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RESEARCH ARTICLE

Repeated burns fail to restore pine regeneration to the natural range of variability in a Sierra Nevada mixed-conifer forest, U.S.A.

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Fire-exclusion has acted as a major perturbation on dry conifer forests in the western United States, increasing tree density and, in mixed-conifer forests, the dominance of shade-tolerant species. Restoration efforts aim to reverse these effects by reducing stand density, restoring relative proportions of tree species, and reintroducing recurrent fire, but there are limited long-term data on the effects of repeated burning on tree regeneration. We analyzed two decades of seedling and overstory data from the Teakettle Experimental Forest in the southern Sierra Nevada, California, United States to determine how thinning and repeated burning affect seedling establishment and overstory recruitment. Across treatments, pine seedling densities remained much lower than shade-tolerant seedling densities. We found repeated burns led to modest increases in sugar pine (*Pinus lambertiana*) and substantial increases in incense-cedar (*Calocedrus decurrens*) seedling densities 4 years postburn. No significant differences in seedling densities among repeated burning treatments were detected for Jeffrey pine (*P. jeffreyi*) or white fir (*Abies concolor*). Estimates of natural midstory recruitment were much higher among white fir and incense-cedar than pines, even following treatments. However, postharvest planting increased rates of pine midstory recruitment in overstory thinned treatments. Our results suggest that fire-exclusion may have shifted the ecosystem out of its initial domain of attraction, creating a forest dominated by shade-tolerant species that exhibits hysteresis by resisting a return to a natural range of variability even after restoring structure and process. Planting pine species may be effective at overcoming this resistance to restore the forest to a pine-dominated state.

Key words: domain of attraction, hysteresis, Jeffrey pine, prescribed fire, sugar pine

Implications for Practice

- Fire-suppressed forests may exhibit hysteresis and resist a return to a historic domain of attraction following repeated restoration treatments.
- Thinning treatments may be leaving too many shade-tolerant individuals, leading to substantial shade-tolerant species regeneration.
- Planting pine following burning and thinning may be required to maintain pine midstory recruitment in Sierra Nevada mixed-conifer forests.

Introduction

Humans have been manipulating ecosystems with fire for millennia and, until recently, tended to increase fire frequency to suit our objectives (Knight et al. 2022). In the past century, human land use and fire suppression have decreased fire in historically frequent-fire forests, resulting in dense forests with abundant fuels (Hagmann et al. 2021). Hotter, drier conditions under climate change, combined with increased forest mortality, have made these forests even more flammable (Goodwin et al. 2021; Juang et al. 2022), increasing societal demand for forest restoration to reduce the risk of high-severity fire (Prichard et al. 2021). Forest restoration in dry western conifer forests has long been predicated on the idea that restoring forest structure and fire as a process will not only reduce the chance of uncharacteristic wildfire but also restore ecosystems to their natural range of variability and allow for system-level ecological resilience to changing climate (Hardy & Arno 1996; North et al. 2021). Yet, increasingly, there is evidence suggesting forest restoration may be insufficient to achieve the full suite of resilience objectives (Schmidt et al. 2006; Zald et al. 2008; Scheller et al. 2018).

The mixed-conifer forests of the Sierra Nevada historically burned at high frequency, on the order of years to decades, largely as low intensity surface fires (Van de Water & Safford 2011). While these forests were once dominated by

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large pines, timber harvesting and more than a century of fire-exclusion has resulted in a shift towards the dominance of smaller-diameter, shade-tolerant trees and an increase in overall forest density (North et al. 2007; Safford & Stevens 2017; Hagmann et al. 2021). The loss of large pines in Sierran mixed-conifer forests has important negative consequences for a variety of ecosystem services (Safford & Stevens 2017; Jones et al. 2018). The accumulation of fuels and structural homogenization following fire-exclusion can increase the chance of high-severity fire (Koontz et al. 2020; Hagmann et al. 2021), and high tree density can make trees more vulnerable to drought because of increased water competition and cause higher rates of disease transmission and insect outbreaks (Smith et al. 2005; Bottero et al. 2017; Robbins et al. 2022). Thus, these structural changes can decrease the resilience of forests to disturbances (Furniss et al. 2022; North et al. 2022; Zald et al. 2022).

The increasing proportion of fires burning at high-severity is challenging both ecosystems and society (Singleton et al. 2019). High-severity fires can threaten homes and structures near the wildland–urban interface, accelerate soil erosion, and degrade water quality (Elliott & Vose 2006; Theobald & Romme 2007; Hohner et al. 2019). High rates of tree mortality increase carbon emissions, and areas affected by severe fires can experience postfire regeneration failure that drives a transition from forest to nonforest vegetation types (Coop et al. 2020). Increasingly, society is investing in forest restoration to reduce the risk of uncharacteristic fire.

Forest restoration efforts can be informed by ecological stability theory, which proposes that ecosystems can recover from perturbations, remaining in a stable state within a “domain of attraction” (Holling 1973; Van Meerbeek et al. 2021). Fire-exclusion has acted as a substantial perturbation on western forests, shifting ecosystems away from historical densities and species composition. In an effort to push forests back towards the original domain of attraction and restore dry-conifer forests to a natural range of variability, managers use thinning and burning treatments to reduce density and reestablish frequent-fire regimes (North et al. 2012; Prichard et al. 2021). Mechanical thinning treatments decrease stand density and increase mean tree diameter by removing small trees and favoring large fire-tolerant pines (Agee & Skinner 2005; North et al. 2007). Prescribed burns consume surface fuels, while also reducing small trees and shrub cover (Agee & Skinner 2005). These restoration treatments are implemented with the goal of removing the perturbation of fire-suppression and allowing the ecosystem to recover to a presuppression state.

Ensuring the sustained presence of large pines in Sierran mixed-conifer forest following restoration treatments requires adequate pine regeneration, making regeneration density a useful predictor of future forest composition. Achieving this goal requires sufficient pine seedling establishment and survival while reducing shade-tolerant seedling establishment and survival. Restoration treatments attempt to address this objective by modifying the regeneration environment to favor pine regeneration. Thinning to reduce overstory canopy cover increases light availability, which can desiccate shade-tolerant seedlings and facilitate establishment of shade-intolerant pines (Zald et al. 2008; Bigelow et al. 2011). Prescribed fire consumes the surface litter layer, exposing soil and creating conditions that support greater rates of seedling establishment by species that prefer mineral soil, such as pines (Kilgore 1973; Zald et al. 2008; Legras et al. 2010).

Despite efforts to promote pine regeneration, the effects of first-entry burning and thinning treatments on mixed-conifer regeneration in the southern Sierra Nevada were not indicative of a return to a pine-dominant domain of attraction (Zald et al. 2008). White fir and incense-cedar seedling frequencies significantly increased after burning and understory thinning, while pine seedling frequencies did not change significantly (Zald et al. 2008). Sown-seed pine germinant survival was highest on burned plots, but seed rain densities for shade-tolerant species were orders of magnitude higher than pine seed rain (Zald et al. 2008).

