

Short-term effects of single-entry prescribed fire in California's yellow-pine and mixed conifer forests

Ashley R. Grupenhoff^{a,*}, Tessa Putz^b, John Williams^c, Becky Estes^d,
Rut Domènech^b, Joe Restaino^e, Hugh D. Safford^b

^a Department of Natural Resources and Environmental Sciences, Cal Poly San Luis Obispo, San Luis Obispo, CA 93407, USA

^b Department of Environmental Science and Policy, University of California, Davis, CA 95616, USA

^c The Nature Conservancy in California, Sacramento, CA, USA

^d Eldorado National Forest, USDA Forest Service, Placerville, CA, USA

^e Fire and Resource Assessment Program, California Department of Forestry and Fire Protection, Sacramento, CA, USA

ARTICLE INFO

Dataset link: [California prescribed fire monitoring program: 2019–2024](#)

Keywords:

Fuel consumption
Forest restoration
Species diversity
Tree mortality
Ladder fuels
Fuel treatment

ABSTRACT

Prescribed fire is an important tool for reducing wildfire risk and restoring forest health in semiarid yellow pine and mixed conifer (YPMC) forests in the western United States (US), which historically experienced frequent low-to moderate-intensity fires. After more than a century of fire exclusion, these forests now tend to support excessive surface fuel loads, dense tree stands, and altered species composition - conditions that promote the potential for high-severity wildfire. To evaluate the short-term effects of prescribed fire as a restoration and fuel reduction strategy, we assessed 12 single-entry prescribed burns across eastern California through the California Prescribed Fire Monitoring Program. We assessed changes in surface fuels, forest structure, and plant diversity before and after prescribed fire using field measurements and Bayesian modeling. We found that prescribed fire reduced total surface fuel loading by an average of 63%, with the greatest reductions in duff (67%) and litter (65%). Fuel consumption was positively associated with pre-fire fuel load, slope, wind speed, and mean annual temperature. Prescribed fire significantly reduced live tree density by 32%, particularly of shade-tolerant and small-diameter trees (<40 cm DBH, 38% reduction), and basal area by 24%. Despite relatively minor change in forest structure, both plant richness and diversity increased significantly two years post-treatment. These findings highlight the value of single-entry prescribed fire for reducing hazardous fuels and stimulating understory biodiversity, while also underscoring its limited capacity to restore forest structure after a single application. Scaling up and sustaining prescribed fire implementation, potentially in combination with other treatments, will be essential for restoring fire-adapted forest ecosystems in the western United States.

1. Background

Prior to Euro-American settlement, much of the seasonally dry forest land base in the western United States experienced frequent low-to-moderate intensity fires set by lightning and Native American ignitions (Agee, 1993; van Wagtenonk et al., 2018; Safford et al., 2021). Since the mid 1800s, fire exclusion, timber harvesting practices, and livestock grazing have greatly altered the fire regime of these forests (van Wagtenonk et al., 1998; Hagmann et al., 2021). Variable fire effects were historically common due to spatially heterogeneous fuel loads, leading to a fine-scaled matrix of mature trees, gaps, and groups of seedlings and saplings that promoted ecological diversity (Larson and

Churchill, 2012; Lydersen et al., 2013; Richter et al., 2019). Today's seasonally dry forests are more likely to support high surface fuel loads, homogeneous stands with high densities of young trees, and a high and increasing proportion of fire-intolerant species (Safford and Stevens, 2017; Hagmann et al., 2021). These changes in fuel conditions and forest structure, in combination with climate warming and drought induced tree mortality, have led to a pronounced increase in larger, higher severity fires (Steel et al., 2015; Westerling, 2018; Williams et al., 2023; Young et al., 2017), posing fundamental threats to biodiversity, ecosystem resilience, and human health and safety (Richter et al., 2019; Steel et al., 2022, 2023; Weeks et al., 2023; Williams et al., 2023).

The basic tenets of ecological restoration, enhancement of forest

* Correspondence to: 1 Grand Ave, San Luis Obispo, CA 93407, USA.

E-mail address: agrupenh@calpoly.edu (A.R. Grupenhoff).

<https://doi.org/10.1016/j.foreco.2026.123771>

Received 17 January 2026; Received in revised form 9 March 2026; Accepted 30 March 2026

Available online 11 April 2026

0378-1127/© 2026 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

resilience, and human asset protection in seasonally dry conifer forests are largely based on replicating the effects of frequent low and moderate severity burning (Covington and Moore, 1994; Arno and Fiedler, 2005; Stephens et al., 2020) either through fire itself (prescribed fire or managed wildfire) or a surrogate for fire's effects, such as hand- or mechanical-thinning. Most comprehensive scientific considerations of fuel reduction in seasonally dry forests have identified some combination of fire surrogates and fire itself as the most effective form of management (Stephens et al., 2009, 2024). Because wildfire behavior under most weather and fuels conditions is driven principally by fine surface fuels (litter and small diameter fuels up to 7.6 cm), reduction of the fine fuel fraction is of paramount importance, followed by reduction of ladder fuels, and opening of the forest canopy (Agee and Skinner, 2005).

Many different techniques and combinations thereof have been proposed and implemented to reduce fuels in seasonally dry forests. From a cost and efficacy basis, however, prescribed fire is consistently identified as a key component, because it most effectively reduces fine fuels, and its cost per area is relatively low (Agee and Skinner, 2005; Stephens and Moghaddas, 2005; Stephens et al., 2009; North et al., 2012; Prichard et al., 2020). With respect to ecological restoration, prescribed fire is a direct way to restore fire to seasonally dry forests that have been missing their keystone ecological process for most of the last century or longer (Biswell, 1989; Covington and Moore, 1994). Prescribed fire, sometimes in combination with mechanical fuel treatment, has been shown to successfully restore structural heterogeneity and increase plant diversity in the short term by removing understory biomass and litter and increasing soil nutrient availability (Knapp et al., 2007; Stephens et al., 2009; Abella and Springer, 2015; Odland et al., 2021). In addition, prescribed burning can increase forest resilience by reducing surface and ladder fuels and mitigating subsequent wildfire severity and large canopy tree mortality (Stephens, 1998; Stephens and Moghaddas, 2005; Vaillant et al., 2009).

In the context of protecting human assets, prescribed fire is frequently deprioritized in favor of mechanical or manual fuel reduction methods. This is because prescribed fire is often avoided near human communities due to high risk aversion and the perception that its fire behavior is less predictable and precisely controlled than mechanical or manual thinning (Hiers et al., 2020). Regulatory and legal boundaries to using fire as a management tool are also difficult to navigate in most western states (Quinn-Davidson and Varner, 2011; Miller et al., 2020; Williams et al., 2024). In addition, prescribed fire, as practiced in the western US, is rarely implemented under conditions that release sufficient energy to kill medium- or large-sized trees or reduce large-diameter woody fuels (Stephens et al., 2020). This limitation also applies when prescribed fire is used as a stand-alone tool in forest management scenarios outside the wildland urban interface that require the removal of larger-stemmed trees (Covington and Wagner, 1998; Vaillant et al., 2009; Stephens et al., 2020). As a result of these issues, prescribed fire has remained a “boutique” tool in the management toolkit in much of the western US, in direct contrast to its widespread use in the midwestern and southeastern US and other nations, such as Australia and South Africa (Levine and Stephens, 2025). Nonetheless, some level of fine fuel reduction is invariably necessary after mechanical or manual work (Safford and Saberi, 2026). Because there is little to no commercial market for small-diameter trees and woody fuels in the western US, managers are often left with few options, making on-site disposal via pile burning the most common solution.

Increased social and political pressures have resulted in a renewed interest in prescribed fire as a management tool. For example, in various US States, recent legislative and regulatory actions have opened the door to more extensive private and tribal use of prescribed fire by mandating easier permitting and certification, as well as enhancing liability protections (Varner et al., 2021; McCormack et al., 2023). In association, there has been a surge in the number of prescribed fire councils and burn associations in the West (Deak et al., 2025). In California, the State Carbon Plan and State Wildfire and Forest Resilience Strategy (Forest

Climate Action Team, 2018; State of California, 2021) have greatly raised the profile of prescribed fire in forest management, and a 2015 MOU between CAL FIRE, the United States Forest Service (USFS), and other state agencies promised to treat 400,000 ha annually.

As the use of fire as a forest management tool regains momentum in the western US, it is increasingly important to assess its effects and its effectiveness. Monitoring is a key component of the adaptive management cycle, but it is rarely practiced under standardized protocols or at sufficiently broad spatial or temporal scales to inform the evolution of management policy and practice. Even when it is, management practices are rarely modified in response (Allen and Gunderson, 2011; Suskind et al., 2012; Reid et al., 2013; Bonner et al., 2021). After the 2012–2016 drought killed hundreds of millions of trees in the Sierra Nevada, a Little Hoover Commission report in 2018 called for a rethinking of California forest management and a massive investment in proaction. The report recommended that “The State of California should lead a policy shift from fire suppression to using fire as a tool” and called for prescribed fire crews and monitoring programs to track progress and facilitate success (Commission LH, 2018). CAL FIRE, the lead State agency in matters relating to vegetation and fire management, responded by hiring and training ten prescribed fire crews based around the state. In collaboration with the University of California, Davis, CAL FIRE also developed the California Prescribed Fire Monitoring Program (CPFMP; Safford et al., 2023; Domènech et al., 2025; Domènech et al., 2026).

A primary focus of the CPFMP is to assess whether prescribed fire, as currently practiced by multiple agencies and organizations, is achieving both ecological and wildfire risk reduction objectives in California's seasonally dry conifer forests. At this point, most prescribed burning in California and the West occurs as one-off events, with reburning either unplanned or not yet on the horizon. Despite recent increases in the area burned, some research suggests that low-intensity single-entry prescribed fires may be insufficient to meet ecological or fuel reduction objectives (Fule et al., 2004; Schwilk et al., 2009; Vaillant et al., 2009; Webster and Halpern, 2010; Nagelson et al., 2025; Domènech et al., 2025). With pre- and post-fire data for numerous prescribed fire events in frequent-fire adapted forest systems, the CPFMP is well equipped to take a closer look at the effects and effectiveness of single-entry fire. In this paper, we analyze and interpret CPFMP pre- and post-fire data from single-entry burns at 12 sites burned by six different land management entities between 2019 and 2022. We asked:

- 1) To what extent did single-entry prescribed fire reduce surface fuels?
- 2) What factors influenced fuel consumption?
- 3) To what extent did prescribed fire alter forest structure and species diversity?

