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Repeated fuel treatments fall short of fire-adapted regeneration objectives in a Sierra Nevada mixed conifer forest, USA

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Abstract

Fire exclusion over the last two centuries has driven a significant fire deficit in the forests of western North America, leading to widespread changes in the composition and structure of these historically fire-adapted ecosystems. Fuel treatments have been increasingly applied over the last few decades to mitigate fire hazard, yet it is unclear whether these fuel-focused treatments restore the fire-adapted conditions and species that will allow forests to persist into the future. A vital prerequisite of restoring fire-adaptedness is ongoing establishment of fire-tolerant tree species, and both the type and reoccurrence of fuel treatments are likely to strongly influence stand trajectories. Here, we leveraged a long-term study of repeated fuel treatments in a Sierra Nevada mixed-conifer forest to examine the regeneration response of six native tree species to the repeated application of common fuel treatments: prescribed fire, mechanical, mechanical plus fire, and untreated controls. Our objectives were to (1) quantify differences in forest structure and composition following the repeated application of alternative fuel treatments that may influence the establishment environment and then (2) identify the stand structure and climate conditions influencing seedling dynamics. We found that both treatment type and intensity are highly influential in shifting forests toward more fire-adapted conditions and determining species-specific regeneration dynamics. Specifically, the conifer species tracked here increased in either colonization or persistence potential following repeated applications of fire, indicating fire may be most effective for restoring regeneration conditions broadly across species. Fire alone, however, was not enough to promote fire-adapted composition, with concurrent mechanical treatments creating more favorable conditions for promoting colonization and increasing abundances of fire-tolerant ponderosa pine. Yet, even with repeated fuel treatment application, establishment of fire-intolerant species far exceeded that of fire-tolerant species over this 20-year study period. Moreover, increasing growing season water stress negatively impacted seedling dynamics across all species regardless of treatment type and intensity, an important consideration for ongoing management under heightened climatic stress. While repeated treatments are waypoints in restoring fire-adapted conditions, more intense treatments via gap-creation or hotter prescribed fires targeting removal of fire-intolerant species will be necessary to sustain recruitment of fire-tolerant species.

KEYWORDS

California black oak, climate, Douglas-fir, fire and fire surrogates, fuel reduction, incense-cedar, mechanical treatments, ponderosa pine, prescribed fire, silviculture, sugar pine, white fir

INTRODUCTION

For nearly two centuries, fire has been largely excluded from fire-adapted forests of western North America (Hagmann et al., 2021; Swetnam et al., 2016; Taylor et al., 2016), catalyzing a massive fire deficit in which fire is less frequent than historical conditions and climate would dictate (Marlon et al., 2012; Parks et al., 2015). This long-term fire deficit has most conspicuously transformed forests that evolved with frequent, low- to moderate-severity fire (<35-year fire return interval, LANDFIRE, 2016) and were, accordingly, historically fuel-limited, structurally heterogenous, and dominated by fire-tolerant species (Larson & Churchill, 2012; Taylor, 2010). Frequent-fire forests are now instead widely characterized as structurally homogenous with high tree densities and surface fuels (Collins et al., 2011; Fulé et al., 2009; Hessburg et al., 2021) and dominated by fire-intolerant species (Knight et al., 2022; Safford & Stevens, 2017). These altered conditions are linked to the emergence of uncharacteristically large and severe wildfires that increase risk to wildland–urban interface communities and burn under regimes misaligned with species' adaptations (Iglesias et al., 2022; Parks & Abatzoglou, 2020).

To mitigate these risks, fuel reduction treatments (henceforth fuel treatments) have been written into legislation (e.g., Collaborative Forest Landscape Restoration Program, 2018; Healthy Forests Restoration Act, 2003) and applied over millions of hectares of western US frequent-fire forests over the last few decades (Schoennagel & Nelson, 2011; USDA Forest Service, 2022). Conceptually, the objective of fuel treatment is to restore the fuel-limited conditions, and more ideally the fire regimes, that historically reduced the probability of crown fire (Agee & Skinner, 2005). Practically, fuel treatments involve the application of fire or fire surrogates (e.g., thinning, mastication) to remove ladder fuels and increase tree spacing, with prescriptions largely resembling pre-commercial thinning operations for even-aged forests (Larson & Churchill, 2024). Treatments generally produce homogenous stands with uniform spacing, limited complexity, and the continued absence of frequent fire (Knapp et al., 2017; Stephens et al., 2021). These fuel reduction strategies effectively mitigate risk and reduce the probability of crown fire (Davis et al., 2024; Hessburg et al., 2021; Prichard et al., 2020; Stephens, Foster, et al., 2023); however, the narrow focus on risk mitigation has obscured the more comprehensive objective of restoring fire-excluded forests to the fire-adapted conditions that will allow them to absorb fire and persist through time (Koontz et al., 2020; Stephens et al., 2021; Ziegler et al., 2017).

Restoring the fire-adaptedness of frequent-fire forests requires a lens of heterogeneity where managers mark to create variable density stands with canopy gap heterogeneity (Knapp et al., 2013, 2017; Larson & Churchill, 2012; Lydersen et al., 2013) while retaining large, fire-tolerant trees (Churchill, 2021; D'Amato et al., 2011). Maintenance of these fire-adapted conditions, in theory, also necessitates the return of fuel treatments at intervals approximating historical fire frequency (e.g., realignment treatments, Stephens et al., 2010). These cornerstones of frequent-fire forest complexity are increasingly integrated into management as we have learned that both structural complexity and treatment longevity are limited under business-as-usual fuel treatments (Reinhardt et al., 2008; Vaillant et al., 2015). For instance, fuel treatment prescriptions now often explicitly return fire or fire surrogates at intervals mimicking the historical, repeated fuel-removal in these once fuel-limited systems (Churchill, 2021; Larson & Churchill, 2024). This repeated application of fuel treatment provides a new opportunity to assess the efficacy of alternative treatment types to meet a forest restoration objective as well as the frequency and/or intensity of application necessary to maintain fire-adapted forest conditions.

Success is best defined by treatments meeting both operationally and ecologically based objectives. Therefore, first creating and then maintaining fire-adapted forest conditions is the key link between accomplishing short-term hazard reduction (i.e., business-as-usual fuel treatments) and achieving long-term resilience (i.e., fire-adapted forest restoration). In particular, a vital pre-requisite of restoring fire-adaptedness is ongoing establishment of fire-tolerant tree species (Addington et al., 2018; York et al., 2012). Meeting this particular objective requires not only the retention of fire-tolerant species as seed or sprouting sources but the creation of a regeneration environment comparable with that once maintained by frequent fire—a structurally complex stand with high light availability and disturbed substrate (Larson & Churchill, 2024; Murphy et al., 2021). Fuel treatments typically do not disturb canopies, limiting light and resulting in regeneration of shade-tolerant, fire-intolerant species (Bigelow et al., 2011; Zald et al., 2008). For fuel treatments to concomitantly meet a forest restoration objective, application must instead target fuels to reduce the probability of crown fire while synchronously creating the forest conditions necessary for promoting, maintaining, and establishing fire-tolerant species (Rossman et al., 2020; Stephens & Moghaddas, 2005). In addition, the regular return of such restoration treatments is likely key to long-term fire-adaptedness and forest resilience.

California's frequent-fire Sierra mixed-conifer (SMC) forests have been the focal point of fuel treatment application to meet these objectives due to their significant departure from historical fire-adapted conditions (van de Water & Safford, 2011) and the corresponding increase in wildfire severity and extent (Safford et al., 2022). Prior to the era of fire exclusion, SMC forests were ignited by lightning and Indigenous peoples roughly every 11–18 years (mean fire return interval [MFRI]; Taylor et al., 2016; van de Water & Safford, 2011), which shaped forests into low density, low fuel ecosystems dominated by fire-adapted structures and fire-tolerant species (Barth et al., 2015; Collins et al., 2011). A priority in SMC forest management is thus restoration of natural ecosystem processes by, in particular, increasing fire-adaptedness via the recruitment of fire-tolerant species, specifically yellow pines—ponderosa pine (*Pinus ponderosa* Laws) and Jeffrey pine (*Pinus jeffreyi* Balf.)—sugar pine (*P. lambertiana* Dougl.), and black oak (*Quercus kellogii* Newb.) (Fitzgerald, 2005; Stephens et al., 2021). Meeting this objective corresponds with reducing surface fuels as well as reducing abundances of fire-intolerant white fir (*Abies concolor* Gord. and Glend.) and incense-cedar (*Calocedrus decurrens* [Torr.] Floren.). Yet, while fuel treatments are actively underway in SMC forest restoration projects, one key piece of uncertainty remains—which treatments (e.g., fire versus mechanical) and at what frequency or intensity create conditions favorable for fire-tolerant species regeneration to go beyond wildfire mitigation, thereby promoting fire-adaptedness and better preparing forests for an uncertain climate future.

To address this knowledge gap, we leveraged an installation of the National Fire and Fire Surrogate Study in the central Sierra Nevada, California (Schwilk et al., 2009). We used a 20-year dataset collected before and after alternative, repeated fuel treatments to investigate demographics of seedling establishment for six native tree species and to identify the primary factors influencing trends. We assessed species-specific seedling dynamics by quantifying metrics that distinguish underlying ecological mechanisms: seedling density, or count per unit area; seedling colonization, or presence at a site previously unoccupied; and seedling persistence, or presence at a site previously occupied (henceforth density, colonization, and persistence, or, collectively, dynamics). Our objectives were to (1) quantify differences in forest structure and composition following the repeated application of alternative fuel treatments (prescribed fire, mechanical, and mechanical plus fire versus untreated control) that may influence the establishment environment and then (2) identify the stand structure and climate conditions influencing seedling dynamics. Quantifying the impact of repeated fuel treatments on seedling dynamics is critical to informing the fuel treatment types and intensities most appropriate for restoring fire-adapted conditions and regenerating fire-tolerant species, particularly given the increasing pace and scale of treatment necessary to reduce high-severity wildfires under both current and extreme future conditions.