These results suggest that first-entry treatments may not provide a sufficient reduction of shade-tolerant species or increase in pine regeneration to support a pine-dominated overstory condition (Zald et al. 2008). It is possible that long-term fire-exclusion was a sufficient perturbation to exceed the Sierran mixed-conifer forest’s threshold of tolerance. Structural and compositional changes may have caused hysteresis, such that the reintroduction of fire, coupled with a reduction in forest density, is unable push the ecosystem back to its original domain of attraction (Beisner et al. 2003; Van Meerbeek et al. 2021).

However, the long-term effects of repeated treatments on Sierra Nevada mixed-conifer regeneration have not been determined. The effects of a first-entry burn following over a century of fire-exclusion may not match the effects of repeated burns that more closely resemble the historic fire regime. Likewise, initial postfire regeneration frequencies may not predict rates of seedling survival and recruitment to larger size classes that ultimately drive future forest composition. The focus of regeneration studies following management activity is often on either the relative differences between species of interest (Zald et al. 2008), or densities required for postharvest regulatory compliance, rather than what is needed to achieve restoration objectives, such as approximating reference conditions or enhancing resilience to stressors. We sought to address these knowledge gaps by using two decades of forest treatment data from the Teakettle Experimental Forest to ask: how do repeated prescribed burns, following initial thinning treatments, affect regeneration in a Sierra Nevada mixed-conifer forest? We predicted that thinning and repeated burning treatments would have positive effects on pine seedling densities and negative effects on shade-tolerant white fir and incense-cedar seedling densities due to increased posttreatment light and substrate availability. Because of this expected trend, we predicted that thinning and burning treatments would lead to a stand structure and species composition that approximates the natural range of variability for the ecosystem, returning it to its original domain of attraction.

Methods

Study Site Description

This study was conducted at the Teakettle Experimental Forest, an old-growth, mixed-conifer forest located in the southern

Sierra Nevada of California. This site is dominated by red fir (*Abies magnifica*), white fir (*Abies concolor*), sugar pine (*Pinus lambertiana*), incense-cedar (*Calocedrus decurrens*), and Jeffrey pine (*Pinus jeffreyi*) (North et al. 2002). Other species present include bitter cherry (*Prunus emarginata*), California black oak (*Quercus kelloggii*), and canyon live oak (*Quercus chrysolepis*) (North et al. 2002). Elevation ranges from 1,980 to 2,590 m, and annual precipitation averages 110 cm, falling mostly during the winter as snow (North et al. 2002). From 2012 to 2016, the southern Sierra Nevada experienced a severe drought that, in combination with endemic bark beetles, caused species-specific mortality ranging 3–38% of overstory trees at Teakettle (Steel et al. 2021). Large-diameter sugar pines experienced some of the highest mortality rates, while firs and incense-cedar with moderate diameters had the lowest mortality rates (Steel et al. 2021).

Prior to the last widespread fire in 1865, the mean fire return interval at Teakettle was 17.3 years and the forest overstory was dominated by sugar pine and Jeffrey pine (North et al. 2005; North et al. 2007). Following fire-exclusion, forest density also increased from an estimated historic 67 trees per hectare (TPH) to 469 TPH driven by ingrowth of shade-tolerant white fir and incense-cedar (North et al. 2007).

Treatments and Experimental Design

In 1998, the Teakettle Experiment was established to investigate the effects of prescribed burning and mechanical thinning on Sierra Nevada mixed-conifer forests (North et al. 2002). The experiment uses a full-factorial design with two levels of burning (burned and unburned) and three levels of thinning (no thin, understory thin, and overstory thin) for a total of six treatment combinations, including a control treatment. Prior to treatments, a systematic intensive sample of plots was established within Teakettle Experimental Forest, and tree species, DBH, and canopy cover data from this sample were used to constrain treatment units to areas of similar forest overstory composition and structure (North et al. 2002). This was confirmed prior to treatment implementation, with overall and species-specific basal area from stem maps being found to be similar between treatment combinations (Zald et al. 2008), although there was slightly higher overall basal area in understory thin units, driven by differences in white fir basal area. The only significant differences in pre-treatment basal area occurred between the control and the understory thin and burn/understory thin treatments, with both understory thin treatments having significantly higher total basal area (Zald et al. 2008). Each treatment combination was replicated over three 4 ha treatment units where mid and overstory conditions were statistically similar prior to treatment. The understory thin treatment removed all trees between 25 and 75 cm diameter at breast height (DBH), following treatment recommendations developed in the 1990s for the California spotted owl (Verner et al. 1992). Overstory thinning treatments, based on a common harvest prescription prior to the 1990s, left 22 evenly spaced trees greater than 100 cm DBH per hectare, as well as all trees less than 25 cm DBH. Thinning treatments were completed in 2000–2001, resulting in mean live basal area reductions of 32% for the understory thin and 61% for the overstory thin (North et al. 2007; Zald et al. 2008, Fig. 1). Overstory thinned plots were planted proportionally to their pre-treatment overstory dominance with 2-year-old bare-root stock of white fir, sugar pine, and Jeffrey pine seedlings in 2002 following common postharvest practices.

Prescribed burning followed thinning, with the first-entry burn conducted during fall 2001, and the second-entry burn conducted during fall 2017. Following typical management prescriptions, burning was applied after the first substantial rain to avoid overstory ignition yet still consume surface fuels and small trees. The time between prescribed fires approximated the mean historical fire return interval for this site.

Following both the first and second-entry treatments, overstory thinned plots had significantly higher direct and diffuse light availability than control treatment units, while light availability in burn-only treatment units did not vary significantly from the control (Odland et al. 2021). Burning significantly decreased litter depth and increased bare soil cover while thinning alone did not (Innes et al. 2006; Odland et al. 2021). While the 2012–2016 drought increased surface fuels across treatments, the second-entry burn returned surface fuel levels to pre-drought ranges on burned treatment units (Goodwin et al. 2020). After both first and second-entry treatments, shrub cover was found to be significantly higher in thinned plots than in control plots, and the largest increases in shrub cover were observed on plots that were both thinned and burned (Odland et al. 2021). While thinning and burning moved treatment units towards historic stem densities, a lower density of large trees than was present historically prevented treatments from fully achieving historic conditions (North et al. 2007). Out of all treatment combinations, the burn/understory thin treatment most closely resembled historic conditions (North et al. 2007).

Data Collection

Trees greater than 5 cm DBH were tagged, measured, and mapped pre-treatment (1999–2001), posttreatment (2002–2004), 10-years posttreatment (2011–2012), 15-years posttreatment (2016–2017) and postsecond-entry burn (2018–2019) within each 4-ha treatment unit. Species, status (live or dead), decay class, and DBH were recorded for each mapped tree. Treatment-unit basal area estimates by species were calculated from DBH measurements.