2. Methods

2.1. Study site

This study encompasses 12 project sites across eastern California, sampled by the CPFMP between 2019 and 2022 that were treated with prescribed fire (Fig. 1). We focus on areas burned in mixed conifer or yellow pine forest types (we collectively refer to these as “YPMC”), which are the most widespread seasonally dry conifer forest types in California, southern Oregon, western Nevada, and northern Baja California, Mexico (the North American Mediterranean Climate Zone, or NAMCZ). Similar forests also occur in eastern Washington and Oregon; Arizona, New Mexico, and southern Colorado; and smaller areas in the northern Rockies. YPMC forests in the NAMCZ historically experienced frequent, low-to-moderate intensity fires. The dominant species – ponderosa pine (*Pinus ponderosa* Laws.), Jeffrey pine (*Pinus jeffreyi* Grev. & Balf.), sugar pine (*Pinus lambertiana* Dougl.), and black oak (*Quercus kelloggii* Newb.) – were well-adapted to this fire regime, exhibiting traits such as highly flammable foliage, thick bark, self-pruning lower branches, hypogeal germination, and well-protected cones (Safford

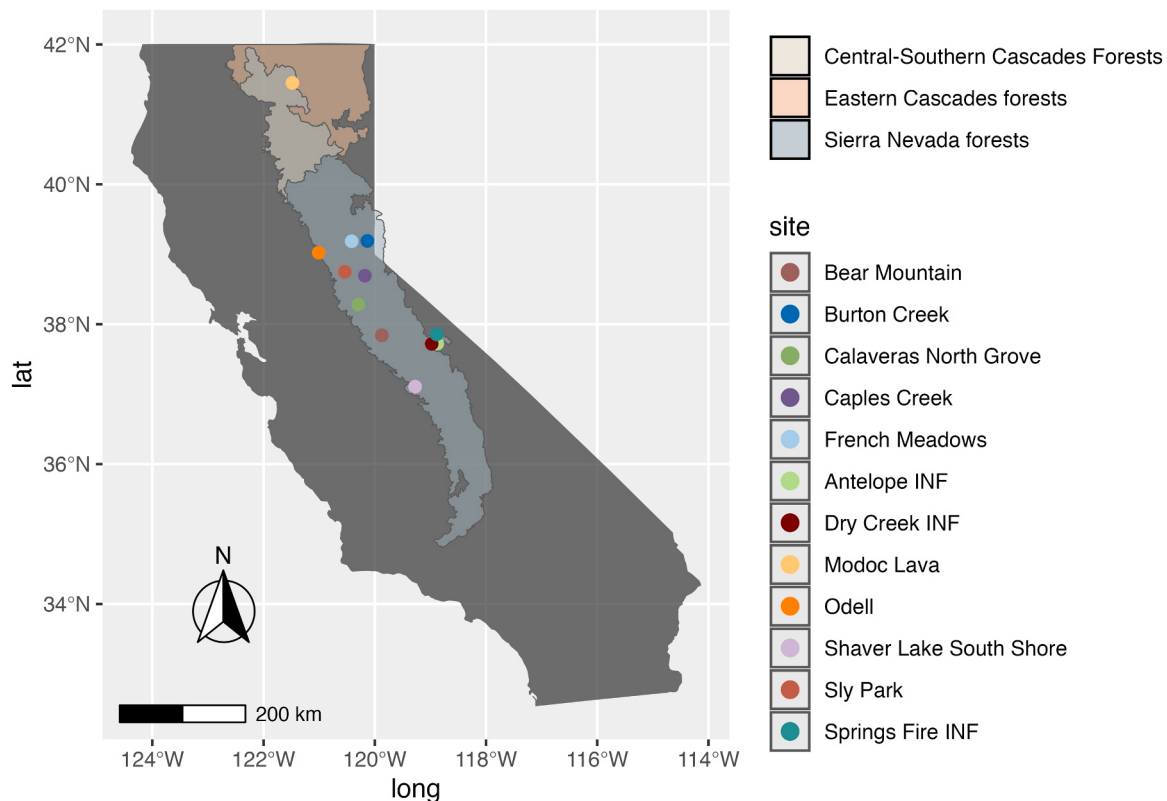


Fig. 1. Location of plot locations (black dots) across northern California. Colored polygons represent the geographic extent of regions within yellow pine and mixed conifer (YPMC) forest types: Sierra Nevada (blue), Eastern Cascades (orange), and Southern Cascades (tan).

et al., 2021). Pre-Euroamerican fire return intervals averaged 5–15 years, and fires rarely resulted in more than 15% of the tree canopy being killed (Van de Water and Safford, 2011; Safford and Stevens, 2017). Other, less fire-tolerant tree species include white fir (*Abies concolor* Gord. & Glend), Douglas-fir (*Pseudotsuga menziesii* Franco), and incense-cedar (*Calocedrus decurrens* (Torr.) Floren.), all of which have become more common since fire exclusion policies were implemented. Modern wildfires often kill more than 30–40% of canopy trees due to higher forest densities and fuel loads, as well as the contemporary dominance of fire-intolerant trees (Safford et al., 2022).

The climate across our NAMCZ study sites is Mediterranean, with the majority of precipitation occurring in winter and spring, and less than 50% of precipitation arriving as snow at most sites (Jeffrey pine-dominated sites are the exception). Precipitation at our sites ranges from 360 to 2247 mm. Mean minimum temperatures in January range from -10.3 – 5.2 °C and mean maximum temperatures in July range from 21.5 to 35.6 °C (Table 1).

All study sites were located in forests that have experienced prolonged fire exclusion, with no recorded fire for at least 75 years prior to treatment. These conditions reflect a substantial departure from the historical range of variability in fire frequency (Safford and Stevens, 2017). The one exception was Bear Mountain, which experienced wildfire during the 2013 Rim Fire. Prior to prescribed burning, all sites underwent some level of unit preparation, typically involving the establishment of control lines and selective clearing around sensitive cultural or ecological features.

2.2. Field measurements

Across each of the 12 sites, 0.04 ha permanent plots were stratified across burn units ($n = 270$), using a modification of the US Forest

Service Common Stand Exam (USFS, 2012). Field data collected included quantification of overstory and understory structure, standing and downed trees, surface fuels and woody debris, and ground cover. All measurements were taken prior to prescribed burns, one year post-burn, and two years post-burn (when applicable). Surface and woody debris were also measured within 1–2 weeks after prescribed fire to capture immediate fire effects.

Tree measurements were collected for all trees greater than 7.62 cm diameter at breast height (DBH) in the 0.04 ha plot. Species, status (live or dead), DBH, height, and height-to-live-crown were recorded. For snags, only DBH and height were recorded. Ocular estimates of percentage cover by trees, shrubs, grasses, and herbs were made in the full 0.04 ha plot. Cover was recorded as a continuous value rather than in categorical classes to support calculation of diversity metrics. To minimize observer bias, all ocular cover estimates were collected by a single trained and experienced crew lead. Ground cover data were estimated for the following categories: rock (particles >2 mm diameter), bedrock, bare ground, litter, basal vegetation, and woody debris.

In the full 0.04 ha plot, vegetation composition was recorded by identifying all species present in the plot and estimating the percent cover for each species before prescribed fire, one year post-fire, and two years post-fire. Plant life history data for each species were obtained from the USFS Fire Effects Information System or the University of California Jepson Herbarium. Species were classified by origin (native, non-native) and lifeform (tree, shrub, forb, graminoid, fern). We calculated local species richness (calculated as the mean number of species per 0.04 ha plot) and the Shannon diversity index (which gives weight to rare species) by plant origin (native or non-native) using the *vegan* package in R (R Core Team, 2021; Oksanen et al., 2023).

Surface fuels were measured using the planar intercept method (Brown, 1974) at each plot before prescribed fire, immediately

Table 1
Description of 11 study sites that were treated with prescribed fire. Species codes: ABCO *Abies concolor*, ABMA *Abies magnifica*, ARME *Arbutus menziesii*, CADE *Calocedrus decurrens*, PICO *Pinus contorta*, PIJE *Pinus jeffreyi*, PILA *Pinus lambertiana*, PIPO *Pinus ponderosa*, PSME *Pseudotsuga menziesii*, QUKE *Quercus kelloggii*, SEGI *Sequoiadendron giganteum*.

Site	Ownership	Elevation (m)	Mean annual precip (mm)	January mean minimum (°C)	July mean maximum (°C)	Burn Units	Description	Dominant tree species	Number of plots	Burn Date	Type of Fire
Antelope INF	Inyo NF	2300	400	-9.0	26.7	2	Jeffrey pine	PIJE	19	June 23–25, 2023	Prescribed fire
Bear Mountain	Stanislaus NF	1500	982	0.1	29.3	4	Mixed conifer	PIPO, CADE, PILA, QUKE	27	September 25–30, 2019	Prescribed fire
Burton Creek	California State Parks	2100	1003	-4.9	25.2	1	Mixed conifer	ABCO, ABMA, PICO, PIJE	5	November 13 2019	Prescribed fire
Calaveras	California State Parks	1500	1371	0.3	28.7	3	Giant sequoia/mixed conifer	SEGI, PILA, ABCO, CADE, QUKE, PIPO	34	May 16, 2022 & October 23–26, 2022	Prescribed fire
North Grove Caples Creek	Eldorado NF	1981	1629	-4.9	24.6	1	Mixed Conifer	ABMA, ABCO, PIPO, PIJE	108	September 30, 2019 - October 25, 2019	Prescribed fire/Wildfire
Dry Creek INF	Inyo NF	2300	469	-10.1	26.2	2	Jeffrey pine/lodgepole pine	PIJE, PICO	11	November 15–18, 2021	Prescribed fire
French Meadows	Tahoe National Forest / The Nature Conservancy	1500–2200	1970	-3.1	24.9	1	Mixed conifer	ABCO, ABMA, PILA, CADE, PIPO, PIJE	11	May 16–19, 2021	Prescribed fire
Modoc Lava	Modoc NF	1500	625	-4.2	29.4	3	Ponderosa pine	PIPO, ABCO, CADE	16	May 10–11, 2021	Prescribed fire
Odell	Private	573	1125	2.5	33.0	1	Ponderosa pin	PIPO, QUKE	5	February 28, 2022	Prescribed fire
Shaver Lake	Southern California Edison	1737	964	-0.5	27.8	1	Mixed conifer	ABCO, CADE, PIPO, PILA	12	May 19, 2022	Prescribed fire
South Shore Sly Park	Sierra Pacific Industries	1200	1373	-0.5	32.0	2	Mixed conifer/ponderosa pine plantation	PIPO, CADE, PSME, QUKE	11	Feb 11, 2020	Prescribed fire
Spring Fire INF	Inyo NF	2400	521	-9.6	24.6	1	Jeffrey pine/lodgepole pine	PIJE, PICO	33	July 26–Aug 20, 2019	Managed wildfire

post-burn, one year post-burn, and two years post-burn. Four 11.3-meter transects were established at N, S, E, and W azimuths from the plot center, and sampling commenced at the distal end of the transects. Woody material was tallied by 1-, 10-, 100-, and 1000-hour fuel classes used in the National Fire-Danger Rating System (diameters: 0–0.6 cm, 0.6–2.5 cm, 2.5–7.59 cm, and >7.6 cm respectively). Fine woody debris (1-, 10-, and 100-hour fuels) was sampled from 0 to 2 m (1- and 10-hour) and 0–4 m (100-hour). Coarse woody debris (1000-hour fuels) was sampled from 0 to 11.3 m. For all pieces of coarse woody debris (1000-hour fuel classes) that intersected the transect line, the diameter, length, and decay class were recorded individually. Duff and litter fuel depths (cm) were measured at 0 and 4 m from the beginning of each sub-transect, for a total of 8 measurements. Litter is the layer of recently deposited undecomposed material, and duff consists of fermenting and decomposing organic material.

