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Post-fire resurveys reveal predictability of long-term conifer recruitment in severely burned California dry forests

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ABSTRACT

High severity fire is far outpacing post-fire reforestation capacity across the American West, highlighting the need to better understand when and where natural regeneration is sufficient to meet short- and long-term reforestation goals. The vast majority of available post-fire data represents regeneration in the first few years following a fire, raising the question of how well recovery trajectories can be predicted from early post-fire snapshots. We utilize a unique dataset from seven wildfires and 78 plots surveyed twice following stand-replacing fire in two California ecoregions, the northern Sierra Nevada and Klamath Mountains, to ask (1) how are post-fire vegetation and conifer densities changing over time and (2) how well do relatively early post-fire sampling efforts and biophysical factors (availability of seed source, shrub competition, and microclimate) explain longer-term (12–23 year) conifer recovery in California dry forests. Change in conifer seedling density between survey periods was highly variable. Overall, densities of all conifer species during the first decade after fire provided reliable estimates of longer-term conifer recovery in northern California dry forests, though in different ways for different species. Early post-fire seedling density readily explained longer-term densities for less shade-tolerant species, yellow pine (*Pinus ponderosa* and *Pinus jeffreyi*) and Douglas-fir (*Pseudotsuga menziesii*). In contrast, early seedling density was a poor predictor for shade-tolerant species, predominantly white fir (*Abies concolor*), with site conditions better explaining longer-term density. In general, the probability of a site experiencing net seedling mortality between surveys was highest in sites with high shrub cover and the probability of net recruitment increased with decreasing heat load, suggesting a continued role of microclimate and competition in forest recovery long after the initial post-fire period. Our results lend support to the use of relatively early post-fire surveys to infer longer-term forest recovery trajectories for forest management planning and can help refine reforestation prioritization tools.

1. Introduction

Increasing fire activity across the American West has led to larger areas burning in high severity, stand replacing-fires. In dry California forests, the proportion of forest burned at high severity (> 75 % basal area mortality) has increased by more than three times the pre-settlement mean (Miller et al., 2012; Williams et al., 2023), largely due to changes in climate and forest structure resulting from over a century of active fire-exclusion. Increased fire activity, coupled with rising temperatures and moisture deficits, has heightened concern about the potential for large-scale forest loss and transition to shrub and/or grass dominated states where forest resistance and resilience mechanisms are overcome (Coop et al., 2020). This is especially concerning in large stand-replacing patches lacking nearby seed sources and thus having limited potential for natural conifer recruitment (Coop et al., 2020; Welch et al., 2016; Gill et al., 2022).

Reforesting disturbed forest ecosystems is a land management priority across the West, with high severity wildfires making up over 80 %

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of current reforestation needs (Forest Service, 2022). Current rates of forest loss are far outpacing reforestation capacity, highlighting the need to better understand how natural regeneration contributes to forest recovery (North et al., 2019). Early assessments of conifer recruitment are important given that costs of planting increase and success rates decrease with time since disturbance (McDonald and Fiddler, 1993; Smith et al., 1997). However, because of dynamic early seral processes, using short-term post-fire surveys to estimate long-term recovery trends may lead to over- or underestimates of stocking rates and misjudged recovery, complicating post-fire management planning. While numerous studies document patterns and drivers of tree regeneration within the first several years after fire, far fewer investigate changes in post-fire regeneration over longer time scales (> 10 years after fire) and little is known about how well observations from early post-fire periods explain long-term outcomes.

Early seral communities following high severity fire have multiple possible pathways of development depending on propagule pressure, productivity, and the strength of competitive interactions. While some research has found that tree recruitment in the first 3–5 years after fire is especially important in conifer forests, presumably because of early post-fire competition (Hankin et al., 2019; Harvey et al., 2016), conifers can continue recruiting for decades to centuries following wildfire if a seed source is available and conditions are suitable for establishment (Airey-Lauvaux et al., 2016; Tepley et al., 2013; Tubbesing et al., 2020; Ursell and Safford, 2022). For example, in California mixed conifer forests, firs (*Abies* spp.) have been shown to continue establishing for decades and at higher densities than pines (Airey-Lauvaux et al., 2016), likely owing to their greater shade-tolerance and dispersal ability (Safford and Stevens, 2017). Alternatively, conifer density may decline after early post-fire recruitment if seedlings die during subsequent drought or from other causes (Young et al., 2019; McCord et al., 2020). Despite this potential for continuing changes in tree density over the first few decades after high severity fire, we know little about when and where longer-term post-fire establishment and seedling mortality occur, or the factors influencing shifts in regeneration trajectories after the initial post-fire recruitment. Beyond changing tree density, differential long-term recruitment or mortality of seedlings among species could shift forest composition away from a desired state, demonstrating the importance of understanding the extent to which seedling recruitment and mortality over time can be explained by short-term post-fire dynamics, and how these processes contribute to long-term forest trends.

Here, we evaluate the factors influencing long-term forest regeneration trajectories in severely burned areas using a unique data set with observations at two time points following high severity fire from seven fires in California dry forests. The resurvey design allows us to directly measure changes in tree seedling density and cover of plant functional types over a potentially critical time period in forest succession (6–23 years post-fire). It also allows us to evaluate associations with potential drivers of successional change. We ask (1) how is early seral forest vegetation (i.e. shrub, forb, and graminoid cover and conifer seedling densities) changing over time and (2) how well do early post-fire conifer seedling density and biophysical factors (including availability of seed source, shrub competition, and site condition) explain longer-term post-fire conifer recovery, seedling mortality, and recruitment? We expected long-term conifer densities to increase over time for shade tolerant species with greater dispersal ability. Shade tolerance can benefit conifer establishment among rapidly growing shrubs (Tubbesing et al., 2020). In contrast, we expected densities of shade intolerant species to be more stable over time, given that their establishment after the early post-fire years is often inhibited by light competition and a lack of bare mineral soil (Rodman et al., 2020; Welch et al., 2016). Our findings will contribute to our understanding of the trajectories of forest recovery following high severity fire and will help inform post-fire monitoring and management efforts by demonstrating the extent to which early post-fire monitoring effects explain longer-term trends.

2. Methods

2.1. Study area

Data were collected from seven wildfires in two northern California study areas: yellow pine mixed conifer forests of the Sierra Nevada ecoregion and mixed evergreen forests of the southern Klamath Mountains ecoregion (Fig. 1, Table 1). Lithology within the wildfire perimeters is dominated by Mesozoic granitoid rocks and Tertiary volcanics in the Sierra Nevada sites (the Pendola and Moonlight Fires also include some Mesozoic metamorphic rocks), and the Klamath Mountain site is found on Paleozoic metamorphic rocks (State of California, 2015). Our study areas all experience a Mediterranean climate characterized by cool, wet winters and warm, dry summers. Mean annual precipitation ranges across the study region from approximately 650 to 2150 mm/yr and mean temperatures range from 4.7 to 14.9 °C (Table 1) (Daly and Bryant, 2013).