METHODS

Study site

The FFS installation on the University of California, Berkeley's 1800-ha Blodgett Forest Research Station (hereafter Blodgett) spans a 1100- to 1400-m elevation range within the mixed-conifer zone on the western slope of the Sierra Nevada range near Georgetown, CA (38°54′45″ N, 120°39′27″ W). The dominant overstory species are black oak, Douglas-fir (*Pseudotsuga menziessi* [Mirb.] Franco), incense-cedar, ponderosa pine, sugar pine, and white fir, which represent a broad spectrum of light, moisture, fire, and reproductive adaptations (Table 1). Generally speaking, fire-tolerant tree species of SMC forests are shade-intolerants that require both high light and disturbed substrate for successful establishment (Stevens et al., 2020; Van Mantgem et al., 2006). Common shrub species include deer brush (*Ceanothus integerrimus*), whitethorn ceanothus (*C. cordulatus*), and Sierra gooseberry (*Ribes roezlii*). Blodgett's onsite weather station documented an average of 136 cm of precipitation per year during our sampling period from 2001 to 2020 (Appendix S1: Figure S1), with the vast majority (~70%) falling as rain between November

TABLE 1 Microsite preferences, fire adaptations, and regeneration characteristics for six common overstory tree species of Sierra Nevada mixed-conifer forests.

		Microsite			Fire		Regeneration		
Common name	Scientific name	Shade tolerance	Drought tolerance	Substrate preference	Seedling tolerance	Mature tolerance	Seed production timeline	Masting frequency	Dispersal strategy
California black oak	*Quercus kellogii*	Low	High	Generalist	Low	Moderate	2 years	2–6 years	Primary sprouting, gravity, animal caching
Douglas- fir	*Pseudotsuga menziesii*	Moderate	Low	Mineral soil	Low	High	1 year	7 years	Wind
Incense- cedar	*Calocedrus decurrens*	High	Moderate	Generalist	Low	High	1 year	3–6 years	Wind
Ponderosa pine	*Pinus ponderosa*	Low	High	Mineral soil	High	High	2 years	2–5 years	Wind
Sugar pine	*Pinus lambertiana*	Moderate	Low	Generalist	Low	High	2 years	3–5 years	Gravity, animal caching
White fir	*Abies concolor*	High	Low	Mineral soil	Low	Low	2 years	3–9 years	Wind

Note: Sourced from Bonner and Karrfalt (2008), Burns and Honkala (1990), and the Fire Effects Information System (2023).

and March. Over the sampling period, mean daytime temperatures were 7°C (±2.3°) during winter months and 24°C (±0.7°) during summer months. Soils are deep and well-drained sandy loams derived from andesitic and granitic parent material (Moghaddas & Stephens, 2007). The topography covers a range of aspects, with slopes averaging less than 30%.

Blodgett's disturbance history is comparable to that of most SMC forests. Before European settlement and widespread fire exclusion, fire was the primary disturbance altering forest structure and composition, with fires burning every 5–15 years (Stephens & Collins, 2004). Fire return was regular and often planned, as Indigenous peoples, including the Nisenan and Washoe Tribes, managed regional forests with fire to meet a variety of cultural resource objectives before being forcefully removed and persecuted in the mid- to late-1800s (Taylor et al., 2016). Logging occurred across most of Blodgett beginning in the 1850s up until the university acquired the property in 1933. Blodgett has since been managed with the suite of silvicultural strategies commonly applied across California, including various fuel treatments.

Treatments

The FFS study was established to compare outcomes of alternative fuel treatments in meeting hazardous fuel reduction objectives (see McIver et al., 2012 for comprehensive details on study design). A multi-disciplinary scientific group defined the conditions desired following FFS treatments, with the overarching goal of producing forest conditions that resist wildfire and begin the process of forest restoration while maintaining habitat for a diverse set of wildlife species. Average desired conditions (range) were thus defined as crown cover of 45% (40%–55%), basal area (BA) of 29 m^2 ha^{-1} (28–34 m^2 ha^{-1}), maintenance of an even species mix of residual conifers, surface fuel load <22 tons ha^{-1}, and 2–5 snags >30 cm DBH ha^{-1}. No spatial heterogeneity was included in these desired conditions.

At Blodgett, a factorial design was implemented to compare effects of three repeated, alternative fuel treatments to an untreated control: prescribed fire (hereafter Fire), mechanical thinning and mastication (Mech), and mechanical treatment followed by prescribed fire (Mech + Fire). The 12 stands (3 stands/treatment × 4 treatments) average 19 ha in size (range 13–29 ha, total area by treatment ranges 50–65 ha). Control units represent the lowest intensity treatment, with no canopy disturbance, while Mech + Fire units represent the highest intensity treatment by combining multiple fuel reduction methods in the canopy and understory. Total BA was relatively comparable across all units prior to initial treatments (Table 2), although species composition varied slightly among units (Table 2). In particular, black oak had higher BA in the Control and Mech + Fire stands at study initiation, while sugar pine BA was highest in the Control and lowest in the Mech + Fire (Table 2).

TABLE 2 Mean basal area (BA) in square meters per hectare.

Species	Treatment	2001	2003	2009	2016	2020
BO	Control	5.4 (1.2)	5.5 (1.3)	5.2 (1.2)	4.8 (1.1)	5.5 (1.3)
	Fire	2.3 (0.6)	1.9 (0.5)	1.6 (0.6)	1.3 (0.5)	1.1 (0.4)
	Mech	4.3 (1)	3.9 (0.9)	3.9 (1.1)	3.7 (0.9)	3.7 (0.9)
	Mech + Fire	7.0 (1.2)	4.3 (0.8)	3.9 (0.8)	2.1 (0.5)	1.5 (0.4)
DF	Control	9.6 (1.5)	9.8 (1.5)	10.2 (1.9)	11.8 (1.6)	13.5 (2)
	Fire	9.8 (1.2)	10.5 (1.3)	10.0 (1.4)	10.2 (1.3)	10.5 (1.6)
	Mech	11.7 (1.2)	9.6 (1.1)	11.6 (1.5)	12.4 (1.4)	10.7 (1.5)
	Mech + Fire	6.5 (0.9)	5.0 (0.9)	5.0 (1)	5.7 (0.9)	5.2 (1.2)
IC	Control	14.0 (1.2)	14.9 (1.2)	16.0 (1.5)	15.9 (1.4)	16.6 (1.6)
	Fire	9.9 (1)	9.5 (1)	10.1 (1.2)	9.7 (1.1)	10.5 (1.3)
	Mech	10.8 (1.1)	6.9 (0.9)	7.2 (1)	7.7 (1)	9.2 (1.2)
	Mech + Fire	8.8 (1.2)	4.5 (0.7)	5.4 (1)	5.8 (0.9)	5.6 (1)
PP	Control	8.4 (1.4)	8.7 (1.5)	10.4 (1.8)	9.5 (1.4)	9.3 (1.8)
	Fire	4.8 (0.8)	4.8 (0.8)	5.5 (1.1)	7.1 (1.1)	6.6 (1.2)
	Mech	2.2 (0.6)	2.2 (0.7)	3.3 (1)	3.9 (0.8)	2.7 (0.9)
	Mech + Fire	11.6 (1.4)	10.5 (1.2)	11.7 (1.5)	13.0 (1.4)	13.8 (1.7)
SP	Control	2.5 (0.7)	2.7 (0.7)	3.0 (0.9)	3.1 (0.8)	3.8 (1.1)
	Fire	5.0 (1)	5.1 (1.1)	5.6 (1.4)	5.0 (1.1)	6.0 (1.4)
	Mech	7.5 (1.5)	7.7 (1.5)	9.7 (2)	9.7 (1.8)	9.8 (2)
	Mech + Fire	8.3 (1.6)	7.4 (1.5)	8.2 (1.7)	6.9 (1.5)	5.8 (1.4)
WF	Control	12.6 (1.4)	12.9 (1.4)	14.5 (1.8)	13.4 (1.5)	14.2 (1.7)
	Fire	11.7 (1)	12.1 (1)	12.9 (1.4)	11.5 (1.2)	12.0 (1.3)
	Mech	11.2 (1.2)	8.7 (1.1)	10.0 (1.4)	8.7 (1.1)	9.1 (1.4)
	Mech + Fire	9.6 (1.1)	6.8 (0.9)	5.5 (1)	4.9 (0.8)	4.4 (0.9)
Other	Control	1.4 (0.5)	1.4 (0.5)	1.0 (0.4)	1.8 (0.6)	2.2 (0.7)
	Fire	1.9 (0.8)	1.6 (0.7)	1.4 (0.7)	0.8 (0.3)	0.4 (0.2)
	Mech	1.1 (0.6)	1.0 (0.6)	0.6 (0.3)	2.8 (1)	1.5 (0.6)
	Mech + Fire	0.1 (0.1)	0.1 (0.1)	0.1 (0.1)	0.8 (0.4)	0.1 (0.1)
Total	Control	53.8 $(4.8)^{1a}$	55.7 $(4.8)^{2ab}$	60.3 $(5.2)^{2ab}$	60.4 $(4.4)^{3ab}$	63.7 $(4.8)^{3b}$
	Fire	45.6 $(4.5)^{1a}$	45.5 $(4.5)^{1a}$	47.0 $(5.1)^{1a}$	45.9 $(4.3)^{12a}$	47.3 $(4.6)^{2a}$
	Mech	48.8 $(4.7)^{1b}$	40.0 $(4.8)^{1a}$	46.4 $(5.2)^{1ab}$	48.8 $(4.5)^{2b}$	46.8 $(5)^{2ab}$
	Mech + Fire	51.8 $(4.8)^{1b}$	38.4 $(4.8)^{1a}$	39.7 $(5.1)^{1a}$	39.1 $(4.5)^{1a}$	36.4 $(5.1)^{1a}$

Note: Parentheses show standard errors for individual species BA. For total BA, parentheses show 95% confidence intervals of the estimated marginal mean BA. Superscript numbers reflect significant differences ($p \leq 0.05$) among treatments within years. Superscript letters reflect significant differences among years and within treatments. Fire stands were treated three times: fall 2002, 2009, and 2017. Mech stands were masticated and thinned in 2001 and again in 2017–2019. Mech + Fire stands were thinned, masticated, and burned in 2001–2002 and masticated and burned in 2017–2019.

