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Thinning and prescribed burning increase shade-tolerant conifer regeneration in a fire excluded mixed-conifer forest

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ABSTRACT

Fire exclusion and past management have altered the composition, structure, and function of frequent-fire forests throughout western North America. In mixed-conifer forests of the California Sierra Nevada, fire exclusion has exacerbated the effects of drought and endemic bark beetles, resulting in extensive mortality of fire-adapted pine species. Thinning and prescribed fire are widely used in these forests to reduce fuels, moderate fire behavior, and restore ecosystems. Tree regeneration influences future forest composition and structure, and therefore future resilience to disturbances, but long-term effects of thinning and prescribed burning on tree regeneration after prolonged fire exclusion are poorly understood. We measured tree regeneration one year prior to, and periodically for 16 years following thinning and prescribed burning in a mixed-conifer forest in the Sierra Nevada, California, USA. We asked three questions. How did the composition and density of tree regeneration change after thinning and prescribed burning? Did pretreatment vegetation types influence conifer regeneration density after treatments? Did planting after overstory thinning increase regeneration density of native pine species?

Sixteen years after treatments, combined natural regeneration of shade-tolerant white fir (*Abies concolor*) and incense-cedar (*Calocedrus decurrens*) averaged 2,032 trees per hectare (tph) after understory thinning, and 7,745 tph after understory thinning combined with prescribed burning, increases of 37 % and 146 % from pretreatment densities. In contrast, combined natural regeneration of white fir and incense-cedar averaged 497 tph after overstory thinning, 780 tph after overstory thinning with prescribed burning, 113 tph after prescribed burning alone, and 807 tph in untreated controls, all of which were declines from pretreatment densities. Natural regeneration of white fir and incense-cedar was consistently an order of magnitude greater than Jeffrey pine (*Pinus jeffreyi*) and sugar pine (*Pinus lambertiana*), whose combined densities 16 years after treatments averaged 37 tph across treatments and did not significantly respond to thinning and/or prescribed burning. Natural conifer regeneration after treatments varied by pre-treatment vegetation type (closed canopy, *Ceanothus cordulatus* shrub dominated, and open sparse), with large increases of natural regeneration after understory thinning in closed canopy and *Ceanothus* shrub vegetation types. Planting increased sugar pine regeneration density after overstory thinning, marginally increased Jeffrey pine regeneration after overstory thinning combined with prescribed burning, and increased white fir regeneration after overstory thinning with and without burning. No treatments reduced white fir and incense-cedar natural regeneration while simultaneously increasing natural pine regeneration, suggesting new thinning, burning, and planting approaches may be required to meet regeneration restoration objectives.

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Table 1
Mean density (trees per hectare) of natural regeneration by species, treatment combination and measurement year.

Species	Treatment	2000	2002	2005	2011	2017
White fir	UN	1268	1311	1078	861	702
White fir	UU	1249	240	904	659	291
White fir	UO	376	66	93	101	70
White fir	BN	1191	714	2676	760	1055
White fir	BU	1974	737	2688	2079	1664
White fir	BO	1117	19	322	337	318
Incense-cedar	UN	132	128	159	109	105
Incense-cedar	UU	237	66	2366	2571	1741
Incense-cedar	UO	310	140	303	376	427
Incense-cedar	BN	714	272	512	388	396
Incense-cedar	BU	1175	469	6450	6981	6081
Incense-cedar	BO	842	39	233	322	462
Jeffrey pine	UN	16	16	12	8	4
Jeffrey pine	UU	0	0	4	16	19
Jeffrey pine	UO	16	0	35	43	50
Jeffrey pine	BN	8	0	8	16	31
Jeffrey pine	BU	4	0	58	43	27
Jeffrey pine	BO	16	0	43	70	74
Sugar pine	UN	124	132	159	113	78
Sugar pine	UU	66	19	62	85	58
Sugar pine	UO	58	19	27	89	97
Sugar pine	BN	47	50	89	93	81
Sugar pine	BU	19	0	31	47	27
Sugar pine	BO	12	0	16	43	23

Treatment combinations are UN = unburned no thin control, UU = unburned understory thin, UO = unburned overstory thin, BN = burned no thin, BU = burned understory thin, BO = burned overstory thin. Note: density values in this table are treatment level arithmetic means, and different from model estimated marginal means presented in results sections 3.2 and 3.4.

1. Introduction

Across western North America, pine and mixed-conifer forests historically had frequent low- to mixed-severity fire regimes (Brown et al., 2008; Fulé et al., 2003; Heyerdahl et al., 2011; Merschel et al., 2018; North et al., 2007; Veblen et al., 2000). Loss of indigenous burning and fuel harvesting, preferential harvesting of large fire resilient pine species, and broad fire exclusion policies have altered forest ecosystem composition and structure (Hagmann et al., 2021; Knight et al., 2022; Markwith and Paudel, 2021). Historically, the yellow pine (*Pinus ponderosa* Lawson & C. Lawson and *Pinus jeffreyi* Balf.) and mixed-conifer forests of the California Sierra Nevada had fire return intervals of 7–12 years (Van de Water and Safford, 2011), but aggressive fire exclusion and the logging of large old trees have led to increased canopy cover, stand densities, and spatial continuity of forest fuels (Knapp et al., 2013; Lydersen and Collins, 2018; North et al., 2012, 2007; Parsons and DeBenedetti, 1979; Stephens et al., 2015). These changes in forest composition and structure have increased susceptibility to drought and endemic bark beetles (Fettig et al., 2019; Robbins et al., 2022; Voelker et al., 2019; Young et al., 2017), reallocated and destabilized carbon stocks (Earles et al., 2014; Goodwin et al., 2020; Hurteau et al., 2019), created fuel conditions more conducive to extreme fire behavior (Goodwin et al., 2021; Stephens et al., 2022; Stephens et al., 2018), and increased overall fire severity and the size of high-severity patches (Miller et al., 2009; Steel et al., 2015; Stevens et al., 2017).

In response, federal and state policies have focused on reducing wildfire risk to communities, restoring ecosystem properties, and increasing forest resilience to biotic and climate stressors (California Forest Management Task Force, 2021; USDA Forest Service, 2022a). Individually and in combination, thinning and prescribed fire are widely used to reduce fuels, modify fire behavior, and restore ecosystems (Agee and Skinner, 2005; Fernandes and Botelho, 2003; Kalies and Yocom Kent, 2016; Reinhardt et al., 2008). Many studies in the Sierra Nevada have shown thinning and prescribed burning can restore some elements of forest structure (Knapp et al., 2017; North et al., 2007), reduce fuels and moderate fire behavior (Low et al., 2021; Safford et al., 2012b; Stephens et al., 2012), increase tree growth and reduce tree mortality (Bernal et al., 2023; Knapp et al., 2021; Steel et al., 2021; Vernon et al., 2018; Wenderott et al., 2022; Zald et al., 2022), and stabilize forest carbon (Goodwin et al., 2020; Hurteau and North, 2009). However thinning and prescribed burning in these forests can have more complex effects on regeneration (May et al., 2023; Zald et al., 2008), understory vegetation (Goodwin et al., 2018; Odland et al., 2021; Wayman and North, 2007), soils (Ma et al., 2004; Ryu et al., 2009), and wildlife (Meyer et al., 2007a). In frequent fire forests, ecological restoration and fuel reduction can have potentially convergent or divergent objectives (Stephens et al., 2021), with restoration often focused on individual species and/or spatial variability of forest structure (Addington et al., 2018; May et al., 2023; North et al., 2012), and fuel reduction focused on the reduction of potential fire behavior by altering the amount and spatial arrangement of fuels (Agee and Skinner, 2005). With increased frequency and severity of disturbances associated with a changing climate, restoration and fuel reduction objectives may alternatively converge to promote operational resilience, focusing on large reductions in tree densities to create stands with desired tree species and those trees largely free of competition (North et al., 2022).

In assessing restoration and fuel reduction treatment efficacy in Sierra mixed conifer forests, there is a scarcity of mid- to long-term (greater than 5 years to over a decade) studies of forest regeneration responses to thinning and prescribed burning. Tree regeneration is a critical life history stage where establishment, survival, and growth are highly sensitive to disturbance, seed dispersal and fecundity, environmental conditions, and resource availability (Clark et al., 1998; Grubb, 1977). In combination with growth and mortality, tree reproductive capacity is a key demographic process controlling forest composition, structure and change (Bell et al., 2014; Brown and Wu, 2005; Liang et al., 2017; Vilà-Cabrera et al., 2011). Regeneration dynamics during the reorganization phase after disturbance can be a critical short time window shaping long-term successional pathways (Seidl and Turner, 2022), and short-term regeneration responses after fuel reduction and restoration treatments can be used to assess initial treatment effectiveness and make inferences about long-term (multi-decadal) forest dynamics (Hurteau et al., 2014; Zald et al., 2008). However, initial post-disturbance regeneration may not be indicative of longer-term regeneration trajectories (Gill et al., 2017), due to factors such as distances to seed sources, water stress, topography, and temporal variability of seed production (Peters et al., 2005; Stevens-Rumann and Morgan, 2019). Furthermore, wildfires and climate change are anticipated to negatively impact tree regeneration success in many forests of western North America (Davis et al., 2019; Stevens-Rumann et al., 2022), yet management activities that reduce fire severity may partially offset climate-driven declines in tree regeneration (Davis et al., 2023a), highlighting the need for empirical information about mid- to long-term regeneration responses to restoration and fuel reduction treatments to reduce uncertainty and inform management and policy.

Frequent-fire forests display consistent spatial patterns often characterized by patches of tree clumps, gaps, and lower density larger trees (Abella and Denton, 2009; Fry et al., 2014; Larson and Churchill, 2012; Lydersen et al., 2013). Compared to historical conditions, the contemporary size distribution of these vegetation patches in Sierra Nevada mixed-conifer forests is characterized by fewer small gaps (less than 0.1 ha in size), a lower proportion of individual open grown trees, and larger clumps of more trees (Lydersen et al., 2013). Different vegetation patch types within treatments can influence short-term regeneration responses to thinning and burning (Zald et al., 2008), and spatial heterogeneity of vegetation can promote resilience to wildfire (Koontz et al., 2020), but fire exclusion and traditional silvicultural practices have reduced heterogeneity in many Sierra mixed-conifer forests (Fry et al., 2014; Lydersen et al., 2013; Lydersen and Collins, 2018). Understanding how regeneration varies by vegetation patches within thinning and burning treatments is important to determining how long-term heterogeneity

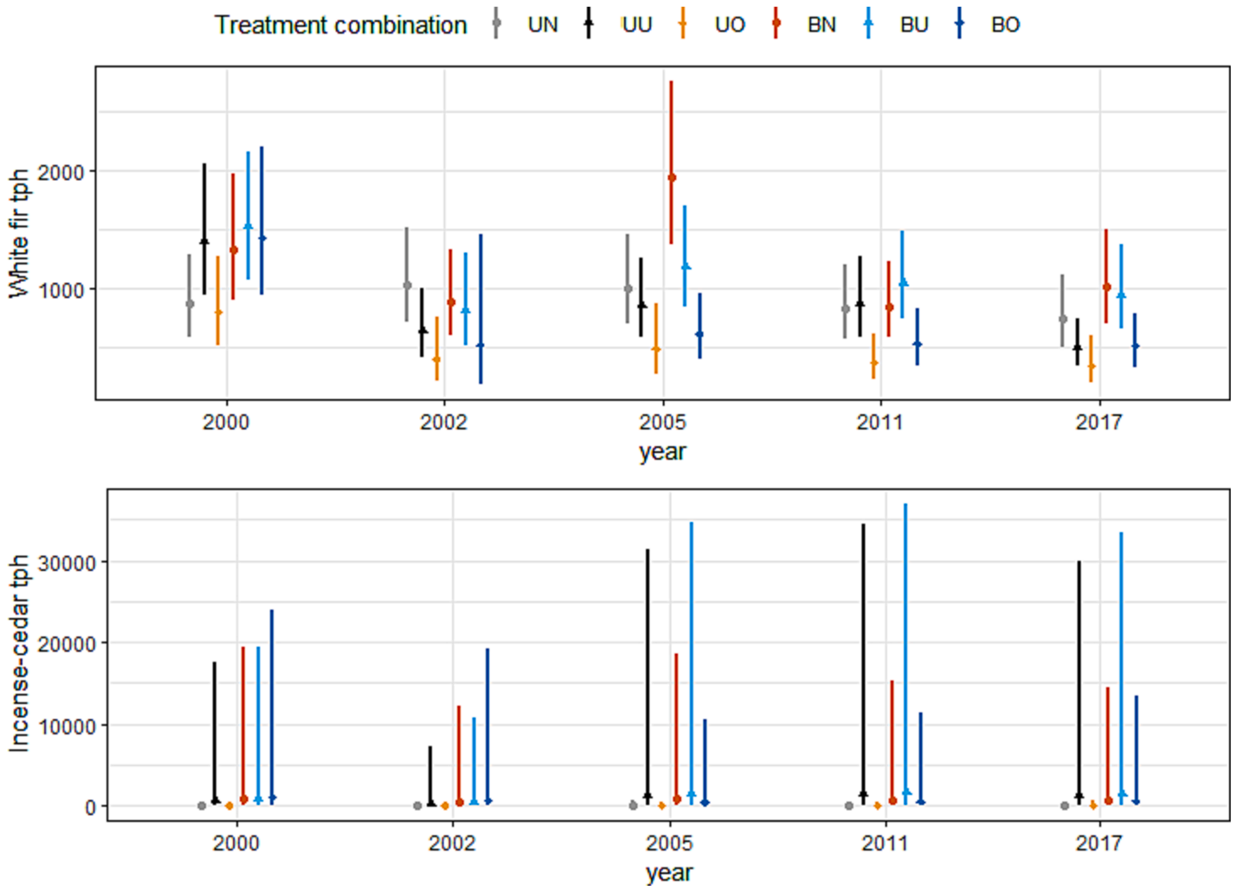

Fig. 1. Estimated marginal means of natural regeneration density (trees per hectare, tph) by year and treatment combination for white fir (*Abies concolor*) and incense-cedar (*Calocedrus decurrens*). Vertical lines are 95 % confidence intervals. Treatment combinations are UN = unburned no thin control, UU = unburned understory thin, UO = unburned overstory thin, BN = burned no thin, BU = burned understory thin, BO = burned overstory thin.

may change in forests after fuel reduction and restoration activities.

Tree planting was and continues to be a common practice in western U.S. forests after whole stand harvest or high severity wildfire, as well as in non-stocked areas believed capable of supporting forests. Standard reforestation practices have focused on high planting density, regular spacing, site preparation, and management of competing vegetation to achieve full site occupancy of fast growing conifers that outcompete shrub vegetation (Schubert and Adams, 1971). Planting has been suggested to restore declining pine species in Sierra Nevada mixed-conifer forests (May et al., 2023; Zald et al., 2008), and has been used to restore declining tree species in other forest types characterized by frequent fire (Barnett, 1999). However, dense regularly spaced planting can result in spatially homogenous forests vulnerable to high severity wildfire (Donato et al., 2006; Zald and Dunn, 2018), highlighting how current post-disturbance reforestation practices may fail to enhance resilience to fire and climate stress (North et al., 2019). With a focus on planting after high severity wildfire, less attention has been given to how planting after fuel reduction and restoration treatments influences the composition and abundance of forest regeneration.

Our study addresses these knowledge gaps by examining long-term (16 year) regeneration dynamics in a factorial experiment of first entry prescribed burning and thinning treatments in a mixed-conifer forest of the Sierra Nevada, USA. We build on previous work which examined pretreatment and short-term (1–3 year) post-treatment natural regeneration, microsite conditions, vegetation patch types, and seed quantity (Gray et al., 2005; Zald et al., 2008). These prior studies found pretreatment regeneration was dominated by shade-tolerant white fir (*Abies concolor* (Gord. & Glend.) Lindl. Ex Hildebr.) and incense-cedar (*Calocedrus decurrens* (Torr.) Florin). The combination of thinning and prescribed fire resulted in initial microsite conditions favorable to germination of Jeffrey pine and sugar pine (*Pinus lambertiana* Douglas). Yet three years after treatments, regeneration of pine species remained low. Seed rain for white fir and incense-cedar was 5–26 times greater than pine species, creating ecological inertia in shifting regeneration towards pine species even when treatments created favorable microsite conditions. Understory thinning and prescribed burning resulted in large increases in regeneration of shade-tolerant species. In this study, we extend analyses of regeneration to 16-years after thinning and burning to ask three questions. First, how did tree regeneration composition and density change after thinning and prescribed burning? Second, did pretreatment vegetation patch types influence conifer regeneration density after treatments? And third, did planting after overstory thinning increase regeneration density of pine species? Within the context of forest regeneration, restoration and fuel reduction goals included: reductions in the abundance of shade tolerant fir and incense-cedar regeneration, sufficient regeneration to maintain pine species, and maintenance or enhancement of vegetation spatial heterogeneity. For the three questions above we hypothesized that:

H1.1. Natural white fir and incense-cedar regeneration density would decline over time since treatment, but continue to dominate total regeneration.
H1.2. Natural white fir and incense-cedar regeneration density would continue to be highest in untreated controls and lower intensity treatments (i.e. treatments with less basal area removed by thinning and/or killed by prescribed burning).
H1.3. Natural pine regeneration would gradually increase in higher intensity treatments.

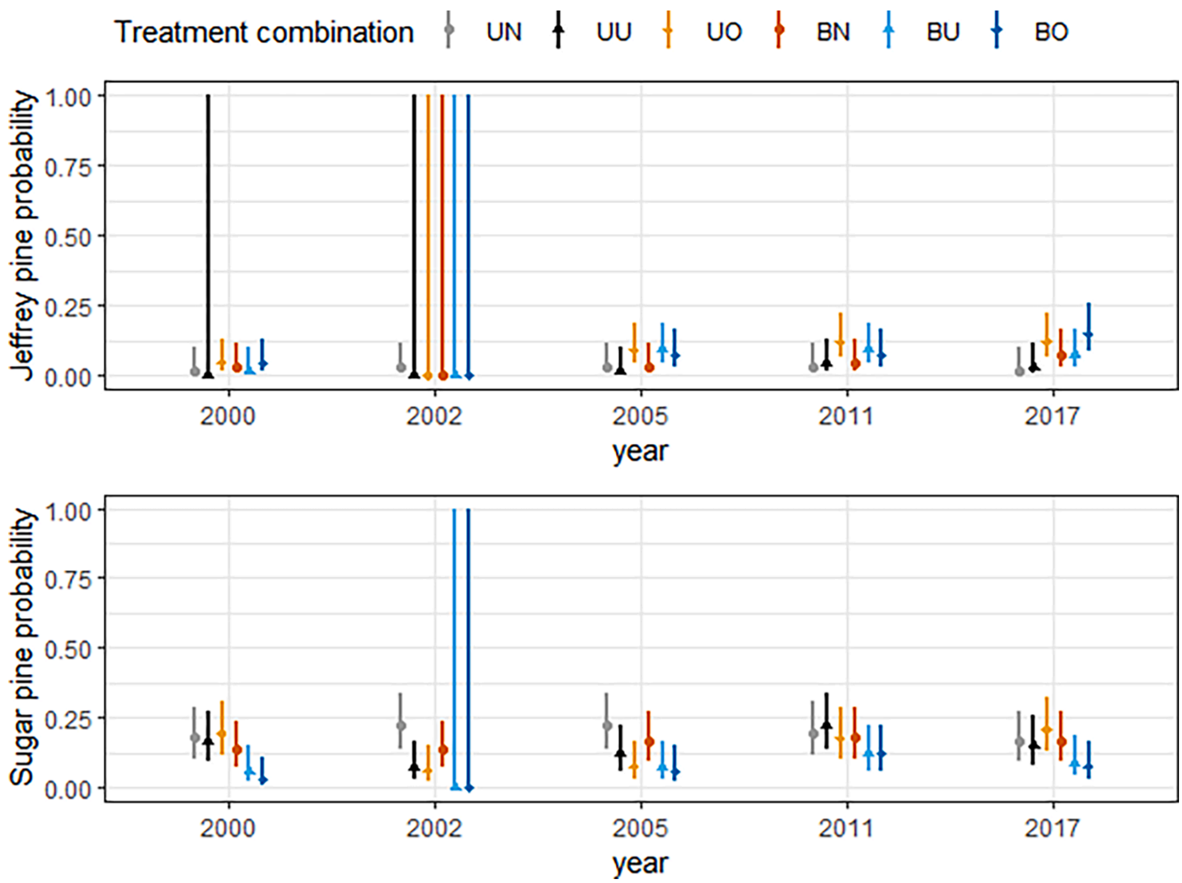

Fig. 2. Estimated marginal mean of the probability natural regeneration presence by year and treatment combination for Jeffrey pine (*Pinus jeffreyi*) and sugar pine (*Pinus lambertiana*). Vertical lines are 95 % confidence intervals. Treatment combinations are UN = unburned no thin control, UU = unburned understory thin, UO = unburned overstory thin, BN = burned no thin, BU = burned understory thin, BO = burned overstory thin.