Measurements of fine woody debris (FWD), coarse woody debris (CWD), litter, and duff were summarized at the transect level (Brown, 1982). These were weighted according to the average proportion of tree species within the plot to account for variation in fuel characteristics across the study areas using the Rfuel package (van Wageningen et al., 1998; Stephens, 2001; Foster et al., 2018). In a few instances, the immediate post-burn fuel load sampled with Brown's protocol was greater than the pre-burn fuel load. For these cases, we treated total consumption as zero.

2.3. Prescribed fire treatments

The primary objective of the prescribed burns was to reduce wildfire risk and restore forest ecosystem health. For each burn day, fire weather indices were obtained from the most representative Remote Automated Weather Station (RAWS) for each site. These indices included temperature (°C), wind speed (m/s), relative humidity (%), and 10-hour dead fuel moisture (%) (Table 2). All prescribed burns remained within prescription parameters, apart from the Caples Creek burn, which started on September 30th, 2019, and was converted to a wildfire on October 10th, 2019. Despite exceeding the planned prescription, it remained within the planned perimeter while burning an additional 2355 acres (Dailey et al., 2019).

2.4. Natural range of variation (NRV) reference values

To determine a benchmark for forest structure and fuel conditions following fire treatments, we summarized natural ranges of variation using data from Safford and Stevens (2017) and Young et al. (2020). We utilize forest structure attributes including surface fuel loading and tree density (Appendix S1: Tables S1–S2). We computed the group mean and 25th to 75th percentiles for each stand attribute (Young et al., 2020).

2.5. Statistical analyses

2.5.1. Prescribed fire effects on surface fuel loading

To determine the effect of prescribed fire on surface fuel loading, we compared surface fuel loads (litter, duff, fine woody debris, and coarse woody debris) before and immediately after prescribed fire using a Wilcoxon signed rank test. We used $\alpha = 0.05$ with a Bonferroni correction to control for bias against repeated testing. Bayesian generalized linear mixed models were used to assess the effect of prescribed burning on fuel consumption. The proportion of fuel consumed ranged from zero (unburned) to one (completely burned); thus, we used a zero/one inflated beta (ZOIB) hierarchical regression model, which allows for zeros, ones, and continuous proportions between the two (Liu and Eugenio, 2018). We considered the following predictors: pre-fire fuel load, density of live trees, density of snags, basal area proportions (pBA) of pine, fir, and incense cedar, relative humidity (%), mean annual precipitation (ppt), mean annual temperature (tmean), slope, and aspect (Eq. 2).

Table 2

Average weather conditions during each prescribed burn. All data are from the nearest Remote Automated Weather Station (RAWS).

Site	RAWS station	Date	Average Temperature (°C) [Min, Max]	Avg wind speed (m/s)	Avg relative Humidity (%)	Avg 10 h fine dead fuel moisture (%)
Antelope INF	Dexter (NWS: 043711)	June 23–25, 2023	11.8 [4.3–19.8]	2.1	43 (19–71)	7.3
Bear Mountain	Crane Flat Lookout (NWS: 044195)	September 25–30, 2019	11.0 [6.6–16.1]	3.1	59 (35–80)	10.6
Burton Creek	Homewood (NWS: 041909)	November 13, 2019	9.9 [6.4–13.8]	0.8	38 (26–51)	7.1
Calaveras North Grove	Cottage (NWS: 043210)	May 16, 2022	8.4 [5.0–15.0]	2.4	54 (44–66)	7.9
Calaveras North Grove	Cottage (NWS: 043210)	October 23–26, 2022	15.0 [11.1–19.4]	3.3	38 (21–62)	7.6
Caples Creek	Owens Camp (NWS: 043611)	September 30, 2019 - October 25, 2019	8.7 [1.2–19.6]	0.8	44 (18–68)	8.6
Dry Creek INF	Crestview (NWS: 043709)	November 15–18, 2021	5.4 [-2.8–14.9]	1.2	49 (18–86)	8.9
French Meadows	Duncan Peak (NWS: 041901)	May 16–19, 2021	9.0 [6.1–13.9]	3.5	80 (50–99)	12.0
Modoc Lava	Round Mountain (NWS: 040221)	May 10–11, 2021	13.5 [4.7–21.1]	2.5	31 (15–64)	6.3
Odell	Secret Town (NWS: 041808)	Feb 8, 2022	13.8 [4.4–24.4]	0.5	30 (13–53)	7.5
Shaver Lake South Shore	Shaver (NWS: 044522)	May 19, 2022	15.2 [6.7–23.9]	0.8	59 (32–94)	11.4
Sly Park	Steely Fork (NWS: 042615)	Feb 11, 2020	12.0 [8.3–20.6]	1.0	24 (14–52)	6.5
Springs Fire INF	Dexter (NWS: 043711)	July 26–Aug 20, 2019	18.8 [11.1–26.8]	2.8	31 (15–51)	5.4

$$\begin{aligned}
& \text{immediate consumption} \sim \text{Beta}(\mu_{ij}, \phi) \\
\text{logit}(\mu_{ij}) = & \alpha + \beta_{\text{prefirefuelload}} \text{prefirefuelload} + \beta_{\text{pBApine}} \text{pBApine} + \beta_{\text{pBAfir}} \text{pBAfir} \\
& + \beta_{\text{pBAcdec}} \text{pBAcdec} + \beta_{\text{prefireDensity}} \text{prefireDensity} \\
& + \beta_{\text{prefireSnag}} \text{prefireSnag} + \beta_{\text{RelativeHumidity}} \text{RelativeHumidity} + \\
& \beta_{\text{windspeed}} \text{windspeed} + \beta_{\text{slope}} \text{slope} + \beta_{\text{aspect}} \text{aspect} + \beta_{\text{ppt}} \text{ppt} + \beta_{\text{tmean}} \text{tmean} \\
& \alpha \sim \text{normal}(0, 100)
\end{aligned} \quad (2)$$

2.5.2. Prescribed fire effects on forest structure

We examined changes in overall tree density and basal area one year after prescribed fire using the same statistical analysis that was performed above. We then applied Bayesian hurdle-gamma regression models to live basal area, live tree density, snag basal area, and snag density to examine shifts in the composition of dominant tree genera (Eq. 3) and diameter class distribution (Eq. 4). Both response variables followed a gamma distribution, with the diameter class model incorporating a hurdle component to address zero-inflation. A random effect for unique site was included in all models to account for non-independence of plots within each site.

$$\begin{aligned}
& \text{forest structure variable} \sim \text{Gamma}(\mu_{ij}, \phi) \\
\text{logit}(\mu_{ij}) = & \alpha + \beta_{\text{pre post fire}} \text{pre post fire} * \beta_{\text{species genera}} \text{Species Genera} + (1|\text{site})
\end{aligned} \quad (3)$$

$$\begin{aligned}
& \text{forest structure variable} \sim \text{Gamma Hurdle}(\mu_{ij}, \phi) \\
\text{logit}(\mu_{ij}) = & \alpha + \beta_{\text{pre post fire}} \text{pre post fire} * \beta_{\text{diamclass}} \text{diamclass} + (1|\text{site}) \\
& \text{HU}_{ij} = \alpha + \beta_{\text{diamclass}} \text{diamclass}
\end{aligned} \quad (4)$$

2.5.3. Prescribed fire effects on species richness and diversity

To determine the effect of prescribed fire on understory species richness and Shannon diversity, we compared understory species richness and diversity before, one year after, and two years after prescribed fire. Four models were created to estimate native richness, non-native richness, native Shannon diversity, and non-native Shannon diversity. For species richness, we used a negative binomial distribution due to the right-skewed distribution of the data and the fact that richness was overdispersed. For Shannon diversity, we used a Gaussian distribution since the data met the assumptions of normality.

We fit all models with *brms* in R (Bürkner, 2017; R Core Team, 2021). Continuous independent variables were centered and scaled prior to

analysis. We used weakly informative priors with 4 chains, each with 3000 iterations and a warmup of 1000. Trace plots and R-hat values were assessed to confirm proper mixing and model convergence. We define significant differences as instances when the 95% highest posterior density intervals (HPDI) did not cross zero. Contrasts before and after prescribed fire were estimated using the *marginalEffects* package (Arel-Bundock et al., 2024).

3. Results

3.1. Prescribed fire reduced fuels in yellow pine mixed conifer (YPMC) forests

Pre-fire total fuel loading averaged 105.6 Mg/ha (10.44 Mg/ha to 481.52 Mg/ha) and was significantly reduced by an average of 63% immediately after burning ($p < 0.001$). Fuel loads remained significantly lower than pre-fire conditions one and two year post-fire for all fuel categories ($p < 0.05$; Fig. 2). Fine woody debris (FWD) was reduced by 56%, coarse woody debris (CWD) by 58%, litter depth by 65%, and duff depth by 67% immediately post-fire (Fig. 2, $p < 0.001$). Litter and duff depth increased significantly one year post-fire, however, these categories remained 48% and 58% lower, respectively, than pre-fire conditions. Variation in immediate post-fire fuel consumption was best explained by pre-fire fuel load (95% HPDI: 0.22 [0.16, 0.28]), wind speed (-0.35 [-0.62, -0.08]), slope (0.30 [0.04, 0.55]), and mean annual temperature (-0.47 [-0.70, -0.23]; Fig. 3).