Gridpoints were established within each treatment unit to concentrate a variety of measurements including tree regeneration. Two of the units for each treatment were gridded using 50 m spacing for a total of 9 gridpoints, and the third was gridded using 25 m spacing for a total of 49 gridpoints, resulting in 67 gridpoints per treatment combination. We counted live seedlings within a 3.5-m radius of the gridpoint centers, creating a 38.5 m^2 regeneration microplot. We divided the microplot into four quadrants (NE, SE, SW, NW) and recorded the number of seedlings within each quadrant. We defined seedlings as all trees with a height greater than 5 cm and a DBH of less than 5 cm and assigned these seedlings to three size classes based on height: A (5–50 cm), B (50–138 cm), and C (138+ cm). Because of the

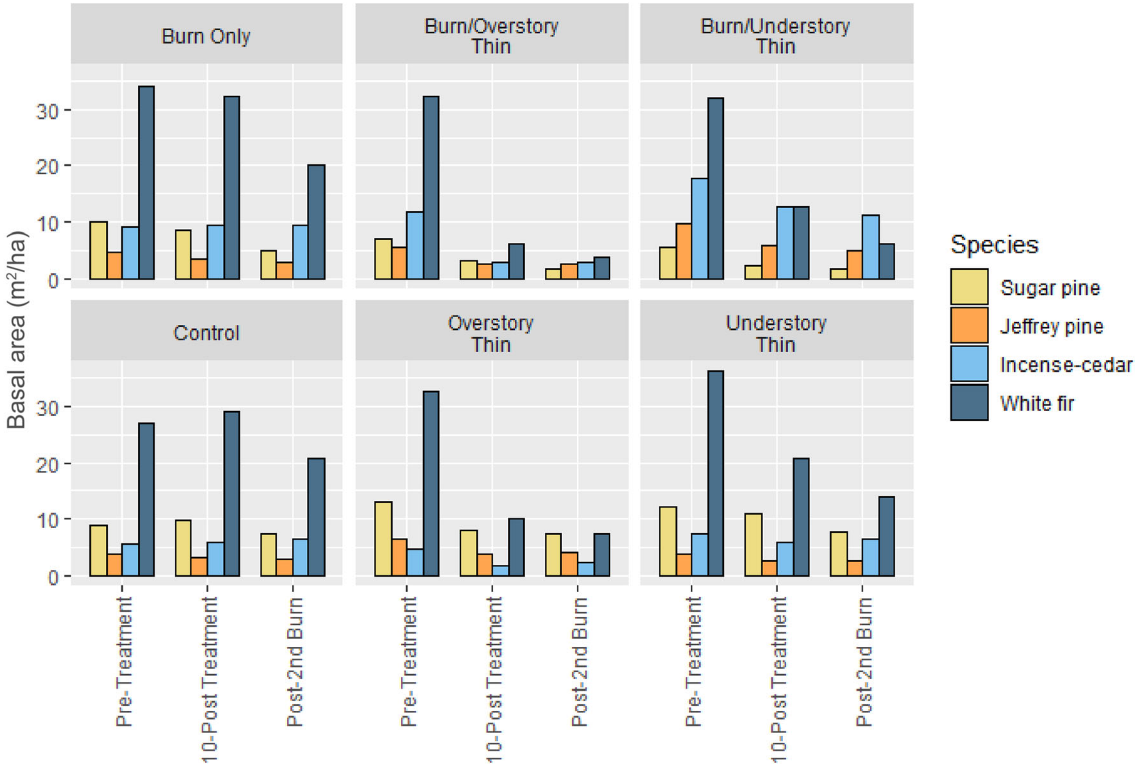

Figure 1. Live overstory basal area by species (m^2/ha) for each thinning and burning treatment combination, across three sampling periods: pre-treatment (2000–2002), posttreatment/predrought (2011) and postsecond burn/postdrought (2017–2018). Initial thinning and burning treatments occurred in 2000–2001, and a second-entry burn occurred in 2017.

ephemeral nature of first-year germinants, we excluded seedlings of less than 5 cm height from our counts. We recorded trees with a DBH greater than 5 cm that had previously been recorded as seedlings as a size class D to continue tracking these individuals. We identified planted seedlings by referencing azimuths and distances from the gridpoint center recorded at the time of planting. A full survey of regeneration microplots was repeated 11 times from 2000 to 2021. Prior to treatments, solar radiation, shrub cover, and soil moisture at grid points were similar between treatment combinations (Zald et al. 2008). Overall and species-specific regeneration frequency (proportion of quadrants occupied per gridpoint) were similar between treatments prior to treatment implementation (Zald et al. 2008). Exceptions to this include somewhat lower incense-cedar regeneration frequency in untreated control units.

As the prescribed burns did not uniformly burn all surface area throughout entire treatment units, percent cover of ash and char were recorded after the burn in a 10 m^2 plot around each gridpoint to determine which individual gridpoints were affected. The first-entry burn reached 72% of gridpoints in the understory thin-burn plots, 76% of gridpoints in the overstory thin-burn, and 25% of gridpoints in the burn-only treatment (Odland et al. 2021). The second-entry burn reached 19% of gridpoints in the understory thin-burn, 24% of gridpoints in the overstory thin-burn, and 36% of gridpoints in the burn-only treatment (Odland et al. 2021). See Table S1 for total number of gridpoints by burn frequency for each treatment.

Statistical Analysis

All statistical analyses for this study were conducted in R version 4.0.2 (R Core Team 2020). We limited our analysis to the four most common mixed-conifer tree species present in all treatment units: white fir, incense-cedar, Jeffrey pine, and sugar pine.

To quantify the effects of the second-entry burn on natural seedling densities, we created a Gamma hurdle mixed-effects model for each species using the “glmmTMB” package (Brooks et al. 2022). In each model, we used seedling density (TPH; excluding planted seedlings) as the response variable. Fixed effects included year (2017, 2018, 2019, 2021), initial thinning treatment and the number of burns experienced by each gridpoint (burn sum) as a three-way interactive term and treatment unit-level basal area of the modeled species. Main effects and all two-way interactions were also included in model outputs. Gridpoints with a burn sum of 1 burned only once in either 2001 or 2017, but small sample sizes within these categories prohibited separation based on burn year. We included treatment unit as a random effect to account for preexisting variability in slope, aspect, elevation, and burn conditions among treatment units. We specified the error distribution family of each model as “ziGamma,” creating a hurdle model to account for a high number of gridpoints with no regeneration detected, with the assumption that the observed zero-inflation is structural and constant across treatments. We assessed model fit (i.e., quantile–quantile plots of model residuals, residual versus predicted values, outlier tests, dispersion tests, and Kolmogorov–Smirnov goodness-of-fit tests) using the "DHARMa" package (Hartig & Lohse 2022). We used the "emmeans" package to calculate estimated marginal means for each thinning and burning combination from each species' seedling density model (Lenth et al. 2022).

