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# Plant community response to thinning and repeated fire in Sierra Nevada mixed-conifer forest understories

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ABSTRACT

Fire suppression in the western United States has significantly altered forest composition and structure, resulting in a higher risk of stand-replacing fire, large-scale drought mortality, and bark beetle outbreaks. Mechanical thinning and prescribed fire are common treatments designed to reduce high-severity fire risk, but few studies have tracked long-term understory plant community response to these treatments with repeated fire application that emulates historic fire regimes. We evaluate changes in understory plant diversity and composition, as well as light availability, soil moisture, and litter depth over two decades following a factorial field experiment crossing thinning and two applications of prescribed fire at the Teakettle Experimental Forest (TEF) in the southern Sierra Nevada. We compare responses in experimental fuels treatments against those in nearby old-growth, mixed-conifer forests with restored low-severity fire regimes in Yosemite and Kings Canyon National Parks. We hypothesized that 1) understory plant richness, evenness, and beta diversity would increase with each burn event; 2) repeated fire after initial thinning would produce the highest understory plant diversity; 3) the second burn would reduce shrub cover, especially in the initially thinned treatments that demonstrated vigorous *Ceanothus cordulatus* growth after initial treatments; 4) the second burn would increase light availability and bare ground while reducing litter depth; and 5) treatments with initial thinning followed by multiple prescribed burns would show the greatest similarities to reference forests in diversity metrics, shrub cover, and environmental conditions. Although initially local (10 $m^2$-scale) understory plant richness and diversity increased most following thinning combined with prescribed fire, this treatment did not generate understory conditions similar to those in nearby reference forests over the long term. Vigorous shrub growth resulted in low understory evenness and beta diversity over time, which a secondary burn treatment did not alter. Burning without thinning retained a more heterogeneous understory following initial treatment. Two years after the second burn treatment, this burning without thinning resulted in high understory richness and evenness similar to reference forest understories. Our results suggest management treatments may need to focus on creating heterogeneity in burn effects to limit shrub cover and foster more diverse understory communities.

## 1. Introduction

Fire suppression in the western United States has significantly altered forest composition and structure, greatly increasing tree density–especially of small trees–and homogenizing stand structure and wildlife habitat (North et al., 2009; Safford and Stevens, 2017). The resulting dense, fuel-loaded forests have a higher risk of stand-replacing fire than forests with a more heterogeneous stand structure (Koontz et al., 2020) and are less resilient to large-scale drought and bark beetle events (Fettig et al., 2019). Common fuels reductions treatments such as mechanical thinning and prescribed fire can reduce wildfire severity under moderate weather conditions (Safford et al., 2012; Stephens et al., 2009) and can also increase structural heterogeneity and understory plant diversity, at least in the short term (Abella and Springer, 2015).

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These effects are important for biodiversity conservation efforts in the Sierra Nevada, where over half of California's vascular plant species are found (Potter, 1998). While several experiments have examined the short-term effects of thinning and prescribed fire on understory plant diversity in mixed conifer forests (Abella and Springer, 2015), few studies to date have assessed these changes for the same plots over multiple decades, or with repeated fire application to more accurately emulate the historic fire regimes.

Mechanical thinning and prescribed fire, two frequently applied approaches for reducing fuels and modifying forest structure, are likely to have different effects on understory plant communities depending on how they are implemented and their effect on the understory environment (Abella and Springer, 2015). Canopy cover, available light, shrub cover, tree basal area, litter and slash cover, bare ground cover, soil moisture, and soil nutrients are all associated with changes in understory plant communities (Abella and Springer, 2015; Bohlman et al., 2016; North et al., 2005b). Mechanical thinning treatments typically reduce tree density, but the impact of thinning on other environmental conditions such as surface fuels loads, soil disturbance, and canopy cover depends on the methods employed (i.e., whole tree harvest, lob and scatter limbs and tree tops, skidder yarding, feller buncher) (Abella and Springer, 2015). Prescribed fire typically removes litter and slash, reduces understory biomass, and alters soil nutrient availability but, depending on fire extent and intensity, may or may not reduce canopy cover or increase understory light availability (Abella and Springer, 2015; He et al., 2019). Fire also plays an important role in controlling understory composition by consuming or killing propagules of fire-sensitive species, while stimulating germination or resprouting in fire-dependent species (Stephan et al., 2010). Thinning is often used prior to burning to provide better control of the prescribed fire's intensity and to facilitate more complete, and often more uniform, burn spread (Ryan et al., 2013). Regardless of the approach used, these fuel reduction treatments appear to have the largest impact on understory plant richness and cover when they substantially alter the understory environment (Abella and Springer, 2015). Community-level changes result from how different species are affected by changes in these factors, often collectively assessed with a variety of diversity metrics.

Most diversity indices measure both the number of species observed in a given area (richness) and their relative abundance compared to other species (evenness). Richness increases when new species colonize a site, and is more sensitive to rare species than evenness. Richness is also sensitive to the scale at which it is measured because larger sampling units are more likely to detect rare species than small sampling units (Magurran, 2013). Evenness increases when species are more equally represented, and may increase with higher abundance of rare plants, or through reduction in abundant species that dominate a site. As a composite index, changes in diversity can be difficult to decipher unless its two components, richness and evenness, are reported. Beta diversity is a measure of how similar the community composition is among different locations; it increases when there are fewer shared species between sites and can reflect variation within a group of sites or turnover along a spatial, temporal, or environmental gradient (Anderson et al., 2011).

Initial results from long-term experimental treatments in an old-growth, mixed conifer forest in the Sierra Nevada indicate that thinning followed by prescribed fire showed the greater gains in understory plant richness and herbaceous cover than thinning or prescribed fire alone (Wayman and North, 2007). However, these combined treatments at Teakettle Experimental Forest (TEF) became heavily dominated by shrubs after 11 – 15 years (Goodwin et al., 2018). *Ceonothus cordulatus*, which accounted for 66% of all understory plant cover at TEF in 2016, readily resprouts from belowground lignotubers following fire with moderate fuel consumption, and requires high temperatures to germinate seeds stored in the soil (Kauffman and Martin, 1990; Quick and Quick, 1961). These characteristics allow *C. cordulatus* to respond rapidly to higher fire intensities and can dominate plant communities

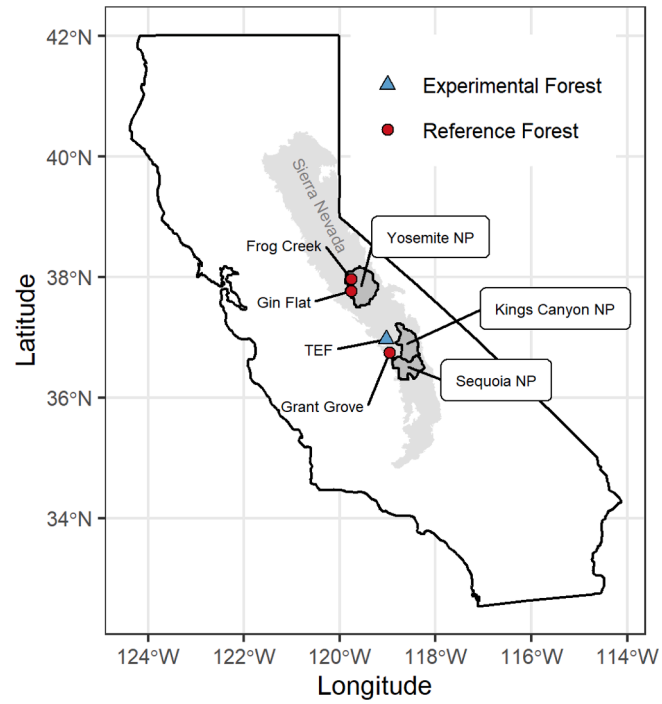


**Fig. 1.** Map of the Teakettle Experimental Forest (TEF) and old-growth mixed-conifer reference forests with active fire regimes.

following wildfire. *C. cordulatus* may also increase after thinning via vegetative release (Goodwin et al., 2018). Resulting homogenous shrub patches can create a positive feedback by increasing risk of high-severity fire when they reburn (Coppoletta et al., 2016; Keyser et al., 2020).

In mid-elevation Sierra Nevada mixed conifer forests, fires were historically frequent (12–20 year fire return interval), and burned at low severity with some high-severity patches (Safford and Stevens, 2017). As research from TEF demonstrates, a single application of treatments has relatively short-lived efficacy for increasing understory plant richness. Given the ecological role of repeated fire in this ecosystem, repeated burning may be necessary to restore understory plant communities and environments. A study of stands with one or two applications of prescribed fire–but no thinning–over a 20-year period in Sequoia and Kings Canyon National Parks found that two applications of prescribed fire increased understory plant community diversity without significantly elevating shrub cover (Webster and Halpern, 2010). This research suggests that regular burning may maintain large-scale heterogeneity, but it remains unclear if thinning followed by multiple burns will yield a similar diverse understory after initial vigorous shrub response.

In this study, we evaluate changes in understory plant diversity and composition over two decades, including two fuels reduction treatments at TEF in 2000–2001 and in 2017. We compare second-entry fire effects to initial treatment effects on multiple diversity metrics, shrub response, and relevant environmental variables. We also compare diversity, shrubs, and environmental variables in experimental fuels treatments at TEF against those in nearby old-growth mixed conifer forests with active fire regimes in Yosemite and Kings Canyon National Parks (hereafter reference forests; Fig. 1). In particular, we focused on the following four questions:

*Q1) How did understory plant diversity respond to second-entry fire compared to initial thinning and burn treatments?* We hypothesized that local (10 $m^2$-scale) understory plant diversity, richness, and evenness would increase with each burn event, regardless of initial thinning, due to increased fire-stimulated herbaceous plant abundance and a reduction in dominant shrubs, and that diversity would remain highest in the thin and burn treatments following the second entry burn. We further hypothesized that beta diversity would increase following the second

**Table 1**
Mean values for environmental variables following initial treatments (2003) and second-entry burn treatments (2019) across all treatment types at Teakettle Experimental Forest (TEF) and reference forests with recent (3–7 ya) and older fires (13–20 ya). Standard deviations are shown in parentheses. Asterisks indicate unequal mean rank values for an environmental variable across treatments in a given year (Kruskal-Wallis test, $p < 0.05$). Different letters following mean values indicate significant pair-wise differences between treatments (Bonferroni corrected Dunn's post-hoc analysis, $p < 0.05$).