3.2. Prescribed fire effects on forest structure

Prescribed fire significantly reduced live tree density, particularly among fir species and trees in small diameter classes (<40 cm DBH; Figs. 4,5). Pre-fire live tree density averaged 317 stems/ha (range: 0–1334 stems/ha) and had a significant mean reduction of 32% after prescribed fire (Wilcoxon rank sum: $p < 0.001$). Live basal area averaged 41 m²/ha (0–269 m²/ha) before prescribed fire and had a significant reduction of 23% one year after treatment (Wilcoxon rank sum: $p = 0.004$). Snag density increased significantly by 37% after prescribed fire, with an average of 66 stems/ha (0–593 stems/ha) before fire and 125 stems/ha (0–1310 stems/ha) after fire (Wilcoxon rank sum: $p < 0.001$). Snag basal area, however, had no significant change after

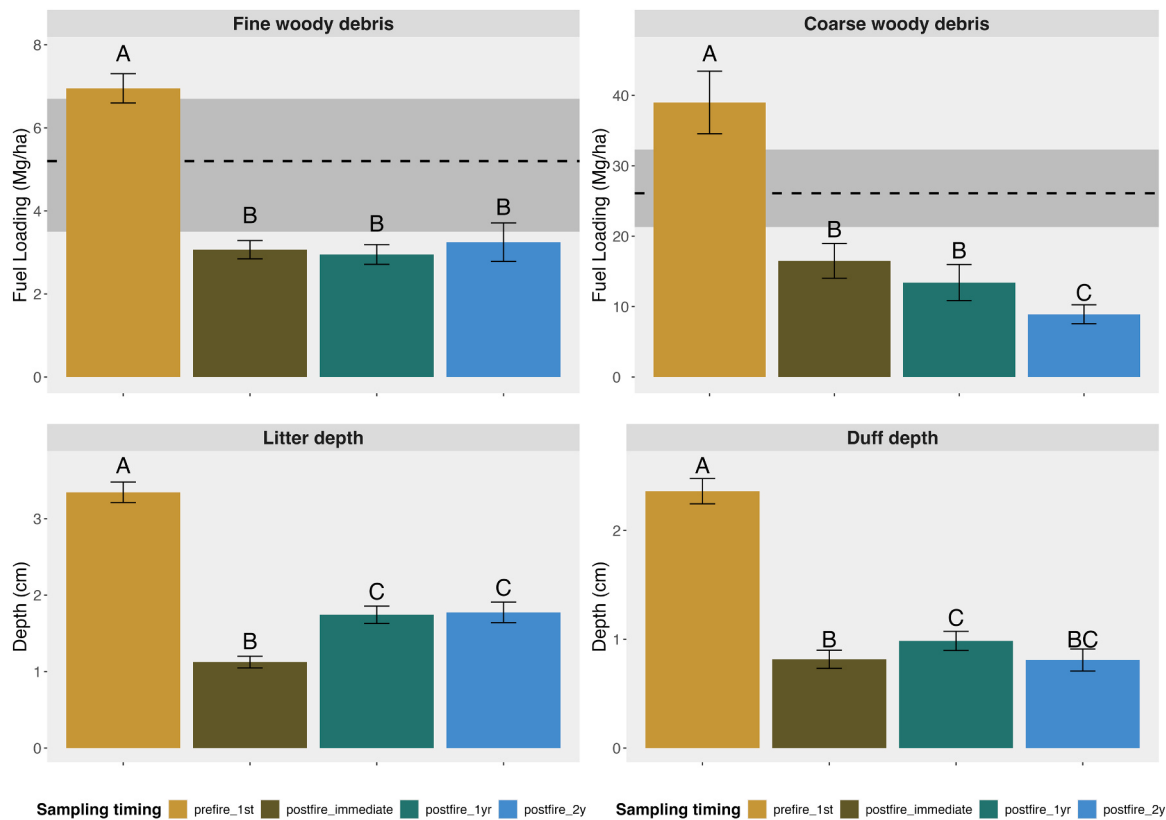


Fig. 2. Changes in surface fuel loading after prescribed fire by fuel class: fine woody debris, coarse woody debris, litter, and duff. Bar values are the mean surface fuel loading values and ± 1 standard error. Shared letters indicate fuel loads and depths are not different from one another. The gray band represents the natural range of variation for yellow pine and mixed-conifer forests, with the NRV mean represented by the dashed line (see *Methods*).

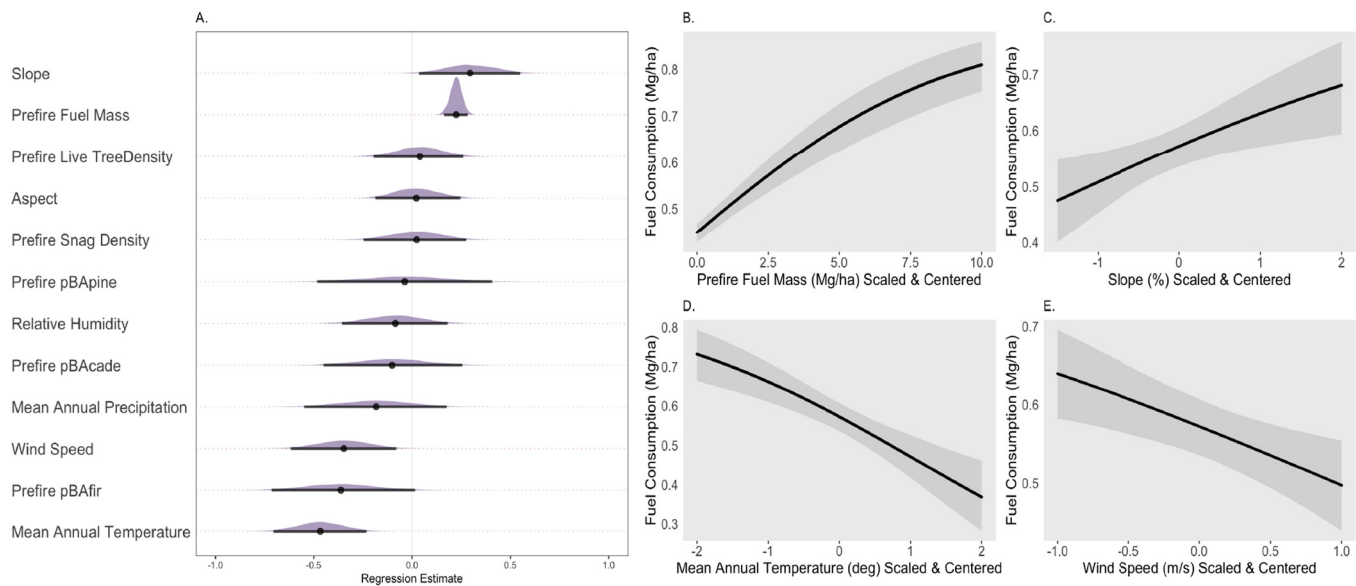


Fig. 3. Regression estimates associated with fuel consumption after prescribed fire (A). Values are coefficient estimates with corresponding error bars from the final model of total fuel consumption. pBA refers to the proportion of basal area for dominant tree genera. Fuel consumption varies with starting fuel conditions (B), slope (C), mean annual temperature (D), and wind speed (E). Predicted values from the top-ranked Bayesian model with 95% credible intervals.

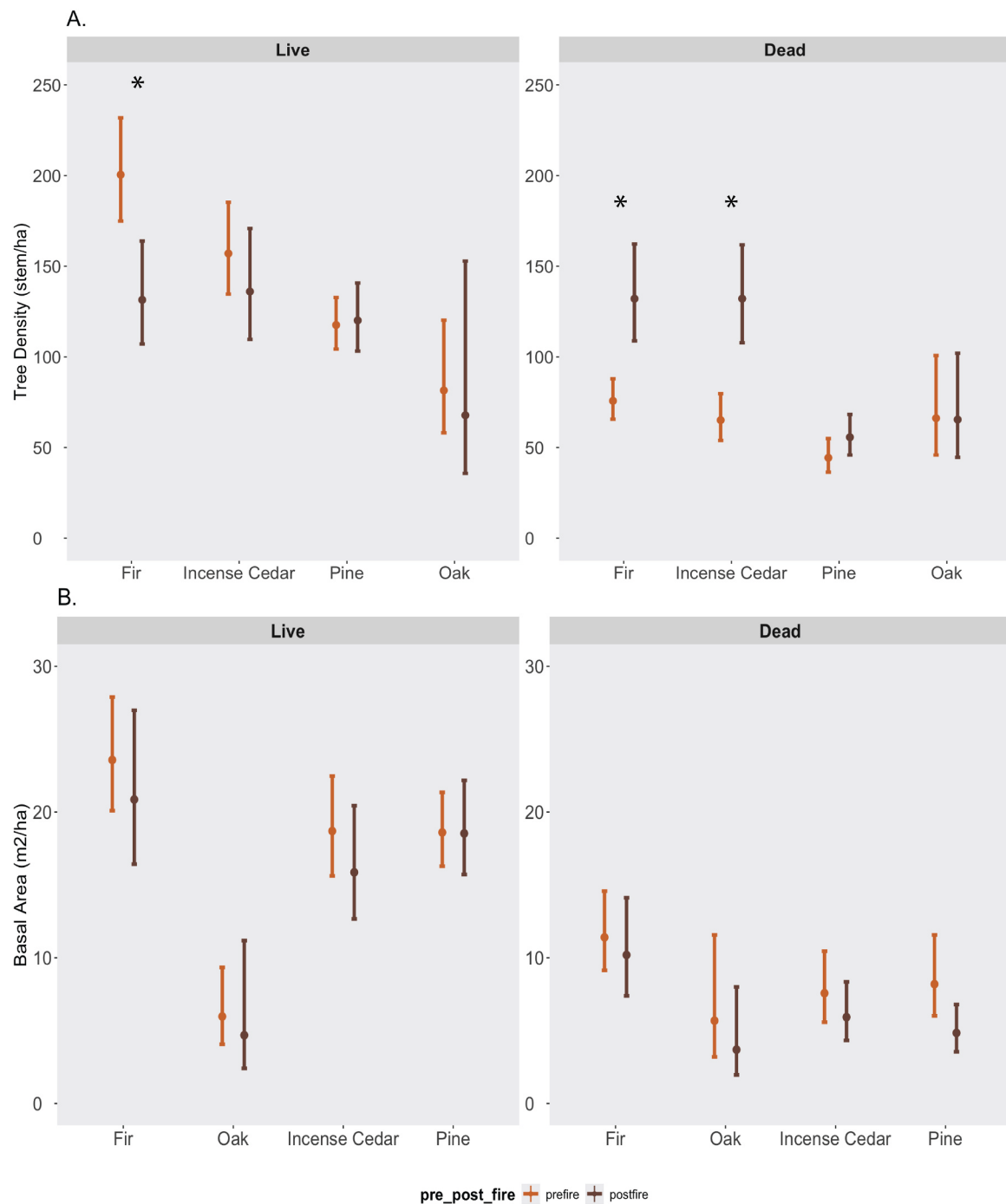


Fig. 4. Pre-treatment (orange) and one year post-treatment (brown) live and dead tree density (stems/ha) across common tree species (A) and live and dead basal area (m²/ha) across common genera (B). Predicted values from the top-ranked Bayesian model with 95% credible intervals. Asterisk indicates that 95% credible intervals for differences between groups do not cross zero.

prescribed fire and averaged 9.3 m²/ha (0–194 m²/ha) before fire and 8.0 m²/ha (0–111) after fire (Wilcoxon rank sum: $p = 0.45$).

