

Changing Fire Regimes and Fire Management Strategies in California's Diverse
Ecosystems

By

ASHLEY GRUPENHOFF
DISSERTATION

Submitted in partial satisfaction of the requirements for the degree of

DOCTOR OF PHILOSOPHY

in

Ecology

in the

OFFICE OF GRADUATE STUDIES

of the

UNIVERSITY OF CALIFORNIA

DAVIS

Approved:

Hugh Safford, Chair

Andrew Latimer

Brandon Collins

Committee in Charge

2023

Abstract

Mitigating the effects of massive wildfires is one of the most critical forest conservation goals of our generation, and perhaps the most important in western North America. Changes in climate and Euro-American fire suppression have altered the natural fire regime across the western US. Chaparral-dominated ecosystems that historically experienced infrequent high-intensity fire are currently threatened by an increase in wildfire frequency driven by increased urbanization of wildlands, warming temperatures, and invasion of non-native species. Dry conifer forests, on the other hand, are experiencing fewer fires due to fire suppression policies, but these policies have resulted in fuel accumulations and forest densification. The warming climate is leading to drier fuels and more severe fire weather, and when fires escape control today, they tend to burn large areas at high severity, which pose enormous threats to biodiversity, human health, and the economy. To address these issues, fuel treatments such as prescribed fire, hand thinning, and mechanical surrogates for fire (e.g thinning, mastication) have been implemented to restore forest resilience by reducing surface and canopy fuels and restoring natural disturbance processes in historically frequent-fire forests.

In my first chapter of this dissertation, I examined the impact of increased fire frequency on the composition and abundance of herbaceous and woody species in chaparral plant communities in the Interior Coast Range of northern California. In my second chapter, I document and analyze patterns in fuel dynamics after fuel treatments across dry conifer forests in the western US using 1,932 observations from 65 published studies. My third chapter concludes this dissertation by quantifying the current effectiveness of prescribed fire as a management strategy by documenting changes in surface fuel loading, stand structure, and resulting species diversity. Understanding the ecological consequences of human-driven changes to fire regimes, and the consequent management strategies to combat them, are

crucial for projecting future fire activity under various climate change scenarios and land management strategies.

Acknowledgements

First and foremost I want to acknowledge the many people who provided constant encouragement and support throughout the PhD experience. I would like to thank my advisor, Hugh Safford, and my committee members Andrew Latimer and Brandon Collins for their mentorship throughout this process. Hugh struck a perfect balance between guiding my research while providing me the autonomy to navigate and solve challenges independently. Thank you to Andrew Latimer, whose expertise and thoughtful observations continued to push me to think critically. Special thanks to Brandon Collins, whose discussions on salient fire ecology papers significantly enriched the depth of this research. I would like to thank Xiaoli Dong and Malcolm North, for their support and critiques at the early stages of my graduate degree. Their thoughtful feedback and encouragement helped shape this work.

To the Safford lab who have supported me throughout this whole process. I especially want to thank Tara Ursell, Sara Winsemius, Jonah Weeks, Emily Brodie, and Rebecca Wayman, who provided me invaluable feedback on writing, ideas, and analyses. This group helped me grow as a scientist, instilling a sense of joy and confidence along the way. To my cohort-mates and the ecology graduate group community for camaraderie, costumes, and wealth of institutional knowledge. They made this process more enjoyable and memorable. To Wesley Brooks and the GGE Statistical Support group, with whom I gained a deep love and understanding of statistics.

This dissertation would not have been possible without many colleagues, technicians, and staff. Thank you to John Williams and Joe Restaino, who worked with me on the Prescribed Fire Monitoring Program. Their knowledge and insight guided my research to be not only ecologically relevant, but also applicable to management. This project would not have been

possible without the many, resilient crew members who worked tirelessly, including Kylie Mosher, Marty Malate, Pete Murphy, Vanessa Stevens, Natalia Rico, Montserrat Valencia, Marcel Safford, and Robbie Heumann.

My research was made possible by a wide range of funding sources, including the CAL FIRE Forest Health Research Grant, Henry A. Jastro Research Fellowship, Northern California Botanists Scholarship, Davis Botanical Society Grant, CNPS Mary DeDecker Botanical Grant, the Mildred E. Mathias Graduate Research Grant, and an agreement with CAL FIRE FRAP for funding the California Prescribed Fire Monitoring Program. Many thanks to GGE and ESP staff, including Angie Nguyen, Sheline Calvert, and Lauren Schroeder, who helped me with paperwork and funding. To Shane Waddell for help and support at Stebbins Cold Canyon and Quail Ridge UC Natural Reserves.

To my mother, Deb Grupenhoff, for her unwavering support and encouragement at each step of this process. A special thanks to my partner, Reed Kenny, for the continual support, laughter, amazing adventures, and delicious food throughout graduate school. His deep support and understanding during challenging times was crucial to my success.

The study sites on which I conducted research for this dissertation were on the tribal lands of the Patwin and Miwok (chapter 1) and Modoc Nation, Washoe, Northern Paiute, Mountain Maidu, Northern Pomo, and Miwok tribal lands (chapter 3). These people lived and managed these lands for time immemorial, actively using fire management to shape vegetation and promote wildlife habitat. The forced removal of Indigenous people disrupted this deep knowledge and colonialism continues to erect significant barriers to their ability to perform cultural burning today.

Table of Contents

Abstract	ii
Acknowledgements	iv
Table of Contents	vi
Introduction	1
Chapter 1: Frequent fire in California chaparral reduces post-fire shrub regeneration and native plant diversity	5
Abstract	6
Introduction	7
Methods	9
Results	14
Discussion	17
Conclusion	21
Acknowledgments	21
Literature Cited	22
Figures and Tables	27
Supplemental Figures	35
Chapter 2: Fuel treatment effects on fuel loads in western US dry conifer forests: a meta-analysis	37
Abstract	38
Introduction	39
Methods	41
Results	46
Discussion	50
Conclusion	57
Literature Cited	58
Figures	74
Supplemental information	85
Chapter 3: First entry prescribed fire has greatest effects on surface fuels but limited effect in altering forest structure	94
Introduction	95
Methods	97
Results	103
Discussion	104
Literature cited	108
Figures and Tables	114

Introduction

Mitigating the effects of massive wildfires is one of our generation's most critical forest conservation goals and perhaps the most important in western North America. There is a vast diversity of fire regimes on Earth, each with specific characteristics, such as frequency, severity, size, and seasonality, that vary over time and space. However, factors that have driven these patterns in the past have been severely altered by changes in climate and Euro-American fire suppression (McLauchlan et al. 2020). These changes have resulted in larger, higher severity fires that pose enormous threats to biodiversity, human health, and the economy (Safford et al. 2022; Steel et al. 2023; Weeks et al. 2023; Williams et al. 2023)

Sclerophyllous shrubland ecosystems in the world's Mediterranean climate zones (MCZs) are a widespread vegetation type and provide invaluable ecosystem services to surrounding human-dominated communities (Underwood et al. 2018). Chaparral shrublands of the North American MCZ historically burned at high intensity with a mean fire return interval of 30-100 years before Euro-American settlement (Van de Water and Safford 2011). Despite its resilience to periodic fire events, alteration of the natural fire regime can lead to the transition from chaparral to oak woodland or grassland. A common successional pathway we see today is a transition to disturbance-tolerant non-native grassland due to an increase in fire frequency (Zedler et al. 1983; Keeley and Fotheringham 2001; Syphard et al. 2019). Increasing temperatures and reduced precipitation are likely to exacerbate the size and frequency of catastrophic fires by altering the amount and distribution of fuels and creating a shorter fire-return interval than historically was present (Franklin et al. 2004; Syphard et al. 2019). This altered fire regime threatens biodiversity (Pausas et al. 2004) and increases fire risk to communities living in the wildland-urban interface (Syphard et al. 2008). Once a chaparral stand

has undergone type conversion, it has a low chance of reverting back to its historical condition, even if actively managed (Allen et al. 2020; Dewees et al. 2022).

For my first chapter, I examined the impact of increased fire frequency on the composition and abundance of herbaceous and woody species in the Interior Coast Range of northern California. I investigated the impact of higher fire frequencies than previously reported in the scientific literature for California by sampling fifty-four 250-m² plots to assess postfire regeneration of chaparral shrubs and plant community composition. Our findings reveal that three fires in quick succession significantly reduced post-fire native woody regeneration, with obligate seeding species experiencing a 99% reduction and facultative species showing an 83% reduction in regeneration in the most frequently burned plots. Further, the overall marginal effect of an increase in one short interval fire decreased the proportion of native species cover by 12% and richness and Shannon diversity both by 4%. Consequently, areas with higher fire recurrence exhibited a more homogeneous landscape, dominated by a similar group of non-native species.

Fire is still a natural disturbance process in dry conifer forests in the western US, however the characteristics that define the fire regime of these forests are quite different from that of chaparral. These forests are experiencing fewer fires due to fire suppression policies, but these policies have resulted in fuel accumulations and forest densification. The warming climate is leading to drier fuels and more severe fire weather, and when fires escape control today, they tend to burn large areas at high severity, which pose enormous threats to biodiversity, human health, and the economy (Lohman et al. 2007; Steel et al. 2022, 2023; Weeks et al. 2023; Williams et al. 2023).

Yellow pine and mixed-conifer (YPMC) forests, for example, are the dominant vegetation type in the Sierra Nevada mountain ranges and typically experienced frequent (10-15 years) fire that was generally low-to-moderate severity prior to Euro-American settlement (Van de Water and Safford 2011). Variable fire effects were 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 species diversity (Larson and Churchill 2012; Knapp et al. 2013; Richter et al. 2019). However, many of these forests have experienced an increase in tree density and shifts in species composition in the absence of fire. Decades of fire suppression and timber harvesting have resulted in structural and compositional changes, leading to high surface fuel loads, high densities of small stems, and an increasing proportion of fire-intolerant species such as *Abies concolor* and *Calocedrus decurrens* (Safford and Stevens 2017). This has increased the number of massive, catastrophic fires in many western fire-adapted forests, posing severe threats to humans and ecological values.

To address these issues, fuel treatments such as prescribed fire, hand thinning, and mechanical surrogates for fire (e.g thinning, mastication) have been implemented to restore forest resilience by reducing surface and canopy fuels and restoring natural disturbance processes in historically frequent-fire forests (Agee and Skinner 2005; North et al. 2012; Stephens et al. 2012). Despite the expanding use of fuel treatments, significant gaps still exist in our understanding of the dynamic change in fuels after treatment as well as their effectiveness in achieving quality objectives such as shifts in species composition and spatial patterns to resemble historical patterns prior to Euro-American colonization.

My second two chapters focus on questions relating to fuel treatment effectiveness in dry conifer forests of the western US. For my second chapter, I documented and analyzed patterns in fuel dynamics after fuel treatments across dry conifer forests in the western US by conducting a meta-analysis using 1,932 observations from 65 published papers. Overall, I found that fuel treatments successfully reduce fuel loads across dry conifer forests; however this effect varied across fuel treatment types. Treatments including thinning followed by prescribed fires (THIN+BURN), when compared to treatments including only thinning (THIN) and prescribed fires (BURN), were the most successful in reducing overstory fuel loads while simultaneously mitigating the build up of surface fuels after thinning. BURN treatments, despite having limited

impact on overstory fuels, were the most effective at reducing surface fuel loads even after a single entry. These findings underscore the effectiveness of fuel treatments in altering fuel loads across different forest types, with treatment type and initial stand conditions being key factors influencing outcomes.

My third chapter concludes this dissertation by quantifying the current effectiveness of prescribed fire as a management strategy in YPMC forests which historically experienced frequent low-to-moderate intensity fire. We documented changes in surface fuel loading, stand structure, and resulting species diversity before and after prescribed fire at 12 project sites across northern and central California. We found that first-entry prescribed fire was successful at reducing surface fuels in YPMC forests, however, there was limited effect on forest structure. Despite this lack of change in overstory structure, we found a significant increase in native and nonnative species richness and Shannon diversity two years after treatment.

Chapter 1: Frequent fire in California chaparral reduces post-fire shrub regeneration and native plant diversity

Ashley R. Grupenhoff^{1*} & Hugh D. Safford^{1,2}

¹Department of Environmental Science and Policy, University of California, 1 Shields Ave,
Davis, California 95616, USA

²Vibrant Planet, Incline Village, Nevada, USA

Abstract

Fire is crucial for maintaining species diversity and resilience in fire-adapted shrublands of the world's Mediterranean climate zones (MCZs), which include the chaparral shrublands of the North American MCZ. Chaparral generally experiences high intensity burning, with long intervals between fires (30-100 years) typical under undegraded conditions. Modern fire frequencies are much higher, however, driven by high density of human ignitions and a progressively longer, warmer, and seasonally drier fire season. This departure from historical patterns has major implications for biodiversity, leading to exotic invasion, decreased ecosystem services, and potential type conversion of shrubland to grassland. We studied the impact of increased fire frequencies on the composition and abundance of herbaceous and woody species in the Interior Coast Range of northern California. Our study area is one of the most frequently burned areas in the state, which afforded us the opportunity to investigate higher fire frequencies than heretofore reported in the scientific literature for California. We surveyed fifty-four 250-m² plots to assess changes in plant community composition and postfire regeneration of chaparral shrubs across a wide range of fire frequencies, including plots that have burned up to six times in the past 30 years. Our findings reveal that three subsequent fires significantly reduced post-fire native woody regeneration, with obligate seeding species experiencing a 99% reduction and facultative species showing an 83% reduction in regeneration in the most frequently burned plots. Moreover, the overall marginal effect of an increase in one short interval fire decreased the proportion of native species cover by 12% and richness and Shannon diversity both by 4%. Consequently, areas with higher fire recurrence exhibited a more homogeneous landscape, dominated by a similar group of non-native species.

Keywords: *chaparral, fire frequency, post-fire regeneration, species diversity*

Introduction

Fire is vital for maintaining biodiversity in many fire-adapted ecosystems around the world, but interactions between anthropogenic drivers such as rapid climate warming, disturbance regime interventions, and land use change are causing major changes in the spatial-temporal pattern of fire (hereafter, fire regime) (UNEP 2022). In the North American Mediterranean Climate Zone (NAMCZ), the climate is warming and becoming seasonally drier and more variable, extreme fire weather conditions are more common, and there is an increase in urbanization and population growth (Keeley and Fotheringham 2001; Abatzoglou and Williams 2016; Molinari et al. 2018; Syphard et al. 2018). Changes in climate and increased urbanization have altered natural fire regimes across the region, posing serious risks to the NAMCZ, especially chaparral shrublands (Molinari et al. 2018; Park et al. 2018; Syphard et al. 2019).

Chaparral shrublands are a widespread vegetation type in the NAMCZ that provide numerous ecosystem services and are considered to be biodiversity hotspots (Rundel 2018; Underwood et al. 2018). Because the shrub canopy is short and mostly connected to surface fuels, California chaparral mostly burns at high intensity (Keeley and Safford 2016). Chaparral vegetation is adapted to moderately infrequent fire, with paleodata and modeling studies suggesting an optimal fire return interval range between 30 and 90 years (Van de Water and Safford 2011). Despite its resilience to periodic fire events, alteration of the natural fire regime can lead to the transition from chaparral to oak woodland or grassland. In some cases, chaparral can transition to woodland or forest after very long intervals without fire (Callaway and Davis 1993; Safford et al. 2021). A common successional pathway we see today, however, is a transition to disturbance-tolerant non-native grassland due to an increase in fire frequency (Zedler et al. 1983; Keeley and Fotheringham 2001; Syphard et al. 2019). Studies in southern California show that large areas of lowland and lower montane chaparral have been converted

to exotic grassland, driven by an increase in short-interval fires and recurrent drought (D'Antonio and Vitousek 1992; Keeley and Brennan 2012; Park et al. 2018; Syphard et al. 2019).

Uncharacteristically short fire return intervals threaten chaparral resilience and persistence by eliminating species without adaptations to short fire return intervals. Many plants adapted to fire-prone ecosystems have traits that allow them to survive and regrow after fire or to rapidly recolonize burned areas (He et al. 2019). Postfire recovery includes factors such as regrowth, reproduction, dispersal, germination, and establishment, all of which are mediated by how plant traits interact with fire severity (McLauchlan et al. 2020). In chaparral, postfire recovery involves regeneration initiated by germination of the dormant seed bank, resprouting from lignotubers and other vegetative structures, or wind dispersal. Native woody species are commonly divided into obligate seeders (species incapable of vegetative regeneration and which germinate from the dormant seed bank in the first postfire year), obligate resprouters (which lack a dormant seed bank but regenerate vegetatively), and facultative seeders (which have post-fire germination coupled with resprouting). Increased fire frequency may induce substantial mortality for obligate seeders since these species often require a decade or more to replenish the seed bank (Zedler et al. 1983; Jacobsen et al. 2004). Some studies have also shown that even resprouting chaparral species will be eliminated if fire is frequent enough (Haidinger and Keeley 1993; Keeley and Brennan 2012).

Shifts in species composition and type conversion to nonnative grassland have large-scale implications for ecosystem resilience, regional and local biodiversity, and ecosystem services such as primary production, carbon sequestration, nutrient cycling, pollination, erosion mitigation, and habitat provision (Rundel 2018; Underwood et al. 2018). As such, understanding the nuanced effects of fire recurrence on biodiversity and recovery is necessary for understanding the extent and future trajectories of chaparral type conversion. To date, no study has examined these effects at sites that have burned more than three times in the past

few decades. Additionally, only a handful of studies have focused on the Coast Range of northern California, one of the most frequently burned locations in the whole state.

Our study took place in the footprint of the 2020 Hennessy Fire, the largest of the fires composing the LNU Lightning Complex. The landscape burned by the Hennessy has a rich fire history: 38% of the Hennessy Fire had burned in the previous 10 years, the highest proportion of any 2020 fire, and more than 50% had burned at least once in the last 20 years (Safford et al. 2022). Some areas in the Putah and Cache Creek drainages had burned 6 times since 1985, and up to 4 times in the previous 7 years, which makes these areas among the most frequently burned wildlands in all of California. This provides a unique research opportunity, as to this point, no published studies in California have evaluated the impacts of more than three fires on chaparral resilience.

To better understand when chaparral communities lose resilience to invasion, we asked two primary questions: 1) How does fire frequency affect the diversity and cover of native and non-native species; and 2) What are the consequences of higher burn frequency on shrub seedling establishment and resprouting success? Based on results from previous studies, we hypothesized (1) a reduction in species diversity and local richness in areas with more than 2 short interval fires and (2) decreased native shrub regeneration and resprout growth of native shrubs. Specifically, we hypothesized higher burn frequency would lead to a reduction in the probability of obligate and facultative seedling regeneration after 2 short interval fires (2a) and a reduction in resprout growth of facultative species after 3 short interval fires (2b).

Methods

Study Site

The study was conducted in the Interior Coast Range of northern California which supports a diverse mosaic of chaparral, oak woodland, and grassland. Intact chaparral vegetation is dominated by drought-tolerant, sclerophyllous shrubs. Our study focused on

Adenostoma fasciculatum (chamise) chaparral and mixed chaparral stands. Nearly pure stands of chamise-dominated chaparral occur on sandstone substrates on xeric exposures with shallow soils, while mixed chaparral stands occur on more mesic exposures with deeper soils and include chamise as well as other co-dominant species such as *Ceanothus* spp., *Heteromeles arbutifolia*, *Arctostaphylos* spp., and *Quercus berberidifolia*.

Historic mean fire-return intervals in California chaparral have been estimated between 30-90 years (Van de Water and Safford 2011) and the ignition sources prior to European colonization were primarily Indigenous peoples who burned in grasslands and chaparral for foods, medicines, and ceremonial items (Anderson and Keeley 2018); lightning ignitions certainly occurred but were relatively rare, as they are today (van Wagtendonk and Cayan 2008). Today, human ignition sources are typically due to accidents from power lines, vehicles, and campfires (Syphard and Keeley 2015; Anderson and Keeley 2018).

We sampled post-fire chaparral plant communities after the 2020 LNU Lightning Complex Fire, which was one of the largest fires in California history, burning 124,000 hectares in Napa, Yolo, Solano, and Lake Counties (Safford et al. 2022). We focused on the area burned in the Hennessy Fire, which ignited by lightning on August 17th and was extinguished in early October. In total, 54 plots were sampled at Quail Ridge UC Natural Reserve (38°30' N, 122°08' W), Cold Canyon UC Natural Reserve (38°30' N, 122°06' W), Cache Creek Regional Park (38°54' N, 122°18' W), and Bobcat Ranch Audubon Reserve (38°31' N, 122°04' W) (Fig. 1.1). All sites are between 260-540 m elevation and occur on inceptisols (mostly Maymen and Millsholm soil series) on sandstone substrates (California Soil Web; <https://casoilresource.lawr.ucdavis.edu/gmap/>). The study area experiences a Mediterranean climate with an annual average of 630-760 mm precipitation, mean January minimum and maximum temperatures are 3°C and 14°C, respectively, and mean July minimum and maximum temperatures are 15°C and 34°C (30-year average, 800-m resolution, PRISM Climate Group 2022).

The study area has a variable fire history, ranging from never burned to six prior burns in the past 30 years (Table 1.1). Plot locations were stratified across a fire frequency gradient and aspect, with an equal number of plots on cool (N and E aspects) and warm (S and W aspects) slopes. GIS layers from the USDA Forest Service were used to extract the date of origin and fire size for fires that occurred during the past 30 years. Fire frequency was calculated using the California Fire Return Interval Departure (FRID) database (Safford et al. 2011). Since these fire perimeters generally ignore unburned patches within fires that are less than hundreds of acres in size, we used Google Earth historical imagery to examine the landscape for unburned patches after each fire and we adjusted the FRID database fire frequencies accordingly. Heat load index was calculated for each transect using aspect and slope to account for the amount of solar radiation received (McCune and Keon 2002). Precipitation and temperature point estimates were extracted for each transect using the 4 km resolution PRISM dataset (PRISM Climate Group 2022).

Sampling Design & Processing

At each of the 54 plots, 50 x 5-m belt transects were established following (Safford and Harrison 2004; Werner et al. 2022). Sites were visited in the spring of 2021 and 2022. All plant species were recorded within the entire 250-m² transect to measure the overall richness of native and exotic plant species. Five 1-m² quadrats were sampled at 10-m intervals along the transect line, measuring: the percent cover of all native and exotic species; number and height of shrub seedlings; resprout height; percent cover of rock, bare soil, and litter; and litter depth. All variables collected at the 1-m² scale were averaged to give a transect-level value. Plant life history data for each species were obtained from the USDA Forest Service Fire Effects Information System or the University of California Jepson Herbarium. Species were classified by origin (native, non-native), lifeform (tree, shrub, forb, graminoid, fern), and fire regeneration strategy (obligate seeder (OS), facultative seeder (FS), obligate resprouter (OR)). The

proportion of native species cover, richness, and diversity were calculated at each transect each year (2021 & 2022). We calculated the proportion of native plant cover in each plot as the total native cover/(total native cover + total exotic cover). Additionally, we calculated the proportion of local species richness (calculated as the mean number of species per 250 m² plot) and the proportion of Shannon-Wiener diversity (which gives weight to rare species) using the vegan package in R (R Core Team 2021; Oksanen et al. 2023).

Fire severity was estimated in each belt transect by measuring the stem diameter (1 cm from the terminus) of four stems from a randomly chosen *Adenostoma fasciculatum* (chamise) individual rooted in or adjacent to each quadrat (Perez and Moreno 1998). Additionally, five more individuals were measured at the entire 250m² transect scale. In cases when chamise was not present we used *Heteromeles arbutifolia* or *Quercus berberidifolia* individuals. We measured heterogeneity in fire severity within each belt transect by calculating the coefficient of variation for the five quadrats within a transect.

Statistical analyses

Species cover, diversity, and composition (H1)

Bayesian generalized linear mixed models were used to investigate the interaction between fire frequency on the proportion of native species cover, richness, and diversity for both survey years using a Beta Binomial likelihood (Equation 1), which accommodates values between 0 and 1. To determine which environmental covariates to add to the model, we used the expected log pointwise predictive density (ELPD) to measure leave-one-out cross-validation for our goodness of fit measure. The covariates that we evaluated were fire frequency (numBurn), mean annual precipitation, mean annual temperature, heat load index, slope and aspect. We verified that independent variables were not highly correlated using the Spearman correlation coefficient (Supplemental Fig. 1). We first fit the proportion of native species cover with each individual predictor separately and added significant predictors in order of ELPD to

determine whether they significantly increased ELPD of the resulting model. Non-metric multidimensional scaling (NMDS) was used to visualize compositional differences between areas with variable fire recurrence as a part of the vegan package in R (R Core Team 2021; Oksanen et al. 2023). This ordination uses rank-order correlation and Bray-Curtis dissimilarities to model the differences among treatments based on species composition and abundance of all plant species.

Equation 1:

$$\begin{aligned}
 \text{prop. native cover}_{i,j} &\sim \text{Beta}(\mu_{i,j}, \phi) \\
 \text{logit}(\mu_{i,j}) &= \alpha + \beta_{\text{numBurn}} \text{numBurn} + \beta_{\text{numBurn}} \text{numBurn}^2 + \beta_{\text{SurveyYear}} \text{SurveyYear} \\
 \alpha &\sim \text{student_t}(3, 0, 2.5)
 \end{aligned}$$

Shrub regeneration (H2a)

We used a similar modeling procedure to understand how fire frequency influenced shrub regeneration and resprout growth. We fit seedling presence/absence using multiple Bayesian generalized linear models with Bernoulli likelihood (Equation 2). Like species diversity, we used the ELPD as a measure of leave-one-out cross-validation for our goodness of fit measure to compare. We first fit the presence/absence of a seedling with each individual predictor separately and added significant predictors in order of ELPD to determine whether they significantly increased ELPD of the resulting model. The covariates that we evaluated were fire frequency (numBurn), mean annual precipitation, mean annual temperature, heat load index, aspect, and slope. For seedling presence/absence, we calculated the area under the receiver operating curve (AUC) with the ROCR package in R, which is a commonly used method to evaluate model fit (Sing et al. 2005). AUC values >0.8 indicate good model prediction while values near 0.5 indicate the model is not better than random chance. We created a separate model for facultative and obligate seeding species, and for each individual species separately.

Equation 2:

$$\begin{aligned} presence &\sim \text{Bernoulli}(\rho_i) \\ \text{logit}(\rho_i) &= \alpha + \beta_{numBurn} numBurn + \beta_{SurveyYear} SurveyYear \\ a &\sim \text{student}_t(3, 0, 1) \\ \beta &\sim \text{normal}(0,1) \end{aligned}$$

Resprout growth (H2b)

To test how the growth of resprouting *A. fasciculatum* was impacted by fire frequency, we fit resprout height one year after fire with a Gaussian distribution (Equation 3). After ELPD measure of leave-one-out cross validation model selection, the final model included covariates for heat load index and the diameter of the largest stem (an indicator of prefire size). Resprout growth was square root transformed to meet assumptions of normality.

Equation 3:

$$\begin{aligned} \text{resprout growth} &\sim N(\mu_i, \sigma) \\ \mu_i &= \alpha + \beta_{numBurn} numBurn + \beta_{hli} Heat\ load\ index + \beta_{diam\ largest\ stem} Diam\ largest\ stem \\ a &\sim \text{normal}(0, 1) \\ \beta &\sim \text{normal}(0,1) \end{aligned}$$

All models were created using the brm function in the brms package (Bürkner 2017) in R version 4.1.1 (R Core Team 2021). Continuous independent variables were centered and scaled prior to analysis. We used mildly regularizing priors to prevent overfitting with 4 chains, each with 2000 iterations and a warmup of 1000. Trace plots and R-hat values were assessed to confirm proper mixing and model convergence.

Results

Fire severity

Mean and maximum fire severity, as well as the heterogeneity of fire severity, were reduced with increased fire frequency (>2 in the past 30 years) (Fig. 1.2, Table 1.2). Fire severity, which is inversely related to the diameter of the measured stem termini, was high in

sites that only burned once before the Hennessy Fire, but low in all other fire frequency classes (differences among FF = 3, 4, 5, and 6 were not statistically significant from each other).

Species cover, diversity, and composition (H1)

In total, 223 species were found throughout the study area. As predicted, we found that the proportion of native species cover, the proportion of native richness, and the proportion of native Shannon diversity declined with increased fire recurrence in both survey years (Fig. 1.3). The effect of fire recurrence was strongest for the proportion of native cover ($\beta_{\text{numburn}} = -1.17$; CIs = -1.67 to -0.67) and moderately strong for the proportion of native species richness ($\beta_{\text{numburn}} = -0.50$; CIs = -0.86 to -0.15) and Shannon diversity ($\beta_{\text{numburn}} = -0.65$; CIs = -1.14 to -0.16) (Supplemental Table 1.1). The overall average marginal effect of a 1-unit increase in fire frequency decreased the proportion of native cover by 12%, the proportion of native richness by 4%, and the proportion of native Shannon diversity by 4%.

This effect of fire frequency, however, varied at higher and lower levels of fire frequency for all diversity metrics (Fig. 1.3). At lower levels of fire frequency, a one-unit increase in frequency led to a significant 16% decrease in the proportion of native cover (Fig. 1.3b). In contrast, a frequency of 5 fires in the past 30 years resulted in a slight 5% *increase* in the proportion of native cover. The pattern of native richness and Shannon diversity closely align with the findings for native cover. For lower levels of fire frequency, a one-unit increase is associated with a 7% and 9% decrease in native richness and Shannon diversity, respectively. However, as fire frequency rises to higher levels there is a slight shift to a 2% increase in native richness and a 1% increase in Shannon diversity.

Plots in areas with different fire frequencies had different species assemblages. The NMDS ordination of species composition resulted in an overlapping cluster of plots with higher fire recurrence (>2 short interval fires) that contain more non-native herbaceous species, while plots with lower fire recurrence (≤ 2 short interval fires) contained more native herbaceous

species and shrubs (Fig. 1.4). Species characteristic of the high fire frequency plots included *Avena barbata*, *Centaurea melitensis*, *Erodium cicutarium*, and *Festuca myuros* (Fig. 1.4), all classic dominant species in the exotic annual grassland that characterizes highly disturbed sites in lowland California. Plots with higher fire recurrence had smaller clusters compared to areas with low fire recurrence, indicating a shift from a more heterogeneous post-fire landscape to a more homogeneous landscape with many similar non-native species.

Shrub regeneration (H2a)

Increased fire frequency in chamise chaparral reduced shrub seedling regeneration, as expected (Fig. 1.5). In plots with higher fire frequency (FF=6), seedling regeneration for FS declined by 83% and OS regeneration declined by 99% when compared to plots with lower fire frequency (FF=1). OS species, including *Ceanothus oliganthus* and *Ceanothus cuneatus*, were almost completely eliminated in areas with >2 fires in the past 30 years (Fig. 1.5). We found a strong negative association between fire frequency and the presence of OS regeneration ($\beta_{\text{numburn}} = -0.92$; CIs = -1.43 to -0.49; Fig. 1.5a) and a significant, albeit less strong, negative association between fire frequency and the presence of FS regeneration ($\beta_{\text{numburn}} = -0.33$; CIs = -0.47 to -0.19; Fig. 1.6a). Fire frequency significantly reduced the presence of *Ceanthous cuneatus* ($\beta_{\text{numburn}} = -1.10$; CIs = -1.65 to -0.64; Fig. 1.5b) and *Ceanthous oliganthus* ($\beta_{\text{numburn}} = -1.20$; CIs = -2.27 to -0.41; Fig. 1.5c). The effect of fire frequency on FS regeneration was species-specific and significantly reduced the presence of *Adenostoma fasciculatum* ($\beta_{\text{numburn}} = -0.70$; CIs = -1.02 to -0.40; Fig. 1.6b) and *Lepechinia calycina* seedlings ($\beta_{\text{numburn}} = -0.66$; CIs = -1.00 to -0.35; Fig. 1.6d). Despite an overall decrease in presence of FS regeneration due to fire frequency, we found a slight qualitative increase in *Eriodictyon californicum* seedlings ($\beta_{\text{numburn}} = 0.05$; CIs = -0.18 to 0.28) but this effect was not significant (Fig. 1.6c).