| | | TEF Treatment | | | | | | Reference Forest | | Kruskal-Wallis Test | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Environmental Variable | Year | Control | Understory Thin | Overstory Thin | Burn | Under + Burn | Over + Burn | Old Fire | Recent Fire | sig | P Value |
| Direct Light (PPFD) ($\mu$mol s$^{-1}$ m$^{-2}$) | 2003 | 14.2 a (5.99) | 16.4 ab (5.31) | 19.0 b (6.41) | 14.4 a (5.73) | 17.5 ab (5.11) | 22.3 c (4.02) | | | * | <0.0001 |
| | 2019 | 14.8 e (6.69) | 16.3 ce (5.90) | 19.9 bd (6.73) | 17.3 cde (6.00) | 22.4 ab (5.57) | 24.4 a (4.50) | 19.4 bcd (5.42) | 17.8 cde (4.77) | * | <0.0001 |
| Diffuse Light (PPFD) ($\mu$mol s$^{-1}$ m$^{-2}$) | 2003 | 0.98 b (0.33) | 1.21 a (0.26) | 1.38 a (0.32) | 0.93 b (0.30) | 1.30 a (0.27) | 1.60 c (0.24) | | | * | <0.0001 |
| | 2019 | 1.05 c (0.36) | 1.18 cd (0.30) | 1.39 b (0.36) | 1.19 bcd (0.36) | 1.64 a (0.33) | 1.76 a (0.28) | 1.4 b (0.36) | 1.32 bd (0.27) | * | <0.0001 |
| Soil Moisture (% VWC) | 2003 | 8.33 ac (7.85) | 9.23 b (4.01) | 11.8 bc (10.3) | 7.25 a (5.80) | 9.51 abc (5.38) | 7.42 abc (3.21) | | | * | <0.0001 |
| | 2019 | 6.10 c (8.17) | 4.70 bc (6.46) | 4.84 abc (7.28) | 4.29 abd (8.40) | 4.72 abc (6.88) | 1.89 d (1.67) | 2.7 ad (3.61) | 2.87 ad (4.18) | * | <0.0001 |
| Litter Depth (cm) | 2003 | 3.21 bd (3.16) | 2.89 abd (2.81) | 3.61 d (3.18) | 1.66 a (1.80) | 1.77 ab (1.66) | 0.71 c (1.14) | | | * | <0.0001 |
| | 2019 | 4.88 d (3.15) | 5.44 d (3.27) | 4.37 bd (3.18) | 1.55 c (1.62) | 3.12 ab (2.26) | 2.49 ac (1.96) | 2.66 abc (2.05) | 2.43 ac (1.88) | * | <0.0001 |
| Bare Ground (%) | 2003 | 7.82 b (16.54) | 14.66 bc (25.84) | 11.61 bc (22.72) | 17.00 bc (25.00) | 38.19 a (30.50) | 64.36 d (27.74) | | | * | <0.0001 |
| | 2019 | 7.21 bc (13.66) | 6.58 b (13.99) | 8.66 abc (13.44) | 25.94 d (23.25) | 13.37 abc (20.25) | 24.57 ad (26.74) | 10.23 abc (16.46) | 12.48 ac (18.96) | * | <0.0001 |

burn event, regardless of initial thinning, due to overlapping patchy effects from multiple burns increasing heterogeneity within burn treatments. Finally, we hypothesized that treatment effects on local diversity, richness, and evenness would change over time.

*Q2) How did shrub cover respond to second-entry fire compared to initial thinning and burn treatments, and what patterns can help explain rapid shrub response after initial thin with burn treatments?* We hypothesized that the second burn would reduce shrub cover, especially in the initially thinned treatments that demonstrated vigorous *C. cordulatus* growth after initial treatments, and that increases in shrub cover following initial treatments are associated with shrub expansion into sites where thinning removed trees, reducing competition for light and water.

*Q3) How did ecologically relevant environmental variables respond to second-entry fire compared to initial thinning and burn treatments?* We hypothesized that the second burn would increase light availability and bare ground cover while reducing litter depth, especially in the unthinned treatment where more small trees remain to burn.

*Q4) Which fuel reduction treatment combination best replicates the understory plant diversity, shrub cover, and abiotic conditions in reference forests with active fire regimes?* We hypothesized that treatments with initial thinning followed by multiple prescribed burns would show the greatest similarities to reference forests in diversity metrics, shrub cover, and environmental conditions.

Understanding the effects of thinning and repeated burning in forests in which fire has been suppressed can be used to inform management that reduces risk of high-severity fire while promoting understory plant diversity.

## 2. Materials and methods

### 2.1. Study sites

#### 2.1.1. Teakettle experimental forest

The Teakettle Experimental Forest (TEF) is an old-growth, mixed-conifer forest in the southern Sierra Nevada, located in the High Sierra Ranger District of the Sierra National Forest (36°58′N, 119°2′W) at 1,880–2,485 m in elevation (Fig. 1). Typical of mixed-conifer forests, overstory tree species include shade tolerant species such as white fir (*Abies concolor*), red fir (*A. magnifica*), and incense-cedar (*Calocedrus decurrens*), and shade-intolerant, fire resistant species such as Jeffrey pine (*Pinus jeffreyi*), and sugar pine (*Pinus lambertiana*) (North et al., 2002). Patches of montane red fir forest are present in TEF, but this experiment took place entirely within in the mixed-conifer forest type, which makes up approximately two thirds of the experimental forest (North et al., 2002; Wayman and North, 2007). TEF soils are predominantly poorly developed and granite-based Inceptisols and Entisols with coarse, sandy-loam texture. The climate is typical of the southern Sierra Nevada with hot, dry summers (17.1 °C mean temperature) and cool, moist winters (1.2 °C mean temperature). Precipitation averages 1,250 mm per year, primarily as snow between November and April. Fires historically occurred every 17 years on average until 1865, after which no fires larger than 3 ha occurred in TEF (Fiegener, 2002; North et al., 2005a). There is no history of significant logging prior to experimental thinning treatments, except for limited hazard tree and sugar pine removal during early white pine blister rust control efforts (North et al., 2002; Smith et al., 2005).

A long-term field experiment testing the effects of different combinations of burning and thinning treatments was established at TEF in 1998. Forest plots were thinned according to the following treatments: no thin, thinning all trees between 25 and 75 cm diameter at breast height as described by Verner et al. (1992) (hereafter understory thin), and a heavier thinning treatment cutting all trees > 25 cm DBH but leaving 20 large (>75 cm) evenly spaced trees per hectare (hereafter overstory thin). Thinning treatments were crossed with prescribed burning and no prescribed burning for a full-factorial design with 6 treatments. Each treatment was replicated in three 200 m × 200 m plots (Fig. A.1). Thinning treatments were randomly assigned, but burn treatments were applied to two clusters of adjacent plots due to logistical constraints. Burn treatments were thinned in 2000 and burned in 2001, and unburned treatments were thinned in 2001.

The 2001 and 2017 prescribed fires were conducted by Sierra National Forest personnel under the following general prescription parameters: 10–15% 10-hr fuel, 50–75% relative humidity, 0–10 °C air temperature, and 0–5 m s$^{-1}$ wind speed. Both prescribed burns were conducted after the first fall precipitation (2 cm in 2001 and 1.2 cm in 2017), with actual daytime temperatures of 10–15 °C and relative humidity ranging from 25% (afternoon) to 70% (3am) (Innes et al., 2006; North pers. observation). Gridpoints were classified as either locally

**Table A1**
Fire summary of initial and second-entry fire treatments at Teakettle Experimental Forest. A total of 67 gridpoints are located within each burn treatment. Burned ground cover values represent the mean (standard deviation) of all 67 gridpoints in each burned treatment.

| Thin Treatment | Initial Fire (2001) | | Second-Entry Fire (2017) | |
|---|---|---|---|---|
| | # Gridpoints Burned | Burned Ground Cover (%) | # Gridpoints Burned | Burned Ground Cover (%) |
| No Thin | 17 | 4.7 (11.8) | 24 | 6.0 (13.7) |
| Understory Thin | 48 | 23.7 (28.8) | 13 | 3.0 (8.1) |
| Overstory Thin | 51 | 27.2 (33.6) | 16 | 2.4 (8.5) |

burned or unburned using a threshold of at least 1% ash or char ground cover following initial treatments and second-entry burns to assess the fire extent in each treatment. Fire did not uniformly impact plots within the burn treatments, and the initial burn treatment (2001) affected a much larger proportion of grid points in the thinned than in the unthinned plots. The reverse was true for the second-entry burn treatment (2017). The percentage of gridpoints in each treatment that burned in 2001 and 2017 was 72% and 19% in the understory thin-burn, 76% and 24% in the overstory thin-burn, and 25% and 36% in the unthinned treatment, respectively (Table A.1).

#### 2.1.2. Old-growth mixed-conifer reference forests

We identified old-growth mixed-conifer forest sites with frequent, low-severity fire regimes (hereafter reference forests) in the central and southern Sierra Nevada with similar forest type and topographic conditions to TEF. We located these sites using ArcGIS 10.6 by overlapping the mixed-conifer forest type in the CalVeg database, with a 1830–2290 m elevation range in the USGS National Elevation Dataset and an active fire regime consisting of at least three fires between 1960 and 2018 including at least one fire since 1990. We overlapped fire events from the CAL FIRE Fire and Resource Assessment Program's Fire Perimeter database to create polygons with unique fire histories and identify areas of low- to moderate-severity fire effects similar to the historic fire regime. We selected reference forest plots based on similar slope and aspect to TEF plots, and no history of logging, with a preference for plots closer to TEF over those further away to maximize overlap in regional species pools. We then visited plots to confirm mixed-conifer forest overstory species composition similar to TEF. Giant sequoia (*Sequoiadendron giganteum*) can be a local component of Sierra Nevada mixed-conifer forest and occurs near our reference forest sites in Kings Canyon National Park. For comparability with TEF conditions, we located our reference forest plots away from mature giant sequoia groves and excluded all gridpoints with giant sequoia greater than 30 cm DBH present within 12.6 m.

We selected three locations based on the above criteria: Gin Flat (37°46′ N, 119°46′ W) and Frog Creek (37°58′ N, 119°46′ W) in Yosemite National Park, and Grant Grove (36°45′ N, 118°58′ W) in Kings Canyon National Park (Fig. 1). See Appendix B for a full comparison of physical variables, tree species composition and understory plant composition between reference forest sites and TEF. We sampled three plots, delineated by distinct fire histories, at each location (9 plots total) in 2018 and 2019, as described below.

### 2.2. Experimental structure

Data were collected in a nested structure within plots. Within each plot at TEF, permanent sample gridpoints were mapped in a grid using a surveyor's total station and monumented for resampling. Two replicates per treatment had nine gridpoints spaced 50 m apart and one replicate per treatment was intensively sampled at 49 gridpoints spaced 25 m apart, for a total of 402 gridpoints.