Prior to treatment, tree density and basal varied by genus and diameter class, with 69% of trees in small diameter classes (<20 cm and 20–40 cm DBH) and fir species accounting for 63% of stems (Figs. 4,5). Results from the Bayesian mixed-effects model, which accounted for site-level variability, indicated a significant reduction in live fir density after fire (95% HPDI: 0.36 [0.10, 0.60]), but no significant changes in density for other genera (Fig. 4A). The density of both dead fir and incense cedar significantly increased one year post fire (fir: -0.51 [-0.77 , -0.27]; incense cedar: -0.64 [-0.94 , -0.35]; Fig. 4A). Despite the

reduction in live fir density, the Bayesian model did not detect a significant change in live or dead basal area across genera (Fig. 4B), underlining that reductions were concentrated among smaller trees and did not substantially affect overall basal area.

Prescribed fire significantly reduced the density of live trees < 20 cm DBH by 55% (0.34, [0.13, 0.55]) and those 20–40 cm DBH by 24% (0.16, [0.00, 0.32]), while larger diameter classes remained unaffected one year post fire (Fig. 5A). Likewise, the density of dead small diameter trees increased one year post-fire (<20 cm: -0.7302 [-0.9212 , -0.5178]; 20–40 cm: -0.4003 [-0.6023 , -0.1877]; Fig. 5A). Prescribed fire also significantly reduced the live basal area of trees < 20 cm DBH by 52%

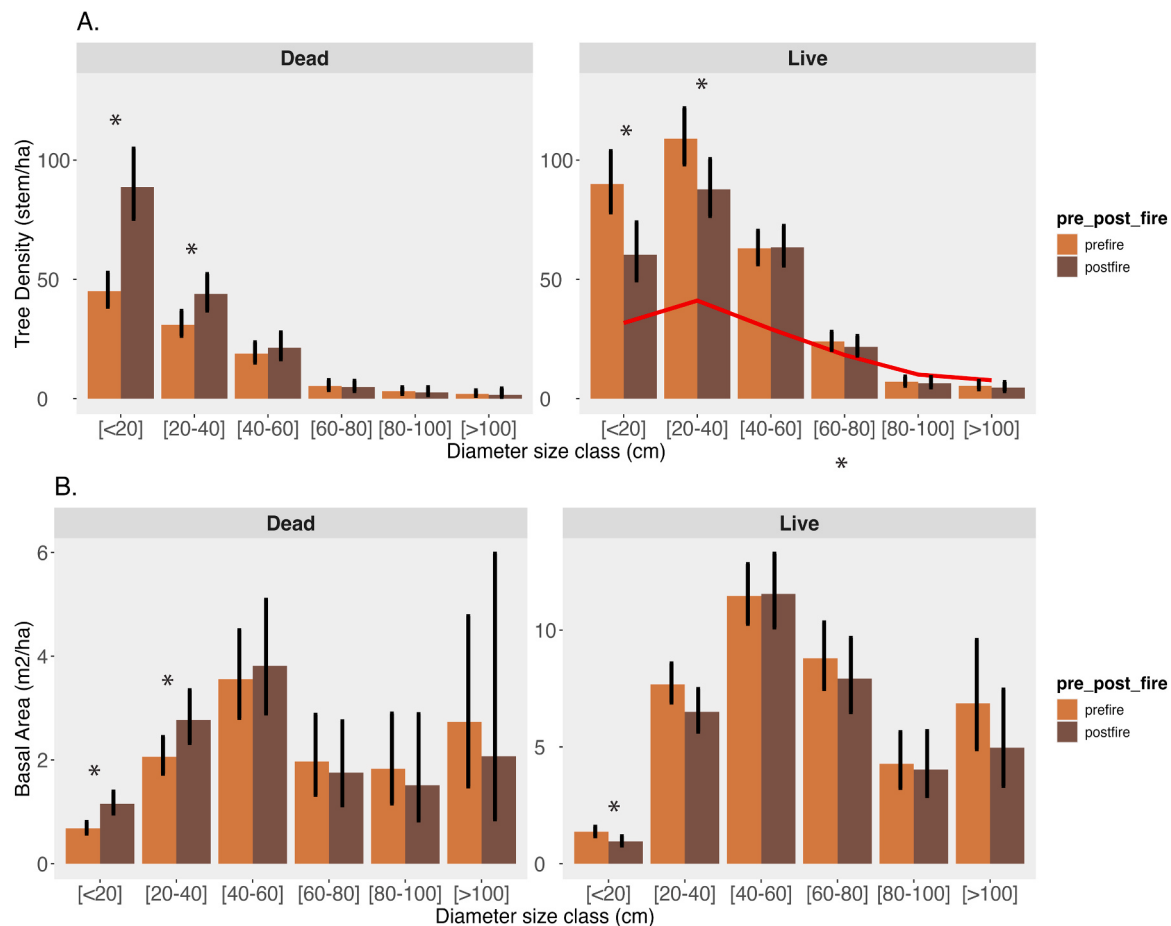


Fig. 5. Pre-treatment (orange) and one year post-treatment (brown) live and dead tree density (stems/ha) across diameter class (A) and live and dead basal area (m²/ha) across diameter class (B). Predicted values from the top-ranked Bayesian model with 95% credible intervals. Asterisk indicates that 95% credible intervals for differences between groups do not cross zero. The red line designates the mean NRV size distribution for yellow pine and mixed-conifer forests (see *Methods*).

one year post fire (0.30 [0.09, 0.52]), with no significant changes in larger diameter classes (Fig. 5B). Despite a reduction in the live basal area of only < 20 cm DBH size classes, dead basal area increased in both < 20 cm and 20–40 cm size classes (<20 cm: 0.528 [0.319, 0.770]; 20–40 cm: 0.851 [0.318, 1.453]; Fig. 5B).

3.3. Short-term effects (1–2 years) of prescribed fire treatment on native and non-native species richness and diversity

Despite relatively modest changes to forest structure, species richness and Shannon diversity significantly increased two years post-fire (Fig. 6). Average native species richness increased significantly from 15 species (SE = 0.7) pre-fire to 21 species (SE = 1.9) two years post-fire (95% HPDI: -0.93 [-1.20, -0.68]), but native species richness one year post-fire was not significantly different from pre-fire levels (Fig. 6A). Although pre-fire non-native richness was substantially lower at 0.26 species (SE = 0.05), it also increased significantly by 87% two years post-fire (-3.36 [-4.81 to -2.16]), with no significant difference between pre-fire and one year post-fire (Fig. 6B).

Native Shannon diversity increased significantly one year after prescribed fire (-0.27 [-0.45 to -0.08]; Fig. 6C). However, native diversity at one year post-fire was not significantly different from that observed two years post-fire, indicating that the increase in diversity was sustained over time but did not continue to rise. In contrast, non-native Shannon diversity followed a pattern more closely aligned with non-native species richness, with a significant increase two years post-fire relative to pre-fire conditions (-0.39 [-0.43, -0.25]; Fig. 6D).

4. Discussion

Our study aimed to evaluate the effectiveness of single-entry prescribed fire in altering surface fuels, forest structure, and understory plant diversity in California's YPMC forests that were historically sustained by frequent fire. Our findings highlight that one prescribed fire significantly reduced surface fuels and increased species diversity two years post-fire. Overall, prescribed fire significantly reduced tree density, with the reduction primarily affecting fir species and small-diameter trees (<40 cm DBH). While reductions in tree density - especially of smaller diameter trees - is critical to reducing the risk of high severity fire, such trees contribute little to stand basal area, so there were minimal changes in this variable post-fire. Nevertheless, the structural changes that did occur appeared to contribute to the promotion of a range of native understory species, with Shannon diversity increasing significantly one year post-fire, and species richness significantly increasing by the second year.

One primary objective of prescribed fire is to reduce surface fuels, to reduce subsequent fireline intensity and crown fire potential in the event of a wildfire (Agee and Skinner, 2005; Stephens et al., 2009). We found that prescribed fire successfully reduced surface fuels, with the most significant reductions in duff (67%) and litter (65%). Overall, pre-fire litter plus duff depth was 5.53 cm, 28% greater than the Young et al. (2020) NRV estimate (Table S1). This depth increases the likelihood of longer-duration heating at the base of trees and higher probability of cambial injury (Stephens and Finney, 2002). The observed surface fuel loads immediately after prescribed fire were consistent with conditions expected under frequent, low- to moderate-severity fire regimes.