Forest types vary with aspect and elevation, but in all cases they include multiple conifer and hardwood species. Low- and middle-elevation forests on the west slope of the Sierra Nevada (Pendola, Freds, and Power Fires) are dominated by mixed conifer forest, including ponderosa pine (*P. ponderosa*), Douglas-fir (*Pseudotsuga menziesii*), sugar pine (*P. lambertiana*), incense cedar (*Calocedrus decurrens*) and white fir (*Abies concolor*), along with canyon live oak (*Quercus chrysolepis*), California black oak (*Quercus kelloggi*), and Pacific madrone (*Arbutus menziesii*). At higher elevations and on the east side of the Sierra Nevada (Moonlight, Gondola, and Showers Fires), the species mixes are broadly similar, but Jeffrey pine (*P. jeffreyi*) mostly replaces ponderosa pine, Douglas-fir becomes rare or absent, red fir (*A. magnifica*) begins to appear, and oaks and madrone are less dominant or absent. In the southern Klamath Mountains (Sims Fire), the landscape is dominated by so-called "mixed evergreen" forests, which are dominated by Douglas-fir and a mix of evergreen (and deciduous) broadleaf species such as tanoak (*Notholithocarpus densiflorus*), canyon live oak, black oak, Pacific madrone, and in drier areas, Oregon white oak (*Quercus garryana*) (North et al., 2016). We restricted our study sites to the yellow pine and Douglas-fir zones given that these species are particularly important for post-fire management throughout the region. In all cases, the forests we sampled developed under frequent low-severity and mixed-severity fire regimes which include scattered patches of high severity burning (Halofsky et al., 2011; Safford et al., 2021). However, uncharacteristically large, stand-replacing fires in the last few decades have left many areas dominated by seed-banking shrubs and re-sprouting hardwoods and shrubs including multiple species in the genera *Ceanothus* (ceanothus) and *Arctostaphylos* (manzanita) (Welch et al., 2016; Fig. 1).

We monitored long-term forest regeneration trajectories within the seven wildfire perimeters in areas that burned at high severity ($\geq$ 75 % basal area mortality) between 1999 and 2007. Study fires ranged in size from 294 to > 18,000 ha and varied in topography, elevation, and environmental conditions (Table 1). All fires burned prior to the extreme California drought lasting from 2012 to 2015 and many post-fire seedlings were exposed to the effects of that drought (Robeson, 2015). Prior to burning, most of the area in the seven fires had been unburned for over a century, and none of the plots we resampled had experienced a fire since at least 1908 (CalFire, 2023). Due to the long-term lack of fire, forests at the time of burning were generally notably denser than would have been expected under the natural fire regime, before the imposition of fire exclusion policies in the early 20th century (Safford et al., 2021).

2.2. Focal species

For this study, we focused on the conifer species that were the most common at our study sites: yellow pines (ponderosa and Jeffrey pine), white fir, and Douglas-fir. These species differ in their drought and shade tolerance and resistance to fire, but all species rely on seed dispersal from surviving trees for post-fire regeneration. Yellow pines are highly

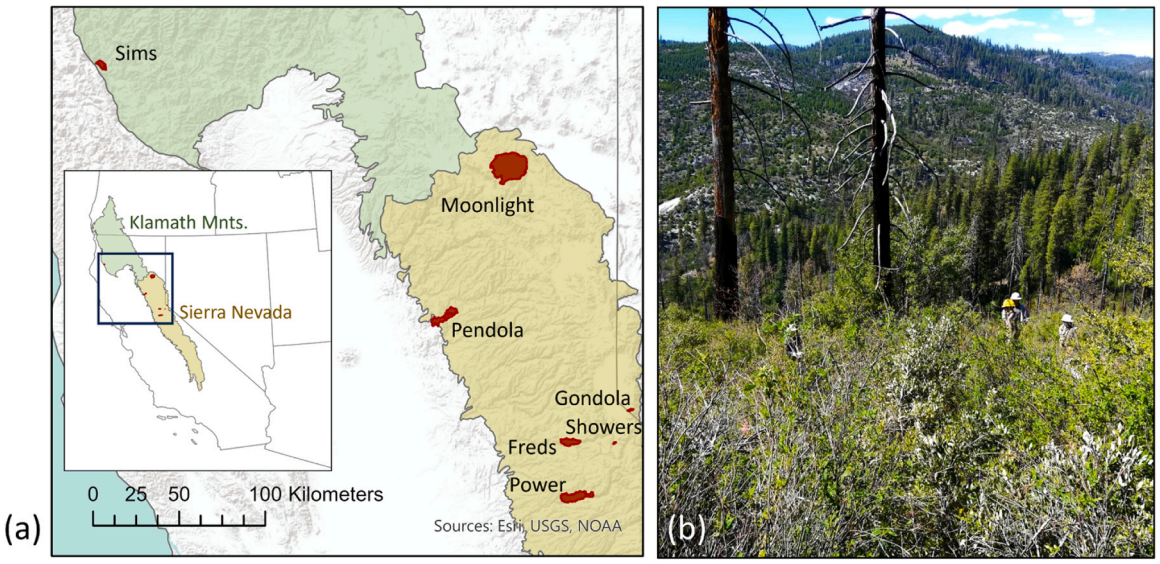

Fig. 1. (a) Study fires located in two northern California, USA, ecoregions: Klamath Mountains and the Sierra Nevada. **(b)** Shrubs dominate a patch of severely burned mixed conifer forest 18 years following the Power fire.

Table 1
Description of 7 surveyed fires in northern California, USA.

Fire	Fire year	Area (ha)	Elevation range (m)	Mean precip. (mm)	Mean temp.°C	Initial survey yr (s); yrs after fire	resurvey yr(s); yrs between surveys	No. re-surveyed plots, *n*	Plot size (m^2) used for veg. cover
Freds[s]	2004	1716	1385–1879	1607	11.0	2012–13; 8–9	2022; 10	3	405
Gondola[s]	2002	272	2098–2578	763	5.7	2008; 6	2019; 11	11	Not used
Moonlight[s]	2007	18,216	1645–2092	773	7.9	2014; 7	2022; 8	7	405
Pendola[s]	1999	4975	608–916	1523	14.5	2010–11; 11–12	2022; 11–12	3	60
Power[s]	2004	5144	1421–1906	1413	11.6	2014; 10	2022; 8	15	405
Showers[s]	2002	294	2112–2300	1343	6.3	2009; 7	2019; 10	10	Not used
Sims[k]	2004	1192	481–945	1413	12.8	2010; 6	2016–17; 6–7	29	60
All fires	Range: 1999–2007	Range: 272–18,216	Range: 481–2578	Mean: 1267	Mean: 10.3	Range: 6–12 yrs after fire	Range: 6–12 yrs between surveys	Total: 78	

Note: Superscript 's' = fire is located in the Sierra Nevada ecoregion. Superscript 'k' = fire is located in the Klamath Mountains ecoregion.

shade-intolerant and often establish in open areas following disturbance. These pines have thick bark when young which aids survival to frequent low-severity fire (Safford and Stevens, 2017). White fir is shade-tolerant and readily establishes in forest understories in addition to in open areas after disturbance (Safford and Stevens, 2017). Douglas-fir is generally less shade tolerant than white fir, but often establishes in the understory (Minore, 1979) and is more shade tolerant than yellow pines. Drought tolerant oaks, shrubs, and adult pines are often more prevalent at lower elevations and south-facing slopes, while firs are more abundant in moister north-facing slopes and at higher elevations (Stephens et al., 2018).