To estimate rates of long-term tree survival in the initial decades after establishment, we calculated midstory recruitment for each 4 ha treatment unit from 2002–2003 (postfirst-entry burn) to 2018–2019 (postsecond-entry burn). Here we have defined "midstory recruitment" as any seedlings (including planted seedlings) crossing the 5 cm DBH threshold, the diameter at which they exceed our defined seedling size and become part of the stem map. We averaged the sum of new individuals of each species added to the midstory per treatment unit between the postfirst-entry burn and postsecond-entry burn measurement periods to obtain treatment-wide mean midstory recruitment rates. Only new individuals added to the stem dataset with a DBH < 20 cm were considered new recruitment for each measurement period to exclude any overstory individuals that were initially missed in the stem map (Fig. S1). We then calculated a mean per year per hectare rate of midstory recruitment for each treatment and species. We scaled this rate over 100 years to provide estimates of long-term midstory recruitment for each species. Additionally, we calculated midstory recruitment rates within regeneration microplots of planted and natural pine seedlings independently over the duration of the experiment (2002–2021). As the stem map for each treatment unit did not differentiate between planted and natural regeneration, regeneration microplots provided an estimate of the proportion of planted trees recruited to the midstory on planted plots.

Results

Second-Entry Burn Seedling Density Models

In our analysis of naturally regenerated seedlings, incense-cedar had higher densities after the second-entry burn than sugar pine and white fir, which were both higher than Jeffrey pine (Fig. 2). For model coefficient estimates and p-values for main effects and interactions with the lowest p-values, see Tables S1–S4. Estimated marginal means provide mean seedling density estimates that reflect the combined effects of all interactions and main effects.

Our results were suggestive that burning increased sugar pine 4 years postburn (coefficient estimate [β] = 0.55, $p = 0.051$), and live basal area of sugar pine had a small positive effect on seedling densities ($\beta = 0.07$, $p = 0.023$) (Table S1). For unthinned treatments 4 years postburn, we found significantly higher estimated marginal mean sugar pine seedling densities following two burns than one burn ($p = 0.009$) or no burns ($p = 0.009$).

For Jeffrey pine regeneration, the interaction of number of burns and understory thinning overall had negative effects ($\beta = -1.11, p = 0.045$), along with understory thinning 2 years postburn ($\beta = -1.14$, $p = 0.049$) and 4 years postburn ($\beta = -1.19$, $p = 0.027$) (Table S2). However, the interaction of burning and understory thinning was positive 2 years postburn ($\beta = 1.60$, $p = 0.032$) and 4 years postburn ($\beta = 1.36$, $p = 0.022$). Ultimately, we did not observe any significant differences in estimated marginal mean Jeffrey pine seedling densities between any treatments within the 4-year period (Fig. 2).

For incense-cedar, we found a small positive effect of mature incense-cedar basal area on seedling density ($\beta = 0.138$, $p < 0.001$) (Table S3). We found a positive effect of the year 2021, 4 years postburn ($\beta = 0.932, p = 0.016$), a timeframe that allowed sufficient time for postfire seed dispersal and seedling establishment. We found overall positive effects of understory thinning ($\beta = 0.862, p = 0.037$), and the number of burns 4 years postburn ($\beta = 1.395$, $p < 0.025$). However, we found negative effects of the interaction of number of burns and both understory thinning ($\beta = -2.152$, $p < 0.003$) and overstory thinning ($\beta = -1.672$, $p = 0.021$) 4 years postburn. On unthinned plots 4 years postburn, we found a significant increase in estimated marginal mean incense-cedar densities following two burns compared to one ($p < 0.001$) or no burns ($p < 0.001$) (Fig. 2).

We found no significant effects of treatments on white fir seedling densities throughout the duration of the study (2017 prior to second burn to 2021 4 years after second burn), and estimated marginal means showed no significant differences in white fir seedling densities between treatments (Fig. 2).

Midstory Recruitment Rates

We used stem map recruitment records to estimate 100-year midstory recruitment rates, calculated by scaling mean midstory recruitment rates from 2002 to 2019. In the control, burn only, and burn/understory thin treatments, estimates of pine recruitment ranged from 0 to 10 TPH century^{-1}, while white fir and incense-cedar rates ranged from 38 to 144 TPH century^{-1} (Fig. 3). In the understory thin treatments, we found higher rates of sugar pine recruitment (41 TPH century^{-1}), but the lowest rates of Jeffrey pine recruitment (2 TPH century^{-1}), while maintaining high rates of white fir (164 TPH century^{-1}) and incense-cedar recruitment (133 TPH century^{-1}). However, we saw a more even species abundance of midstory recruitment in plots that were planted following initial treatments. Sugar pine and Jeffrey pine had higher mean recruitment rates in the overstory thin (sugar pine 31, Jeffrey pine 66 TPH century^{-1}) and burn/overstory thin (sugar pine 52, Jeffrey pine 126 TPH century^{-1}) treatments because of planting. Incense-cedar and white fir overstory recruitment remained in a similar range for the overstory thin (incense-cedar 124, white fir 101 TPH century^{-1}) and burn/overstory thin treatments (incense-cedar 58, white fir 138 TPH century^{-1}).

While treatment unit stem map records did not differentiate planted versus natural recruitment, we tracked the origin of seedlings occurring on regeneration microplots to provide an estimate of the contribution of planted seedlings to midstory recruitment (Fig. 4). Within regeneration microplots in planted treatment units in 2021, planted seedlings made up 75% of live sugar pine and 89% of live Jeffrey pine that recruited to the midstory since 2002, the year of planting. When including unplanted treatment