Shrub resprout growth (H2b)

In contrast to hypothesis 2b, we did not see any significant difference in *A. fasciculatum* resprout growth with increased fire frequency ($\beta_{\text{numburn}} = 0.00$; CIs = -0.02 to 0.01; Fig. 1.7). Despite a reduction in live individuals, postfire height was around 0.4 meters 1-year after fire for all levels of fire frequency. Heat load index and the diameter of the largest stem improved model fit, but did not have a strong association with resprout growth ($\beta_{\text{hli}} = 0.00$; CIs = -0.02 to 0.01; $\beta_{\text{diam largest stem}} = -0.01$; CIs = -0.03 to 0.00)

Discussion

Our results are consistent with other studies that show a reduction in native shrub regeneration and species diversity after multiple, short-interval fires in chaparral shrublands (Zedler et al. 1983; Haidinger and Keeley 1993; Jacobsen et al. 2004; Keeley and Brennan 2012). Yet our study is the first to examine how such high fire frequencies – up to six times in the past 30 years – may be impacting chaparral vegetation in the NAMCZ. Our findings highlight how uncharacteristically high fire recurrence (>2 short interval fires) in chaparral reduced fire severity, resulting in a reduction in native woody regeneration and homogenization of the plant community. We found that a diverse mix of native shrub and herb species are being replaced with a smaller, more homogeneous set of non-native annual species. Overall, these results highlight the complex relationship between fire frequency and diversity metrics, showcasing how different levels of fire frequency can impact native cover, richness, and Shannon diversity in varying ways.

It is important to note that the occurrence of short intervals between fires, rather than fire frequency per se, is a key component to type conversion (Jacobsen et al. 2004; Syphard et al. 2019). Our study examines the effect of fire frequency, and because short interval fires are more likely to occur when fire is more frequent, we cannot parse a partial causality between the two in this study. All of our sites that burned more than three times in the past 30 years were also the sites that had the shortest fire return intervals (between 2 and 5 years). Short fire return

intervals reduce fire intensity, promoting non-native species persistence and reducing regeneration of native chaparral shrubs (Keeley et al. 2006). This has negative consequences for obligate seeding shrubs that require at least 10 years to mature before replenishing the seed bank (Zedler et al. 1983; Jacobson et al. 2004), and in particular for the genus *Ceanothus*, which tends to germinate best under higher fire intensities that are only possible in the presence of a woody fuel load (Moreno and Oechel 1991; Le Fer and Parker 2005). Despite our inability to parse the importance of fire return interval and fire frequency independently, assessing fire frequency by itself is still relevant given the increasingly common condition of frequent fire in chaparral and that the two are very often linked.

How does fire frequency affect the diversity and cover of native and non-native species?

Our study confirms that increased fire frequency in chaparral facilitates a reduction in the proportion of native species cover, richness, and Shannon diversity. Consequently, plots with higher fire recurrence exhibit a more homogeneous landscape, dominated by a set of similar non-native species. This result is in line with the body of research in southern California, showing that high fire frequency, and subsequent short fire intervals, promote non-native invasion (Keeley 2006; Syphard et al. 2019). It is generally known that in chaparral landscapes, shrub canopy closure and the presence of a non-native seedbank at the time of fire are important drivers of non-native invasion (D'Antonio et al. 2001; D'Antonio and Kark 2002; Keeley et al. 2005). We observed a decrease in fire intensity – which is inversely related to the diameter of the measured stem termini – with an increase in fire frequency. This lower intensity fire diminishes the heat filter that kills the non-native species pool and promotes native germination (Keeley et al. 2008; Keeley and Brennan 2012).

Prior studies in California chaparral have only examined the impacts of up to three short-interval fires. Our study is the first to show the effect of up to six fires in the past 30 years.

Note that at the most highly departed sites (FF=6), there is a slight increase in the proportion of all diversity metrics. This was an unexpected result and is likely due to a transition to grassland vegetation type. Highly departed sites are primarily dominated by non-native grasses and forbs (e.g., *Avena barbata*, *Bromus madritensis*, *Erodium* spp.). Nonetheless, we found a slight increase in native richness and cover at the higher end of the fire frequency gradient (>5 fires in the past 30 years), driven mostly by disturbance-tolerant native species that are common in California grassland systems (e.g., *Acmispon* spp., *Madia* spp., *Dichelostemma* spp.). Despite this increase in native forbs, we observed no perennial grasses characteristic of native California grasslands at these sites (e.g., *Stipa* spp., *Melica* spp.). Further, these plots still exhibited lower diversity metrics than sites with low fire frequency (<2 fires in the past 30 years). Another caveat to this finding is that, due to a lack of interspersed sites with FF =2-5, there could be certain site effects driving this increase in diversity.

What are the consequences of higher burn frequency on shrub seedling establishment and resprouting success?

As predicted, we found a reduction in both OS and FS regeneration. OS species, such as *C. oliganthus* and *C. cuneatus*, were almost completely eliminated in areas with more than 2 fires in the past 30 years (99% reduction). These results are consistent with other studies in southern California, showing that obligate seeding shrubs often require a decade or more between fires in order to reach maturity and replenish the seedbank (Zedler et al. 1983; Jacobsen et al. 2004; Keeley and Brennan 2012). Our observed reduction in fire severity with short-interval fires confirm a departure from the high-intensity fires that are typical of undegraded chaparral and vital for the survival and recruitment of many chaparral shrub species (Park and Jenerette, 2019).

While all obligate seeding species declined with high fire frequency, facultative species as a group showed reduced regeneration (83% reduction) but displayed species-specific responses, with some species persisting at high levels of fire frequency. We found that *A. fasciculatum* re-established well from seedlings after up to 3 fires in the past 30 years. Still, seedling regeneration declined and was almost completely eliminated in areas with fire frequency ≥ 5 . This result contrasts with research in southern California, reporting a drastic reduction in *A. fasciculatum* seedlings after just two short interval fires (Zedler et al. 1983; Keeley and Brennan 2012). Despite our prediction that all facultative seeding species regeneration would be eliminated after 2 short interval fires, there was little effect on *Eriodictyon californicum* regeneration. We found a slight increase in seedling regeneration at the most highly departed sites. This is not necessarily surprising, considering *Eriodictyon sp.* is a principal invader in many disturbed sites (Mooney and Hobbs 1986). While grouping regeneration by functional type (OS, FS) can be very useful, species-specific responses are vital to consider (Keeley et al. 2006).

Contrary to our expectations, and findings from research in southern California (Zedler et al. 1983; Keeley and Brennan 2012), we found no reduction in resprout growth with increased fire frequency. Other variables that play an essential role in determining the vigor of resprouting shrubs. For example, the survival and vigor of resprouting shrubs in northern California are especially sensitive to pre-fire drought and can exacerbate the effect of short-interval fire (Werner et al. 2022). While the lack of environmental variation (e.g., temperature, precipitation) and temporal scope across our sites makes it difficult to parse out the exact cause of reduced resprout vigor, we can fully understand the consequences of increased fire frequency, which did not have a strong impact on resprout vigor. While resprouting species are well adapted for repeat fires, they can be extirpated after some time (Zedler et al. 1983, Keeley and Brennan 2012). Assessing shrub mortality, in addition to resprout success, is vital to consider.

Conclusion

Much of the species diversity in the NAMCZ – a global biodiversity hotspot – is centered in chaparral-dominated shrublands. There is a rich diversity of endemic species restricted to chaparral and loss of this habitat type has major implications on many ecosystem services such as flood control, erosion reduction, carbon sequestration, nutrient cycling, pollination, primary production, and habitat provision (Rundel 2018; Underwood et al. 2018). Here we provide insights into the effects of altered fire regimes on chaparral plant communities, using a broader fire frequency gradient than has been previously studied.

Our study provides empirical evidence that an increase in fire frequency, and the associated increase in shorter fire return intervals, precipitates a shift in the local vegetation. Initially characterized by a distinctive assemblage of native woody and herbaceous species, we observed a shift to a homogenized community dominated by a smaller set of non-native annual species. Areas dominated by nonnative grasses increase fine fuel loads, leading to more frequent fires that burn at lower intensity. The shift in fire behavior allows the nonnative seedbank to persist, leading to a repeating “grass-fire cycle” (D’Antonio and Vitousek 1992). Once a community has undergone type conversion, it has a greatly reduced probability of reverting to its previous state, even if actively managed (Allen et al. 2018; Dewees et al. 2022). Identifying areas that are in severe danger of type conversion, but are still intact, enhances the possibility of preventative management (Allen et al. 2018). In chaparral, reducing fire frequency is paramount to conserving native species and preserving ecosystem services, using the entirety of the integrated fire management spectrum (Safford et al. 2018).

Acknowledgments

Many thanks to Sam Vaillancourt, Marcela Cathcart, and Reed Kenny for field support, Andrew Latimer and Hannah Fertel for general analysis advice, and Sara Winsemius and Tara Ursell for

reviewing this manuscript. We thank Shane Waddell, the University of California Natural Reserve System, and the U.S. Bureau of Land Management for access to study sites. Funding was provided by CAL FIRE (8GG20807) and the UC Davis Jastro-Shields Graduate Research Award.

Literature Cited

- Abatzoglou JT, Williams AP (2016) Impact of anthropogenic climate change on wildfire across western US forests. *Proc Natl Acad Sci* 113:11770–11775.
<https://doi.org/10.1073/pnas.1607171113>
- Allen EB, Williams K, Beyers JL, et al (2018) Chaparral Restoration. In: Underwood EC, Safford HD, Molinari NA, Keeley JE (eds) *Valuing Chaparral: Ecological, Socio-Economic, and Management Perspectives*. Springer International Publishing, Cham, pp 347–384
- Anderson MK, Keeley JE (2018) Native Peoples' Relationship to the California Chaparral. In: Underwood EC, Safford HD, Molinari NA, Keeley JE (eds) *Valuing Chaparral: Ecological, Socio-Economic, and Management Perspectives*. Springer International Publishing, Cham, pp 79–121
- Bürkner P-C (2017) brms: An R Package for Bayesian Multilevel Models Using *Stan*. *J Stat Softw* 80:. <https://doi.org/10.18637/jss.v080.i01>
- Callaway RM, Davis FW (1993) Vegetation Dynamics, Fire, and the Physical Environment in Coastal Central California. *Ecology* 74:1567–1578. <https://doi.org/10.2307/1940084>
- D'Antonio C, Levine J, Thomsen M, others (2001) Ecosystem resistance to invasion and the role of propagule supply: a California perspective. *J Mediterr Ecol* 2:233–246
- D'Antonio CM, Kark S (2002) Impacts and extent of biotic invasions in terrestrial ecosystems. *Trends Ecol Evol* 17:202–204. [https://doi.org/10.1016/S0169-5347\(02\)02454-0](https://doi.org/10.1016/S0169-5347(02)02454-0)
- D'Antonio CM, Vitousek PM (1992) Biological Invasions by Exotic Grasses, the Grass/Fire

- Cycle, and Global Change. *Annu Rev Ecol Syst* 23:63–87.
<https://doi.org/10.1146/annurev.es.23.110192.000431>
- Deweese SL, D'Antonio CM, Molinari N (2022) Determining potential drivers of vegetation change in a Mediterranean environment. *Ecosphere* 13:e4313.
<https://doi.org/10.1002/ecs2.4313>
- Environment UN (2022) Spreading like Wildfire: The Rising Threat of Extraordinary Landscape Fires. In: UNEP - UN Environ. Programme.
<http://www.unep.org/resources/report/spreading-wildfire-rising-threat-extraordinary-landscape-fires>. Accessed 17 Sep 2023
- Haidinger TL, Keeley JE (1993) Role of High Fire Frequency in Destruction of Mixed Chaparral. *Madroño* 40:141–147
- He T, Lamont BB, Pausas JG (2019) Fire as a key driver of Earth's biodiversity. *Biol Rev* 94:1983–2010. <https://doi.org/10.1111/brv.12544>
- Jacobsen A, Davis S, Fabritius S (2004) Fire frequency impacts non-sprouting chaparral shrubs in the Santa Monica Mountains of southern California. *Ecol Conserv Manag Mediterr Clim Ecosyst* Millpress Rotterdam Neth
- Keeley JE (2006) Fire severity and plant age in postfire resprouting of woody plants in sage scrub and chaparral. *Madroño* 53:373–379
- Keeley JE, Baer-Keeley M, Fotheringham CJ (2005) Alien plant dynamics following fire in Mediterranean-climate California shrublands. *Ecol Appl* 15:2109–2125.
<https://doi.org/10.1890/04-1222>
- Keeley JE, Brennan T, Pfaff AH (2008) Fire Severity and Ecosystem Responses Following Crown Fires in California Shrublands. *Ecol Appl* 18:1530–1546.
<https://doi.org/10.1890/07-0836.1>
- Keeley JE, Brennan TJ (2012) Fire-driven alien invasion in a fire-adapted ecosystem. *Oecologia* 169:1043–1052. <https://doi.org/10.1007/s00442-012-2253-8>

- Keeley JE, Fotheringham CJ (2001) Historic Fire Regime in Southern California Shrublands. *Conserv Biol* 15:1536–1548. <https://doi.org/10.1046/j.1523-1739.2001.00097.x>
- Keeley JE, Fotheringham CJ, Baer-Keeley M (2006) Demographic Patterns of Postfire Regeneration in Mediterranean-Climate Shrublands of California. *Ecol Monogr* 76:235–255. [https://doi.org/10.1890/0012-9615\(2006\)076\[0235:DPOPRI\]2.0.CO;2](https://doi.org/10.1890/0012-9615(2006)076[0235:DPOPRI]2.0.CO;2)
- Keeley JE, Safford HD (2016) Fire as an ecosystem process: Chapter 3
- Le Fer D, Parker VT (2005) The Effect of Seasonality of Burn on Seed Germination in Chaparral: The Role of Soil Moisture. *Madroño* 52:166–174
- McCune B, Keon D (2002) Equations for potential annual direct incident radiation and heat load. *J Veg Sci* 13:603–606. <https://doi.org/10.1111/j.1654-1103.2002.tb02087.x>
- McLauchlan KK, Higuera PE, Miesel J, et al (2020) Fire as a fundamental ecological process: Research advances and frontiers. *J Ecol* 108:2047–2069. <https://doi.org/10.1111/1365-2745.13403>
- Molinari NA, Underwood EC, Kim JB, Safford HD (2018) Climate Change Trends for Chaparral. In: Underwood EC, Safford HD, Molinari NA, Keeley JE (eds) *Valuing Chaparral: Ecological, Socio-Economic, and Management Perspectives*. Springer International Publishing, Cham, pp 385–409
- Mooney HA, Hobbs RJ (1986) Resilience at the individual plant level. In: Dell B, Hopkins AJM, Lamont BB (eds) *Resilience in mediterranean-type ecosystems*. Springer Netherlands, Dordrecht, pp 65–82
- Moreno JM, Oechel WC (1991) Fire intensity and herbivory effects on postfire resprouting of *Adenostoma fasciculatum* in southern California chaparral. *Oecologia* 85:429–433. <https://doi.org/10.1007/BF00320621>
- Oksanen J, Simpson GL, Blanchet FG, et al (2023) *vegan: Community Ecology Package*
- Park IW, Hooper J, Flegal JM, Jenerette GD (2018) Impacts of climate, disturbance and topography on distribution of herbaceous cover in Southern California chaparral: Insights

- from a remote-sensing method. *Divers Distrib* 24:497–508.
<https://doi.org/10.1111/ddi.12693>
- Perez B, Moreno JM (1998) Methods for quantifying fire severity in shrubland-fires. *Plant Ecol* 139:91–101
- PRISM Climate Group, Oregon State University, <https://prism.oregonstate.edu>, data created 4 Feb 2014, accessed 16 Dec 2022.
- R Core Team (2021) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria
- Rundel PW (2018) California Chaparral and Its Global Significance. In: Underwood EC, Safford HD, Molinari NA, Keeley JE (eds) *Valuing Chaparral*. Springer International Publishing, Cham, pp 1–27
- Safford H, van de Water K, Schmidt D (2011) California fire return interval departure (FRID) map metadata: description of purpose, data sources, database fields, and their calculations. USDA For Serv Pac Southwest Reg Vallejo
- Safford HD, Butz RJ, Bohlman GN, et al (2021) Fire Ecology of the North American Mediterranean-Climate Zone. In: Greenberg CH, Collins B (eds) *Fire Ecology and Management: Past, Present, and Future of US Forested Ecosystems*. Springer International Publishing, Cham, pp 337–392
- Safford HD, Harrison S (2004) Fire effects on plant diversity in serpentine vs. sandstone chaparral. *Ecology* 85:539–548
- Safford HD, Paulson AK, Steel ZL, 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>
- Sing T, Sander O, Beerenwinkel N, Lengauer T (2005) ROCr: visualizing classifier performance in R. *Bioinformatics* 21:3940–3941. <https://doi.org/10.1093/bioinformatics/bti623>
- Syphard AD, Brennan TJ, Keeley JE (2018) Chaparral Landscape Conversion in Southern

- California. In: Underwood EC, Safford HD, Molinari NA, Keeley JE (eds) Valuing Chaparral: Ecological, Socio-Economic, and Management Perspectives. Springer International Publishing, Cham, pp 323–346
- Syphard AD, Brennan TJ, Keeley JE (2019) Drivers of chaparral type conversion to herbaceous vegetation in coastal Southern California. *Divers Distrib* 25:90–101.
<https://doi.org/10.1111/ddi.12827>
- Syphard AD, Keeley JE (2015) Location, timing and extent of wildfire vary by cause of ignition. *Int J Wildland Fire* 24:37. <https://doi.org/10.1071/WF14024>
- Underwood EC, Safford HD, Molinari NA, Keeley JE (eds) (2018) Valuing Chaparral: Ecological, Socio-Economic, and Management Perspectives. Springer International Publishing, Cham
- Van de Water KM, Safford HD (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>
- van Wagtenonk JW, Cayan DR (2008) Temporal and Spatial Distribution of Lightning Strikes in California in Relation to Large-Scale Weather Patterns. *Fire Ecol* 4:34–56.
<https://doi.org/10.4996/fireecology.0401034>
- Werner CM, Harrison SP, Safford HD, et al (2022) Extreme pre-fire drought decreases shrub regeneration on fertile soils. *Ecol Appl* 32:e02464. <https://doi.org/10.1002/eap.2464>
- Zedler PH, Gautier CR, McMaster GS (1983) Vegetation Change in Response to Extreme Events: The Effect of a Short Interval between Fires in California Chaparral and Coastal Scrub. *Ecology* 64:809–818. <https://doi.org/10.2307/1937204>

Figures and Tables

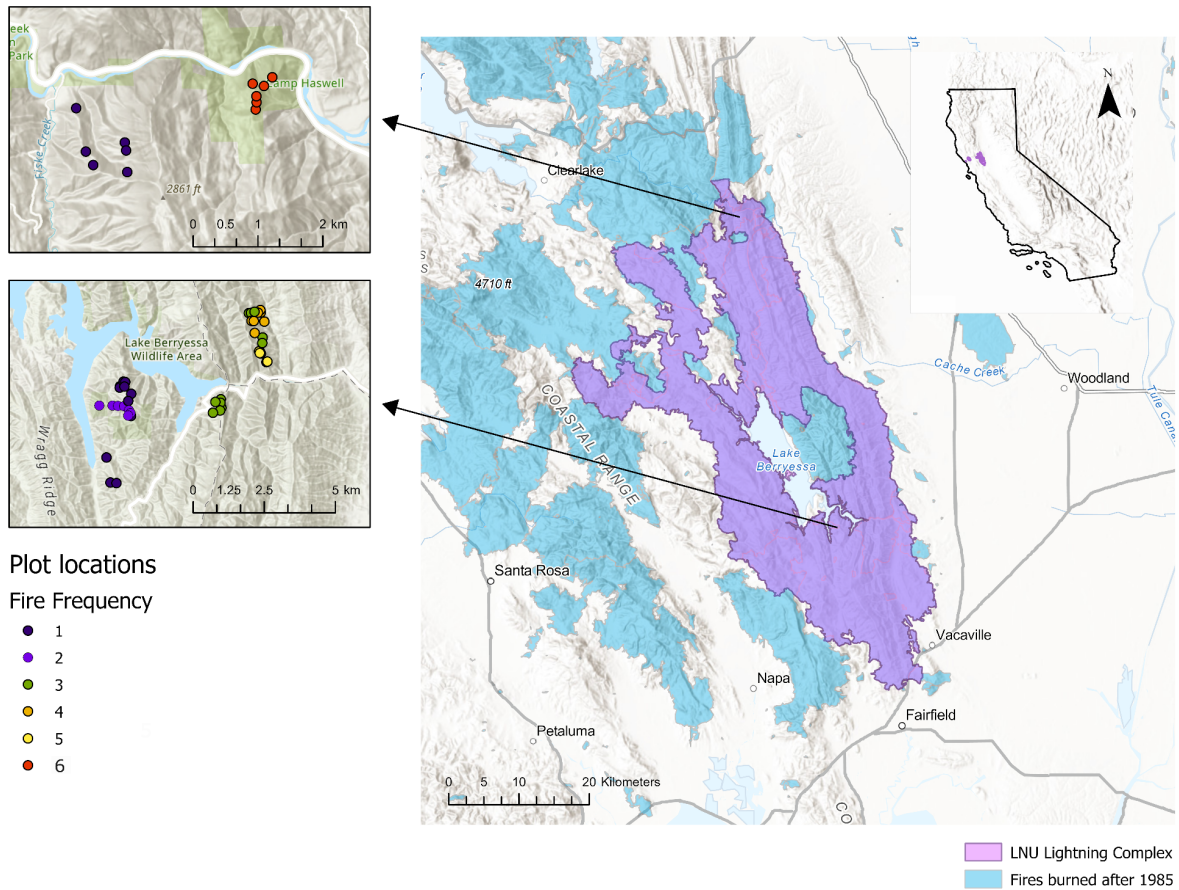


Fig. 1.1. Map of LNU Lightning complex (purple polygon) with locations of prior fires burned since 1985 (light blue polygons). The figures to the left show plot locations, which were distributed across a fire frequency gradient of 1 total burn (blue) up to 6 total burns in the past 30 years (red).

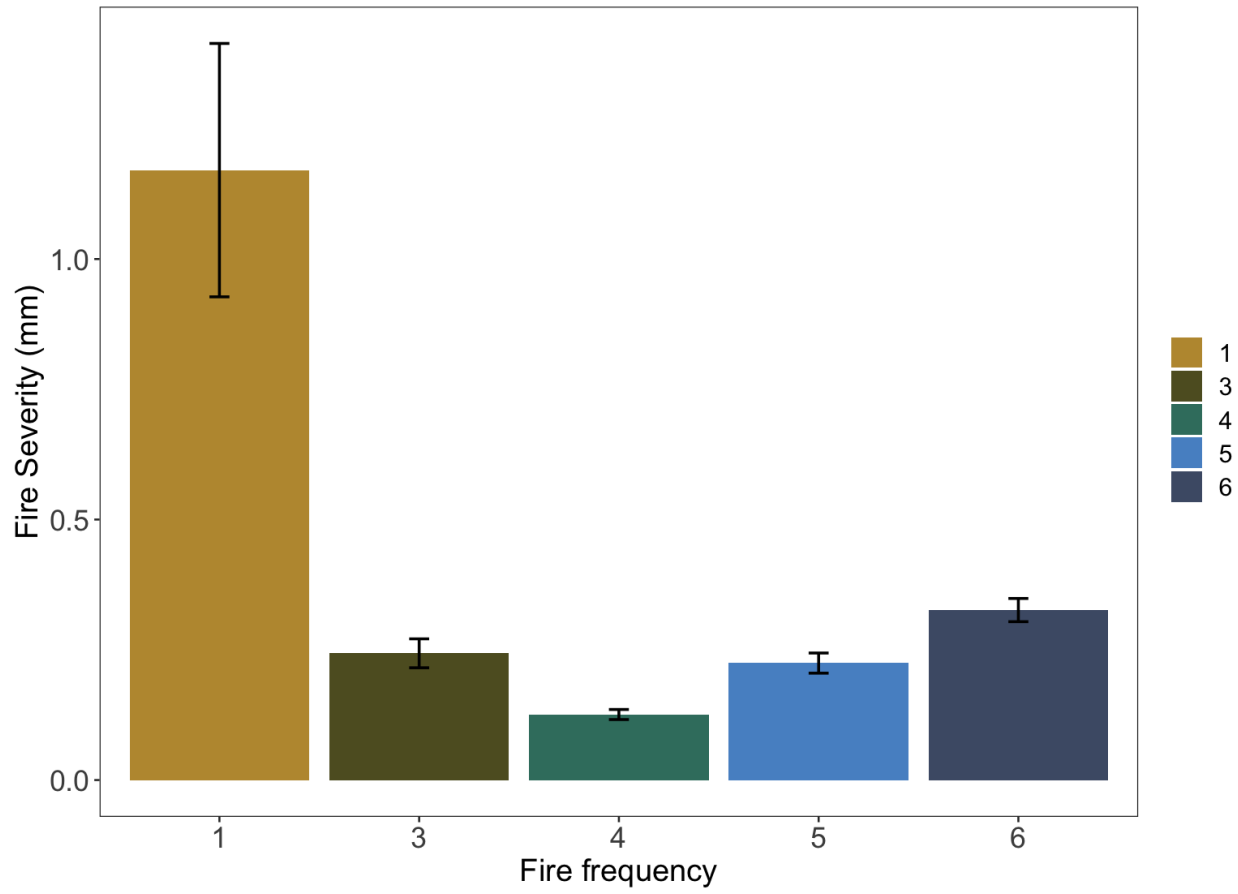


Fig 1.2: Measures of mean fire severity (mm) (\pm SE) decrease with increased fire frequency.

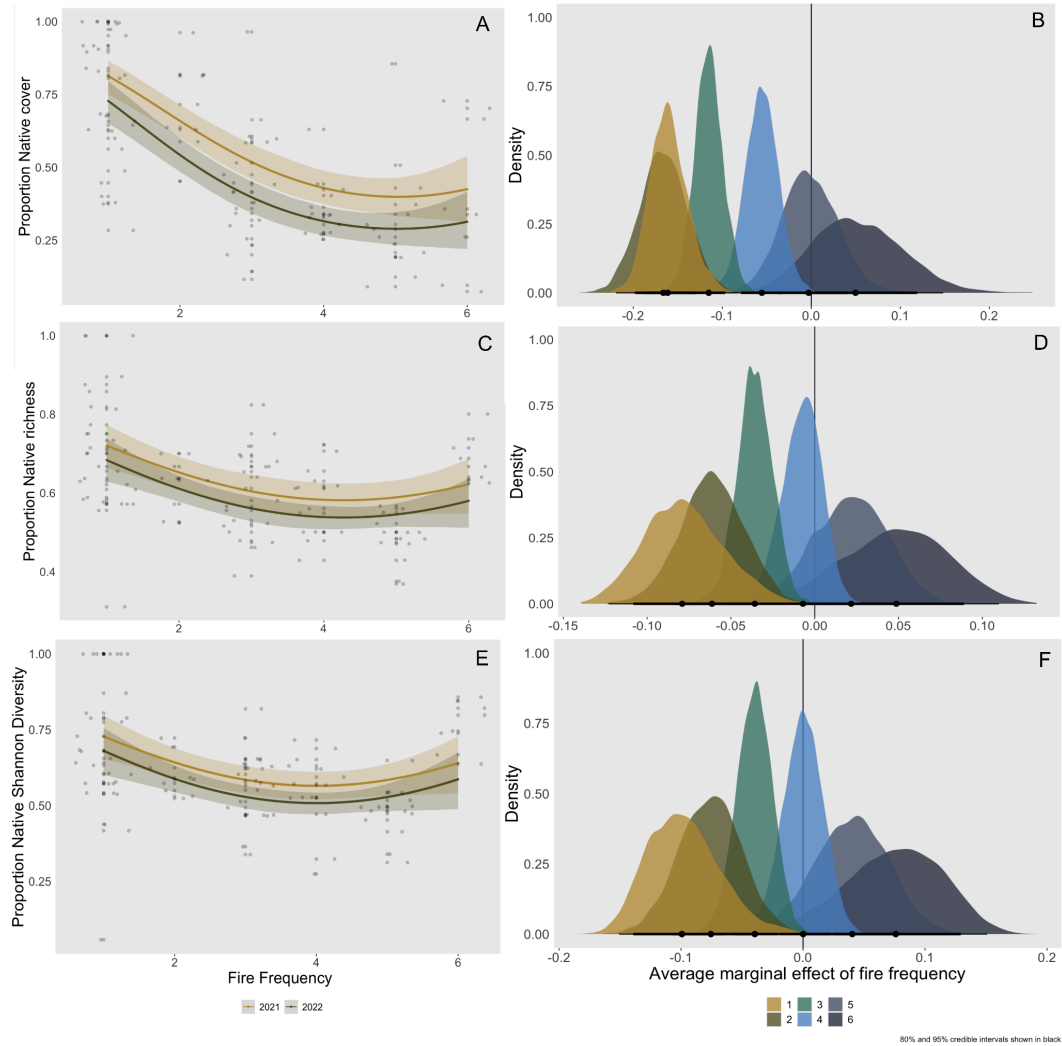


Fig 1.3: Proportion of native species cover (A), richness (C), and Shannon diversity (E) at the plot level declines with increased fire frequency after both survey years. Predicted values from the top-ranked Bayesian model with 95% credible intervals, as well as raw values (grey circles, n=103).

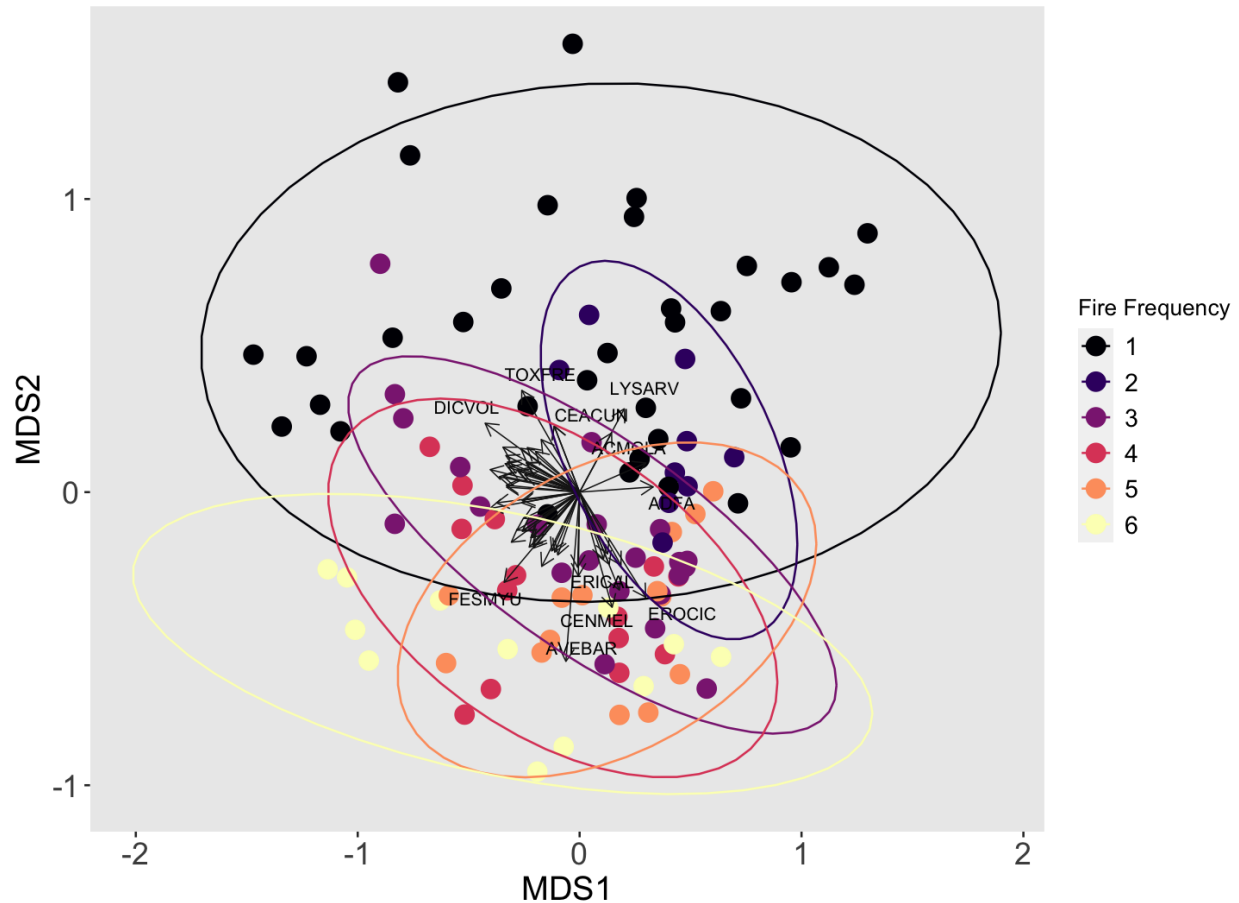


Fig 1.4: Non-metric multidimensional scaling plot (NMDS) of Bray-Curtis dissimilarity matrix across fire frequency. Each point represents a survey point. Plots with higher fire recurrence (pink, orange, and yellow) are more clustered together, indicating that they have a more similar species composition than plots with lower fire recurrence (black, dark blue, purple). Labeling priority was given to more abundant and frequent species. Species codes: ACMGLA *Acmispon glaber*, ACMWRA *Acmispon wrangelianus*, ADFA *Adenostoma fasciculatum*, ASTGAM *Astragalus gambeliana*, AVEBAR *Avena barbata*, CEACUN *Ceanothus cuneatus*, GENMEL *Centaurea melitensis*, CLAUNG *Clarkia unguiculata*, DICVOL *Dichelostemma volubile*, ERICAL *Eriodictyon californicum*, ERODIC *Erodium cicutarium*, ESCCAE *Eschscholzia caespitosa*, FESMYU *Festuca myuros*, LYSARV *Lysimachia arvensis*, MELTOR *Melica torreyana*, NEMMEN *Nemophila menziesii*, STARIG *Stachys rigida*, TOXFRE *Toxicodendron fremontii*, TRIMIC *Trifolium microcephalum*, TRIMIC2 *Trifolium microdon*. Final stress of three dimensional solution = 0.166 after 24 iterations.

