbour & Billings, 2000). Where shade-tolerant species are bounded below by shade-intolerant species such as pines and broadleaved species (e.g., in parts of the Rocky Mountains and eastern Cascade range), fire may facilitate the upward movement of montane species while simultaneously limiting the reproduction of resident subalpine species (Meier et al., 2012). Thus, the impacts of increased incidence of fire in subalpine forest will probably depend on the relative abundance and orientation of fire-related life history traits in montane and subalpine forest bands.

CONCLUSIONS AND IMPLICATIONS FOR MANAGEMENT

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-dispersed and animal-dispersed seeds like Jeffrey pine may be more likely to move upslope into small high-severity patches. Such patterns suggest that fire within the natural range of variation for California subalpine forests may advantage subalpine

specialist five-needle pines over encroaching red fir, while simultaneously providing establishment opportunities for Jeffrey pine in newly climatically available habitat.

Although there is little direct management in subalpine forests due to constraints on access and actions in the federally protected wilderness, our results provide the context for decisions regarding the suppression of wildfire ignitions. We show that fires, such as those sampled here, with 18%–27% high severity in small patches (<200 m radius), can stimulate regeneration and reduce red fir encroachment in large populations of foxtail pine. Thus, our work supports letting wildfires burn into California subalpine forests under moderate weather conditions, as long as recent fire return intervals are not appreciably shorter than ecologically desirable (see, e.g., Safford & Van De Water, 2014). We also provide evidence that seed availability is important for the regeneration of subalpine trees, indicating that, with predicted changes in climate, the large high-severity patches causing regeneration failure at lower elevations may become a problem in subalpine forests as well (Alizadeh et al., 2021; Hansen et al., 2018; Harvey et al., 2016; Welch et al., 2016). Ultimately, decisions regarding wildfire use for resource benefit will require detailed knowledge of fire history, current conditions, and—we propose—the ecology, orientation, and regeneration niche of local tree species.

AUTHOR CONTRIBUTIONS

Emily G. Brodie, Hugh D. Safford, and Andrew M. Latimer conceived the study. Emily G. Brodie, Jesse E. D. Miller, and Sara Winsemius collected field data. Sara Winsemius produced fire severity maps. Joseph A. E. Stewart produced seed availability maps and consulted with Emily G. Brodie regarding data analysis. Emily G. Brodie wrote the manuscript and all authors contributed substantially to revisions.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Brodie & Miller, 2023) are available in Dryad at <https://doi.org/10.25338/B8RD26>. Maps of projected climatic suitability of montane species suitability were downloaded from <https://charcoal2.cnre.vt.edu/climate/species/index.php> by clicking on links to maps for “Red Fir” and “Jeffrey Pine.”

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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