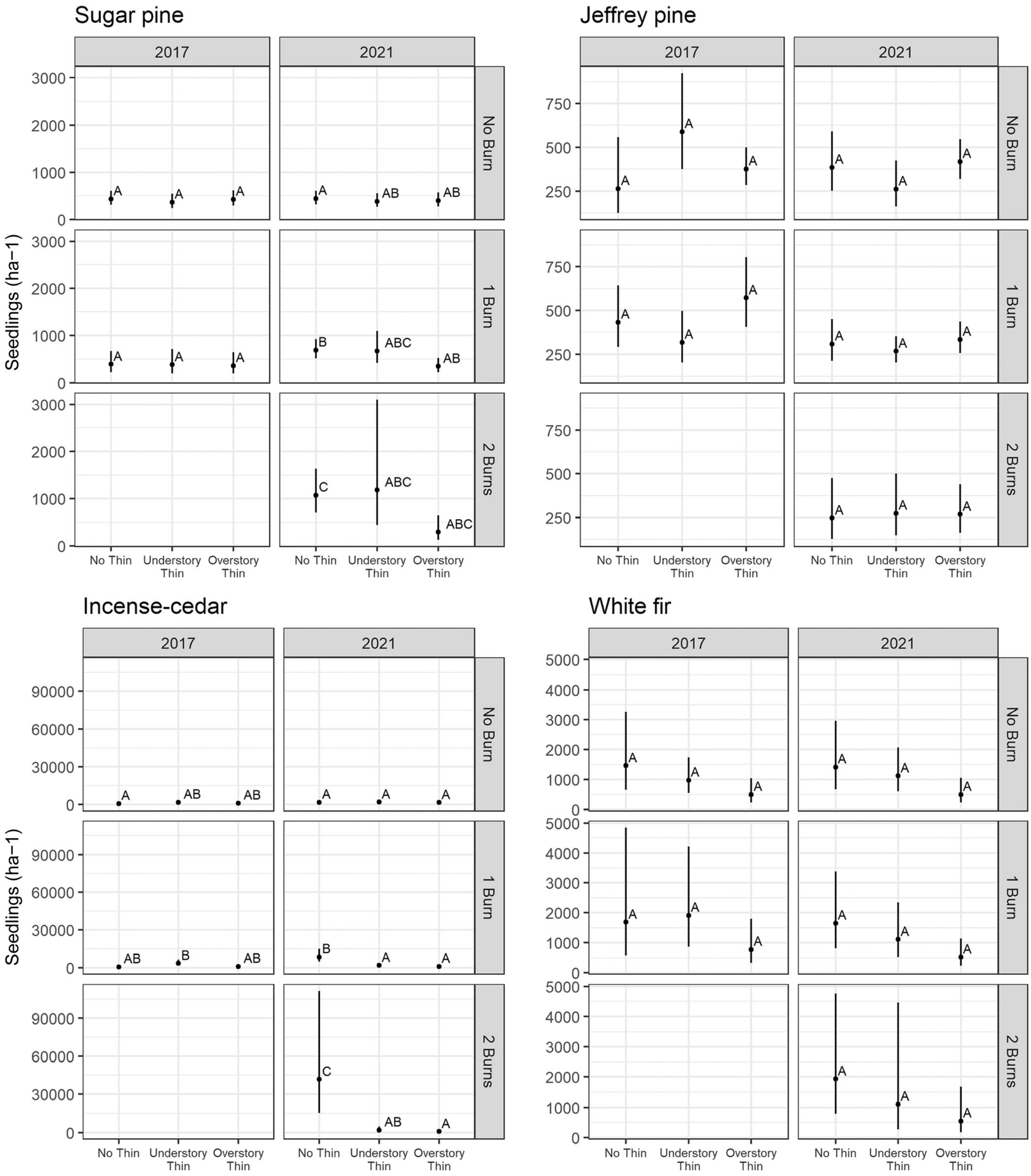

Figure 2. Estimated marginal means seedling density by species for each burn and thinning treatment combination from 2017 (presecond burn) and 2021 (4 years postsecond burn). Marginal means are estimated using a Gamma hurdle, mixed-effects model predicting seedling density, with burn sum, thinning treatment, year, and conspecific basal area as fixed effects. Letters differentiate significant differences ($p < 0.05$) in pairwise comparisons between treatments and number of burns and are meant to be compared within a year. Error bars represent ±95% CI.

units, planted sugar pines made up 50% of total sugar pine midstory recruitment on regeneration microplots. As no other Jeffrey pine midstory recruitment was detected on unplanted regeneration microplots, planted seedlings also made up 89% of total Jeffrey pine midstory recruitment on regeneration microplots across treatments.