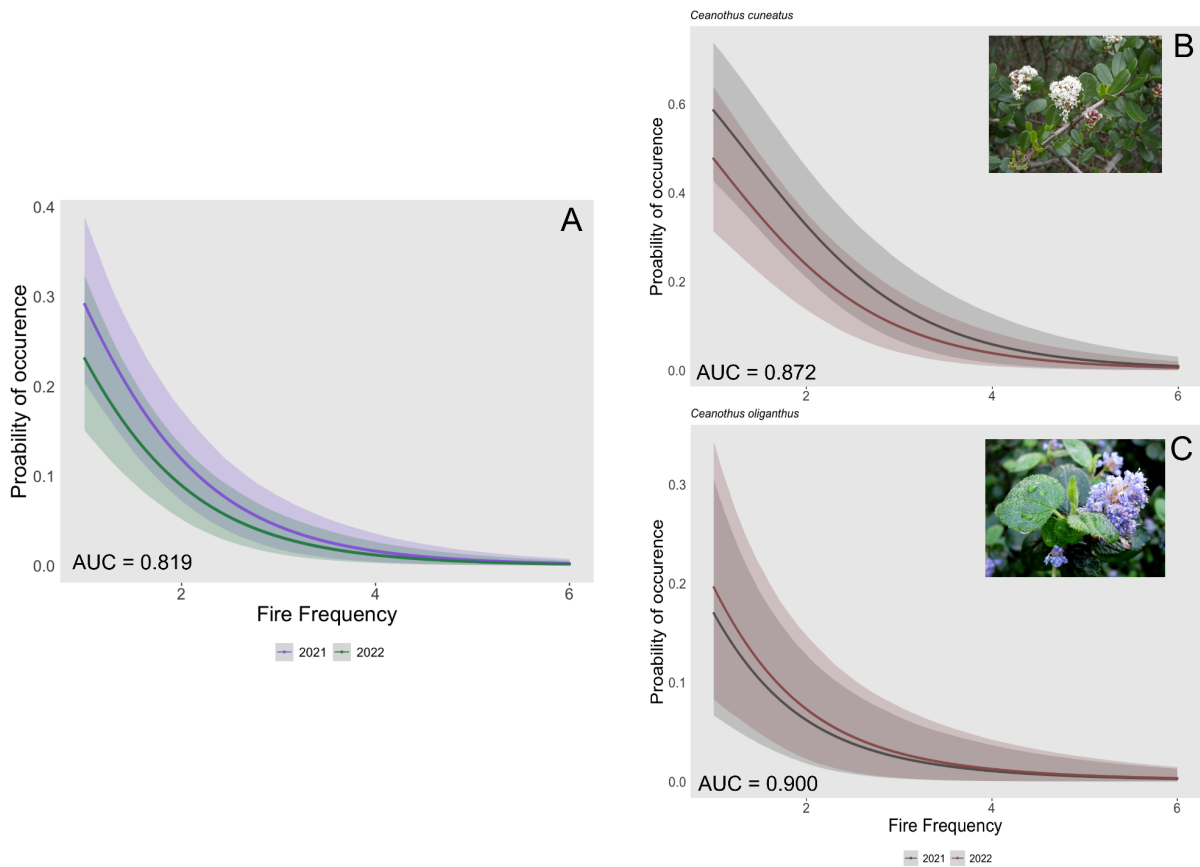


Fig 1.5: The probability of occurrence of an obligate seedling (A), including *Ceanothus cuneatus* (B) and *Ceanothus oliganthus* (C), declines with increased fire frequency in both survey years (2021 & 2022). The probability of occurrence is the presence of at least one seedling in the 250m² plot. Error bars show 95% CIs. The area under the receiver operating curve (AUC), a measure of model accuracy ranging from 0-1, noted in the bottom left.

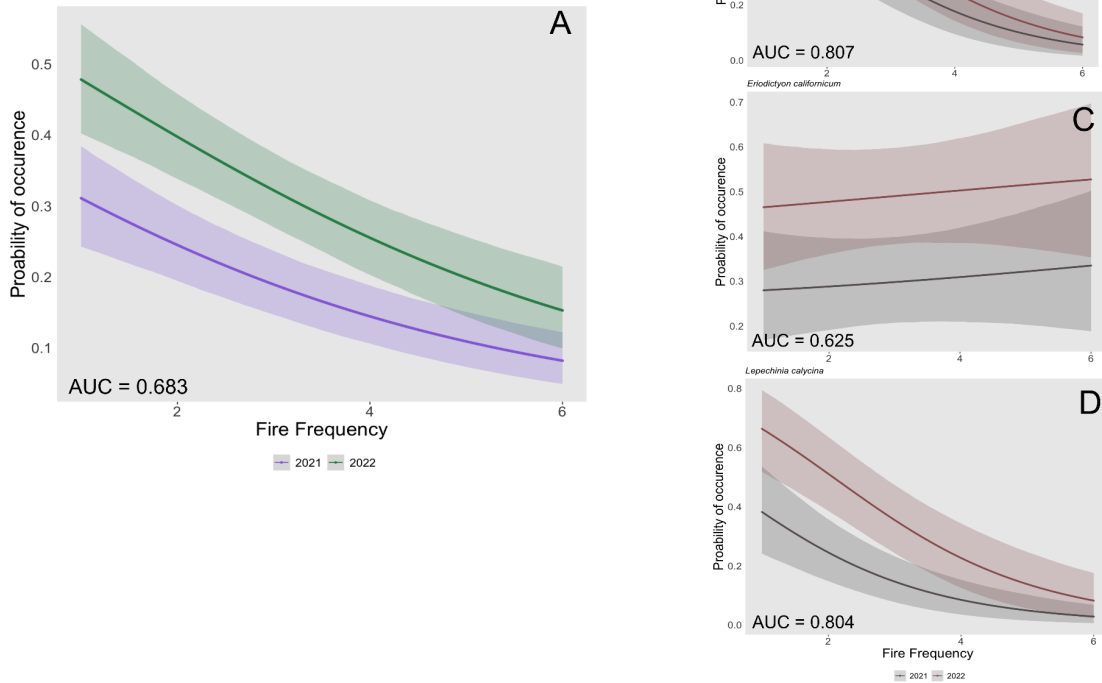


Fig 1.6: The probability of occurrence of a facultative seedling (A) declines with increased fire frequency in both survey years (2021 & 2022). This relationship was species-dependent, and fire frequency had little change on the probability of occurrence of an *Eriodictyon californicum* seedling (C) but decreased the probability of occurrence for *Adenostoma fasciculatum* (B) and *Lepechinia calycina* (D) seedlings. The probability of occurrence is the presence of at least one seedling in the 250m² plot. Error bars show 95% CIs. The area under the receiver operating curve (AUC), a measure of model accuracy ranging from 0-1, is noted in the bottom left.

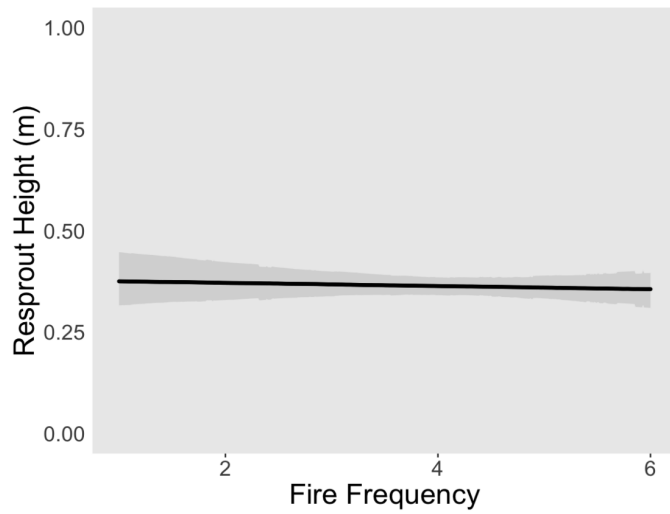


Fig. 1.7: Resprout height (m) of *Adenostoma fasciculatum* does not significantly change with increased fire frequency. Error bars show 95% CIs. Picture of *Adenostoma fasciculatum* individual that has experienced 3 short interval fires in the past 30 years.

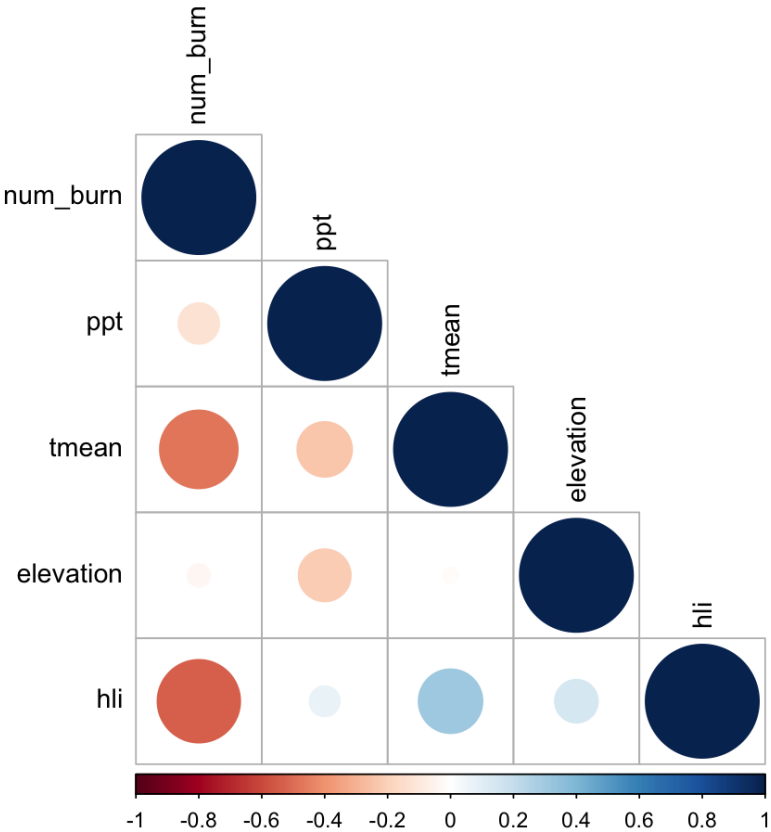
Table 1.1: Description of all study sites included in the analysis.

Site	Jurisdiction	Fire History (since 1980)	Shortest interval between fire	Fire frequency (since 1985)
Bobcat Ranch	Audubon Canyon Ranch	2020 (Hennessey), 2018 (County), 2016 (Cold), 2014 (Monticello), 2007 (Braye)	2	3,4,5
Quail Ridge	UC Natural Reserve	2020 (Hennessey), 2005 (Pleasure)	15	1,2
Cold Canyon	UC Natural Reserve	2020 (Hennessey), 2015 (Wragg), Miller (1988)	5	3
Cache Creek	BLM	2020 (Hennessey), 2012 (sixteen complex), 2004 (Rumsey), 2002 (Sixteen), 1999 (Rumsey), 1987 (Haswell)	2	1,6

Table 1.2: Fire severity (mm) (\pm SE), which is inversely related to the diameter of the measured stem termini, across fire frequency gradient.

Fire frequency	1	3	4	5	6
Mean fire severity (mm)	1.17 \pm 0.24	0.24 \pm 0.03	0.13 \pm 0.01	0.22 \pm 0.02	0.32 \pm 0.02
Coefficient of variation in mean fire severity (%)	88.1	40.6	21.1	28.9	18.3
Maximum fire severity (mm)	2.45 \pm 0.48	0.49 \pm 0.07	0.21 \pm 0.03	0.40 \pm 0.04	0.47 \pm 0.02
Coefficient of variation in max fire severity (%)	83.3	50.0	54.4	19.7	12.0

Supplemental Figures



Supplemental Figure 1.1: Correlation plot of covariates included in this analysis. Spearman's Rank Correlation Coefficients

Supplemental Table 1.1: Model summary for Bayesian model fit for the proportion of native species cover, proportion of native species richness, and proportion of native Shannon diversity.

Native Species Cover	Estimate	Est.Error	Lower 95% CI	Upper 95% CI	Rhat	Bulk_ESS
Intercept	2.54	0.42	1.72	3.33	1.00	2335
Num_burn	-1.17	0.26	-1.67	-0.67	1.00	2165
Num_burn ²	0.12	0.04	0.04	0.19	1.00	2200
2022 SurveyYear	-0.49	0.17	-0.83	-0.16	1.00	4612

Native Species Richness	Estimate	Est.Error	Lower 95% CI	Upper 95% CI	Rhat	Bulk_ESS
Intercept	1.39	0.30	0.81	1.98	1.00	1596
Num_burn	-0.50	0.18	-0.86	-0.15	1.00	1484
Num_burn ²	0.06	0.03	0.01	0.11	1.00	1439
2022 SurveyYear	-0.18	0.11	-0.40	0.04	1.00	2856

Native Shannon Diversity	Estimate	Est.Error	Lower 95% CI	Upper 95% CI	Rhat	Bulk_ESS
Intercept	1.56	0.41	0.77	2.40	1.00	2615
Num_burn	-0.65	0.25	-1.14	-0.16	1.00	2523
Num_burn ²	0.08	0.04	0.01	0.15	1.00	2535
2022 SurveyYear	-0.23	0.13	-0.49	0.02	1.00	6148

Chapter 2: Fuel treatment effects on fuel loads in western US dry conifer forests: a meta-analysis

Ashley R. Grupenhoff,^{1*} Derek J. N. Young,² Michele Barbato,³ Andrew M. Latimer²

¹Department of Environmental Science and Policy, University of California, Davis, California 95616, USA

²Department of Plant Sciences, University of California, Davis, CA 95616, USA

³Department of Civil & Environmental Engineering, University of California, Davis, CA 95616 USA

Abstract

Background

Fuel treatments are vital tools for reducing wildfire hazard, and their use has expanded in response to the increasing risk and occurrence of severe wildfires across western dry conifer forests. A number of systematic reviews have documented the effectiveness of fuel treatments in reducing future wildfire severity, yet few have synthesized the evidence on how treatments affect multiple dimensions of fuel loads across the western United States (US). Focusing on western US dry conifer forest types, we conducted a meta-analysis using 1,932 observations from 65 published papers to (1) test the effect of different fuel treatment types on fuel loads, and (2) synthesize patterns of post-treatment fuel loads.

Results

Overall, fuel treatments reduced fuel loads across western US dry conifer forest types; however, this effect varied across fuel treatment types. Treatments including thinning followed by prescribed fires (THIN+BURN), when compared to treatments including only thinning (THIN) and prescribed fires (BURN), were the most successful in reducing overstory fuel loads while simultaneously mitigating the build up of surface fuels after thinning. BURN treatments, despite having limited impact on overstory fuels, were the most effective at reducing surface fuel loads even after a single entry. Post-treatment fuel conditions, although not significantly related to forest type, were influenced by starting stand conditions that interacted with fuel treatment.

Conclusions

Our findings underscore the effectiveness of fuel treatments in altering fuel loads across different forest types, with treatment type and initial stand conditions being key factors influencing outcomes. The success of fuel treatments, especially in landscapes with heavy fuel loads, highlights their potential as a valuable tool in managing fire risk and restoring forest health. In synthesizing post-treatment fuel data, we provide vital information for improving fire behavior predictions and wildfire management strategies in response to future climate change.

Keywords: *Fuel treatment, fuel loads, meta-analysis, wildfire*

Introduction

Dry conifer forests in the western US have experienced a massive increase in the annual average area burned by wildfire, driven primarily by a shift to warmer and drier conditions and fuel accumulations linked to a century or more of fire exclusion (Westerling 2018; Abatzoglou et al. 2021). Consequently, these conditions have resulted in fuel loads that far exceed historical levels and forests with a more homogeneous composition and structure (Hessburg et al. 2005; Stephens et al. 2012b; Hessburg et al. 2016). This altered forest landscape has given rise to uncharacteristically large and severe ‘megafires’ that are detrimental to biodiversity, ecosystem and human health, and the economy (Lohman et al. 2007; Steel et al. 2022, 2023; Weeks et al. 2023; Williams et al. 2023). To address these issues, fuels treatments such as prescribed fire, hand thinning, and mechanical surrogates (e.g., woody debris removal and/or mechanical thinning) have been implemented to restore forest resilience by reducing surface and canopy fuel loads, thereby mitigating the potential impact of future wildfires (Agee and Skinner 2005; Stephens et al. 2012b).

Areas treated with fuel reduction methods have been shown to experience lower fire severity compared to untreated stands in similar weather conditions (Safford et al. 2012; Martinson and Omi 2013; Prichard et al. 2020). However, different fuel treatments can have varied effects and effectiveness over time. These outcomes are dependent on factors such as site productivity and rate of fuel accumulation (Prichard et al. 2017), which can alter treatment longevity (Vaillant et al., 2015). Having a more accurate quantitative picture of resulting changes in fuel attributes after treatment will aid in modeling the effects of fuel treatments on fire behavior and informing wildfire management strategies in response to changing environmental conditions.

Despite the expanding use of fuel treatments, significant gaps exist in our understanding of the dynamic change in fuels after treatment, and of the role of fuels in fire spread and growth (Omi, 2015). To address these knowledge gaps, there has been a growing emphasis on examining the ecological implications of different fuel treatment options. One notable example is the Fire and Fire Surrogate (FFS) study, a long-term experiment evaluating the effects and effectiveness of mechanical thinning and prescribed burning for reducing fuels across western US forest types that historically experienced frequent, low-to-moderate intensity fires (Schwilk et al., 2009; Stephens et al., 2009; Weatherspoon and McIver, 2000). Whereas the FFS study provides invaluable information on how effective fuel treatments are in reducing fuels, meta-analyses complement such experiments by compiling published evidence across broader areas and forest types while incorporating a wider range of observational and experimental studies.

A limited number of reviews have previously examined the effects of thinning and burning treatments in mitigating subsequent fire intensity and restoring natural fire behavior in western dry conifer forests (Fulé et al. 2012; Martinson and Omi 2013; Ott et al. 2023). Fulé et al. (2012), for example, examined how fuels treatments restore natural fire behavior and Martinson and Omi (2013) examined the effect of fuel treatments on subsequent fire intensity and severity in western US forests. While these reviews show that fuel treatments effectively restore low-severity fire behavior, they do not synthesize empirical post-treatment fuel data. We expand on these reviews by including more recent studies and focus primarily on empirical data rather than modeled fire behavior. The goals of the present meta-analysis are first to test the effectiveness of different treatment types in reducing fuel loads, and second to quantify post-treatment fuel loads in treated areas. Specifically we ask: (1) How effective are fuel treatments in reducing fuels? (2) What is the state of fuels after fuel treatments? (3) Are post-treatment fuel levels influenced by pre-treatment stand conditions or forest type?

Methods

Literature search

We conducted a literature search following the steps suggested by Harrer et al. (2021). We searched the Web of Science database on February 7, 2022, for papers that included all combinations of the following search terms: fuel load, duff load, litter load AND fuels treatments, thinning, prescribed burning, managed wildfire AND western forests, mixed conifer, yellow-pine, pine-oak, ponderosa pine, Jeffrey pine, dry conifer forests. We selected studies that met the following criteria:

1. Studies were located in western dry forests of the US dominated by ponderosa pine (*Pinus ponderosa*), Jeffrey pine (*Pinus jeffreyi*), pine-oak (*Quercus* spp.), mixed-conifer, or Douglas-fir (*Pseudotsuga menziesii*).
2. Fuel treatments included thin-only, burn-only (prescribed fire or managed wildfire), mastication only, thin and burn, or mastication and burn, since these are overwhelmingly the most common treatments applied in these forests.
3. The study design included control-impact (CI), before-after (BA), and before-after control-impact (BACI) studies. We excluded studies that lacked controls or pre-treatment data.
4. The study measured one or more of the following outcome variables, which are important for modeling fire behaviors: tree density, tree basal area, canopy cover, canopy bulk density, canopy base height, surface fuels (1, 10, 100-hour fuels, coarse woody debris (CWD), litter, and duff), vegetation cover (shrub and herbaceous), seedling density, sapling density, snag density, and snag basal area.

After removing duplicates, we scanned the abstracts of the remaining 406 papers and removed papers that did not fit our inclusion criteria, leaving 65 papers that were included in the analysis. Generally, discarded papers had the wrong treatment effect (effect of wildfire or forest pests/pathogens), wrong outcome variables (no post-treatment fuels data given), or post-treatment fuels data that were simulated based on pre-treatment fuels. Although simulated studies can test treatment effectiveness in areas in which direct experimentation with fuel treatments may be difficult, we omitted these studies since one of our goals was to synthesize empirical observations of post-treatment fuel loads.

Data extraction

Fuel load means, standard deviations, and sample sizes across different treatment groups were extracted from each study that met the inclusion criteria previously described. In addition to recording fuel loads and the associated fuel treatment conducted, we noted site characteristics including forest type, ecoregion, time since treatment, prior history, and management jurisdiction. In cases in which summary statistics were not documented, we extracted data using `WebPlotDigitizer v. 4.3` (Rohatgi 2022). Using plot locations noted in the study, we extracted the ecoregion using the ‘Terrestrial Ecoregions of the World’ dataset in R (Dinerstein et al. 2017). Ecoregions denote useful boundaries that incorporate distinct biogeographic assemblages and ecological habitats. We noted methodological variables that could affect the outcome of the study (before-after, control-treatment), the size of the plot, and sample size. For the purpose of this analysis, we broadly categorized studies into treatments:

1. “BURN RX” - prescribed fires that were low-to-moderate severity and had little to no overstory mortality (N = 45 papers)

2. “BURN MW” - managed wildfires that were low-to-moderate severity and had little to no overstory mortality (N = 3 papers)
3. “THIN” - small to intermediate diameter trees were removed (N = 33 papers)
4. “MAST” - mastication, i.e., vegetation was chopped, ground, or chipped and left on soil surface (N = 3 papers)
5. “THIN+BURN” - thinning was conducted followed by prescribed fire (N = 31 papers)
6. “MAST+BURN” - mastication was conducted followed by low-to-moderate severity burning (N = 1 paper)
7. “THIN+MAST” – thinning was conducted followed by mastication (N = 1 paper)
8. “FULL” - a combination of thinning, mastication or raking fuels, and low-to-moderate severity prescribed fire (N = 3 papers)

To quantify untreated fuel loads, some studies used values measured prior to treatment in the plots that were ultimately treated, some used values measured in control plots at the same time (post-treatment) when the treated plots were measured, and some included both. To represent untreated fuel loads, we used values measured prior to treatment when available and values measured at control plots otherwise. Our assessments of treatment effects compare reported untreated fuel loads (as previously defined) against reported post-treatment fuel loads.

Meta-analysis

To examine the change in fuel loads due to treatments, we summarized the absolute and relative change in fuel loads across forest types and ecoregions. Given the limited number of studies examining fuel loads after treatments involving MAST or BURN_MW, we include only BURN_RX (henceforth, BURN), THIN, and THIN+BURN in this analysis. We used a response ratio (*RR*) for our effect size calculation, which is designed to measure relative differences and

is more appropriate for our questions of interest than the commonly-used Hedges' g (Hedges and Olkin 2014) because it allows for calculating the magnitude and significance of an overall effect across studies (Hedges et al. 1999; Mosquera et al. 2000). The metric we used is defined as:

$$\ln(RR) = \ln\left(\frac{x_A}{x_B}\right) \quad (1)$$

in which $\underline{x_A}$ is the post-treatment fuel load mean and $\underline{x_B}$ is the untreated fuel load mean.

Negative values indicated studies in which the fuel treatment reduced the fuel load. Positive values indicate studies in which the fuel treatment led to a higher fuel load. The natural logarithm could not be calculated when the mean value for any of the treatments or untreated fuel loads was zero. In these cases, we substituted zero with the minimum possible value (e.g., 0.0 Mg/ha surface fuel load was replaced with 0.001 Mg/ha), similar to Thapa et al. (2018). More than one $\ln(RR)$ was calculated for one study in which multiple treatment types, forest types, and/or fuel variables were reported. These effect sizes were considered as independent observations. In some cases, multiple fuel treatments shared the same untreated value (no fuel treatment), leading to non-independence. To account for this situation, we created a Bayesian hierarchical model with treatment type as a fixed effect and a random intercept that varied by study (Bürkner 2017; McElreath 2020).

We used the `brm` function in the `brms` package (Bürkner 2017) in R version 4.1.1 (R Core Team 2021) to fit a mixed-effects model for each fuel variable with $\ln(RR)$ as the response variable, *treatment type* as a fixed effect, and two random effects: (i) *study ID*, to control for non-independence among fuel load values from the same study; and (ii) *forest type*, to account for variation in pre-treatment fuel accumulation across different forest types (Equation 2).

In a meta-analysis, individual effect sizes are typically weighted by the inverse of the sampling variance to increase the weight of studies with greater precision. Many studies

included in this analysis did not report information on within-study variability (standard error or standard deviation). To include these studies, we used an alternative weighting scheme (w) that uses experimental replications (Adams et al. 1997; Basche and DeLonge 2017; Thapa et al. 2018). Effect size weights were incorporated into the model by combining the number of experimental replicates with their estimated effect size using the se function (Bürkner 2017). For interpretation, $\ln(RR)$ values were back-transformed to mean effect sizes ($RR = e^{\ln(RR)}$) and expressed as percentage change in fuel load due to fuel treatment, ΔFL , as follows:

$$\Delta FL = 100 * (RR - 1) \quad (2)$$

We used a similar modeling procedure to predict post-treatment fuel loads across various starting fuel conditions and forest types. We fit post-treatment fuel load using multiple Bayesian generalized linear models for each fuel variable, with *treatment type* and *untreated fuel load* as fixed effects, and two random effects: (i) *study ID*, to control for non-independence among fuel load values from the same study; and (ii) *forest type*, to account for variation in pre-treatment fuel load across different forest types (Bürkner 2017; McElreath 2020).

For all models, we specified normal prior distributions for the true pooled effect size (μ) and a half-Cauchy distribution with a mean of 0 and a standard deviation of 2 for the between-study heterogeneity (τ). We used these half-Cauchy parameters to reflect high levels of between-study heterogeneity (McElreath 2020). Each model was run for 5000 iterations following a warm-up period of 1000 iterations (which was discarded for the analysis). Convergence was checked with Gelman-Rubin diagnostics based on posterior predictive checks and inspection of the potential scale reduction factor (\hat{R}) values of the parameter estimates (Gelman and Rubin 1992). We considered the treatment effect to be significantly different from zero if the 95% confidence interval did not cross zero (McElreath 2020).

Detection of publication bias

Publication bias is generally assessed using funnel plots that compare effect sizes and sampling variances to check for asymmetry in the data (Egger et al. 1997). However, since sampling variances were not available in some of the studies included, we indirectly evaluated bias toward publishing positive or negative results using histograms of the individual effect sizes (Basche and DeLonge 2017; Thapa et al. 2018). Histograms of the overall effect size estimates showed equal distribution between slightly positive and slightly negative values, suggesting that the effects of publication bias are negligible (Fig. S2.1).

Results

Studies quantifying change in fuel load due to treatment

Our literature search incorporated many studies that quantified the change in fuels after a variety of fuel treatments across dry conifer forests in the western US (Fig. 2.1). We found a total of 65 published papers, representing 95 distinct studies out of 406 (16%) papers found in the literature, which met our search criteria and had quantitative data suitable for a meta-analysis. Figs. 2.2 and 2.3 report the number of studies that quantify the fuel state in terms of different fuel variables (Fig. 2.2), fuel treatment methods (Fig. 2.3A), and western US dry forest types (Fig. 2.3B). It is noteworthy that several studies evaluated more than one fuel variable, forest type, and treatment type; thus, they are counted multiple times in Figs. 2.2 and 2.3. 94% (61/65) of relevant publications were published after 2000. Sierra mixed conifer and yellow pine forests were the predominant forest types, with each accounting for 32% (21/65) of papers (Fig. 2.3B). Most articles quantified fuel loads at short time scales, with 92% (60/65) of articles considering observations between 0-4 years post-treatment and only 6.2% (4/65) quantifying fuel loads after over 20 years post-treatment (Fig. 2.4). We retrieved a total of $N = 1,971$ effect sizes $\ln(RR)$, most of which came from studies that compared pre-treatment to

post-treatment fuel loads ($n = 1224$, where n denotes the number of observations), with median time between pre-treatment and treatment measurement of 1 year, and median time between treatment and post-treatment measurement of 1 year. Other effect sizes were calculated from control sites ($n = 747$). Forest structure variables were the most frequently reported, with 10% ($n = 200$) of the total observations representing tree density and 7% ($n = 140$) representing basal area. Woody surface fuel load also had a high frequency of observations, with 1-hour fuel loads comprising 5% of observations ($n = 90$), 10-hour fuel loads at 5% ($n = 96$), 100-hour fuel loads at 6% ($n = 114$), and 10% representing CWD ($n = 195$).

Effectiveness of fuel treatments in reducing fuel loads

The most commonly reported forest structure (or “overstory fuel”) variables, including tree density, basal area, canopy bulk density (CBD), canopy base height (CBH), and canopy cover, were significantly reduced in both THIN and THIN+BURN treatments; however, they were not as significantly reduced in BURN treatments (Fig. 2.5A, Table S2.2). On average THIN+BURN treatments strongly reduced all overstory fuel variables, i.e.: tree density by 73%, with $\ln(RR) = -1.32$ and 95% credible intervals (CIs) = -1.59 to -1.06; basal area by 46%, with $\ln(RR) = -0.61$ and CIs = -0.76 to -0.46; canopy bulk density by 56%, with $\ln(RR) = -0.83$ and CIs = -1.18 to -0.48; and canopy cover by 39%, with $\ln(RR) = -0.50$ and CIs = -0.83 to -0.17. The effect of THIN treatments was less substantial than THIN+BURN treatments, but they still reduced tree density by 59%, with $\ln(RR) = -0.90$ and CIs = -1.18 to -0.61; basal area by 41%, with $\ln(RR) = -0.53$ and CIs = -0.74 to -0.31; canopy bulk density by 55%, with $\ln(RR) = -0.79$ and CIs = -1.19 to -0.43; and canopy cover by 26%, with $\ln(RR) = -0.30$ and CIs = -0.63 to 0.05. The lowest confidence was found for the canopy cover treatment effect, for which the credible interval includes zero (i.e., no statistically significant effects). Canopy base height (CBH), which is inversely related to the amount of canopy fuel available to propagate fire vertically into the

upper canopy, significantly increased in THIN+BURN treatments by 115%, with $\ln(RR) = 0.76$ and CIs = 0.24 to 1.29, and in THIN treatments by 79%, with $\ln(RR) = 0.58$ and CIs = 0.16 to 1.00. BURN treatments had little to no effect on canopy cover and canopy bulk density; however, they significantly reduced tree density by 32%, with $\ln(RR) = -0.39$ and CIs = -0.66 to -0.14, and marginally reduced basal area by 8%, with $\ln(RR) = -0.08$ and CIs = -0.16 to -0.02. CBH moderately increased by 40% in BURN treatments with $\ln(RR) = 0.34$, and CIs = -0.03 to 0.72.