For reference forest sites, we sampled 15 gridpoints in each of the 3 plots in each location for a total of 135 gridpoints. The 15 gridpoints were arranged on a grid to fit within irregularly shaped, overlapped footprints of past fires, with 25 m (4 plots) or 50 m (5 plots) spacing between gridpoints. We marked all gridpoints to ensure repeated measures in the same locations. We sampled vegetation, ground cover, and environmental data at each gridpoint using identical sampling methods in TEF and reference forests, as described below.

### 2.3. Plant diversity response to initial and second entry treatments (Q1)

We collected vegetation data at all 402 gridpoints at TEF in each year during the following time periods: 1999 (2 years prior to initial treatment), 2002–2004 (1–3 years after initial treatment), 2006 (5 years after initial treatment), 2011–2013 (10–12 years after initial treatment), 2016–2017 (15–16 years after initial treatment), and 2018–2019 (17–18 years after initial treatment/1–2 years after second entry burn treatment). We visually estimated the cover (%) of each plant species within a 10 $m^2$ circular area (1.78 m radius) centered on each gridpoint in mid-June through early July in each sampling year, coincident with peak blooming period for the region. Plot size was determined as approximately the largest area that produced consistent cover estimates between trained field technicians. We used movable 1.78 m poles to determine plot perimeters and ensure consistent recording of species present. We collected unknown taxa outside of the plot and identified them using the Jepson Manual first edition (Hickman, 1993) in 1999–2012 and the Jepson Manual second edition (Baldwin et al., 2012) in 2013–2019. Due to field constraints, certain taxa could not be reliably identified to species in the field. These were primarily species that rely on minute anatomical differences to distinguish or that do not develop characteristics necessary to reliably distinguish during our sampling window, such as many members of the order Poales or species in the genus *Cryptantha*. Taxa that we could not identify to species were identified to genus or to family. In total, we identified 18 taxa to genus. Of these, 8 taxa occurred in at least 5 out of 5118 gridpoint-years sampled in TEF and reference forests: *Cryptantha* (n = 926 gridpoint-years), *Boechera* (n = 50), *Salix* (n = 31), *Galium* (n = 17), *Hackelia* (n = 14), *Viola* (n = 8), *Castilleja* (n = 5), and *Delphinium* (n = 5). We also recorded 3 taxa to family in the order Poales: Poaceae (n = 1010), Cyperaceae (n = 65), and Juncaceae (n = 30).

Plant diversity metrics were calculated using the vegan package in R (Oksanen et al., 2019). Gridpoint-scale (10 $m^2$) richness, diversity, and evenness were calculated at each gridpoint in each year. We chose antilog Shannon-Wiener diversity index, $e^{H'}$, to measure diversity because it does not weight diversity towards rare species or abundant species and can be intuitively interpreted as the "effective number of species", which behaves predictably when manipulated mathematically (Jost, 2006). We use diversity divided by richness ($e^{H'}/S$) as a simple representation of evenness that accounts for the portion of diversity not explained by richness (Jost, 2006). We calculated average beta diversity—the variation in species composition among gridpoints—within each plot in each year. We chose the Raup-Crick dissimilarity index for beta diversity because it helps to differentiate variation in community dissimilarity from variation in local richness by comparing pair-wise differences in species composition to a null model (Chase et al., 2011; Raup and Crick, 1979).

We compared understory plant diversity, richness, evenness, and beta diversity between the six treatment combinations at TEF two years after initial treatments (2003) and second entry burns (2019). We also compared each diversity metric within each treatment at four points in time: before and after initial treatments (1999 and 2003) and before and after second entry burns (2016 and 2019). Due to the non-normal distribution of environmental data, we used Kruskal-Wallis tests with Dunn's post-hoc tests to identify differences in conditions between treatments within the same year, and Friedman's Tests with post-hoc Wilcoxon's tests to compare repeated measures of our response

variables over time within treatments, with gridpoint as the grouping variable for repeated measures. To control for potential bias against repeated testing effects, we adjusted all p-values using Bonferroni corrections (Armstrong, 2014).

Due to differences in fine-scale fire behavior and spread between initial treatments and second-entry burns (Fig. A.1; Table A.1), we tested whether one or two gridpoint-scale fire events increased local richness, evenness, and diversity using a Bayesian linear regression model approach. This approach allows us to account for uncertainty in the nested structure of our sampling design and estimate the effect sizes of our treatments through sampling the joint posterior distribution of our models (Kruschke and Liddell, 2018; McElreath, 2020). We fit multilevel Bayesian linear regression models using the brms package (Bürkner, 2017) to compare effects of burn and thin treatment combinations on changes from pre-treatment values in local richness, evenness, and diversity following initial treatments in 2000 and 2001 and second-burn treatments in 2017. We calculated the change in richness, evenness, and diversity from pre-treatment values at each gridpoint in each year using the formula:

$$\Delta\,[diversity\,metric]_{gridpoint} = [diversity\,metric]_{gridpoint,\,year} - [diversity\,metric]_{gridpoint,1999}$$

and used those values as the response variables in each model. Since gridpoints are nested spatially within plots and temporally within years, we include random effects for plot and year in each model. We include fixed effects for initial thin treatment, number of burn events, and their interactions as predictor variables in each model. Number of burn events was determined using a threshold of 1% ash or char ground cover to indicate the presence or absence of fire during each burn event. We did not consider our ash and char values to be an accurate measure of fire severity at each gridpoint, so we did not include them as a predictor in our models beyond this metric of fire presence or absence. We used weakly-informative, regularizing priors in all models to aid in model convergence and avoid biasing our posterior distribution towards extreme parameter values (Lemoine, 2019). See the supplemental materials for all priors included in the model (Table S.2). Joint posterior distributions were sampled using MCMC sampling with 3 chains of 2000 iterations, and 1000 warm-up samples. We diagnosed model convergence using trace plots and Gelman-Rubin diagnostic values $< 1.01$ for all model parameters (Gelman and Rubin, 1992, Table S.2).

To examine how fire and thinning treatment effects vary over time, we compared models without a fixed effect term for time since disturbance to those with linear and polynomial fixed effect terms for time since disturbance and interactions between time since disturbance and thin and burn treatments using leave-one-out cross validation (Vehtari et al., 2017). See supplemental materials for model comparisons (Table S.1) and all model parameters for the best-fitting models (Table S.2).

We used the posterior distributions from the best-fitting models for each response variable to evaluate our hypotheses that greater numbers of burn events at the gridpoint scale would result in higher local diversity, richness, and evenness. We simulate the effects of thinning and prescribed burning on local diversity, richness, and evenness by fitting the model for each combination of thinning treatment and number of burn events for the 1–18 year period following a single burn and the 1–2 year period following two burns. The result of these simulations is posterior linear prediction distributions of the effect on local diversity, richness, and evenness for each scenario. For each combination of thinning treatment and number of burn events, the effect of treatment is expressed as the difference from pre-treatment (1999) values for the included time period.

Probabilistic results concerning the effect of burn number are calculated using model posterior distributions. For example, contrasts between categories (e.g., change in richness within untreated vs. twice burned gridpoints) were calculated as the difference between estimated marginal means of posteriors for each category using the emmeans package in R (Lenth, 2020). The probability an effect was positive or negative was calculated as the proportion of the parameter posterior distribution above or below zero.

### 2.4. Shrub response to initial and second entry treatments (Q2)

Understory plant species were classified as herbaceous plants or shrubs (Baldwin et al., 2012), and total percent cover was calculated for each group at each gridpoint for each year with vegetation sampling.

We compared shrub cover between the six treatment combinations at TEF two years after initial treatments (2003) and second entry burns (2019). We also compared shrub cover within each treatment at four points in time: before and after initial treatments (1999 and 2003) and before and after second entry burn (2016 and 2019). We used Kruskal-Wallis tests with Bonferroni corrected Dunn's post-hoc tests to identify differences in conditions between treatments within the same year, and Friedman's Tests with Bonferroni corrected post-hoc Wilcoxon's tests to compare repeated measures of our response variables over time within treatments, with gridpoint as the grouping variable for repeated measures.

To explore whether the observed increase in shrub cover following initial treatments (Goodwin et al., 2018) may be due to expanded shrub presence in patches that were previously dominated by tree cover, we plotted mean shrub cover over time for each combination of initial thinning and burning in different initial vegetation patch types. Previous TEF studies found three different vegetation patch types influential on understory ecosystem processes including soil nutrient cycling, soil respiration, and litter accumulation before and after treatments (Erickson et al., 2005; Ryu et al., 2009). We identified gridpoints that were clearly representative of these three distinct pre-treatment vegetation patch types: open (canopy closure $< 45\%$, total shrub cover $< 10\%$, $n = 64$), shrub dominated (canopy closure $< 45\%$, total shrub cover $> 30\%$, $n = 50$), and tree dominated (canopy closure $> 65\%$, total shrub cover $< 10\%$, $n = 64$). We did not conduct a formal statistical analysis on shrub cover over time by vegetation patch type due to the low number of available data points for some combinations of treatment and vegetation patch type.

### 2.5. Environmental variable response to initial and second entry treatments (Q3)

We recorded latitude, longitude, slope, and aspect at each gridpoint in 1999. Aspect was transformed to reflect difference from southwest as a relative measure of heat load using the equation $(1\text{-}\cos[\theta\text{-}45])/2$ where $\theta$ is the azimuth measured from true north (Beers et al., 1966).

We sampled ground variables at the time of vegetation sampling for each gridpoint in each year where vegetation was sampled. We visually estimated the cover (%) of bare ground, rock, litter (<1 cm diameter), sticks (1 – 5 cm diameter), and coarse woody debris (>5cm diameter) for each of two, broad decay classes—largely intact (decay classes 1–3; (Maser et al., 1988) and substantially decomposed (decay classes 4–5; (Maser et al., 1988)—within a 10 $m^2$ circular area centered on each gridpoint. We recorded litter depth at 3 random locations within 1.78 m of each gridpoint and averaged the values. In the year following each burn treatment, we visually estimated the cover (%) of ash and char material within the same 10 $m^2$ circular area centered on each gridpoint to indicate fire occurrence and severity at each gridpoint.