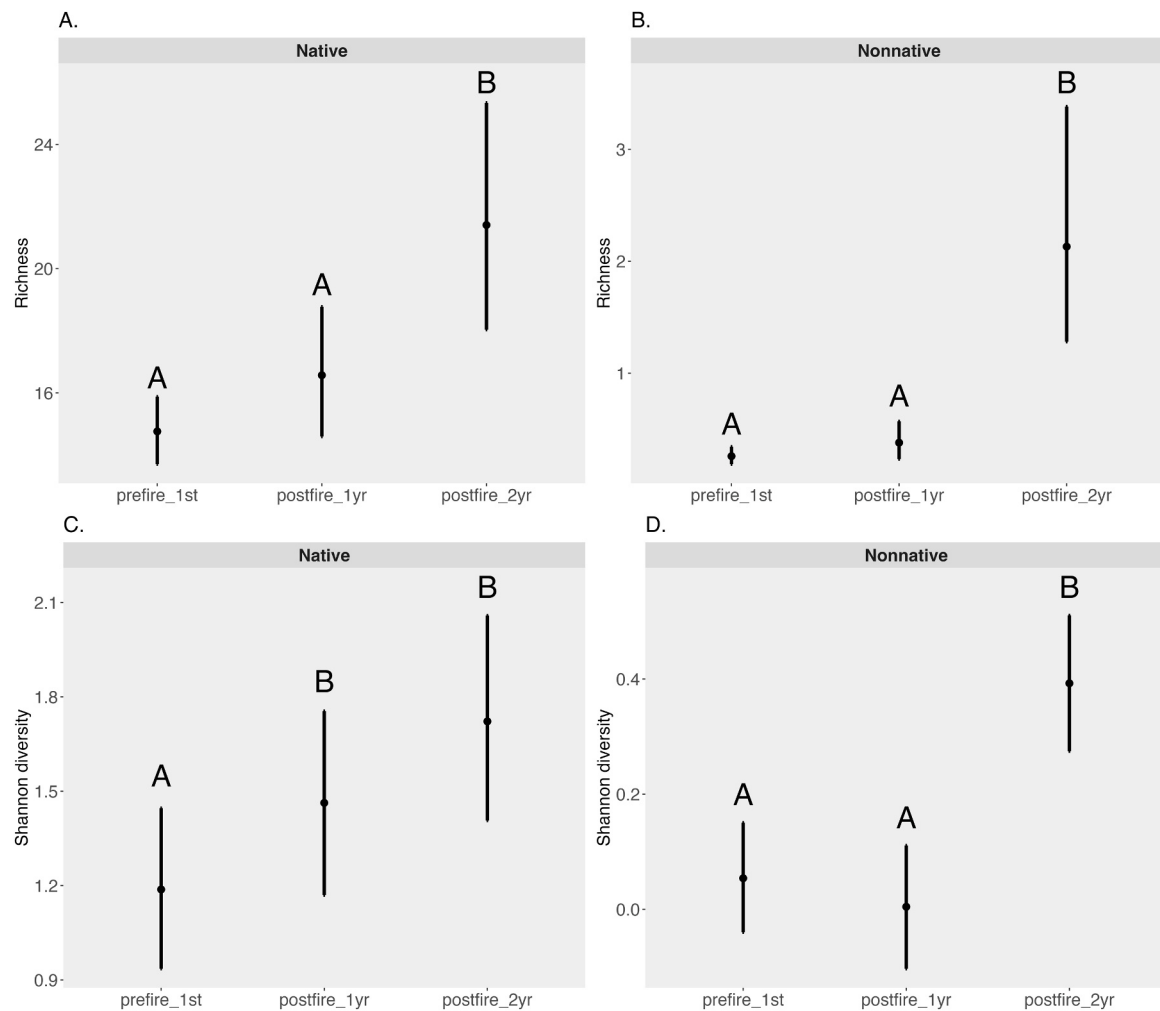


Fig. 6. Native (A, C) and non-native (B, D) species richness and diversity before, 1 year after prescribed fire, and 2 years after prescribed fire. Mean predicted values from the top-ranked Bayesian model with 95% credible intervals are plotted. Shared letters indicate diversity indices are not different from one another.

Moreover, these reduced fuel levels persisted, remaining significantly lower than pre-fire conditions one and two years post-treatment. This suggests that prescribed fire can effectively reset surface fuels towards the lower bound of their historical range, moderating future fire behavior and sustaining fuel loadings that more closely reflect fire-resilient conditions.

Pre-fire fuel load, slope, wind speed, and mean annual temperature were significant drivers of fuel consumption as measured immediately after fire, corroborating findings from previous studies in Sierra Nevada YPMC forests (Lydersen et al., 2015; Levine et al., 2020). Among these variables, pre-fire fuel load emerged as a primary driver of consumption, highlighting the importance of initial fuel conditions in shaping fire effects. These results align with prior research demonstrating that single-entry prescribed burns, which are typically conducted in stands with higher fuel loading, tend to achieve greater surface fuel consumption than follow-up burns (Levine et al., 2020; Katuna et al., 2024).

Because our study focused specifically on single-entry burns in long unburned forests, study sites likely exhibited relatively homogenous and continuous fuel beds compared to areas with a history of fire. Such fuel continuity can promote more complete fuel combustion and higher overall consumption (Miller and Urban, 1999; Moghaddas and Stephens, 2007; Levine et al., 2020). This relatively uniform fuel structure likely canceled out finer-scale variability associated with overstory characteristics.

In contrast to other studies in Sierra Nevada YPMC forests that have documented species-specific influences on fuel consumption (van

Wagtendonk and Moore, 2010; Lydersen et al., 2015; Levine et al., 2020), our results suggest that prolonged fire exclusion and the resulting accumulation of surface fuels homogenizes the fuel bed. The influence of species-specific traits on fuel dynamics may be more apparent during multiple-entry burns, once fuels have been partially reduced and site heterogeneity becomes more pronounced (van Wagtendonk and Moore, 2010; Lydersen et al., 2015; Levine et al., 2020).

We found modest changes to forest structure after prescribed fire, with significant reductions only in firs and in small diameter trees (<40 cm DBH). Based on historical and modern reference data, YPMC stands prior to widespread Euro-American settlement supported an average of about 160 trees/ha, with a range of 60–328 trees/ha, and a basal area of about 35 m²/ha, with a range of 21–54 m²/ha (Safford and Stevens, 2017; Young et al., 2020). Total live tree density at our sites (317 trees/ha) was higher than the upper end of the NRV range prior to prescribed fire. One year post-fire it was reduced to 215 trees/ha, closer to but still notably above the NRV mean. Although our short term monitoring period captured limited overstory mortality, substantial duff consumption observed in portions of the burn units may increase the potential for delayed mortality (Thies et al., 2006; Hood et al., 2007). This lagged mortality could further reduce stand density in the coming years, shifting forest structure closer to NRV conditions. In this study, we were unable to assess longer-term mortality, but continued monitoring of these sites would provide a valuable opportunity to evaluate delayed mortality.

Most prescribed burns in California YPMC forests are conducted

under relatively mild weather and fuel moisture conditions, typically within a 10-hour dead fuel moisture range of approximately 5–15%, when the potential for extreme fire behavior is low. The relatively limited overstory mortality observed in this study suggests that current low-to-moderate single-entry prescribed fires in California mixed conifer forests are generally not sufficiently hot to return current forest structure to densities that are near the NRV mean (Schwilk et al., 2009; Fulé et al. 2012; Waring et al., 2016; Domènech et al., 2025). Such conservative burning is an understandable precaution to prevent escape, especially in stands with prolonged time periods since last fire. Nevertheless, it highlights the need for forest managers to be thinking of second-entry fire even as they are planning the first entry. While this study shows that single-entry prescribed fire induces some change in forest structure by reducing shade-tolerant and small diameter trees, other studies have found that multiple-entry fire (Webster and Halpern, 2010; Hankin and Anderson, 2022) and thinning prior to prescribed fire (Wayman and North, 2007; Schwilk et al., 2009; Fulé et al. 2012) can induce higher levels of structural change.

Several variables are associated with changes to the understory plant community after prescribed fire, including canopy cover, litter cover, soil moisture, soil nutrients, and available light (Wayman and North, 2007; Abella and Springer, 2015; Dudney et al., 2021). While mechanical thinning treatments can successfully alter some environmental conditions and increase understory diversity (Wayman and North, 2007; Knapp et al., 2017; Odland et al., 2021), fire more profoundly promotes native biodiversity by exposing bare mineral soil, altering soil nutrient availability, stimulating germination through heat and smoke, reducing shading, and generally increasing heterogeneity in understory conditions (Kauffman and Martin, 1990; Abella et al., 2007). Fire-induced changes to the forest floor, including duff consumption, may also contribute to understory response; however, we did not explicitly evaluate these mechanistic pathways in the present study. Further reductions in canopy cover and repeated burning are necessary to increase understory floral diversity and maintain it in the long term (Abella and Springer, 2015; Knapp et al., 2017). We found a significant increase in non-native species richness two years after prescribed fire; however, the magnitude of this change was small, with an average of only two non-native species added per site over the two-year period. While non-native species can increase substantially after mechanical thinning or thinning followed by burning (Collins et al., 2007; Schwilk et al., 2009), our observation of a minimal increase in non-native species highlights an additional ecological benefit of burn-only treatments. In addition, other work in the Sierra Nevada has found that post-management increases in non-native species are not permanent and may decrease with time since treatment (Bohlman et al., 2016).

Our findings are from 12 prescribed fires across a broad geographic and institutional scope. Across our diverse sites, we found single-entry prescribed fire to be effective in reducing surface fuels but much less in restoring forest structure back to historical levels. Repeat treatments of prescribed fire or judicious combinations with mechanical or manual thinning may be necessary to restore conditions more typical of frequent-fire forests (Sackett, 1980; Stephens et al., 2009, 2020; Waring et al., 2016). Considered in concert with the work of other research groups, we contend that these findings are generally applicable to the management of YPMC and related seasonally dry forest types across California and western North America, providing important metrics on how single-entry prescribed fire affects surface fuels and ecological variables, like forest structure and plant diversity.

The continuity and expansion of long-term monitoring programs, such as the CPFMP, are critical for supporting effective forest and fuel management. Long-term datasets are essential not only for documenting short-term treatment effects, but also for understanding the longevity of fuel reductions and other ecological changes following prescribed fire. This underlines the importance of planning and implementing prescribed fire as a repeated management process rather than a single-entry treatment. Improving the consistency and transparency of reporting

practices will strengthen the scientific foundation of prescribed fire management by enabling broader synthesis across studies, facilitating adaptive management, and ensuring that clearly communicated outcomes inform future treatments (Bonner et al., 2021).

CRedit authorship contribution statement

Tessa Putz: Writing – review & editing, Data curation. **Ashley R. Grunehoff:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Formal analysis, Data curation, Conceptualization. **Becky Estes:** Writing – review & editing, Data curation. **John Williams:** Writing – review & editing, Project administration, Data curation. **Joe Restaino:** Writing – review & editing, Project administration, Data curation, Conceptualization. **Rut Domènech:** Writing – review & editing, Data curation. **Hugh D. Safford:** Writing – review & editing, Writing – original draft, Supervision, Project administration, Methodology, Funding acquisition, Data curation, Conceptualization.

Declaration of Competing Interest

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

Acknowledgements

Many thanks to the field crew members for assisting with field data collection, including Kylie Mosher, Martin Malate, Pete Murphey, Natalia Rico, Robbie Heumann, Marcel Safford, Vanessa Stevens, Montserrat Valencia, and Melanie Schlueter. Much appreciation to all the land managers who facilitated our data collection, site visits, and participation in prescribed fire projects. Funding was provided through the CALFIRE agreement #8CA043659.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2026.123771.