Surface fuels showed an opposite pattern to that of overstory fuel loads, with moderate to significant reduction in BURN treatments, slight increases in THIN treatments, and moderate reduction in THIN+BURN treatments (Fig. 2.5B, Table S2.2). BURN treatments significantly reduced litter and duff load by 69%, with $\ln(RR) = -1.17$ and CIs = -1.69 to -0.56; 100-hour fuels by 56%, with $\ln(RR) = -0.82$ and CIs = -1.15 to -0.45; and rotten CWD by 90%, with $\ln(RR) = -2.26$ and CIs = -3.43 to -0.92. Conversely, the reduction in sound CWD, 10-hour fuels, and 1-hour fuels after BURN treatments was not statistically significant (Table S2.2). THIN treatments exhibited varying effects. They substantially increased rotten CWD, with $\ln(RR) = 2.01$ and CIs = -0.85 to 4.96 which indicates a considerable variability and low confidence as the CIs crossed zero. They also resulted in slight increases of 100-hour fuels by 36%, with $\ln(RR) = 0.31$ and CIs = -0.25 to 0.86; 10-hour fuels by 31%, with $\ln(RR) = 0.27$ and CIs = -0.38 to 0.91; and sound CWD by 108%, with $\ln(RR) = 0.73$ and CIs = -0.63 to 2.04, although these results were not statistically significant. Additionally, slight non-significant reductions were noted in 1-hour fuels, with $\ln(RR) = -0.39$ and CIs = -1.31 to 0.61; and in litter/duff, with $\ln(RR) = -0.35$ and CIs = -1.31 to 0.63. For THIN+BURN treatments, minimal effects were observed on most surface fuel variables, except for a substantial but statistically non-significant 69% reduction in litter and duff, with $\ln(RR) = -1.18$ and CIs = -2.36 to 0.04.

Effects of starting fuel conditions and forest type on post-treatment fuel loads

Fuel treatments reduced tree density and basal area relative to untreated stands. However, the relative differences in post-treatment fuel loads among THIN, BURN, and THIN+BURN treatments depended greatly on the starting fuel conditions (Fig. 2.6). We found that the starting conditions and fuel treatment interacted to affect post-treatment tree density and basal area (Fig. 2.6). The effect of untreated tree density on post-treatment tree density alone was positive ($\beta_{\text{control_fuel_load}} = 0.60$, CIs = 0.49 to 0.70), but the interaction between starting stand conditions and post-treatment tree density varied with fuel treatment method such that THIN+BURN ($\beta_{\text{control_fuel_load:thin+burn}} = -0.56$, CIs = -0.63 to -0.50) and THIN ($\beta_{\text{control_fuel_load:thin}} = -0.16$, CIs = -0.22 to -0.10) treatments were more likely to have a greater effect on reducing tree density than BURN treatments at higher initial stand densities (Fig. 2.6A, 2.7A). Similarly, the effect of untreated basal area on post-treatment basal area was positive ($\beta_{\text{control_fuel_load}} = 1.31$, CIs = 1.19 to 1.44); however, unlike tree density, the interaction with fuel treatment was similar across all fuel treatments (Fig. 2.6B, 2.7B).

Models with random effects for forest type were better at predicting post-treatment tree density ($R^2 = 0.80$) and basal area ($R^2 = 0.94$); however there were only slight differences in post-treatment overstory fuels across forest types (Fig. 2.8). Statistically significant differences were observed in post-treatment tree density between forest type after THIN and BURN treatments ($Pr = 0.95$), but no statistically significant differences were observed after THIN+BURN treatments (Fig. 2.8A). Post-treatment basal area was similar across all forest types except for the Sierra mixed conifer forest type, which had a significantly higher post-treatment basal area than all other forest types (Fig. 2.8B; $Pr = 0.95$).

Surface fuels showed a reduction in both BURN and THIN+BURN treatments when compared to untreated stands across all fuel variables, but an increase in THIN treatments. Similar to overstory fuels, starting fuel conditions and fuel treatment interacted to affect post-treatment fine and CWD (Fig. 2.9). The effect of both untreated CWD and fine woody

debris (FWD) on their post-treatment counterparts alone was positive (CWD: $\beta_{\text{control_fuel_load}} = 0.33$, CIs = 0.27 to 0.39; FWD: $\beta_{\text{control_fuel_load}} = 1.41$, CIs = 1.36 to 1.48), but this effect varied with fuel treatment such that BURN and THIN+BURN treatments had a greater effect on reducing CWD and FWD at higher initial fuel loads (Fig. 2.9, 2.10, Tables S2.4-2.5).

Post-treatment surface fuel loads varied slightly across forest types. Models with a random effect for forest type were better at predicting post-treatment CWD ($R^2 = 0.77$) and FWD ($R^2 = 0.89$). CWD and FWD were not significantly different across all forest types after BURN and THIN+BURN treatments, but significant differences were observed after THIN treatments (Fig. 2.11; $P = 0.95$). CWD load in Sierra mixed conifer forest types was moderately higher than in yellow pine, rocky mountain mixed conifer, and pacific northwest (PNW) mixed conifer forest types after thinning (Fig. 2.11A). FWD, on the other hand, was moderately higher in yellow pine forest types after thinning (Fig. 2.11B).

Discussion

This meta-analysis aims to document and synthesize patterns in fuel dynamics after fuel treatments across western US dry conifer forests characterized by historically frequent fire regimes. Our results show that, in general, fuel treatments reduced fuel loads across western US dry forest types. Consistent with prior literature, this effect depended on treatment type and the fuel variable in question (Fulé et al. 2012; North et al. 2012; Martinson and Omi 2013; Omi 2015; Ott et al. 2023). Furthermore, our findings underscore the role of starting stand conditions, which interact with fuel treatments to influence resulting post-treatment fuel loads. In our analysis of 65 publications that met our criteria, we observed significant reductions in the most commonly reported overstory fuels following THIN and THIN+BURN treatments. Notably, THIN treatments exhibited the highest levels of surface fuel load among all treatment types, leading to surface fuel loads that were on average higher than control fuels loads, although with high

variability. Conversely, BURN treatments yielded significant reductions in surface fuels, but had a smaller impact on overstory fuels, although they did substantially reduce tree density. Fuel treatments demonstrate successful reduction in fuel loads, but this study shows the intricate interplay between treatment type, starting conditions, and the resulting changes in fuel components.

Effectiveness of fuel treatments in reducing fuels

Fuel treatments are, in part, designed to reduce crown fire potential, which is dependent primarily on canopy fuels and canopy base height (van Wagner 1977). While THIN+BURN and THIN treatments had the greatest effect on reducing overstory fuel loads, BURN treatments demonstrated smaller effects on overstory fuel variables, with the exception of tree density. Generally, smaller and shorter trees with thinner bark are the most vulnerable to low- to moderate-severity prescribed fire, which is why we see this significant reduction in tree density but a limited reduction in basal area and canopy bulk density (Hood et al. 2007; Hurteau and North 2009; Jain et al. 2012).

While previous research has demonstrated that BURN treatments can substantially reduce overstory fuels (Youngblood et al. 2008; Battaglia et al. 2008), the effectiveness of these treatments is highly influenced by factors such as weather conditions, fuel moistures, and initial stand conditions (Jain et al., 2012). Additionally, mortality thresholds can vary depending on the tree species involved (Hood et al. 2007). While multiple-entry burns can hold potential for reducing overstory fuel loads and restoring historic stand structures for fire hazard mitigation, THIN+BURN and THIN treatments are currently the most effective option for reducing overstory fuels in a single entry. Despite the effectiveness of some prescribed fire programs across the western US, there remain several limiting factors preventing their widespread use at meaningful levels. These factors include concerns related to risk, resource limitations, and regulatory constraints (Miller et al. 2020; Williams et al. 2023).

Fuel treatments also aim to reduce surface fuels, thereby lowering fireline intensity and diminishing the likelihood of crown fire (Agee and Skinner, 2005; Stephens et al., 2009). Despite successful reductions in overstory fuel loads, THIN treatments led to a slight increase in surface fuel loads. Conversely, BURN treatments were the most successful in reducing fine and coarse woody surface fuels when compared to both THIN+BURN and THIN treatments. As with overstory fuels, this effect depended on the fuel variables and fuel treatment used. Rotten CWD was significantly and substantially reduced by BURN treatments, but sound CWD was minimally and non-significantly reduced. This result could be explained by the higher level of combustibility and consumption of rotten CWD (Hyde et al. 2011, 2012). Rotten logs have a lower heat conductivity and oxygen availability, key factors in smoldering consumption (Carvalho et al. 2002; Hyde et al. 2012). Conversely, THIN treatments moderately increased most fine and coarse woody fuels except for litter, duff, and 1 hour fuel loads. Mechanical thinning produces FWD and CWD as a byproduct, typically increasing surface fuel loads at least over the short term (Agee and Skinner 2005; Johnston et al. 2021). The lower levels of litter, duff, and 1-hour fuels in thinned areas may result from higher decomposition rates produced by aerating the duff layer and mixing it with mineral soil (Johnston et al. 2021). It is important to note that the pattern of changes to different surface fuel pools is likely influenced by the specific harvesting method employed (Chiono et al., 2012; Stephens and Moghaddas, 2005a), a factor that was not considered in our analysis. THIN+BURN effects were intermediate due in part to the combination of fuel accumulation after thinning and fuel consumption after burning. On net, THIN+BURN treatments tend to substantially (69%) reduce litter and duff levels, but do not consistently reduce fine and coarse woody surface fuel loads.

State of fuels after fuel treatments and influence of pre-treatment stand conditions and forest type

Our analysis revealed that post-treatment fuel loads were highest in stands with higher starting fuel loads, irrespective of the fuel treatment applied. The influence of starting fuel conditions on post-treatment fuels varied depending on fuel treatment and fuel variable. We observed a limited effect of starting fuel conditions on post-treatment tree density following THIN+BURN treatments, as well as on post-treatment CWD following BURN and THIN+BURN treatments. These findings suggest that such treatments can be effective in achieving a target tree density and CWD loading regardless of starting conditions, underscoring the benefit of investing in fuel treatments, particularly in landscapes characterized by heavy fuel loads. These results are consistent with previous research demonstrating the cost-effectiveness of different fuel treatment strategies, with significant positive impacts evident in landscapes with the highest fuel loads (Chew et al. 2003). It is noteworthy that, for some fuel variables (especially basal area), untreated fuel loads also varied substantially among treatment types. This variation may in part reflect the fact that managers usually rule out some treatment methods under certain pre-treatment conditions (e.g., BURN in a highly overstocked stand). This result emphasizes the importance of evaluating treatment effectiveness also in terms of a response ratio, which takes into account the relative changes in fuel variables as a result of a fuel treatment.

Consistent with other research, we found little variation in post-treatment fuel loads across forest types (Fulé et al., 2012; Stephens et al., 2009). The forest types included in this analysis are all western US dry conifer forests that were historically fuel limited systems and experienced frequent, low-to-moderate intensity fires (Swetnam and Baisan 1996; Metlen et al. 2018; Safford et al. 2021). Disruption to this historical fire regime due to fire suppression has occurred across all of these forest types, generally producing a shift to high surface fuel load, high tree density, and forest homogeneity (van Wagner 1977; Covington and Moore 1994; Swetnam et al. 1999; Wagtenonk 2018). In line with Fulé et al. (2012), we found that post-treatment fuels were more influenced by type of fuel treatment and starting fuel load than by forest type.

Beyond the data: additional fuel treatment effectiveness considerations

Due to the paucity of studies examining the state of fuel loads after mastication, managed wildfire, and multiple entry prescribed burns, we were unable to include these studies in the analysis. Mastication treatments – mechanical fuel treatments that chop, grind, or chip vegetation – reduce canopy and ladder fuels but result in an increase in surface fuels (Kane et al. 2006). Mastication followed by prescribed burning has been found to adequately reduce both canopy and surface fuel loads (Reiner et al., 2009; Stephens and Moghaddas, 2005a); however, there is a high degree of variability in post-mastication fuel load, leading to variable fire behavior during prescribed burns (Bradley et al. 2006; Kane et al. 2006), and the potential for severe burning in wildfires (Safford 2008). Wildfires managed for restoration (hereafter, managed wildfire) have also increased as a restoration option to reduce hazard fuels and restore historical spatial structure (Stephens et al. 2016). Generally, managed wildfires are more intense than first-entry prescribed fire, and are more likely to reduce canopy fuels in addition to surface fuels. Yet few empirical studies exist that quantify fuels after managed wildfire. Lastly, with extremely high surface and canopy fuel load, multiple entry treatments may be necessary for successfully reducing fuels to moderate levels (Peterson et al. 2003). More research is needed to understand variation in fuel loads after mastication, managed wildfire, and multiple entry prescribed fires.

In order to incorporate as many studies as possible, we did not parse the fine-scale variations in treatment design (e.g., type of harvest system used, spring vs. fall burn), which have been shown to influence the effectiveness of fuel reduction. For instance, Stephens et al. (2009) found that the type of harvest system used, along with the residual fuels left in the unit, significantly impacted the efficacy of thinning in reducing passive and active crown fire potential. Whole-tree harvesting typically results in fewer residual surface fuels when compared to other methods, such as helicopter yarding or harvester-forward operations (Agee and Skinner, 2005;

Stephens et al., 2009). Additionally, research has shown that early-season burns consume less fuel and have lower fire intensity than late-season burns, leading to higher post-fire fuels (Knapp et al. 2005, 2007). Lastly, a recent meta-analysis synthesizing simulation studies comparing treatment scenarios in North America found treatment extent, placement, size, prescription intensity, and timing to be important factors determining treatment effectiveness (Ott et al., 2023). Due to the lack of qualified studies incorporating these factors we were unable to include them in the analysis. Despite our inability to account for fine scale variation in fuel treatment characteristics, the fact that we were able to find strong effects of fuel treatments in reducing fuels suggest that coarse-scale treatment type definitions capture a significant amount of variation in outcomes.

Across all surface fuel variables, the effect of fuel treatment was highly variable. Almost all studies that quantified surface fuels used coarse-scale methods, such as Brown's transects, that are generally fast and simple to use (Brown 1974; Lutes et al. 2006) and moderately repeatable (Hazard and Pickford 1986). Although this method can be precise at a coarse scale, it can be highly variable among fuel size classes and among forest types (Sikkink and Keane 2008). CWD can be especially variable, and transect length is one of the main parameters affecting the precision of the estimate (Hazard and Pickford, 1986). Some treatment areas may require more transects to reduce variance.

Management implications

The results reported and analyzed in the present study corroborate and fortify the existing body of evidence supporting the effectiveness of fuel treatments in reducing fuel loads. Currently, fire exclusion in western US conifer forests has led to the accumulation of surface fuels and increased continuity of vertical and horizontal stand structure, subsequently increasing their susceptibility to high-severity wildfire (van Wagner 1977; Collins et al. 2011). Further,

ongoing climate change will likely exacerbate this issue as the fire season extends and these areas become warmer and drier (Westerling 2018; Stephens et al. 2020). The success of fuel treatments, especially in landscapes with heavy fuel loads, highlights their potential as a valuable tool in managing fire risk and restoring forest health. Generally, we found that, when compared to THIN and BURN treatments, THIN+BURN treatments are the best at reducing overstory fuel loads while simultaneously mitigating the build up of surface fuels after thinning. These findings corroborate the results from the Fire and Fire Surrogate study (Schwilk et al., 2009; Stephens et al., 2009; Weatherspoon and McIver, 2000). Whereas THIN treatments also decreased overstory fuels, albeit to a lesser extent than THIN+BURN treatments, they resulted in the highest surface fuel loads when compared to BURN and THIN+BURN treatments. Because decomposition is relatively slow in most of the non-coastal western US – especially in California, which mostly lacks summer precipitation (Safford and Stevens 2017) – higher fuel load plus annual accumulations can result in long-term increases in fire hazard in such stands. However, it is worth noting that a study at Blodgett Forest, in a wet part of the Sierra Nevada (1800 mm annual precipitation), showed that decomposition was sufficient to significantly reduce fine fuels to low fire hazard within 7 years after fuels treatment (Stephens et al. 2012a). Despite having limited impacts on overstory fuels, BURN treatments were most successful in reducing fine and woody surface fuels and resulted in the lowest levels of post-treatment surface fuel loads, while also reducing tree density.

These findings offer a nuanced perspective on how fuel treatments alter fuels, highlighting the importance of initial stand conditions while revealing a lesser importance of forest type. Accurate fuel load estimates are vital for wildland fire behavior prediction models (e.g., FLAMMAP, (Finney 2006)), emission models (e.g., FOFEM, (Reinhardt et al. 1997)), and smoke-dispersion models (e.g., BlueSky, (Larkin et al. 2009)), especially given the projected increase in severe wildfires due to a warming climate (Westerling 2018). The fuel load estimates

we compile and summarize here can be used for projecting efficacy under various future climate scenarios as well as predicting potential fire behavior and the effects of future wildland fires. Accurate pre- and post-treatment fuel data is indispensable for effective wildfire management strategies, and for comparing different treatment methods

Conclusion

This meta-analysis provides insights into fuel dynamics following fuel treatments in western US dry conifer forests with historically frequent fire regimes. Our findings underscore the effectiveness of fuel treatments in altering fuel loads across different forest types, with treatment type and initial stand conditions being key factors explaining outcomes given current management approaches. Our results strongly suggest initial THIN+BURN treatments for maximum effectiveness in reducing overstory fuels; however, BURN treatments were the most successful at reducing surface fuels, whereas THIN treatments tend to increase surface fuel loads. Additionally, our study highlights the importance of considering initial fuel loads when predicting treatment impacts, as post-treatment fuel levels were highest in stands with heavier initial fuel loads. This effect, however, varied depending on fuel treatment and fuel variable. The dependence on initial conditions highlights the need for future treatments to use more intensive prescriptions in more fuel-loaded stands for a given target post-treatment fuel load. Consistent with other research, fuel treatment effectiveness was not significantly influenced by forest type.

Despite the extensive body of literature supporting fuel treatment effectiveness, there is a need for more empirical post-treatment fuel data to complement simplified fire behavior models used in simulation studies. Such data are vital for more accurate fire behavior predictions and to inform wildfire management strategies in response to changing environmental conditions with future climate change. In some places, there is a need for more intensive fuel treatment data collection and standardization of methods. Our study also identifies the need for further research on other fuel treatment options, such as mastication, managed wildfire, and

multiple entry prescribed burns, which were not adequately represented in the analyzed studies. Overall, we provide critical insights into fuel treatment effectiveness, which can be instrumental in mitigating wildfire risk and restoring forest health in western US dry conifer forests. Further research and refinement of fuel treatment strategies are essential in effectively managing these ecosystems in the face of increasing wildfire risks and changing environmental conditions.

Acknowledgements

The authors gratefully acknowledge the support by the University of California Office of the President (UCOP) Lab Fees program through award LFR-20-651032, and by the Electric Power Research Institute, Inc. (EPRI) through award DKT200194. We thank Wesley Brooks for statistical advice and Brandon Collins and Hugh Safford for reviewing this manuscript. Any opinions, findings, conclusions, or recommendations expressed in this publication are those of the writers and do not necessarily reflect the views of the sponsoring agencies.

Authors' contributions

AL, DY, and MB conceived the research idea and AG, AL, and DY designed methodology. AG compiled, analyzed, interpreted the data, and wrote the first draft of the manuscript. All authors contributed to and approved the final manuscript.

Literature Cited

- Abatzoglou JT, Battisti DS, Williams AP, et al (2021) Projected increases in western US forest fire despite growing fuel constraints. *Commun Earth Environ* 2:227.
<https://doi.org/10.1038/s43247-021-00299-0>
- Adams DC, Gurevitch J, Rosenberg MS (1997) Resampling Tests for Meta-Analysis of Ecological Data. *Ecology* 78:1277–1283.
[https://doi.org/10.1890/0012-9658\(1997\)078\[1277:RTFMAO\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1997)078[1277:RTFMAO]2.0.CO;2)
- Agee JK, Lolley MR (2006) Thinning and Prescribed Fire Effects on Fuels and Potential Fire Behavior in an Eastern Cascades Forest, Washington, USA. *Fire Ecol* 2:3–19.
<https://doi.org/10.4996/fireecology.0202003>
- Agee JK, Skinner CN (2005) Basic principles of forest fuel reduction treatments. *For Ecol Manag* 211:83–96. <https://doi.org/10.1016/j.foreco.2005.01.034>
- Basche A, DeLonge M (2017) The Impact of Continuous Living Cover on Soil Hydrologic Properties: A Meta-Analysis. *Soil Sci Soc Am J* 81:1179–1190.
<https://doi.org/10.2136/sssaj2017.03.0077>
- Bastian HV (2001a) Effects of low intensity prescribed fires on ponderosa pine forests in wilderness areas of Zion National Park, Utah. Vance Regina K Edminster Carlet B Covington W Wallace 25–27
- Bastian HV (2001b) The effects of a low intensity fire on a mixed conifer forest in Bryce Canyon National Park, Utah. In: *Ponderosa Pine Ecosystems Restoration and Conservation: Steps Toward Stewardship: Conference Proceedings, Flagstaff, AZ, April 25-27, 2000*. US Department of Agriculture, Forest Service, Rocky Mountain Research Station
- Battaglia MA, Rocca ME, Rhoades CC, Ryan MG (2010) Surface fuel loadings within mulching treatments in Colorado coniferous forests. *For Ecol Manag* 260:1557–1566.
<https://doi.org/10.1016/j.foreco.2010.08.004>

- Battaglia MA, Smith FW, Shepperd WD (2008) Can prescribed fire be used to maintain fuel treatment effectiveness over time in Black Hills ponderosa pine forests? *For Ecol Manag* 256:2029–2038. <https://doi.org/10.1016/j.foreco.2008.07.026>
- Bradley T, Gibson J, Bunn W (2006) Fuels management and non-native plant species: an evaluation of fire and fire surrogate treatments in a chaparral plant community. Joint Fire Science Program
- Brown JK (1974) Handbook for inventorying downed woody material. Gen Tech Rep INT-16 Ogden UT US Dep Agric For Serv Intermt For Range Exp Stn 24 P 016:
- Bürkner P-C (2017) brms: An R Package for Bayesian Multilevel Models Using *Stan*. *J Stat Softw* 80:. <https://doi.org/10.18637/jss.v080.i01>
- Busse M, Gerrard R (2020) Thinning and Burning Effects on Long-Term Litter Accumulation and Function in Young Ponderosa Pine Forests. *For Sci* 66:761–769. <https://doi.org/10.1093/forsci/fxaa018>
- Campbell J, Alberti G, Martin J, Law BE (2009) Carbon dynamics of a ponderosa pine plantation following a thinning treatment in the northern Sierra Nevada. *For Ecol Manag* 257:453–463. <https://doi.org/10.1016/j.foreco.2008.09.021>
- Cansler CA, Swanson ME, Furniss TJ, et al (2019) Fuel dynamics after reintroduced fire in an old-growth Sierra Nevada mixed-conifer forest. *Fire Ecol* 15:16. <https://doi.org/10.1186/s42408-019-0035-y>
- Carvalho ER, Gurgel Veras CA, Carvalho Jr JA (2002) Experimental investigation of smouldering in biomass. *Biomass Bioenergy* 22:283–294. [https://doi.org/10.1016/S0961-9534\(02\)00005-3](https://doi.org/10.1016/S0961-9534(02)00005-3)
- Chew J, Jones JG, Stalling C, et al (2003) Combining Simulation and Optimization for Evaluating the Effectiveness of Fuel Treatments for Four Different Fuel Conditions at Landscape Scales. In: Arthaud GJ, Barrett TM (eds) *Systems Analysis in Forest Resources: Proceedings of the Eighth Symposium, held September 27–30, 2000,*

- Snowmass Village, Colorado, U.S.A. Springer Netherlands, Dordrecht, pp 35–46
- Chiono LA, O'Hara KL, De Lasaux MJ, et al (2012) Development of Vegetation and Surface Fuels Following Fire Hazard Reduction Treatment. *Forests* 3:700–722.
<https://doi.org/10.3390/f3030700>
- Collins BM, Everett RG, Stephens SL (2011) Impacts of fire exclusion and recent managed fire on forest structure in old growth Sierra Nevada mixed-conifer forests. *Ecosphere* 2:art51.
<https://doi.org/10.1890/ES11-00026.1>
- Covington WW, Moore MM (1994) Postsettlement Changes in Natural Fire Regimes and Forest Structure. *J Sustain For* 2:153–181. https://doi.org/10.1300/J091v02n01_07
- Crotteau JS, Keyes CR, Hood SM, et al (2018) Fuel dynamics after a bark beetle outbreak impacts experimental fuel treatments. *Fire Ecol* 14:13.
<https://doi.org/10.1186/s42408-018-0016-6>
- Crotteau JS, Keyes CR, Hood SM, Larson AJ (2020) Vegetation dynamics following compound disturbance in a dry pine forest: fuel treatment then bark beetle outbreak. *Ecol Appl* 30:.
<https://doi.org/10.1002/eap.2023>
- Dinerstein E, Olson D, Joshi A, et al (2017) An Ecoregion-Based Approach to Protecting Half the Terrestrial Realm. *BioScience* 67:534–545. <https://doi.org/10.1093/biosci/bix014>
- Egger M, Smith GD, Schneider M, Minder C (1997) Bias in meta-analysis detected by a simple, graphical test. *BMJ* 315:629–634. <https://doi.org/10.1136/bmj.315.7109.629>
- Finney MA (2006) An Overview of FlamMap Fire Modeling Capabilities. Andrews Patricia Butl Bret W Comps 2006 Fuels Manag- Meas Success Conf Proc 28-30 March 2006 Portland Proc RMRS-P-41 Fort Collins CO US Dep Agric For Serv Rocky Mt Res Stn P 213-220 041:
- Fonda RW, Binney EP (2011) Vegetation Response to Prescribed Fire in Douglas-Fir Forests, Olympic National Park. *Northwest Sci* 85:30–40. <https://doi.org/10.3955/046.085.0103>
- Fule PZ, Cocke AE, Heinlein TA, Covington WW (2004) Effects of an intense prescribed forest

- fire: is it ecological restoration? *Restor Ecol* 12:220–230
- Fulé PZ, Covington WW, Smith HB, et al (2002) Comparing ecological restoration alternatives: Grand Canyon, Arizona. *For Ecol Manag* 170:19–41.
[https://doi.org/10.1016/S0378-1127\(01\)00759-9](https://doi.org/10.1016/S0378-1127(01)00759-9)
- Fulé PZ, Covington WW, Stoddard MT, Bertolette D (2006) “Minimal-Impact” Restoration Treatments Have Limited Effects on Forest Structure and Fuels at Grand Canyon, USA. *Restor Ecol* 14:357–368. <https://doi.org/10.1111/j.1526-100X.2006.00144.x>
- Fulé PZ, Crouse JE, Roccaforte JP, Kalies EL (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>
- Gelman A, Rubin DB (1992) Inference from Iterative Simulation Using Multiple Sequences. *Stat Sci* 7:. <https://doi.org/10.1214/ss/1177011136>
- Goodwin MJ, North MP, Zald HSJ, Hurteau MD (2018) The 15-year post-treatment response of a mixed-conifer understory plant community to thinning and burning treatments. *For Ecol Manag* 429:617–624. <https://doi.org/10.1016/j.foreco.2018.07.058>
- Harrer M, Cuijpers P, Furukawa T, Ebert D (2021) *Doing Meta-Analysis with R: A Hands-On Guide*. Chapman and Hall/CRC, New York
- Harrod RJ, Peterson DW, Povak NA, Dodson EK (2009) Thinning and prescribed fire effects on overstory tree and snag structure in dry coniferous forests of the interior Pacific Northwest. *For Ecol Manag* 258:712–721. <https://doi.org/10.1016/j.foreco.2009.05.011>
- Hartsough BR, Abrams S, Barbour RJ, et al (2008) The economics of alternative fuel reduction treatments in western United States dry forests: Financial and policy implications from the National Fire and Fire Surrogate Study. *For Policy Econ* 10:344–354.
<https://doi.org/10.1016/j.forpol.2008.02.001>
- Havrilla CA, Faist AM, Barger NN (2017) Understory Plant Community Responses to Fuel-Reduction Treatments and Seeding in an Upland Piñon-Juniper Woodland. *Rangel*

- Ecol Manag 70:609–620. <https://doi.org/10.1016/j.rama.2017.04.002>
- Hazard JW, Pickford SG (1986) Simulation Studies on Line Intersect Sampling of Forest Residue, Part II. For Sci 32:447–470. <https://doi.org/10.1093/forestscience/32.2.447>
- Hedges LV, Gurevitch J, Curtis PS (1999) The Meta-Analysis of Response Ratios in Experimental Ecology. Ecology 80:1150–1156.
[https://doi.org/10.1890/0012-9658\(1999\)080\[1150:TMAORR\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1999)080[1150:TMAORR]2.0.CO;2)
- Hedges LV, Olkin I (2014) Statistical Methods for Meta-Analysis. Academic Press
- Hessburg PF, Agee JK, Franklin JF (2005) Dry forests and wildland fires of the inland Northwest USA: Contrasting the landscape ecology of the pre-settlement and modern eras. For Ecol Manag 211:117–139. <https://doi.org/10.1016/j.foreco.2005.02.016>
- Hessburg PF, Spies TA, Perry DA, et al (2016) Tamm Review: Management of mixed-severity fire regime forests in Oregon, Washington, and Northern California. For Ecol Manag 366:221–250. <https://doi.org/10.1016/j.foreco.2016.01.034>
- Hille MG, Stephens SL (2005) Mixed conifer forest duff consumption during prescribed fires: tree crown impacts. For Sci 51:417–424
- Hood SM, Keyes CR, Bowen KJ, et al (2020) Fuel Treatment Longevity in Ponderosa Pine-Dominated Forest 24 Years After Cutting and Prescribed Burning. Front For Glob Change 3:78. <https://doi.org/10.3389/ffgc.2020.00078>
- Hood SM, McHugh CW, Ryan KC, 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>
- Huffman DW, Fulé PZ, Crouse JE, Pearson KM (2009) A comparison of fire hazard mitigation alternatives in pinyon–juniper woodlands of Arizona. For Ecol Manag 257:628–635.
<https://doi.org/10.1016/j.foreco.2008.09.041>
- Huffman DW, Stoddard MT, Springer JD, et al (2019) Stand Dynamics of Pinyon-Juniper Woodlands After Hazardous Fuels Reduction Treatments in Arizona. Rangel Ecol Manag 72:757–767. <https://doi.org/10.1016/j.rama.2019.05.005>

- Hull IT, Shipley LA, Berry SL, et al (2020) Effects of fuel reduction timber harvests on forage resources for deer in northeastern Washington. *For Ecol Manag* 458:117757.
<https://doi.org/10.1016/j.foreco.2019.117757>
- Hunter ME, Iniguez JM, Lentile LB (2011) Short- and Long-Term Effects on Fuels, Forest Structure, and Wildfire Potential from Prescribed Fire and Resource Benefit Fire in Southwestern Forests, USA. *Fire Ecol* 7:108–121.
<https://doi.org/10.4996/fireecology.0703108>
- Hurteau M, North M (2009) Fuel treatment effects on tree-based forest carbon storage and emissions under modeled wildfire scenarios. *Front Ecol Environ* 7:409–414.
<https://doi.org/10.1890/080049>
- Hyde JC, Smith AMS, Ottmar RD, et al (2011) The combustion of sound and rotten coarse woody debris: a review. *Int J Wildland Fire* 20:163–174. <https://doi.org/10.1071/WF09113>
- Hyde JC, Smith AMS, Ottmar RD, et al (2012) Properties affecting the consumption of sound and rotten coarse woody debris in northern Idaho: a preliminary investigation using laboratory fires. *Int J Wildland Fire* 21:596–608. <https://doi.org/10.1071/WF11016>
- Jain TB, Battaglia MA, Han H-S, et al (2012) A comprehensive guide to fuel management practices for dry mixed conifer forests in the northwestern United States. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ft. Collins, CO
- Johnston JD, Olszewski JH, Miller BA, et al (2021) Mechanical thinning without prescribed fire moderates wildfire behavior in an Eastern Oregon, USA ponderosa pine forest. *For Ecol Manag* 501:119674. <https://doi.org/10.1016/j.foreco.2021.119674>
- Kane JM, Knapp EE, Varner JM (2006) Variability in Loading of Mechanically Masticated Fuel Beds in Northern California and Southwestern Oregon. Andrews Patricia Butl Bret W Comps 2006 Fuels Manag- Meas Success Conf Proc 28-30 March 2006 Portland Proc RMRS-P-41 Fort Collins CO US Dep Agric For Serv Rocky Mt Res Stn P 341-350 041:

- Keifer M (1998) Fuel load and tree density changes following prescribed fire in the giant sequoia-mixed conifer forest: the first 14 years of fire effects monitoring. In: Proceedings of the Tall Timbers Fire Ecology Conference. pp 306–309
- Keifer M, van Wagtenonk JW, Buhler M (2006) Long-term surface fuel accumulation in burned and unburned mixed-conifer forests of the Central and Southern Sierra Nevada, CA (USA). *Fire Ecol* 2:53–72. <https://doi.org/10.4996/fireecology.0201053>
- Knapp E, Bernal A, Kane J, et al (2021) Variable thinning and prescribed fire influence tree mortality and growth during and after a severe drought. *For Ecol Manag* 479:.. <https://doi.org/10.1016/j.foreco.2020.118595>
- Knapp EE, Keeley JE, Ballenger EA, Brennan TJ (2005) Fuel reduction and coarse woody debris dynamics with early season and late season prescribed fire in a Sierra Nevada mixed conifer forest. *For Ecol Manag* 208:383–397. <https://doi.org/10.1016/j.foreco.2005.01.016>
- Knapp EE, Lydersen JM, North MP, Collins BM (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>
- Knapp EE, Schwilk DW, Kane JM, Keeley JE (2007) Role of burning season on initial understory vegetation response to prescribed fire in a mixed conifer forest. *Can J For Res* 37:11–22. <https://doi.org/10.1139/x06-200>
- Kobziar L, Moghaddas J, Stephens SL (2006) Tree mortality patterns following prescribed fires in a mixed conifer forest. *Can J For Res* 36:3222–3238. <https://doi.org/10.1139/x06-183>
- Korb JE, Stoddard MT, Huffman DW (2020) Effectiveness of Restoration Treatments for Reducing Fuels and Increasing Understory Diversity in Shrubby Mixed-Conifer Forests of the Southern Rocky Mountains, USA. *Forests* 11:508. <https://doi.org/10.3390/f11050508>

- Larkin NK, O'Neill SM, Solomon R, et al (2009) The BlueSky smoke modeling framework. *Int J Wildland Fire* 18:906–920. <https://doi.org/10.1071/WF07086>
- Levine JI, Collins BM, York RA, 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>
- Lohman DJ, Bickford D, Sodhi NS (2007) The Burning Issue. *Science* 316:376–376.
<https://doi.org/10.1126/science.1140278>
- Low KE, Collins BM, Bernal A, et al (2021) Longer-term impacts of fuel reduction treatments on forest structure, fuels, and drought resistance in the Lake Tahoe Basin. *For Ecol Manag* 479:118609. <https://doi.org/10.1016/j.foreco.2020.118609>
- Lutes DC, Keane RE, Caratti JF, et al (2006) FIREMON: Fire effects monitoring and inventory system. Gen Tech Rep RMRS-GTR-164 Fort Collins CO US Dep Agric For Serv Rocky Mt Res Stn 1 CD 164:. <https://doi.org/10.2737/RMRS-GTR-164>
- Martinson EJ, Omi PN (2013) Fuel treatments and fire severity: A meta-analysis. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ft. Collins, CO
- Mason GJ, Baker TT, Cram DS, et al (2007) Mechanical fuel treatment effects on fuel loads and indices of crown fire potential in a south central New Mexico dry mixed conifer forest. *For Ecol Manag* 251:195–204. <https://doi.org/10.1016/j.foreco.2007.06.006>
- McElreath R (2020) *Statistical Rethinking: A Bayesian Course with Examples in R and STAN*, 2nd edn. Chapman and Hall/CRC, New York
- McIver JD, Adams PW, Doyal JA, et al (2003) Environmental Effects and Economics of Mechanized Logging for Fuel Reduction in Northeastern Oregon Mixed-Conifer Stands. *West J Appl For* 18:238–249. <https://doi.org/10.1093/wjaf/18.4.238>
- Metlen KL, Skinner CN, Olson DR, et al (2018) Regional and local controls on historical fire regimes of dry forests and woodlands in the Rogue River Basin, Oregon, USA. *For Ecol*

- Manag 430:43–58. <https://doi.org/10.1016/j.foreco.2018.07.010>
- Miller RK, Field CB, Mach KJ (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 EEY, Stephens SL (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>
- Morici KE, Bailey JD (2021) Long-Term Effects of Fuel Reduction Treatments on Surface Fuel Loading in the Blue Mountains of Oregon. *Forests* 12:1306.
<https://doi.org/10.3390/f12101306>
- Mosquera I, Côté IM, Jennings S, Reynolds JD (2000) Conservation benefits of marine reserves for fish populations. *Anim Conserv* 3:321–332.
<https://doi.org/10.1111/j.1469-1795.2000.tb00117.x>
- North M, Collins BM, 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>
- North M, Hurteau M, Innes J (2009) Fire suppression and fuels treatment effects on mixed-conifer carbon stocks and emissions. *Ecol Appl* 19:1385–1396.
<https://doi.org/10.1890/08-1173.1>
- Odland MC, Goodwin MJ, Smithers BV, 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>
- Omi PN (2015) Theory and Practice of Wildland Fuels Management. *Curr For Rep* 1:100–117.
<https://doi.org/10.1007/s40725-015-0013-9>
- Ott JE, Kilkenny FF, Jain TB (2023) Fuel treatment effectiveness at the landscape scale: a systematic review of simulation studies comparing treatment scenarios in North America. *Fire Ecol* 19:10. <https://doi.org/10.1186/s42408-022-00163-2>

- Perrakis DDB, Agee JK (2006) Seasonal fire effects on mixed-conifer forest structure and ponderosa pine resin properties. 36:17
- Peterson DL, Johnson M, Agee J, et al (2003) Fuels planning: managing forest structure to reduce fire hazard. In: Proceedings of the Second International Wildland Fire Ecology and Fire Management Congress, Orlando, Florida. p 10
- Prichard SJ, Kennedy MC, Wright CS, et al (2017) Predicting forest floor and woody fuel consumption from prescribed burns in southern and western pine ecosystems of the United States. For Ecol Manag 405:328–338.
<https://doi.org/10.1016/j.foreco.2017.09.025>
- Prichard SJ, Povak NA, Kennedy MC, Peterson DW (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>
- R Core Team (2021) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria
- Raymond CL, Peterson DL (2005) Fuel treatments alter the effects of wildfire in a mixed-evergreen forest, Oregon, USA. 35:15
- Reiner A, Vaillant N, Fites-Kaufman J, Dailey S (2009a) Mastication and prescribed fire impacts on fuels in a 25-year old ponderosa pine plantation, southern Sierra Nevada. For Ecol Manag 258:2365–2372. <https://doi.org/10.1016/j.foreco.2009.07.050>
- Reiner AL, Vaillant NM, Fites-Kaufman J, Dailey SN (2009b) Mastication and prescribed fire impacts on fuels in a 25-year old ponderosa pine plantation, southern Sierra Nevada. For Ecol Manag 258:2365–2372. <https://doi.org/10.1016/j.foreco.2009.07.050>
- Reinhardt ED, Keane RE, Brown JK (1997) First Order Fire Effects Model: FOFEM 4.0, user's guide. Gen Tech Rep INT-GTR-344 Ogden UT US Dep Agric For Serv Intermt Res Stn 65 P 344:. <https://doi.org/10.2737/INT-GTR-344>
- Ritter S, Morici K, Stevens-Rumann CS (2023) Efficacy of Prescribed Fire as a Fuel Reduction

- Treatment in the Colorado Front Range. *Can J For Res* cjfr-2022-0259.
<https://doi.org/10.1139/cjfr-2022-0259>
- Roccaforte J, Fule P, Covington W (2008) Landscape-scale changes in canopy fuels and potential fire behaviour following ponderosa pine restoration treatments. *Int J WILDLAND FIRE* 17:293–303. <https://doi.org/10.1071/WF06120>
- Roccaforte JP, Fulé PZ, Covington WW (2010) Monitoring Landscape-Scale Ponderosa Pine Restoration Treatment Implementation and Effectiveness. *Restor Ecol* 18:820–833.
<https://doi.org/10.1111/j.1526-100X.2008.00508.x>
- Rohatgi A (2022) Webplotdigitizer: Version 4.6
- Sackett SS (1980) Reducing natural ponderosa pine fuels using prescribed fire: two case studies. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station
- Safford H (2008) Fire Severity in Fuel Treatments American River Complex fire, Tahoe National Forest, California. Rep USDA For Serv Pac Southwest Reg Fire Aviat Manag Staff
- Safford HD, Butz RJ, Bohlman GN, et al (2021) Fire Ecology of the North American Mediterranean-Climate Zone. In: Greenberg CH, Collins B (eds) *Fire Ecology and Management: Past, Present, and Future of US Forested Ecosystems*. Springer International Publishing, Cham, pp 337–392
- Safford HD, Stevens JT (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 HD, Stevens JT, Merriam K, et al (2012) Fuel treatment effectiveness in California yellow pine and mixed conifer forests. *For Ecol Manag* 274:17–28.
<https://doi.org/10.1016/j.foreco.2012.02.013>
- Saud P, Cram D, Smallidge S, Baker T (2018) Coarse Woody Debris Following Silviculture Treatments in Southwest Mixed-Conifer Forest. *FORESTS* 9:.

<https://doi.org/10.3390/f9060347>

Schwilk DW, Keeley JE, Knapp EE, 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>

Sikkink PG, Keane RE (2008) A comparison of five sampling techniques to estimate surface fuel loading in montane forests. *Int J Wildland Fire* 17:363. <https://doi.org/10.1071/WF07003>

Smith JE, McKay D, Brenner G, et al (2005) Early impacts of forest restoration treatments on the ectomycorrhizal fungal community and fine root biomass in a mixed conifer forest: Prescribed fire and EMF species richness. *J Appl Ecol* 42:526–535. <https://doi.org/10.1111/j.1365-2664.2005.01047.x>

Smith JE, McKay D, Niwa CG, et al (2004) Short-term effects of seasonal prescribed burning on the ectomycorrhizal fungal community and fine root biomass in ponderosa pine stands in the Blue Mountains of Oregon. *Can J For Res* 34:2477–2491. <https://doi.org/10.1139/x04-124>

Stanton S (2009) Western Dwarf Mistletoe and Prescribed Fire Behavior-A Case Study from Crater Lake National Park. *NORTHWEST Sci* 83:189–199. <https://doi.org/10.3955/046.083.0303>

Steel ZL, Fogg AM, 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 ZL, Jones GM, Collins BM, 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>

Stephens S, Finney M (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, Moghaddas J, Edminster C, et al (2009a) Fire treatment effects on vegetation

- structure, fuels, and potential fire severity in western US forests. *Ecol Appl* 19:305–320.
<https://doi.org/10.1890/07-1755.1>
- Stephens SL, Collins BM, Biber E, Fulé PZ (2016) U.S. federal fire and forest policy: emphasizing resilience in dry forests. *Ecosphere* 7:e01584.
<https://doi.org/10.1002/ecs2.1584>
- Stephens SL, Collins BM, Roller G (2012a) Fuel treatment longevity in a Sierra Nevada mixed conifer forest. *For Ecol Manag* 285:204–212.
<https://doi.org/10.1016/j.foreco.2012.08.030>
- Stephens SL, Mclver JD, Boerner REJ, et al (2012b) The Effects of Forest Fuel-Reduction Treatments in the United States. *BioScience* 62:549–560.
<https://doi.org/10.1525/bio.2012.62.6.6>
- Stephens SL, Moghaddas JJ (2005a) 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 SL, Moghaddas JJ (2005b) Experimental fuel treatment impacts on forest structure, potential fire behavior, and predicted tree mortality in a California mixed conifer forest. *For Ecol Manag* 215:21–36. <https://doi.org/10.1016/j.foreco.2005.03.070>
- Stephens SL, Moghaddas JJ (2005c) Fuel treatment effects on snags and coarse woody debris in a Sierra Nevada mixed conifer forest. *For Ecol Manag* 214:53–64.
<https://doi.org/10.1016/j.foreco.2005.03.055>
- Stephens SL, Moghaddas JJ, Edminster C, et al (2009b) Fire treatment effects on vegetation structure, fuels, and potential fire severity in western U.S. forests. *Ecol Appl* 19:305–320.
<https://doi.org/10.1890/07-1755.1>
- Stephens SL, Westerling AL, Hurteau MD, et al (2020) Fire and climate change: conserving seasonally dry forests is still possible. *Front Ecol Environ* 18:354–360.
<https://doi.org/10.1002/fee.2218>

- Stoddard MT, Roccaforte JP, Meador AJS, et al (2021) Ecological restoration guided by historical reference conditions can increase resilience to climate change of southwestern U.S. Ponderosa pine forests. *For Ecol Manag* 493:119256.
<https://doi.org/10.1016/j.foreco.2021.119256>
- Swetnam TW, Allen CD, Betancourt JL (1999) Applied Historical Ecology: Using the Past to Manage for the Future. *Ecol Appl* 9:1189–1206.
[https://doi.org/10.1890/1051-0761\(1999\)009\[1189:AHEUTP\]2.0.CO;2](https://doi.org/10.1890/1051-0761(1999)009[1189:AHEUTP]2.0.CO;2)
- Swetnam TW, Baisan C (1996) Historical fire regime patterns in the southwestern United States since AD 1700. UNITED STATES DEPARTMENT OF AGRICULTURE FOREST SERVICE GENERAL TECHNICAL REPORT RM
- Swim SL, Walker RF, Johnson DW, et al (2014) Evaluation of Mechanized Thinning and Prescribed Fire Effects on Long-Term Fuels Accumulations in Uneven-Aged Jeffrey Pine. *J Sustain For* 33:827–859. <https://doi.org/10.1080/10549811.2014.966919>
- Thapa R, Mirsky SB, Tully KL (2018) Cover Crops Reduce Nitrate Leaching in Agroecosystems:A Global Meta-Analysis. *J Environ Qual* 47:1400–1411.
<https://doi.org/10.2134/jeq2018.03.0107>
- Vaillant N, Noonan-Wright E, Reiner A, et al (2015a) Fuel accumulation and forest structure change following hazardous fuel reduction treatments throughout California. *Int J WILDLAND FIRE* 24:361–371. <https://doi.org/10.1071/WF14082>
- Vaillant NM, Noonan-Wright EK, Reiner AL, et al (2015b) Fuel accumulation and forest structure change following hazardous fuel reduction treatments throughout California. *Int J Wildland Fire* 24:361. <https://doi.org/10.1071/WF14082>
- Vakili E, Hoffman CM, Keane RE, et al (2016) Spatial variability of surface fuels in treated and untreated ponderosa pine forests of the southern Rocky Mountains. *Int J Wildland Fire* 25:1156. <https://doi.org/10.1071/WF16072>
- van Wagner CE (1977) Conditions for the start and spread of crown fire. *Can J For Res*

7:23–34. <https://doi.org/10.1139/x77-004>

Wagtendonk JW van (2018) *Fire in California's Ecosystems*. Univ of California Press

Walker RB, Coop JD, Parks SA, Trader L (2018) Fire regimes approaching historic norms reduce wildfire-facilitated conversion from forest to non-forest. *Ecosphere* 9:.
<https://doi.org/10.1002/ecs2.2182>

Walker RF, Fecko RM, Frederick WB, et al (2006) Thinning and Prescribed Fire Effects on Forest Floor Fuels in the East Side Sierra Nevada Pine Type. *J Sustain For* 23:99–115.
https://doi.org/10.1300/J091v23n02_06

Waring KM, Hansen KJ, Flatley WT (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>

Weatherspoon CP, Mclver J (2000) A national study of the consequences of fire and fire surrogate treatments. USDA For Serv Pac Southwest Res Stn Redd Calif USA

Webster KM, Halpern CB (2010) Long-term vegetation responses to reintroduction and repeated use of fire in mixed-conifer forests of the Sierra Nevada. *Ecosphere* 1:art9.
<https://doi.org/10.1890/ES10-00018.1>

Weeks J, Miller JED, Steel ZL, 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 AL (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

Westlind DJ, Kerns BK (2017) Long-Term Effects of Burn Season and Frequency on Ponderosa Pine Forest Fuels and Seedlings. *Fire Ecol* 13:42–61.
<https://doi.org/10.4996/fireecology.130304261>

- Williams JN, Safford HD, 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>
- Youngblood A, Wright C, Ottmar R, McIver J (2008) Changes in fuelbed characteristics and resulting fire potentials after fuel reduction treatments in dry forests of the Blue Mountains, northeastern Oregon. *For Ecol Manag* 255:3151–3169. <https://doi.org/10.1016/j.foreco.2007.09.032>
- Zald HSJ, Gray AN, North M, Kern RA (2008) Initial tree regeneration responses to fire and thinning treatments in a Sierra Nevada mixed-conifer forest, USA. *For Ecol Manag* 256:168–179. <https://doi.org/10.1016/j.foreco.2008.04.022>

Figures

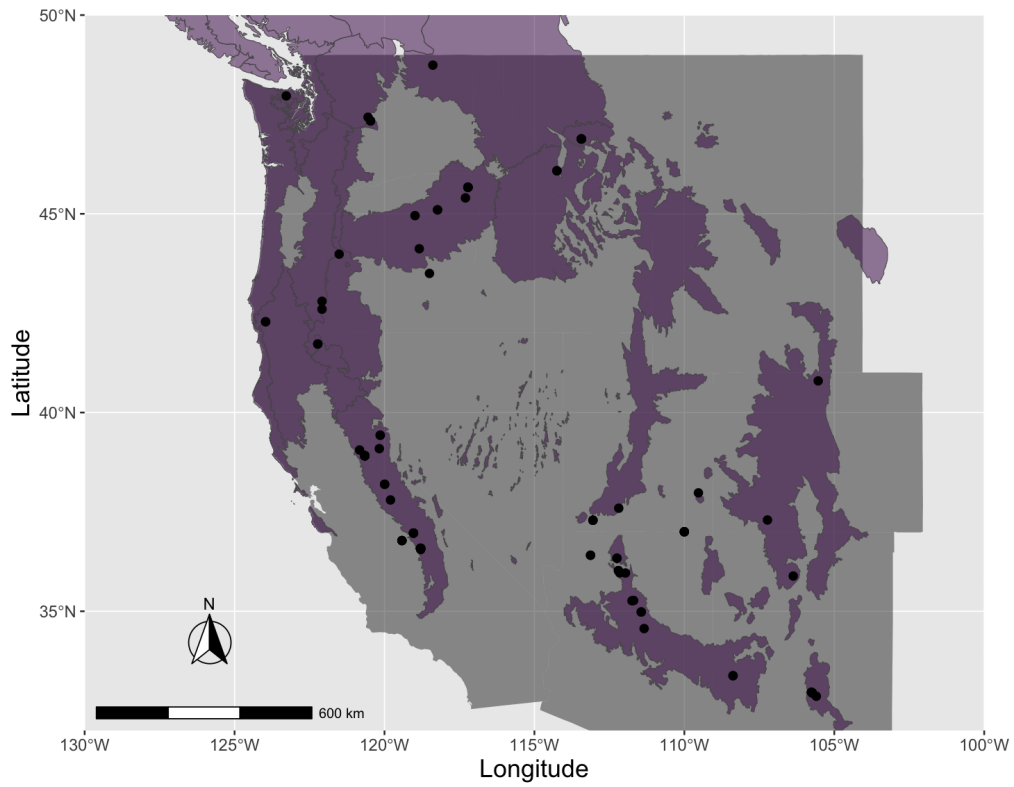


Figure 2.1. Map of the 95 study locations included in the meta-analysis. The geographic distribution of temperate conifer forests is shown by the purple polygons. The dark gray area indicates the region of interest for this study. The black dots represent the locations of the observations for the available references included in this study.

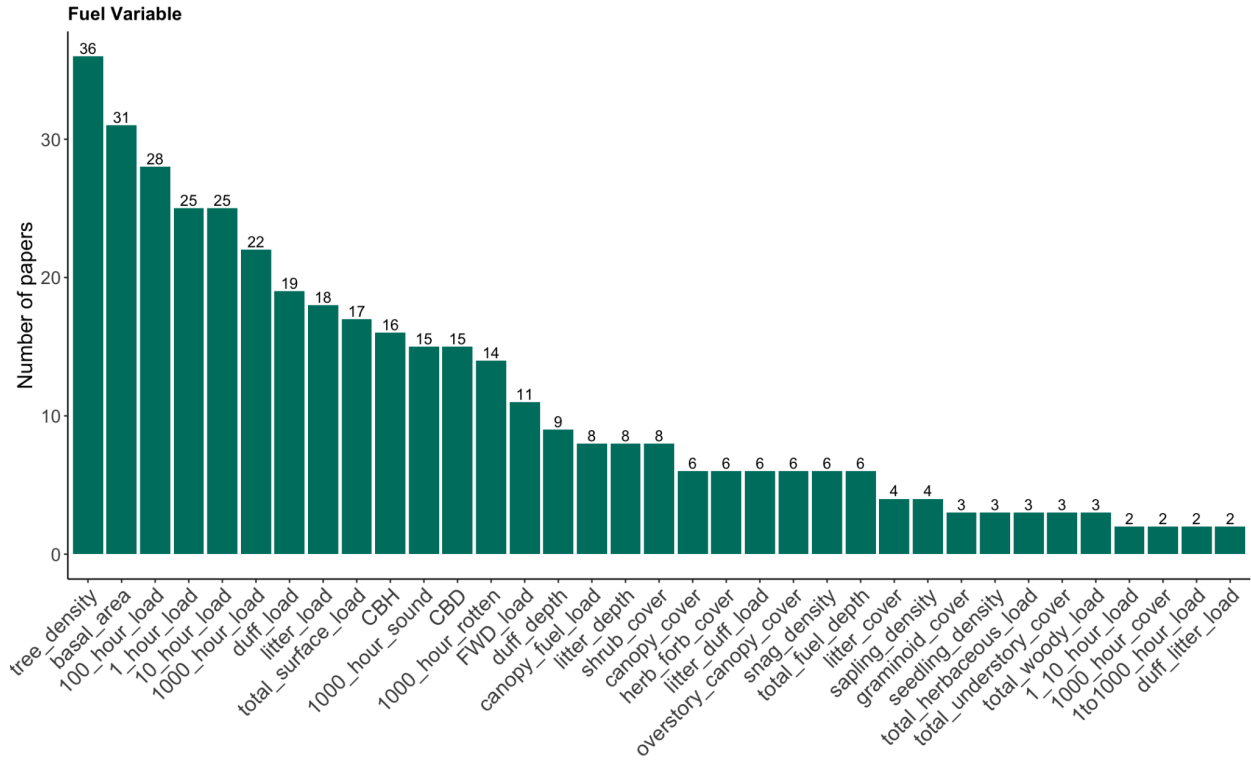


Figure 2.2. Number of identified papers that quantify fuel loading in terms of different fuel variables. Several studies evaluated more than one fuel variable, forest type, and treatment type. Treatment types represented by single studies were removed from the analysis.

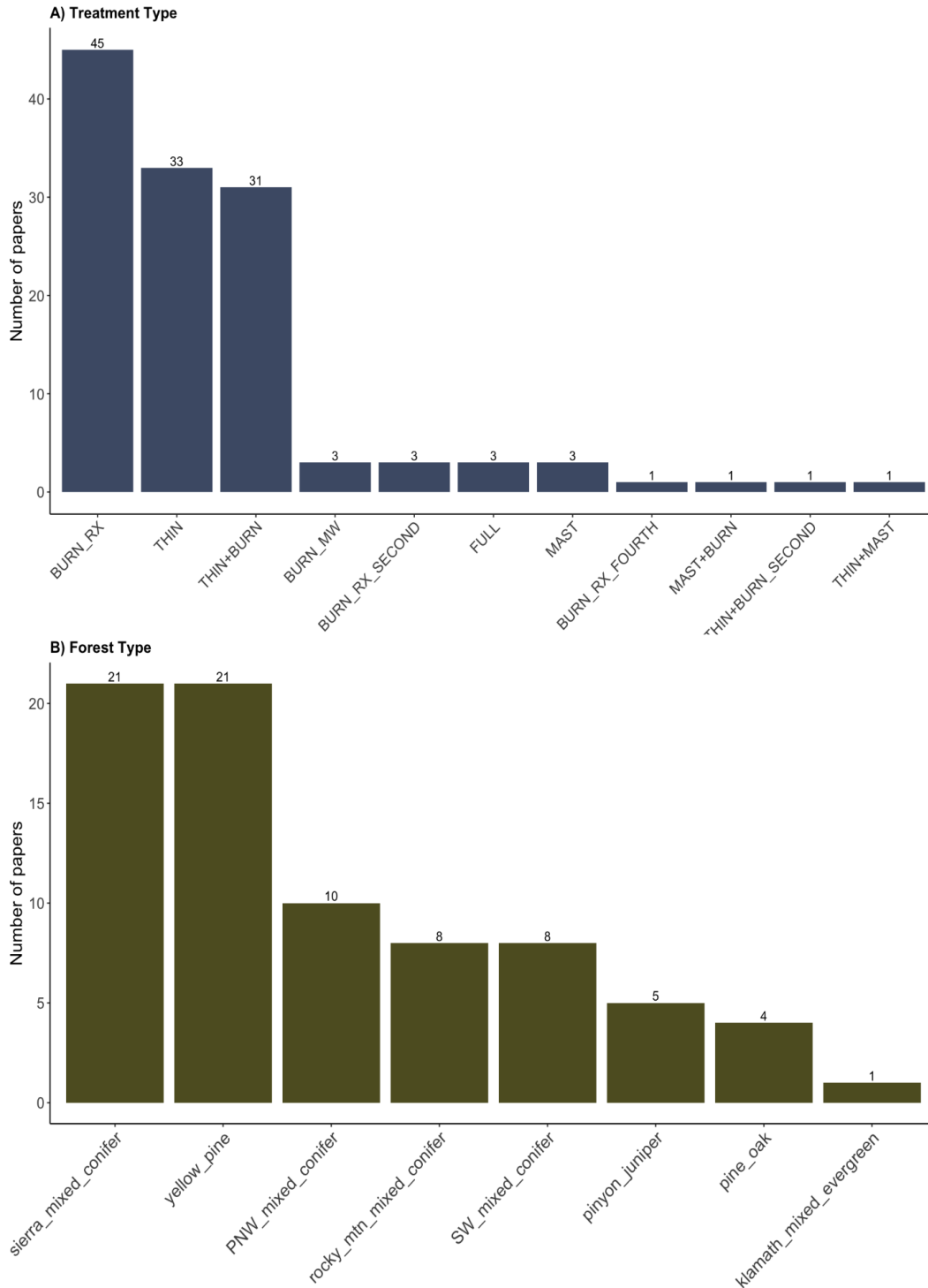


Figure 2.3. Number of identified papers that quantify fuel loading in terms of: (A) different fuels treatment methods and (B) different western US dry forest types. Several studies evaluated more than one fuel variable, forest type, and treatment type. Treatment types represented by single studies were removed from the analysis.

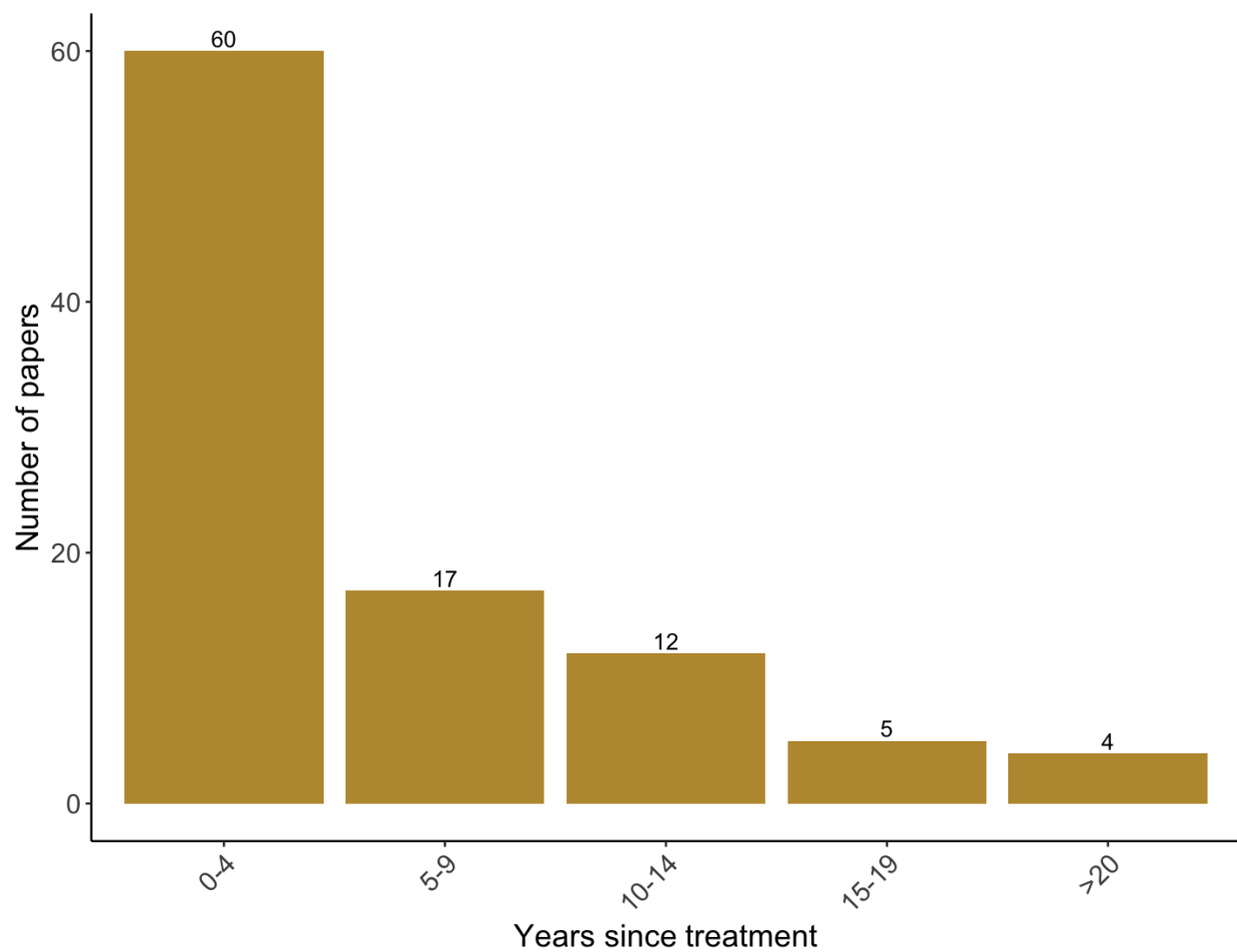


Figure 2.4. Number of papers that quantify the state of fuels after fuel treatments classified by considered temporal scales. Several papers considered more than one temporal scale.