H2.1. Pretreatment vegetation types would mediate natural conifer regeneration after thinning and prescribed burning, with densities highest in previously closed canopy patches, and lowest in previously shrub and open dominated patches, consistent with moderated light conditions in previously closed canopy conditions, greater competition in shrub patches, and less moisture availability in shrub dominated and open patches.

H.3.1. Planting would increase long-term regeneration density for the three species planted (white fir, Jeffrey pine, and sugar pine).

2. Material and methods

2.1. Study area and experimental design

The study was conducted at the Teakettle Experimental Forest (hereafter "Teakettle"), in the Sierra National Forest approximately 80 km east of Fresno, California, USA. Elevation ranges from 1900 to 2600 m, and soils are well-drained Dystric and Lithic Xeropsamments derived from granitic rock, with exposed granitic rock throughout the study area (USDA Forest Service and Soil Conservation Service, 1993). Teakettle has a Mediterranean climate of hot dry summers and cool wet winters, with mean annual precipitation of 125 cm falling largely as snow between November and April (North et al., 2002). Teakettle mixed-conifer forests are dominated by white fir (*Abies concolor* (Gord. & Glend.) Lindl. Ex Hildebr.), incense-cedar (*Calocedrus decurrens* (Torr.) Florin), sugar pine (*Pinus lambertiana* Dougl.), and Jeffrey pine (*Pinus jeffreyi* Grev. & Balf). Red fir (*Abies magnifica* A. Murr.), California black oak (*Quercus kelloggii* Newberry), and bitter cherry (*Prunus emarginata* Dougl. Ex Hook.) are also present.

Before the last recorded fire in 1865, mean fire return interval was 17.3 years (North et al., 2005). Fire exclusion greatly increased the density of shade-tolerant white fir and incense-cedar, resulting in a negative exponential diameter distribution and highly clustered stem distributions at multiple spatial scales (North et al., 2007). Prior to treatments, basal area and stem density were 56.4 m^2/ha and 469 tph, with proportional stem density dominated by white fir (67.6 %), followed by incense-cedar (13.4 %), sugar pine (7.9 %), Jeffrey pine (6.2 %), and red fir (3.0 %). Tree species proportional representation was marginally affected by treatments, with no differences between treatments for white fir, sugar pine, or Jeffrey pine, while the proportional density of incense-cedar increased after thinning combined with prescribed burning. Within these broad composition and structure conditions are distinct vegetation patch types: closed canopy forests, mountain whitethorn (*Ceanothus cordulatus* Kellogg) dominated shrub patches, open canopy gaps, and shallow soil/rock outcrops previously found to have different above and belowground environmental conditions (Ma et al., 2004; North et al., 2002).

Treatments were established as a factorial design with two levels of prescribed burning and three levels of thinning, resulting in six treatment combinations: unburned and no thin control (UN); unburned understory thin (UU); unburned overstory thin (UO); burned no thin (BN); burned understory thin (BU); and burned overstory thin (BO). Three replicate 4 ha treatment units were assigned to each of the six treatment combinations (18 total treatment units). Thinning was randomly assigned to treatment units, while burning was assigned with restricted randomization due to fire line and containment considerations. Burned and thinned treatments were thinned in 2000 and burned in 2001, while unburned and thinned treatments were thinned in 2001. Treatments follow a gradient of intensity with respect to post-treatment basal area,

Table 2
Pretreatment median and 95% confidence intervals of vegetation and environmental variables by patch type.

	CECO dominated	Closed canopy	Open	p
Number of plots	54	240	108	
canopy cover (%)	50.0 (2.3–86.0)	84.0 (53.9–100.0)	36.5 (0.0–66.3)	<0.001
litter cover (%)	2.5 (0.3–13.8)	4.3 (0.5–20.0)	0.8 (0.0–8.5)	<0.001
bare soil cover (%)	0.0 (0.0–7.0)	0.0 (0.0–7.0)	1.0 (0.0–90.0)	<0.001
rock cover (%)	0.0 (0.0–3.4)	0.0 (0.0–50.0)	0.0 (0.0–96.6)	<0.001
large wood cover (%)	0.0 (0.0–60.1)	1.0 (0.0–65.1)	0.0 (0.0–46.3)	0.212
small wood cover (%)	1.0 (0.0–9.0)	7.0 (0.2–61.2)	2.0 (0.0–25.0)	<0.001
Arctostaphlyos patula cover (%)	0.0 (0.0–13.4)	0.0 (0.0–10.3)	0.0 (0.0–76.6)	0.01
Ceanothus cordulatus cover (%)	60.0 (35.0–99.3)	0.0 (0.0–25.0)	0.0 (0.0–30.0)	<0.001
Symphoricarpos mollis cover (%)	0.0 (0.0–0.0)	0.0 (0.0–5.1)	0.0 (0.0–10.3)	0.211
Prunus emarginata cover (%)	0.0 (0.0–40.2)	0.0 (0.0–0.1)	0.0 (0.0–24.9)	0.003
Ribes roezlii cover (%)	0.0 (0.0–0.0)	0.0 (0.0–3.0)	0.0 (0.0–3.6)	0.503
soil moisture (October 1998)	4.3 (2.7–7.5)	3.9 (2.0–8.1)	4.5 (2.7–17.2)	<0.001
soil moisture (May 1999)	10.8 (6.4–20.2)	12.0 (6.4–31.1)	12.3 (6.8–28.4)	0.025
soil depth (cm)	90.5 (13.9–163.7)	80.3 (15.0–182.9)	48.4 (1.8–143.2)	<0.001

Note: CECO = *Ceanothus cordulatus*, p values associated with Kruskall-Wallis tests.

tree density, and substrate disturbance with increased intensity from no thin to understory thinned, and overstory thinned, with the addition of prescribed burning having a lesser effect, but one that increases with thinning intensity. Understory thinning followed guidelines in the California spotted owl report (Verner, 1992), removing intermediate sized trees 25–76 cm diameter at breast height (DBH, 1.37 m) while retaining at least 40 % canopy cover, retaining 40 % basal area, or no harvest of trees greater than 76 cm DBH, whichever constraint was most restrictive. Initially designed to minimize impacts to spotted owl habitat, this thinning prescription has been used since the 1990s for fuel reduction treatments (USDA Forest Service, 2022b; USDA Forest Service, 2004). While this thinning can more strictly be characterized as a midstory thinning due to the removal of intermediate size classes of trees, or as a free thinning due to additional diameter and canopy cover retention specifications, we are referring to this treatment as an understory thinning to convey its focus on removal of smaller diameter trees in relation to stand level diameter distributions, while also maintaining consistency with definitions in prior published studies at Teakettle. Immediately after treatments, basal area was 41.2 m^2/ha for understory thinning and 37.5 m^2/ha for understory thinning combined with prescribed burning. Overstory thinning removed trees >25 cm DBH while retaining ~22 large trees (>100 cm DBH) per hectare. This thinning was widely practiced in national forests of the Sierra Nevada prior to the 1990′s thinning guidelines in the California spotted owl report. Traditionally, this would have been part of a regeneration harvest such as a seed tree or a shelterwood prescription, with eventual harvest of the residual overstory after natural advanced regeneration. However, these residual trees were often not harvested, effectively resulting in a free thinning method due to the harvest of a wide range of size classes and uniform large tree retention. We refer to this treatment as an overstory thinning to convey its removal of larger diameter trees from upper canopy positions, while also maintaining consistency with definitions in prior published studies at Teakettle. Immediately after treatments, basal area was 22.7 m^2/ha for overstory thinning and 17.2 m^2/ha for overstory thinning combined with prescribed burning. Consistent with prescription guidelines of the time, overstory thinned plots were planted in the summer of 2002 with 2-year-old bare root stock of white fir, sugar pine, and Jeffrey pine. The planting prescription called for densities of the three species to be proportional to their relative pretreatment basal area, and our initial posttreatment survey in 2002 found 74 % percent of planted regeneration to be white fir (305 tph), 20 % sugar pine (83 tph), and 5 % Jeffrey pine (22 tph). Burning was applied in late October 2001 under mild fire weather conditions, resulting in slow creeping surface fire intended to consume surface fuels with little to no overstory mortality, confirmed by basal area of 53.7 m^2/ha after burning alone, which was not significantly different from pretreatment basal area. Additional details of treatment effects on forest composition and structure at Teakettle can be found in North et al. (2007). In addition to thinning and prescribed burning, from 2011 to 2017 tree mortality from synergistic effects of drought and bark beetles resulted in 13 % to 31 % reductions in live tree carbon across experimental units (Goodwin et al., 2020), with increased mortality for sugar pines and firs, larger diameter trees, and trees with higher levels of local competition (Steel et al., 2021).

2.2. Regeneration, vegetation, and microsite environmental sampling

A permanent sampling grid was established in the treatment units, with 49 grid points established on a 25 m × 25 m spacing in one of the three replicate plots per treatment combination, and 9 grid points established on a 50 m × 50 m spacing in the remaining two plots per treatment combination, for a total of 67 grid points per treatment combination. Prior to treatments, canopy cover, understory vegetation cover, substrate cover, soil moisture, and soil depth were collected at all grid points. Cover of shrubs and herbs by species, substrate cover (coarse woody debris by decay class, mineral soil, litter, rock), and litter depth were recorded within a 1.78 m radius microplot at each grid point during the pretreatment summers of 1998–1999 (Wayman and North, 2007). Pretreatment canopy cover above each grid point was estimated using digital hemispherical photography (Gray et al., 2005). Volumetric soil water content in the upper 15 cm of soil was measured in mid-Oct. 1998 and mid-May 1999 using time domain reflectometry with permanently installed 30-cm probes inserted at a 30° angle (Zald et al., 2008). Soil depth was measured using a 2 m steel tile probe, calibrated using five soil pits of various soil depths to bedrock, with five randomly selected soil depth measurements within a 2 m radius of each grid point (Meyer et al., 2007b). Cluster analysis of pretreatment vegetation and environmental data previously found four distinct vegetation patch types (North et al., 2002). Due to the similar environmental conditions of the open and rock outcrop patch types, and their low sample numbers within all treatment combinations, these two patch types were merged, resulting in three pretreatment patch types (closed canopy, *Ceanothus* shrub dominated, and open patches). Prior to treatments, closed canopy vegetation patches types were the most frequent across treatment combinations, but there was substantial variation between treatment combinations, with 45–75 % of microplots within closed canopy, 15–39 % within open, and 9–16 % within *Ceanothus* shrub dominated patches.

Regeneration was tallied on 3.5 m radius regeneration microplots centered on each grid point prior to treatments (summer of 2000) and periodically for nineteen years after treatments (summers of 2002, 2003, 2004, 2005, 2011, 2016, 2017, 2018, 2019, 2021). Burned treatment units were reburned in the Fall of 2017 (May et al., 2023). For this study we were only interested in the effects of thinning and initial entry prescribed burning prior to 2017 reburns, and for simplification analyses of regeneration only included a subset of measurement years (2000, 2002, 2005, 2011, and 2017). Initially, all trees at least 5 cm tall and less than 5 cm DBH were counted by species. The 5 cm minimum height cutoff excluded the more temporally variable pool of first-year germinants. Regeneration that grew past the initial pretreatment 5 cm DBH cutoff continued to be tallied as regeneration in subsequent measurement

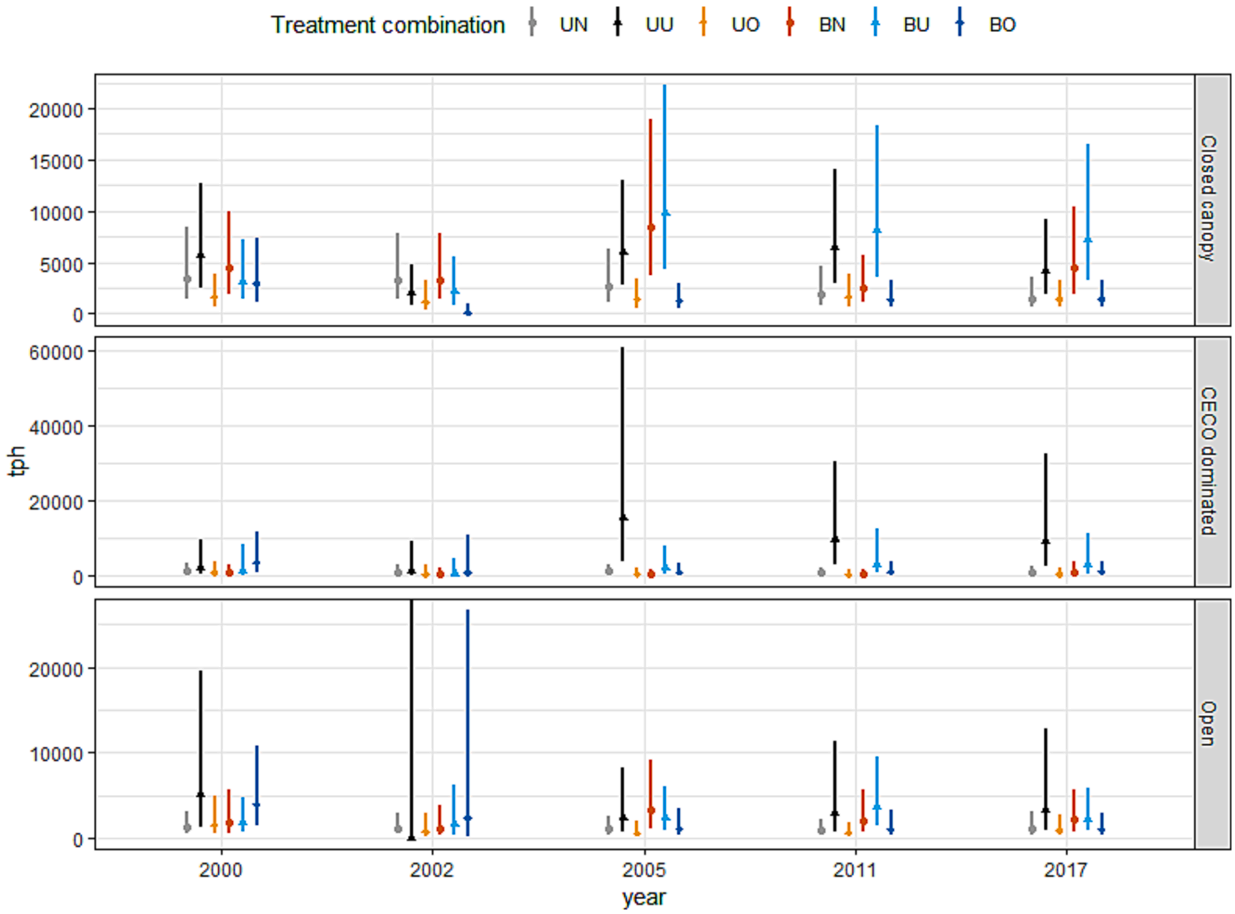

Fig. 3. Estimated marginal means of natural conifer regeneration density by year, treatment combination, and pretreatment vegetation patch type. Error bars are 95 % confidence intervals. UN = unburned no thin control, UU = unburned understory thin, UO = unburned overstory thin, BN = burned no thin, BU = burned understory thin, BO = burned overstory thin.

Table 3
Mean (and 95 % confidence intervals) of natural versus combined (natural + planted) regeneration density by species, treatment, and year.

Species	Year	Treatment	Natural regeneration		Combined regeneration		z	p
			Mean	95 % CI	Mean	95 % CI		
White fir	2002	BO	19.39	(1.94–42.71)	608.99	(531.46–682.66)	1378	0.0000
White fir	2017	BO	318.07	(190.03–471.34)	461.63	(316.19–626.51)	276	0.0000
White fir	2002	UO	65.94	(25.22–114.47)	391.76	(306.46–475.14)	528	0.0000
White fir	2017	UO	69.85	(44.63–97.01)	128.04	(79.55–186.24)	45	0.0061
Jeffrey pine	2002	BO	0.00	(0–0)	54.33	(31.04–83.43)	55	0.0035
Jeffrey pine	2017	BO	73.72	(38.81–114.5)	108.61	(62.07–157.14)	15	0.0579
Jeffrey pine	2002	UO	0.00	(0–0)	11.64	(3.88–21.34)	6	0.1489
Jeffrey pine	2017	UO	50.45	(27.16–77.61)	73.72	(40.74–112.49)	6	0.1814
Sugar pine	2002	BO	0.00	(0–0)	124.13	(79.47–178.4)	105	0.0010
Sugar pine	2017	BO	23.28	(11.59–38.81)	65.96	(32.98–104.72)	15	0.0579
Sugar pine	2002	UO	19.40	(5.82–32.99)	143.54	(96.93–197.89)	105	0.0010
Sugar pine	2017	UO	96.99	(52.38–149.34)	131.90	(77.6–194.01)	21	0.0310

Note: UO = unburned overstory thin, BO = burned overstory thin.

years. In overstory thinned treatment units, planted seedlings were identified in regeneration microplots shortly after they were planted in the summer of 2002, and their distance and azimuth from microplot centers recorded to distinguish them from natural regeneration in subsequent years. For all tree species, regeneration count data were converted to density (trees per hectare, tph).

2.3. Statistical analyses

All statistical analyses were conducted in R version 4.2.1 (R Development Core Team, 2020). Regeneration was present for eight species, but very low frequency of canyon live oak, and spatially constrained distributions of red fir, California black oak, and bitter cherry limited analyses to the four dominant conifer species (white fir, incense-cedar, Jeffrey pine, and sugar pine). Generalized linear mixed models (GLMMs) were used to quantify the effect of treatments on natural regeneration density for white fir and incense-cedar using the glmmTMB package (Magnusson et al., 2017). GLMMs used microplot regeneration density (tph) as the observational unit, included three fixed effects (burn, thin, and year), and all possible interactions among them.