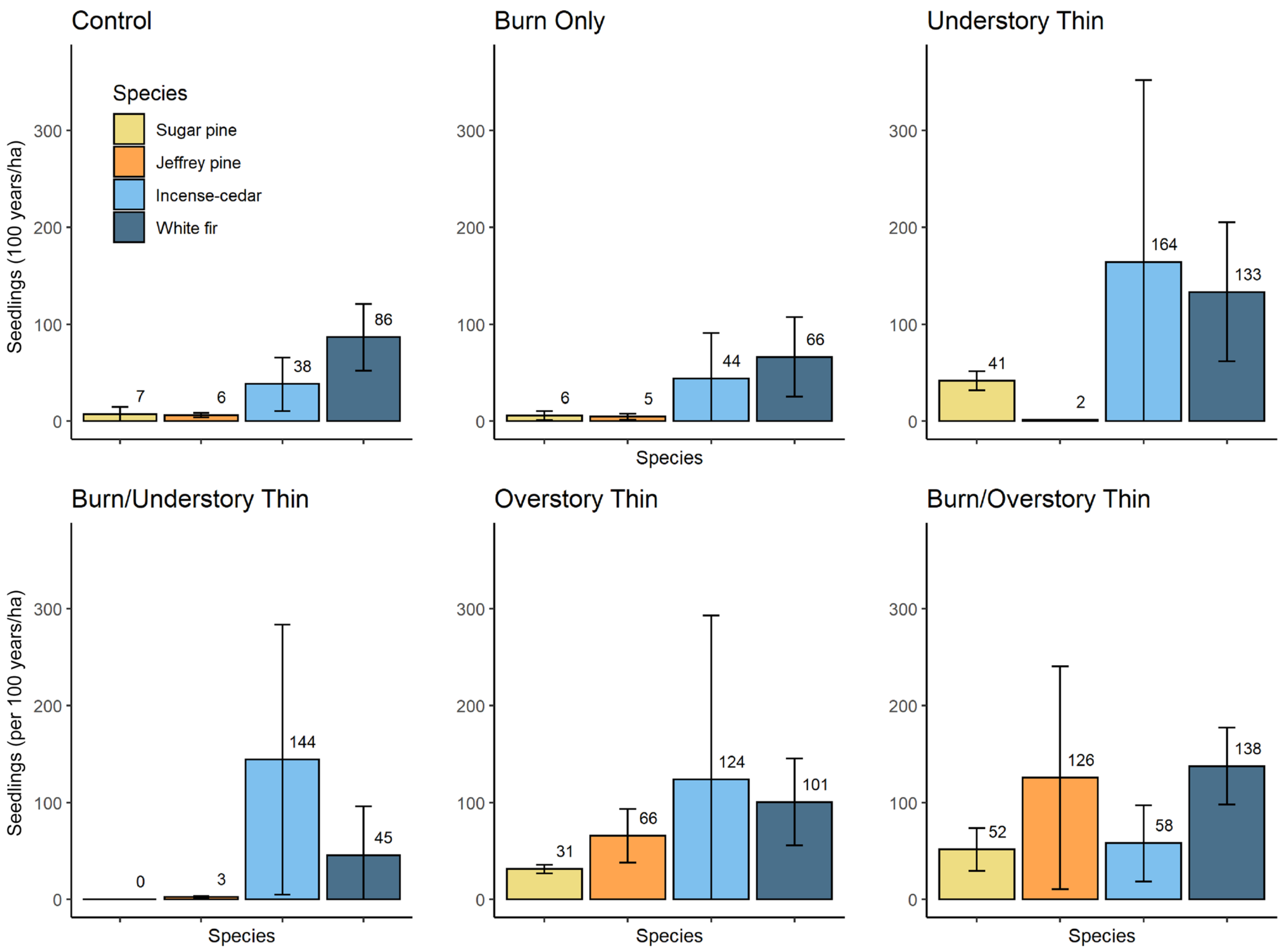

Figure 3. Species-specific rates of midstory recruitment (seedlings surpassing >5 cm DBH) per hectare scaled over 100 years, by treatment. Mean recruitment rates are calculated from records of new trees tagged and mapped plot-wide at each measurement period from 2002–2003 to 2018–2019. Overstory thin and burn/overstory thin plots include recruitment from both planted seedlings and natural seedlings. Error bars represent ± SDS1.

Discussion

A dominant paradigm informing the restoration of fire-suppressed dry-conifer forests has been that by recreating structure similar to reference conditions and reintroducing the ecological process of fire, we can restore the ecosystem. However, our analysis suggests that Sierran mixed-conifer forests may have entered an alternate state that resists efforts to restore and maintain a pine-dominated overstory over the long-term. This observed resistance to returning to the original state is characteristic of hysteresis (Beisner et al. 2003). Similar hysteric states have been documented following fire-exclusion driven changes in tallgrass prairie and predicted due to changes in fire type and frequency in southwestern United States and tropical forests (Collins et al. 2021; Drüke et al. 2021; Keyser et al. 2020). Overcoming hysteresis may require proactive management intervention beyond the removal of the initial fire suppression perturbation (Beisner et al. 2003).

When the modern forest structure at Teakettle was compared to the reconstructed forest structure, North et al. (2007) found that the pre-treatment basal area was similar to the reconstructed basal area, but that pre-treatment stem density was 600% higher the reconstructed stem density. Following the initial thinning and burning treatments, basal area was significantly lower than the reconstructed basal area for every treatment except the burn only (North et al. 2007). We predicted that thinning and repeated burning treatments would have positive effects on pine seedling densities and negative effects on white fir and incense-cedar seedling densities because of decreases in overstory density and changes in the understory environment, but these were not the observed effects. While we saw an increase in sugar pine seedlings as a consequence of burning, Jeffrey pine seedling densities were largely unaffected. Furthermore, incense-cedar regeneration also increased substantially after burning. The second-entry burn had similar effects to the first-entry burn, in that it led to large increases in incense-cedar regeneration and smaller increases in pine regeneration.

Burning increased sugar pine regeneration, likely due to greater light and reduced litter depths favored by sugar pine germinants (Stark 1965). This response is consistent with results from the first-entry burn, after which the burn/no thin treatment

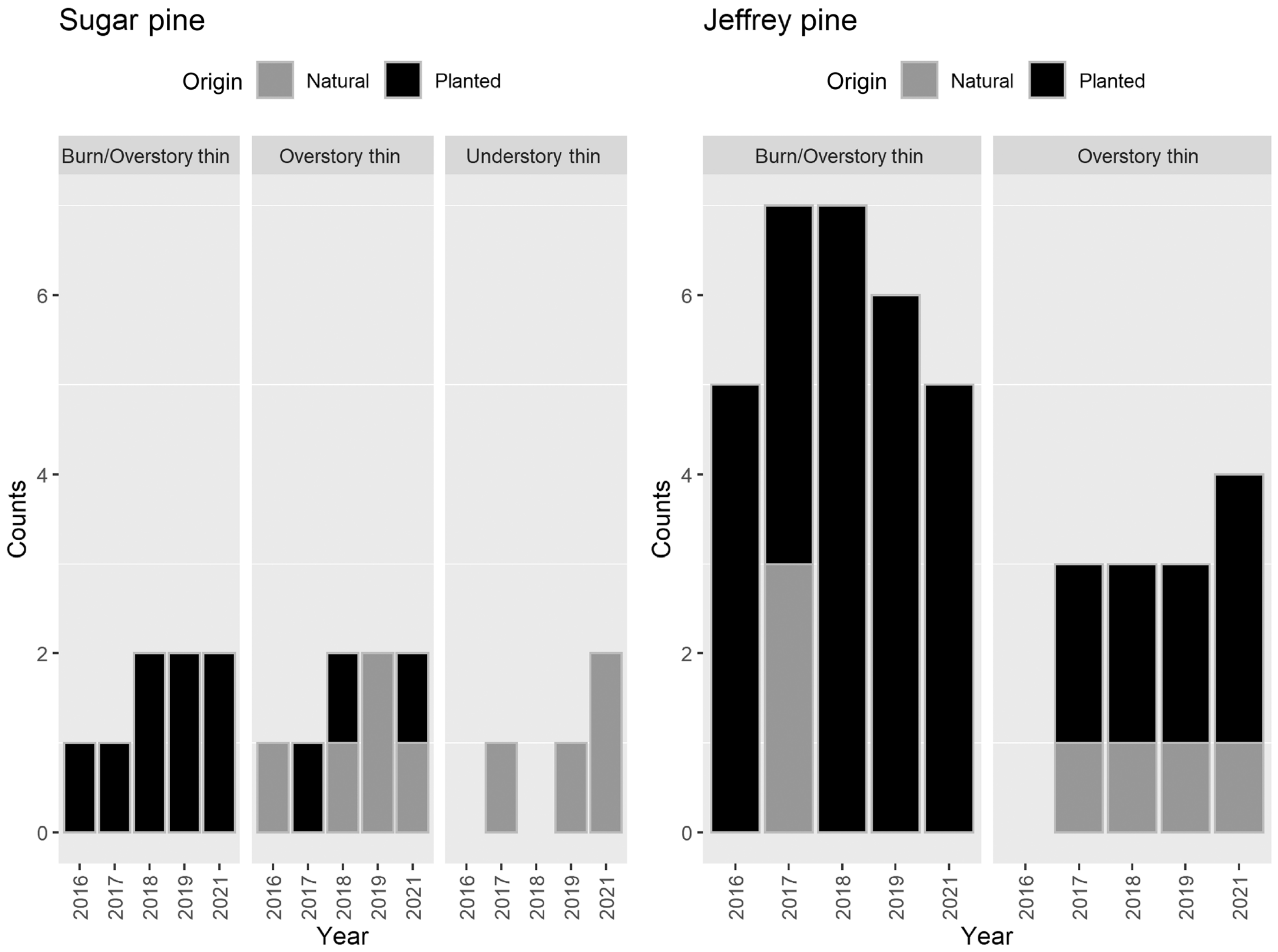

Figure 4. Counts of sugar pine and Jeffrey pine midstory recruitment (>5 cm DBH) detected on regeneration microplots, including only seedlings that crossed this size threshold within the duration of the study (2002–2021). Seedlings were planted in 2002 on overstory thinned plots, with species planted proportionally to pre-treatment overstory dominance. Colors differentiate midstory recruitment counts that were naturally regenerated (gray) from midstory recruitment counts that were originally planted (black). Treatments with no midstory recruitment of these species detected within the duration of the study were not included in the figure.