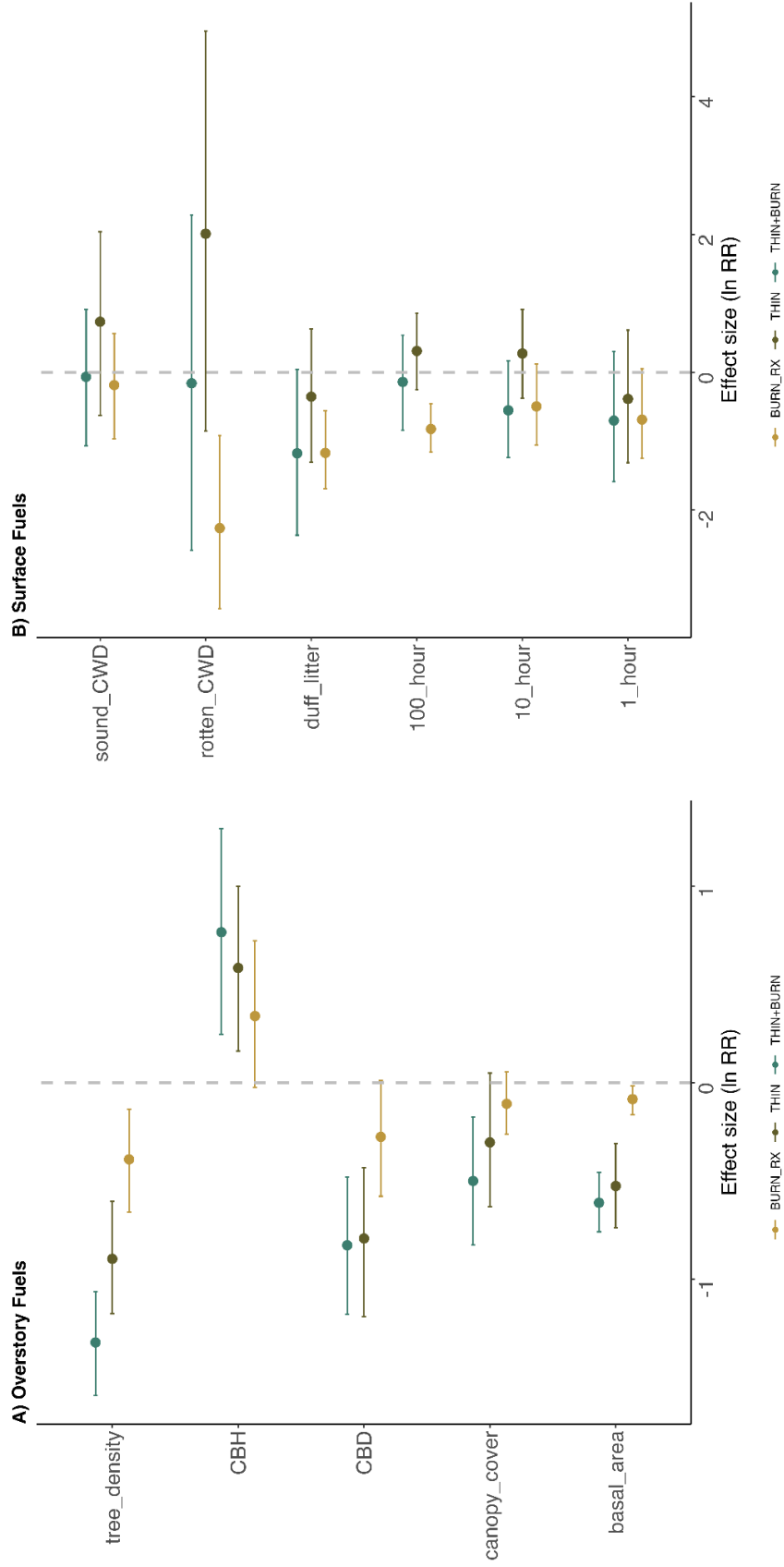


Figure 2.5. Effect of BURN (tan), THIN (brown), and THIN+BURN (blue) treatments on: (A) overstory fuel loads and (B) surface fuels. For each category, the mean and the 95% credible interval for the posterior distribution are plotted. Negative values indicate that the fuel treatment reduced fuel loads.

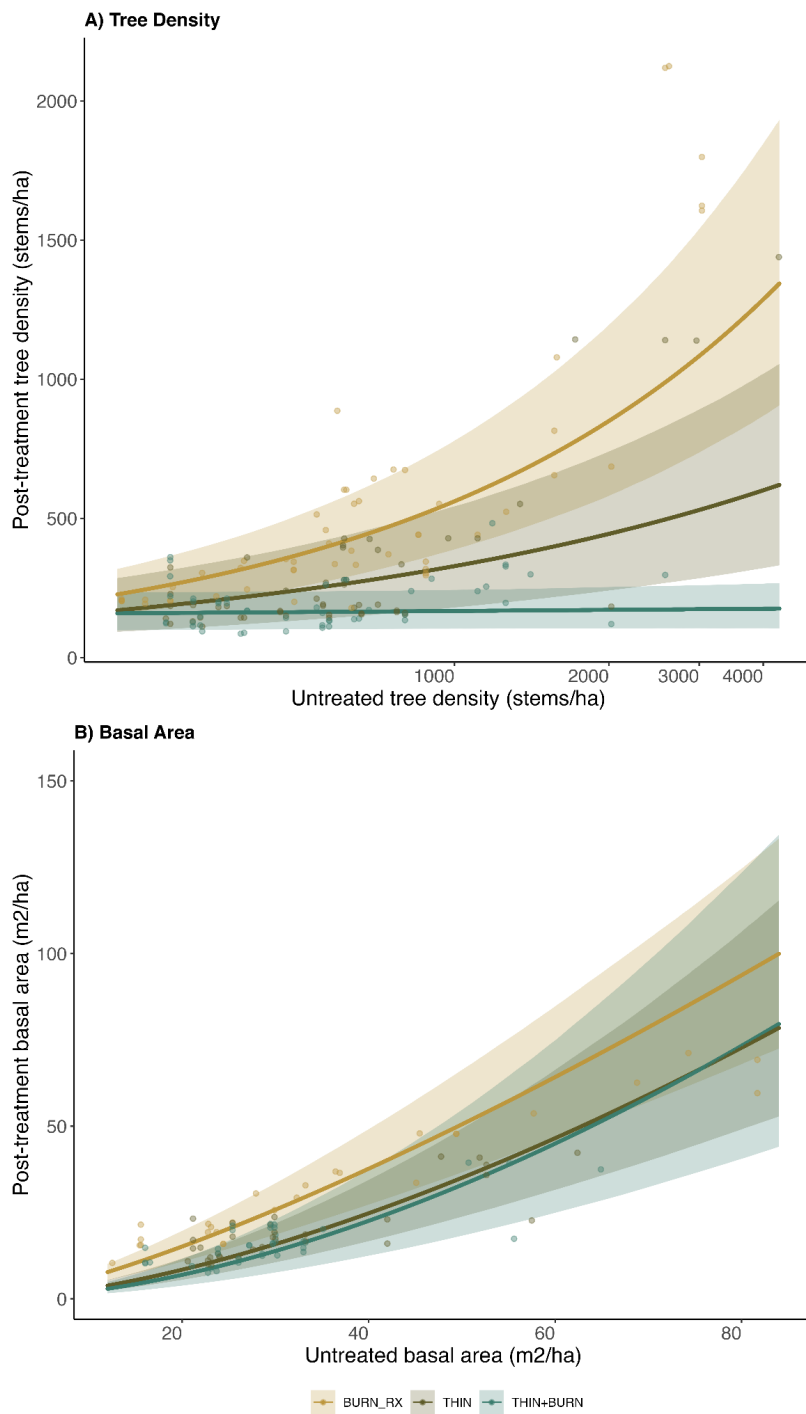


Figure 2.6. Overstory fuel: (A) Post-treatment tree density and (B) basal area vary with starting fuel conditions after BURN (tan), THIN (brown), and THIN+BURN (blue) treatments. Predicted values from the top-ranked Bayesian model with 95% credible intervals, as well as raw values (colored circles).

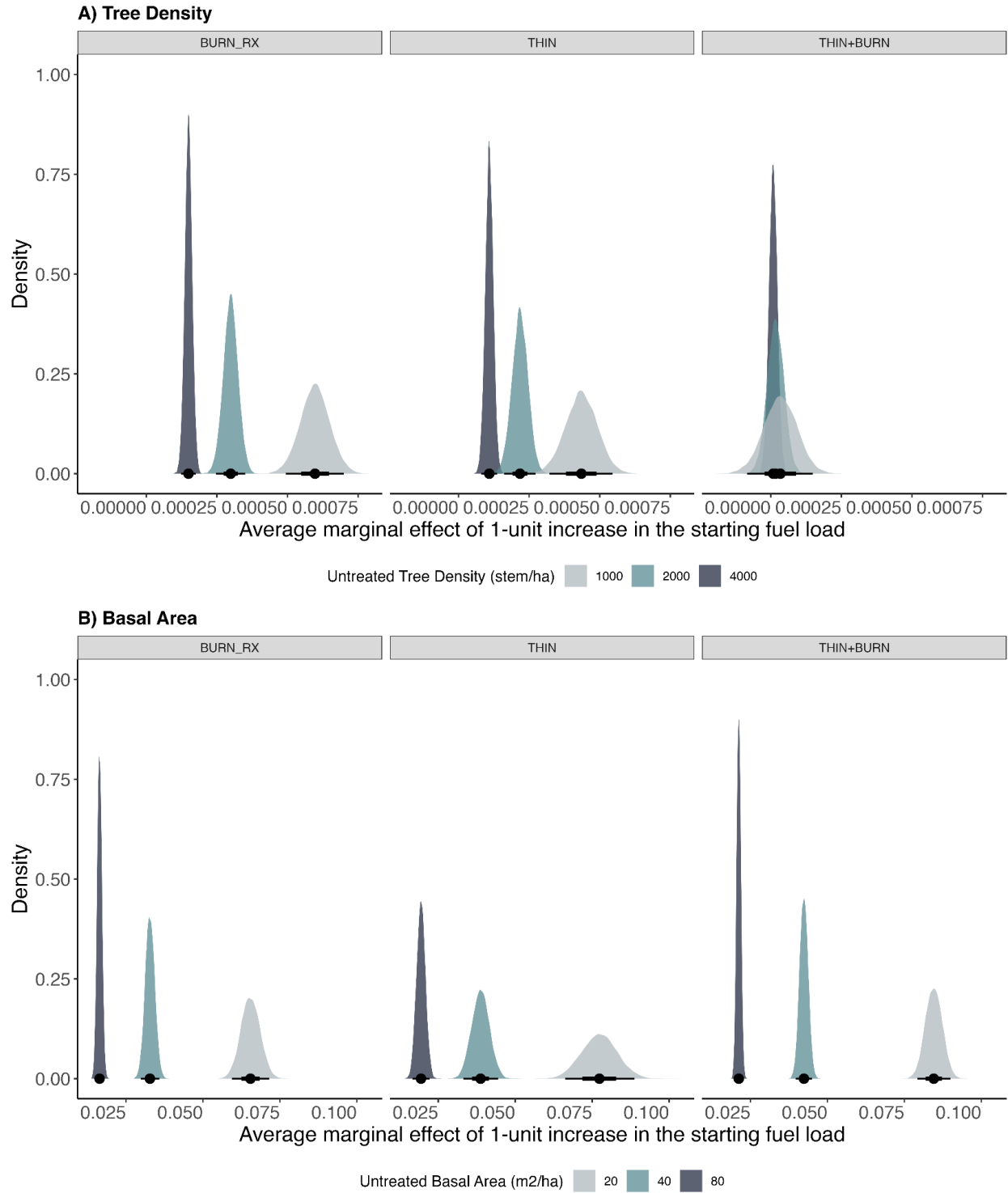


Figure 2.7: Average marginal effect of a 1-unit increase in starting fuel conditions on: (A) tree density and (B) basal area after BURN, THIN, and THIN+BURN treatments varied across high (dark blue), medium (blue), and low (light blue) levels of starting fuel load. Black dots show the mean effect with 80% and 95% confidence intervals shown in black.

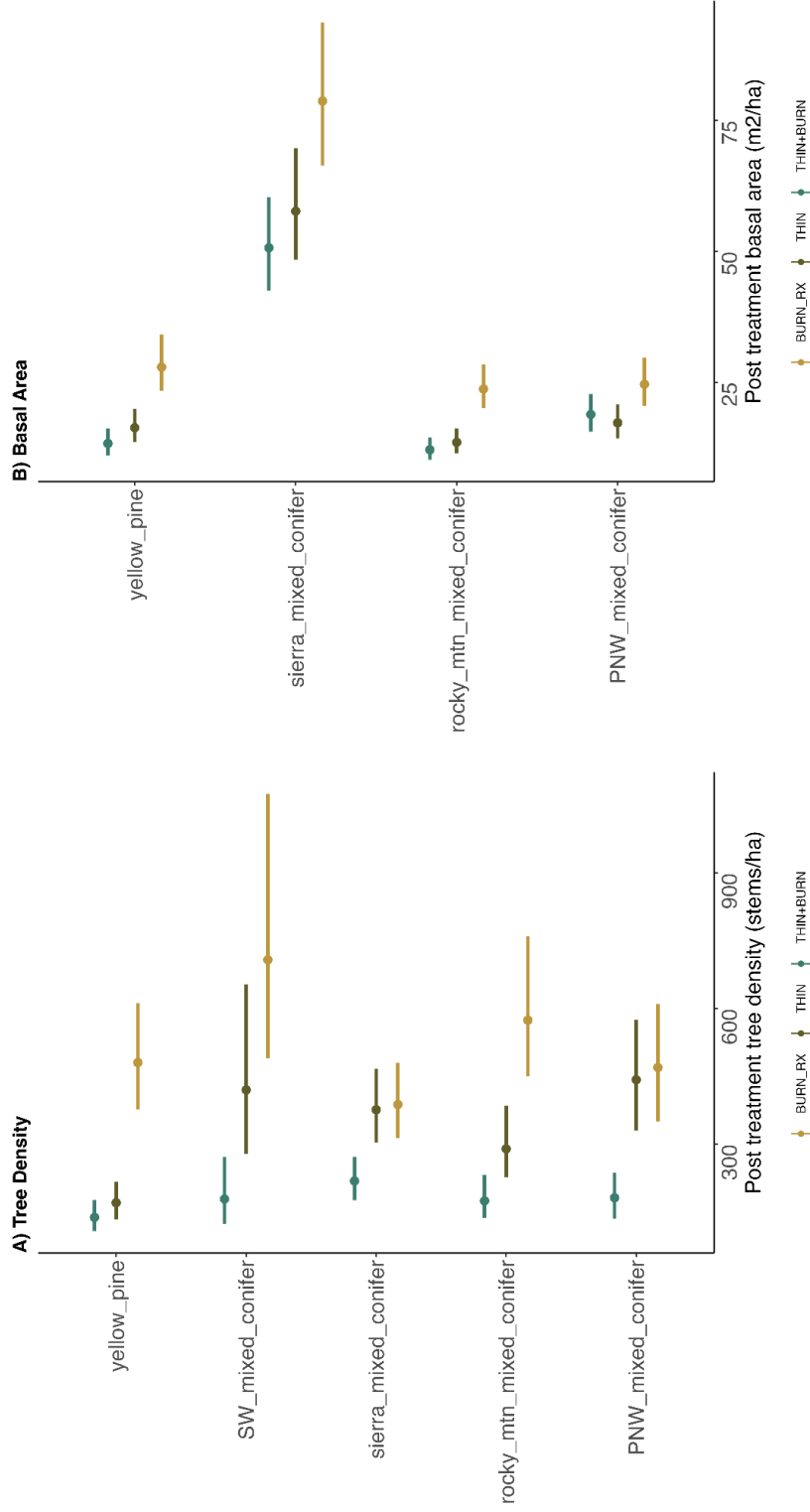


Figure 2.8. Model-fitted post-treatment fuel loads: (A) tree density and (B) basal area for different forest types after BURN (tan), THIN (brown), and THIN+BURN (blue) treatments. Dots show predicted values from the top-ranked Bayesian model and bars show the 95% (thick) credible intervals.

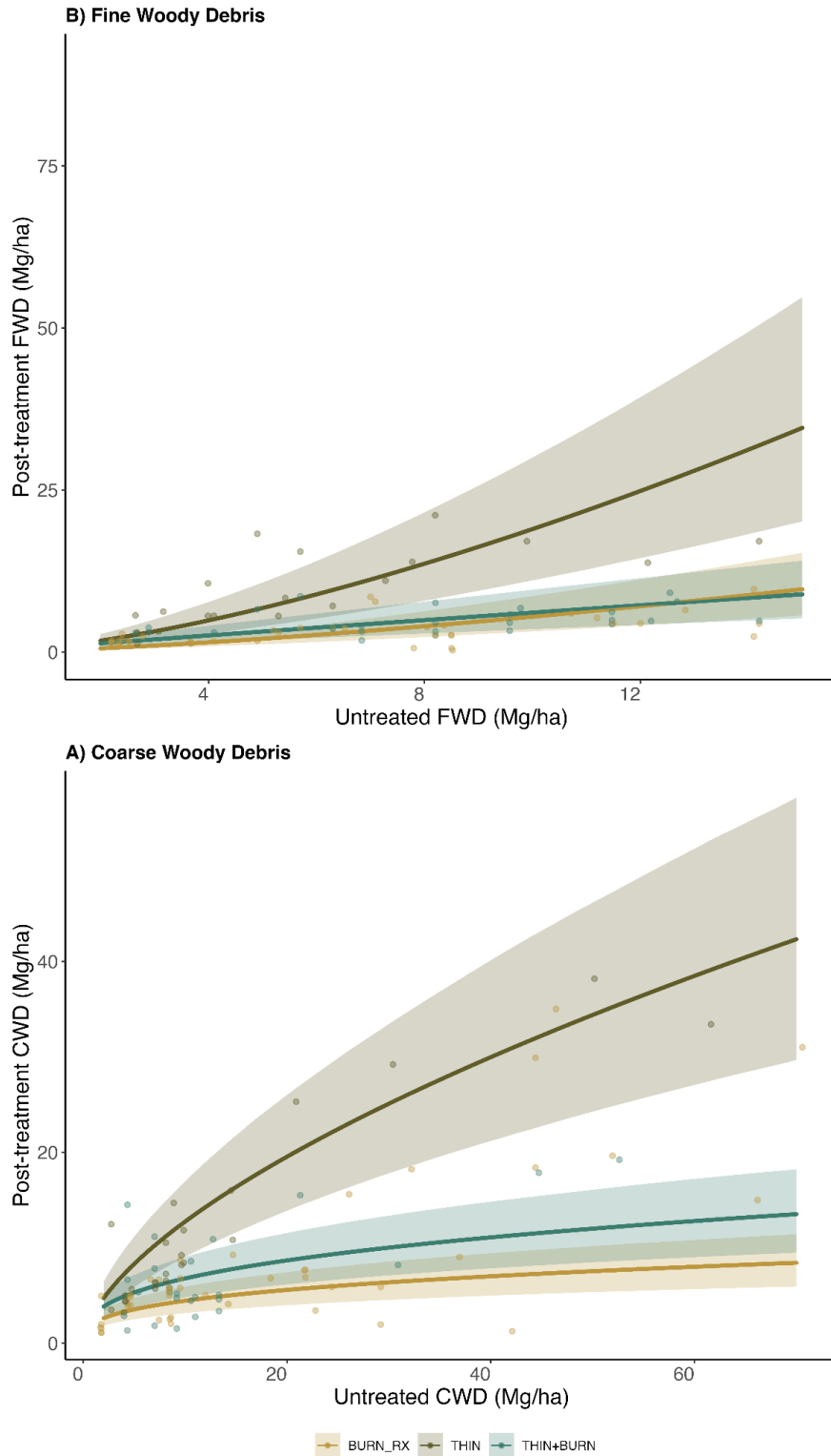


Figure 2.9: Post-treatment fuel load: (A) CWD and (B) FWD vary with starting fuel conditions after BURN (tan), THIN (brown), and THIN+BURN (blue) treatments. Predicted values from the top-ranked Bayesian model with 95% credible intervals, as well as raw values (colored circles).

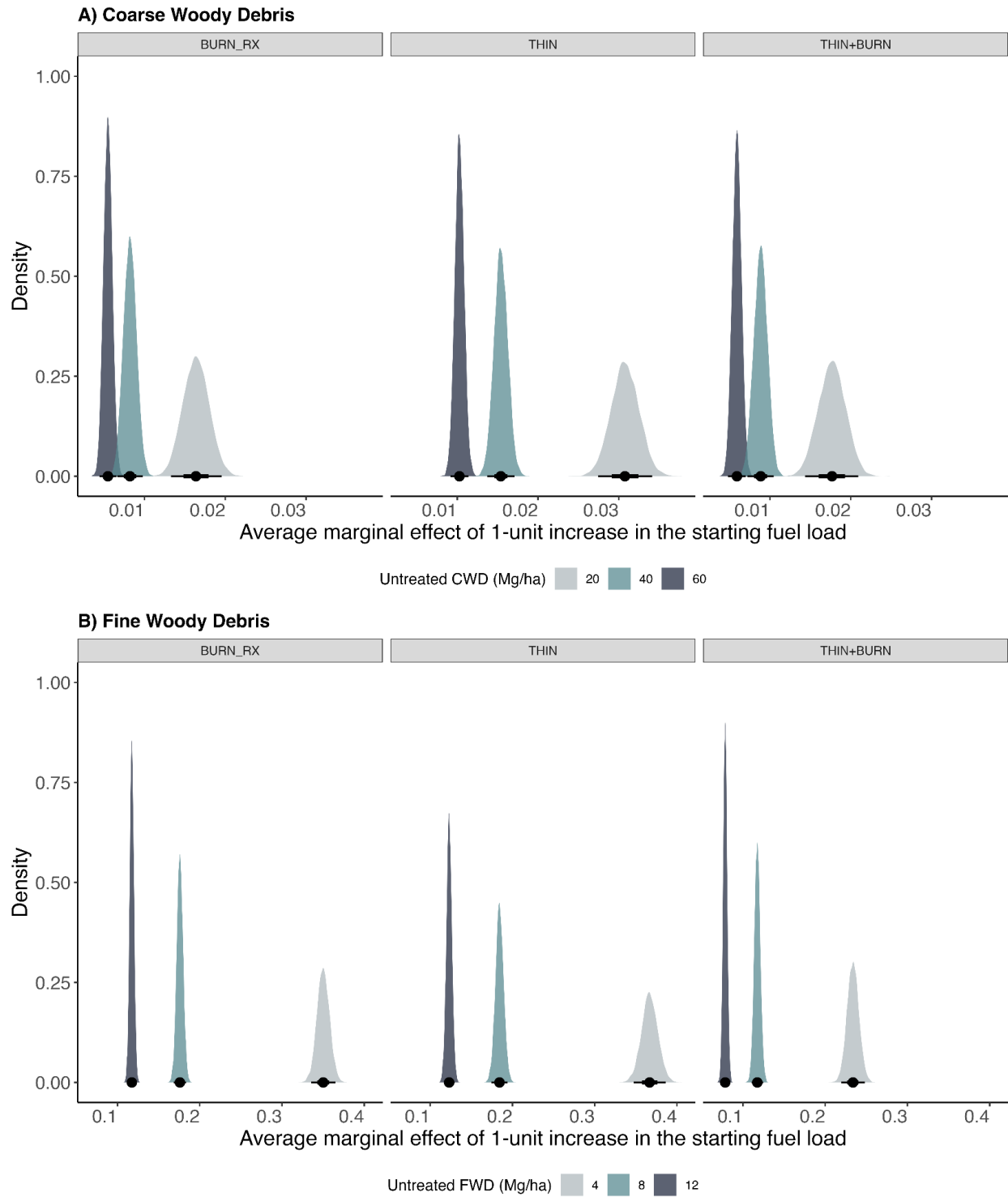


Figure 2.10: The average marginal effect of a 1-unit increase in starting fuel conditions on coarse woody debris (C) and fine woody debris (D) after BURN-only, THIN-only, and THIN+BURN treatments varied across high (dark blue), medium (blue), and low (light blue) levels of starting fuel load. Black dots show the mean effect with 80% and 95% confidence intervals shown in black.

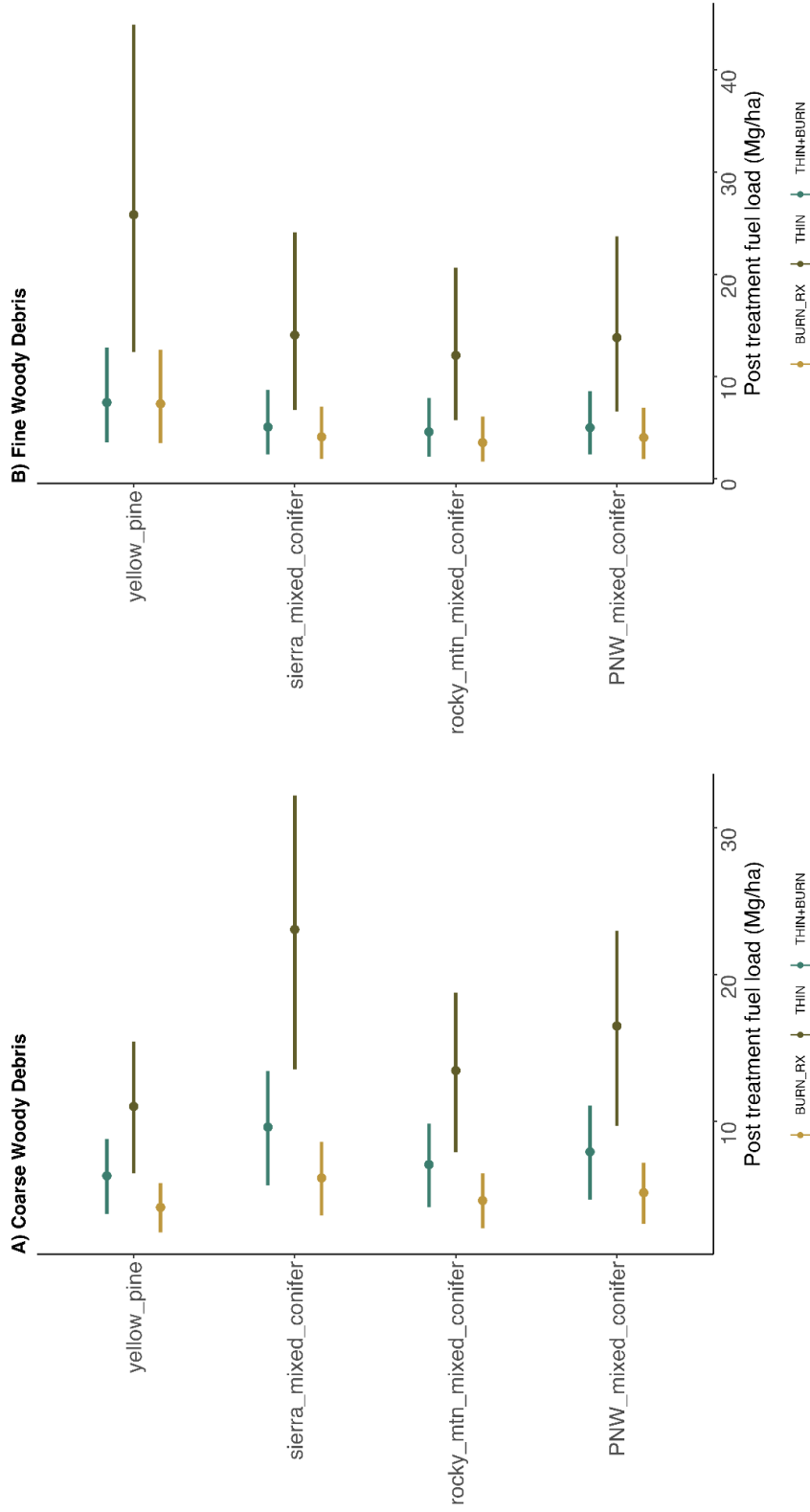


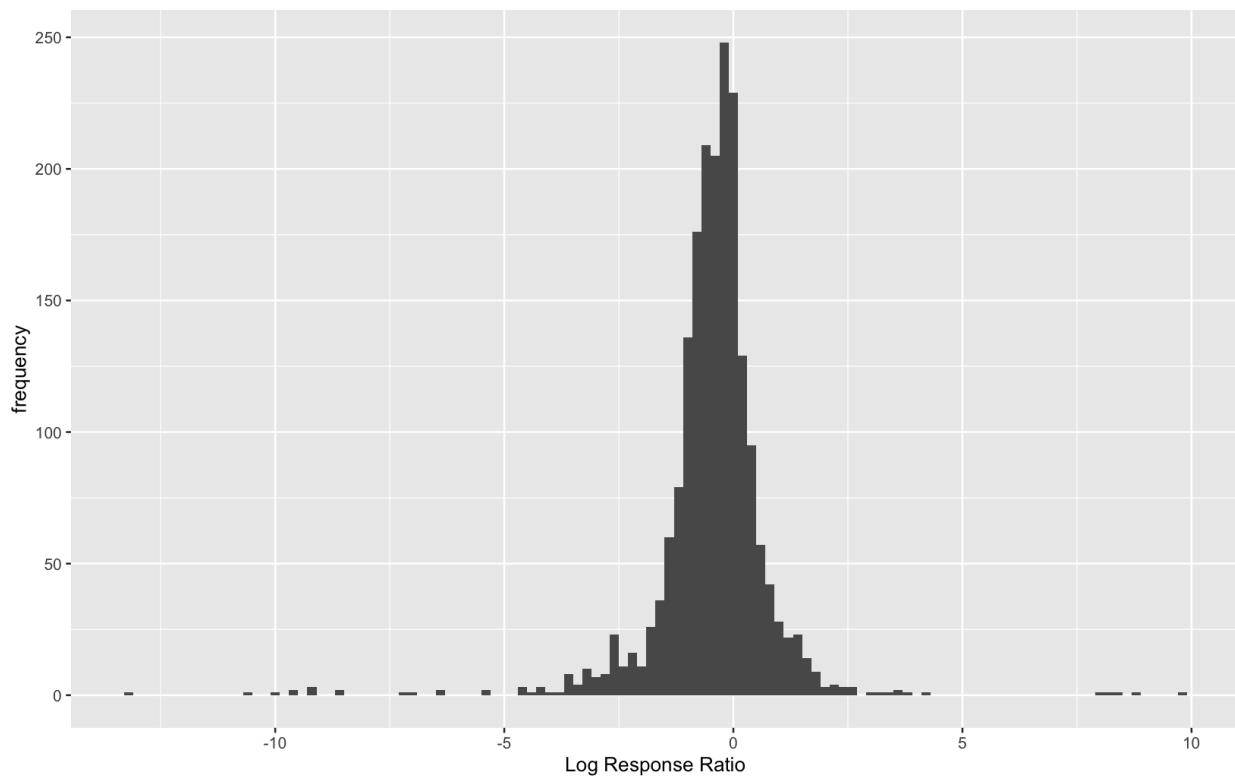
Figure 2.11: Model-fitted post-treatment fuel loads: (A) CWD and (B) FWD for different forest types after BURN (tan), THIN (brown), and THIN+BURN (blue) treatments. Dots show predicted values from the top-ranked Bayesian model and bars show the 95% credible intervals.

Supplemental information

Additional File 1 - Figure S2.1: Histogram of the individual effect sizes for all fuel variables. This histogram shows an approximately equal distribution between positive and negative values, suggesting absence of publication bias.

Additional File 2 - Table S2.1: List of the 65 publications through February 2022 that met all criteria for inclusion in the meta-analysis presented in this study. Study location(s), forest type(s), treatment age(s), treatment type(s), and whether overstory fuels or surface fuel variables were reported.

Additional File 3 - Table S2.2: Effect size, expressed as $\ln(RR)$ of overstory and surface fuel loads after prescribed burning (BURN), thinning (THIN), and thinning and burning (THIN+BURN) treatments. Model estimates, estimated error, and 95% credible intervals (CIs) are reported. Negative values indicate that the fuel treatment reduced fuel loads. Parameters whose 95% CIs do not cross zero are indicated in bold.



Supplemental Fig. S2.1. Histogram of the individual effect sizes for all fuel variables. This histogram shows an approximately equal distribution between positive and negative values, suggesting absence of publication bias.

Supplemental Table S2.1: List of the 65 publications through February 2022 that met all criteria for inclusion in the meta-analysis presented in this study. Study location(s), forest type(s), treatment age(s), treatment type(s), and whether overstory fuels or surface fuel variables were reported.