Abbreviations: BO, black oak; DF, Douglas-fir; IC, incense-cedar; PP, Ponderosa pine; SP, sugar pine; WF, white fir.

The Fire stands were treated in October and November of 2002, 2009, and 2017. The Mech stands were treated with a thin from below followed by mastication. The first set of paired treatments occurred in 2001 and 2002, respectively, followed by repeated treatments of mastication in 2017 and thinning in 2019. Each thinning plus mastication is considered a single entry, implemented in tandem for maintaining low fire hazard. In the Mech + Fire treatments, stands were first thinned and masticated in 2001 and burned in 2002. These stands received secondary rounds of mastication and burning in 2018. Two of the three Mech + Fire stands were burned in October 2018 before unfavorably low relative humidity required postponing burning in the third stand until conditions were again appropriate in January of 2019.

Data collection

Repeated measurements of permanent plots were used to capture a range of ecological responses, including seedling establishment. Plots were established prior to treatments using a systematic 60-m grid (hereafter "full inventory"). At each grid point (20 plots per stand, 60 per treatment type), all trees ≥11.4 cm diameter-at-breast-height (DBH, 1.37 m bole height) within one 11.3 m (0.04 ha) fixed-radius plot were tagged and sampled for species and DBH as well as additional tree-level data not leveraged in this study (see Stephens & Moghaddas, 2005). Seedling data were collected on 0.004-ha nested fixed-radius plots within the 0.04-ha plots (hereafter nested plot). In nested plots, all trees <11.4 cm DBH were tallied by species into eight size classes, but we use only data from the smallest size class (≤30 cm tall) to limit our inference to the most recently established trees. Current year's seedlings (germinants) are not considered "established" and were not tallied due to the ephemeral nature of this size class (Kroiss et al., 2015; Petrie et al., 2015). Given the complexity and destructive nature of this task, we did not differentiate between black oak seedlings that established from seed versus those that sprouted from existing root systems of mature trees. Operational timing occasionally required sampling efforts to span two field seasons, and plots were sampled in 2001, 2003, 2009, 2010, 2013–2014, 2016–2017, 2018–2019, and 2020. The timing of measurements was focused on capturing conditions prior to and immediately following treatments as well as changes between treatments, resulting in variable sampling intervals (1–6 years) over the course of the study.

Given the high spatial variability of seedling establishment, an additional network of subplots was established at 10 random plots from the grid described above to supplement the regeneration dataset. In this effort, a 1-m^2 subplot was installed at 5 m distance from plot center at four azimuths (20°, 110°, 200°, and 290°), creating a cluster of four subplots (hereafter clustered subplots). In each 1-m^2 subplot, seedlings ≤30 cm tall were tallied by species in 2001, 2003, 2004, 2006, 2009, 2016, 2018, and 2020.

To measure changes in the light environment following treatments, we derived percent total transmitted radiation (%TTR) from hemispherical photographs of the canopy (Table 3). Photographs were captured in 2006, 2016, 2018, and 2020 using a Nikon camera with fisheye lens 1 m above ground at 4–7 locations per stand and taken just before sunrise or after sunset. Additional photos were taken in the Mech + Fire stands in 2019 to capture posttreatment conditions after the second round of mastication and prescribed fire. Gap Light Analyzer (Frazer et al., 1999) was used to calculate %TTR from hemispherical photographs. We report light data to demonstrate the effect of treatment intensity on this critical ecological characteristic over time. However, due to the mismatches in sample size and sampling frequency between light measurements and seedling data, we excluded this variable from analyses described below.

Treatment, stand, and climate predictors

Prior to analysis, we summarized or calculated a suite of potential predictors related to treatment, stand, and climate conditions. We first derived a set of variables to capture the effects of treatment, time, and the number of treatments applied. *Treatment* is a categorical variable for treatment type: Control, Fire, Mech, and Mech + Fire. *Time-since-treatment* is the number of growing seasons that have elapsed since the most recent treatment application. *Treatment-number* represents the number of treatment entries since the beginning of the study. We also summarized forest composition and structural data

TABLE 3 Estimated marginal mean % total transmitted radiation (TTR) and 95% confidence intervals.

Treatment	2006	2016	2018	2020
Control	15.4 (5.9)^{a1}	15.7 (5.9)^{a1}	23.6 (5.8)^{b1}	19.2 (6.0)^{ab1}
Fire	24.2 (6.2)^{a12}	22.4 (6.1)^{a1}	29.5 (6.1)^{a1}	23.4 (6.2)^{a12}
Mech	22.1 (5.8)^{ab1}	16.7 (5.8)^{a1}	24.3 (5.9)^{bc1}	30.4 (5.9)^{c2}
Mech + Fire	34.7 (5.8)^{a2}	37.7 (5.5)^{ab2}	42.7 (5.6)^{b2}	51.1 (5.8)^{c3}

Note: Cells that share superscript letters failed Tukey tests for pairwise comparisons among years within treatments, and cells that share superscript numbers show pairwise comparisons within years and among treatments. Fire stands were treated three times: fall 2002, 2009, and 2017. Mech stands were masticated and thinned in 2001 and again in 2017–2019. Mech + Fire stands were thinned, masticated, and burned in 2001–2002 and masticated and burned in 2017–2019.

from overstory plots for each sampling period given that microsite conditions within a stand can influence seedling dynamics. Conspecific BA (in square meters per hectare) was quantified as a surrogate for potential seed availability, while total BA (in square meters per hectare) was selected to characterize competition for light and soil moisture.

Finally, we calculated a suite of climate variables using daily temperature and precipitation data from Blodgett's onsite weather station (Appendix S1: Figure S1). Our statistical models ultimately included two precipitation variables that capture the distinct precipitation "seasons" for the Sierra Nevada, as defined by Williams et al. (2021): growing season (May–October) and cool season (November–April). We additionally calculated total growing season climatic water deficit (CWD) to capture combined water and temperature stress experienced by seedlings (Lutz et al., 2010; Redmond, 2019). The inputs for CWD included monthly precipitation, monthly mean temperature, aspect, slope, and soil-water holding capacity (Soil Survey Staff, 2017). When one or more years elapsed between seedling surveys, data were calculated as the mean of annual sums between surveys. When surveys were conducted in consecutive years, only the single annual sum was used.

Statistical analyses

Our objectives for the analyses were twofold: (1) test for differences among years and among treatments in terms of overstory structure (BA, light) and seedling density and (2) identify key variables that drive the three dimensions of specifies-specific seedling dynamics: density, colonization, and persistence. To compare differences between key forest structure metrics following repeated treatments (Objective 1), we used generalized linear mixed models (Bolker et al., 2009) and multiple pairwise comparisons to test for differences in mean total BA, light, and seedling density among treatments and years. We used a normal error distribution (with an identity link function) to model total BA and light and a negative binomial error distribution (log link function) to model seedling density. Year was treated as a categorical fixed effect. We included an offset term to account for differences in sampling area (0.004 ha nested regeneration plots vs. 1 m^2 clustered subplots) in our seedling density models, calculated as the log of sampling area. We additionally included a random intercept term to accommodate variation among stands. We built these models using the *glmmTMB* package (Brooks et al., 2017). We used the *emmeans* package (Lenth, 2021) to acquire estimated marginal means and post hoc comparisons.

To identify the stand structure and climate conditions further influencing seedling dynamics (Objective 2), we modeled seedling density and occupancy for each species (California black oak, Douglas-fir, incense-cedar, ponderosa pine, sugar pine, white fir) as a function of treatment, stand, and climatic drivers of establishment. Prior to modeling species-specific seedling density and occupancy, we examined pairwise correlation coefficients between all hypothesized predictors to avoid incorporating highly correlated predictors; we found no paired values were >0.65, a conservative retention coefficient, so retained all potential predictors. We then centered all covariate means around 0 and scaled standard deviations to 1 (Appendix S1: Table S1). We used generalized linear mixed models to find expected species-specific seedling densities at plot i in year t as a log-linear function of our predictor variables, with residual error following a negative binomial distribution. We included an offset term to account for differences in sampled area between plots and a random intercept term to capture variation among stands.