We also sampled soil moisture annually at the time of vegetation sampling (mid June – early July) for each gridpoint. From 1999 to 2017, we sampled soil volumetric water content using a Time Domain Reflectometer (TDR) with permanent installed rods at a single location at each gridpoint assessing 0–15 cm and 15–40 cm of the same soil profile (Zald et al., 2008). In 2018–2019 we used a Fieldscout TDR 100 probe to average volumetric water content in the top 12 cm of soil in five locations for each gridpoint (at the gridpoint and 1 m in each cardinal

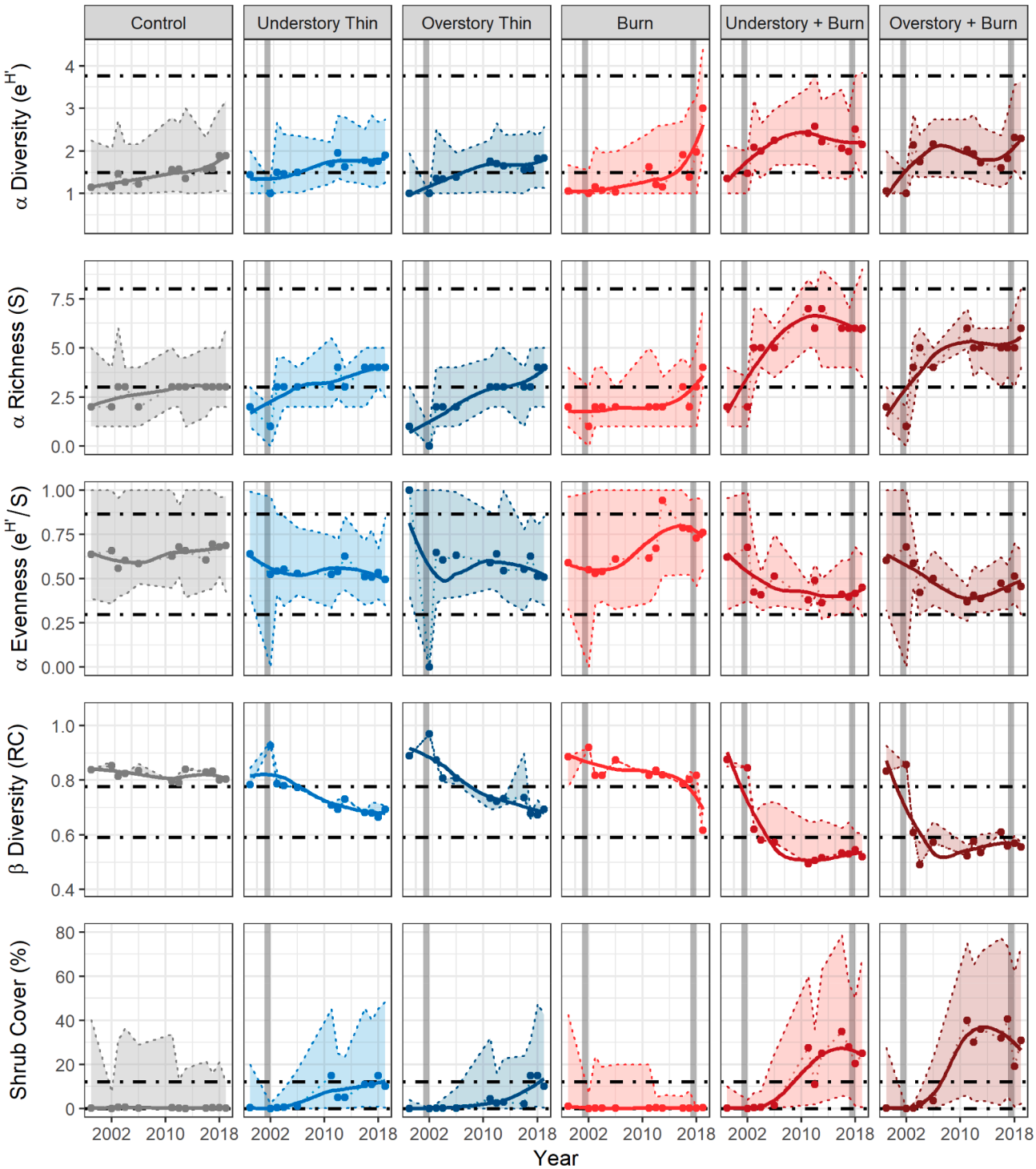


**Fig. 2.** (Top to bottom) local (10 $m^2$) diversity ($e^{H'}$), richness (S), evenness ($e^{H'}/S$), beta diversity (RC), and shrub cover (%) over time for experimental treatments in Teakettle Experimental Forest. Horizontal black dashed lines represent the middle 50% of values in reference forests with active fire regimes for comparison to TEF treatments. Vertical gray lines represent timing of initial treatments in 2000–2001 and second-entry prescribed fire in 2017. Points represent median values in each year, bold lines represent a smoothed trend in median over time (Loess smoothing function, median ~ year), and shaded areas represent the middle 50% of values for each year.

direction) to better account for fine-scale variation in soil water content. TDR sampling locations were flagged in 2018 to ensure repeated sampling of the same soil columns in 2019.

We measured other soil characteristics following initial treatments and second-entry burns. We estimated soil depth over competent bedrock in 2003 by pounding a rod into the soil in five randomly selected locations within 2 m of the gridpoint. We calculated the mean of the three greatest depths to account for erroneous depth measurements produced by buried rocks. We collected soil samples from nine gridpoints in each plot in 2003 and 2019 for nutrient and soil texture analysis. Three soil cores were taken to a depth of 30 cm with a 2 cm wide soil probe at approximately 75 cm from the gridpoint at 0, 120, and 240-degree azimuths. When cores were not able to be taken to the full 30 cm depth, additional cores were collected from within 1.78 m of the

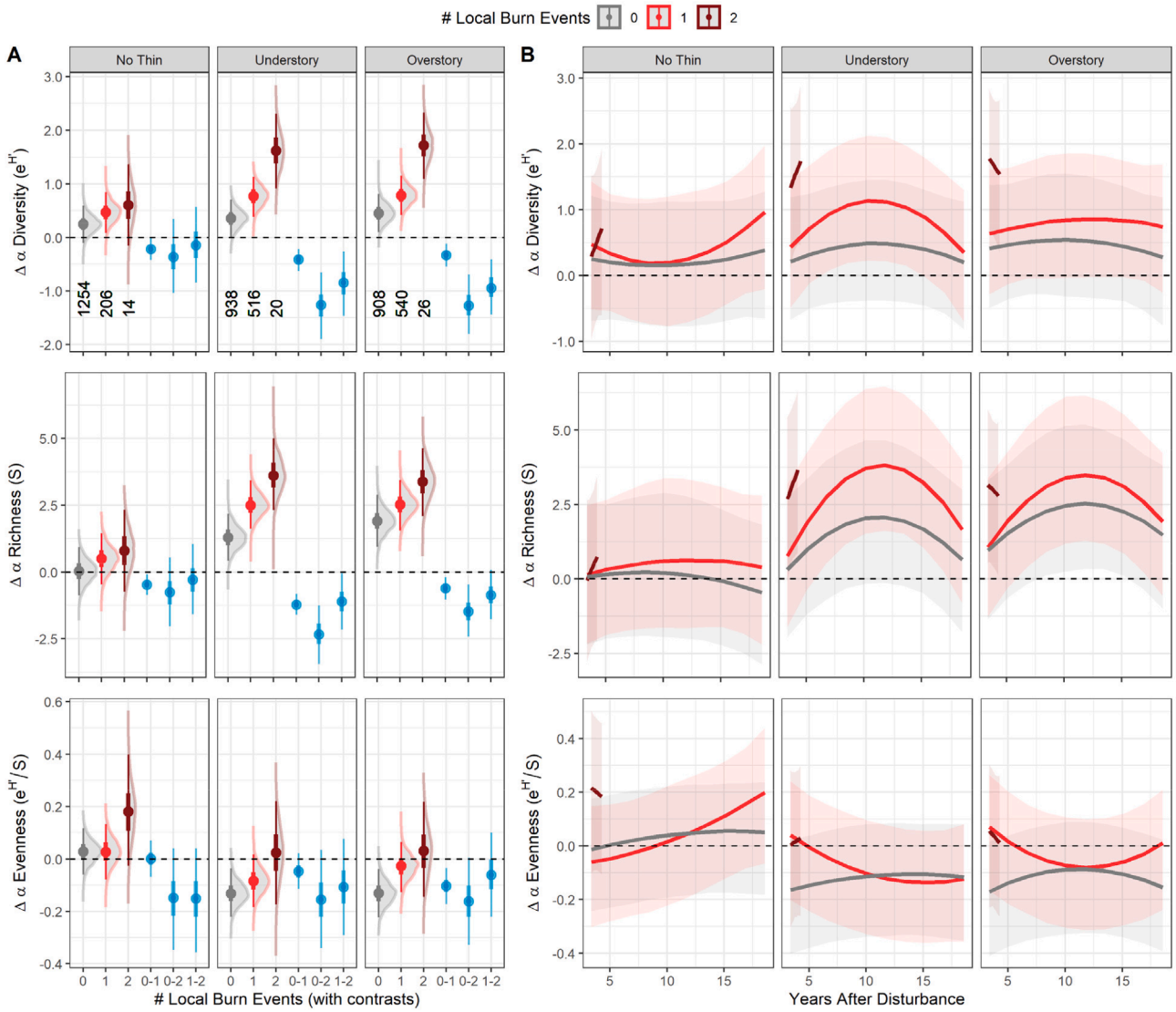


**Fig. 3.** Effects of number of local (10 $m^2$ gridpoint-scale) burn events and initial thin treatment on local understory plant diversity ($e^{H'}$), richness (S), and evenness ($e^{H'}$/S) at TEF. Marginal effects of burn number and thin treatment are shown on (A) overall change in each diversity metric and (B) change in each diversity metric over time since most recent disturbance. Response variable values indicate difference between pre-treatment (1999) values and 1–18 years post-treatment (1–2 years post treatment for 2 fire events); a value of zero indicates no predicted change from pre-treatment. For (A), Points and intervals indicate median and 50% and 95% credible intervals for model fits for each treatment. Shaded areas indicate distributions of estimated marginal means for each. Number of data points in each group is indicated in black. Contrasts between numbers of burns are shown in blue for each initial thin treatment, with 50% and 95% credible intervals to indicate differences between treatment effects. For (B), lines and shaded areas indicate median and 95% credible intervals for model fits for each combination of over time. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

gridpoint until sufficient soil was collected to complete all analyses, and core depths recorded. Soil samples from each gridpoint were combined in a waterproof bag and kept on ice for up to 8 days. They were then air dried and analyzed by the UC Davis Analytical Laboratory for total carbon and nitrogen (Horwitz, 2010), Bray phosphorus (the recommended method for low pH soils: (Olsen and Sommers, 1982), and particle size (2019 only, (Sheldrick and Wang, 1993).