Citation	Location	State	Forest Type	Treatment Age (years)	Treatment Type										Fuel variables			
					BUR N_R X	BUR N_M W	THI N	THIN +BUR N	MA ST	MAST +BUR N	THIN +MA ST	FUL L	Overstory fuels	Surface fuels				
Agee and Lolley, 2006	Okanogan-Wenatchee NF	WA	PNW mixed conifer	1	x		x		x							x		x
Bastian, 2001	Zion NP	UT	yellow pine (PIPO)	0.1, 1, 2	x													x
Bastian, 2001b	Bryce Canyon NP	UT	SW mixed conifer	0.1, 1, 2	x													x
Battaglia et al., 2010	Southern Rocky Mountains and Colorado Plateau	CO	yellow pine (PIPO), pinyon juniper, SW mixed conifer	3.5						x								x
Busse and Gerrard, 2020	Deschutes NF	OR	yellow pine (PIPO)	0.01, 1, 4, 5, 8, 9, 11, 13, 15, 20, 24	x			x										x
Campbell et al., 2009	Tahoe NF	CA	yellow pine (PIPO) plantation	3, 16				x										x
Cansler et al., 2019	Yosemite NP	CA	sierra mixed conifer	1						x								x
Crotteau et al., 2018	University of Montana's Lubrecht Experimental forest	MT	rocky mountain mixed conifer, yellow pine (PIPO)	1	x			x										x
Crotteau et al., 2020	University of Montana's Lubrecht Experimental forest	MT	rocky mountain mixed conifer	1, 3, 4	x			x										x
Fonda and Binney, 2011	Olympic NP	WA	PNW mixed conifer	0.1, 1, 2, 3	x													x

Fulé et al., 2002	Kaibab NP, Grand Canyon	AZ	pine oak	.1, 1	x		x	x	x	x
Fule et al., 2004	Kaibab Plateau	AZ	SW mixed conifer	1, 7		x		x		x
Fule et al., 2006	Grand Canyon	AZ	pine oak, SW mixed conifer	1	x		x		x	
Goodwin et al., 2018	Teakettle Experimental Forest	CA	sierra mixed conifer	1, 10, 15	x	x		x		x
Harrod et al., 2009	Okanogan-Wenatchee NF	WA	PNW mixed conifer	1	x	x		x		
	Okanogan-Wenatchee NF, Lubrecht		PNW mixed conifer, rocky mountain							
	Experimental Forest, Blue Mountains, Goosenest	WA, OR, MT, CA, AZ	PNW mixed conifer, sierra mixed conifer, yellow pine (PIPO)	0.5, 1	x	x		x		x
Hartsough et al., 2008	Experimental Forest, Blodgett Forest, SEKI NP, Coconino NF									
Havrilla et al., 2017	Shay Mesa, Upper Colorado Plateau	UT	pinyon juniper	1, 2, 6			x			x
Hille and Stephens, 2005	Blodgett Forest	CA	sierra mixed conifer	0.02	x					x
Hood et al., 2020	Lick Creek Demonstration forest	MT	rocky mountain mixed conifer	1, 12, 22		x		x		x
Huffman et al., 2009	Kaibab NF	AZ	pinyon juniper	1	x	x		x		x
Huffman et al., 2019	Kaibab NF	AZ	pinyon juniper	1, 5, 11	x	x		x		x
Hull et al., 2020	Colville NF	WA	rocky mountain mixed conifer	11		x			x	
Hunter et al., 2011	Gila NF	NM	yellow pine (PIPO), pinyon juniper	5	x	x				x

Johnston et al., 2021	Blue Mountains	OR	yellow pine (PIPO)	1, 2, 3, 4, 5	x				x
Keifer, 1998	SEKI NP	CA	sierra mixed conifer	.02, 1, 5, 10	x			x	x
Keifer et al., 2006	SEKI NP	CA	yellow pine (PIPO), sierra mixed conifer	.02, 1, 5, 10	x			x	x
Knapp et al., 2005	SEKI NP	CA	sierra mixed conifer	1	x				x
Knapp et al., 2017	stanislaus-tuolumne experimental forest	CA	sierra mixed conifer	1, 3	x			x	
Knapp et al., 2021	stanislaus-tuolumne experimental forest	CA	sierra mixed conifer	1, 5	x			x	
Kobziar et al., 2006	Blodgett Forest	CA	sierra mixed conifer	0.7	x				x
Korb et al., 2020	San Juan Mountains	CO	SW mixed conifer	1, 5, 10	x			x	x
Levine et al., 2020	Blodgett Forest	CA	sierra mixed conifer	0.08, 0.5	x				x
Low et al., 2021	Lake Tahoe	CA	sierra mixed conifer	1, 10	x			x	
Mason et al., 2007	Lincoln NF	NM	SW mixed conifer	1, 2	x			x	x
McIver et al., 2003	La Grande	OR	SW mixed conifer	1	x			x	x
Moghaddas and Stephens, 2007	Blodgett Forest	CA	sierra mixed conifer	1	x			x	x
Morici and Bailey, 2021	Blue Mountains	OR	PNW mixed conifer	4, 15	x			x	x
North et al., 2009	Teakettle Experimental Forest	CA	sierra mixed conifer	2	x			x	x
Odland et al., 2021	Teakettle Experimental Forest	CA	sierra mixed conifer	1, 2, 15, 18	x			x	x
Perrakis and Agee, 2006	Crater Lake NP	OR	PNW mixed conifer	1	x				x

Author	Year	State	Forest Name	Forest Type	Area (ha)	Yellow Pine (PIPO)	Other	Notes
Prichard et al., 2017	1	AZ, OR, WA, MT	North Cascades NP, Okanogan NF, Umatilla NF, Wallowa-Whitman NF, Malheur NF, Ochoco NF, Deschutes NF, Crater Lake NP, Lubrecht Experimental Forest	yellow pine (PIPO)		x		
Raymond and Peterson, 2005	2	OR	Siskiyou NF	klamath mixed evergreen		x	x	
Reiner et al., 2009	1	CA	SEKI NP	yellow pine (PIPO)		x	x	
Ritter et al., 2023	1	CO	Arapaho-Roosevelt NF and Ben Delatour Scout Ranch	rocky mountain mixed conifer		x		
Roccaforte et al., 2008	1	AZ	canyon-parahant national monument	pine oak		x		
Roccaforte et al., 2010	1	AZ	canyon-parahant national monument	pine oak		x		
Sackett, 1980	1	AZ	Long Valley Experimental Forest	yellow pine (PIPO)		x		
Saud et al., 2018	5, 7	NM	Lincoln NF	SW mixed conifer		x	x	
Smith et al., 2004	0.08, 0.8, 1, 1.83	OR	Malheur NF	yellow pine (PIPO)		x		
Smith et al., 2005	1	OR	Wallowa-Whitman NF	PNW mixed conifer		x	x	
Stanton, 2009	1	OR	Crater Lake NP	PNW mixed conifer		x		
Stephens and Finney, 2002	0.1	CA	SEKI NP	sierra mixed conifer		x		

Stephens and Moghaddas, 2005b	Blodgett Forest	CA	sierra mixed conifer	0.5	x	x	x	x	x
Stephens and Moghaddas, 2005c	Blodgett Forest	CA	sierra mixed conifer	0.7	x	x	x	x	x
Stephens et al., 2009	Blodgett Forest, Lubrecht Experimental Forest, Goosenest Experimental Forest, Blue Mountains, SW Plateau, SEKI	CA, MT, WA, OR, AZ	sierra mixed conifer, rocky mountain mixed conifer, PNW mixed conifer, yellow pine (PIPO)	0.5, 1	x	x	x	x	x
Stoddard et al., 2021	Colorado Plateau	AZ	yellow pine (PIPO)	5, 10, 20				x	
Swim et al., 2014	Tahoe NF	CA	yellow pine (PIJE)	0.5, 7.5	x	x	x	x	x
Vaillant et al., 2015	Inyo NF, Klamath NF, Lake Tahoe Basin Management Unit, Lassen NF, Modoc NF, Mendocino NF, Plumas NF, San Bernardino NF, Shasta-Trinity NF, Stanislaus NF, Tahoe NF, Pike-San Isabel NF, Bluewater (AZ), Flagstaff (AZ), Red Feather Lakes (CO), Heil	CA	sierra mixed conifer, yellow pine	1, 2, 8	x	x	x	x	x
Vakili et al., 2016	Bluewater (AZ), Flagstaff (AZ), Red Feather Lakes (CO), Heil	CO, AZ	yellow pine (PIPO)	3				x	x

Valley Ranch (CO)										
Walker et al., 2006	Tahoe NF	CA	yellow pine (PIJE)	1						x
Walker et al., 2018	Sante Fe NF & Bandelier National Monument	NM	rocky mountain mixed conifer	1	x					x
Waring et al., 2016	Zion NP	UT	yellow pine (PIPO)	0.03, 1, 2, 5, 10	x					x
Webster and Halpern, 2010	SEKI NP	CA	sierra mixed conifer	2, 5, 10, 20	x					x
Westlind and Kerns, 2017	Malheur NF	OR	yellow pine (PIPO)	1	x					x
Youngblood et al., 2008	Blue Mountains	OR	PNW mixed conifer	1, 3, 6, 8	x					x
Zald et al., 2008	Teakettle Experimental Forest	CA	sierra mixed conifer	1, 2, 3	x					x

Supplemental Table S2.2: Effect size, expressed as $\ln(RR)$ of overstory and surface fuel loads after prescribed burning (BURN), thinning (THIN), and thinning and burning (THIN+BURN) treatments. Model estimates, estimated error, and 95% credible intervals (CIs) are reported. Negative values indicate that the fuel treatment reduced fuel loads. Parameters whose 95% CIs do not cross zero are indicated in bold.

	Fuel treatment	Estimate	Est. Error	Lower 95%	Upper 95%	
Overstory fuel variables	Tree density	-0.39	0.16	-0.66	-0.14	
		BURN				
		THIN	-0.90	0.18	-1.18	-0.61
		THIN+BURN	-1.32	0.17	-1.59	-1.06
	Basal area	BURN	-0.08	0.05	-0.16	-0.02
		THIN	-0.53	0.14	-0.74	-0.31
	Canopy cover	THIN+BURN	-0.61	0.10	-0.76	-0.46
		BURN	-0.11	0.11	-0.26	0.06
		THIN	-0.30	0.23	-0.63	0.05
		THIN+BURN	-0.50	0.21	-0.83	-0.17
CBD	BURN	-0.28	0.19	-0.58	0.01	
	THIN	-0.79	0.24	-1.19	-0.43	
CBH	THIN+BURN	-0.83	0.22	-1.18	-0.48	
	BURN	0.34	0.23	-0.03	0.72	
	THIN	0.58	0.27	0.16	1.00	
	THIN+BURN	0.76	0.33	0.24	1.29	
Surface fuel variables	1 hour	BURN	-0.69	0.41	-1.25	0.05
		THIN	-0.39	0.61	-1.31	0.61
	10 hour	THIN+BURN	-0.70	0.59	-1.58	0.30
		BURN	-0.50	0.38	-1.06	0.12
		THIN	0.27	0.41	-0.38	0.91

	THIN+BURN	-0.55	0.45	-1.23	0.17
100 hour	BURN	-0.82	0.23	-1.15	-0.45
	THIN	0.31	0.36	-0.25	0.86
	THIN+BURN	-0.14	0.45	-0.84	0.53
Rotten CWD	BURN	-2.26	0.78	-3.43	-0.92
	THIN	2.01	1.77	-0.85	4.96
	THIN+BURN	-0.16	1.50	-2.58	2.28
Sound CWD	BURN	-0.19	0.48	-0.97	0.56
	THIN	0.73	0.83	-0.63	2.04
	THIN+BURN	-0.07	0.65	-1.07	0.91
Duff and litter	BURN	-1.17	0.36	-1.69	-0.56
	THIN	-0.35	0.61	-1.31	0.63
	THIN+BURN	-1.18	0.76	-2.36	0.04

Chapter 3: First entry prescribed fire has greatest effects on surface fuels but limited effect in altering forest structure

Ashley R. Grupenhoff,^{1*} John Williams,¹ Joe Restaino,² Tessa Putz,¹ Hugh D. Safford^{1,3}

¹Department of Environmental Science and Policy, University of California, Davis, California 95616, USA

²Fire and Resource Assessment Program, California Department of Forestry and Fire Protection,
Sacramento California, USA

³Vibrant Planet, Incline Village, Nevada, USA

Introduction

Historically, dry forests in the western United States experienced frequent low-to-moderate intensity fires, however, fire suppression and the enforced cessation of Indigenous burning practices have altered the fire regime of these forests. 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). Yet decades of fire suppression and harvesting of old, fire-tolerant trees have resulted in high surface fuel loads, high densities of young trees, and an increasing proportion of fire-intolerant species. These changes in fuel conditions and structural changes, in combination with climate warming, have led to a massive increase in larger, higher severity fires (Agee and Skinner 2005; Westerling 2018; Williams et al. 2023), posing enormous threats to biodiversity, ecosystem resilience, and human health (Richter et al. 2019; Steel et al. 2022, 2023; Weeks et al. 2023; Williams et al. 2023).

Prescribed fire and managed wildfire are generally recognized to restore forest resilience by decreasing fire risk and restoring natural disturbance processes in historically frequent-fire yellow pine and mixed conifer (YPMC) forests (Biswell 1989; Agee and Skinner 2005; Schwilk et al. 2009; Stephens et al. 2009). While prescribed fire can successfully reduce surface and ladder fuels, thereby reducing the potential for passive crown fire and future wildfire severity (Agee and Skinner 2005; Stephens and Moghaddas 2005; Stephens et al. 2009; Prichard et al. 2020), its efficacy in restoring a more fire resistant forest structure has been highly variable. Some studies have found that when compared to treatments in which thinning was conducted before, fire alone was insufficient in restoring the more open forest structure characteristic of pre-Euro-American settlement (Covington and Wagner 1998). Other studies, however, have found that prescribed fire alone was successful in restoring structural heterogeneity and plant

diversity in the short term by removing understory biomass and soil nutrients available (Abella and Springer 2015).

In addition to reducing fire risk and restoring historic stand structure, there is a push to manage forests to maintain biodiversity (Hunter 1999). This is especially relevant in California, where over half of its plant diversity is found in the understory plant community of the Sierra Nevada (Potter 1998). Many studies have shown that the largest increases in understory species diversity and richness were observed after thinning followed by prescribed fire, when compared to thinning or prescribed fire alone (Collins et al. 2007; Wayman and North 2007; Schwilk et al. 2009). Yet these treatments have also been shown to lead to the highest abundance and richness of exotic species, while burn-only treatments did not induce enough disturbance necessary for exotic species to establish (Metlen and Fiedler 2006; Knapp et al. 2007; Collins et al. 2007).

Tree thinning followed by prescribed fire treatments has been shown to successfully restore forest structure while simultaneously reducing surface fuel loads (Pollet and Omi 2002; Moghaddas and Stephens 2007; Stephens et al. 2009; Fulé et al. 2012). However, there are many economic and ecological constraints to thinning. For one, thinning is more expensive than prescribed fire, and these costs are likely going to increase (North et al. 2012). Additionally, mechanical equipment can have adverse effects on the landscape by disturbing soil properties and introducing non-native species (Battles et al. 2001; Dudley et al. 2021). Prescribed fire alone can be successful at reducing potential fire behavior through the reduction of surface and ladder fuels (Stephens and Moghaddas 2005; Vaillant et al. 2009).

With a push to increase prescribed fire use, it is vital to understand the effectiveness of prescribed fire in achieving qualitative objectives such as wildfire risk mitigation and improved ecological resilience. While the breadth of research examining prescribed fire effects has grown substantially in the past few decades (e.g., The National Fire and Fire Surrogate study; (Schwilk et al. 2009; Stephens et al. 2009), there are still few studies examining regional trends.

Despite increases in the area burned, some studies have found that low-intensity first-entry prescribed fires are not sufficient for effectively meeting ecological objectives (Fule et al. 2004; Schwilk et al. 2009; Webster and Halpern 2010). We use data from the California Prescribed Fire Monitoring Program (CPFMP), a joint effort by the University of California Davis and CAL FIRE, to examine whether current prescribed fire practices are meeting quality objectives in yellow pine and mixed conifer (YPMC) forests. Specifically, we ask: 1) To what extent does current prescribed fire reduce surface fuels? 2) What factors most influence fuel consumption in YPMC forests? 3) To what extent does current prescribed fire alter forest structure and species diversity? 4) What environmental variables best explain prescribed fire effects on native and nonnative species?

Methods

Study site

This study includes 19 project sites across northern and central California sampled by the CPFMP (Fig 3.1). We focus on areas burned in mixed conifer or yellow pine forest types, which historically experienced low to moderate intensity, frequent fire. Presettlement fire return intervals in these forests were frequent, burning every 12-20 years (Safford and Stevens 2017). The average elevation of the study sites is 1984 meters and ranges from 566 to 2669 meters. Vegetation in these forests is dominated by yellow pines, which include ponderosa pine (*Pinus ponderosa* Laws) and Jeffrey pine (*P. jeffreyi* Grev. & Balf.), white fir (*Abies concolor* Gord. & Glend), sugar pine (*Pinus lambertiana* Dougl.), California black oak (*Quercus kelloggii* Newb.), Douglas-fir (*Pseudotsuga menziesii* Franco), and incense-cedar (*Calocedrus decurrens* (Torr.) Floren.). Some stands of red fir (*A. magnifica* A. Murray bis) were found at higher elevations and at moister sites. Climate across the study sites is Mediterranean, with the majority of precipitation occurring in winter and spring. Precipitation at the sites ranges from 360 to 2247

mm. Mean minima in January range from -10.3 to 5.2 °C and mean maxima in July range from 21.5 to 35.6 °C (Table 3.1).

Field measurements

In each of the 19 sites, 0.04 ha permanent plots were stratified across burn units (overall n=697). Field data were collected using a modified version of the USDA Forest Service (USFS) common stand exam (“CSE”; USDA Forest Service 2012). This protocol includes quantification of overstory and understory structure, standing and downed trees, surface fuels and woody debris, and ground cover. Measurements were taken before and after prescribed burns. Of the 697 plots implemented, 245 of these burned.

Vegetation measurements

Tree measurements were collected for all trees greater than 7.62 cm diameter at breast height (DBH) in the 0.04 ha plot before and one year after prescribed burn treatments. Species, status (live or dead), DBH, height, and height-to-live-crown were recorded. For all snags, DBH and height were recorded. A smaller 0.006 ha circular plot, sampled at the CSE plot center, was used to record the number, species, height, and status of all saplings (>1.4 m tall) and seedlings (<1.4 m tall). Ocular estimates of percentage cover by trees, shrubs, grasses, and herbs were made in the full 0.04 ha plot. Ground cover data were estimated for the following categories: rock (particles >2 mm diameter), bare ground, litter, basal vegetation, and woody debris.

In the full 0.04 ha plot, vegetation composition was recorded by identifying all plants to the species level and estimating the percent cover for each species. 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, introduced) 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 (gives weight to rare

species) by plant origin (native or introduced) using the vegan package in R (R Core Team 2021; Oksanen et al. 2023).

Ground and surface fuel load

Surface fuels were measured using the planar intercept method (Brown 1982) at each plot before and immediately after prescribed burn treatments. Four 11.4-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. Fine 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 respectively). 1- and 10-hour fuel classes were sampled between meters 0 and 2; 100-hour fuels were sampled between 0 and 4 m; and 1000-hour fuels were sampled between 0 and 11.4 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 0 and 4 m from the beginning of each sub-transect, for a total of 8 measurements. Litter is the layer of undecomposed material, and duff consists of fermenting and decomposing organic material.

Fine woody material, CWD, and litter and duff measurements were summarized at the transect scale and were weighted based on the average basal area proportion of tree species in the plot to account for differences in fuel characteristics across study areas (Van Wagtenonk et al. 1998; Stephens 2001). In order to normalize fuel consumption by pre-burn fuel loads, we calculated consumption as a proportion (Equation 1). In a few instances, the post-burn fuel load as sampled with Brown's protocol, was greater than the pre-burn fuel load. For these cases, we treated total consumption as zero.

$$\text{Equation 1: } \frac{\text{PreFire Fuel load} - \text{PostFire Fuel load}}{\text{PreFire Fuel load}}$$

Prescribed fire treatments

Of the 19 project sites, 12 were treated with prescribed fire. The primary objective of these burns was to reduce fire risk and restore forest health. Fire weather indices on burn day were obtained from the most representative Remote Automated Weather Station (RAWS) for each site. Fire weather-related measures include temperature, wind speed, relative humidity, fuel moisture, and days since precipitation (Table 3.1).

Statistical analyses

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. Due to the non-normal distribution of the fuel data, Kruskal-Wallis tests were performed to identify differences before and after prescribed fire.

Mechanisms associated with fuel consumption

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); therefore, 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, canopy cover, basal area proportions of pine, fire, and incense cedar, fuel moisture percent, relative humidity, days since last precipitation, elevation, slope, and aspect. Many of these variables are highly correlated, so to reduce multicollinearity, we identified all predictor variables that were correlated ($R > 0.5$) and retained the variable from each highly correlated pair that showed the highest correlation with fuel consumption (Equation 2).

Equation 2: immediate consumption $\sim \text{Beta}(\mu_{ij}, \phi)$

$$\begin{aligned} \text{logit}(\mu_{ij}) = & \alpha + \beta_{\text{prefire mass}} \text{prefire mass} + \beta_{\text{pBA pine}} \text{pBA pine} + \beta_{\text{pBA fir}} \text{pBA fir} + \\ & \beta_{\text{pBA cade}} \text{pBA cade} + \beta_{\text{prefireTreeDen}} \text{prefire TreeDen} + \\ & \beta_{\text{prefireSnagDen}} \text{prefireSnagDen} + \beta_{\text{elevation}} \text{elevation} + \\ & \beta_{\text{slope}} \text{slope} + \beta_{\text{aspect}} \text{aspect} + \beta_{\text{fuelmoisture}} \text{fuelmoisture} \\ & \alpha \sim \text{normal}(0, 100) \end{aligned}$$

Prescribed fire effects on forest structure

To determine how forest structure differed before and after prescribed fire, we modeled two forest structure variables (basal area and tree density) of dominant tree genera using a Bayesian gamma regression model (Equation 3) and diameter size class using a Bayesian hurdle-gamma regression model (Equation 4). Both response variables have a gamma distribution, and we used a hurdle model for the diameter size class due to the occurrence of zeros. We included a random effect for each site to account for the non-independence of plots within each site.

Equation 3: forest structure variable $\sim \text{Gamma}(\mu_{ij}, \phi)$

$$\text{logit}(\mu_{ij}) = \alpha + \beta_{\text{pre post fire}} \text{pre post fire} * \beta_{\text{species genera}} \text{Species Genera} + (1|\text{site})$$

Equation 4: forest structure variable $\sim \text{Gamma Hurdle}(\mu_{ij}, \phi)$

$$\text{logit}(\mu_{ij}) = \alpha + \beta_{\text{pre post fire}} \text{pre post fire} * \beta_{\text{diamclass}} \text{diamclass} + (1|\text{site})$$

$$HU_{ij} = \alpha + \beta_{\text{diamclass}} \text{diamclass}$$

Prescribed fire effects on species richness and diversity

We fit species accumulation curves to ensure that understory vegetation was adequately sampled (Fig. 3.2). To determine the effect of prescribed fire on understory species richness and Shannon diversity, we compared understory species richness and diversity before, 1 year after, and 2 years after prescribed fire. Four models were created estimating native richness, introduced richness, native Shannon diversity, and introduced 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 (variance > mean). For Shannon diversity, we used a Gaussian distribution since the data met assumptions of normality.

Mechanisms associated with post-fire species richness and diversity

To test mechanisms associated with immediate effects on species richness and diversity, we modeled native and introduced species richness and Shannon diversity as a function of possible environmental covariates. The covariates we included were elevation (m), slope (degree), aspect, canopy cover (%), live tree density, litter depth (cm), bare soil (%), and pre-treatment richness or Shannon diversity to account for pretreatment conditions. We used a negative binomial distribution to model richness and a Gaussian distribution for Shannon diversity.

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 those instances when the 95% credible intervals did not cross zero.

Results

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

Prefire total surface fuel loading averaged 42.4 Mg/ha (2.6 Mg/ha to 282 Mg/ha) and was reduced by an average of 70% immediately after burning. Out of all fuel variables, litter and duff contributed the most to total surface fuel loading before fire (87%) and after fire (81.3%). Prescribed fire significantly reduced fine woody debris (FWD) by 55%, coarse woody debris (CWD) by 60%, litter load by 66%, and duff by 75% (Fig. 3.3, $p < 0.05$). The most important predictors were prefire fuel mass ($\beta_{\text{prefire fuel mass}} = 0.20$, CIs = 0.15 to 0.27), elevation ($\beta_{\text{elevation}} = 0.50$, CIs = 0.22 to 0.78), live tree density ($\beta_{\text{live tree density}} = 0.20$, CIs = 0.00 to 0.38, and snag density ($\beta_{\text{snag density}} = 0.31$, CIs = 0.11 to 0.49) (Fig. 3.4).

Prescribed fire had a limited effect on forest structure

Overall prescribed fire did not significantly reduce tree density or basal area of live trees and snags (Table 3.4). Pre-fire live tree density averaged 331 stems/ha (25 to 1334 stems/ha) and had a nonsignificant mean reduction of 24% after prescribed fire. Snag density showed a nonsignificant increase by 61% after prescribed fire, with an average of 114 stems/ha (25 to 593 stems/ha) before fire and 184 stems/ha (24 to 1310 stems/ha) after fire. Live basal area averaged 43 m²/ha (0.20 to 269 m²/ha) before prescribed fire and was reduced by a (nonsignificant) average of 8.6% one year after treatment. Snag basal area had no significant change after prescribed fire and averaged 15.8 m²/ha (0.12 to 194 m²/ha) before fire and 14.3 m²/ha (0.12 to 111) after fire.

Prior to treatment, tree density and basal area varied across genera and size classes. Most trees were in small size class distribution categories (<20 cm and 20-40 cm dbh), and mostly fir species (Fig. 3.6). Prescribed fire treatments reduced the density of fir species by 11% ($\beta_{\text{prepostfire:fir_spp}} = 0.12$, CIs = -0.07 to 0.30), however, this was not significant (Fig. 3.6A). There

were no significant reductions in basal area across genera (Fig. 3.6C). Prescribed fire moderately reduced the density of trees <20 cm dbh by 31% ($\beta_{\text{prepostfire};[<20]} = 0.38$, CIs = 0.19 to 0.57) and trees 20-40 cm dbh by 15% ($\beta_{\text{prepostfire};[20-40]} = 0.16$, CIs = 0.01 to 0.31; Fig. 3.6B). All other size classes did not significantly change. The largest proportion of basal area was in the 20-40 cm dbh size class (Fig. 3.6D). Despite a 27% reduction in basal area of the smallest size class (<20 cm dbh), there were no significant reductions across any size class.

Immediate effects (1-2 years) of prescribed fire treatment on native and non-native species richness and diversity

Both native and non-native species richness increased after prescribed fire. However, this effect was not significant until two years post-treatment (Fig. 3.7). Average prefire native species richness was 15 ± 0.7 and significantly increased to 21 ± 1.9 (an increase of 30%) two years after prescribed fire ($\beta_{\text{prefire-postfire2yr}} = -0.93$, CIs = -1.20 to -0.68). Nonnative richness was substantially lower at 0.26 ± 0.05 species, but this also significantly increased by 87% ($\beta_{\text{prefire-postfire2yr}} = -3.36$, CIs = -4.81 to -2.16). Comparably to species richness, native Shannon diversity increased after fire, however it was significantly different only one year after fire ($\beta_{\text{prefire-postfire1yr}} = -0.36$, CIs = -0.55 to -0.20, Fig. 3.7). Nonnative Shannon diversity followed similar trends to nonnative species richness and significantly increased 2 years after prescribed fire ($\beta_{\text{prefire-postfire2yr}} = -0.34$, CIs = -0.43 to -0.25).

Discussion

This paper aims to evaluate the effectiveness of prescribed fire in altering surface fuels and certain ecological variables in California's YPMC forests that were historically maintained by frequent fire (Safford and Stevens 2017). Our findings highlight that first-entry prescribed fire significantly reduced surface fuels but had a limited effect on forest structure. Overall, prescribed fire did not significantly reduce tree density or basal area of live trees or snags.

Nevertheless, species richness and Shannon diversity significantly increased two years post-fire.

One main objective of prescribed fire is to reduce surface fuels, which can reduce fireline intensity and crown fire potential (Agee and Skinner 2005; Stephens et al. 2009). We found that prescribed fire successfully reduced coarse and woody surface fuel variables, with the most significant reductions in duff and litter (75% and 66%, respectively). It is important to note that while prefire fuel loadings across all study sites were similar to that of a fire-excluded Sierra Nevada forest, CWD and litter loads were lower than previously reported (Lydersen et al. 2015; Cansler et al. 2019). With the lack of large, down trees at most sites, unit preparation and local firewood collecting may explain these low fuel loads (Stephens 2004).

Prefire fuel mass, elevation, and overstory trees significantly influenced fuel consumption immediately after fire, corroborating other studies in Sierra Nevada YPMC forests (Lydersen et al. 2015; Levine et al. 2020). The significance of prefire fuel mass highlights the importance of starting fuel conditions in fuel consumption. This finding supports other studies that showed that starting fuel load and number of burn entries impact burn efficacy (Levine et al. 2020). While we have limited data on multiple-entry burns in this study, first-entry burns with higher starting fuel loads had the most significant consumption. This finding is likely due to a more homogeneous fuel bed, which allows for more complete fuel consumption (Miller and Urban 1999; Moghaddas and Stephens 2007; Levine et al. 2020).

Overstory live tree density and snag density were significant covariates for fuel consumption. An increase in tree density results in higher fuel production and alters microclimate conditions such as temperature and relative humidity, which is why we most likely see this increase in fuel consumption (Keane 2008; Fry and Stephens 2010; Lydersen et al. 2015). Unlike other studies in YPMC forests in the Sierra Nevada, we found little influence of species composition variables on fuel consumption (Van Wagtendonk and Moore 2010; Lydersen et al. 2015; Levine et al. 2020). This is likely due to the high levels of surface fuels that

have accumulated after almost a century of fire suppression, creating a homogenous fuel bed that cancels out any effect of fine-scale variation in overstory composition. As such, the effect of species composition will likely be more critical during multiple-entry burns (Van Wagtendonk and Moore 2010; Lydersen et al. 2015; Levine et al. 2020)

We found no significant changes to forest structure after prescribed fire. However, there were slight, albeit non-significant, reductions of trees in small-size class distribution categories (<40 cm dbh) and fir species. The prescribed burns were conducted under mild conditions when extreme fire behavior was low. This lack of mortality suggests that current low-to-moderate first-entry prescribed fire may not be sufficient to drive structural change (Schwilk et al. 2009; Fulé et al. 2012; Waring et al. 2016). YPMC stands prior to Euro-American settlement had an average of 159 trees/ha, with a range of 60 to 328 trees/ha, and a basal area of 35 m²/ha, with a range of 21 to 54m²/ha (Safford and Stevens 2017). Even after prescribed fire, these sites show higher densities than these historical estimates. Our data show the immediate effects of prescribed fire; however, there may be a lag response in mortality (Thies et al. 2006; Hood et al. 2007). These highly dense stands are at risk for high-severity wildfires and are less resilient to insect outbreaks, such as bark beetles (Fettig et al. 2007) and climate change (Young et al. 2020). While this study shows that first-entry prescribed fire induces little change in forest structure, 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 tree mortality.

Despite the lack of significant changes to forest structure, species richness and Shannon diversity significantly increased two years post-fire. Many variables are associated with changes to the understory plant community, such as 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 to change understory diversity long-term, fire has an essential role by altering soil

nutrient availability and stimulating germination through heat and smoke (Kauffman and Martin 1990; Abella et al. 2007). These fire-specific germination cues, in addition to a reduction to surface fuels, are likely the reason we see a significant increase in diversity two years after treatment. Further reduction in canopy cover may be necessary for substantially increasing the understory flora in the long term (Knapp et al. 2007; Abella and Springer 2015).

We found a significant increase in non-native species richness two years after prescribed fire, but this was a minimal increase of only two nonnatives on average. Non-native species generally increase substantially after mechanical thinning and thinning followed by burning treatments (Collins et al. 2007; Schwilk et al. 2009; Dudley et al. 2021). The minimal increase in non-native species is an added benefit of burn-only treatments; however, recruitment of these disturbance-tolerant species may have long-lasting effects on the understory community (Dudney et al. 2021)

Our findings are from 12 prescribed fires across a broad geographic scope. While we are able to compare burn effects across sites with variable environmental conditions, we are unable to parse apart specific within-stand variables linked to fuel consumption and changes to species diversity. Despite this, these findings apply to the management of most YPMC forests in the Sierra Nevada and provide important metrics to which current prescribed fire is altering surface fuels and ecological variables such as forest structure and species diversity. Continuity and expansion of long-term monitoring programs, such as the CPFMP, will be vital for informing fire managers.

While the primary goal of prescribed fire is to mitigate future stand-replacing fires by reducing fuel loads, it can also successfully restore stand structure and composition to restore ecosystem resilience. We found prescribed fire to be effective at reducing surface fuels but ineffective at incorporating spatial and structural heterogeneity (Larson and Churchill 2012). Repeat treatments of prescribed fire may be necessary to restore conditions typical of frequent-fire forests (Sackett 1980; Stephens et al. 2009, 2020; Waring et al. 2016).