Second, a dynamic site-occupancy modeling framework (Royle & Kéry, 2007) was used to model species-specific seedling occupancy (occupancy = 1, absence = 0) for each plot i and year t. This framework allowed us to derive probabilities for two distinct processes, colonization and persistence, for each species. We assumed that unoccupied plots were colonized with seedlings each year with probability ϕ_t (i.e., colonization), while occupied plots would maintain seedling occupancy with probability γ_t (i.e., persistence).

$$z(i,t) \sim \text{Bernoulli}\left(\psi_{i,t}\right), \tag{1}$$

$$\psi_{i,t} = z(i,t-1) \times \gamma_{i,t} + (1 - z(i,t-1)) \times \phi_{i,t}, \tag{2}$$

$$\begin{aligned}\text{logit}\left(\gamma_{i,t}, \phi_{i,t}\right) = {} & \beta_0 + \beta_1 \times \text{Treatment}_i + \beta_2\left(\text{Treatment}_i \times \text{Timesince treatment}_{i,t}\right) + \beta_3 \times N \text{ treatments} + \\ & \beta_4 \times \text{Conspecific } BA_{i,t} + \beta_5 \times \text{Total } BA_{i,t} + \beta_6 \times \text{Growing PPT}_{i,t} + \beta_7 \times \text{Cool } PPT_{i,t} + \beta_8 \times \text{Growing } CWD_{i,t} + \varepsilon_i\end{aligned} \tag{3}$$

where $z(i, t)$ is the occupancy status in time t (Equation 1). Thus, when $z(i, t-1) = 0$, ψ_t takes on the parameter for colonization (ϕ), and when $z(i, t-1) = 1$,

ψ_t takes on the parameter value for persistence (γ) (Equation 2). ε represents the random intercept to capture variation among stands and plots (Appendix S2). Both ϕ_t and γ_t were modeled as logit-linear functions (Equation 3) of the same covariates used in the density model specified above (Appendix S1: Table S2).

Because we rely on plot-level occupancy data rather than tagged individuals, we focus on how predictor variables drive changes for the recently established cohort as a whole at the plot level. Our conclusions thus apply to the flux in the presence or absence of this cohort through time, not recruitment beyond the seedling stage. We therefore do not attempt to make inferences about the mechanisms by which individual trees exit this size class (mortality or growth) but rather infer whether or not a plot is "stocked" by a species while also tracking stocking changes between sampling events. In this context, colonization refers to seedling establishment at a plot that was previously lacking seedlings, while persistence refers to continued seedling establishment or seedling survival and growth up to 30 cm in height.

Both models—seedling density and dynamic seedling occupancy—were fit in a Bayesian framework using JAGS, version 4.3.0 (Plummer 2017), to generate joint posterior distributions using Markov chain Monte Carlo (MCMC), which was called from R using the *jagsUI* package (Kellner, 2021; R Core Team, 2021). We used vague normal priors for estimating parameter means and vague gamma priors for variances (Appendix S2). We checked for convergence of MCMC chains using visual examination of traceplots and ensuring potential scale reduction factors (PSRFs) less than 1.1 (Brooks & Gelman, 1998). We evaluated goodness-of-fit using the *DHARMa* package in R (Hartig, 2020). In addition, we calculated r-squared values for each species-specific count and occupancy model (Appendix S2). Regression coefficients for which 90% credible intervals (computed using "highest posterior density," HPD) overlapped zero were considered to have no interpretable effect.

RESULTS

Post-treatment forest composition and structure

In the absence of treatment, Controls maintained the highest BA over the 20-year study period while also maintaining the highest relative BAs of black oak and all shade-tolerant conifers (Douglas-fir, incense-cedar, white fir) as compared to treated stands (Table 2). In contrast, total BA was 25% lower in Fire, 27% lower in Mech, and 43% lower in Mech + Fire after repeated treatment as compared to Controls. Within treatments, only Mech + Fire achieved a significant reduction in total BA between 2001 and 2020 ($t = 4.8$, $p < 0.0001$), while only Controls experienced an overall increase ($t = -3.2$, $p = 0.01$). Fire and Mech maintained relatively constant total BAs between 2001 and 2020 despite repeated treatment (Table 2). All three fuel treatments increased residual ponderosa pine BA, although the BA response was greatest in Mech + Fire. Shade-tolerant species BA (Douglas-fir, incense-cedar, white fir) declined in both Mech and Mech + Fire due to targeted removal of these species as well as sensitivity to fire treatments, with decreased black oak BA in Fire only (Table 2). Sugar pine BA increased under all treatments except Mech + Fire where some large sugar pines were lost during and after treatment; this species-specific mortality was previously attributed to heightened fire intensity in post-masticated fuels either killing trees directly or weakening trees and leading to subsequent bark beetle attack (Stark et al., 2013), and we found continued depressed sugar pine BA in the years following.

Over the 20-year window of repeated treatment and monitoring, species-specific seedling abundances varied over time and as a function of treatment type, although all species saw increased densities in 2006 (Figure 1; Appendix S1: Table S1). Densities of fire-intolerant seedlings (Douglas-fir, white fir, and incense-cedar) remained in highest abundance and generally saw greater posttreatment increases as compared to fire-tolerant ponderosa and sugar pines (Figure 1a–e). Black oak was generally the most abundant species in Mech and Controls. In Fire and Mech + Fire, black oak densities were generally lower than fire-intolerant species and higher than pines.

Declines in seedling densities were detected across most species and treatments immediately after the initial treatment entries in 2002 (Figure 1a–f). However, by 2006, many species rebounded to or exceeded pre-treatment densities. For example, Douglas-fir in Fire ($t = -12.79$, $p < 0.000$) and incense-cedar ($t = -11.16$, $p < 0.0001$) and ponderosa pine in Mech + Fire ($t = -10.44$, $p < 0.0001$) exceeded pre-treatment densities within 4 years. In 2016, prior to a round of treatments, seedling densities were higher in Fire and Mech + Fire for Douglas-fir, incense-cedar, and ponderosa pine as compared to 2001 pretreatment levels. By 2016, only Douglas-fir ($t = -3.49$, $p = 0.002$) and sugar pine ($t = -3.15$, $p = 0.009$) had higher seedling densities in Mech as compared to Control.

By 2020, seedling densities for most species and treatments were at or below pre-treatment levels (Figure 1), potentially attributable to the limited time since last treatment application—3 years since the most recent

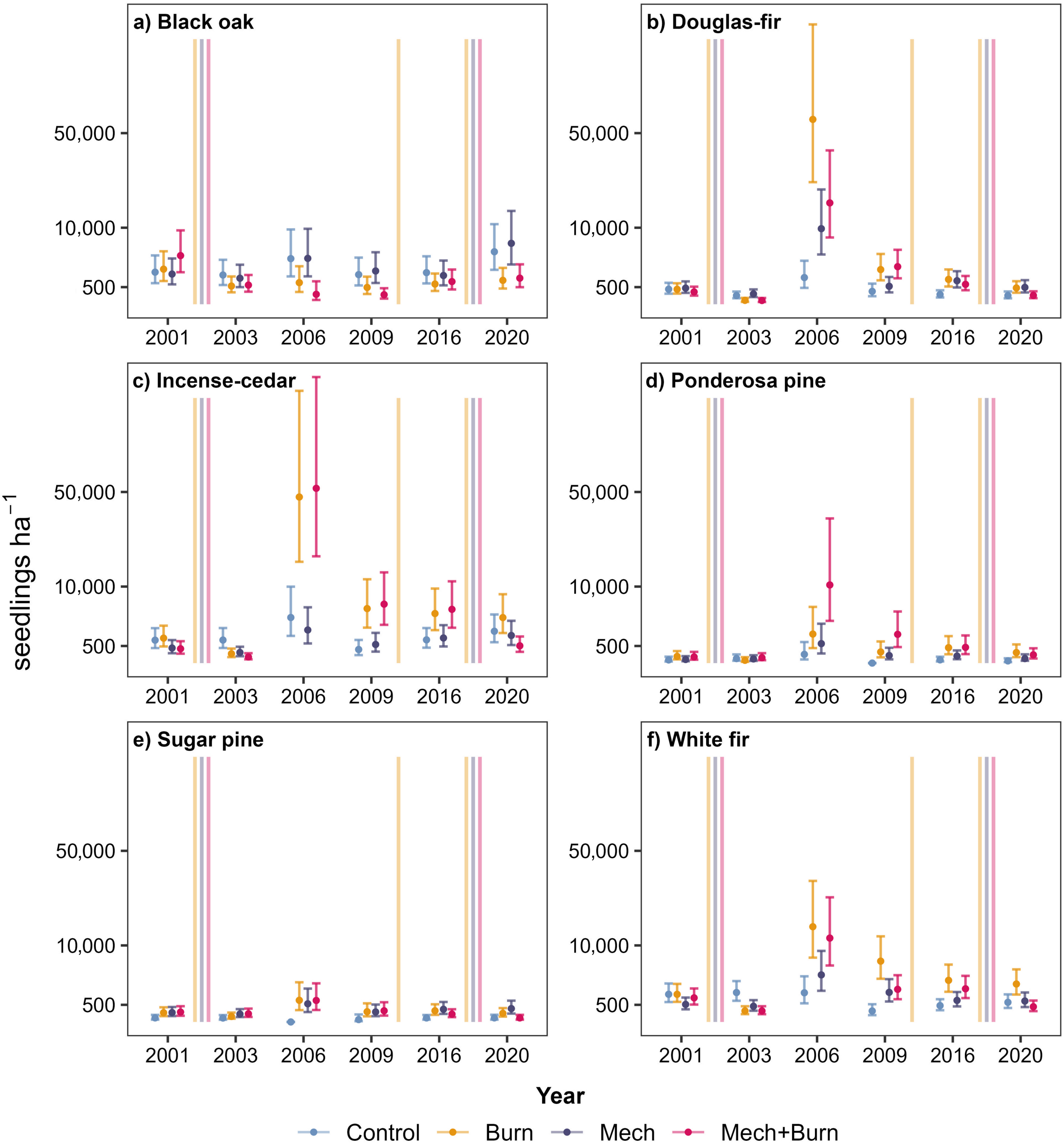

FIGURE 1 Estimated marginal mean seedling density and 95% confidence intervals for the four Fire and Fire Surrogate treatment groups. Vertical bars between years broadly indicate treatment timing relative to seedling measurements. Fire stands were treated three times: fall 2002, 2009, and 2017. Mech stands were masticated and thinned in 2001 and again in 2017–2019. Mech + Fire stands were thinned, masticated, and burned in 2001–2002 and masticated and burned in 2017–19. *Y*-axes are square-root-transformed. Appendix S1: Table S1 is a tabular presentation of this figure.