2.3. Survey plots

The project aim from the original surveys was to determine rates of natural regeneration in areas that had not been replanted after burning. Plots were installed in a 200 × 200 m gridded pattern across a fire severity gradient and a range of aspects, slopes, and elevations within areas that met the initial field sampling conditions (i.e. USFS lands, non-wilderness, and untreated after fire) totaling over 1400 plots (Welch et al., 2016). Plots were located and surveyed following the Forest Service's Common Stand Exam protocol (USDA Forest Service, 2012) using a fixed 4.4 m (14.3 ft) radius (60^2 m area) circular regeneration sampling plot. Within each regeneration plot, site characteristics were documented including slope, aspect, and dominant vegetation. The diameter at breast height (dbh) of surviving pre-fire trees was recorded and post-fire seedlings and saplings of all tree species were aged and tallied for each species within each age class. Post-fire seedlings and saplings (trees less than 7.6 cm dbh; USDA Forest Service, 2012), were combined for analysis and are hereafter called "seedlings". The size of the regeneration plot was chosen so that presence of a single seedling per plot represents a fully stocked site for these forest types.

Seedling age was determined by counting bud scars and/or branch whorls on each individual. While this method is not entirely accurate and has been found to underestimate age, especially for older trees, it is often used as a best method for non-destructive field tree aging for the dominant species included in this study (Hankin et al., 2018; Urza and Sibold, 2013). Non-destructive sampling was necessary for tracking forest recovery over time in re-surveyed plots. We determined the establishment year for each seedling by subtracting the age of the seedling from the survey year. The number of years that a seedling established post-fire was determined by subtracting the establishment year from the fire year.

Foliar cover of vegetation lifeform (shrubs, graminoids, and forbs) was visually estimated to the nearest percent either within a 405 m^2 circular plot that encompassed the smaller regeneration plot or within the 60 m^2 regeneration plot depending on the fire and the initial sampling method (Table 1). In plots where hardwoods and shrubs were recorded separately, these covers were combined as "shrub cover" for analysis given that regenerating hardwoods were often documented as

"shrubs'' when in their multi-stemmed, basally resprouting form. In addition to total shrub cover, percent cover by species of dominant shrub species was recorded for species that occupied at least 10 % foliar cover of the plot. We characterized abiotic site conditions by calculating "heat load" for each plot from a 30 m resolution elevation model (Landfire, 2019) following McCune and Grace (2002). This method calculates potential annual direct incident radiation using aspect (radians E of N), slope (radians), and latitude. Burn severity was characterized in the field during the initial post-fire survey based on percent tree basal area mortality within each plot (Welch et al., 2016). Distance to nearest live seed source (single, reproductive tree) present at the time of fire was recorded for each tree species using a laser rangefinder.

Sample plots were resurveyed 6–12 years following the initial survey protocol by locating rebar or pin flags at plot center and repeating the initial measurements. We selected plots for resurveys that (1) burned at high severity with $\geq$ 75 % canopy mortality at least five years prior to the initial survey (Welch et al., 2016), (2) did not receive post-fire management including salvage logging, planting, or vegetation removal, and (3) had a permanent marker at plot center. Post-fire management was determined in the field and using spatial data from the Forest Service Forest Activity Tracking System database (FACTS; USDA Forest Service, 2022). Plot data from multiple collection efforts were standardized and compiled prior to analysis. In total, we compiled 78 resurveyed plots from seven fires and four fire years (Table 1). While over 1400 plots were initially established, very few plots met our complete requirements as only a small subset of plots burned at high severity, most plots lacked permanent plot markers and many re-burned or received post-fire management after the initial sample. Only one fire, Sims, was located in the Klamath Mountains; the remaining six fires were situated in the northern Sierra Nevada (Fig. 1). At the time of the resurvey, minimum distance to live seed source varied from 0 (live trees present in the plot) to > 400 m. On average, plots were 104 m from the nearest seed source, with 50 % of plots > 44 m from a seed source and 25 % of plots > 119 m from a seed source.

Given functional similarities between species, difficulty differentiating species of the same genus at early regeneration stages, and low frequency of seedlings of some species, we performed conifer density analyses at the genus level. For example, all pine seedlings (*Pinus* spp.) were combined for analysis. Uncommon seedling genera, including incense-cedar (*Calocedrus* spp.), were excluded from genus specific analyses given insufficient sample sizes, but were included in total conifer density. We chose not to evaluate trends in post-fire hardwood recovery in this study given inconsistencies in their inclusion as post-fire seedlings in the initial data collection efforts and the strong management focus on conifers in this region.

2.4. Data analysis

We tested for differences in early seral vegetation cover between the two survey periods using generalized linear mixed models (GLMMs) with data from both sampling periods included in the response (discrete, non-negative data) and a two-level factor for survey period (initial/revisit) as a predictor variable. A plot level random effect was included to account for repeated observations at the same plot. We used a 'Tweedie' family distribution with a log-link (Tweedie, 1984) because evaluation of residuals revealed non-normality in the lifeform and shrub species data. The Tweedie family is a flexible distribution with a compound Poisson-gamma structure often used to fit non-negative data with excess zeros, common in cover data (Tweedie, 1984). We fit separate models for each vegetation lifeform (shrubs, graminoids, and forbs) and ecoregion. To characterize the composition in more detail, we modeled cover of dominant shrub genera/species: manzanita, ceanothus and poison oak (*Toxicodendron diversilobum*). Post-fire seedling counts from the initial survey and resurvey were modeled using GLMMs with a negative binomial distribution with a two-level factor for survey period as a predictor and a random effect for plot. Negative binomial families can be used for over-dispersed count data with excess zeros as was observed in our conifer seedling count data (DeGroot, 1986). Separate models were fit for each conifer species – pine, fir, and Douglas-fir. To test for differences in mean cover/counts between survey periods, post-hoc comparisons comparing the estimated marginal means of our two survey periods (resurvey - initial survey) for each model were performed using 'emmeans' (Russell, 2021). Tests were performed on the log scale.

We chose to model structure and seedling data for the Sims fire (Klamath Mountains) separately from the fires in the Sierra Nevada because of its distinct composition, geography, and ecology. Data from the Sims fire (survey plots = 37) was used exclusively to fit the Douglas-fir model given that pine and true fir were absent from nearly all Sims survey plots and Sims was the only fire that recorded Douglas-fir seedlings in the initial sampling effort (although adult Douglas-fir trees were present within the Pendola burn perimeter). The pine and fir models were fit with data from the six study fires in the Sierra Nevada (n = 49 resurveyed plots). To account for variability in sampling efforts in the pine and fir models, we included explanatory variables for the time between the fire and the initial survey and the time between surveys. For a subset of the vegetation lifeform models (shrub, forb, and graminoid), we excluded data from two fires, Showers and Gondola (n = 21 plots), which had insufficient data available from the initial survey.

To investigate how well seedling density from the initial survey (6–12 years after fire) explained longer-term conifer regeneration, we modeled seedling count at the time of resurvey (response variable) as a function of seedling count at the initial survey and biophysical predictor variables using GLMMs with a negative binomial family. Biophysical predictors consisted of heat load, distance to seed source (resurvey), and shrub cover (resurvey). Density of initial seedlings was square root transformed to improve normality of residuals and all predictors were scaled and centered to improve convergence and comparability of effect sizes. As with the density models described above, we fit separate models for genus and ecoregion. In the pine and fir models, the time between the fire and the initial survey and time between surveys were included as explanatory variables to account for multiple survey years. To evaluate how well the variability in seedling density at the resurvey was explained by initial seedling density, we calculated partial r^2 for initial seedling density using differences in Nakagawa marginal r^2 for models with and without initial seedling count with the 'performance' package (Lüdecke et al., 2021).