Fig. 4. Example of planted pine regeneration within a burned overstory thinned treatment unit at Teakettle Experimental Forest. Photo was taken in 2016, 15 years after treatments and 14 years after planting. Treatment unit has a moderate slope and southwest aspect. Note very little canopy retention, dense shrub cover dominated by *Ceanothus cordulatus*, and extensive planted Jeffrey pine and sugar pine regeneration in the midground. Minimal canopy retention is due to a combination of thinning in 2000, prescribed burning in 2001, and additional mortality during 2012–2016 from drought and endemic bark beetles. Photo credit Harold Zald.

Table A1
Fixed effects of generalized linear mixed effects model of white fir natural regeneration density.

Effect	Component	Group	Term	β	95 % CI		SE	Z	p
fixed	conditional		(Intercept)	864.798	583.455	1281.803	173.637	33.681	0.000
fixed	conditional		thinU	1.615	0.929	2.808	0.456	1.699	0.089
fixed	conditional		thinO	0.932	0.512	1.698	0.285	−0.229	0.819
fixed	conditional		burnB	1.534	0.879	2.677	0.436	1.506	0.132
fixed	conditional		year2002	1.197	0.860	1.665	0.202	1.065	0.287
fixed	conditional		year2005	1.162	0.841	1.606	0.192	0.910	0.363
fixed	conditional		year2011	0.954	0.686	1.326	0.160	−0.280	0.780
fixed	conditional		year2017	0.860	0.599	1.234	0.159	−0.820	0.412
fixed	conditional		thinU:burnB	0.713	0.332	1.530	0.278	−0.869	0.385
fixed	conditional		thinO:burnB	1.160	0.504	2.672	0.494	0.349	0.727
fixed	conditional		thinU:year2002	0.385	0.226	0.656	0.105	−3.512	0.000
fixed	conditional		thinO:year2002	0.412	0.204	0.832	0.148	−2.472	0.013
fixed	conditional		thinU:year2005	0.528	0.325	0.859	0.131	−2.572	0.010
fixed	conditional		thinO:year2005	0.520	0.268	1.011	0.176	−1.929	0.054
fixed	conditional		thinU:year2011	0.649	0.397	1.061	0.163	−1.725	0.085
fixed	conditional		thinO:year2011	0.480	0.261	0.883	0.149	−2.363	0.018
fixed	conditional		thinU:year2017	0.417	0.247	0.705	0.112	−3.268	0.001
fixed	conditional		thinO:year2017	0.503	0.262	0.963	0.167	−2.073	0.038
fixed	conditional		burnB:year2002	0.560	0.342	0.918	0.141	−2.300	0.021
fixed	conditional		burnB:year2005	1.258	0.769	2.057	0.316	0.914	0.361
fixed	conditional		burnB:year2011	0.670	0.412	1.092	0.167	−1.606	0.108
fixed	conditional		burnB:year2017	0.895	0.525	1.526	0.244	−0.407	0.684
fixed	conditional		thinU:burnB:year2002	2.075	0.954	4.514	0.823	1.841	0.066
fixed	conditional		thinO:burnB:year2002	1.309	0.355	4.831	0.872	0.404	0.686
fixed	conditional		thinU:burnB:year2005	1.009	0.496	2.052	0.365	0.024	0.981
fixed	conditional		thinO:burnB:year2005	0.563	0.232	1.366	0.255	−1.271	0.204
fixed	conditional		thinU:burnB:year2011	1.654	0.817	3.349	0.595	1.399	0.162
fixed	conditional		thinO:burnB:year2011	1.212	0.527	2.786	0.515	0.452	0.651
fixed	conditional		thinU:burnB:year2017	1.934	0.909	4.114	0.745	1.713	0.087
fixed	conditional		thinO:burnB:year2017	0.913	0.376	2.214	0.413	−0.202	0.840
random	conditional	plot	sd_(Intercept)	1.634	1.494	1.788	0.075	10.688	0.000
random	conditional	gridpt:plot	sd_(Intercept)	0.968	0.877	1.069			
random	conditional	plot	sd_(Intercept)	0.000	0.000				

Note: β = beta coefficient representing the degree of change in the regeneration density for every 1-unit of change in the predictor variable.

Table A2
Estimated marginal means, standard error (SE) and 95 % confidence interval (95 % CI) of regeneration density (tph) by treatment combination and year from generalized linear mixed effects model of white fir natural regeneration density.

Treatment	Year	Response	SE	95 % CI	
BN	2000	1326.496	267.086	893.962	1968.305
BO	2000	1434.552	311.375	937.475	2195.193
BU	2000	1527.248	271.582	1077.817	2164.084
UN	2000	864.798	173.637	583.455	1281.803
UO	2000	806.238	186.271	512.630	1268.009
UU	2000	1396.790	277.649	946.090	2062.196
BN	2002	889.505	180.087	598.159	1322.759
BO	2002	518.201	272.697	184.741	1453.559
BU	2002	818.241	193.757	514.422	1301.496
UN	2002	1034.842	199.114	709.732	1508.876
UO	2002	397.114	131.383	207.635	759.506
UU	2002	643.626	146.430	412.077	1005.284
BN	2005	1939.041	346.624	1365.923	2752.632
BO	2005	613.656	138.923	393.754	956.368
BU	2005	1189.679	214.454	835.584	1693.828
UN	2005	1004.952	188.240	696.153	1450.728
UO	2005	487.387	146.056	270.890	876.910
UU	2005	857.453	167.438	584.780	1257.266
BN	2011	848.529	157.726	589.446	1221.488
BO	2011	534.108	118.112	346.254	823.878
BU	2011	1049.184	187.669	738.917	1489.729
UN	2011	825.076	157.492	567.564	1199.425
UO	2011	369.512	96.444	221.545	616.303
UU	2011	865.155	168.500	590.625	1267.289
BN	2017	1020.582	199.278	696.054	1496.417
BO	2017	506.278	113.301	326.510	785.022
BU	2017	947.791	179.200	654.296	1372.936
UN	2017	743.318	151.231	498.879	1107.529
UO	2017	348.323	95.373	203.666	595.726
UU	2017	500.754	100.857	337.429	743.131

UN = unburned no thin control, UU = unburned understory thin, UO = unburned overstory thin, BN = burned no thin, BU = burned understory thin, BO = burned overstory thin.

Individual microplots nested within treatment units were included in models as random effects. Histograms of natural regeneration density by species showed a high frequency of microplots had no regeneration, while when present, regeneration density appeared to have a negative binomial or gamma distribution. Therefore, GLMMs for white fir and incense-cedar were first evaluated with the same fixed and random effects and two different response variable distributions (zero-inflated Gamma, and zero-inflated negative binomial). Models were evaluated based on Akaike Information Criterion (AIC) values, as well as model diagnostics (quantile-quantile plots of model residuals, residual versus predicted values, outliers, and zero-inflation) using the DHARMa package (Hartig and Hartig, 2017). For white fir, both gamma and negative binomial distribution models had comparable AIC values (ΔAIC = 1.2), and for incense-cedar the negative binomial distribution had the lowest AIC values (gamma distribution model, ΔAIC = 7.2). All models had acceptable model diagnostics, so we chose to present results from zero-inflated negative binomial models for both white fir and incense-cedar. Marginal and conditional coefficients of determination for mixed models were calculated using the performance package (Lüdecke et al., 2021; Nakagawa and Schielzeth, 2013). Model coefficients and associated 95 % confidence intervals were exponentiated to calculate the estimated marginal means of fixed effects on regeneration density. Pairwise comparisons of within year estimated marginal means of regeneration density between treatment combinations were calculated using the Tukey HSD method and 95 % confidence intervals with the emmeans package (Lenth et al., 2018).

For Jeffrey pine and sugar pine, GLMMs of natural regeneration density failed to converge on a solution, likely due to the low proportion of microplots with natural pine regeneration in any given year. The percent of microplots with natural regeneration was much higher for white fir (mean across years = 39.8 %, range across years = 24.1–44.8

Table A3
Pairwise comparison of white fir natural regeneration density between treatments within years from generalized linear mixed effects model.

Treatment Contrast	Year	Ratio	SE	z.ratio	p
BN/BO	2000	0.925	0.274	−0.265	1.000
BN/BU	2000	0.869	0.233	−0.525	0.995
BN/UO	2000	1.645	0.504	1.625	0.582
BN/UU	2000	0.950	0.269	−0.183	1.000
BU/BO	2000	1.065	0.299	0.223	1.000
BU/UO	2000	1.894	0.552	2.192	0.241
UN/BN	2000	0.652	0.185	−1.505	0.661
UN/BO	2000	0.603	0.178	−1.713	0.523
UN/BU	2000	0.566	0.152	−2.123	0.275
UN/UO	2000	1.073	0.328	0.229	1.000
UN/UU	2000	0.619	0.175	−1.699	0.533
UO/BO	2000	0.562	0.178	−1.819	0.454
UU/BO	2000	0.974	0.286	−0.091	1.000
UU/BU	2000	0.915	0.244	−0.335	0.999
UU/UO	2000	1.732	0.528	1.804	0.463
BN/BO	2002	1.716	0.968	0.958	0.931
BN/BU	2002	1.087	0.339	0.268	1.000
BN/UO	2002	2.240	0.869	2.080	0.298
BN/UU	2002	1.382	0.421	1.063	0.896
BU/BO	2002	1.579	0.911	0.792	0.969
BU/UO	2002	2.061	0.838	1.778	0.480
UN/BN	2002	1.163	0.325	0.542	0.994
UN/BO	2002	1.997	1.119	1.235	0.820
UN/BU	2002	1.265	0.386	0.770	0.973
UN/UO	2002	2.606	0.997	2.504	0.123
UN/UU	2002	1.608	0.479	1.595	0.602
UO/BO	2002	0.766	0.476	−0.428	0.998
UU/BO	2002	1.242	0.712	0.378	0.999
UU/BU	2002	0.787	0.258	−0.731	0.978
UU/UO	2002	1.621	0.651	1.203	0.836
BN/BO	2005	3.160	0.910	3.994	0.001
BN/BU	2005	1.630	0.413	1.928	0.385
BN/UO	2005	3.978	1.387	3.960	0.001
BN/UU	2005	2.261	0.598	3.086	0.025
BU/BO	2005	1.939	0.560	2.291	0.197
BU/UO	2005	2.441	0.853	2.553	0.109
UN/BN	2005	0.518	0.134	−2.540	0.113
UN/BO	2005	1.638	0.481	1.680	0.545
UN/BU	2005	0.845	0.219	−0.650	0.987
UN/UO	2005	2.062	0.728	2.048	0.315
UN/UU	2005	1.172	0.317	0.587	0.992
UO/BO	2005	0.794	0.298	−0.614	0.990
UU/BO	2005	1.397	0.417	1.120	0.873
UU/BU	2005	0.721	0.191	−1.234	0.820
UU/UO	2005	1.759	0.629	1.580	0.612
BN/BO	2011	1.589	0.459	1.603	0.596
BN/BU	2011	0.809	0.208	−0.824	0.963
BN/UO	2011	2.296	0.736	2.595	0.098
BN/UU	2011	0.981	0.264	−0.072	1.000
BU/BO	2011	1.964	0.558	2.378	0.164
BU/UO	2011	2.839	0.898	3.301	0.012
UN/BN	2011	0.972	0.259	−0.105	1.000
UN/BO	2011	1.545	0.451	1.490	0.671
UN/BU	2011	0.786	0.206	−0.919	0.942
UN/UO	2011	2.233	0.722	2.485	0.128
UN/UU	2011	0.954	0.260	−0.174	1.000
UO/BO	2011	0.692	0.236	−1.078	0.890
UU/BO	2011	1.620	0.477	1.638	0.573
UU/BU	2011	0.825	0.218	−0.730	0.978
UU/UO	2011	2.341	0.762	2.613	0.094
BN/BO	2017	2.016	0.598	2.364	0.169
BN/BU	2017	1.077	0.292	0.273	1.000
BN/UO	2017	2.930	0.985	3.198	0.017
BN/UU	2017	2.038	0.571	2.540	0.113
BU/BO	2017	1.872	0.547	2.145	0.264
BU/UO	2017	2.721	0.905	3.010	0.031
UN/BN	2017	0.728	0.205	−1.125	0.871
UN/BO	2017	1.468	0.444	1.271	0.801
UN/BU	2017	0.784	0.218	−0.876	0.952
UN/UO	2017	2.134	0.728	2.223	0.227
UN/UU	2017	1.484	0.425	1.381	0.739
UO/BO	2017	0.688	0.243	−1.058	0.898
UU/BO	2017	0.989	0.298	−0.036	1.000
UU/BU	2017	0.528	0.146	−2.312	0.189
UU/UO	2017	1.438	0.489	1.068	0.894

UN = unburned no thin control, UU = unburned understory thin, UO = unburned overstory thin, BN = burned no thin, BU = burned understory thin, BO = burned overstory thin.

%) and incense-cedar (33.1 %, 14.2–41.5 %) compared to sugar pine (14.1 %, 8.2–17.2 %) and Jeffrey pine (5.2 %, 0.1–7.7 %). Therefore, we quantified treatment effects for the two pine species as the log odds of natural regeneration presence with mixed effects logistic models in the lme4 package (Bates et al., 2015). Logistic models had a binomial distribution with a logit link function, three fixed effects (burn, thin, and year), all possible interactions among fixed effects, and treatment units as a random effect. Model diagnostics were assessed in the same manner as for GLMMs of white fir and incense-cedar, and coefficients of determination for generalized linear mixed models for binary outcomes calculated (Tjur, 2009). Model coefficients and associated 95 % confidence intervals were exponentiated to calculate the estimated marginal means of fixed effects on regeneration probability of occupancy (presence). Pairwise comparisons of within year estimated marginal means of regeneration probability between treatment combinations were calculated using the Tukey HSD method and 95 % confidence intervals with the emmeans package (Lenth et al., 2018).

The median and 95 % confidence intervals of microplot environmental and vegetation cover variables were calculated for each patch type, and differences in environmental and vegetation variables between patch types assessed using Kruskall-Wallis tests. GLMM was used to quantify the effect of treatments and pretreatment vegetation patch type on total natural conifer regeneration density. GLMM models included four fixed effects (burn, thin, vegetation type, and year), and all possible interactions among them. Individual treatment units were included as a random effects term. As with GLMMs of white fir and incense-cedar, two models were developed with different response variable distributions, and these were evaluated based on their AIC values and model diagnostics. The model using a zero-inflated negative binomial distribution had the lowest AIC values (second best model had ΔAIC value of 25.8) and acceptable model diagnostics. Estimated marginal means and within group comparisons of regeneration density by treatment combination and patch type in each year were calculated as described above for GLMMs of white fir and incense-cedar.

To quantify the effect of tree planting on regeneration density, we calculated the natural and combined (natural + planted) regeneration density for each of the three planted species (white fir, Jeffrey pine, and sugar pine) at each microplot in the burned and unburned overstory thinned treatment units, for measurements taken immediately after treatments (2002) and sixteen years after treatment (2017). Natural versus combined regeneration on microplots were treated as paired (dependent) samples, while visual assessment of histograms indicated regeneration densities were not normally distributed. For these reasons, differences in densities between natural versus combined regeneration were quantified using Wilcoxon signed-rank tests. Tests were conducted separately for each of the three species, in each of the two treatment combinations, for the 2002 and 2017 measurement years.

3. Results

3.1. Regeneration density by species and treatment over time

Overall, natural regeneration density across treatments (excluding controls) and measurement years was dominated by shade-tolerant species, with mean densities across post-treatment years (2002, 2005, 2011, 2017) of 790 tph for white fir and 1530 tph for incense-cedar, versus 27 tph for Jeffrey pine, and 48 tph for sugar pine (Table 1). Sixteen years after treatments, mean regeneration density declined from 2000 pretreatment levels in untreated controls for all species, with greater declines for white fir (-45 %) and Jeffrey pine (-75 %) versus

Table A4
Fixed effects of generalized linear mixed effects model of incense-cedar fir natural regeneration density.

Effect	Component	Group	Parameter	β	95 % CI		SE	Z	p
fixed	conditional		(Intercept)	18.126	0.680	483.220	30.363	1.730	0.084
fixed	conditional		thinU	40.597	0.424	3882.760	94.465	1.592	0.111
fixed	conditional		thinO	1.101	0.011	112.339	2.599	0.041	0.967
fixed	conditional		burnB	45.922	0.485	4347.660	106.617	1.648	0.099
fixed	conditional		year2002	1.062	0.689	1.636	0.234	0.271	0.786
fixed	conditional		year2005	1.190	0.767	1.844	0.266	0.776	0.438
fixed	conditional		year2011	0.921	0.603	1.407	0.199	−0.381	0.704
fixed	conditional		year2017	1.005	0.626	1.613	0.243	0.019	0.985
fixed	conditional		thinU:burnB	0.025	0.000	14.499	0.081	−1.138	0.255
fixed	conditional		thinO:burnB	1.128	0.002	691.403	3.694	0.037	0.971
fixed	conditional		thinU:year2002	0.378	0.184	0.777	0.139	−2.646	0.008
fixed	conditional		thinO:year2002	0.604	0.311	1.175	0.205	−1.485	0.138
fixed	conditional		thinU:year2005	1.527	0.824	2.833	0.481	1.344	0.179
fixed	conditional		thinO:year2005	0.643	0.342	1.206	0.206	−1.376	0.169
fixed	conditional		thinU:year2011	2.175	1.195	3.959	0.664	2.545	0.011
fixed	conditional		thinO:year2011	0.933	0.509	1.708	0.288	−0.226	0.821
fixed	conditional		thinU:year2017	1.727	0.919	3.245	0.556	1.697	0.090
fixed	conditional		thinO:year2017	1.020	0.541	1.921	0.330	0.061	0.951
fixed	conditional		burnB:year2002	0.581	0.304	1.111	0.192	−1.643	0.100
fixed	conditional		burnB:year2005	0.803	0.434	1.486	0.252	−0.698	0.485
fixed	conditional		burnB:year2011	0.853	0.458	1.591	0.271	−0.500	0.617
fixed	conditional		burnB:year2017	0.746	0.388	1.437	0.249	−0.876	0.381
fixed	conditional		thinU:burnB:year2002	2.365	0.910	6.149	1.153	1.766	0.077
fixed	conditional		thinO:burnB:year2002	1.727	0.383	7.779	1.326	0.711	0.477
fixed	conditional		thinU:burnB:year2005	1.233	0.538	2.827	0.522	0.495	0.621
fixed	conditional		thinO:burnB:year2005	0.712	0.293	1.730	0.323	−0.750	0.453
fixed	conditional		thinU:burnB:year2011	1.124	0.493	2.561	0.472	0.278	0.781
fixed	conditional		thinO:burnB:year2011	0.651	0.271	1.561	0.291	−0.963	0.336
fixed	conditional		thinU:burnB:year2017	1.337	0.575	3.112	0.576	0.675	0.500
fixed	conditional		thinO:burnB:year2017	0.738	0.303	1.798	0.335	−0.669	0.504
fixed	zero inflation		(Intercept)	2.093	1.902	2.304	0.102	15.129	0.000
random	conditional	gridpt:plot	sd_(Intercept)	1.070	0.958	1.194			
random	conditional	plot	sd_(Intercept)	2.733	1.836	4.066			

Note: β = beta coefficient representing the degree of change in the regeneration density for every 1-unit of change in the predictor variable.