We assessed light availability with hemispherical canopy photographs in 1999, 2002, and 2019. Photographs were taken at each gridpoint with a Sigma 4.5 mm F2.8 EX DC HSM Circular Fisheye lens. All photographs were taken from the gridpoint at breast height using a leveled tripod at dawn or dusk, with the top of the picture oriented to true north. Photographs were corrected for exposure and analyzed for percent canopy cover and direct, diffuse, and total photosynthetically active photon flux density (PPFD) (μmol $s^{-1}$ $m^{-2}$) using the Hemiphot.R package in R (ter Steege, 2018). For a given gridpoint, PPFD is calculated from the latitude, elevation, and the tracking angle of the sun over the course of a year.

In order to determine which environmental variables were most closely associated with understory community composition, we conducted a NMDS (non-metric multi-dimensional scaling) ordination analysis on our vegetation data from 1999, 2003, 2016, and 2019 using the vegan package (Oksanen et al., 2019). Full details of this analysis can be found in the supplemental material. We calculated environmental loadings for each environmental variable described above using the envfit function with 999 permutations. Environmental variables with significant loading values were then used in subsequent comparisons of treatment effects.

We then compared direct and diffuse light availability, soil moisture, litter depth, and bare ground cover between the six treatment combinations at TEF two years after initial treatments (2003) and second entry burns (2019). We used Kruskal-Wallis tests with Bonferroni corrected Dunn's post-hoc tests to identify differences in conditions between treatments.

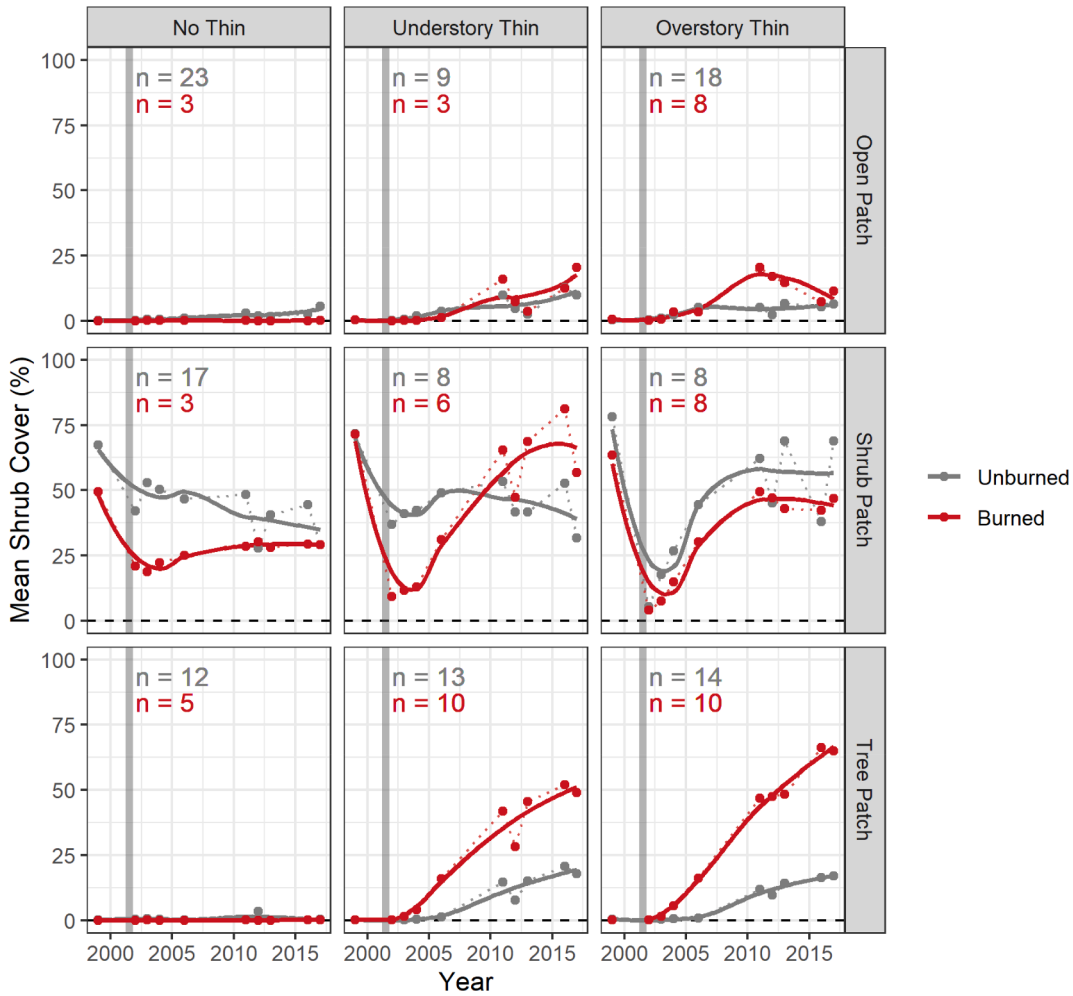


**Fig. 4.** Mean shrub cover over time in gridpoints that were originally open patches (canopy closure < 45%, total shrub cover < 10% %, n = 64), shrub dominated patches (canopy closure < 45%, total shrub cover > 30%, n = 50), and tree dominated patches (canopy closure > 65%, total shrub cover < 10%, n = 64) prior to treatment. Gridpoints are further separated by thinning treatment and whether they burned in the initial burn treatment. Thin dashed lines and points represent median shrub cover values for each year and solid lines represent the Loess-smoothed median shrub cover over time. Vertical gray lines represent initial thinning and/or burning treatments in 2000 – 2001. The number of gridpoints for each combination of thin treatment and original vegetation patch type is shown for unburned gridpoints (gray) and burned gridpoints (red) in the upper left corner of each panel. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

### *2.6. Comparing TEF treatments to frequent-fire reference forests (Q4)*

We collected vegetation, ground cover, and soil moisture data each year at all 135reference forest gridpoints in 2018 and 2019. We collected latitude, longitude, slope, and aspect for each gridpoint in 2018. Hemispherical canopy photographs were taken at all reference forest gridpoints and soil samples were collected for nutrient and soil texture analysis from nine gridpoints in each reference forest plot (81 gridpoints total) in 2019.

We compared treatment outcomes with reference forest conditions by comparing understory plant diversity, richness, evenness, beta diversity, shrub cover, litter depth, soil moisture, and direct and diffuse light availability between all TEF treatments two years after each treatment (2003 and 2019) and reference forests with recent fires (3–7 years old), and reference forests with older fires (13–20 year-old fires). We used Kruskal-Wallis tests with Bonferroni corrected Dunn's post-hoc tests to identify differences in conditions between treatments and reference forests two years after second-entry burn treatments at TEF.

All data analysis was performed in R version 3.6.3 (R Development Core Team, 2011), unless otherwise noted.

## 3. Results

### *3.1. Plant diversity response to initial and second entry treatments (Q1)*

Thinning and burning effects on understory plant diversity over time differed by both treatment type and diversity metric (Fig. 2). Two years after the initial treatments (2003), thin-burn treatments increased richness the most (adding a median 2–3 species per gridpoint), and the burn-only and overstory thin treatments displayed smaller, but still significant, increases relative to pre-treatment conditions (1999) (Wilcoxon's post hoc of the Friedman test, adjusted $p < 0.05$). Evenness, however, decreased significantly in the overstory thin treatment following initial treatments ($p < 0.05$). For diversity ($e^{H'}$) (combining richness and evenness), the largest increases occurred in the thin-burn treatments following initial treatment, with smaller, but significant, increases in other treatments ($p < 0.05$).

In contrast, richness increased significantly in the burn-only and overstory thin-burn treatments from one year prior to second-entry fire (2016) to two years after second-entry fire (2019) (adjusted $p < 0.05$), but there was no significant increase in the understory thin-burn treatment. Evenness ($e^{H'}/S$) did not change significantly for any treatment following second-entry fire, with the burn-only treatment retaining

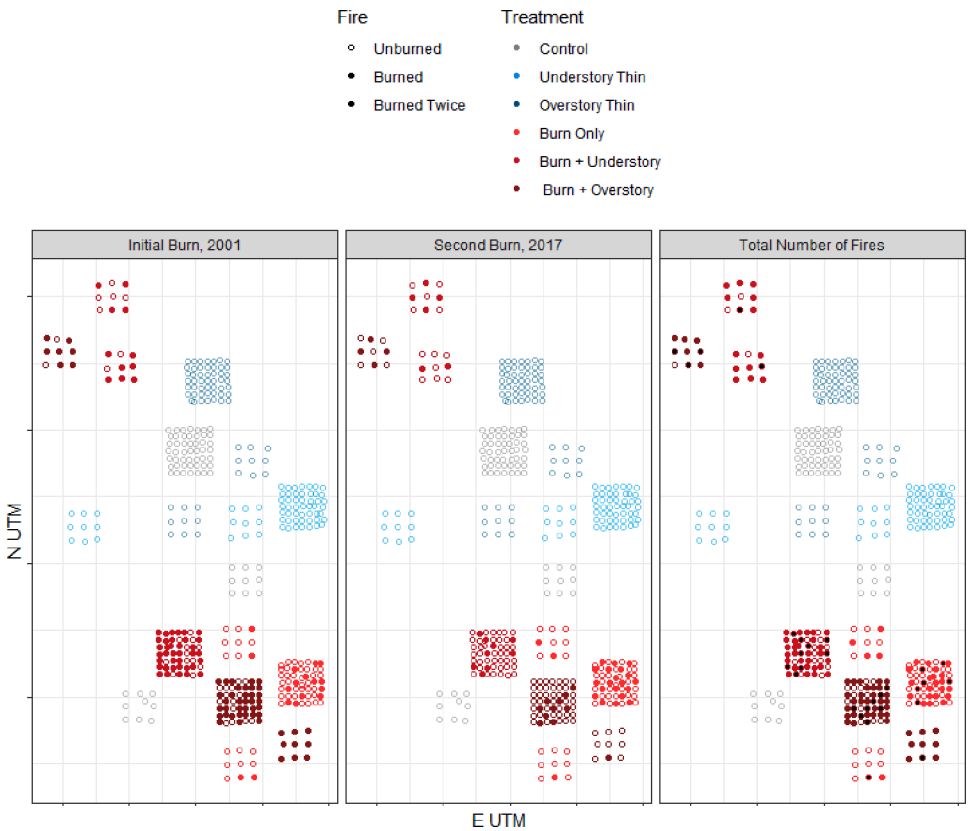


**Fig. A1.** Fire history at Teakettle Experimental Forest. Closed circles represent gridpoints with ≥ 1% ash or char ground cover post-fire. Open circles represent gridpoints with ≤ 1% ash or char ground cover post-fire.

significantly higher evenness than all thinned treatments (Dunn's post hoc of the Kruskal-Wallis test, adjusted $p < 0.05$; Table C. 1). Following the second burn, gridpoint-scale diversity ($e^{H'}$) increased most in the burn-only treatment (+1.2 effective species on average) due to increased richness and high evenness, with smaller but still significant increases in the overstory thin-burn treatment ($p < 0.05$).