We evaluated the probability of a plot experiencing net mortality and net recruitment of conifer seedlings between surveys using logistic GLMMs with a binomial family. Net mortality and net recruitment were calculated as binary variables describing plots where the total conifer seedling count at the resurvey was lower (net mortality) and higher (net recruitment) than the total count at the initial survey. All conifer seedlings were combined for these analyses. As in the previous models, we included shrub cover (resurvey), heat load, and distance to seed source as biophysical predictors. We used the minimum distance to seed source recorded for any conifer species at the plot during the resurvey. Time between the fire and the initial survey and time between surveys were included as explanatory variables, and study fire was included as a random effect to account for variability between fires. Initial seedling count was included in the mortality model to evaluate potential density dependence (i.e. the relationship between population growth and population density). All models were fit with the package 'glmmTMB' (Brooks et al., 2017) and assumptions were checked using the 'Dharma' package (Hartig, 2022) in R version 4.3.0.

3. Results

3.1. Timing of seedling establishment

Conifer seedling densities and timing of seedling establishment, determined by bud scar seedling aging, varied by species and study fire.

However, we observed seedling establishment of all three species throughout the period of extreme drought (2012–2016) (Fig. 2). Fir seedling recruitment was highest and most continuous in the highest elevation study fires, Gondola and Showers. The highest number of fir and Douglas-fir seedlings established in the first five years after burning, although these seedlings were largely recorded only in the initial survey. No years were substantially more favorable for conifer establishment across multiple fires and species. Pine establishment appeared to peak in 2008 and 2009, but these were only apparent in the initial survey within the Freds and Showers fires (which are close both geographically and floristically) and did not correspond with peaks in Douglas-fir or true fir establishment (Fig. 2). Pine regeneration was nearly absent from the Pendola fire (the lowest elevation study fire in the Sierra). Care should be taken when comparing establishment dates from repeat surveys because determining seedling ages (and thus establishment year) from bud scars can be inexact and accuracy tends to decline with seedling age (Urza and Sibold, 2013). For this reason, we chose not to statistically evaluate seedling mortality or timing of establishment based on budscars.

3.2. Trends in post-fire vegetation cover

Post-fire cover of shrubs (including many hardwoods, see methods) varied between ecoregions and across plots, with the Sierra Nevada fires generally having much higher shrub cover than the Klamath fire after burning (Fig. 3). In the Sierra, median shrub cover exceeded 55 % by the initial survey (Fig. 3), increasing from presumably near zero cover immediately following high severity fire to the initial survey (8.1 years post-fire on average). Shrub cover accumulated more slowly in the Sims fire in the Klamath Mountains, reaching a median cover of only 8 % six years after burning. In the Sierra, we observed little change in mean cover of total shrubs, forbs, or graminoids between post-fire surveys after adjusting for time since fire to initial survey and time between surveys by holding these variables at their means (Table 2), suggesting that most of the non-conifer growth occurs in the first decade after fire in this region. In the Klamath, mean shrub cover increased to 165 % the initial survey cover and mean forb cover decreased to about half the initial survey between 6 and 12 years after fire (Table 2).

Shrub composition also differed between the ecoregions at the time of the resurvey, with higher cover of manzanita and ceanothus in the Sierra and higher cover of poison oak in the Klamath (Fig. 3). Mean cover of dominant shrub genera, ceanothus and manzanita, nearly doubled in the Sierra, after accounting for repeated measures and adjusting for time between surveys (Table 2). In the Klamath, mean ceanothus cover increased slightly over time and poison oak increased over nine times the initial survey cover (Table 2; Fig. 3). Increases in dominant shrub genera may not reflect changes in total shrub cover given that many shrub and shrubby hardwood species were present across the two regions.

3.3. Trends in post-fire seedling densities

Conifer seedling density for all species ranged from 0 to 1.9 seedlings/m^2 at the time of the initial survey and from 0 to 1.7 seedlings/m^2 at the time of the resurvey (Fig. 4). At the initial survey, 74 % of study plots had conifer seedlings present, increasing to 82 % of plots at the resurvey. Whether or not a site was fully stocked (presence of at least one seedling per plot) varied between survey periods and by species. Overall, 45 % of plots with no conifer seedlings at the initial survey (9 out of 20 plots across both ecoregions) gained at least one seedling of