Table A5
Estimated marginal means, standard error (SE) and 95 % confidence interval (95 % CI) of regeneration density (tph) by treatment combination and year from generalized linear mixed effects model of incense-cedar natural regeneration density.

Treatment	Year	Response	SE	95 % CI	
UN	2000	18.126	30.363	0.680	483.220
UU	2000	735.873	1189.033	31.004	17465.673
UO	2000	19.960	33.596	0.737	540.544
BN	2000	832.390	1338.140	35.641	19440.506
BU	2000	836.799	1341.827	36.116	19388.452
BO	2000	1034.130	1657.880	44.664	23943.668
UN	2002	19.243	32.207	0.724	511.568
UU	2002	295.064	480.090	12.161	7159.463
UO	2002	12.807	21.603	0.470	349.335
BN	2002	513.522	828.281	21.758	12119.841
BU	2002	461.194	741.189	19.766	10761.123
BO	2002	665.869	1140.772	23.180	19128.143
UN	2005	21.562	36.098	0.810	573.753
UU	2005	1336.993	2151.559	57.060	31327.608
UO	2005	15.261	25.663	0.565	412.068
BN	2005	795.451	1279.081	34.032	18592.613
BU	2005	1505.956	2410.526	65.362	34697.451
BO	2005	452.204	724.241	19.591	10437.629
UN	2011	16.693	27.941	0.628	443.870
UU	2011	1474.280	2371.411	63.009	34494.996
UO	2011	17.143	28.789	0.638	460.840
BN	2011	653.944	1052.057	27.934	15308.884
BU	2011	1607.096	2571.735	69.810	36996.979
BO	2011	492.858	788.990	21.383	11359.660
UN	2017	18.210	30.518	0.682	486.208
UU	2017	1276.483	2052.611	54.609	29837.657
UO	2017	20.453	34.341	0.761	549.471
BN	2017	624.085	1002.510	26.786	14540.702
BU	2017	1448.844	2317.982	62.979	33330.780
BO	2017	583.615	933.648	25.375	13423.010

UN = unburned no thin control, UU = unburned understory thin, UO = unburned overstory thin, BN = burned no thin, BU = burned understory thin, BO = burned overstory thin.

incense cedar (-21 %) and sugar pine (-37 %). For white fir, all treatment combinations reduced regeneration density from 2000 pretreatment levels, with the greatest reductions in unburned overstory thins (-81 %), unburned understory thins (-77 %), and burned overstory thins (-72 %), while burning alone (-11 %) and burned understory thins (-16 %) had only small reductions from pretreatment levels and 2016 regeneration densities were greater than 1000 tph. Incense-cedar densities increased after understory thins (636 %) and burned understory thins (417 %), resulting in regeneration densities in excess of 1600 tph, while burning alone and burned overstory thins both resulted in moderate reductions (-45 %) in regeneration densities. For Jeffrey pine, regeneration density increased in all combinations of thinning and burning, but total regeneration densities remained low, with the greatest densities found in burned overstory thins (47 tph), followed by unburned overstory thins (32 tph), burned understory thins (32 tph), burning alone (14 tph), unburned understory thins (10 tph) and untreated controls (10 tph). For sugar pine, regeneration density increased in all combinations of thinning and burning except unburned understory thins (-12 %), but total regeneration densities remained low, with the greatest densities found in untreated controls (120 tph), followed by burning alone (79 tph), unburned overstory thins (58 tph), unburned understory thins (56 tph), burned understory thins (26 tph) and burned overstory thins (20 tph).

3.2. White fir and incense-cedar nature regeneration in response to treatments

Despite large differences in mean treatment level densities, high within treatment and between year variability resulted in a limited number of significant differences in white fir regeneration density between treatments in any given year, and no combination of thinning

Table A6
Pairwise comparison of incense-cedar natural regeneration density between treatments within years from generalized linear mixed effects model.

Treatment Contrast	Year	Ratio	SE	z.ratio	p
BN/BO	2000	0.805	1.827	−0.096	1.000
BN/BU	2000	0.995	2.259	−0.002	1.000
BU/BO	2000	0.809	1.835	−0.093	1.000
UN/BN	2000	0.022	0.051	−1.648	0.566
UN/BO	2000	0.018	0.041	−1.744	0.502
UN/BU	2000	0.022	0.050	−1.653	0.563
UN/UO	2000	0.908	2.143	−0.041	1.000
UN/UU	2000	0.025	0.057	−1.592	0.604
UO/BN	2000	0.024	0.056	−1.603	0.597
UO/BO	2000	0.019	0.045	−1.698	0.533
UO/BU	2000	0.024	0.055	−1.607	0.594
UU/BN	2000	0.884	2.015	−0.054	1.000
UU/BO	2000	0.712	1.620	−0.149	1.000
UU/BU	2000	0.879	2.002	−0.056	1.000
UU/UO	2000	36.867	85.997	1.546	0.634
BN/BO	2002	0.771	1.815	−0.110	1.000
BN/BU	2002	1.113	2.535	0.047	1.000
BU/BO	2002	0.693	1.627	−0.156	1.000
UN/BN	2002	0.037	0.087	−1.413	0.719
UN/BO	2002	0.029	0.069	−1.480	0.677
UN/BU	2002	0.042	0.097	−1.369	0.746
UN/UO	2002	1.503	3.548	0.172	1.000
UN/UU	2002	0.065	0.152	−1.170	0.851
UO/BN	2002	0.025	0.058	−1.582	0.611
UO/BO	2002	0.019	0.046	−1.643	0.570
UO/BU	2002	0.028	0.065	−1.538	0.639
UU/BN	2002	0.575	1.316	−0.242	1.000
UU/BO	2002	0.443	1.047	−0.344	0.999
UU/BU	2002	0.640	1.463	−0.195	1.000
UU/UO	2002	23.038	53.981	1.339	0.763
BN/BO	2005	1.759	3.992	0.249	1.000
BN/BU	2005	0.528	1.198	−0.281	1.000
BU/BO	2005	3.330	7.541	0.531	0.995
UN/BN	2005	0.027	0.063	−1.554	0.629
UN/BO	2005	0.048	0.110	−1.314	0.778
UN/BU	2005	0.014	0.033	−1.834	0.444
UN/UO	2005	1.413	3.332	0.147	1.000
UN/UU	2005	0.016	0.037	−1.778	0.480
UO/BN	2005	0.019	0.045	−1.699	0.532
UO/BO	2005	0.034	0.078	−1.459	0.690
UO/BU	2005	0.010	0.024	−1.978	0.355
UU/BN	2005	1.681	3.824	0.228	1.000
UU/BO	2005	2.957	6.713	0.477	0.997
UU/BU	2005	0.888	2.015	−0.052	1.000
UU/UO	2005	87.610	203.873	1.922	0.388
BN/BO	2011	1.327	3.011	0.125	1.000
BN/BU	2011	0.407	0.923	−0.396	0.999
BU/BO	2011	3.261	7.381	0.522	0.995
UN/BN	2011	0.026	0.059	−1.580	0.612
UN/BO	2011	0.034	0.078	−1.462	0.689
UN/BU	2011	0.010	0.024	−1.973	0.358
UN/UO	2011	0.974	2.294	−0.011	1.000
UN/UU	2011	0.011	0.026	−1.931	0.383
UO/BN	2011	0.026	0.061	−1.566	0.621
UO/BO	2011	0.035	0.081	−1.448	0.698
UO/BU	2011	0.011	0.025	−1.958	0.367
UU/BN	2011	2.254	5.129	0.357	0.999
UU/BO	2011	2.991	6.788	0.483	0.997
UU/BU	2011	0.917	2.081	−0.038	1.000
UU/UO	2011	86.001	199.945	1.916	0.392
BN/BO	2017	1.069	2.424	0.030	1.000
BN/BU	2017	0.431	0.977	−0.371	0.999
BU/BO	2017	2.483	5.617	0.402	0.999
UN/BN	2017	0.029	0.068	−1.522	0.650
UN/BO	2017	0.031	0.072	−1.497	0.667
UN/BU	2017	0.013	0.029	−1.889	0.409
UN/UO	2017	0.890	2.099	−0.049	1.000
UN/UU	2017	0.014	0.033	−1.830	0.446
UO/BN	2017	0.033	0.076	−1.471	0.683
UO/BO	2017	0.035	0.081	−1.445	0.699
UO/BU	2017	0.014	0.033	−1.837	0.442
UU/BN	2017	2.045	4.649	0.315	1.000
UU/BO	2017	2.187	4.961	0.345	0.999
UU/BU	2017	0.881	1.998	−0.056	1.000
UU/UO	2017	62.410	145.064	1.778	0.480

UN = unburned no thin control, UU = unburned understory thin, UO = unburned overstory thin, BN = burned no thin, BU = burned understory thin, BO = burned overstory thin.

and/or burning resulted in significantly lower regeneration density versus untreated controls in any year. The GLMM model of white fir natural regeneration density had a marginal $R^2 = 0.052$ and conditional $R^2 = 0.314$. Neither burning or year had a significant fixed individual effect on density, understory thinning only had a marginal fixed effect on density (β = 1.615, Z = 1.699, p = 0.089), but interactions between thinning, burning and year were important (Table A1). White fir regeneration density was not different between treatment combinations prior to treatment in 2000 or in the first year after treatment in 2002, but differences became apparent over time (Fig. 1, Tables A2 and A3). Four years after treatments (2005), burned unthinned treatments had the highest white fir regeneration density (mean 1940 tph, 1366–2753 % CI), significantly higher than found in unburned overstory thins (mean 487 tph, 271–877 95 % CI, t = -3.959, p = 0.001), burned overstory thins (mean 613 tph, 394–956 95 % CI, t = 3.994, p = 0.001), and unburned understory thins (mean 857 tph, 585–1257 95 % CI, t = -3.086, p = 0.025). White fir regeneration density in burned understory thins (mean 1190 tph, 835–1694 95 % CI) and untreated controls (mean 1005 tph, 696–1451 95 % CI) were not different than any other treatment combination. Ten years after treatments (2011), burned understory thins had the highest white fir regeneration density (mean 1049 tph, 739 – 1490 95 % CI), significantly higher than found in unburned overstory thins (mean 370 tph, 222–616 95 % CI, t = -3.301, p = 0.012), and marginally higher than in unburned understory thins (mean 865 tph, 591–1267 95 % CI, t = 2.613, p = 0.093), and burning alone (mean 849 tph, 589–1221 95 % CI, t = -2.595, p = 0.098). White fir regeneration density in burned overstory thins (mean 534 tph, 346–824 95 % CI) and untreated controls (mean 825 tph, 568–1199 95 % CI) were not different than any other treatment combination. Sixteen years after treatments (2017), burned unthinned treatments had the highest white fir regeneration density (mean 1021 tph, 696 – 1496 95 % CI), significantly higher than in unburned overstory thins (mean 348 tph, 204–596 95 % CI, t = -3.198, p = 0.017), which in turn had significantly lower density than burned understory thins (mean 948 tph, 654–1373 95 % CI, t = -3.010, p = 0.031). White fir regeneration density in untreated controls (mean 743 tph, 499–1108 95 % CI), burned overstory thins (mean 506 tph, 327–785 95 % CI), and unburned understory thins (mean 501 tph, 337 – 743 95 % CI) were not different than any other treatment combination.

The GLMM model of incense-cedar natural regeneration density had a marginal $R^2 = 0.18$ and conditional $R^2 = 0.64$. Thinning did not have a significant individual effect on density, and burning only had a marginal effect (β = 45.922, z = 1.648, p = 0.099), but interactions between thinning, burning and year were important (Table A4). Despite large differences in mean treatment level densities, incense-cedar regeneration density was extremely variable, resulting in no differences in regeneration density between treatment combinations prior to treatment in 2000 or in any year after treatment (Fig. 1, Tables A5 and A6). Four years after treatments (2005), burned understory thinned treatments had the highest incense-cedar regeneration density (mean 1506 tph, 65 – 34,697 95 % CI), followed by unburned understory thins (mean 1337 tph, 57 – 31,328 95 % CI), burning alone (mean 795 tph, 34 – 18,593 95 % CI), burned overstory thins (mean 452 tph, 20 – 10,438 95 % CI), untreated controls (mean 22 tph, 1 – 574 95 % CI), and unburned overstory thins (mean 15 tph, 1 – 574 95 % CI). Ten years after treatments (2011), burned understory thinned treatments had the highest incense-cedar regeneration density (mean 1607 tph, 70 – 36,997 95 % CI), followed by unburned understory thins (mean 1474 tph, 63 – 34,495 95 % CI), burning alone (mean 654 tph, 28 – 15,309 95 % CI), burned overstory thins (mean 493 tph, 21 – 11,360 95 % CI), unburned overstory thins (mean 17 tph, 1 – 461 95 % CI), and untreated controls (mean 17 tph, 1 – 444 95 % CI). Sixteen years after treatments (2017), burned understory thinned treatments had the highest incense-cedar regeneration density (mean 1449 tph, 63 – 33,331 95 % CI), followed by

Table A7
Fixed effects of logistic mixed effects model of Jeffrey pine natural regeneration presence.

Effect	Group	Parameter	β	95 % CI		SE	Z	p
fixed		(Intercept)	0.015	0.002	0.109	0.015	−4.158	0.000
fixed		thinU	0.000	0.000	Inf	0.000	−0.003	0.998
fixed		thinO	3.094	0.314	30.524	3.613	0.967	0.334
fixed		burnB	2.031	0.180	22.947	2.512	0.573	0.567
fixed		year2002	2.031	0.180	22.947	2.512	0.573	0.567
fixed		year2005	2.031	0.180	22.947	2.512	0.573	0.567
fixed		year2011	2.031	0.180	22.947	2.512	0.573	0.567
fixed		year2017	1.000	0.061	16.325	1.425	0.000	1.000
fixed		thinU:burnB	16899331.745	0.000	Inf	98258346445.693	0.003	0.998
fixed		thinO:burnB	0.492	0.026	9.184	0.735	−0.475	0.635
fixed		thinU:year2002	0.492	0.000	Inf	4049.049	0.000	1.000
fixed		thinO:year2002	0.000	0.000	Inf	0.000	−0.003	0.997
fixed		thinU:year2005	16899335.565	0.000	Inf	98258368656.951	0.003	0.998
fixed		thinO:year2005	1.033	0.062	17.246	1.484	0.023	0.982
fixed		thinU:year2011	52282321.893	0.000	Inf	303986839504.182	0.003	0.998
fixed		thinO:year2011	1.424	0.088	23.113	2.025	0.249	0.804
fixed		thinU:year2017	69693263.410	0.000	Inf	405219858655.896	0.003	0.998
fixed		thinO:year2017	2.893	0.129	64.992	4.593	0.669	0.504
fixed		burnB:year2002	0.000	0.000	Inf	0.000	−0.003	0.997
fixed		burnB:year2005	0.492	0.021	11.340	0.788	−0.443	0.658
fixed		burnB:year2011	0.750	0.036	15.575	1.161	−0.186	0.853
fixed		burnB:year2017	2.621	0.101	68.085	4.356	0.580	0.562
fixed		thinU:burnB:year2002	3.958	0.000	Inf	46013.798	0.000	1.000
fixed		thinO:burnB:year2002	135963785.103	0.000	Inf	1314119482171.880	0.002	0.998
fixed		thinU:burnB:year2005	0.000	0.000	Inf	0.002	−0.003	0.998
fixed		thinO:burnB:year2005	1.665	0.039	70.715	3.185	0.267	0.790
fixed		thinU:burnB:year2011	0.000	0.000	Inf	0.000	−0.003	0.998
fixed		thinO:burnB:year2011	0.793	0.021	30.228	1.473	−0.125	0.901
fixed		thinU:burnB:year2017	0.000	0.000	Inf	0.000	−0.003	0.998
fixed		thinO:burnB:year2017	0.494	0.011	21.627	0.952	−0.366	0.714
random	plot	sd_(Intercept)	0.000					

Note: β = beta coefficient representing the degree of change in the odds ratio of non-zero regeneration for every 1-unit of change in the predictor variable.

Table A8
Estimated marginal means, standard error (SE) and 95 % confidence interval (95 % CI) of regeneration probability of occurrence by treatment combination and year from logistic mixed effects model of Jeffrey pine natural regeneration occurrence.

Treatment	Year	Response	SE	95 % CI	
BN	2000	0.030	0.021	0.007	0.112
BO	2000	0.045	0.025	0.015	0.130
BU	2000	0.015	0.015	0.002	0.098
UN	2000	0.015	0.015	0.002	0.098
UO	2000	0.045	0.025	0.015	0.130
UU	2000	0.000	0.000	0.000	1.000
BN	2002	0.000	0.000	0.000	1.000
BO	2002	0.000	0.000	0.000	1.000
BU	2002	0.000	0.000	0.000	1.000
UN	2002	0.030	0.021	0.007	0.112
UO	2002	0.000	0.000	0.000	1.000
UU	2002	0.000	0.000	0.000	1.000
BN	2005	0.030	0.021	0.007	0.112
BO	2005	0.075	0.032	0.031	0.167
BU	2005	0.090	0.035	0.041	0.185
UN	2005	0.030	0.021	0.007	0.112
UO	2005	0.090	0.035	0.041	0.185
UU	2005	0.015	0.015	0.002	0.098
BN	2011	0.045	0.025	0.015	0.130
BO	2011	0.075	0.032	0.031	0.167
BU	2011	0.090	0.035	0.041	0.185
UN	2011	0.030	0.021	0.007	0.112
UO	2011	0.119	0.040	0.061	0.221
UU	2011	0.045	0.025	0.015	0.130
BN	2017	0.075	0.032	0.031	0.167
BO	2017	0.149	0.044	0.082	0.256
BU	2017	0.075	0.032	0.031	0.167
UN	2017	0.015	0.015	0.002	0.098
UO	2017	0.119	0.040	0.061	0.221
UU	2017	0.030	0.021	0.007	0.112

UN = unburned no thin control, UU = unburned understory thin, UO = unburned overstory thin, BN = burned no thin, BU = burned understory thin, BO = burned overstory thin.

unburned understory thins (mean 1276 tph, 55 – 29,838 95 % CI), burning alone (mean 624 tph, 27 – 14,541 95 % CI), burned overstory thins (mean 584 tph, 25 – 13,423 95 % CI), unburned overstory thins (mean 20 tph, 1 – 549 95 % CI), and untreated controls (mean 18 tph, 1 – 486 95 % CI).

3.3. *Jeffrey pine and sugar pine nature regeneration in response to treatments*

Logistic model fit was low for Jeffrey pine (R^2 = 0.037), mean modelled probability of occurrence across all years was 4.6 %, and no combination of burning, thinning, or year was associated with changes in the probability of Jeffrey pine natural regeneration (Fig. 2, Tables A7–A9). Models for Jeffrey pine had high uncertainty resulting in confidence intervals ranging from 0 to 1 (0 to 100 % probability of occurrence), especially in the first year after treatments (2002). Prior to treatments, Jeffrey pine probability of occupancy was highest in unburned overstory thins (mean 0.05, 0.03–0.13 95 % CI) and burned overstory thins (mean 0.05, 0.03–0.13 95 % CI), followed by burning alone (mean 0.03, 0.01–0.11 95 % CI), untreated controls (mean 0.02, 0.00–0.10 95 % CI), burned understory thins (mean 0.02, 0.00–0.10 95 % CI), and unburned understory thins (mean 0.00, 0.00–1.00 95 % CI). Sixteen years after treatments, Jeffrey pine probability of occupancy was highest in burned overstory thins (mean 0.15, 0.08–0.26 95 % CI), followed by unburned overstory thins (mean 0.12, 0.06–0.22 95 % CI), burned understory thins (mean 0.07, 0.03 – 0.17 95 % CI), burning alone (mean 0.07, 0.03–0.17 95 % CI), unburned understory thins (mean 0.02, 0.01–0.11 95 % CI), and untreated controls (mean 0.01, 0.00–0.09 95 % CI).