Data availability

Research Link Provided

California prescribed fire monitoring program: 2019–2024 (Dryad)

References

- Abella, S.R., Springer, J.D., 2015. Effects of tree cutting and fire on understory vegetation in mixed conifer forests. *FEM* 335, 281–299. <https://doi.org/10.1016/j.foreco.2014.09.009>.
- Abella, S.R., Springer, J.D., Covington, W.W., 2007. Seed banks of an Arizona Pinus ponderosa landscape: responses to environmental gradients and fire cues. *Can. J. Res* 37, 552–567. <https://doi.org/10.1139/X06-255>.
- Agee J.K. (1993) Fire ecology of Pacific Northwest forests. Island press Washington, DC.
- Agee, J.K., Skinner, C.N., 2005. Basic principles of forest fuel reduction treatments. *For. Ecol. Manag.* 211, 83–96. <https://doi.org/10.1016/j.foreco.2005.01.034>.
- Allen, C.R., Gunderson, L.H., 2011. Pathology and failure in the design and implementation of adaptive management. *J. Environ. Manag.* 92, 1379–1384. <https://doi.org/10.1016/j.jenvman.2010.10.063>.
- Arel-Bundock, V., Greifer, N., Heiss, A., 2024. How to Interpret Statistical Models Using *marginalEffects* for R and Python. *J. Stat. Soft* 111. <https://doi.org/10.18637/jss.v111.i09>.
- Arno S.F., Fiedler C.E. (2005) Mimicking nature's fire: restoring fire-prone forests in the west. Island Press, Washington.
- Biswell, H.H., 1989. Prescribed burning. *California wildlandsvegetation management* Berkeley. University of California Press, p. 255.
- Bohlman, G.N., North, M., Safford, H.D., 2016. Shrub removal in reforested post-fire areas increases native plant species richness. *For. Ecol. Manag.* 374, 195–210. <https://doi.org/10.1016/j.foreco.2016.05.008>.
- Bonner, S.R., Hoffman, C.M., Kane, J.M., et al., 2021. Invigorating prescribed fire science through improved reporting practices. *Front Glob. Change* 4, 750699. <https://doi.org/10.3389/ffgc.2021.750699>.

- Brown J.K. (1974) Handbook for inventorying downed woody material. Gen Tech Rep INT-16 Ogden, UT: US Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station 24 p 016:
- Brown J.K. (1982) Handbook for Inventorying Surface Fuels and Biomass in the Interior West. U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station.
- Bürkner, P.-C., 2017. brms: An R Package for Bayesian Multilevel Models Using Stan. *J. Stat. Soft.* 80. <https://doi.org/10.18637/jss.v080.i01>.
- Collins, B.M., Moghaddas, J.J., Stephens, S.L., 2007. Initial changes in forest structure and understory plant communities following fuel reduction activities in a Sierra Nevada mixed conifer forest. *For. Ecol. Manag.* 239, 102–111. <https://doi.org/10.1016/j.foreco.2006.11.013>.
- Commission L.H. (2018) Voting System Security: Pamela Smith's Testimony to the Little Hoover Commission (2018).
- Covington W., Wagner P.K. (1998) Conference on Adaptive Ecosystem Restoration and Management: Restoration of Cordilleran Conifer Landscapes of North America. DIANE Publishing.
- Covington, W.W., Moore, M.M., 1994. Postsettlement Changes in Natural Fire Regimes and Forest Structure. *J. Sustain. For.* 2, 153–181. https://doi.org/10.1300/J091v02n01_07.
- Dailey S., Reiner A., Ewell C. (2019) 2019 Caples Fire First Order Fire Effects.
- Deak, A., Fawcett, J.E., Quinn-Davidson, L., et al., 2025. Burning from the ground up: the structure and impact of Prescribed Burn Associations in the United States. *Int. J. Wildland Fire* 34. <https://doi.org/10.1071/WF24178>.
- Domènech, R., Castellnou, M., Resco de Dios, V., et al., 2025. The hidden variable: impacts of human decision-making on prescribed fire outcomes. *J. Environ. Manag.* 395, 127866. <https://doi.org/10.1016/j.jenvman.2025.127866>.
- Domènech, R., Naimeh, A.M., Putz, T., et al., 2026. California prescribed fire monitoring program: 2019–2024. *Sci. Data* 13, 225. <https://doi.org/10.1038/s41597-025-06509-0>.
- Dudney, J., York, R.A., Tubbesing, C.L., et al., 2021. Overstory removal and biological legacies influence long-term forest management outcomes on introduced species and native shrubs. *For. Ecol. Manag.* 491, 119149. <https://doi.org/10.1016/j.foreco.2021.119149>.
- Forest Climate Action Team (2018) California Forest Carbon Plan: Managing Our Forest Landscapes in a Changing Climate.
- Foster D., Stephens S., Moghaddas J., van Wagtenonk J. (2018) Rfuels: forest fuels from Brown's transects. R Berkeley, CA (<https://github.com/danfo/sterfue/Rfuels>).
- Fule, P.Z., Cocke, A.E., Heinlein, T.A., Covington, W.W., 2004. Effects of an intense prescribed forest fire: is it ecological restoration? *Restor. Ecol.* 12, 220–230.
- Fulé, P.Z., Crouse, J.E., Roccaforte, J.P., Kalies, E.L., 2012. Do thinning and/or burning treatments in western USA ponderosa or Jeffrey pine-dominated forests help restore natural fire behavior? *For. Ecol. Manag.* 269, 68–81. <https://doi.org/10.1016/j.foreco.2011.12.025>.
- Hagmann, R.K., Hessburg, P.F., Prichard, S.J., et al., 2021. Evidence for widespread changes in the structure, composition, and fire regimes of western North American forests. *Ecol. Appl.* 31, e02431. <https://doi.org/10.1002/eap.2431>.
- Hankin, L.E., Anderson, C.T., 2022. Second-Entry Burns Reduce Mid-Canopy Fuels and Create Resilient Forest Structure in Yosemite National Park, California. *Forests* 13, 1512.
- Hiers, J.K., O'Brien, J.J., Varner, J.M., et al., 2020. Prescribed fire science: the case for a refined research agenda. *s42408-020-0070-8* *fire Ecol.* 16, 11. <https://doi.org/10.1186/s42408-020-0070-8>.
- Hood, S.M., McHugh, C.W., Ryan, K.C., et al., 2007. Evaluation of a post-fire tree mortality model for western USA conifers. *Int. J. Wildland Fire* 16, 679–689. <https://doi.org/10.1071/WF06122>.
- Katuna, T.A., Collins, B.M., Stephens, S.L., 2024. Prescribed fires effects on actual and modeled fuel loads and forest structure in southern coast redwood (*Sequoia sempervirens*) forests. *fire Ecol.* 20, 100. <https://doi.org/10.1186/s42408-024-00331-6>.
- Kauffman, J.B., Martin, R.E., 1990. Sprouting Shrub Response to Different Seasons and Fuel Consumption Levels of Prescribed Fire in Sierra Nevada Mixed Conifer Ecosystems. *For. Sci.* 36, 748–764. <https://doi.org/10.1093/forestscience/36.3.748>.
- Knapp, E.E., Schwilk, D.W., Kane, J.M., Keeley, J.E., 2007. Role of burning season on initial understory vegetation response to prescribed fire in a mixed conifer forest. *Can. J. Res* 37, 11–22. <https://doi.org/10.1139/x06-200>.
- Knapp, E.E., Lydersen, J.M., North, M.P., Collins, B.M., 2017. Efficacy of variable density thinning and prescribed fire for restoring forest heterogeneity to mixed-conifer forest in the central Sierra Nevada, CA. *For. Ecol. Manag.* 406, 228–241. <https://doi.org/10.1016/j.foreco.2017.08.028>.
- Larson, A.J., Churchill, D., 2012. Tree spatial patterns in fire-frequent forests of western North America, including mechanisms of pattern formation and implications for designing fuel reduction and restoration treatments. *For. Ecol. Manag.* 267, 74–92. <https://doi.org/10.1016/j.foreco.2011.11.038>.
- Levine, B., Stephens, S.L., 2025. Australia and the United States have many similarities and differences in prescribed fire management: learning from each other. *Fire Ecol.* 21, 50. <https://doi.org/10.1186/s42408-025-00395-y>.
- Levine, J.I., Collins, B.M., York, R.A., et al., 2020. Forest stand and site characteristics influence fuel consumption in repeat prescribed burns. *Int. J. Wildland Fire* 29, 148. <https://doi.org/10.1071/WF19043>.
- Liu, F., Eugenio, E.C., 2018. A review and comparison of Bayesian and likelihood-based inferences in beta regression and zero-or-one-inflated beta regression. *Stat. Methods Med. Res.* 27, 1024–1044. <https://doi.org/10.1177/0962280216650699>.
- Lydersen, J.M., North, M.P., Knapp, E.E., Collins, B.M., 2013. Quantifying spatial patterns of tree groups and gaps in mixed-conifer forests: reference conditions and long-term changes following fire suppression and logging. *For. Ecol. Manag.* 304, 370–382. <https://doi.org/10.1016/j.foreco.2013.05.023>.
- Lydersen, J.M., Collins, B.M., Knapp, E.E., et al., 2015. Relating fuel loads to overstorey structure and composition in a fire-excluded Sierra Nevada mixed conifer forest. *Int. J. Wildland Fire* 24, 484. <https://doi.org/10.1071/WF13066>.
- McCormack, P.C., Miller, R.K., McDonald, J., 2023. Prescribed burning on private land: reflections on recent law reform in Australia and California (NULL-NULL). *Int. J. Wildland Fire* 33. <https://doi.org/10.1071/WF22213>.
- Miller C., Urban D.L. (1999) Interactions between forest heterogeneity and surface fire regimes in the southern Sierra Nevada. 29:
- Miller, R.K., Field, C.B., Mach, K.J., 2020. Barriers and enablers for prescribed burns for wildfire management in California. *Nat. Sustain* 3, 101–109. <https://doi.org/10.1038/s41893-019-0451-7>.
- Moghaddas, E.E.Y., Stephens, S.L., 2007. Thinning, burning, and thin-burn fuel treatment effects on soil properties in a Sierra Nevada mixed-conifer forest. *For. Ecol. Manag.* 250, 156–166. <https://doi.org/10.1016/j.foreco.2007.05.011>.
- Nagelson, P.B., York, R.A., Shoemaker, K.T., et al., 2025. Repeated fuel treatments fall short of fire-adapted regeneration objectives in a Sierra Nevada mixed conifer forest, USA. *Ecol. Appl.* 35, e3075. <https://doi.org/10.1002/eap.3075>.
- North, M., Collins, B.M., Stephens, S., 2012. Using Fire to Increase the Scale, Benefits, and Future Maintenance of Fuels Treatments. *J. For.* 110, 392–401. <https://doi.org/10.5849/jof.12-021>.
- Odland, M.C., Goodwin, M.J., Smithers, B.V., et al., 2021. Plant community response to thinning and repeated fire in Sierra Nevada mixed-conifer forest understories. *For. Ecol. Manag.* 495, 119361. <https://doi.org/10.1016/j.foreco.2021.119361>.
- Oksanen J., Simpson G.L., Blanchet F.G., et al (2023) *vegan: Community Ecology Package*.
- Prichard, S.J., Povak, N.A., Kennedy, M.C., Peterson, D.W., 2020. Fuel treatment effectiveness in the context of landform, vegetation, and large, wind-driven wildfires. *Ecol. Appl.* 30, e02104. <https://doi.org/10.1002/eap.2104>.
- Quinn-Davidson, L.N., Varner, J.M., 2011. Impediments to prescribed fire across agency, landscape and manager: an example from northern California. *Int. J. Wildland Fire* 21, 210–218. <https://doi.org/10.1071/WF11017>.
- R Core Team (2021) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Reid, T., Hazell, D., Gibbons, P., 2013. Why monitoring often fails to inform adaptive management: a case study. *Ecol. Manag. & Restor.* 14, 224–227. <https://doi.org/10.1111/emr.12065>.
- Richter, C., Rejmánek, M., Miller, J.E.D., et al., 2019. The species diversity × fire severity relationship is hump-shaped in semiarid yellow pine and mixed conifer forests. *Ecosphere* 10, e02882. <https://doi.org/10.1002/ecs2.2882>.
- Sackett, S.S., 1980. Reducing natural ponderosa pine fuels using prescribed fire: two case studies. USDA For. Serv. Rocky Mt. For. Range Exp. Station.
- Safford, H.D., Saberi, S., 2026. Fuel treatment effects on fire severity during the Caldor Fire (2021), Lake Tahoe, California, USA. *For. Ecol. Manag.* 603, 123424. <https://doi.org/10.1016/j.foreco.2025.123424>.
- Safford H.D., Stevens J.T. (2017) Natural range of variation for yellow pine and mixed-conifer forests in the Sierra Nevada, southern Cascades, and Modoc and Inyo National Forests, California, USA. U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Albany, CA.
- Safford, H.D., Butz, R.J., Bohlman, G.N., et al., 2021. *Fire Ecology of the North American Mediterranean Climate Zone*. In: Greenberg, C.H., Collins, B. (Eds.), *Fire Ecology and Management: Past, Present, and Future of US Forested Ecosystems*. Springer International Publishing, Cham, pp. 337–392.
- Safford, H.D., Paulson, A.K., Steel, Z.L., et al., 2022. The 2020 California fire season: A year like no other, a return to the past or a harbinger of the future? *Glob. Ecol. Biogeogr.* 31, 2005–2025. <https://doi.org/10.1111/geb.13498>.
- Safford, H.D., Grunehoff, A., Williams, J.N., Putz, T., Restaino, J., 2023. Measuring success: Monitoring program assesses benefits of prescribed burning. *Wildfire Mag. Qtrt* 1, 14–23.
- Schwilk, D.W., Keeley, J.E., Knapp, E.E., et al., 2009. The national Fire and Fire Surrogate study: effects of fuel reduction methods on forest vegetation structure and fuels. *Ecol. Appl.* 19, 285–304. <https://doi.org/10.1890/07-1747.1>.
- State of California (2021) California's wildfire and forest resilience action plan.
- Steel, Z.L., Fogg, A.M., Burnett, R., et al., 2022. When bigger isn't better—Implications of large high-severity wildfire patches for avian diversity and community composition. *Divers. Distrib.* 28, 439–453. <https://doi.org/10.1111/ddi.13281>.
- Steel, Z.L., Jones, G.M., Collins, B.M., et al., 2023. Mega-disturbances cause rapid decline of mature conifer forest habitat in California. *Ecol. Appl.* 33, e2763. <https://doi.org/10.1002/eap.2763>.
- Steel, Z.L., Safford, H.D., Viers, J.H., 2015. The fire frequency-severity relationship and the legacy of fire suppression in California forests. *Ecosphere* 6 (1), 8.
- Stephens, S.L., 1998. Evaluation of the effects of silvicultural and fuels treatments on potential fire behaviour in Sierra Nevada mixed-conifer forests. *For. Ecol. Manag.* 105, 21–35. [https://doi.org/10.1016/S0378-1127\(97\)00293-4](https://doi.org/10.1016/S0378-1127(97)00293-4).
- Stephens, S.L., 2001. Fire history differences in adjacent Jeffrey pine and upper montane forests in the eastern Sierra Nevada. *Int. J. Wildland Fire* 10, 161–167. <https://doi.org/10.1071/wf01008>.
- Stephens, S.L., Finney, M.A., 2002. Prescribed fire mortality of Sierra Nevada mixed conifer tree species: effects of crown damage and forest floor combustion. *For. Ecol. Manag.* 162, 261–271. [https://doi.org/10.1016/S0378-1127\(01\)00521-7](https://doi.org/10.1016/S0378-1127(01)00521-7).
- Stephens, S.L., Moghaddas, J.J., 2005. Silvicultural and reserve impacts on potential fire behavior and forest conservation: Twenty-five years of experience from Sierra Nevada mixed conifer forests. *Biol. Conserv.* 125, 369–379. <https://doi.org/10.1016/j.biocon.2005.04.007>.