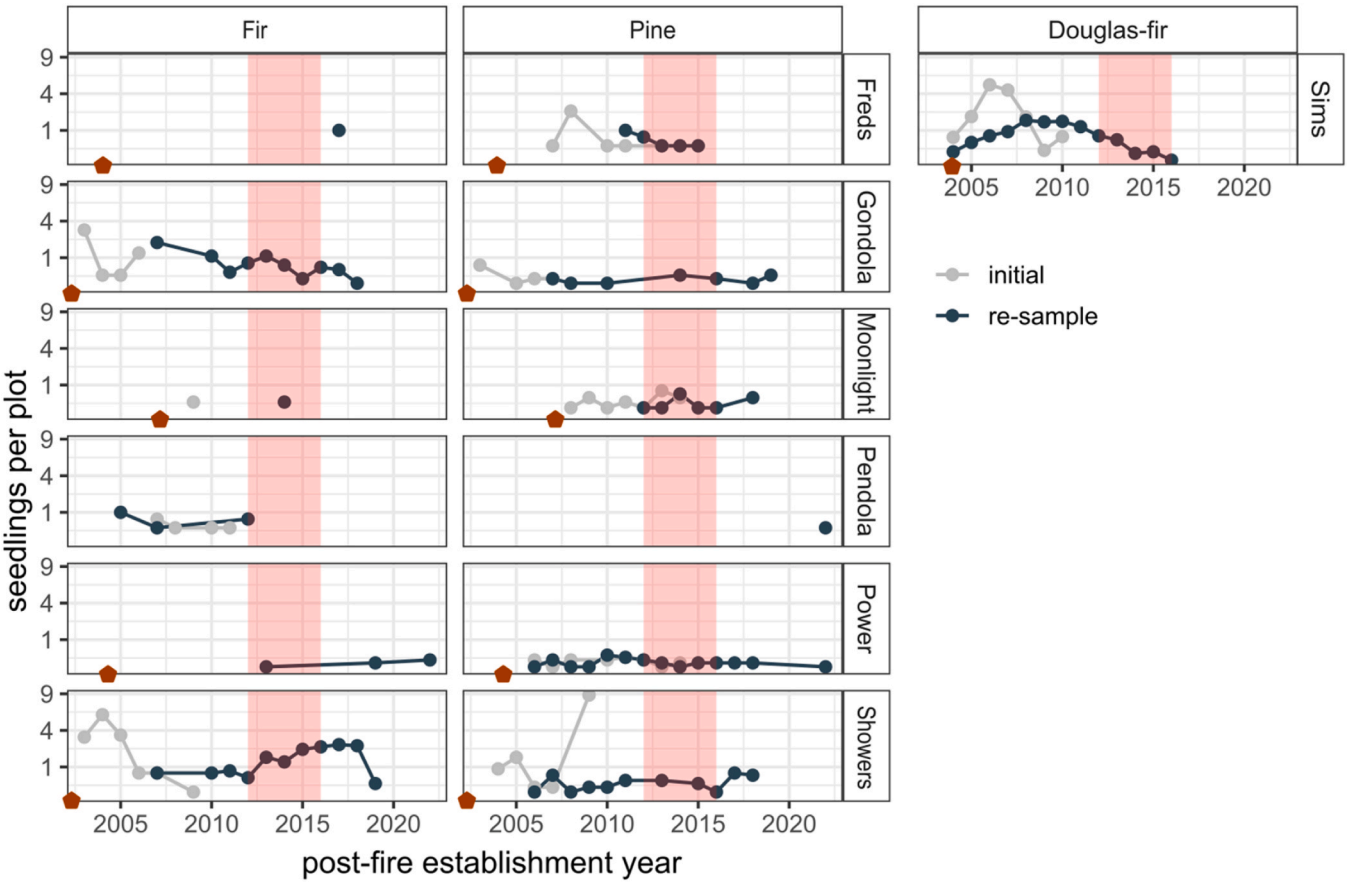

Fig. 2. Conifer seedling density by establishment year and survey period for each fire. Red shading indicates the 2012–2016 period of extreme drought in California. Red polygons indicate the year the fire occurred. Pendola burned in 1999, but the oldest observed seedlings established in 2005.

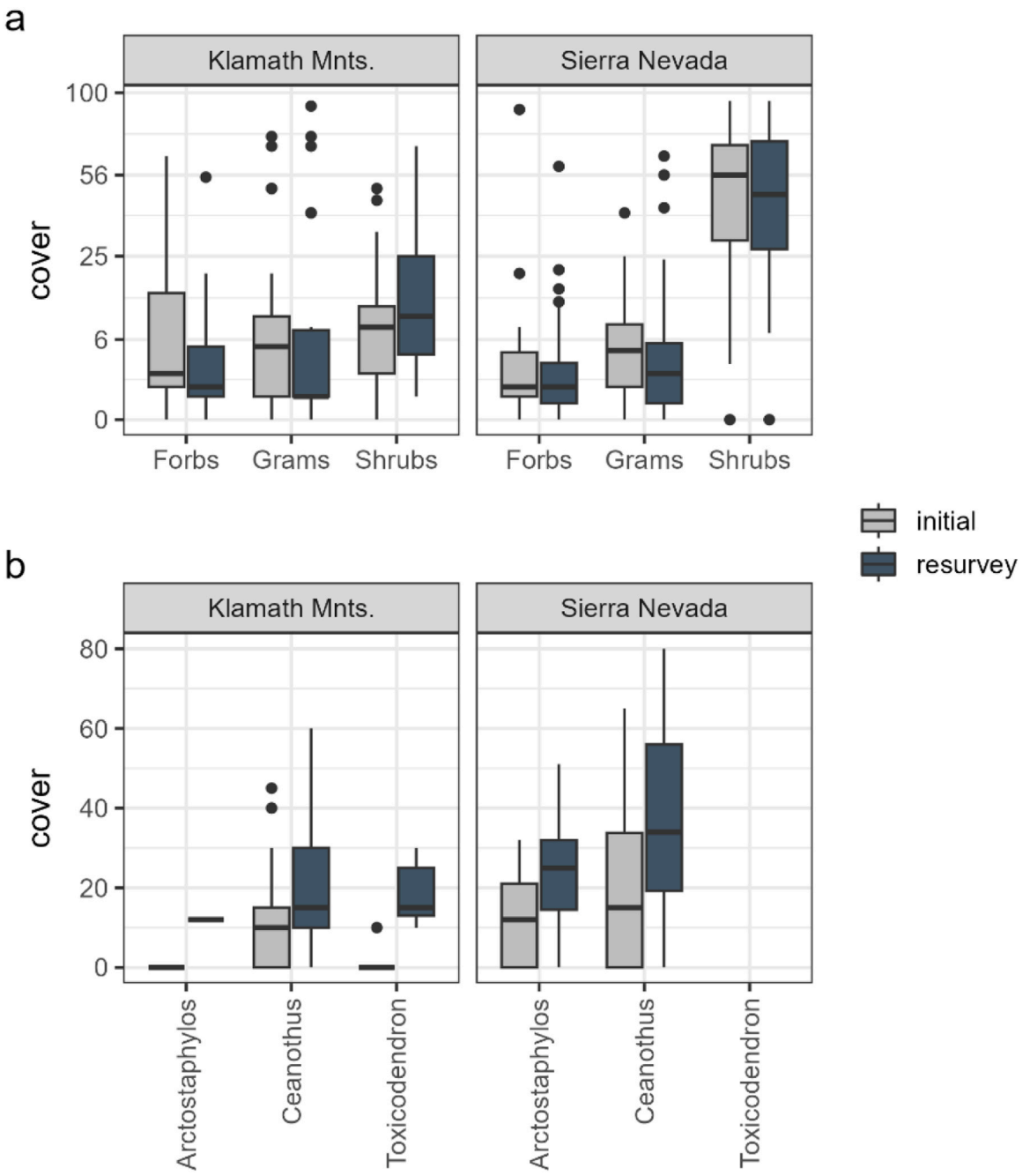

Fig. 3. Percent cover of (a) lifeform and (b) dominant shrub species by ecoregion and post-fire survey period.

any genus by the time of the resurvey. Of plots that had at least one seedling in the initial survey, only 5 % (3 out of 58 plots) lost all seedlings by the time of resurvey. We observed slightly higher rates of loss for pine and Douglas-fir seedlings. Of the 24 plots where pine seedlings were present in the initial survey, 5 plots (21 % of initial presence plots) lost all pine seedlings by the time of the resurvey. Douglas-fir were present in 26 plots in the initial survey, and 3 of these (11.5 % of initial presence plots) lost all Douglas-fir by the time of the resurvey.

Changes in seedling density between survey periods was highly variable (Fig. 4), and this variation led to high uncertainty in model estimates. While we did not observe strong evidence to suggest that seedling density is increasing or decreasing across our study area over time (i.e. no trends in seedling densities were significant at a 0.05 alpha level), overall, mean pine seedling density at the resurvey decreased to 85 % ($p = 0.48$) of the density at the initial survey and estimated mean fir seedling density increased to 161 % ($p = 0.31$) of the initial survey after adjusting for variability in time between fires (Table 2). In the Klamath, Douglas-fir seedling estimated mean density decreased to 81 % ($p = 0.23$) of the density at the initial survey over the six-year period between surveys, but with high variability between plots (Table 2). These trends remained similar when we removed outlying occurrences of over 60 seedlings per plot (density > 1 seedling m^{-2}) for each species (one observation for each species).

3.4. Drivers of post-fire seedling density, mortality, and recruitment

Overall, variability in seedling density for our focal genera 12–23 years after fire was well explained by relatively simple models (r^2 0.57–0.82). However, different genera responded differently to initial seedling density and environmental variables (Fig. 5). Seedling density

Table 2
Pairwise comparisons from GLMMs comparing mean change in post-fire lifeform cover and seedling densities between the initial survey and resurvey for fires in the Sierra Nevada and Klamath Mountains ecoregions. Sierra models adjust for variability in the time since fire to the initial survey and the time between surveys by holding variables at their means, 8.1 and 9.4 years, respectively. Two fires, Gondola and Showers, were excluded from the shrub, forb, and graminoid models because they had insufficient data from the initial survey.