units saw the greatest increases in sugar pine seedlings (Zald et al. 2008). Despite the increase following burning, sugar pine seedling densities remained much lower than incense-cedar and most white fir seedling densities in corresponding treatments. These results aligned with previous research which showed no increase or comparatively minimal increases in sugar pine following burning or thinning (Van Mantgem et al. 2004; Walker et al. 2012; Tubbesing et al. 2019). We found a small but significant positive effect of live sugar pine basal area on seedling densities, indicating that the presence of more mature individuals increases seedling establishment. This result is consistent with previous research suggesting seed availability may be limiting for pine species (Zald et al. 2008).

Jeffrey pine seedlings were rare across treatments, leading to small sample sizes for analysis. While we did detect significant effects of burning and understory thinning, the estimated marginal mean seedling densities of Jeffrey pine were low and did not vary significantly by treatment. Similarly, earlier research found no significant effects of treatments on Jeffrey pine regeneration 3-years after the first-entry treatments (Zald et al. 2008). In the northern Sierra, a study investigating the effects of burning and thinning also reported much lower seedling densities of pines than shade-tolerant species following treatments (Tubbesing et al. 2019). In the eastern Sierra, thinning was shown to favor shade-tolerant species establishment over Jeffrey pine, but a significant increase in Jeffrey pine was detected after prescribed burning (Walker et al. 2012). Likewise, in a sown seed experiment, higher rates of Jeffrey pine germination were observed on burned treatment units (Zald et al. 2008). At a lower-elevation site dominated by Jeffrey pine with a minor white fir component, thinning and burning were followed by abundant Jeffrey pine-dominated recruitment (Salverson et al. 2011). These results suggest that limited Jeffrey pine regeneration in our experiment may be the result of seed source limitation and, potentially, the dominance of shade-tolerant species in both the overstory and regeneration may have outweighed treatment benefits.

We found no significant effects of treatments on white fir seedling densities following the second-entry burn. In contrast, the results of first-entry treatments at Teakettle showed significant effects of thinning and burning on white fir regeneration, with the greatest increases in white fir frequency in the burn/no thin and burn/understory thin treatment units (Zald et al. 2008). Likewise, other studies in Sierran mixed-conifer forests found increases in fir density following treatments (Tubbesing et al. 2019; Nagelson 2021), despite a preference for dense shade (Stark 1965). However, a study of ponderosa pine/white fir forests in northern Arizona found that while white fir seedling densities were high after a first-entry burn, they were significantly reduced following the second entry burn (Higgins et al. 2015). This wide range of documented treatment effects suggests that white fir post-treatment seedling densities may vary depending on factors such as treatment-entry and intensity, and forest composition.

While the burn/understory thin treatment had the most incense-cedar regeneration following the first-entry (Zald et al. 2008), 4 years after the second-entry burn, we found 23-fold greater incense-cedar estimated marginal mean seedling densities in the Burn Only treatment compared to the control. This large difference may be attributed to increased substrate and light availability because high overstory mortality rates from the drought resulted in a reduction of live tree basal area that may have had similar effects on light availability as the initial thinning events (Steel et al. 2021). Previous research provides evidence that incense-cedar regeneration is facilitated by thinning and fire events (Walker et al. 2012; Welch et al. 2016; Nagelson 2021) and can survive well under a wide range of conditions (Stark 1965). We also found incense-cedar regeneration was positively correlated with live incense-cedar basal area, indicating the importance of seed availability.

Our estimation of long-term midstory recruitment rates by species did not support our initial hypothesis. We predicted that burning and thinning treatments would lead to a stand structure and species composition that approximates the natural range of variability for the ecosystem. However, our data suggests natural midstory recruitment rates for pines are likely insufficient to reach historic densities of overstory pines. Historically the Teakettle Experimental Forest supported around 18 mature sugar pine, 15 Jeffrey pine, 10 incense-cedar, and 23 white fir per hectare (North et al. 2007). Our estimates of midstory recruitment rates in control, burn only, and burn/understory Thin treatments give low mean recruitment rates for pines (3–9 TPH century^{-1}). These results align with those of a previous study that found declines in three out of four sugar pine populations evaluated with no increases after prescribed fire and predicted possible local extinctions in four generations (Van Mantgem et al. 2004). Understory Thin only treatments experienced higher rates of sugar pine recruitment (44 TPH century^{-1}) but the lowest rates of Jeffrey pine recruitment (2 TPH century^{-1}). Midstory recruitment rates for incense-cedar and white-fir are comparatively much higher (39–231 TPH century^{-1}) for these treatments and suggest that removal or significant mortality of these individuals would be needed to reach historic densities. A potential contributing factor to the high levels of white fir recruitment may be that following the initial thinning and burning treatments, white fir accounted for a significantly higher percent of the stem density compared to the reconstructed forest. This was also true for incense-cedar in the burn/understory thin and burn/overstory thin treatments (North et al. 2007). These differences in overstory tree density and our recruitment results suggest that the initial treatments may have not gone far enough in reducing white fir and incense-cedar density.

These results suggest that Sierran mixed-conifer forests may have entered an alternative state dominated by shade-tolerant species. Suppression-related perturbations of natural fire regimes may have exceeded the ecosystem's tolerance threshold, resulting in a shift out of the initial pine-dominated domain of attraction and towards one that favors the persistence of fir and incense-cedar. The observed resistance to a return to the natural range of variability even after the removal of the perturbation reinforces the idea that a domain of attraction shift has occurred. Advanced regeneration of shade-tolerant species that established under fire-suppressed conditions and survived burning and thinning treatments likely contribute to this resistance. Even if we assume 100% survival of the mid-story pine recruitment that we estimated, recruitment in most treatments would be insufficient to approximate species-specific stem density distribution that occurred prior to fire-exclusion (North et al. 2007) because mid-story estimated recruitment rates for white fire and incense-cedar are considerably higher. However, overstory thin treatment units that were planted following initial treatments had much higher pine midstory recruitment rates (32–148 TPH century^{-1}). Regeneration microplot records show that most pine recruited to the midstory in overstory thin treatments were planted, suggesting that the increase in pine recruitment in these treatments can largely be attributed to planted pine survival rather than overstory thinning creating more favorable conditions for natural regeneration. Given these results, it is possible that planting pine, in addition to removing shade-tolerant species, may be an effective means of shifting forest composition back into a domain of attraction that encompasses the natural range of variability, if thinning and burning alone do not overcome resistance in the system.