We did not have the statistical power to detect significant differences in beta diversity with only three plots in each treatment at TEF, but our data do not support our hypothesis that beta diversity would increase following second entry burn treatments at TEF. They instead show a decrease in beta diversity following initial thin treatments with fire (Fig. 2). Thin treatments without fire show a more gradual decline in beta diversity, while the burn-only treatment maintained high beta diversity until after the second burn treatment.

Results of our hierarchical Bayesian models were consistent with our hypothesis that repeated local fire events would increase understory plant diversity and richness at the local scale (Fig. 3). Contrasts of estimated marginal means for the effect of burn number and thinning treatment on richness and evenness across the 1–18 year period following initial treatment and the 1–2 year period following the second entry burn indicate that one local fire event was much more likely to result in a greater increase in local diversity and richness than no fire in both unthinned (Pr. = 0.98) and initially thinned (Pr. > 0.99) treatments. Two local fire events were much more likely to result in a greater increase in diversity than one or zero fires in both thinned treatments (Pr. > 0.99). The small number of gridpoints that experienced two fire events in understory thin treatments were much more likely to have greater increases in richness than their unburned (Pr. > 0.999) and once-burned counterparts (Pr. = 0.98). Gridpoints that experienced two fires in overstory thin treatments were also more likely to result in greater increases in richness than no fire (Pr. > 0.999), and somewhat more likely than those with one fire event (Pr. = 0.96).

Richness and evenness responded differently to thinning and burning, and we found less evidence to support our hypothesis that greater numbers of fire events at the local scale would increase evenness. Gridpoints with at least one burn event were less likely to experience decreases in evenness than unburned gridpoints in the overstory thin treatment (Pr. > 0.99 for one burn event; Pr. = 0.97 for two burn events). Both thin treatments resulted in decreases in evenness without burning (Pr. > 0.99 for understory thin; Pr. = 0.99 for overstory thin), but one or two burn events reduce this effect and there was little difference between understory and overstory thinning treatments.

Model comparison results support our hypothesis that influence of thinning and burning on diversity, richness, and evenness would change over time. Models with quadratic fixed effects for time since treatment were significantly better at predicting diversity, richness, and evenness than models with no fixed effects or linear fixed effects for time (Table S.1 in supplemental materials). Both thinning treatments with and without fire had a significant non-linear effect on richness and diversity over time, peaking ~ 12 years after disturbance (Fig. 3). Both thinning treatments have an immediate negative effect on evenness, while thinning followed by appears to exhibit a decline in evenness over time.

### 3.2. Shrub response to initial and second entry treatments (Q2)

Eight species of shrubs occurred in at least 2% of gridpoint-years sampled at TEF: *C. cordulatus*, *Ribes rozellii*, *Arctostaphylos patula*, *Prunus emarginata*, *Symphorocarpus mollis*, *Ribes Viscosissimum*, *Chrysolepis sempervirens*, and *Corylus cornuta*. *C. cordulatus* is the most abundant, accounting for 63% of all understory plant cover recorded at TEF.

We did not find support for our hypothesis that second-entry burn treatments would reduce shrub cover. Shrub cover showed a delayed

response to and was not significantly different between any treatments or the control in 2003, two years after initial treatments (Fig. 2, Table C.1). Shrub cover showed a significant reduction (Wilcoxon's post hoc of the Friedman test, adjusted $p < 0.05$) in the overstory thin and burn treatment in the initial treatment, and non-significant reductions in all other treatments. However, in the subsequent 13 years, shrub cover increased significantly in all thinned treatments ($p < 0.05$), with the greatest increases observed in the treatments that were burned following thinning. Shrub cover did not reduce significantly in any second-entry burn treatment, regardless of initial thinning, and two years after second-entry burn, shrub cover was significantly higher (Dunn's post hoc of the Kruskal-Wallis test, adjusted $p < 0.5$) in all thinned treatments than in the control or the burn only treatment.

The shrub cover response over time at individual gridpoints is consistent with our hypothesis that shrub presence would expand in vegetation patches that were previously dominated by tree cover. The largest increases in shrub cover were found in previously tree-dominated gridpoints after thinning; those which also burned showed earlier and larger increases in shrub cover (Fig. 4). We found little change or slight increases in shrub cover in the open gridpoints regardless of thin or burn treatment, and a gradual return to near original shrub cover in shrub-dominated gridpoints that were thinned, regardless of burn treatment. Although very few un-thinned gridpoints actually burned in the initial prescribed fire ($n = 17$), all but one of these burned gridpoints maintained or decreased their shrub cover.

### 3.3. Environmental variable response to initial and second entry treatments (Q3)

Thinning treatments and fire together had the greatest effect on direct and diffuse light availability in the understory. In 2003, following initial treatments, both direct light and diffuse light availability were significantly higher (Dunn's post hoc of the Kruskal-Wallis test, adjusted $p < 0.05$) in the overstory thin and the overstory thin and burn treatment than in the control, and significantly higher in the overstory thin and burn treatment than in all other treatments (Table 1). The understory thin and understory thin and burn treatments had significantly higher diffuse light (but not direct light) than the control. In 2019, after 16 years and subsequent second-entry burn treatments, direct light and diffuse light availability were significantly higher ($p < 0.05$) in the overstory thin, overstory thin and burn, and understory thin and burn treatments than the control and other treatments. Relative to the controls, neither direct nor diffuse light was significantly higher in the burn only treatment after either of the two burn treatments.

Burn treatments at TEF resulted in decreased average litter depth and increased bare ground, while thinning treatments did not (Table 1). In 2003, litter depth was significantly lower ($p < 0.05$) in the burn only and overstory thin and burn treatment than in the control, and significantly lower ($p < 0.05$) in the overstory thin and burn treatment than in all other treatments. Bare ground cover was significantly higher ($p < 0.05$) in both thinned and burned treatments than in the control. In 2019, all burned treatments had significantly lower ($p < 0.05$) litter depth than in the control, while the burn-only and overstory thin and burn treatments had significantly higher ($p < 0.05$) bare ground cover than in the control.

Soil moisture was highly variable between gridpoints, and therefore we were not able to detect consistent patterns in treatment effects (Table 1). Soil moisture was significantly higher ($p < 0.05$) in the understory thin treatment than the control in 2003, but no other treatment differed significantly. In 2019, soil moisture was significantly lower ($p < 0.05$) in the burn only and overstory thin and burn treatments than in the control, and no other treatments differed significantly from the control.

### 3.4. Comparing TEF treatments to frequent-fire reference forests. (Q4)

Initially, thin treatments with burning approximated local (10 $m^2$) plant diversity in reference forests more closely than thin-only and burn-only treatments, but all burned treatments approximated local reference forest plant diversity after second-entry burns (Fig. 2, Table C.1). Thin treatments with burning did not significantly differ in local diversity, richness, or evenness from reference forests (measured in 2018 and 2019) after initial treatments. The control, both thin treatments without fire, and the burn-only treatment had significantly lower richness and diversity (Dunn's post hoc of the Kruskal-Wallis test, adjusted $p < 0.05$) than reference forests, but did not differ in evenness. By 2016, both thin treatments with burning maintained similar richness to reference forests, but the overstory thin and burn treatment had significantly lower diversity ($p < 0.05$), and the understory thin and burn treatment had significantly lower evenness ($p < 0.05$) than reference forests. All other treatments at TEF had significantly lower diversity and richness ($p < 0.05$) than reference forests, but the burn-only treatment had significantly higher evenness ($p < 0.05$) than reference forests. After the second-entry burn treatment, none of the three burned treatments had significantly lower diversity, richness, or evenness than reference forests, and the burn-only treatment had significantly higher evenness ($p < 0.05$) than reference forests.

We did not have the statistical power to detect significant differences in beta diversity with only three plots in each treatment at TEF and nine plots in reference forests, but our data point to a decrease in beta diversity following initial thin treatments with fire to below reference forest levels (Fig. 2). Thin treatments without fire show a more gradual decline in beta diversity, while the burn-only treatment maintained high beta diversity until after the second burn treatment.

Shrub cover diverged from reference forest levels over time in all thinned treatments at TEF, with or without fire (Fig. 2). In 2003, following initial treatments, shrub cover was significantly lower ($p < 0.05$) in the overstory thin treatment without burning than in reference forests (sampled in 2019), and no other treatments differed from reference forests. However, by 2016 all thinned treatments except for overstory thin without fire had significantly higher shrub cover than reference forests ($p < 0.05$). This high shrub cover remained two years after the second-entry burn treatment in 2019, when all thinned treatments, with or without fire, had higher shrub cover than reference forests.

Thin-only treatments consistently emulated the light conditions in reference forests, but when fire was applied, different thin treatments most closely emulated reference forests after initial treatments and second-entry burns (Table 1). In 2003, following initial treatments, neither direct nor diffuse light availability significantly differed from reference forests (measured in 2019) in the understory thin treatments, with or without fire, or the overstory thin treatment without fire. The burn-only treatment and control had significantly lower ($p < 0.05$) direct and diffuse light than in reference forests. The overstory thin and burn treatment was significantly higher in both light conditions than in reference forests with recent fires ($p < 0.05$). In 2019, following second-entry burn treatments, neither direct nor diffuse light availability significantly differed compared with reference forests in the either thin treatment without fire, or the burn-only treatment. The overstory thin and burn treatment had significantly higher direct and diffuse light than in reference forests ($p < 0.05$), while the understory thin and burn treatments were significantly higher in both light conditions than in reference forests with recent fires ($p < 0.05$).

Litter depth in 2003 was significantly lower in the overstory thin and burn treatment than in reference forests ($p < 0.05$), and did not differ in other treatments. Bare ground cover was significantly higher ($p < 0.05$) in both thinned treatments with fire, and significantly lower ($p < 0.05$) in the control and overstory thin treatment without fire. Litter depth in burn treatments at TEF two years after the second-entry burn (2019) did not significantly differ from litter depth in reference forests, regardless of initial thin treatment. All unburned treatments at TEF had

significantly higher ($p < 0.05$) litter depth in 2019 than in reference forests. Bare ground cover was significantly higher ($p < 0.05$) in the burn-only treatment, and not significantly different in the thin treatments with fire. Burn-only treatments at TEF had significantly lower total soil C than in reference forests ($p < 0.05$), and significantly lower total soil N than in reference forests with older fires ($p < 0.05$). No treatments had significantly different soil P than reference forests.