Model (response variable)	Ratio (resurvey/ initial)	Standard error	p-value
Sierra (fires = 6, resurveyed plots = 49)			
Shrub cover (fires = 4, n = 28)	1.01	0.09	0.91
Forb cover (fires = 4, n = 28)	0.97	0.23	0.88
Graminoid cover (fires = 4, n = 28)	1.00	0.29	1.00
Arctostaphylos spp. cover	2.05	0.67	**0.03**
Ceanothus spp. cover	1.82	0.34	**<0.01**
Pine seedling density	0.85	0.19	0.48
Fir seedling density	1.61	0.75	0.31
Klamath (fires = 1, resurveyed plots = 29)			
Shrub cover	1.65	0.33	**0.01**
Forb cover	0.52	0.14	**0.01**
Graminoid cover	0.73	0.16	0.17
Toxicodendron pubescens cover	9.3	10.9	0.06
Ceanothus spp. cover	1.59	0.59	0.21
Douglas-fir seedling density	0.81	0.14	0.23

Note: Bold values indicate $p < 0.05$.

at the initial survey explained a large amount of variance in resurvey seedling density for pine and Douglas-fir after accounting for heat load, shrub cover, and distance to seed source, with resurvey density increasing substantially with higher initial density (initial pine seedling density partial $r^2 = 0.31$; initial Douglas-fir seedling density partial $r^2 = 0.46$). This was not the case for true fir seedling density at the resurvey, which had a weaker relationship to initial seedling density (initial fir density partial $r^2 = 0.001$). Variability in fir seedling density 12–23 years after fire was most strongly associated with heat load and shrub cover, with density decreasing in plots with higher heat loads and shrub cover (Fig. 5). Pine and Douglas-fir density also decreased with increasing heat load, but these trends had higher variability (indicated by wider confidence intervals). Resurvey fir and Douglas-fir seedling density declined slightly with increasing distance to seed source, however the strength of this effect on fir density was uncertain due to high variability (Fig. 5). Mean fir seedling density tended to increase with increasing time between sampling periods, while mean density of pine seedlings tended to decrease, although with high variability between sites (Fig. 5). We found little evidence to suggest that the time from fire to initial survey influenced resurvey seedling density (Fig. 5).

The probability of net seedling mortality and recruitment for all conifers between the initial survey and resurvey varied with some biophysical variables. The probability of a plot experiencing a net decline in conifer seedlings between the two surveys (net mortality) increased with increasing seedling density at the initial survey (log-odds for an increase of 10 seedlings = 0.7, $p = 0.006$) and increasing shrub cover at the resurvey ($p = 0.029$) (Fig. 6a). The probability of a plot experiencing an increase in seedlings between the two surveys (net recruitment) decreased with increasing heat load ($p = 0.033$) (Fig. 6b). We found no evidence to suggest that distance to seed source (Fig. 6c) or shrub cover at the resurvey substantially influenced the probability of net recruitment between the two surveys (Appendix 1).

4. Discussion

Our study provides evidence that relatively early post-fire monitoring, during the first decade after fire, can provide a reliable estimate of longer-term conifer recovery in northern California dry forests, though in different ways for different species groups. For less shade-tolerant species – yellow pines and Douglas-fir – early seedling density readily explained longer-term densities. In contrast, for shade-tolerant true firs, early seedling density was a poor predictor and instead site conditions better explained longer-term recovery.

The fact that we observed initial pine and Douglas-fir density to strongly predict later density indicates that these genera may establish during an initial post-fire period when shrubs are less abundant. Establishment of shade-intolerant species, including ponderosa pine, is known to be inhibited by competing vegetation and litter/duff cover (Rodman et al., 2020; Welch et al., 2016), both of which are initially low after high severity fire but accumulate quickly over time. In alignment with this interpretation, ponderosa pine recruitment post-fire was more continuous over time under lower shrub cover (vs. higher shrub cover) in mixed conifer forests across the western US (Davis et al., 2019). Interestingly, shrub cover did not generally appear to influence the probability of a plot experiencing net recruitment of conifers between the two surveys in our study. This could be because shrub cover was already relatively high in the majority of our sites by the first survey. Our resurvey data revealed that shrub cover remained high between surveys, with dominant species (ceanothus, manzanita, and poison oak) increasing over time, consistent with observations of continued growth and shrub persistence decades to centuries after fire (Duren and Muir, 2010; Nagel and Taylor, 2005).

It is important to highlight that although initial regeneration conditions can enable prediction of longer-term recovery trajectories, seedling densities are unlikely to remain constant through time. Conifer densities in more productive forests typically decrease over time as post-fire trees grow, intraspecific competition increases, and light and space become more limiting (Oliver, 1981). In our study, change in conifer density over time was highly variable, with many sites experiencing net mortality between surveys, suggesting that site factors continue to play an important role in long-term forest recovery after initial establishment. These declines were more strongly driven by competition from shrubs than microclimate conditions (i.e. heat load). Although many plots experienced some seedling mortality, overall no genera declined in seedling density consistently across the study area, suggesting that most sites are not yet in a stem exclusion phase of stand development. This may be in part due to high shrub cover, as shrubs are known to not only reduce establishment success, but also reduce growth and survival of conifers in early seral forests, particularly for shade intolerant pine species (Airey-Lauvaux et al., 2016; Tubbesing et al., 2020). For example, it took over 25 years for conifers to emerge from the shrub canopy and for post-fire conifer growth rates to increase following severe fire in California forests (Airey-Lauvaux et al., 2016). Future studies could examine shrub influence on seedling growth and emergence by tracking growth of individual seedlings over time.

In contrast to Douglas-fir and pine, true fir density continued to increase for decades after fire, despite high shrub cover, although fir density at the resurvey was lower in sites with higher shrub cover and we observed high variability between sites. White fir, the most abundant fir in our study, can continue to establish beneath the shrub canopy long after an initial disturbance (Nagel and Taylor, 2005; Ursell and Safford, 2022), and often recruits at higher densities than pine in severely burned areas where shrubs establish quickly after fire (Airey-Lauvaux et al., 2016; Nagel and Taylor, 2005). Similarly, in a post-fire regeneration study in California montane forests, red fir frequency increased substantially with time since fire, while yellow pine frequency was unrelated to time since fire (Brodie et al., 2023). Along with lower light requirements, white fir has smaller seeds than yellow pines, higher seed production (Fowells and Schubert, 1956; Greene and Johnson, 1996), and greater dispersal ability (Safford and Stevens, 2017) which likely contribute to more continuous post-fire establishment periods.