Fit for the logistic model was low for sugar pine (R^2 = 0.038), with

Table A9
Pairwise comparison of Jeffrey pine natural regeneration probability of occurrence between treatments within years from logistic mixed effects model.

Treatment Contrast	Year	Ratio	SE	z.ratio	p
BN/BO	2000	0.656	0.610	−0.453	0.998
BN/BU	2000	2.031	2.512	0.573	0.993
BN/UO	2000	0.656	0.610	−0.453	0.998
BN/UU	2000	69693252.911	405219785443.703	0.003	1.000
BU/BO	2000	0.323	0.378	−0.967	0.928
BU/UO	2000	0.323	0.378	−0.967	0.928
UN/BN	2000	0.492	0.609	−0.573	0.993
UN/BO	2000	0.323	0.378	−0.967	0.928
UN/BU	2000	1.000	1.425	0.000	1.000
UN/UO	2000	0.323	0.378	−0.967	0.928
UN/UU	2000	34318651.185	199540070121.087	0.003	1.000
UO/BO	2000	1.000	0.835	0.000	1.000
UU/BO	2000	0.000	0.000	−0.003	1.000
UU/BU	2000	0.000	0.000	−0.003	1.000
UU/UO	2000	0.000	0.000	−0.003	1.000
BN/BO	2002	0.920	7335.589	0.000	1.000
BN/BU	2002	1.042	8563.953	0.000	1.000
BN/UO	2002	0.904	7170.178	0.000	1.000
BN/UU	2002	1.022	8357.999	0.000	1.000
BU/BO	2002	0.883	7116.537	0.000	1.000
BU/UO	2002	0.867	6956.722	0.000	1.000
UN/BN	2002	68196241.493	392233799570.508	0.003	1.000
UN/BO	2002	62765249.942	346324526550.385	0.003	1.000
UN/BU	2002	71059717.173	417195453309.523	0.003	1.000
UN/UO	2002	61619979.245	336888880651.859	0.003	1.000
UN/UU	2002	69693518.490	405221929977.083	0.003	1.000
UO/BO	2002	1.019	7912.004	0.000	1.000
UU/BO	2002	0.901	7218.909	0.000	1.000
UU/BU	2002	1.020	8424.898	0.000	1.000
UU/UO	2002	0.884	7056.481	0.000	1.000
BN/BO	2005	0.382	0.326	−1.127	0.871
BN/BU	2005	0.313	0.261	−1.391	0.733
BN/UO	2005	0.313	0.261	−1.391	0.733
BN/UU	2005	2.031	2.512	0.573	0.993
BU/BO	2005	1.220	0.771	0.314	1.000
BU/UO	2005	1.000	0.605	0.000	1.000
UN/BN	2005	1.000	1.015	0.000	1.000
UN/BO	2005	0.382	0.326	−1.127	0.871
UN/BU	2005	0.313	0.261	−1.391	0.733
UN/UO	2005	0.313	0.261	−1.391	0.733
UN/UU	2005	2.031	2.512	0.573	0.993
UO/BO	2005	1.220	0.771	0.314	1.000
UU/BO	2005	0.188	0.208	−1.507	0.660
UU/BU	2005	0.154	0.169	−1.709	0.526
UU/UO	2005	0.154	0.169	−1.709	0.526
BN/BO	2011	0.581	0.437	−0.722	0.979
BN/BU	2011	0.477	0.348	−1.016	0.913
BN/UO	2011	0.346	0.242	−1.516	0.654
BN/UU	2011	1.000	0.835	0.000	1.000
BU/BO	2011	1.220	0.771	0.314	1.000
BU/UO	2011	0.725	0.414	−0.563	0.993
UN/BN	2011	0.656	0.610	−0.453	0.998
UN/BO	2011	0.382	0.326	−1.127	0.871
UN/BU	2011	0.313	0.261	−1.391	0.733
UN/UO	2011	0.227	0.184	−1.829	0.447
UN/UU	2011	0.656	0.610	−0.453	0.998
UO/BO	2011	1.681	1.006	0.868	0.954
UU/BO	2011	0.581	0.437	−0.722	0.979
UU/BU	2011	0.477	0.348	−1.016	0.913
UU/UO	2011	0.346	0.242	−1.516	0.654
BN/BO	2017	0.460	0.266	−1.346	0.759
BN/BU	2017	1.000	0.657	0.000	1.000
BN/UO	2017	0.595	0.356	−0.868	0.954
BN/UU	2017	2.621	2.242	1.127	0.871
BU/BO	2017	0.460	0.266	−1.346	0.759
BU/UO	2017	0.595	0.356	−0.868	0.954
UN/BN	2017	0.188	0.208	−1.507	0.660
UN/BO	2017	0.086	0.092	−2.301	0.193
UN/BU	2017	0.188	0.208	−1.507	0.660
UN/UO	2017	0.112	0.120	−2.037	0.321
UN/UU	2017	0.492	0.609	−0.573	0.993
UO/BO	2017	0.773	0.394	−0.506	0.996

(*continued on next page*)

Table A9 (*continued*)

Treatment Contrast	Year	Ratio	SE	z.ratio	p
UU/BO	2017	0.175	0.140	−2.188	0.243
UU/BU	2017	0.382	0.326	−1.127	0.871
UU/UO	2017	0.227	0.184	−1.829	0.447

UN = unburned no thin control, UU = unburned understory thin, UO = unburned overstory thin, BN = burned no thin, BU = burned understory thin, BO = burned overstory thin.

mean modelled probability of occurrence across all years of 12.8 %, and no combination of burning, thinning, or year was associated with changes in the probability of sugar pine natural regeneration, although interactions between thinning, and year fixed effects were important (Fig. 2, Tables A10–A12). Prior to treatments, sugar pine probability of occupancy was highest in unburned overstory thins (mean 0.19, 0.12–0.31 95 % CI), followed by untreated controls (mean 0.18, 0.1–0.29 95 % CI), unburned understory thins (mean 0.16, 0.09 – 0.27 95 % CI), burning alone (mean 0.13, 0.07–0.24 95 % CI), burned understory thins (mean 0.06, 0.02–0.15 95 % CI), and burned overstory thins (mean 0.03, 0.01–0.11 95 % CI). Sixteen years after treatments, sugar pine probability of occupancy was highest in unburned overstory thins (mean 0.21, 0.13–0.32 95 % CI), followed by burning alone (mean 0.16, 0.09–0.27 95 % CI), untreated controls (mean 0.16, 0.09 – 0.27 95 % CI), unburned understory thins (mean 0.15, 0.08–0.26 95 % CI), burned understory thins (mean 0.08, 0.04–0.19 95 % CI), and burned overstory thins (mean 0.07, 0.03–0.17 95 % CI).

3.4. Pretreatment environmental conditions in vegetation patch types

Prior to treatments, patch types had distinctly different environmental and vegetation conditions (Table 2). Closed canopy patches had high canopy cover (84 %), low amounts of bare soil (0.0 %), little shrub competition (0 % cover for any shrub species), and deep soil (80.3 cm). *Ceanothus cordulatus* dominated patches unsurprisingly had high cover of their namesake (60 %), while also having lower canopy cover (50 %), less litter cover (2.5 % versus 4.3 %), less small wood cover (1 % versus 7 %), and similar soil depth compared to closed canopy patches. Open patches had the lowest canopy cover (37 %) lowest litter cover (1 %), highly variable bare soil (0 – 90 %) and rock cover (0 – 97 %), and the shallowest soil (48.4 cm).

3.5. Conifer natural regeneration in response to treatments and pretreatment vegetation types

The GLMM model of conifer natural regeneration density in relation to vegetation patch types and treatment combinations had a marginal R^2 = 0.568 and conditional R^2 = 0.633. Only the closed canopy patch fixed effect had a significant individual effect on density (β = 2.747, Z = 2.061, p = 0.0399), but interactions between thinning, patch type and year were important (Table A13). Conifer regeneration density was not different between treatment combinations prior to treatment in 2000 or in the first year after treatment in 2002, but differences became apparent over time (Fig. 3, Tables A14 and A15). In 2002, closed canopy vegetation patches in burned overstory thins had marginally lower conifer regeneration density (mean 120 tph, 14–1042 95 % CI), compared to closed canopy patches in burning alone (mean 3324 tph, 1407–7852 95 % CI, t = 2.8, p = 0.057) or untreated controls (mean 3319 tph, 1408–7826 95 % CI, t = 2.799, p = 0.058). Four years after treatments (2005), treatments resulted in significant differences in conifer regeneration density in closed canopy and *Ceanothus* shrub dominated patches, but not open patches. In closed canopy patches, burned overstory thins had lower conifer density (mean 1227 tph, 509–2958 95 % CI) than burned understory thins (mean 9776 tph, 4300–22225 95 % CI, t = 3.378, p = 0.010) or burning alone (mean 8371 tph, 3703–19823 95 % CI, t = 3.137, p = 0.021), and marginally lower than unburned understory thins (mean 5990 tph, 2753–13034 95 % CI, t = 2.647, p = 0.086). Unburned overstory thins in closed canopy patches had lower

Table A10
Fixed effects of logistic mixed effects model of sugar pine natural regeneration presence.

Effect	Group	Parameter	β	95 % CI		SE	Z	p
fixed		(Intercept)	−1.522	−2.147	−0.898	0.319	−4.778	0.000
fixed		thinU	−0.105	−1.004	0.794	0.459	−0.229	0.819
fixed		thinO	0.098	−0.771	0.968	0.444	0.222	0.825
fixed		burnB	−0.341	−1.280	0.599	0.479	−0.711	0.477
fixed		year2002	0.279	−0.569	1.128	0.433	0.645	0.519
fixed		year2005	0.279	−0.569	1.128	0.433	0.645	0.519
fixed		year2011	0.098	−0.771	0.968	0.444	0.222	0.825
fixed		year2017	−0.105	−1.004	0.794	0.459	−0.229	0.819
fixed		thinU:burnB	−0.789	−2.312	0.735	0.778	−1.014	0.310
fixed		thinO:burnB	−1.716	−3.513	0.081	0.917	−1.872	**0.061**
fixed		thinU:year2002	−1.169	−2.572	0.233	0.716	−1.634	0.102
fixed		thinO:year2002	−1.612	−3.064	−0.160	0.741	−2.176	**0.030**
fixed		thinU:year2005	−0.650	−1.947	0.647	0.662	−0.982	0.326
fixed		thinO:year2005	−1.373	−2.757	0.012	0.706	−1.944	**0.052**
fixed		thinU:year2011	0.286	−0.941	1.512	0.626	0.457	0.648
fixed		thinO:year2011	−0.197	−1.427	1.033	0.628	−0.314	0.754
fixed		thinU:year2017	−0.008	−1.303	1.287	0.661	−0.012	0.990
fixed		thinO:year2017	0.198	−1.036	1.431	0.629	0.314	0.753
fixed		burnB:year2002	−0.279	−1.585	1.027	0.666	−0.419	0.675
fixed		burnB:year2005	−0.043	−1.321	1.234	0.652	−0.067	0.947
fixed		burnB:year2011	0.242	−1.038	1.523	0.653	0.371	0.711
fixed		burnB:year2017	0.341	−0.970	1.652	0.669	0.509	0.610
fixed		thinU:burnB:year2002	−15.527	−4028.424	3997.370	2047.434	−0.008	0.994
fixed		thinO:burnB:year2002	−14.438	−4186.437	4157.562	2128.610	−0.007	0.995
fixed		thinU:burnB:year2005	0.653	−1.455	2.762	1.076	0.607	0.544
fixed		thinO:burnB:year2005	1.862	−0.553	4.276	1.232	1.511	0.131
fixed		thinU:burnB:year2011	0.132	−1.856	2.121	1.015	0.130	0.896
fixed		thinO:burnB:year2011	1.339	−0.879	3.558	1.132	1.183	0.237
fixed		thinU:burnB:year2017	0.210	−1.867	2.287	1.060	0.198	0.843
fixed		thinO:burnB:year2017	0.530	−1.760	2.820	1.168	0.454	0.650
random	plot	sd_(Intercept)	0.000					

Note: β = beta coefficient representing the degree of change in the odds ratio of non-zero regeneration for every 1-unit of change in the predictor variable.

Table A11
Estimated marginal means, standard error (SE) and 95 % confidence interval (95 % CI) of regeneration probability of occurrence by treatment combination and year from logistic mixed effects model of sugar pine natural regeneration occurrence.

Treatment	Year	Response	SE	95 % CI	
BN	2000	0.134	0.042	0.071	0.238
BO	2000	0.030	0.021	0.007	0.112
BU	2000	0.060	0.029	0.023	0.149
UN	2000	0.179	0.047	0.105	0.289
UO	2000	0.194	0.048	0.116	0.306
UU	2000	0.164	0.045	0.093	0.273
BN	2002	0.134	0.042	0.071	0.238
BO	2002	0.000	0.000	0.000	1.000
BU	2002	0.000	0.000	0.000	1.000
UN	2002	0.224	0.051	0.140	0.339
UO	2002	0.060	0.029	0.023	0.149
UU	2002	0.075	0.032	0.031	0.167
BN	2005	0.164	0.045	0.093	0.273
BO	2005	0.060	0.029	0.023	0.149
BU	2005	0.075	0.032	0.031	0.167
UN	2005	0.224	0.051	0.140	0.339
UO	2005	0.075	0.032	0.031	0.167
UU	2005	0.119	0.040	0.061	0.221
BN	2011	0.179	0.047	0.105	0.289
BO	2011	0.119	0.040	0.061	0.221
BU	2011	0.119	0.040	0.061	0.221
UN	2011	0.194	0.048	0.116	0.306
UO	2011	0.179	0.047	0.105	0.289
UU	2011	0.224	0.051	0.140	0.339
BN	2017	0.164	0.045	0.093	0.273
BO	2017	0.075	0.032	0.031	0.167
BU	2017	0.090	0.035	0.041	0.185
UN	2017	0.164	0.045	0.093	0.273
UO	2017	0.209	0.050	0.128	0.323
UU	2017	0.149	0.044	0.082	0.256

UN = unburned no thin control, UU = unburned understory thin, UO = unburned overstory thin, BN = burned no thin, BU = burned understory thin, BO = burned overstory thin.

conifer density (mean 1404 tph, 577–3420 95 % CI) than burned understory thins ($t = 3.140$, $p = 0.021$) or burning alone ($t = 2.899$, $p = 0.044$). Within closed canopy patches, no combination of thinning and/or burning resulted in significantly different conifer regeneration densities than found in closed canopy patches of untreated controls (mean 2717 tph, 1175–6285 95 % CI). Within *Ceanothus* shrub dominated patches, unburned understory thins had higher conifer regeneration density (mean 15,598 tph, 4002–60802 95 % CI), compared to burning alone (mean 506 tph, 156–1641 95 % CI, $t = -3.734$, $p = 0.003$), unburned overstory thins (mean 526 tph, 136 – 2034 95 % CI, $t = 3.463$, $p = 0.007$), burned overstory thins (mean 1063 tph, 335 – 3377 95 % CI, $t = 2.949$, $p = 0.038$), or untreated controls (mean 1198 tph, 439–3269 95 %, $t = -2.974$, $p = 0.035$). Within *Ceanothus* shrub patches, conifer regeneration densities in burned understory thins (mean 2074 tph, 526–8175 95 % CI) did not differ from any other treatment combination.

Ten years after treatments (2011), there were significant differences in conifer regeneration density in closed canopy and *Ceanothus* shrub dominated patches, but not open patches. In closed canopy patches, burned overstory thins had lower conifer density (mean 1388 tph, 599–3217 95 % CI) than burned understory thins (mean 8154 tph, 3630–18318 95 % CI, $t = 2.973$, $p = 0.035$), and marginally lower than unburned understory thins (mean 6417 tph, 2938–14015 95 % CI, $t = 2.615$, $p = 0.094$). Burned understory thins also had marginally higher regeneration density than unburned overstory thins (mean 1642 tph, 696–3874 95 % CI, $t = 2.662$, $p = 0.083$). Within closed canopy patches, no combination of thinning and/or burning resulted in significantly different conifer regeneration densities than found in closed canopy patches of untreated controls (mean 1950 tph, 827–4595 95 % CI) or burning alone (mean 2524 tph, 1124 – 5671 95 % CI). Within *Ceanothus* shrub dominated patches, unburned understory thins had much higher

Table A12
Pairwise comparison of sugar pine natural regeneration probability of occurrence between treatments within years from logistic mixed effects model of sugar pine natural regeneration occurrence.