Fire, 1 year since the most recent Mech, and 2 years since the most recent Mech + Fire. Black oak was the only species with an increase in Controls between 2001 and 2020 ($t = -3.41$, $p = 0.009$), while only Douglas-fir showed a decline in Controls over this temporal window ($t = 2.93$, $p = 0.04$). The increase in black oak seedlings is consistent with the higher black oak BA in Controls at study initiation and over time.

Treatments also influenced light conditions over time (Table 3). Light availability (%TTR) did not change significantly between 2006 and 2020 in Control and Fire, while Mech ($t = -2.9$, $p = 0.02$) and Mech + Fire ($t = -5.9$, $p = <0.0001$) experienced 27% and 32% relative increases in light over this time, respectively. Mech + Fire also had the highest light availability (51.1%, range 33.3–81.8; Table 3) compared to other treatments in 2020, suggesting that Mech + Fire most effectively created and maintained light availability to the forest floor.

Density and occupancy models

Treatment

Conifer dynamics (i.e., expected densities plus colonization and persistence probabilities) were generally lower in Control and higher in Fire, relative to within-species global averages (Figure 2b–f). Treatments also produced species-specific responses that should be considered when determining appropriate fuel treatments to meet species objectives. Fire, specifically, led to increases in expected densities and both colonization and persistence probabilities for Douglas-fir and white fir (Figure 2b,f) and increases in expected densities and colonization probabilities for incense-cedar, ponderosa pine, and sugar pine (Figure 2c–e). Only black oak, our single hardwood, decreased in expected densities and both colonization and persistence probabilities with Fire (Figure 2a). Mech + Fire was also beneficial for regeneration dynamics of Douglas-fir and incense-cedar but most notably so for ponderosa pine (Figure 2b–d). Compared with all other species, ponderosa pine experienced the strongest increase in expected density and colonization probability in Mech + Fire against the species' global average (Figure 2d). Mech + Fire additionally decreased expected densities and persistence of white fir (Figure 2f), a common objective in fuel treatment application. Mech generally hindered conifer regeneration, with the exception of nominal increases in Douglas-fir and sugar pine (Figure 2b,e), but had a positive effect on expected black oak densities and occupancy probabilities (Figure 2a). Black oak was the only species with all three dynamics higher in the Controls. The strongest decrease in expected ponderosa pine seedling density and occupancy probability over time was attributed to Controls (Figures 3d and 4).

The influence of time since treatment was highly variable among species, although conifers were increasingly likely to persist at sites with increasing time since Mech + Fire, especially incense-cedar (Figures 2c and 3c). Across all six species, the probability of colonization increased with time since Fire, while expected densities increased for all conifers (Figure 3). Sugar pine and white fir had the strongest positive responses to time since Fire, although incense-cedar and ponderosa pine also increased in expected densities and occupancy probabilities. Douglas-fir colonization and persistence probabilities increased with time since Fire. Increasing time since Mech had a positive effect on black oak, incense-cedar, and sugar pine persistence (Figures 2a,c,e and 3a,c,e). Time since study initiation in Controls increased expected black oak densities and occupancy probabilities (Figures 2a and 3a) while also marginally increasing incense-cedar persistence (Figures 2c and 3c.). All other species declined in expected seedling densities over time in Controls.

Higher number of treatment applications favored black oak dynamics (density, colonization, and persistence) as well as conifer persistence, with the exception of ponderosa pine (Figure 2a,d). Expected densities and colonization probabilities decreased with increasing number of treatments for ponderosa pine. More treatment applications were also associated with lower expected densities for Douglas-fir, sugar pine, and white fir (Figure 2b,e,f).

Stand conditions

Overstory composition was consistent in its influence across the six regenerating tree species assessed here. Conspecific BA was positively influential for all species, indicating that a local seed source contributes to higher expected densities, higher likelihood of establishing new cohorts (colonization), and maintenance of young cohorts (persistence) (Figure 2a–f). The influence of conspecific BA was greatest for expected seedling densities, and the strength of this influence was consistent across all six species. Total BA, a surrogate for canopy cover and light competition, had a slight influence on seedling dynamics for three of the six species, with increasing total BA decreasing expected black oak, sugar pine, and white fir densities but no effect on any aspect of seedling dynamics for Douglas-fir, incense-cedar, or ponderosa pine. Seedling dynamics for ponderosa pine were not impacted by changes in total BA (Figure 2a–f).

Climate

Seasonal precipitation and growing season CWD strongly influenced seedling dynamics for all species (Figure 2a–f). Increasing cool season precipitation increased expected

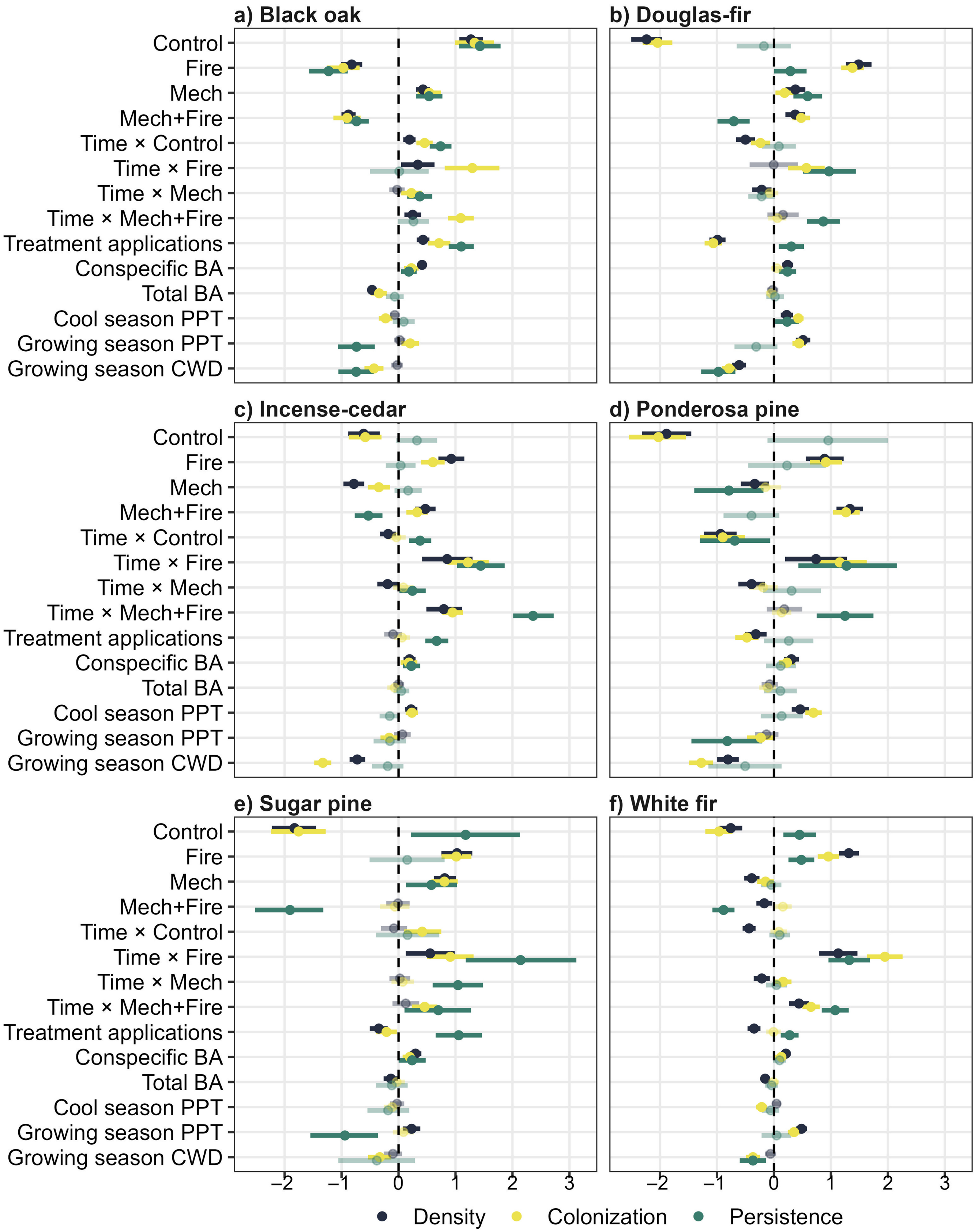

FIGURE 2 Modeled coefficients and 90% credible intervals for species-specific seedling density and occupancy models. Faded bars indicate that the 90% credible interval included zero. BA, basal area; CWD, climatic water deficit; PPT, precipitation; Cool season, November–March; Warm season, April–October.