Our results highlight an important role of topography in post-fire conifer establishment. Cooler sites with lower heat load were more likely to support continued recruitment and establishment of all conifer seedlings after the initial survey, with longer-term fir density appearing especially sensitive to heat load. Conifer recruitment in burned areas is

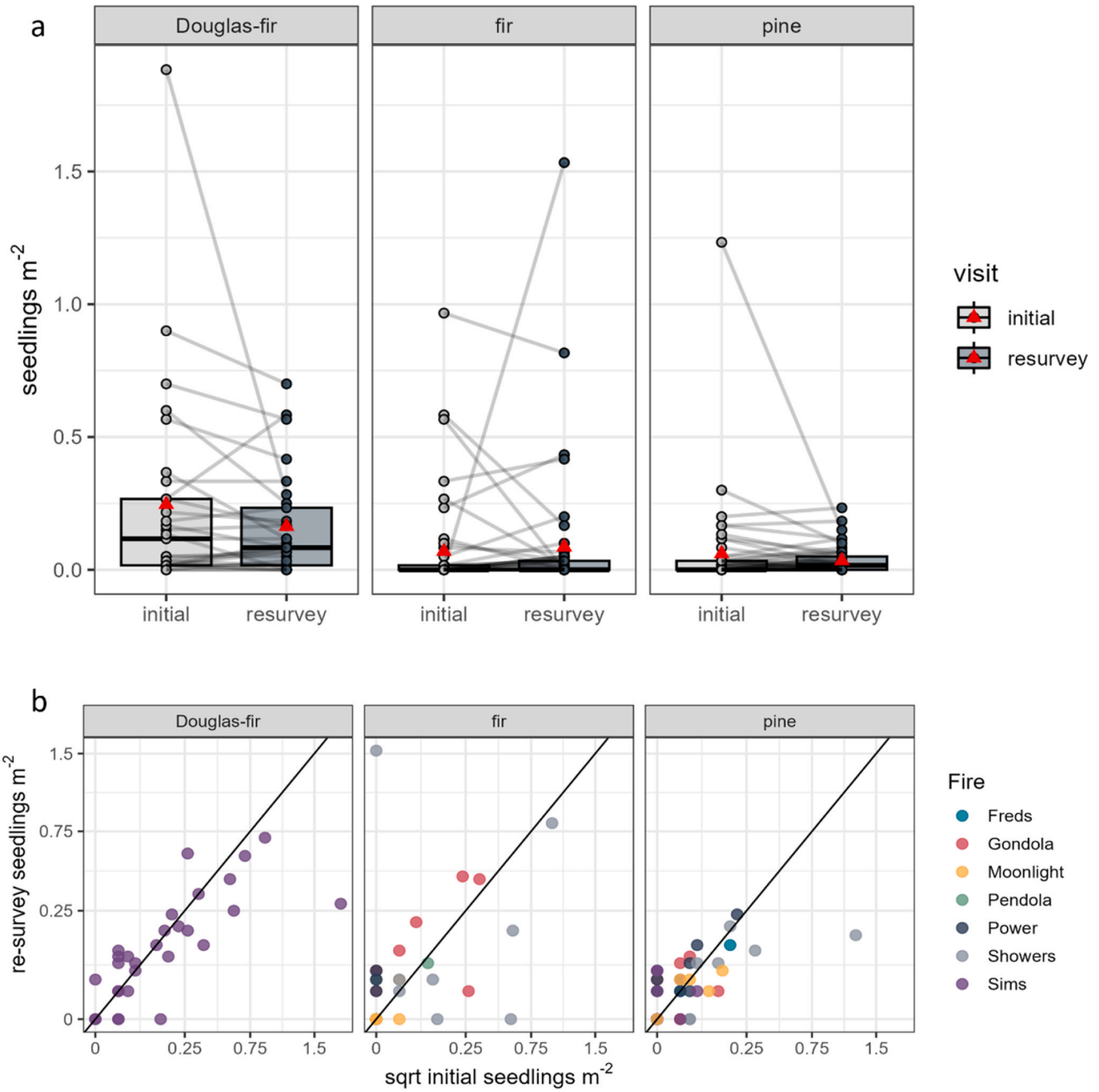

Fig. 4. **(a)** Conifer seedling density (seedlings m^{-2}) boxplots by genera and survey period. Black horizontal lines in boxplots represent group medians. Grey lines connecting points represent difference in density for individual sample plots between surveys. Red triangles denote group means. **(b)** Seedling density for dominant conifers for the initial survey and resurvey periods colored by study fire. Diagonal lines represent 1:1 line for equal seedling densities in the initial survey and resurvey. Points below the line represent declines in seedling density between surveys and points above the line represent increases in seedling density. Note that the seedling density axis in panel b increases exponentially by a power of 2 rather than linearly.

often higher in wetter sites, including north-facing slopes and at higher elevations (Kemp et al., 2019; Shive et al., 2018; Tepley et al., 2017). While we did not have enough variability in fire years to specifically test the effect of post-fire climate on tree seedling density, nearly all our plots were sampled both before and after the 2012–2016 extreme California drought, providing insight into drought effects on seedling recruitment. Seedling densities did not appear to plummet over time even through the period of extreme drought, suggesting that once established, seedlings are relatively robust to post-fire climate conditions.

Establishment of pine and fir did not appear to be greatly reduced during the drought period, indicating that establishment may be explained more strongly by general site condition and seed availability than post-fire weather. This contrasts with regeneration studies from cold forests in the northern Rockies that found lower conifer recruitment during abnormally dry periods (Davis et al., 2019; Harvey et al., 2016; Stevens-Rumann and Morgan, 2019), but is consistent with Young et al. (2019), who found that topography, long-term climate trends, and seed availability were stronger drivers of post-fire regeneration than post-fire weather in dry forests of California. Species and genotypes present in California dry forests are exposed to annual 4–6-month dry periods, thus these seedlings may be less susceptible and more adapted to post-fire drought conditions than those growing in generally less water-limited cold forests. Surprisingly, distance to seed source, a proxy for seed limitation, was not a strong driver of continued recruitment in our study,

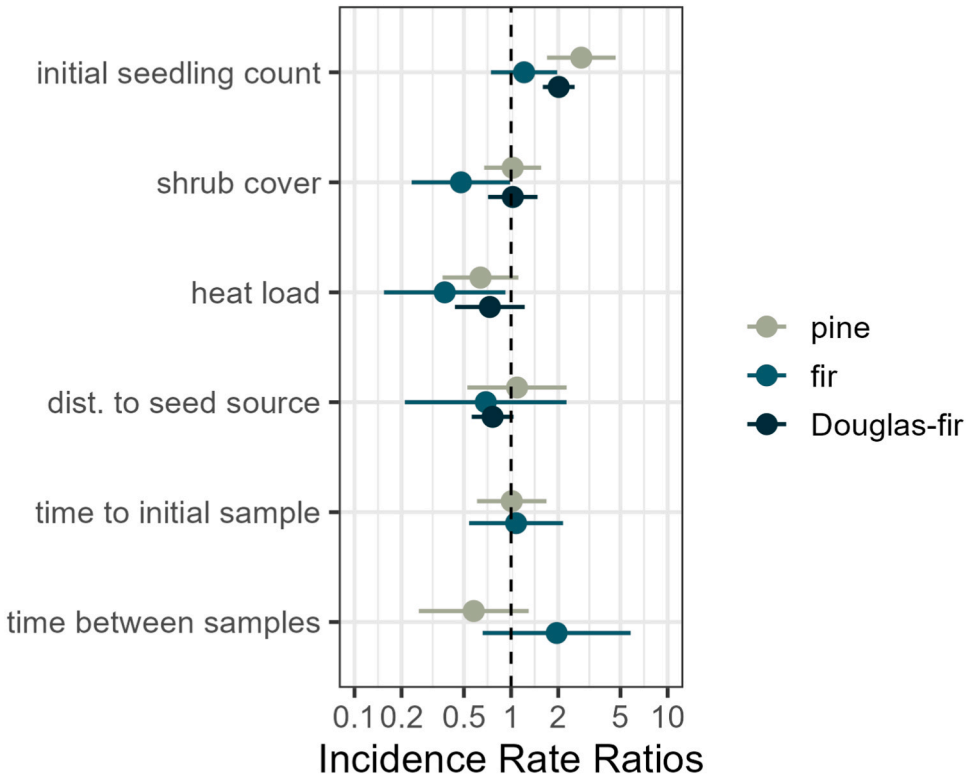

Fig. 5. Estimates and 95 % confidence intervals from GLMMs comparing post-fire conifer seedling density at resurvey to initial survey density and biophysical covariates for pine and fir in the Sierra (n = 49) and Douglas-fir in the Klamath (n = 29).