Treatment Contrast	Year	Ratio	SE	z.ratio	p
BN/BO	2000	5.043	4.046	2.017	0.333
BN/BU	2000	2.444	1.535	1.423	0.713
BN/UO	2000	0.645	0.305	−0.928	0.939
BN/UU	2000	0.790	0.385	−0.484	0.997
BU/BO	2000	2.063	1.824	0.820	0.964
BU/UO	2000	0.264	0.159	−2.217	0.230
UN/BN	2000	1.406	0.674	0.711	0.981
UN/BO	2000	7.091	5.569	2.494	0.126
UN/BU	2000	3.436	2.083	2.037	0.321
UN/UO	2000	0.906	0.402	−0.222	1.000
UN/UU	2000	1.111	0.509	0.229	1.000
UO/BO	2000	7.824	6.115	2.632	0.090
UU/BO	2000	6.384	5.044	2.346	0.176
UU/BU	2000	3.094	1.894	1.845	0.437
UU/UO	2000	0.816	0.369	−0.450	0.998
BN/BO	2002	47106575.865	100271526014.785	0.008	1.000
BN/BU	2002	43582202.090	89231681086.286	0.009	1.000
BN/UO	2002	2.444	1.535	1.423	0.713
BN/UU	2002	1.924	1.129	1.115	0.875
BU/BO	2002	1.081	3192.306	0.000	1.000
BU/UO	2002	0.000	0.000	−0.008	1.000
UN/BN	2002	1.859	0.860	1.340	0.763
UN/BO	2002	87569908.121	186402176722.681	0.009	1.000
UN/BU	2002	81018188.283	165879390110.745	0.009	1.000
UN/UO	2002	4.543	2.695	2.552	0.109
UN/UU	2002	3.577	1.966	2.319	0.186
UO/BO	2002	19274647.812	41028207704.834	0.008	1.000
UU/BO	2002	24481900.948	52112418415.590	0.008	1.000
UU/BU	2002	22650238.000	46374867214.565	0.008	1.000
UU/UO	2002	1.270	0.882	0.344	0.999
BN/BO	2005	3.094	1.894	1.845	0.437
BN/BU	2005	2.436	1.388	1.562	0.624
BN/UO	2005	2.436	1.388	1.562	0.624
BN/UU	2005	1.449	0.725	0.740	0.977
BU/BO	2005	1.270	0.882	0.344	0.999
BU/UO	2005	1.000	0.657	0.000	1.000
UN/BN	2005	1.469	0.648	0.871	0.953
UN/BO	2005	4.543	2.695	2.552	0.109
UN/BU	2005	3.577	1.966	2.319	0.186
UN/UO	2005	3.577	1.966	2.319	0.186
UN/UU	2005	2.127	1.015	1.582	0.611
UO/BO	2005	1.270	0.882	0.344	0.999
UU/BO	2005	2.136	1.364	1.188	0.843
UU/BU	2005	1.681	1.006	0.868	0.954
UU/UO	2005	1.681	1.006	0.868	0.954
BN/BO	2011	1.609	0.794	0.964	0.929
BN/BU	2011	1.609	0.794	0.964	0.929
BN/UO	2011	1.000	0.451	0.000	1.000
BN/UU	2011	0.756	0.327	−0.645	0.988
BU/BO	2011	1.000	0.533	0.000	1.000
BU/UO	2011	0.621	0.307	−0.964	0.929
UN/BN	2011	1.103	0.490	0.222	1.000
UN/BO	2011	1.775	0.865	1.178	0.847
UN/BU	2011	1.775	0.865	1.178	0.847
UN/UO	2011	1.103	0.490	0.222	1.000
UN/UU	2011	0.835	0.355	−0.425	0.998
UO/BO	2011	1.609	0.794	0.964	0.929
UU/BO	2011	2.127	1.015	1.582	0.611
UU/BU	2011	2.127	1.015	1.582	0.611
UU/UO	2011	1.322	0.572	0.645	0.988
BN/BO	2017	2.436	1.388	1.562	0.624
BN/BU	2017	1.997	1.079	1.280	0.796
BN/UO	2017	0.744	0.332	−0.664	0.986
BN/UU	2017	1.120	0.533	0.238	1.000
BU/BO	2017	1.220	0.771	0.314	1.000
BU/UO	2017	0.372	0.195	−1.889	0.409
UN/BN	2017	1.000	0.466	0.000	1.000
UN/BO	2017	2.436	1.388	1.562	0.624
UN/BU	2017	1.997	1.079	1.280	0.796
UN/UO	2017	0.744	0.332	−0.664	0.986
UN/UU	2017	1.120	0.533	0.238	1.000

(*continued on next page*)

Table A12 (*continued*)

Treatment Contrast	Year	Ratio	SE	z.ratio	p
UO/BO	2017	3.275	1.813	2.143	0.265
UU/BO	2017	2.175	1.257	1.346	0.759
UU/BU	2017	1.784	0.978	1.055	0.899
UU/UO	2017	0.664	0.303	−0.898	0.947

UN = unburned no thin control, UU = unburned understory thin, UO = unburned overstory thin, BN = burned no thin, BU = burned understory thin, BO = burned overstory thin.

conifer regeneration density (mean 9934 tph, 3216–30683 95 % CI), compared to burning alone (mean 546 tph, 168–1772 95 % CI, t = -3.485, p = 0.007), unburned overstory thins (mean 464 tph, 120 – 1796 95 % CI, t = 3.409, p = 0.009), and untreated controls (mean 863 tph, 316–2354 95 %, t = -3.171, p = 0.019), and marginally higher than burned overstory thins (mean 1174 tph, 370 – 3727 95 % CI, t = 2.593, p = 0.099). Within *Ceanothus* shrub patches, conifer regeneration densities in burned understory thins (mean 3207 tph, 814–12642 95 % CI) did not differ from any other treatment combination.

Sixteen years after treatments (2017), treatment effects weakened, with fewer significant or marginal differences in conifer regeneration density in closed canopy and *Ceanothus* shrub dominated patches, while still no differences in open patches. In closed canopy patches, burned understory thins had marginal higher conifer density (mean 7280 tph, 3210–16512 95 % CI) than untreated controls (mean 1493 tph, 628–3551 95 % CI, t = -2.606, p = 0.096), unburned overstory thins (mean 1417 tph, 617–3253 95 % CI, t = 2.749, p = 0.066), and burned overstory thins (mean 1425 tph, 618–3286 95 % CI, t = 2.731, p = 0.069). Within closed canopy patches, no combination of thinning and/or burning resulted in significantly different conifer regeneration densities than found in closed canopy patches of unburned understory thins (mean 1950 tph, 827–4595 95 % CI) or burning alone (mean 2524 tph, 1124 – 5671 95 % CI). Within *Ceanothus* shrub dominated patches, unburned understory thins had much higher conifer regeneration density (mean 9295 tph, 2646–32660 95 % CI), compared to unburned overstory thins (mean 546 tph, 141 – 2122 95 % CI, t = 3.004, p = 0.032), and marginally higher than untreated controls (mean 946 tph, 325–2754 95 %, t = -2.714, p = 0.072). Within *Ceanothus* shrub patches, conifer regeneration densities after burning alone (mean 1059 tph, 273–4102 95 % CI), burned understory thins (mean 2892 tph, 734–11403 95 % CI), and burned overstory thins (mean 1210 tph, 381–3845 95 % CI) did not differ from any other treatment combination.

3.6. *Effects of planting on regeneration density after overstory thinning*

One year after treatments (2002), planting increased regeneration density above natural regeneration levels of all three planted species in burned and unburned overstory thinned treatments, except for Jeffrey pine in unburned overstory thinned treatments (Table 3). Most notable was the effect of planting white fir, which resulted in high regeneration density in burned overstory thinned treatments (mean 609 tph, 531–687 95 % CI) versus natural regeneration alone (mean 19 tph, 2–45 95 % CI, z = 1378, p = 0.000). In unburned overstory thinned treatments, combined planted and natural regeneration of white fir (mean 392 tph, 308 – 483 95 % CI) was also much higher than natural regeneration alone (mean 66 tph, 27 – 112 95 % CI, z = 528, p = 0.000). There was no initial natural regeneration of Jeffrey pine in burned or unburned overstory thinned treatments, and no initial natural sugar pine regeneration in burned overstory thinned treatments. Planting increased initial combined regeneration of Jeffrey pine in burned overstory thins (mean 54 tph, 31–80 95 % CI, z = 55, p = 0.004), but not in unburned overstory thins (mean 12 tph, 4–21 95 % CI, z = 6, p = 0.149). Planting increased initial combined regeneration of sugar pine in burned overstory thins (mean 124 tph, 78–173 95 % CI, z = 105, p = 0.000) and unburned overstory thins (mean 144 tph, 93–198 95 % CI, z = 105, p = 0.000).

Sixteen years after treatments (2017), initial effects of planting were largely unchanged, although overall white fir regeneration density declined, Jeffrey pine regeneration increased, and changes in sugar pine regeneration varied by treatment combination. Combined white fir regeneration density was higher in burned overstory thins (mean 462 tph, 324–626 95 % CI) versus natural regeneration alone (mean 318 tph, 190–466 95 % CI, z = 276, p = 0.000). In unburned overstory thinned treatments, combined regeneration of planted and natural white fir regeneration declined greatly since 2002 (mean 128 tph, 81 – 184 95 % CI), but was still greater than natural regeneration alone (mean 70 tph, 45 – 95 95 % CI, z = 45, p = 0.006). For Jeffrey pine in burned overstory thinned treatments, planting marginally increased regeneration density (mean 109 tph, 64 – 157 95 % CI) versus natural regeneration alone (mean 74 tph, 39 – 111 95 % CI, z = 15, p = 0.058), but planting did not increase regeneration density in unburned overstory thin treatments (mean 74 tph, 39 – 113 95 % CI) versus natural regeneration alone (mean 50 tph, 27 – 78 95 % CI, z = 6, p = 0.181), although there was previously no natural Jeffrey pine regeneration in unburned overstory thinned treatments in 2002. Combined planted and natural sugar pine regeneration was still marginally higher in burned overstory thin treatments (mean 66 tph, 31–103 95 % CI) versus natural regeneration alone (mean 23 tph, 12–39 95 % CI, z = 15, p = 0.058), and combined sugar pine regeneration was still higher in unburned overstory thin treatments (mean 132 tph, 80–186 95 % CI) versus natural regeneration alone (mean 97 tph, 56–153 95 % CI, z = 21, p = 0.031).

4. Discussion

Sixteen years after prescribed burning and thinning treatments, our study found treatments broadly did not achieve all restoration objectives associated with regeneration composition and abundance. Specifically, no combination of prescribed burning and/or thinning reduced densities of shade-tolerant white fir and incense-cedar natural regeneration while simultaneously increasing densities of Jeffrey pine or sugar pine natural regeneration. High regeneration densities of shade-tolerant species and low densities of pine species suggest prescribed burning and understory thinning treatments, both individually and in combination, in the absence of future disturbance, could reinforce compositional change associated with over a century of fire exclusion. Natural regeneration responses to treatments were mediated by pretreatment vegetation patch types, but understory thinning without burning resulted in large increases in regeneration density in patches that were dominated by shrubs prior to treatment. Of all treatments, only the combination of overstory thinning (with or without burning) and planting increased pine regeneration without increasing natural white fir and incense cedar regeneration. In combination these findings suggest fuel reduction and ecosystem restoration objectives in mixed-conifer forests of the Sierra Nevada are not intrinsically convergent, and with respect to regeneration objectives treatments should consider what total and species-specific cover and basal area reductions are needed to avoid high regeneration densities of shade tolerant species while promoting adequate pine regeneration, and under what conditions planting pines may be required to maintain them in the regeneration pool.

4.1. *Treatment effects on natural regeneration composition and abundance*

Our findings are largely consistent with initial and short-term regeneration after treatments at Teakettle Experimental Forest (Zald et al., 2008), indicating that in the absence of future disturbances, current composition and abundance trajectories are unlikely to change, unlike some forest types and disturbance combinations that can result in delayed regeneration (Gill et al., 2017; Stevens-Rumann et al., 2022). Large increases in regeneration of shade-tolerant white fir and incense-cedar after first entry burning and/or understory thinning have also

Table A13
Fixed effects of generalized linear mixed effects model of conifer natural regeneration density in relation to treatment, year, and pretreatment vegetation patch type.

Effect	Component	Group	Parameter	β	95 % CI		SE	Z	p
fixed	cond	NA	(Intercept)	1263.315	448.192	3560.900	667.941	13.507	0.000
fixed	cond	NA	thinU	1.658	0.264	10.419	1.555	0.540	0.590
fixed	cond	NA	thinO	0.790	0.141	4.417	0.694	−0.269	0.788
fixed	cond	NA	burnB	0.626	0.114	3.433	0.544	−0.540	0.589
fixed	cond	NA	patchClosed	2.747	1.051	7.182	1.347	2.061	0.039
fixed	cond	NA	patchOpen	0.976	0.354	2.691	0.505	−0.047	0.963
fixed	cond	NA	year2002	0.921	0.316	2.688	0.503	−0.150	0.881
fixed	cond	NA	year2005	0.949	0.325	2.772	0.519	−0.096	0.923
fixed	cond	NA	year2011	0.683	0.233	1.999	0.374	−0.696	0.487
fixed	cond	NA	year2017	0.749	0.241	2.326	0.433	−0.500	0.617
fixed	cond	NA	thinU:burnB	1.094	0.060	19.952	1.620	0.061	0.952
fixed	cond	NA	thinO:burnB	5.731	0.472	69.513	7.297	1.371	0.170
fixed	cond	NA	thinU:patchClosed	0.988	0.179	5.465	0.862	−0.013	0.989
fixed	cond	NA	thinO:patchClosed	0.605	0.124	2.959	0.490	−0.620	0.535
fixed	cond	NA	thinU:patchOpen	2.487	0.318	19.458	2.610	0.868	0.385
fixed	cond	NA	thinO:patchOpen	1.572	0.256	9.647	1.455	0.489	0.625
fixed	cond	NA	burnB:patchClosed	2.037	0.417	9.954	1.649	0.879	0.379
fixed	cond	NA	burnB:patchOpen	2.412	0.407	14.291	2.189	0.970	0.332
fixed	cond	NA	thinU:year2002	0.800	0.075	8.579	0.968	−0.185	0.853
fixed	cond	NA	thinO:year2002	0.556	0.056	5.506	0.651	−0.501	0.616
fixed	cond	NA	thinU:year2005	7.848	0.986	62.455	8.305	1.947	0.052
fixed	cond	NA	thinO:year2005	0.555	0.076	4.030	0.561	−0.582	0.561
fixed	cond	NA	thinU:year2011	6.942	1.007	47.854	6.838	1.967	0.049
fixed	cond	NA	thinO:year2011	0.682	0.094	4.925	0.688	−0.380	0.704
fixed	cond	NA	thinU:year2017	5.926	0.769	45.634	6.172	1.708	0.088
fixed	cond	NA	thinO:year2017	0.731	0.099	5.410	0.747	−0.306	0.759
fixed	cond	NA	burnB:year2002	0.896	0.135	5.946	0.865	−0.113	0.910
fixed	cond	NA	burnB:year2005	0.675	0.107	4.269	0.635	−0.418	0.676
fixed	cond	NA	burnB:year2011	1.011	0.160	6.406	0.952	0.012	0.991
fixed	cond	NA	burnB:year2017	1.789	0.243	13.178	1.822	0.571	0.568
fixed	cond	NA	patchClosed:year2002	1.038	0.276	3.906	0.702	0.055	0.956
fixed	cond	NA	patchOpen:year2002	1.043	0.260	4.175	0.738	0.059	0.953
fixed	cond	NA	patchClosed:year2005	0.825	0.222	3.074	0.554	−0.286	0.775
fixed	cond	NA	patchOpen:year2005	0.868	0.219	3.444	0.610	−0.202	0.840
fixed	cond	NA	patchClosed:year2011	0.822	0.218	3.100	0.557	−0.289	0.773
fixed	cond	NA	patchOpen:year2011	1.079	0.271	4.291	0.760	0.108	0.914
fixed	cond	NA	patchClosed:year2017	0.575	0.144	2.286	0.405	−0.786	0.432
fixed	cond	NA	patchOpen:year2017	1.262	0.287	5.544	0.953	0.308	0.758
fixed	cond	NA	thinU:burnB:patchClosed	0.396	0.026	6.018	0.550	−0.667	0.505
fixed	cond	NA	thinO:burnB:patchClosed	0.244	0.023	2.543	0.292	−1.180	0.238
fixed	cond	NA	thinU:burnB:patchOpen	0.213	0.010	4.693	0.336	−0.980	0.327
fixed	cond	NA	thinO:burnB:patchOpen	0.301	0.022	4.075	0.400	−0.903	0.367
fixed	cond	NA	thinU:burnB:year2002	0.813	0.021	32.090	1.525	−0.110	0.912
fixed	cond	NA	thinO:burnB:year2002	0.587	0.014	24.464	1.117	−0.280	0.780
fixed	cond	NA	thinU:burnB:year2005	0.288	0.011	7.478	0.478	−0.749	0.454
fixed	cond	NA	thinO:burnB:year2005	0.837	0.051	13.811	1.197	−0.125	0.901
fixed	cond	NA	thinU:burnB:year2011	0.466	0.020	11.084	0.754	−0.472	0.637
fixed	cond	NA	thinO:burnB:year2011	0.697	0.042	11.477	0.996	−0.252	0.801
fixed	cond	NA	thinU:burnB:year2017	0.254	0.009	6.927	0.429	−0.812	0.417
fixed	cond	NA	thinO:burnB:year2017	0.346	0.019	6.255	0.511	−0.719	0.472
fixed	cond	NA	thinU:patchClosed:year2002	0.462	0.035	6.162	0.611	−0.584	0.559
fixed	cond	NA	thinO:patchClosed:year2002	1.324	0.100	17.484	1.743	0.213	0.831
fixed	cond	NA	thinU:patchOpen:year2002	0.000	0.000	Inf	0.000	−0.037	0.970
fixed	cond	NA	thinO:patchOpen:year2002	0.934	0.053	16.374	1.365	−0.047	0.963
fixed	cond	NA	thinU:patchClosed:year2005	0.171	0.017	1.685	0.200	−1.513	0.130
fixed	cond	NA	thinO:patchClosed:year2005	1.949	0.206	18.403	2.232	0.582	0.560
fixed	cond	NA	thinU:patchOpen:year2005	0.073	0.005	1.129	0.102	−1.873	0.061
fixed	cond	NA	thinO:patchOpen:year2005	0.819	0.063	10.670	1.073	−0.152	0.879
fixed	cond	NA	thinU:patchClosed:year2011	0.289	0.033	2.515	0.319	−1.124	0.261
fixed	cond	NA	thinO:patchClosed:year2011	2.587	0.277	24.163	2.949	0.834	0.404
fixed	cond	NA	thinU:patchOpen:year2011	0.113	0.008	1.642	0.154	−1.597	0.110
fixed	cond	NA	thinO:patchOpen:year2011	0.775	0.063	9.499	0.991	−0.200	0.842
fixed	cond	NA	thinU:patchClosed:year2017	0.291	0.030	2.791	0.335	−1.071	0.284
fixed	cond	NA	thinO:patchClosed:year2017	2.716	0.287	25.692	3.114	0.871	0.384
fixed	cond	NA	thinU:patchOpen:year2017	0.118	0.007	1.914	0.167	−1.504	0.133
fixed	cond	NA	thinO:patchOpen:year2017	0.851	0.065	11.106	1.115	−0.123	0.902
fixed	cond	NA	burnB:patchClosed:year2002	0.876	0.100	7.657	0.969	−0.119	0.905
fixed	cond	NA	burnB:patchOpen:year2002	0.680	0.056	8.205	0.864	−0.304	0.761
fixed	cond	NA	burnB:patchClosed:year2005	3.581	0.439	29.221	3.836	1.191	0.234
fixed	cond	NA	burnB:patchOpen:year2005	3.130	0.297	32.930	3.758	0.950	0.342
fixed	cond	NA	burnB:patchClosed:year2011	1.005	0.122	8.261	1.080	0.004	0.997
fixed	cond	NA	burnB:patchOpen:year2011	1.397	0.131	14.929	1.688	0.276	0.782
fixed	cond	NA	burnB:patchClosed:year2017	1.300	0.136	12.455	1.499	0.227	0.820
fixed	cond	NA	burnB:patchOpen:year2017	0.691	0.058	8.226	0.873	−0.292	0.770

(*continued on next page*)

Table A13 (*continued*)

Effect	Component	Group	Parameter	β	95 % CI		SE	Z	p
fixed	cond	NA	thinU:burnB:patchClosed:year2002	3.066	0.059	159.815	6.184	0.555	0.579
fixed	cond	NA	thinO:burnB:patchClosed:year2002	0.125	0.001	11.452	0.289	−0.901	0.367
fixed	cond	NA	thinU:burnB:patchOpen:year2002	1.032E + 10	0.000	Inf	6.134E + 12	0.039	0.969
fixed	cond	NA	thinO:burnB:patchOpen:year2002	3.330	0.024	467.148	8.399	0.477	0.633
fixed	cond	NA	thinU:burnB:patchClosed:year2005	4.251	0.127	142.107	7.611	0.808	0.419
fixed	cond	NA	thinO:burnB:patchClosed:year2005	0.243	0.010	5.832	0.394	−0.873	0.383
fixed	cond	NA	thinU:burnB:patchOpen:year2005	4.467	0.080	250.065	9.174	0.729	0.466
fixed	cond	NA	thinO:burnB:patchOpen:year2005	0.439	0.012	16.226	0.809	−0.447	0.655
fixed	cond	NA	thinU:burnB:patchClosed:year2011	4.859	0.158	149.722	8.498	0.904	0.366
fixed	cond	NA	thinO:burnB:patchClosed:year2011	0.670	0.028	15.788	1.080	−0.248	0.804
fixed	cond	NA	thinU:burnB:patchOpen:year2011	5.375	0.098	293.800	10.973	0.824	0.410
fixed	cond	NA	thinO:burnB:patchOpen:year2011	0.703	0.020	25.159	1.283	−0.193	0.847
fixed	cond	NA	thinU:burnB:patchClosed:year2017	5.298	0.150	187.629	9.643	0.916	0.360
fixed	cond	NA	thinO:burnB:patchClosed:year2017	0.703	0.027	18.146	1.166	−0.213	0.832
fixed	cond	NA	thinU:burnB:patchOpen:year2017	6.068	0.101	365.824	12.691	0.862	0.389
fixed	cond	NA	thinO:burnB:patchOpen:year2017	1.030	0.027	38.787	1.907	0.016	0.987
fixed	zi	NA	(Intercept)	0.775	0.709	0.847	0.035	−5.612	0.000
ran_pars	cond	plot	sd_(Intercept)	0.585	0.409	0.838			

Note: β = beta coefficient representing the degree of change in the regeneration density for every 1-unit of change in the predictor variable.

been observed elsewhere in the Sierra Nevada (Tubbesing et al., 2019; Walker et al., 2012), consistent with treatment effects on seed availability, reductions in litter depth and exposure of mineral soil, and moderated light and soil moisture conditions created by high overstory retention (McDonald, 1976; Stark, 1965; Zald et al., 2008). Responses to prescribed burning and understory thinning were notably different between shade-tolerant species. White fir regeneration increased in burned unthinned and burned understory thinned treatments, while incense-cedar increased in understory thinned treatments with or without burning, but incense-cedar regeneration also displayed very high within treatment variability. Different regeneration responses by white fir and incense-cedar may be explained by greater shade tolerance and reduced drought tolerance of white fir versus incense-cedar (Minore, 1979), although at Teakettle incense-cedar occupied shadier and moister microsites than white fir (Zald et al., 2008). Alternatively, greater seed densities and germinant survival for white fir in burned unthinned treatments, and for incense-cedar in burned understory thinned treatments, may explain different regeneration responses to treatments (Zald et al., 2008). As such, different regeneration responses of white fir and incense-cedar to burning and understory thinning may reflect more deterministic effects of treatments on environmental conditions, as well as harder to manipulate and temporally variable seed availability and germinant survival.