Our analysis was subject to several limitations. As with any natural system, our treatment units were not perfect copies and differences between units, even when statistically similar, may have influenced our findings. For example, prior to implementation of the initial thinning and burning treatments, total overstory basal area in the two understory thin treatments was significantly higher than in the control (Zald et al. 2008). While this may have contributed to species-specific differences in regeneration between treatments initially, the thinning and burning treatments altered both total basal area and the distribution of basal area among species, likely limiting the potential effects of any pre-treatment differences in basal area on regeneration 15 years after initial treatment implementation. Our study is used a factorial design with large plots located in a manner as to reduce differences in pre-treatment forest composition and structure. As in most large silvicultural experiments, there are tradeoffs between the size of individual treatment units and the number of treatment unit replicates. In the Teakettle Experiment the importance of capturing within stand heterogeneity was a critical factor in determining plot size, but with the potential downside of reducing treatment replicates and statistical power. While our dataset spans over 20 years, this timeframe is still short on the scale of conifer life spans and limits the temporal inference of our results. Regeneration analyses of less frequent species, such as pines, can also be subject to statistical power limitations. The prescribed burns were not ignited in a pattern with the objective of burning 100% of the area and they moved through treatment units inconsistently, affecting as little as 19% of all microplots for the burn/understory thin treatment. As a result, analysis at the treatment-unit level could not offer an accurate representation of burn effects. Because of this, we chose to use individual microplots as replicates in our models and this approach did not allow us to draw conclusions at the treatment unit scale. Only the inner 10 m^2 (where vegetation and cover were surveyed) of each 38.5 m^2 regeneration microplot was assessed for ash and char cover to establish if the microplot was affected by each fire, potentially misclassifying regeneration microplots that were burned only at the outer edges as unburned.

Regeneration in mixed-conifer forests is known to vary considerably by year due to climate variation, masting cycles, and seed predator populations (Lobo 2014; Pearse et al. 2016). To account for this, our midstory recruitment estimates average a 16-year period in hopes of capturing a range of both high and low years for regeneration to provide a realistic mean estimate. As it likely takes around 15–20 years for seedlings to reach the 5 cm DBH size class, the midstory recruitment rates presented in this study are largely reflective of the effects of the first-entry treatments (2000–2001) rather than the second-entry burn (2017), and some seedlings that established prior to treatment implementation were likely incorporated into calculated midstory recruitment rates. Quantifying the long-term effects of repeated burns on midstory recruitment rates will require additional data collection. Yet, similar postburn effects on seedling densities between the first and second-entry treatments suggest that we may see similar trends in midstory recruitment rates in the coming decades. The years used to calculate midstory recruitment rates (2002–2019) encompassed a severe drought that may have reduced seedling survival and therefore decreased midstory recruitment. Similar drought events, however, are expected to become increasingly frequent in the coming century, making the conditions of this measurement period likely representative of future conditions (McEvoy et al. 2020). Given the substantially higher regeneration densities of shade-tolerant species, managers could increase the proportion of the basal area that is pine either by increasing the harvest intensity of shade-tolerant seed producers or with ***precommercial thinning of shade-tolerant saplings that recruit approximately 10 years after the initial treatment.

Our results are in line with other studies that have found pine regeneration lacking in mixed-conifer forests both in untreated areas and following restoration treatments (Ansley & Battles 1998; van Mantgem et al. 2004; Nagelson 2021). A suggested driver of current regeneration patterns is the historic selective logging of pines leaving behind an overstory dominated by shade-tolerant species (Welch et al. 2016). We observed, however, a dominance of shade-tolerant regeneration at our research site on unthinned control units that have never experienced logging. Declining pine regeneration across multiple regions in recent decades has been linked to climate change, suggesting that our low rates of observed pine establishment may be largely a consequence of changing temperature and moisture patterns (Davis et al. 2019; Stevens-Rumann & Morgan 2019). However, similar regeneration patterns were observed in this experiment from 2000–2004 during a non-drought period, indicating that climate is not the primary driver behind our observations (Zald et al. 2008). Regardless, increasing temperature and drought stress is likely to suppress tree regeneration with additional climate change (Davis et al. 2019).

While natural pine midstory recruitment rates were estimated to be insufficient to restore a pine-dominated overstory, our results suggest that planting pine seedlings may increase overstory recruitment and shift the forest back towards its original domain of attraction. Our results were similar to previous research on ponderosa pine regeneration, which showed higher survival and growth rates for planted pines than naturally-established pines (Shepperd et al. 2006; McDonald et al. 2009). Pines have been shown to have the highest rates of survival among mixed-conifer species once established, and planting bypasses initial impediments to pine regeneration such as high seed predation rates and lack of soil substrate access (Fowells & Stark 1965; Zald et al. 2008). Just as postwildfire reforestation approaches have been reevaluated (North et al. 2019; Meyer et al. 2021), our findings suggest planting after restoration treatments in dry western forests is worth consideration. Planting is frequently used to restore forests following disturbance, but our analysis suggests that there may be benefits to expanding planting to currently forested areas as a means of restoring species compositions (Stevens-Rumann & Morgan 2019). As this project only evaluated planted seedlings on overstory thinned treatment units, further research is needed to determine how planted seedlings fare following burning alone, understory thinning, and combination treatments.

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Supporting Information

The following information may be found in the online version of this article:

Figure S1. Histograms of the DBH of trees recruited to the stem map between post-1st entry treatment measurements and post-2nd entry burn measurements.
Table S1. Table of the number of plots in each burn sum category (0, 1, or 2 burns) by burn treatment.
Table S2. Full mixed model results for ABCO (White fir) seedling densities in TPH (trees per hectare), including intercept and model coefficient estimates, Standard Error (SE), test statistic values, and *p*-values
Table S3. Full mixed model results for CADE (Incense-cedar) seedling densities in TPH (trees per hectare), including intercept and model coefficient estimates, Standard Error (SE), test statistic values, and *p*-values
Table S4. Full mixed model results for PIJE (Jeffrey pine) seedling densities in TPH (trees per hectare), including intercept and model coefficient estimates, Standard Error (SE), test statistic values, and *p*-values
Table S5. Full mixed model results for PILA (Sugar pine) seedling densities in TPH (trees per hectare), including intercept and model coefficient estimates, Standard Error (SE), test statistic values, and *p*-values
Table S6. Estimated marginal means for ABCO (White fir).
Table S7. Estimated marginal means for CADE (Incense-cedar).
Table S8. Estimated marginal means for PIJE (Jeffrey pine).
Table S9. Estimated marginal means for PILA (Sugar pine).

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