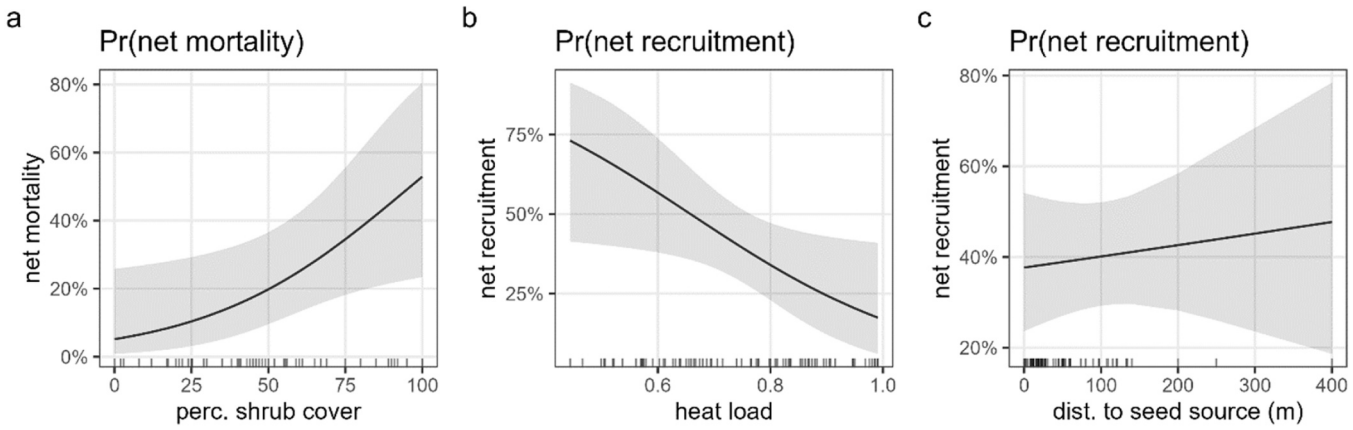

Fig. 6. Marginal effects plots of the probability of (a) net post-fire seedling mortality with shrub cover at the time of the resurvey and the probability of (b) net post-fire recruitment with heat load and (c) distance to seed source at the time of the resurvey.

despite being found to be an important driver of recruitment even decades after wildfire in a previous study within our study area (Ursell and Safford, 2022). This suggests that seed availability may be less limiting for longer-term recruitment than site conditions after controlling for initial site conditions and seed source through our repeated measures study design.

Sampling across many fires and fire years spanning a broad biophysical gradient revealed how variable post-fire conifer regeneration trends can be even within similar forest types. Fir and pine regeneration was highly variable across the Sierra study fires (Fig. 6), further demonstrating that long-term recovery trajectories may depend strongly on site-specific conditions. Differences in establishment and recruitment suggest early pathways may diverge and lead to long-term compositional differences among topographic settings. Given that our Douglas-fir data are from a single fire in the Klamath, our scope is limited to the Sims fire perimeter for this region.

4.1. Conclusions and management implications

Our results indicate that early conditions are reasonably predictive of longer-term outcomes, supporting the value of using early surveys to infer longer-term trends. For example, the mapping tool POSCRPT, used extensively by the USDA Forest Service for predicting post-fire regeneration and informing areas in need of planting in California mixed conifer forests, is currently focused on regeneration five years post-fire (Shive et al., 2018; Stewart et al., 2021), due to site preparation considerations and National Forest Management Act guidance on post-disturbance replanting. Our findings could help refine such tools to

predict both short and longer-term conifer regeneration in Sierra and Klamath forests, for example by demonstrating where mortality or recruitment is likely to occur over time based on initial post-fire seedling density and site conditions.

Long-term seedling densities are relatively predictable based on early density measurements, but it is important to note that "predictable" is not the same as "fixed". Although high long-term pine and Douglas-fir densities are predicted by high initial pine densities, and high long-term fir densities are predicted by low heat load and low shrub cover, long-term seedling densities can differ from short-term densities, with fir density generally increasing over time (although with high variability between sites). While increasing conifer regeneration density overall can accelerate the return to a forest system, continued fir recruitment over time in the Sierra may shift desired species composition towards a more fir dominated system that could have lower resistance to future fires and droughts than a forest dominated by more fire- and drought-tolerant yellow pines (Safford and Stevens, 2017). Fire and drought resistance are common forest management goals, and continued fir recruitment in early post-fire pine dominated sites may not be consistent with desired forest trajectories. However, it is important to note that our results suggest that pine and Douglas-fir are generally not eliminated from post-fire sites when present at the initial survey. The dynamic (yet predictable) nature of these fire-adapted forests highlights the need for continual management with fire or fire surrogates through time.

CRediT authorship contribution statement

Ramona J. Butz: Writing – review & editing, Project administration, Data curation. **Matthew J. Reilly:** Writing – review & editing, Supervision, Investigation. **Derek J. N. Young:** Writing – review & editing, Writing – original draft, Methodology, Data curation, Conceptualization. **Claire M. Tortorelli:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Nina E Venuti:** Writing – review & editing, Project administration, Methodology, Data curation, Conceptualization. **Hugh D. Safford:** Writing – review & editing, Project administration, Methodology, Data curation. **Kevin R. Welch:** Writing – review & editing, Project administration, Methodology, Data curation. **Andrew M. Latimer:** Writing – review & editing, Writing – original draft, Supervision, Resources, Project administration, Methodology, Funding acquisition, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix 1. Results of GLMMs for the probability of post-fire conifer seedling density declining (net mortality) or increasing (net recruitment) between the initial and resurvey

Predictor	Estimate	P.value
Probability of net mortality		
(Intercept)	3.438	0.209
initial seedling count	0.070	**0.006**
percent shrub cover	0.030	**0.029**
heat load	-3.147	0.298
dist. To seed source	-0.001	0.591
yrs. fire to initial survey	-0.682	0.056
yrs. between samples	0.045	0.797
Probability of net recruitment		
(Intercept)	-1.434	0.444
percent shrub cover	-0.006	0.517
heat load	-4.669	**0.033**
dist. to seed source	0.001	0.646
yrs. fire to initial survey	0.360	0.072
yrs. between samples	0.258	0.090

Note: Bold values indicate $p < 0.05$.

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