## 4. Discussion

This study points to key differences in how the type and frequency of fuels-reduction treatments affect plant understory diversity. Although local understory plant richness initially increased most following thinning combined with prescribed fire, this fuels reduction treatment did not generate understory beta diversity and shrub cover most similar to those in reference old-growth, mixed-conifer forests with frequent, low-severity fire regimes. Intense shrub growth after thinning, and especially thinning followed by fire (Goodwin et al., 2018), resulted in low understory evenness and beta diversity over time, which a secondary burn treatment emulating the historic fire return interval did not alter. Vigorous shrub growth may be driven by fire stimulated seed germination and resprouting of *C. cordulatus*, and augmented by thinning's reduction in live tree basal area which reduced competition for light, belowground water, and nutrients (Goodwin et al., 2018; Halpern, 1989). In contrast, multiple burns without thinning retained a more heterogeneous understory more similar to reference forest understories, with low levels of shrub cover, and high local diversity, richness, evenness, and beta diversity, at least in the two years following the second burn treatment. Our results suggest management treatments may need to focus on creating heterogeneity in burn effects to foster diverse forest understories and limit shrub cover.

### 4.1. Limitations

This study has several limitations to consider. First, replication is limited in this type of large-scale field experiment, resulting in low statistical power for comparing plot-level metrics. We try to address these limitations by using hierarchical models that take advantage of the nested structure of our study design to examine finer scale patterns rather than emphasizing plot-level effects. The models include random intercepts for each plot to help account for patterns in the data that may be due to particular differences between plots. In addition, we could not fully randomize the burn treatment due to logistical field constraints (i.e., containment and liability concerns of nine dispersed versus two aggregated units) faced by forest managers implementing the burn. We try to detect burn effects (rather than any potentially autocorrelated plot effects) by comparing pre and post treatment data in our analyses. Second, reference sites for mixed-conifer forests with intact or restored fire regimes are rare (Lydersen and North, 2012) and pose challenges for relevant understory comparisons because individual species may or may not be shared in species pools across locations. We attempted to address these limitations by selecting reference sites as similar as possible to TEF conditions (elevation, slope, aspect, overstory composition, dominant shrub species) and by comparing understory diversity metrics that are not sensitive to individual species identities. Third, we have limited data following the second burn, and we saw from the initial treatments that there is a strong temporal component to understory response. We can only compare the initial effects of the second burn, and we expect that the effects will continue to change over time. Finally, our large, repeated samples required extensive field technician crews which had difficulties identifying some genera to species. We found that data quality and identification consistency precluded more precise measures of certain genera, particularly in the family Poaceae and the genus *Cryptantha*. Therefore, it is likely that we are at least somewhat underreporting species richness and diversity while overreporting evenness across all of our treatments at TEF and the reference forests. This may particularly be the case in the understory thin, understory thin and burn, and overstory thin and burn treatments where Poaceae and *Cryptantha* were more frequently recorded following initial treatment. Correcting for any potential under- or overreporting of diversity would most likely intensify the trends displayed in these treatments, rather than negating them (Fig. 2).

### 4.2. Local understory plant richness, evenness, and diversity following multiple burn events

Understory community response varied greatly between the first and second burn events, likely due to different fire behavior in 2001 and 2017. The second burn had a major effect in the burn-only treatment, but very little effect in the two thinned treatments. We suspect that this may be due to cool, high humidity conditions during the burn and high moisture in shrubs dampening combustion. Local richness showed conflicting trends with local evenness and beta diversity in our study, indicating that many of the sites that gained species locally following thinning and prescribed fire also became more dominated by a small subset of similar species across sites. Other studies have also suggested different metrics of diversity frequently show divergent responses to disturbance, even when presenting the results from the same experiment (Li et al., 2004; Svensson et al., 2012). These trends are also influenced by the spatial scale at which the data is collected (Chase and Leibold, 2002). Small sampling areas, like those used in this study, are less sensitive to rare species, so our results are likely driven by changes in more abundant understory species found at TEF and reference forests. Some research has found that the relationship between spatial scale and diversity indices can change following disturbance(Dumbrell et al., 2008), suggesting the need for further research that compares diversity indices across multiple scales in order to fully understand treatment impacts on diversity.

We found some support for our hypotheses that multiple burn events would increase local understory plant richness and evenness relative to one or zero burn events at TEF. Gridpoints that did experience more fire did show increased local richness, but more fire only increased evenness in the most heavily thinned treatments (Fig. 3). We may not see substantial treatment-level responses to second-entry burn in initially thinned treatments because so few of those gridpoints actually burned in the second fire. This difference in burn behavior often occurs between repeated prescribed fire applications (Waring et al., 2016) and highlights how variable second-entry fire can be due to fuel loading and shrub regrowth following initial burning. Compounding these effects, fuels were elevated in the burn-only plots because mortality from California's 2012–2016 drought was higher in these stands due to their higher density (Steel et al., 2021). Our results suggest that for managed forests where prescribed burning is often cautiously applied, understory restoration may require more time and repeated burning.

### 4.3. Shrub response

The observed reductions in beta diversity and local evenness after initial treatment in this study are correlated with the growth of shrubs as an understory dominant and a shift toward open shrub-dominated community types over $\sim 10 - 12$ years following thinning and burning. Contrary to our hypothesis, the second burn treatment did not substantially reduce shrub cover in any of our treatments.

Other studies of shrub-layer responses to fire have found shrubs to mediate understory plant richness and diversity after wildfires over multiple decades (Bohlman et al., 2016; Webster and Halpern, 2010). This large increase in shrub cover in our thin-burn treatments may be analogous to conditions following wildfires in similar mixed-conifer forests, where high severity fire and shrub cover can create a positive feedback loop that induces type conversion from conifer forest to an alternate stable state of montane chaparral (Coppoletta et al., 2016). Results from TEF's thin-burn treatments agree with a recent analysis of fire severity effects on understory diversity in Sierra Nevada yellow pine and mixed-conifer forests, in which moderate - high severity patches

(>50–75% basal area mortality) had the highest richness and diversity (Richter et al., 2019). The study also found that evenness and beta diversity declined with greater fire severity, with fire-stimulated *C. cordulatus* as an indicator species for moderate-high severity fire (Richter et al., 2019). Despite relatively low levels of crown scorch in initial burn treatments compared to a high severity wildfire (Innes et al., 2006), thin-burn treatments may emulate high-severity burn conditions by releasing shrubs from competition with trees, while stimulating both abundant re-sprouting and germination of soil-banked seed (Halpern, 1989; Huffman and Moore, 2004).

### 4.4. Understory plant community conditions at reference forests

Our comparison of understory plant communities at TEF and reference forests did not fully support our hypothesis that multiple fires after initial thinning would best replicate understory plant diversity, shrub cover, and environmental conditions at reference forests. Thinning (at either level) followed by burning did best replicate reference forest local diversity metrics (Fig. 2, Table C.1) and environmental characteristics (Table 1) after the initial treatments. However, these combined thin and burn treatments had lower beta diversity than reference forests, and their light environment and shrub cover diverged from those in reference forests over time, where near-zero median shrub cover indicates that shrubs remain concentrated in discrete patches rather than widespread.

Once a second fire was introduced all of the burn treatments, regardless of initial thinning, at least approximated local understory diversity, richness, and evenness. However, the burn-only treatment had the highest local diversity and retained higher evenness and beta diversity than the initially thinned treatments. The burn-only treatment also closely matched the light environment and shrub cover of reference forests following the second burn treatment. These results highlight the important temporal dynamics of forest response to disturbance, including management treatments. Treatments that maximize short-term increases in understory plant diversity may or may not remain similar to target conditions over the long term.

### 4.5. Management implications

Patchiness at multiple scales within prescribed fire treatments may be beneficial to maintaining diverse understories across larger spatial scales. Congruent with other studies of understory plant community response to fire in mixed-conifer forests, richness was enhanced where treatment was more intense, leading to greater local reduction in litter and shrub cover and greater increases in light availability at intermediate scales. While these treatments became more homogeneous at the 4 ha plot scale over time, spatial and temporal variability in fire behavior may maintain beta diversity in the landscape by retaining species associated with mesic, closed-canopy conditions (North et al., 2005b). This also fits with the recently proposed framework that increased pyrodiversity, or diversity of fire histories, at the landscape scale supports increased biodiversity (He et al., 2019).

Conversion from mixed-conifer forest to shrub-field communities is an undesirable outcome of high severity wildfire for many forest managers in the Sierra Nevada, and would be an unintended outcome of forest restoration and fuels reduction treatments designed to reduce the risk of high-severity fire in these forests. A previous analysis in the TEF found shrub cover positively correlated with reduction in live tree basal area associated with thinning and subsequent mortality in the 2012–2016 drought (Goodwin et al., 2018).

In fire-suppressed forests, significant increases in shrub cover following mechanical thinning and burning treatments are a management concern because of their reduction in understory diversity and potential to increase subsequent fire intensity if burned when shrubs are dry. While the sample sizes in our preliminary analysis of shrub response in open, shrub, and tree dominated gridpoints are small (Fig. 4), our results suggest how thinning and burning at TEF may promote dominance by shrubs. Fire may have stimulated the seed bank of the dominant shrub *C. cordulatus*, after decades of seed accumulation due to fire suppression. Meanwhile, both fire and mechanical thinning may facilitate shrub growth from surviving plants and new seed germination in sites previously occupied by trees whose shade precluded shrubs. Previous research at TEF has shown that trees often occupy microsites with deeper soils and higher soil moisture availability (Meyer et al., 2007) in contrast to open areas with high surface temperatures and scant soil moisture. More research is needed to investigate this pattern but our results do suggest caution for managers using mechanical thinning. Removal of small trees that have infilled sites in fire-suppressed forests may not trigger an aggressive shrub cover response, but removal of large trees, which often indicate wet, productive sites (Fricker et al., 2019), could facilitate rapid shrub expansion into microsites where low-light conditions from tree cover previously precluded shrub expansion.

Achieving target understory conditions may require more than a single prescribed burn, irrespective of the thinning treatment. Similarly, we caution that treatments that maximize local understory plant diversity may not be the best treatments to achieve target understory conditions over the long term. Our results are consistent with those of other long-term studies of prescribed fire in Sequoia and Kings Canyon National Parks, where understory plant diversity responses often needed long time periods (10 – 20 years) after fire or even multiple fire events to become fully apparent (Webster and Halpern, 2010). Restoring the understory conditions and plant communities in fire-suppressed mixed-conifer forests may take multiple treatments over many years.