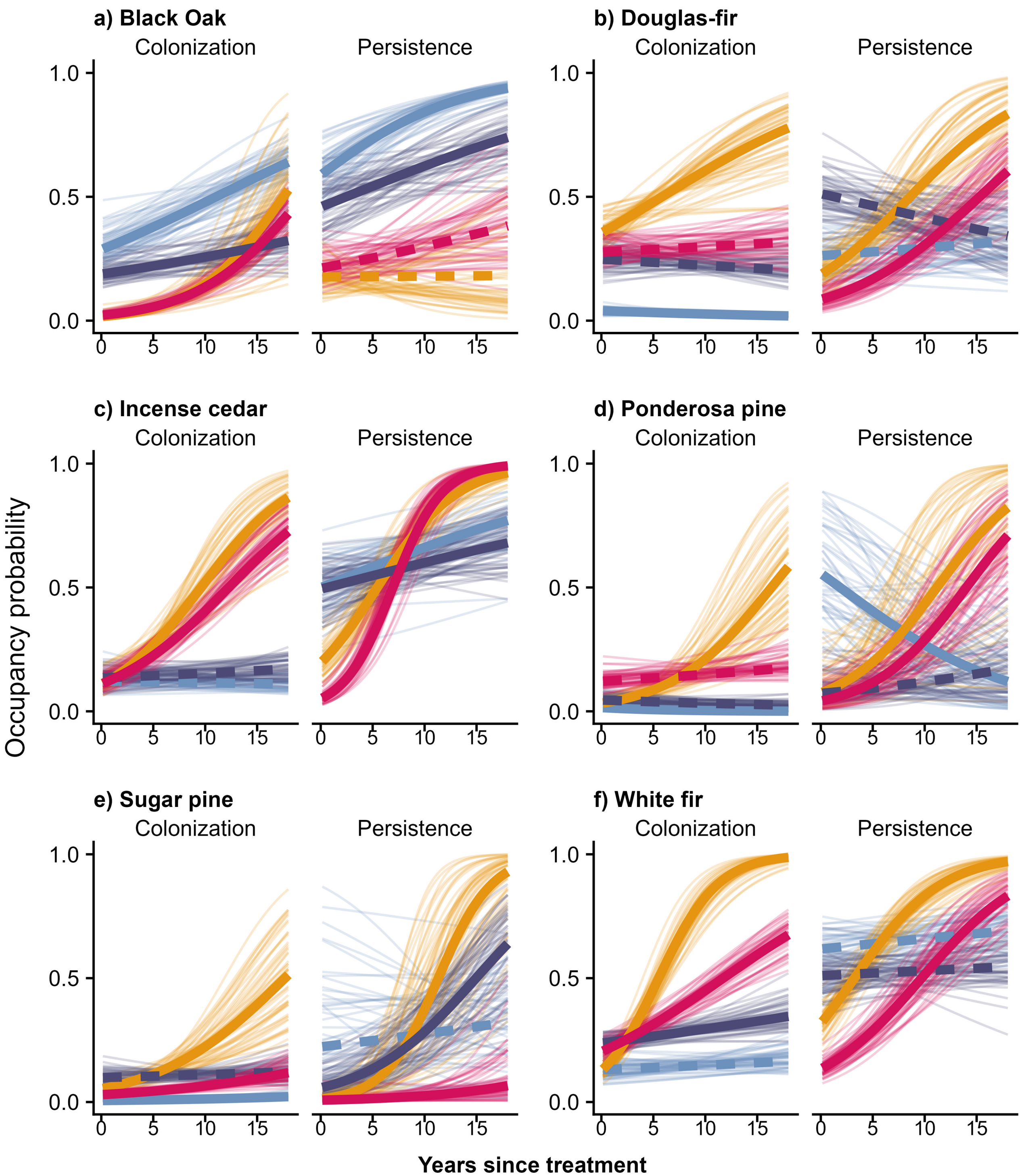

FIGURE 3 Probability of colonization and persistence as a function of years since treatment application when all other covariates are set to their means. Thin lines are random draws from the posterior distribution, thick lines show the posterior median, and thick hashed lines indicate that the 90% credible interval (CI) includes zero. For the Control, the "treatment" is considered to have taken place in 2001 when the study was established.

densities and colonization probabilities for Douglas-fir, incense-cedar, and ponderosa pine (Figures 2b–d and 4a). Douglas-fir persistence probabilities also increased with increasing cool season precipitation. Black oak and white fir colonization probabilities were, on the other hand, negatively impacted by increasing cool season precipitation (Figures 2a,f and 4a). Increasing growing season precipitation increased colonization rates for all

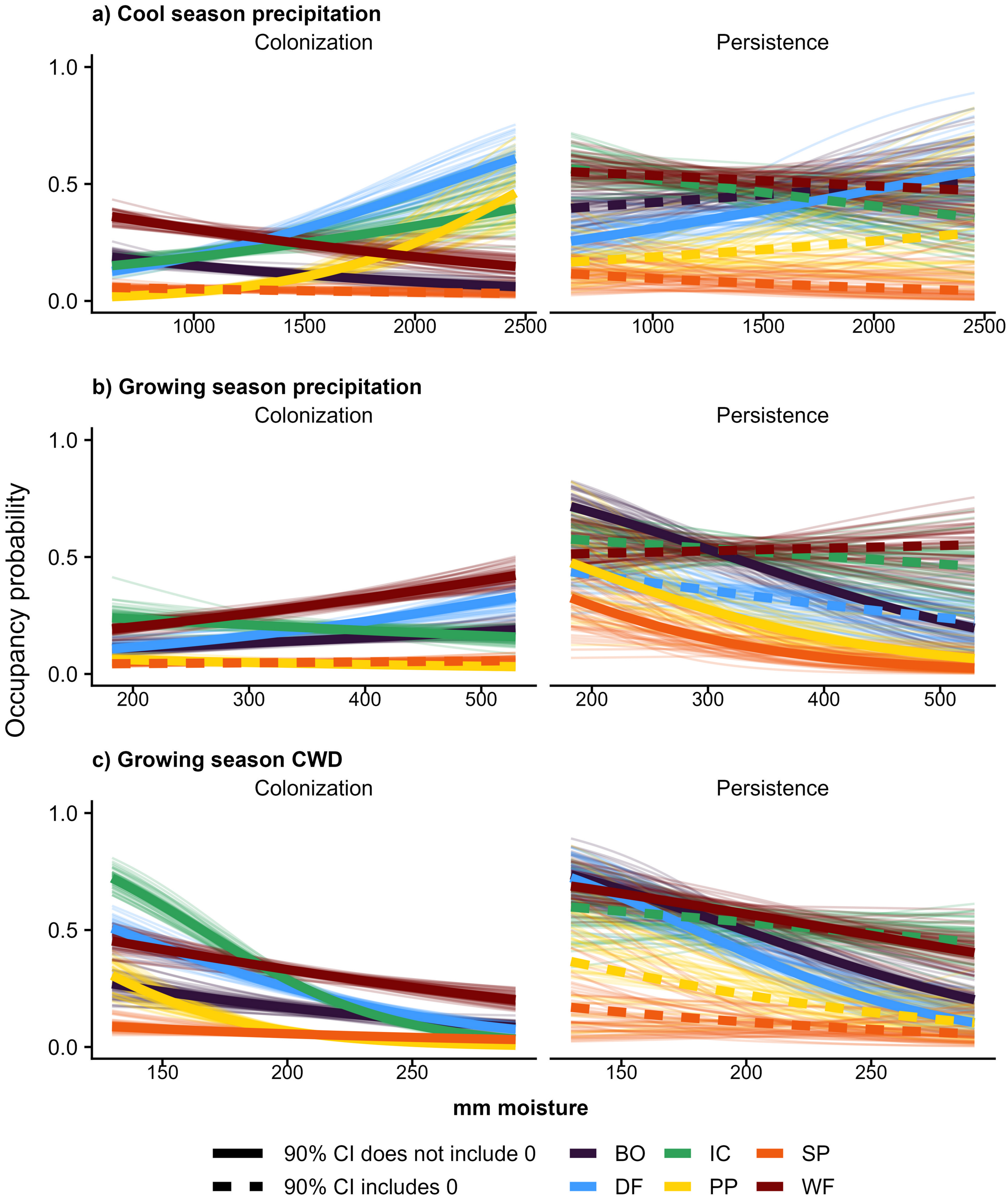

FIGURE 4 Probability of colonization and persistence as a function of (a) cool season (November–March) precipitation, (b) growing season (April–October) precipitation, and (c) growing season climatic water deficit (CWD). Thin lines are random draws from the posterior distribution, thick lines show the posterior median, and thick hashed lines indicate that the 90% credible interval (CI) includes zero. BO, black oak; DF, Douglas-fir; IC, incense-cedar; PP, Ponderosa pine; SP, sugar pine; WF, white fir.

but ponderosa pine and incense-cedar, which experienced decreasing colonization or neutral effects, respectively (Figure 2c,d; Figure 4b). Persistence probability was negatively impacted by increasing growing season precipitation for black oak, ponderosa pine, and sugar pine (Figures 2a,d,e and 4b). Only Douglas-fir, sugar pine, and white fir increased in expected densities with greater growing season precipitation (Figures 2b,e,f and 4b). Increasing CWD was generally negatively impactful, reducing colonization rates across all species and driving lower expected densities for Douglas-fir, incense-cedar, and ponderosa pine (Figures 2b–d and 4c), suggesting that moisture stress is a strong limiting factor in seedling establishment. Persistence probabilities were negatively impacted by increasing CWD for only black oak, Douglas-fire and fir, and white fir (Figures 2a,b,f and 4c).