Overstory thinning (with or without burning) was the only treatment that did not increase regeneration densities of white fir or incense-cedar, although it also did not significantly lower regeneration densities of either species below that found in untreated controls. Overstory thinning may have initially improved substrate suitably for regeneration by exposing mineral soil and reducing litter depth, but it also greatly increased light levels, reduced seed rain of white fir, and reduced germinant survival of incense-cedar (Zald et al., 2008). This is consistent with high stand-level light and thermal microsite conditions inhibiting the establishment of more shade-tolerant and moisture-sensitive species (Gray and Spies, 1997; Keyes et al., 2009; McDonald, 1976). From 2005 to 2017, natural regeneration densities of white fir and incense-cedar remained surprisingly stable after overstory thinning (Table 1), despite large increases in *Ceanothus cordulatus* shrub cover, especially for burned overstory thinned treatments (Goodwin et al., 2018). This may result from an interaction between competitive and facultative roles of dense shrub vegetation (Keyes et al., 2009; Oakley et al., 2006; Royo and Carson, 2006; Skinner and Chang, 1996; Tubbesing et al., 2022), or may simply reflect tree establishment occurring prior to extensive shrub development, versus delayed regeneration as has been seen in large shrub patches after wildfires (Shatford et al., 2007; Welch et al., 2016; Zhang et al., 2006).

Across all treatments, natural regeneration densities were low for both Jeffrey pine and sugar pine (Table 1), and no combination of burning and thinning increased the probability of natural regeneration of either pine species. Poor natural pine regeneration and its lack of response to treatment is despite the presence of large pine seed sources, and increased germinant survival of pines in sown-seed plots in burned and thinned treatment combinations (Zald et al., 2008). For sugar pine, these findings are consistent with other studies showing limited effectiveness of prescribed fire and thinning treatments in promoting its natural regeneration (Levine et al., 2016; Moghaddas et al., 2008; van Mantgem et al., 2004), while elevated mortality and inadequate midstory recruitment suggest declining demographic trends across much of sugar pine's geographic distribution (Fettig et al., 2019; Goheen and Goheen, 2014; May et al., 2023; van Mantgem et al., 2004). Low regeneration density of Jeffrey pine after overstory thinning was somewhat unexpected, as it tends to establish on more open and dry microsites with bare mineral soil (Johnson et al., 2014; Salverson et al., 2011; Stark, 1965; Walker et al., 2012; Zald et al., 2008). At Teakettle, initial Jeffrey pine germinant survival tended to be higher with increased treatment intensity, but lower on bare open sites (Zald et al., 2008). Both Jeffrey and sugar pine seed densities were low across treatments relative to white fir and incense-cedar, but cone counts suggest 2003 may have been a mast year for Jeffrey pine (Zald et al., 2008). Masting in pine species such as Jeffrey and sugar pine can increase dispersal distances, overwhelm seed predation, and increase seed survival (Vander Wall, 2002). In combination, it appears overstory thin treatments initially created light and substrate environmental conditions beneficial to Jeffrey pine regeneration, but seed density after treatments in 2001–2003 was insufficient to substantively increase regeneration, even with a potential mast year two years after treatments in 2003.

4.2. Mediation of regeneration responses by pretreatment vegetation patch types

Pretreatment vegetation patch type mediated overall conifer regeneration responses to treatments, with closed canopy patches displaying the greatest responses to treatments, intermediate responses to treatments occurring within *Ceanothus cordulatus* dominated patches, and treatments having no significant effect on regeneration density within open patches. Plots in shrub and open patches occurred in close proximity to closed canopy forests, so it is unlikely seed dispersal was a limiting factor within any vegetation type, given potential wind and animal dispersal distances (Greene and Johnson, 1989; Vander Wall, 1992). Mediation of regeneration responsiveness to treatments is consistent with gradients of pretreatment resource availability and potential vegetation competition, with greater soil depth and less shrub

Table A14
Estimated marginal means, standard error (SE) and 95 % confidence interval (95 % CI) of regeneration density (tph) by treatment combination, year, and patch type from generalized linear mixed effects model of conifer natural regeneration density.

Treatment	Year	Vegetation Patch Type	Response	SE	95 % CI	
BN	2000	CECO dominated	790.619	544.981	204.751	3052.867
BO	2000	CECO dominated	3577.437	2190.764	1077.234	11880.478
BU	2000	CECO dominated	1434.226	1314.866	237.823	8649.287
UN	2000	CECO dominated	1263.315	667.941	448.192	3560.900
UO	2000	CECO dominated	997.431	699.662	252.229	3944.301
UU	2000	CECO dominated	2095.185	1621.226	459.805	9547.081
BN	2000	Closed canopy	4424.685	1837.789	1960.364	9986.841
BO	2000	Closed canopy	2953.532	1368.074	1191.422	7321.799
BU	2000	Closed canopy	3140.273	1323.360	1374.858	7172.606
UN	2000	Closed canopy	3470.745	1559.522	1438.631	8373.290
UO	2000	Closed canopy	1658.007	702.728	722.460	3805.034
UU	2000	Closed canopy	5689.297	2328.067	2551.209	12687.358
BN	2000	Open	1861.210	1061.454	608.629	5691.651
BO	2000	Open	3988.798	2036.344	1466.528	10849.102
BU	2000	Open	1788.450	908.178	661.052	4838.584
UN	2000	Open	1233.151	598.673	476.182	3193.443
UO	2000	Open	1530.664	924.821	468.368	5002.328
UU	2000	Open	5086.677	3494.628	1323.260	19553.439
BN	2002	CECO dominated	652.924	416.874	186.807	2282.086
BO	2002	CECO dominated	964.959	1193.962	85.369	10907.277
BU	2002	CECO dominated	770.279	701.306	129.320	4588.080
UN	2002	CECO dominated	1164.088	596.352	426.504	3177.233
UO	2002	CECO dominated	511.275	463.779	86.403	3025.393
UU	2002	CECO dominated	1543.679	1405.862	259.030	9199.514
BN	2002	Closed canopy	3323.780	1457.832	1406.985	7851.904
BO	2002	Closed canopy	120.325	132.515	13.897	1041.812
BU	2002	Closed canopy	2172.462	1022.754	863.421	5466.151
UN	2002	Closed canopy	3319.398	1452.640	1407.846	7826.425
UO	2002	Closed canopy	1167.930	613.034	417.475	3267.411
UU	2002	Closed canopy	2009.645	884.453	848.208	4761.420
BN	2002	Open	1089.834	691.909	314.017	3782.397
BO	2002	Open	2372.061	2929.157	210.869	26683.212
BU	2002	Open	1591.822	1099.072	411.323	6160.356
UN	2002	Open	1184.870	553.026	474.659	2957.741
UO	2002	Open	764.006	530.080	196.119	2976.282
UU	2002	Open	0.000	0.001	0.000	Inf
BN	2005	CECO dominated	506.101	303.791	156.062	1641.259
BO	2005	CECO dominated	1063.429	627.016	334.830	3377.474
BU	2005	CECO dominated	2073.867	1451.423	526.086	8175.332
UN	2005	CECO dominated	1198.493	613.611	439.373	3269.175
UO	2005	CECO dominated	525.293	362.781	135.688	2033.589
UU	2005	CECO dominated	15598.470	10827.267	4001.684	60802.460
BN	2005	Closed canopy	8370.600	3483.460	3702.760	18922.898
BO	2005	Closed canopy	1226.628	550.861	508.687	2957.844
BU	2005	Closed canopy	9775.551	4096.514	4299.710	22225.079
UN	2005	Closed canopy	2717.233	1162.473	1174.817	6284.686
UO	2005	Closed canopy	1404.223	637.668	576.633	3419.583
UU	2005	Closed canopy	5990.265	2375.860	2753.229	13033.161
BN	2005	Open	3235.126	1725.688	1137.212	9203.245
BO	2005	Open	1157.844	653.896	382.764	3502.425
BU	2005	Open	2293.098	1135.488	868.816	6052.260
UN	2005	Open	1014.917	467.663	411.345	2504.121
UO	2005	Open	572.879	365.630	163.983	2001.367
UU	2005	Open	2401.690	1522.061	693.540	8316.916
BN	2011	CECO dominated	545.886	327.992	168.137	1772.316
BO	2011	CECO dominated	1173.637	691.977	369.543	3727.370
BU	2011	CECO dominated	3206.953	2244.444	813.512	12642.160
UN	2011	CECO dominated	862.837	441.808	316.285	2353.852
UO	2011	CECO dominated	464.274	320.505	119.994	1796.340
UU	2011	CECO dominated	9934.155	5716.087	3216.265	30683.867
BN	2011	Closed canopy	2524.377	1042.560	1123.597	5671.499
BO	2011	Closed canopy	1388.085	595.326	598.895	3217.227
BU	2011	Closed canopy	8154.164	3367.201	3629.795	18317.945
UN	2011	Closed canopy	1949.551	852.831	827.135	4595.074
UO	2011	Closed canopy	1642.032	719.120	695.988	3874.014
UU	2011	Closed canopy	6416.928	2557.554	2938.118	14014.743
BN	2011	Open	1936.800	1064.133	659.797	5685.376
BO	2011	Open	1074.021	607.518	354.431	3254.566
BU	2011	Open	3646.071	1792.392	1391.164	9555.908
UN	2011	Open	908.904	418.242	368.831	2239.793
UO	2011	Open	595.500	339.237	194.976	1818.794
UU	2011	Open	2929.256	2011.405	762.555	11252.366
BN	2017	CECO dominated	1058.706	731.652	273.229	4102.277

(continued on next page)

Table A14 (*continued*)

Treatment	Year	Vegetation Patch Type	Response	SE	95 % CI	
BO	2017	CECO dominated	1210.494	713.722	381.139	3844.514
BU	2017	CECO dominated	2892.498	2024.462	733.696	11403.282
UN	2017	CECO dominated	945.850	515.758	324.844	2754.037
UO	2017	CECO dominated	546.163	378.214	140.563	2122.134
UU	2017	CECO dominated	9295.294	5959.680	2645.544	32659.627
BN	2017	Closed canopy	4425.004	1928.434	1883.461	10396.105
BO	2017	Closed canopy	1424.588	607.579	617.528	3286.412
BU	2017	Closed canopy	7280.057	3041.894	3209.736	16512.023
UN	2017	Closed canopy	1493.068	660.096	627.707	3551.421
UO	2017	Closed canopy	1416.551	600.797	616.900	3252.742
UU	2017	Closed canopy	4213.176	1662.484	1944.162	9130.334
BN	2017	Open	2173.795	1077.639	822.703	5743.728
BO	2017	Open	1031.620	537.715	371.402	2865.462
BU	2017	Open	2244.767	1082.520	872.342	5776.382
UN	2017	Open	1164.877	588.115	433.043	3133.494
UO	2017	Open	899.500	505.832	298.765	2708.151
UU	2017	Open	3348.039	2300.976	870.548	12876.211

UN = unburned no thin control, UU = unburned understory thin, UO = unburned overstory thin, BN = burned no thin, BU = burned understory thin, BO = burned overstory thin.

cover in closed canopy patches more conducive to tree regeneration, while high light levels and shallow soils in open patches result in adverse microsite conditions, especially for white fir and incense-cedar which dominated the regeneration pool.

Unburned understory thinned treatments resulted in high densities of natural conifer regeneration in *Ceanothus cordulatus* dominated patches. Shrub patches can suppress tree regeneration via direct competition, as well as facilitate regeneration by mediating seed predation (McDonald and Fiddler, 2010; Royo and Carson, 2006; Shainsky and Radosevich, 1986), reducing heat load and evaporative demand, or via belowground interactions (Barbour et al., 1998; Crockett and Hurteau, 2021; Gómez-Aparicio et al., 2005; Keyes et al., 2009; Oakley et al., 2006). Understory thinning without burning resulted in high canopy retention and an initial increase in bare ground, while shrub cover was initially reduced, and remained low compared to burned and overstory thinned treatments (Goodwin et al., 2018; Zald et al., 2008). This combination of moderated light, exposed substrate, and reduced shrub cover conditions likely promoted high regeneration densities. It is important to note that regeneration in shrub dominated patches after understory thinning in this study applies to stand and small treatment level effects, and not large shrub patches following high-severity wildfire, where conifer seed source limitations and large dense shrub patches can delay and suppress natural regeneration (Welch et al., 2016). Given the order of magnitude greater regeneration of white fir and incense-cedar, our analysis of total conifer regeneration by treatment combination and pretreatment patch type largely reflects the response of shade-tolerant species. However, our data did not allow for the analysis of individual species responses to treatments in different patch types, so we cannot determine if and how pretreatment vegetation may mediate species-specific regeneration after treatment, especially for Jeffrey pine and sugar pine.

4.3. The role of planted regeneration after overstory thinning

Planting after overstory thinning (with or without burning) initially increased regeneration density for all three planted species (white fir, Jeffrey pine, and sugar pine), although 16 years after treatments the effects of planting on regeneration density varied by species. Planting of the three species was roughly proportional to their relative pretreatment basal area in the treatment units, so it is not surprising that planting of white fir at densities over 300 tph resulted in greater increases in regeneration density versus natural regeneration alone. Sugar pine had initial planting densities closer to 100 tph, while Jeffrey pine was planted at approximately 50 tph in the burned overstory thin, but only around 11 tph in the unburned overstory thin. The lower planting densities are reflected in the marginal effects on Jeffrey pine combined regeneration density 16 years after treatments in the unburned overstory thinned treatment, and no effect in the burned overstory thinned treatment. Even with low initial planting densities, planted pines represent a significant proportion (65 % for sugar pine in burned overstory thins, 27–32 % for both species in the other treatments) of total pine regeneration in overstory thinned treatments sixteen years after planting. Height growth of planted conifers has been shown to be much greater than natural regeneration of con-specifics (Holgén and Hånell, 2000; McDonald et al., 2009), which may play an important role in outcompeting dense shrub vegetation and surviving harsh site conditions (Fig. 4). Additionally, after a second entry burn at Teakettle in the fall of 2017, overstory thinned and twice burned treatments with planted pines were the only treatments with midstory recruitment rates sufficient to maintain historical pine densities prior to fire exclusion (May et al., 2023).

4.4. Management implications

In frequent-fire forests, increasing the pace and scale of fuel reduction treatments has become a management priority at state and federal levels (North et al., 2012; State of California, 2020; USDA Forest Service, 2022a). Fuel reduction treatments focus on moderating wildfire behavior and reducing wildfire risk, with restoration of ecological patterns and processes as an important and often convergent management objective (Stephens et al., 2021). There is widespread recognition that initial thinning and burning treatments will require subsequent fire, either prescribed or wildfire managed for resource benefit, to maintain fuel reduction objectives (North et al., 2012). Similarly, our results are indicative of an ecosystem requiring additional inputs to meet ecological pattern and process objectives that are dependent on restoring a pine-dominated ecosystem.

In our study, understory thinning with or without initial entry prescribed burning increased regeneration of shade-tolerant white fir and incense-cedar. Increasing white fir and incense-cedar regeneration density runs counter to restoration objectives of reducing shade-tolerant species and promoting drought and fire adapted pine species, and may also negatively impact fuel reduction treatment longevity by increasing stand densities and ladder fuels (Hood et al., 2020; Tinkham et al., 2016). Understory thinning also resulted in large increases in regeneration in pretreatment shrub patches. From a traditional forestry perspective, high regeneration rates in potentially competing shrub vegetation would be viewed as a success. However, given the importance of vegetation heterogeneity in frequent-fire forests, high regeneration densities in shrub patches after understory thinning suggests thinning with high canopy and basal area retention also poses risks of further homogenizing fine scale vegetation structure via the conversion

Table A15
Pairwise comparison of conifer natural regeneration density between treatments and patch types within years from generalized linear mixed effects model of conifer natural regeneration density.