## CRediT authorship contribution statement

**M.C. Odland:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Visualization, Writing - original draft, Writing - review & editing. **M.J. Goodwin:** Data curation, Writing - review & editing. **B.V. Smithers:** Data curation, Writing - review & editing. **M.D. Hurteau:** Writing - review & editing. **M.P. North:** Conceptualization, Funding acquisition, Methodology, Resources, Supervision, Writing - review & editing.

## Declaration of Competing Interest

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

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## Appendix A

Fig. A1 and Table A1.

## Appendix B

Tables B1-B3.

**Table B1**
Physical and structural characteristics of reference forest sites and Teakettle Experimental Forest in 2019. Mean values for all gridpoints in each location are shown, with standard deviations in parentheses.

| | | | | | | Aspect (Proportion) | | |
|---|---|---|---|---|---|---|---|---|
| Location | Canopy Openness | CWD (%) | Elevation (m) | N UTM (m) | Slope (%) | SW | NE | SE/NW |
| Gin Flat | 0.71 (0.17) | 3.76 (9.06) | 2,146.81 (45.18) | 4,183,097.06 (406.79) | 29 (15) | 0.17 | 0.17 | 0.67 |
| Grant Grove | 0.62 (0.17) | 5.96 (7.56) | 1,981.04 (49.84) | 4,069,138.13 (242.50) | 32 (15) | 0.48 | 0.04 | 0.48 |
| Frog Creek | 0.66 (0.15) | 6.86 (11.05) | 1,995.54 (58.40) | 4,207,617.83 (135.92) | 16 (13) | 0.36 | 0.09 | 0.55 |
| Teakettle | 0.65 (0.21) | 5.96 (9.74) | 2,057.80 (58.39) | 4,092,525.53 (491.63) | 13 (8) | 0.31 | 0.24 | 0.45 |

**Table B2**
Overstory composition of reference forest gridpoints. Species are arranged by proportion of gridpoints where they occur as one of the two most abundant tree species within 12.6 m of the gridpont.

| Species | Proportion |
|---|---|
| Abies concolor | 0.673 |
| Pinus jeffreyi | 0.449 |
| Calocedrus decurrens | 0.422 |
| Pinus lambertiana | 0.347 |
| Abies magnifica | 0.041 |
| Sequoiadendron giganteum | 0.020 |
| Quercus kellogii | 0.007 |

**Table B3**
Understory species composition of Teakettle Experimental Forest and reference forest sites, 2018–2019. The 15 taxa with the highest frequency (proportion of gridpoints present) or relative abundance (proportion of total cover) are shown, and their frequency rank and relative abundance rank are indicated. The 10 of the 15 most frequently observed taxa and 10 of the 15 most abundant taxa are the same between reference forests and Teakettle Experimental Forest.

| | | Teakettle Experimental Forest | | | | Reference Forests | | | |
|---|---|---|---|---|---|---|---|---|---|
| Species | Type | Fr. Rank | Frequency | Ab. Rank | Rel. Abundance | Fr. Rank | Frequency | Ab. Rank | Rel. Abundance |
| Ceanothus cordulatus | Shrub | 1 | 0.48 | 1 | 0.63 | 2 | 0.34 | 1 | 0.57 |
| Gayophytum eriospermum | Herb | 2 | 0.46 | 12 | 0.01 | 1 | 0.53 | 13 | 0.01 |
| Ribes rozellii | Shrub | 3 | 0.37 | 3 | 0.04 | 3 | 0.30 | 4 | 0.03 |
| Poaceae sp. | Graminoid | 4 | 0.28 | 9 | 0.01 | 4 | 0.30 | 5 | 0.03 |
| Cryptantha sp. | Herb | 5 | 0.28 | 15 | 0.01 | 10 | 0.15 | – | 0.00 |
| Arctostaphylos patula | Shrub | 6 | 0.20 | 2 | 0.08 | 12 | 0.13 | 3 | 0.04 |
| Collinsia toreyii | Herb | 7 | 0.19 | – | 0.00 | – | 0.03 | – | 0.01 |
| Monordella odoritissima | Herb | 8 | 0.15 | 11 | 0.01 | – | 0.03 | – | 0.00 |
| Prunus emarginata | Shrub | 9 | 0.13 | 5 | 0.03 | – | 0.04 | 11 | 0.01 |
| Alophyllum integrifollium | Herb | 10 | 0.12 | – | 0.00 | – | 0.01 | – | 0.00 |
| Kellogia galliodes | Herb | 11 | 0.11 | – | 0.00 | – | 0.06 | – | 0.00 |
| Phacelia hastata | Herb | 12 | 0.10 | – | 0.00 | 5 | 0.18 | – | 0.01 |
| Symphorocarpus mollis | Shrub | 13 | 0.09 | 4 | 0.03 | 15 | 0.11 | 12 | 0.01 |
| Pteridium aquillinum | Fern | 14 | 0.09 | 6 | 0.03 | 7 | 0.17 | 2 | 0.09 |
| Eriogonum nudum | Herb | 15 | 0.08 | – | 0.00 | 11 | 0.14 | – | 0.00 |
| Viola pinetorum | Herb | – | 0.06 | – | 0.00 | 6 | 0.18 | – | 0.00 |
| Ribis viscossissimum | Shrub | – | 0.05 | 10 | 0.01 | – | 0.07 | 10 | 0.01 |
| Hierecium albiflorum | Herb | – | 0.05 | – | 0.00 | 8 | 0.16 | – | 0.00 |
| Hossakia crassifolia | Herb | – | 0.04 | 13 | 0.01 | – | – | – | – |
| Corylus cornuta | Shrub | – | 0.03 | 7 | 0.02 | – | 0.00 | – | 0.00 |
| Chrysolepis sempervirens | Shrub | – | 0.03 | 8 | 0.01 | – | 0.01 | – | 0.00 |
| Apocynum androsaemifolium | Shrub | – | 0.02 | – | 0.00 | 9 | 0.15 | 7 | 0.01 |
| Arctostaphylus nevadensis | Shrub | – | 0.01 | 14 | 0.01 | – | 0.02 | 9 | 0.01 |
| Chamaebatia foliolosa | Shrub | – | 0.01 | – | 0.00 | – | 0.02 | 6 | 0.02 |
| Rubus parviflorus | Shrub | – | 0.01 | – | 0.00 | – | 0.02 | 15 | 0.01 |
| Salix sp. | Shrub | – | 0.00 | – | 0.00 | – | 0.05 | 14 | 0.01 |
| Galium aparine | Herb | – | – | – | – | 14 | 0.12 | – | 0.01 |
| Galium trifidum | Herb | – | – | – | – | 13 | 0.13 | – | 0.01 |
| Ceanothus parvifolius | Shrub | – | – | – | – | – | 0.03 | 8 | 0.01 |

## Appendix C

Table C1

**Table C1**
Mean values for diversity metrics and shrub cover two years after initial treatments (2003), 15 years after initial treatments (2016) and two years after second-entry burn treatments (2019) across all treatment types at Teakettle Experimental Forest (TEF) and reference forests. Standard deviations are shown in parentheses. Asterisks indicate unequal mean rank values for an environmental variable across treatments in a given year (Kruskal-Wallis test, $p < 0.05$). Different letters following mean values indicate significant pair-wise differences between treatments (Bonferroni corrected Dunn's post-hoc analysis, $p < 0.05$).

| | | TEF Treatments | | | | | | | Kruskal-Wallis Test | |
|---|---|---|---|---|---|---|---|---|---|---|
| Metric | Year | Control | Understory Thin | Overstory Thin | Burn | Understory + Burn | Overstory + Burn | Reference Forests | sig | p value |
| Richness (S) | 2003 | 4.04 bc (4.14) | 3.37 bc (3.48) | 2.90 c (3.25) | 3.13 bc (2.88) | 5.31 a (3.29) | 4.04 ab (1.97) | 5.90 a (3.93) | * | <0.001 |
| | 2016 | 3.33 bc (2.39) | 3.99 bc (2.30) | 3.06 c (2.49) | 3.19 bc (2.26) | 5.94 a (3.03) | 4.51 ab (2.20) | 5.90 a (3.93) | * | <0.001 |
| | 2019 | 4.15 b (3.13) | 4.21 b (2.61) | 4.07 b (2.70) | 5.10 ab (3.08) | 6.49 a (3.56) | 6.06 a (2.93) | 5.90 a (3.93) | * | <0.001 |
| Diversity (e^H') | 2003 | 2.32 bcd (2.03) | 2.05 bcd (1.50) | 2.08 cd (1.58) | 1.79 c (1.13) | 2.42 ab (1.12) | 2.28 abd (1.03) | 2.90 a (1.87) | * | <0.001 |
| | 2016 | 2.00 a (1.20) | 1.97 a (0.90) | 2.00 a (1.25) | 2.26 a (1.63) | 2.61 ab (1.68) | 2.04 a (1.21) | 2.90 b (1.87) | * | <0.001 |
| | 2019 | 2.70 bc (2.10) | 2.20 bc (1.33) | 2.05 c (1.05) | 3.41 a (1.87) | 2.79 abc (1.83) | 2.85 abc (1.93) | 2.90 ab (1.87) | * | <0.001 |
| Evenness (e^H'/S) | 2003 | 0.61 (0.31) | 0.57 (0.33) | 0.59 (0.38) | 0.59 (0.36) | 0.51 (0.27) | 0.61 (0.24) | 0.58 (0.29) | | 0.373 |
| | 2016 | 0.65 bc (0.31) | 0.56 ac (0.25) | 0.53 ac (0.34) | 0.73 b (0.29) | 0.46 a (0.22) | 0.51 ac (0.24) | 0.58 c (0.29) | * | <0.001 |
| | 2019 | 0.66 bc (0.33) | 0.57 ac (0.28) | 0.57 ac (0.29) | 0.74 b (0.24) | 0.48 a (0.23) | 0.51 a (0.25) | 0.58 ac (0.29) | * | <0.001 |
| Shrub cover (%) | 2003 | 16.26 ab (25.27) | 9.32 ab (19.54) | 3.52 b (10.45) | 14.36 ab (24.71) | 7.36 ab (15.37) | 4.02 ab (9.82) | 13.05 a (23.63) | * | 0.043 |
| | 2016 | 14.08 b (25.40) | 26.79 ac (30.69) | 16.65 bc (27.01) | 8.83 b (18.37) | 42.90 a (36.93) | 40.24 a (38.17) | 13.05 b (23.63) | * | <0.001 |
| | 2019 | 8.35 b (14.20) | 26.16 a (31.22) | 24.87 a (30.36) | 4.79 b (13.09) | 36.23 a (34.42) | 35.83 a (35.31) | 13.05 b (23.63) | * | <0.001 |

## Appendix D. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2021.119361.

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