DISCUSSION

Fire exclusion in the once frequent-fire, and thus fuel-limited, forests of western North America has shifted forests out of their historical fire-adapted condition. Fuel treatments have thus been widely applied to reduce fuels and mitigate fire severity, yet it has been unclear whether business-as-usual treatments go beyond wildfire mitigation to restore fire-adaptedness and better prepare forests for ongoing fire and climate stressors. Tracking 20 years of repeated fuel treatments in a SMC forest, we found that both treatment type and intensity can be influential in shifting forests toward more fire-adapted conditions and fire-tolerant species. Specifically, the conifer species tracked here increased in either colonization or persistence probabilities following the repeated application of fire, indicating that returning fire may be the most effective method of restoring regeneration conditions broadly across species. However, fire alone did less to favor fire-tolerant ponderosa pine or black oak, species targeted in restoration following declines over the last two centuries of fire exclusion. Pairing burning with concurrent mechanical treatments was more effective for promoting colonization and increasing densities of ponderosa pine, while black oak responded most favorably to mechanical treatments alone. Yet, importantly, even with repeated fuel treatment application, establishment of fire-intolerant species exceeded that of fire-tolerant oak or pine. Repeated fuel treatments did shift forests closer to fire-adapted structural and compositional conditions in the canopy but fell short of meeting long-term regeneration objectives. Moreover, higher growing season water stress negatively impacted seedlings of all species regardless of treatment type, an important consideration in ongoing management of temperate forests globally as climatic stress increases and further strains available resources. Restoration of fire-adapted conditions will require a commitment to recurrent, and likely more intense, fuel treatments that rebuild fire-adaptedness in fire-excluded forests by preparing stands both structurally and compositionally to survive and regenerate under current and future stressors.

Treatment effects

In the absence of regular fuel reduction via lightning ignitions and Indigenous burning, fuel treatments are critical for restoring fire-adaptedness in frequent-fire forests (Hessburg et al., 2016; Prichard et al., 2021). Leveraging a 20-year fuel treatment experiment, we uncovered the efficacy of various treatment types to meet a forest restoration objective as well as the importance of both fuel treatment type and intensity in shaping the regenerating community. Untreated stands maintained high levels of shade-tolerant, fire-intolerant species in both the overstory and regenerating communities, a finding consistent with other studies comparing responses among alternative fuel treatments (Hood et al., 2020; Huckaby et al., 2001; Zald et al., 2024). These findings provide another line of evidence that exclusion of fire (and fire surrogates) has fundamentally altered not only frequent-fire forest composition and structure (Collins et al., 2017; Keeling et al., 2006; Naficy et al., 2010; Taylor et al., 2014) but corresponding regeneration dynamics (Larson & Churchill, 2012; May et al., 2023; Rossman et al., 2020) across western North American forests (Hagmann et al., 2021; Haugo et al., 2019). The vast majority of western forest acreage remains in this untreated state where fire and fire surrogates are excluded and where conditions continue to hinder wildfire mitigation efforts and forest restoration objectives (Davis et al., 2024; Lydersen et al., 2019; North et al., 2021).

Regardless, fuel treatments, even at small spatial scales, have the potential to meet both of these key social and ecological needs. Much of our understanding to-date comes from first-entry fuel treatments, which are well-documented to mitigate fire hazard, particularly when thinning and burning are combined (Davis et al., 2024; Prichard et al., 2021). Generally, however, these first-entry treatments have done little to shift forest community composition toward fire-adaptedness (Levine et al., 2016; Moghaddas et al., 2008) and instead led to increases in shade-tolerant, fire-intolerant species establishment (Addington et al., 2018; Fialko et al., 2020; Tubbesing et al., 2019; Zald et al., 2008). This response can be attributed to the low-intensity of many business-as-usual fuel treatments in which treatments are focused on the understory and midstory but do little to increase light conditions favorable to establishment of shade-intolerant, fire-tolerant species (Moghaddas et al., 2008; Zald et al., 2008) even following repeated burning or thinning plus burning treatments (Zald et al., 2024).

Treatments, however, have the potential to modify both the light environment and seed source abundances by repeatedly targeting shade-tolerant, fire-intolerant species for removal from the overstory, as was a primary objective in the National FFS Study. Here, recurrent mechanical treatments increased light availability over time (from 22% to 30%) by reducing stem density and concentrating BA in large trees (Stephens, Hall, et al., 2023). Mechanical treatments followed by fire, as the most intensive fuel treatment, had the greatest effect on BA reduction and the light environment and, accordingly, created the most favorable conditions for ponderosa pine establishment, an effect that persisted over time. Yet, while repeated mechanical plus fire treatments increased available light to the forest floor (from 35% to 51%), light minimums for shade-intolerant ponderosa pine (~40%; York et al., 2012) were barely exceeded (to ~42%) 15 years after the initial treatments. These findings support other recent conclusions on repeat-entry treatments (May et al., 2023; Zald et al., 2024) and reveal that recurrent fuel treatments nudge the forest closer to desired fire-adapted conditions than single-entry treatments.

Outcomes are, however, still not analogous to those created by the historical fire regime in promoting fire-adapted conditions and, importantly, fire-tolerant species (Hutchinson et al., 2012) given that the regenerating community is still dominated by fire-intolerant species even under the most intense management strategy studied here. A defining characteristic of success in restoring fire-adaptedness is thus likely the creation of open, heterogeneous stands with fire-tolerant species dominating the canopy; creation of such post-treatment conditions will require pairing opening of the canopy through higher intensity treatments with simultaneous reduction in fire-intolerant seed source through targeted overstory removals. These criteria for success call for pushing the bounds of business-as-usual fuel treatments by marking and removing more canopy trees in order to mimic the effects of historical SMC mixed-severity fire in which many small and few large canopy gaps were created from periodic fire in the canopy (Lydersen et al., 2013). With this strategy, both operationally and ecologically based objectives will be met as a reduction in canopy continuity will support hazard reduction while concomitantly achieving long-term resilience via fire-adapted forest restoration.

Restoration of fire-adaptedness will undoubtedly be a daunting task given that the inertia driving contemporary forest composition set in after only a few decades of fire exclusion (Brodie et al., 2023). Our results are consistent with this lasting effect of fire exclusion in fire-adapted forests on early shifts in regenerating community composition from fire-tolerant to fire-intolerant species (Brodie et al., 2023; Nowacki & Abrams, 2008) as well as the recent discovery of forest hysteresis despite repeated treatments to restore conditions (May et al., 2023). Nevertheless, we also discovered that returning fire to these longstanding fire-free conditions had positive effects by pushing forests toward lower BAs, higher light conditions, and greater fire-tolerant species abundances in the regenerating community. Although incense-cedar remained the clear winner despite repeated treatment, fire return was beneficial for seedling dynamics across all species. This effect is likely a product of species' adaptations to regenerating under historical postfire high light conditions in disturbed substrate that was free of deep litter (Adili et al., 2013; Brockway & Outcalt, 1998; Owen et al., 2020). Fire was the primary driving force behind these historical establishment conditions that favored shade-intolerant, disturbance-dependent pine (Owen et al., 2020) and oak (Stephens, Hall, et al., 2023) in SMC forests and in other oak-pine forests globally (Gracia et al., 2002; Moreno et al., 2021). Specifically, these species benefit from enhanced light and reduced competition via canopy gaps that would have been periodically created and maintained with an intact fire regime but that are typically not found in conventional fuel treatments (Larson & Churchill, 2012; Pawlikowski et al., 2019). While fire did boost establishment of ponderosa pine in our study, it remained far less abundant in the regenerating community than fire-intolerant species, a finding consistent in other historically fire-dependent forests treated with repeated prescribed fire (Hutchinson et al., 2012; May et al., 2023; Zald et al., 2024). Fire is the key process that shapes composition and structure of these and other western fire-adapted forests (Sugihara et al., 2006), and restoring fire-adaptedness will ultimately require return of fire (Davis et al., 2024; Safford et al., 2021).

Although fire is critical to creating favorable conditions for seedling establishment, our study also reaffirms the need to apply both fire and fire surrogates to overcome the inertia of current forest conditions and create low canopy density conditions for fire-tolerant species (Becker & Lutz, 2016; York et al., 2022) while mitigating fire hazard (Davis et al., 2024). Shifting forest composition in favor of fire-tolerant species will require increasing light availability as well as reducing the seed source of shade-tolerant species that have disproportionately recruited into the overstory (May et al., 2023; North et al., 2007). An intensive approach to further reducing fire-intolerant composition in the canopy is necessary in order to shift the balance of seed supply in favor of fire-tolerant species. Widespread adoption of repeated prescribed fire paired with preparatory mechanical treatments will likely be necessary to achieve significant shifts in forest structure and promote establishment of fire-tolerant species (Battaglia et al., 2008; Kolden, 2019; York et al., 2022). Combining mechanical treatments with fire positively influenced densities and colonization probabilities of ponderosa pine, outperforming the influence of fire alone, and this outcome is consistent with this species' well-documented preference for establishing in historically open post-fire light and substrate conditions (Korb et al., 2019; Malone et al., 2018; Mast et al., 1999; Shepperd & Battaglia, 2002). An additional case for the continued use of mechanical treatments and other fire surrogates is the response it had on fire-tolerant black oak. Counter to expectations for a primarily fire-initiated sprouting species, black oak regeneration responded more favorably to root collar damage via mechanical treatments (McDonald, 1969) than to fire alone. Very little is documented on black oak response to fuel treatments, and this response suggests more research is needed to understand how best to manage and promote this ecologically and culturally important species. Our findings show that black oak dynamics, more consistently than other species, increased with more treatment applications overall, underscoring the importance of repeated treatments in promoting this high-value species.