- Stephens, S.L., Moghaddas, J.J., Edminster, C., et al., 2009. Fire treatment effects on vegetation structure, fuels, and potential fire severity in western US forests. *Ecol. Appl.* 19, 305–320.
- Stephens, S.L., Battaglia, M.A., Churchill, D.J., et al., 2020. Forest Restoration and Fuels Reduction: Convergent or Divergent? *BioScience*, baa134. <https://doi.org/10.1093/biosci/baa134>.
- Stephens, S.L., Foster, D.E., Battles, J.J., et al., 2024. Forest restoration and fuels reduction work: Different pathways for achieving success in the Sierra Nevada. *Ecol. Appl.* 34, e2932. <https://doi.org/10.1002/eap.2932>.
- Susskind, L., Camacho, A.E., Schenk, T., 2012. A critical assessment of collaborative adaptive management in practice. *J. Appl. Ecol.* 49, 47–51. <https://doi.org/10.1111/j.1365-2664.2011.02070.x>.
- Thies, W.G., Westlind, D.J., Loewen, M., Brenner, G., 2006. Prediction of delayed mortality of fire-damaged ponderosa pine following prescribed fires in eastern Oregon, USA. *Int. J. Wildland Fire* 15, 19–29. <https://doi.org/10.1071/WF05025>.
- USFS (2012) Region 5 Common Stand Exam Field Guide. USDA Forest Service, Vallejo, CA. (<http://www.fs.fed.us/nrm/fsveg/index.shtml>).
- Vaillant, N.M., Fites-Kaufman, J.A., Stephens, S.L., et al., 2009. Effectiveness of prescribed fire as a fuel treatment in Californian coniferous forests. *Int. J. Wildland Fire* 18, 165–175. <https://doi.org/10.1071/WF06065>.
- Van de Water, K.M., Safford, H.D., 2011. A summary of fire frequency estimates for California vegetation before Euro-American settlement. *fire Ecol.* 7, 26–58. <https://doi.org/10.4996/fireecology.0703026>.
- Varnier, J.M., Hiers, J.K., Wheeler, S.B., et al., 2021. Increasing Pace and Scale of Prescribed Fire via Catastrophe Funds for Liability Relief. *Fire* 4, 77. <https://doi.org/10.3390/fire4040077>.
- van Wagtenonk, J.W., Moore, P.E., 2010. Fuel deposition rates of montane and subalpine conifers in the central Sierra Nevada, California, USA. *For. Ecol. Manag.* 259, 2122–2132. <https://doi.org/10.1016/j.foreco.2010.02.024>.
- van Wagtenonk, J.W., Benedict, J.M., Sydoriak, W.M., 1998. Fuel bed characteristics of Sierra Nevada Conifers. *West. J. Appl. For.* 13, 73–84. <https://doi.org/10.1093/wjaf/13.3.73>.
- {C}{C}{C}{C}{C}{C}van Wagtenonk J.W., Sugihara N.G., Stephens S.L., Thode A.E., Shaffer K.E., Fites-Kaufman J. {C}{C}{C}{C}{C}{C}(eds). 2018. Fire in California's ecosystems. University of California Press, Berkeley, CA.
- Waring, K.M., Hansen, K.J., Flatley, W.T., 2016. Evaluating prescribed fire effectiveness using permanent monitoring plot data: a case study. *fire Ecol.* 12, 2–25. <https://doi.org/10.4996/fireecology.1203002>.
- Wayman, R.B., North, M., 2007. Initial response of a mixed-conifer understory plant community to burning and thinning restoration treatments. *For. Ecol. Manag.* 239, 32–44. <https://doi.org/10.1016/j.foreco.2006.11.011>.
- Webster, K.M., Halpern, C.B., 2010. Long-term vegetation responses to reintroduction and repeated use of fire in mixed-conifer forests of the Sierra Nevada. *art9 Ecosphere* 1. <https://doi.org/10.1890/ES10-00018.1>.
- Weeks, J., Miller, J.E.D., Steel, Z.L., et al., 2023. High-severity fire drives persistent floristic homogenization in human-altered forests. *Ecosphere* 14, e4409. <https://doi.org/10.1002/ecs2.4409>.
- Westerling A.L. (2018) Wildfire Simulations for California's Fourth Climate Change Assessment: Projecting Changes in Extreme Wildfire Events with a Warming Climate: a Report for California's Fourth Climate Change Assessment. California Energy Commission Sacramento, CA.
- Williams, J.N., Safford, H.D., Enstice, N., et al., 2023. High-severity burned area and proportion exceed historic conditions in Sierra Nevada, California, and adjacent ranges. *Ecosphere* 14, e4397. <https://doi.org/10.1002/ecs2.4397>.
- Williams, J.N., Quinn-Davidson, L., Safford, H.D., et al., 2024. Overcoming obstacles to prescribed fire in the North American Mediterranean climate zone. *Front. Ecol. Environ.* 22, e2687. <https://doi.org/10.1002/fee.2687>.
- Young, D.J.N., Stevens, J.T., Earles, J.M., Moore, J., Ellis, A., Jirka, A.L., Latimer, A.M., 2017. Long-term climate and competition explain forest mortality patterns under extreme drought. *Ecol. Lett.* 20, 78–86.
- Young, D.J.N., Meyer, M., Estes, B., et al., 2020. Forest recovery following extreme drought in California, USA: natural patterns and effects of pre-drought management. *Ecol. Appl.* 30, e02002. <https://doi.org/10.1002/eap.2002>.