Treatment Contrast	Year	Patch	Ratio	SE	z.ratio	p
BN/BO	2000	CECO dominated	0.221	0.204	−1.637	0.574
BN/BO	2000	Closed canopy	1.498	0.932	0.650	0.987
BN/BO	2000	Open	0.467	0.357	−0.996	0.919
BN/BU	2000	CECO dominated	0.551	0.632	−0.519	0.995
BN/BU	2000	Closed canopy	1.409	0.834	0.579	0.992
BN/BU	2000	Open	1.041	0.795	0.052	1.000
BN/UO	2000	CECO dominated	0.793	0.780	−0.236	1.000
BN/UO	2000	Closed canopy	2.669	1.584	1.654	0.562
BN/UO	2000	Open	1.216	1.010	0.235	1.000
BN/UU	2000	CECO dominated	0.377	0.391	−0.940	0.936
BN/UU	2000	Closed canopy	0.778	0.453	−0.431	0.998
BN/UU	2000	Open	0.366	0.327	−1.126	0.871
BU/BO	2000	CECO dominated	0.401	0.442	−0.829	0.962
BU/BO	2000	Closed canopy	1.063	0.665	0.098	1.000
BU/BO	2000	Open	0.448	0.323	−1.114	0.876
BU/UO	2000	CECO dominated	1.438	1.660	0.315	1.000
BU/UO	2000	Closed canopy	1.894	1.132	1.068	0.894
BU/UO	2000	Open	1.168	0.922	0.197	1.000
UN/BN	2000	CECO dominated	1.598	1.388	0.540	0.995
UN/BN	2000	Closed canopy	0.784	0.480	−0.397	0.999
UN/BN	2000	Open	0.663	0.496	−0.550	0.994
UN/BO	2000	CECO dominated	0.353	0.286	−1.287	0.793
UN/BO	2000	Closed canopy	1.175	0.758	0.250	1.000
UN/BO	2000	Open	0.309	0.218	−1.666	0.554
UN/BU	2000	CECO dominated	0.881	0.932	−0.120	1.000
UN/BU	2000	Closed canopy	1.105	0.680	0.163	1.000
UN/BU	2000	Open	0.690	0.484	−0.530	0.995
UN/UO	2000	CECO dominated	1.267	1.113	0.269	1.000
UN/UO	2000	Closed canopy	2.093	1.293	1.196	0.839
UN/UO	2000	Open	0.806	0.625	−0.279	1.000
UN/UU	2000	CECO dominated	0.603	0.565	−0.540	0.995
UN/UU	2000	Closed canopy	0.610	0.371	−0.813	0.965
UN/UU	2000	Open	0.242	0.204	−1.684	0.542
UO/BO	2000	CECO dominated	0.279	0.260	−1.372	0.744
UO/BO	2000	Closed canopy	0.561	0.353	−0.919	0.942
UO/BO	2000	Open	0.384	0.304	−1.211	0.832
UU/BO	2000	CECO dominated	0.586	0.578	−0.542	0.994
UU/BO	2000	Closed canopy	1.926	1.191	1.060	0.897
UU/BO	2000	Open	1.275	1.091	0.284	1.000
UU/BU	2000	CECO dominated	1.461	1.753	0.316	1.000
UU/BU	2000	Closed canopy	1.812	1.065	1.011	0.914
UU/BU	2000	Open	2.844	2.430	1.223	0.826
UU/UO	2000	CECO dominated	2.101	2.194	0.711	0.981
UU/UO	2000	Closed canopy	3.431	2.021	2.093	0.291
UU/UO	2000	Open	3.323	3.040	1.313	0.778
BN/BO	2002	CECO dominated	0.677	0.942	−0.281	1.000
BN/BO	2002	Closed canopy	27.623	32.744	2.800	0.057
BN/BO	2002	Open	0.459	0.638	−0.560	0.994
BN/BU	2002	CECO dominated	0.848	0.943	−0.149	1.000
BN/BU	2002	Closed canopy	1.530	0.985	0.661	0.986
BN/BU	2002	Open	0.685	0.642	−0.404	0.999
BN/UO	2002	CECO dominated	1.277	1.417	0.220	1.000
BN/UO	2002	Closed canopy	2.846	1.947	1.529	0.645
BN/UO	2002	Open	1.426	1.342	0.378	0.999
BN/UU	2002	CECO dominated	0.423	0.471	−0.773	0.972
BN/UU	2002	Closed canopy	1.654	1.027	0.810	0.966
BN/UU	2002	Open	1.231E + 09	7.319E + 11	0.035	1.000
BU/BO	2002	CECO dominated	0.798	1.226	−0.147	1.000
BU/BO	2002	Closed canopy	18.055	21.627	2.416	0.151
BU/BO	2002	Open	0.671	0.949	−0.282	1.000
BU/UO	2002	CECO dominated	1.507	1.936	0.319	1.000
BU/UO	2002	Closed canopy	1.860	1.312	0.880	0.951
BU/UO	2002	Open	2.084	2.039	0.750	0.976
UN/BN	2002	CECO dominated	1.783	1.459	0.707	0.981
UN/BN	2002	Closed canopy	0.999	0.619	−0.002	1.000
UN/BN	2002	Open	1.087	0.856	0.106	1.000
UN/BO	2002	CECO dominated	1.206	1.616	0.140	1.000
UN/BO	2002	Closed canopy	27.587	32.696	2.799	0.058
UN/BO	2002	Open	0.500	0.659	−0.526	0.995
UN/BU	2002	CECO dominated	1.511	1.579	0.395	0.999
UN/BU	2002	Closed canopy	1.528	0.982	0.660	0.986
UN/BU	2002	Open	0.744	0.620	−0.354	0.999
UN/UO	2002	CECO dominated	2.277	2.372	0.790	0.969

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Table A15 (*continued*)

Treatment Contrast	Year	Patch	Ratio	SE	z.ratio	p
UN/UO	2002	Closed canopy	2.842	1.942	1.528	0.646
UN/UO	2002	Open	1.551	1.297	0.525	0.995
UN/UU	2002	CECO dominated	0.754	0.788	−0.270	1.000
UN/UU	2002	Closed canopy	1.652	1.026	0.808	0.966
UN/UU	2002	Open	1.338E + 09	7.957E + 11	0.035	1.000
UO/BO	2002	CECO dominated	0.530	0.813	−0.414	0.998
UO/BO	2002	Closed canopy	9.706	11.838	1.864	0.425
UO/BO	2002	Open	0.322	0.456	−0.800	0.968
UU/BO	2002	CECO dominated	1.600	2.458	0.306	1.000
UU/BO	2002	Closed canopy	16.702	19.803	2.375	0.165
UU/BO	2002	Open	0.000	0.000	−0.037	1.000
UU/BU	2002	CECO dominated	2.004	2.581	0.540	0.995
UU/BU	2002	Closed canopy	0.925	0.597	−0.121	1.000
UU/BU	2002	Open	0.000	0.000	−0.036	1.000
UU/UO	2002	CECO dominated	3.019	3.881	0.860	0.956
UU/UO	2002	Closed canopy	1.721	1.178	0.792	0.969
UU/UO	2002	Open	0.000	0.000	−0.035	1.000
BN/BO	2005	CECO dominated	0.476	0.400	−0.882	0.951
BN/BO	2005	Closed canopy	6.824	4.178	3.137	0.021
BN/BO	2005	Open	2.794	2.171	1.323	0.773
BN/BU	2005	CECO dominated	0.244	0.225	−1.530	0.644
BN/BU	2005	Closed canopy	0.856	0.506	−0.263	1.000
BN/BU	2005	Open	1.411	1.027	0.473	0.997
BN/UO	2005	CECO dominated	0.963	0.882	−0.041	1.000
BN/UO	2005	Closed canopy	5.961	3.671	2.899	0.044
BN/UO	2005	Open	5.647	4.697	2.081	0.297
BN/UU	2005	CECO dominated	0.032	0.030	−3.734	0.003
BN/UU	2005	Closed canopy	1.397	0.803	0.582	0.992
BN/UU	2005	Open	1.347	1.116	0.360	0.999
BU/BO	2005	CECO dominated	1.950	1.785	0.730	0.978
BU/BO	2005	Closed canopy	7.969	4.896	3.378	0.010
BU/BO	2005	Open	1.980	1.488	0.910	0.944
BU/UO	2005	CECO dominated	3.948	3.882	1.397	0.729
BU/UO	2005	Closed canopy	6.962	4.303	3.140	0.021
BU/UO	2005	Open	4.003	3.233	1.717	0.520
UN/BN	2005	CECO dominated	2.368	1.868	1.093	0.884
UN/BN	2005	Closed canopy	0.325	0.194	−1.885	0.411
UN/BN	2005	Open	0.314	0.221	−1.645	0.569
UN/BO	2005	CECO dominated	1.127	0.880	0.153	1.000
UN/BO	2005	Closed canopy	2.215	1.374	1.282	0.795
UN/BO	2005	Open	0.877	0.639	−0.181	1.000
UN/BU	2005	CECO dominated	0.578	0.501	−0.633	0.989
UN/BU	2005	Closed canopy	0.278	0.166	−2.138	0.267
UN/BU	2005	Open	0.443	0.299	−1.205	0.834
UN/UO	2005	CECO dominated	2.282	1.962	0.959	0.931
UN/UO	2005	Closed canopy	1.935	1.207	1.058	0.898
UN/UO	2005	Open	1.772	1.395	0.726	0.979
UN/UU	2005	CECO dominated	0.077	0.066	−2.974	0.035
UN/UU	2005	Closed canopy	0.454	0.265	−1.355	0.754
UN/UU	2005	Open	0.423	0.331	−1.099	0.882
UO/BO	2005	CECO dominated	0.494	0.449	−0.777	0.971
UO/BO	2005	Closed canopy	1.145	0.731	0.212	1.000
UO/BO	2005	Open	0.495	0.422	−0.826	0.963
UU/BO	2005	CECO dominated	14.668	13.358	2.949	0.038
UU/BO	2005	Closed canopy	4.884	2.925	2.647	0.086
UU/BO	2005	Open	2.074	1.761	0.860	0.956
UU/BU	2005	CECO dominated	7.521	7.418	2.046	0.316
UU/BU	2005	Closed canopy	0.613	0.354	−0.848	0.958
UU/BU	2005	Open	1.047	0.843	0.058	1.000
UU/UO	2005	CECO dominated	29.695	29.075	3.463	0.007
UU/UO	2005	Closed canopy	4.266	2.572	2.406	0.154
UU/UO	2005	Open	4.192	3.771	1.594	0.603
BN/BO	2011	CECO dominated	0.465	0.392	−0.909	0.944
BN/BO	2011	Closed canopy	1.819	1.083	1.005	0.917
BN/BO	2011	Open	1.803	1.422	0.748	0.976
BN/BU	2011	CECO dominated	0.170	0.157	−1.921	0.389
BN/BU	2011	Closed canopy	0.310	0.181	−2.007	0.338
BN/BU	2011	Open	0.531	0.392	−0.858	0.956
BN/UO	2011	CECO dominated	1.176	1.076	0.177	1.000
BN/UO	2011	Closed canopy	1.537	0.925	0.714	0.980
BN/UO	2011	Open	3.252	2.574	1.490	0.671
BN/UU	2011	CECO dominated	0.055	0.046	−3.485	0.007
BN/UU	2011	Closed canopy	0.393	0.226	−1.626	0.581
BN/UU	2011	Open	0.661	0.581	−0.470	0.997
BU/BO	2011	CECO dominated	2.732	2.501	1.098	0.882
BU/BO	2011	Closed canopy	5.874	3.498	2.973	0.035

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Table A15 (*continued*)

Treatment Contrast	Year	Patch	Ratio	SE	z.ratio	p
BU/BO	2011	Open	3.395	2.544	1.631	0.578
BU/UO	2011	CECO dominated	6.907	6.791	1.966	0.362
BU/UO	2011	Closed canopy	4.966	2.990	2.662	0.083
BU/UO	2011	Open	6.123	4.607	2.408	0.153
UN/BN	2011	CECO dominated	1.581	1.247	0.580	0.992
UN/BN	2011	Closed canopy	0.772	0.465	−0.429	0.998
UN/BN	2011	Open	0.469	0.336	−1.056	0.899
UN/BO	2011	CECO dominated	0.735	0.574	−0.394	0.999
UN/BO	2011	Closed canopy	1.404	0.861	0.554	0.994
UN/BO	2011	Open	0.846	0.617	−0.229	1.000
UN/BU	2011	CECO dominated	0.269	0.233	−1.514	0.655
UN/BU	2011	Closed canopy	0.239	0.144	−2.380	0.163
UN/BU	2011	Open	0.249	0.168	−2.064	0.306
UN/UO	2011	CECO dominated	1.858	1.597	0.721	0.979
UN/UO	2011	Closed canopy	1.187	0.735	0.277	1.000
UN/UO	2011	Open	1.526	1.118	0.577	0.993
UN/UU	2011	CECO dominated	0.087	0.067	−3.171	0.019
UN/UU	2011	Closed canopy	0.304	0.180	−2.012	0.335
UN/UU	2011	Open	0.310	0.257	−1.415	0.718
UO/BO	2011	CECO dominated	0.396	0.359	−1.022	0.911
UO/BO	2011	Closed canopy	1.183	0.725	0.274	1.000
UO/BO	2011	Open	0.554	0.445	−0.735	0.978
UU/BO	2011	CECO dominated	8.464	6.973	2.593	0.099
UU/BO	2011	Closed canopy	4.623	2.706	2.615	0.094
UU/BO	2011	Open	2.727	2.426	1.128	0.870
UU/BU	2011	CECO dominated	3.098	2.809	1.247	0.814
UU/BU	2011	Closed canopy	0.787	0.452	−0.417	0.998
UU/BU	2011	Open	0.803	0.679	−0.259	1.000
UU/UO	2011	CECO dominated	21.397	19.228	3.409	0.009
UU/UO	2011	Closed canopy	3.908	2.314	2.302	0.193
UU/UO	2011	Open	4.919	4.389	1.786	0.475
BN/BO	2017	CECO dominated	0.875	0.795	−0.147	1.000
BN/BO	2017	Closed canopy	3.106	1.894	1.859	0.428
BN/BO	2017	Open	2.107	1.516	1.036	0.906
BN/BU	2017	CECO dominated	0.366	0.360	−1.022	0.911
BN/BU	2017	Closed canopy	0.608	0.367	−0.824	0.963
BN/BU	2017	Open	0.968	0.670	−0.046	1.000
BN/UO	2017	CECO dominated	1.938	1.897	0.676	0.985
BN/UO	2017	Closed canopy	3.124	1.900	1.873	0.419
BN/UO	2017	Open	2.417	1.812	1.177	0.848
BN/UU	2017	CECO dominated	0.114	0.107	−2.303	0.193
BN/UU	2017	Closed canopy	1.050	0.617	0.083	1.000
BN/UU	2017	Open	0.649	0.550	−0.510	0.996
BU/BO	2017	CECO dominated	2.390	2.187	0.952	0.933
BU/BO	2017	Closed canopy	5.110	3.052	2.731	0.069
BU/BO	2017	Open	2.176	1.545	1.095	0.884
BU/UO	2017	CECO dominated	5.296	5.215	1.693	0.536
BU/UO	2017	Closed canopy	5.139	3.061	2.749	0.066
BU/UO	2017	Open	2.496	1.849	1.234	0.820
UN/BN	2017	CECO dominated	0.893	0.786	−0.128	1.000
UN/BN	2017	Closed canopy	0.337	0.209	−1.750	0.499
UN/BN	2017	Open	0.536	0.379	−0.882	0.951
UN/BO	2017	CECO dominated	0.781	0.628	−0.307	1.000
UN/BO	2017	Closed canopy	1.048	0.644	0.076	1.000
UN/BO	2017	Open	1.129	0.820	0.167	1.000
UN/BU	2017	CECO dominated	0.327	0.290	−1.260	0.807
UN/BU	2017	Closed canopy	0.205	0.125	−2.606	0.096
UN/BU	2017	Open	0.519	0.362	−0.940	0.936
UN/UO	2017	CECO dominated	1.732	1.527	0.623	0.989
UN/UO	2017	Closed canopy	1.054	0.646	0.086	1.000
UN/UO	2017	Open	1.295	0.979	0.342	0.999
UN/UU	2017	CECO dominated	0.102	0.086	−2.714	0.072
UN/UU	2017	Closed canopy	0.354	0.210	−1.750	0.499
UN/UU	2017	Open	0.348	0.297	−1.237	0.818
UO/BO	2017	CECO dominated	0.451	0.410	−0.875	0.953
UO/BO	2017	Closed canopy	0.994	0.598	−0.009	1.000
UO/BO	2017	Open	0.872	0.669	−0.179	1.000
UU/BO	2017	CECO dominated	7.679	6.688	2.341	0.178
UU/BO	2017	Closed canopy	2.957	1.718	1.867	0.423
UU/BO	2017	Open	3.245	2.799	1.365	0.748
UU/BU	2017	CECO dominated	3.214	3.052	1.229	0.823
UU/BU	2017	Closed canopy	0.579	0.333	−0.951	0.933
UU/BU	2017	Open	1.491	1.253	0.476	0.997
UU/UO	2017	CECO dominated	17.019	16.060	3.004	0.032
UU/UO	2017	Closed canopy	2.974	1.723	1.882	0.413
UU/UO	2017	Open	3.722	3.305	1.480	0.677

UN = unburned no thin control, UU = unburned understory thin, UO = unburned overstory thin, BN = burned no thin, BU = burned understory thin, BO = burned overstory thin.

of shrub patches into closed-canopy forests.

Reducing competition down to low residual stand densities and basal area is increasingly recognized as a means of increasing tree vigor, reducing tree mortality, and improving resilience of frequent fire forests (Knapp et al., 2021; North et al., 2022; Steel et al., 2021; Zald et al., 2022). Our study suggests greater reductions in canopy cover and stand densities may also be critical for reducing densities of shade-tolerant regeneration. However, overstory thinning failed to promote natural regeneration of pine species. Of the treatments we evaluated, at best treatments decreased the amount of shade-tolerant species regeneration through overstory thinning treatments alone.

While limited to the overstory thin treatments, our results demonstrate that planting following overstory thinning with or without prescribed burning is a moderately effective means for increasing pine regeneration, approaching recruitment levels needed to maintain pine relative to historical reference conditions (May et al., 2023), and in spite of high shrub cover following overstory thinning (Goodwin et al., 2018). When Teakettle was planted in 2002, silviculturists on National Forests in the Sierra Nevada followed the practice of planting species proportional to overstory composition in response to stakeholder concern that reforestation practices were converting diverse forests into evenly-spaced pine plantations (Mark Smith, pers. comm.). That may still be a concern when reforesting large high-severity wildfire patches lacking nearby seed sources (North et al., 2019), but planting species proportional to overstory composition does not acknowledge how past logging and fire exclusion have shifted many frequent fire forests away from their historic pine composition. Our results question planting practices that perpetuate current forest conditions that are highly departed from historical variability and poorly adapted to fire and climate change. New approaches should consider historically resilient forest structure and composition in the context of resilience in a changing climate. There is a growing body of research on post-wildfire regeneration (Stevens-Rumann and Morgan, 2019; Welch et al., 2016), climate and fire effects on regeneration (Davis et al., 2023b; Stephens et al., 2023), natural regeneration under restored fire regimes (Fertel et al., 2022), and the role of post-fire planting in the frequent fire forests (Coop et al., 2020; Marsh et al., 2022; North et al., 2019). Given the large increases in thinning to meet fuel reduction goals in frequent-fire forests, we believe there is a pressing need to consider new planting strategies after fuel reduction treatments to maintain drought and fire adapted pine species in Sierra Nevada mixed-conifer forests. There is considerable discussion about the relevance of historical reference conditions in promoting resiliency to a changing climate (Coop et al., 2020; Keeley and Stephenson, 2000; Safford et al., 2012a; Stoddard et al., 2021). Within this, there is a need to reevaluate regeneration objectives and guidelines from a focus on density targets to meet full stocking, towards quantitative regeneration guidelines that promote forest resiliency.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Harold S.J. Zald, Carolina J. May, Andrew N. Gray, Malcolm P. North, Matthew D. Hurteau reports financial support was provided by Joint Fire Science Program. Harold S.J. Zald, Carolina J. May, Andrew N. Gray, Malcolm P. North, Matthew D. Hurteau reports financial support was provided by California Department of Forestry and Fire Protection.

Data availability

The data and code that support the findings of this study are openly available in "Data from: Thinning and prescribed burning increase shade-tolerant conifer regeneration in a fire excluded mixed-conifer forest " at https://doi.org/10.5061/dryad.2bvq83bx1.

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Appendix A

Tables A1 – A15.

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