Finally, this study provides evidence suggesting the repeated fuel treatments of the last few decades are simply waypoints in pushing forests from their long-standing fire-excluded state toward desired fire-adapted conditions. The product of past mismanagement—prolonged exclusion of fire starting with prohibition of Indigenous burning in the mid- to late-1800s (Taylor et al., 2016) followed by active fire suppression beginning in the early 1900s (Show & Kotok, 1923) and early logging that targeted the large pines (Laudenslayer & Darr, 1990)—is that of strong ecological momentum (i.e., hysteresis, May et al., 2023) favoring shade-tolerant, fire-intolerant species. Widespread logging of the largest pines reduced the future seed source, while fire exclusion and suppression allowed for forest densification and abundant establishment and recruitment of shade-tolerant species—a massive pendulum swing away from fire-adapted structure and composition. Treatments studied here have arguably begun to shift momentum back toward fire-adapted structure given that all fuel treatments reduced BA and influenced regeneration dynamics toward more fire-adapted conditions. However, increasing management intensity by targeting the removal of fire-intolerant species will be critical to further reducing canopy continuity and increasing available light for regeneration of fire-tolerant species. One notable limitation of this conclusion is the abbreviated temporal window between treatment and our final sampling effort (1–3 years), which may not have provided sufficient time for detecting treatment-induced regeneration responses. These findings are, regardless, consistent with conclusions drawn elsewhere in managed SMC forests that also revealed prescriptions are not yet restoring fire-adapted conditions (May et al., 2023; Zald et al., 2024).

Despite repeated fuel treatments nudging forests closer to fire-adapted conditions, many western forest types remain outside of their natural range of structural and compositional conditions (Haugo et al., 2015; Stephens et al., 2018). Precise numeric estimates for the historical relative proportion of fire-tolerant to fire-intolerant regeneration do not exist, but observations from early in the fire exclusion era describe an abrupt reduction in pine and increase in fir (Greeley, 1907; Show & Kotok, 1923). Stand descriptions from this era point toward frequent fire as the primary determinant of seedling composition that prevented fir regeneration from outpacing pine (Leiberg, 1902; Sudworth, 1900). The path forward is likely a treatment regime that mimics historical fire return intervals (MFRI ~11–18 years; van de Water & Safford, 2011) once fuels are reduced after initial entries, thereby moving stand structure and composition between waypoints over time toward this more fire-adapted target condition (Jeronimo et al., 2019; North et al., 2021).

Stochastic effects—Climate variability and seed availability

Although restoration of fire-adapted conditions is critical to creating favorable establishment conditions, treatments must also synchronize with the key stochastic factors beyond a manager's control—favorable climate plus seed availability and dispersal (Brown & Wu, 2005; Peters et al., 2005). In particular, both the seasonality of precipitation and the period of drought stress strongly influence conifer establishment potential under even the most favorable stand conditions (Puhlick et al., 2012; Stewart et al., 2021), and the species assessed here all declined in colonization and persistence probabilities under increasing moisture stress. Growing season precipitation did little to mitigate this stressor, which may be attributable to species' adaptations to conserve growth under historically dry Mediterranean summers (Warwell & Shaw, 2019). This may be unique to SMC forests, as growing season moisture has been observed as an important driver of seedling establishment in systems where rainfall is more common in summer months (Davis et al., 2019; Rother & Veblen, 2017). In this forest type, cool season precipitation was instead a driver of seedling densities and colonization probabilities for some species, mapping back to the historical temporal window of precipitation (Williams et al., 2021). Periods of abundant cool season precipitation have been linked to establishment pulses for many species, particularly ponderosa pine (League & Veblen, 2006; Puhlick et al., 2012), and our findings indicate that winter precipitation may mask intense growing season moisture stress for some species. Post-treatment climate will remain stochastic, but foresters can and should manage stand structure and composition to create the requisite light conditions so that species can capitalize on favorable periods of co-occurring soil moisture.

Management of stand structure and composition will also prime stands for alignment with the other stochastic factor critical to establishment—seed availability and dispersal. Annual and interannual variations in seed production act as the primary constraint on seedling establishment, and masting species may be further constrained in establishment until climate and seed development align in subsequent years (Redmond et al., 2017; Vander Wall, 2002). Differences in seed production vary among our study species and most certainly among years within species. For example, ponderosa pine and white fir may each produce large cone crops as often as every 2 years (McDonald, 1992), but the relative difference in seed production favors white fir by as much as a factor of two (Franklin et al., 1974; Oliver & Ryker, 1990). Bumper crops in ponderosa pine have been attributed to both warm and wet spring months during the first year of cone development (Krannitz & Duralia, 2004; Mooney et al., 2011); however, cone and seed production tracking over California's 2012–2016 drought revealed that even periods of severe climatic stress do not negatively impact seed production patterns of SMC tree species (Wright et al., 2021). And, here, conspecific BA was a driver of regeneration success across all six species studied. Ideally, foresters would implement treatments during periods of high seed production so that the ensuing seed rain finds suitable seedbed and light conditions. The extended timeline of cone production for pine species in particular makes this technically feasible in small-scale forestry operations, but this practice is likely impractical at scale. Treatments are instead the pathway to creating the light and substrate conditions suitable for seedling establishment when climate and seed production align to produce abundant cone crops.

Although seed production and favorable climate windows may be the first filters on forest composition, the unpredictable and extreme effects of ongoing climate change will further shape demography of establishing cohorts. For instance, the composition of fire-tolerant species may be bolstered during warming and drying events, as these species generally have higher drought and heat tolerances than their fire-intolerant associates (Becker & Lutz, 2023; Hankin et al., 2019). Conversely, systems may be poised to continue re-seeding to fire-intolerant species, as has been documented in both fire-suppressed and postfire environments in the SMC forest type (Tubbesing et al., 2020). Moreover, although ponderosa pine is physiologically adapted to drought (Stone & Jenkinson, 1970; Wambolt, 1973), its establishment trends are still vulnerable to predicted increases in temperature and changes in seasonal moisture (Kolb & Robberecht, 1996). Growing season moisture stress, which we found to negatively impact dynamics for all species, is predicted to increase in the future (IPCC, 2023), further restricting windows for natural regeneration. Planting may ultimately be the best option for establishing a new cohort and would allow managers to more directly steer species composition by planting higher proportions of fire-tolerant species than what is represented in the overstory.

Management implications

If a primary objective of fuel treatment is to restore forests to the fire-adapted conditions historically maintained by Indigenous and natural ignitions, the treatments studied here, despite making some progress, have fallen short of meeting a forest restoration objective. Progress toward this objective is quantifiable in the increased abundance and colonization rates of fire-tolerant species after multiple treatments, yet shortcomings lie in the fact that fire-intolerant species still dominate both the canopy and the regenerating community. Indeed, repeated fuel treatments in this and other SMC forests have not gone far enough to disrupt the status quo, and consequently, shade-tolerant, fire-intolerant species remain dominant even after repeated, targeted removal over many decades. Most notably, although incorporating fire into silvicultural systems (i.e., pyrosilviculture, North et al., 2021; York et al., 2021) is a priority in forest restoration, prescribed fire alone has not yet achieved robust structural changes in the SMC (May et al., 2023; Zald et al., 2024) and or other fire-dependent temperate forests across North America (Crotteau & Keyes, 2020; Hutchinson et al., 2012).

Fuel treatments maintain exceptionally low levels of surface fuel loads and ladder fuel densities and will remain a critical component of wildfire mitigation and forests restoration, but adding a gap-based silvicultural system would bring frequent-fire forests more in alignment with natural disturbance models and promote regeneration of fire-tolerant species (Hart et al., 2024; Jack et al., 2024; Larson & Churchill, 2024). Combining prescribed fire with mechanical treatments that reduce mature tree density and create distinct canopy gaps may be necessary to shift canopy BA, and thus both potential seed supply and light availability, in favor of shade-intolerant, fire-tolerant species. In SMC forests specifically, future waypoint treatments should include larger openings (from 0.1 to 1.0 ha; York, 2024) and an ongoing focus on targeted removal of fire-intolerant species. Targeting fire-intolerant species for removal will serve the two-fold purpose of reducing seed supply of these species while concurrently improving light conditions for fire-tolerant species. Managers aiming to restore fire-adapted forests are advised to combine a group-selection harvest and paired fire surrogate treatment with a follow-up prescribed fire to meet these targeted fire-adaptedness restoration objectives and return the natural disturbance regime to the landscape. This is not only the pathway toward restoring forest resilience but can also provide the necessary foundation upon which prescribed fire may be regularly applied to manage fuels and maintain fire-adaptedness in perpetuity.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code (Nagelson et al., 2024) are available in Dryad at https://doi.org/10.5061/dryad.jsxksn0jd.

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SUPPORTING INFORMATION

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

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