Literature cited

- Abella SR, Springer JD (2015) Effects of tree cutting and fire on understory vegetation in mixed conifer forests. For Ecol Manag 335:281–299.
<https://doi.org/10.1016/j.foreco.2014.09.009>
- Abella SR, Springer JD, Covington WW (2007) Seed banks of an Arizona Pinus ponderosa landscape: responses to environmental gradients and fire cues. Can J For Res 37:552–567. <https://doi.org/10.1139/X06-255>
- Agee JK, Skinner CN (2005) Basic principles of forest fuel reduction treatments. For Ecol Manag 211:83–96. <https://doi.org/10.1016/j.foreco.2005.01.034>
- Battles JJ, Shlisky AJ, Barrett RH, et al (2001) The effects of forest management on plant species diversity in a Sierran conifer forest. For Ecol Manag 146:211–222.
[https://doi.org/10.1016/S0378-1127\(00\)00463-1](https://doi.org/10.1016/S0378-1127(00)00463-1)
- Biswell HH (1989) Prescribed burning. Calif Wildlandsvegetation Manag Berkeley Univ Calif Press 255
- Brown JK (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 Softw 80:. <https://doi.org/10.18637/jss.v080.i01>
- Cansler CA, Swanson ME, Furniss TJ, et al (2019) Fuel dynamics after reintroduced fire in an old-growth Sierra Nevada mixed-conifer forest. Fire Ecol 15:16.
<https://doi.org/10.1186/s42408-019-0035-y>
- Collins BM, Moghaddas JJ, Stephens SL (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>
- Covington W, Wagner PK (1998) Conference on Adaptive Ecosystem Restoration and

Management: Restoration of Cordilleran Conifer Landscapes of North America. DIANE Publishing

- Dudney J, York RA, Tubbesing CL, 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>
- Fettig CJ, Klepzig KD, Billings RF, et al (2007) The effectiveness of vegetation management practices for prevention and control of bark beetle infestations in coniferous forests of the western and southern United States. *For Ecol Manag* 238:24–53. <https://doi.org/10.1016/j.foreco.2006.10.011>
- Fry DL, Stephens SL (2010) Stand-level spatial dependence in an old-growth Jeffrey pine – mixed conifer forest, Sierra San Pedro Mártir, Mexico. *Can J For Res* 40:1803–1814. <https://doi.org/10.1139/X10-122>
- Fule PZ, Cocke AE, Heinlein TA, Covington WW (2004) Effects of an intense prescribed forest fire: is it ecological restoration? *Restor Ecol* 12:220–230
- Fulé PZ, Crouse JE, Roccaforte JP, Kalies EL (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>
- Hankin LE, Anderson CT (2022) Second-Entry Burns Reduce Mid-Canopy Fuels and Create Resilient Forest Structure in Yosemite National Park, California. *Forests* 13:1512
- Hood SM, McHugh CW, Ryan KC, 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>
- Hunter ML (1999) *Maintaining Biodiversity in Forest Ecosystems*. Cambridge University Press
- Kauffman JB, Martin RE (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>
- Keane RE (2008) Biophysical controls on surface fuel litterfall and decomposition in the northern

- Rocky Mountains, USA. *Can J For Res* 38:1431–1445. <https://doi.org/10.1139/X08-003>
- Knapp EE, Schwilk DW, Kane JM, Keeley JE (2007) Role of burning season on initial understory vegetation response to prescribed fire in a mixed conifer forest. *Can J For Res* 37:11–22. <https://doi.org/10.1139/x06-200>
- Larson AJ, 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 JI, Collins BM, York RA, 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 EC (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 JM, Collins BM, Knapp EE, 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>
- Lydersen JM, North MP, Knapp EE, Collins BM (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>
- Metlen KL, Fiedler CE (2006) Restoration treatment effects on the understory of ponderosa pine/Douglas-fir forests in western Montana, USA. *For Ecol Manag* 222:355–369. <https://doi.org/10.1016/j.foreco.2005.10.037>
- Miller C, Urban DL (1999) Interactions between forest heterogeneity and surface fire regimes in the southern Sierra Nevada. 29:

- 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>
- 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>
- Oksanen J, Simpson G L, Blanchet F G, et al (2023) *vegan: Community Ecology Package*
- Pollet J, Omi P N (2002) Effect of thinning and prescribed burning on crown fire severity in ponderosa pine forests. *Int J Wildland Fire* 11:1. <https://doi.org/10.1071/WF01045>
- Potter D A (1998) *Forested Communities of the Upper Montane in the Central and Southern Sierra Nevada*. U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station
- 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>
- R Core Team (2021) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria
- 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 Forest Service, Rocky Mountain Forest and Range Experiment Station
- 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
- 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>
- Steel ZL, Fogg AM, 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 ZL, Jones GM, Collins BM, 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>
- Stephens SL (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 SL (2004) Fuel loads, snag abundance, and snag recruitment in an unmanaged Jeffrey pine–mixed conifer forest in Northwestern Mexico. *For Ecol Manag* 199:103–113. <https://doi.org/10.1016/j.foreco.2004.04.017>
- Stephens SL, Battaglia MA, Churchill DJ, et al (2020) Forest Restoration and Fuels Reduction: Convergent or Divergent? *BioScience* biaa134. <https://doi.org/10.1093/biosci/biaa134>
- Stephens SL, Moghaddas JJ (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 SL, Moghaddas JJ, Edminster C, et al (2009) Fire treatment effects on vegetation structure, fuels, and potential fire severity in western U.S. forests. *Ecol Appl* 19:305–320. <https://doi.org/10.1890/07-1755.1>
- Thies WG, Westlind DJ, 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>
- USDA Forest Service Region 5 (2012) Common Stand Exam Field Guide. USDA Forest Service. <http://www.fs.fed.us/nrm/fsveg/index.shtml>

- Vaillant NM, Fites-Kaufman JA, Stephens SL, 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 Wagtendonk JW, Benedict JM, Sydoriak WM (1998) Fuel Bed Characteristics of Sierra Nevada Conifers. *West J Appl For* 13:73–84. <https://doi.org/10.1093/wjaf/13.3.73>
- Van Wagtendonk JW, Moore PE (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>
- Waring KM, Hansen KJ, Flatley WT (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 RB, 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 KM, Halpern CB (2010) Long-term vegetation responses to reintroduction and repeated use of fire in mixed-conifer forests of the Sierra Nevada. *Ecosphere* 1:art9.
<https://doi.org/10.1890/ES10-00018.1>
- Weeks J, Miller JED, Steel ZL, 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 AL (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 JN, Safford HD, 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>

Young DJN, 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:.
<https://doi.org/10.1002/eap.2002>

Figures and Tables

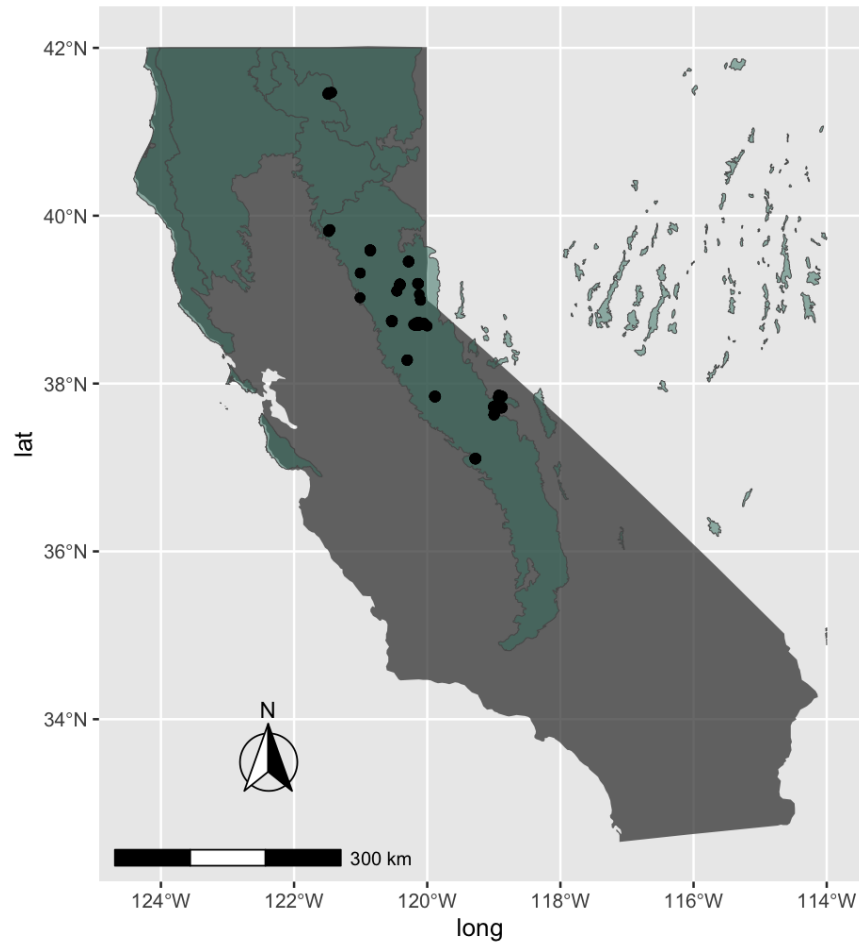


Figure 3.1: Location of plot locations (black dots) across northern California. The geographic distribution of temperate conifer forests is shown by the turquoise polygon.

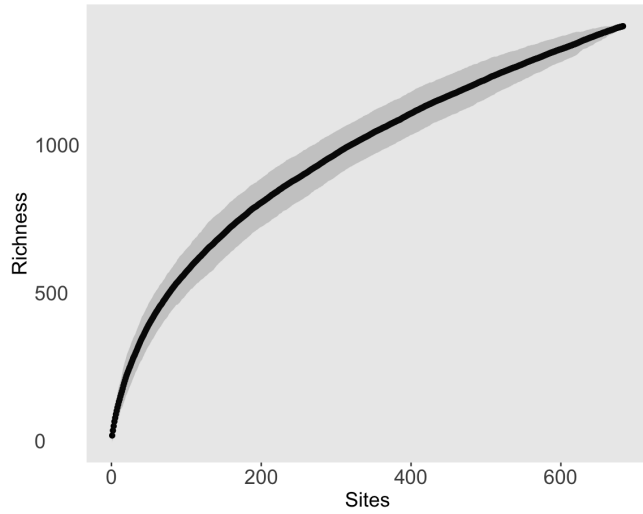


Fig 3.2: Species accumulation curve for understory vegetation sampled before and after prescribed fire treatment.

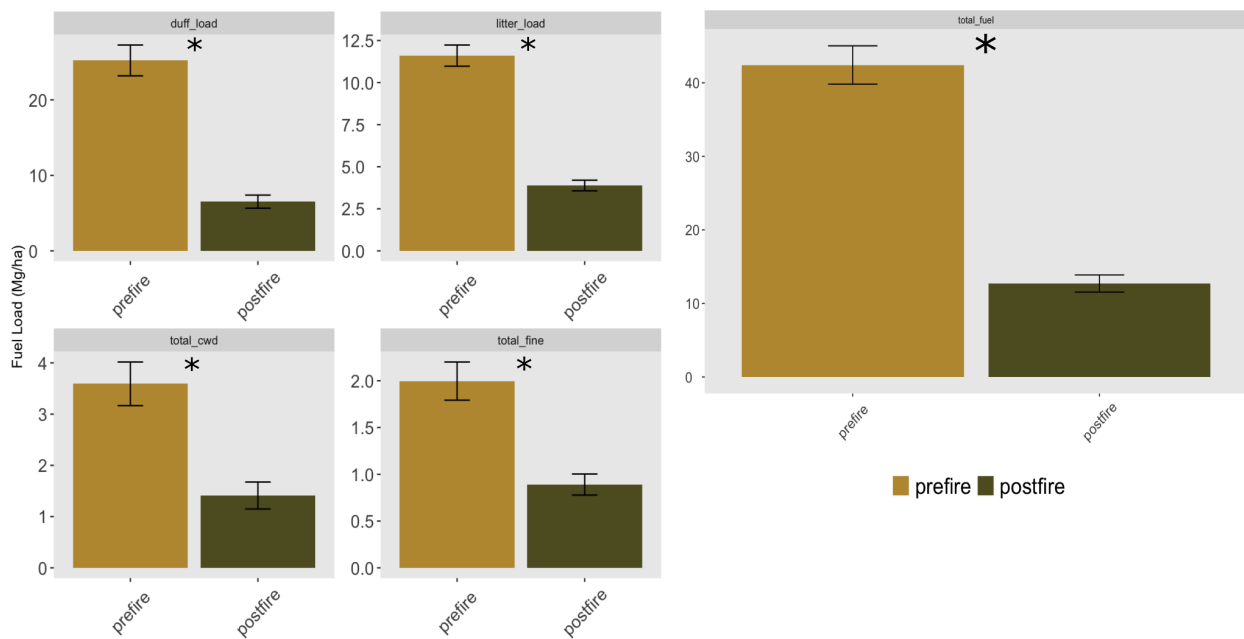


Figure 3.3: Changes in surface fuel loading after prescribed fire. Bar values are the mean surface fuel loading values (Mg/ha) and ± 1 standard error. Stars indicate a significant difference between pre- and post-fire fuel load estimates for each fuel load.

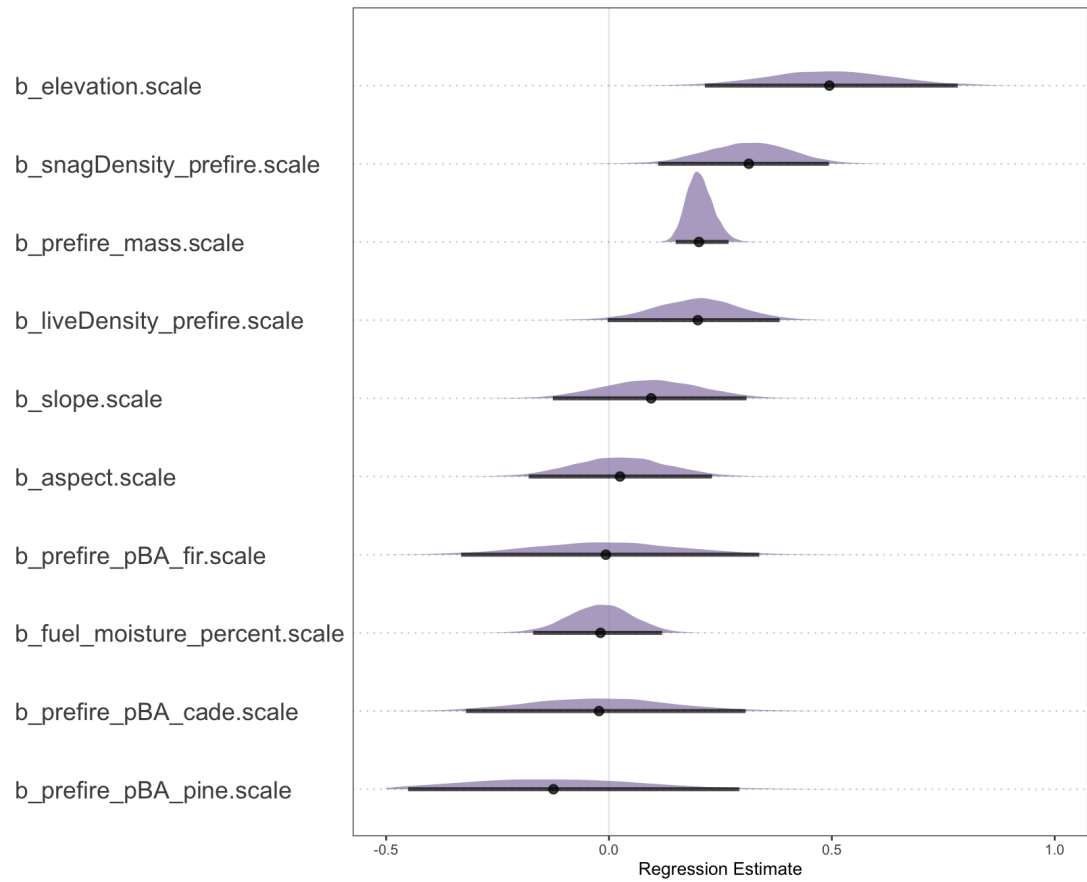


Figure 3.4: Regression estimates associated with fuel consumption after prescribed fire. Values are coefficient estimates with corresponding error bars from the final model of total fuel consumption.

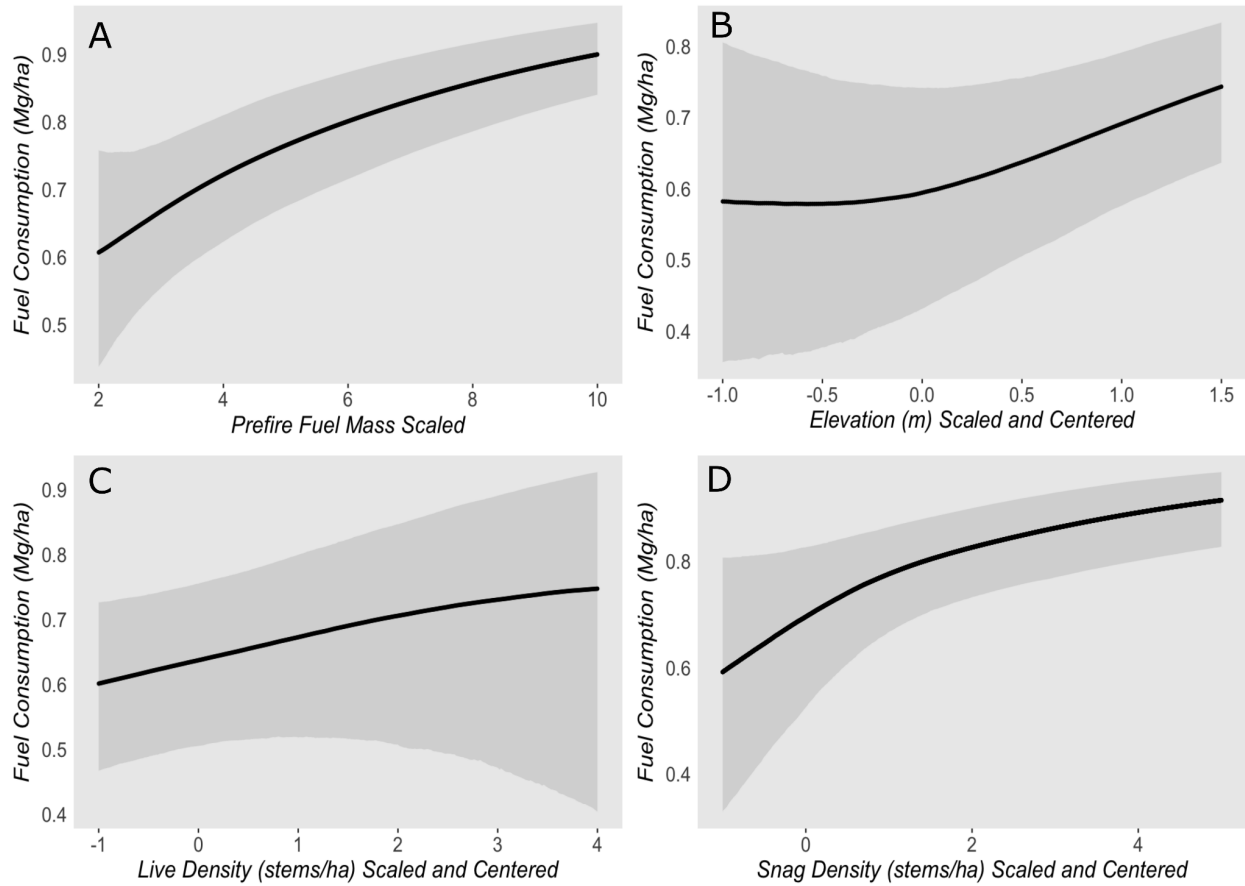


Figure 3.5: Fuel consumption varies with starting fuel conditions (A), elevation (B), live tree density (C), and snag density (D). Predicted values from the top-ranked Bayesian model with 95% credible intervals.

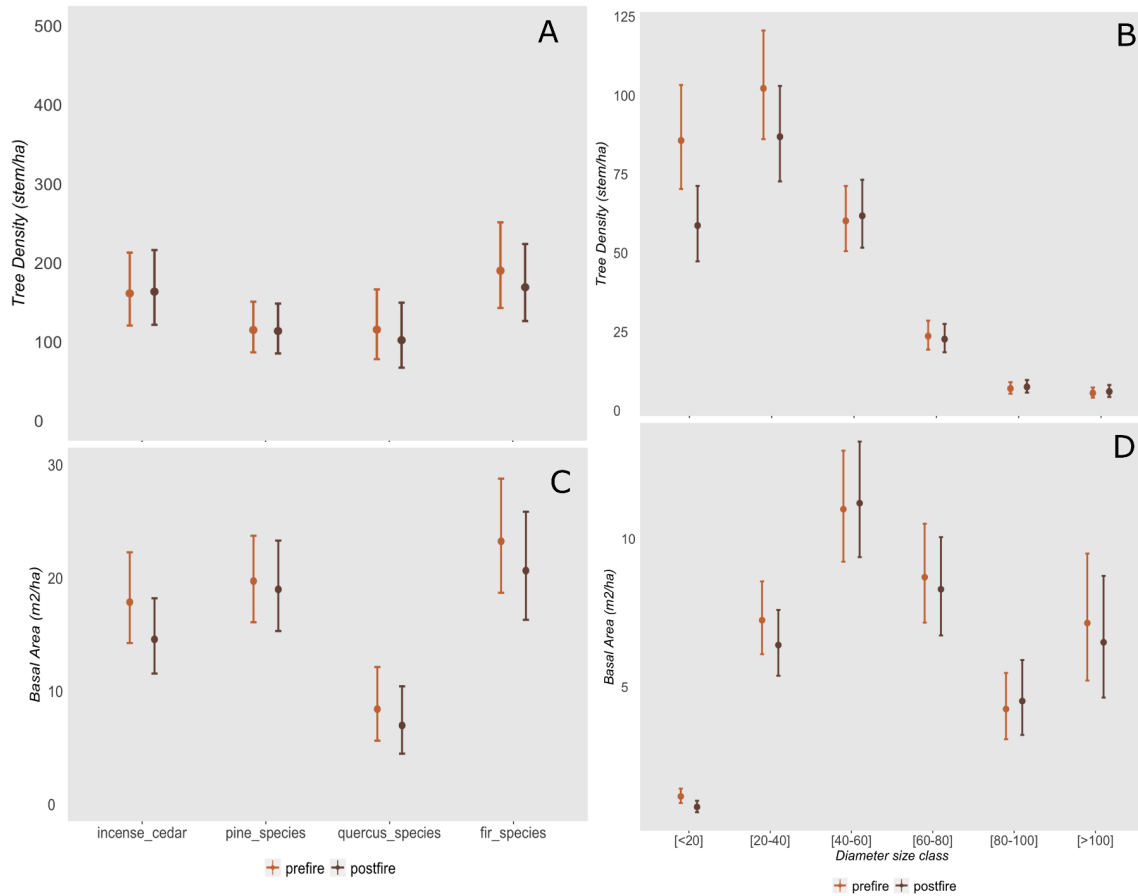


Figure 3.6. Pre-treatment (orange) and one year post-treatment (brown) tree density (stems/ha) across common genera (A), basal area (m²/ha) across common genera (C), tree density (stems/ha) across diameter class (B), and basal area (m²/ha) across diameter class (D). Predicted values from the top-ranked Bayesian model with 95% credible intervals.

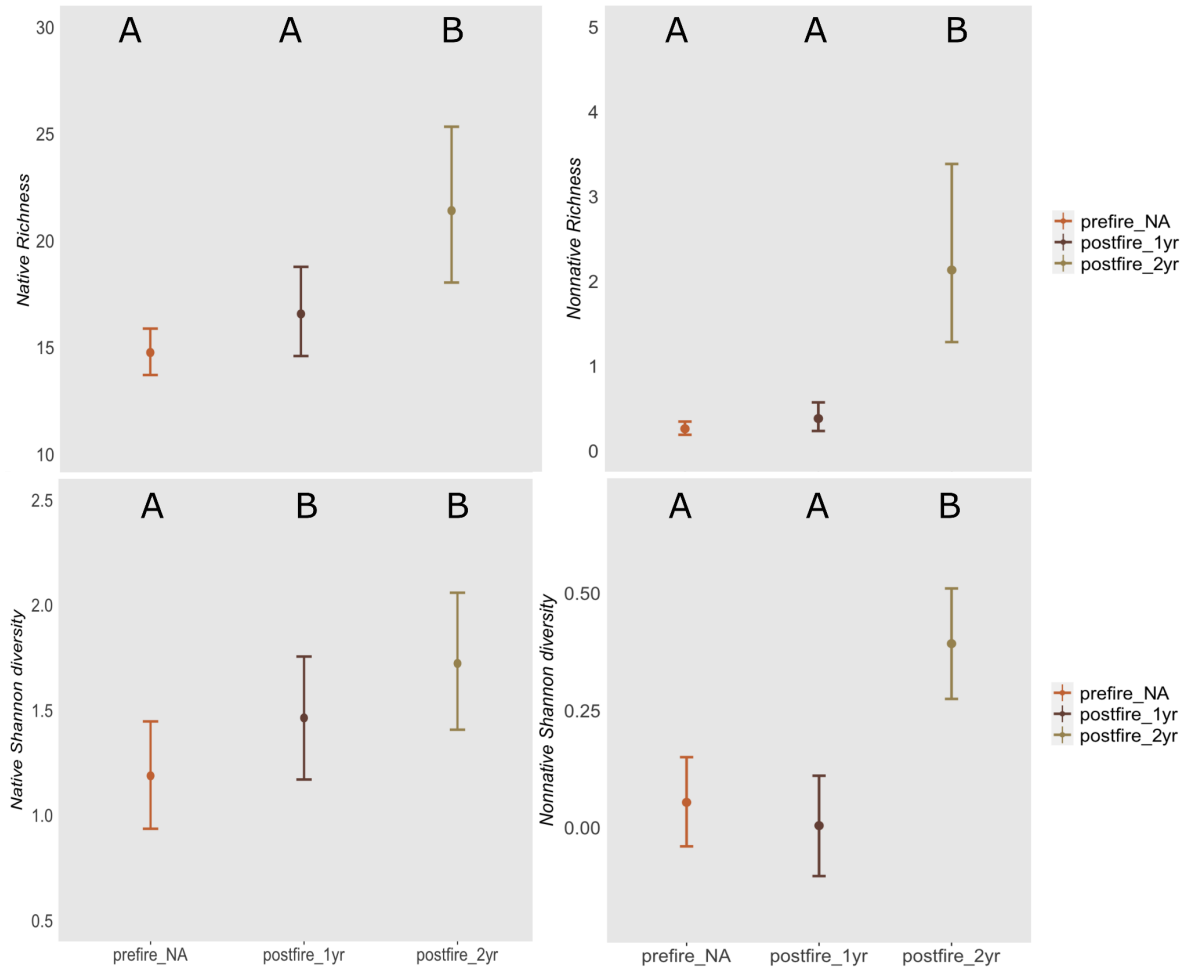


Figure 3.7. Native (left column) and nonnative (right column) species richness and diversity before (orange), 1 year after prescribed fire (brown), and 2 years after prescribed fire (green). Mean predicted values from the top-ranked Bayesian model with 95% credible intervals are plotted. Shared letters indicate diversity indices are not different from one another.

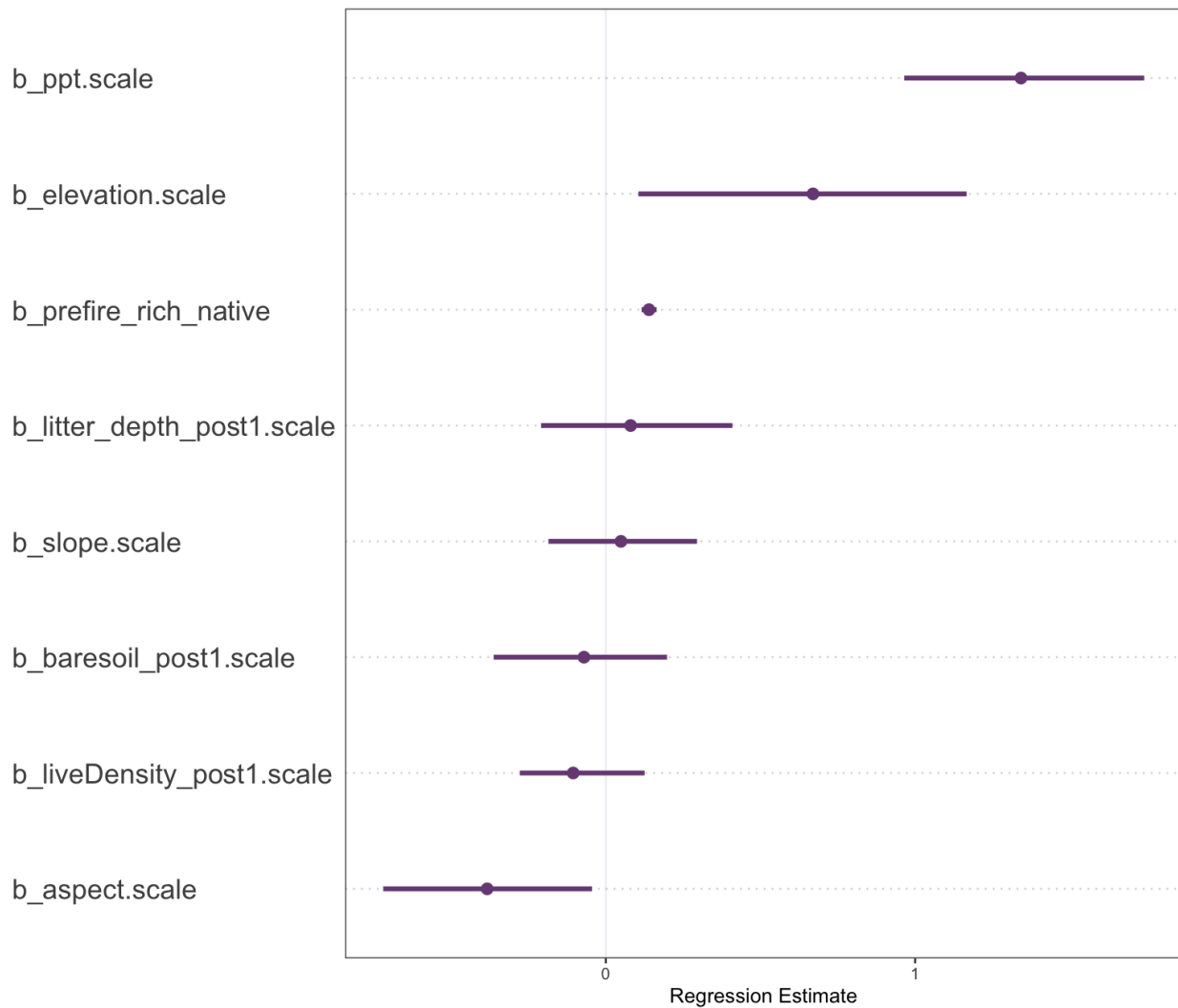


Figure 3.8: Regression estimates associated with native species richness after prescribed fire. Values are coefficient estimates with corresponding error bars from the final model of total fuel consumption.

Table 3.1: Description of 12 study sites that were treated with prescribed fire

Site	Ownership	Elevation (m)	Mean annual precip (mm)	January mean minima (°C)	July mean maxima (°C)	Burn units	Description	Dominant tree species	Number of plots	Burn
Sly Park	Sierra Pacific Industries	1,200	1373	-0.5	32.0	2	Mixed conifer/PIPO plantation	PIPO, CADE, PSME, QUKE	22	January 2020
Burton Creek	California State Parks	2,100	1003	-4.9	25.2	5	Mixed conifer	ABCO, ABMA, PICO, PIJE	47	Fall 2019
French Meadows	The Nature Conservancy	1,500-2,200	1970	-3.1	24.9	12	Mixed conifer	ABCO, ABMA, PILA, CADE, PIPO, PIJE	62	Spring 2021
Springs Fire	Inyo NF	2,400	521	-9.6	24.6	1	Jeffrey pine/lodgepole pine	PIJE, PICO	44	Summer 2019
Dry Creek	Inyo NF	2,300	469	-10.1	26.2	4	Jeffrey pine-lodgepole pine	PIJE, PICO	26	Fall 2018
Lava	Modoc NF	1,500	625	-4.2	29.4	9	Ponderosa pine	PIPO, ABCO, CADE	41	May 2021
Bear Mountain	Stanislaus NF	1,500	982	0.1	29.3	5	Mixed conifer	PIPO, CADE, PILA, QUKE	27	Summer 2013 (Rim Fire) / Fall 2019
Calaveras Big Trees North Grove	California State Parks	1,500	1371	0.3	28.7	3	Mixed conifer	SEGI, PILA, ABCO, CADE, QUKE, PIPO	34	Spring 2022/Fall 2022
Lone Bobcat Woods	Private	1,000	1429	1.6	31.6	3	Mixed conifer	PIPO, CADE, QUKE, ABCO, ARME	7	Spring 2021
Shaver Lake South Shore	Southern California Edison	1737	964	-0.5	27.8	9	Mixed conifer	ABCO, CADE, PIPO, PILA	26	Spring 2022
Caples Creek	Eldorado NF	1,981	1629	-4.9	24.6	n/a	Mixed Conifer	ABMA, ABCO, PIPO, PIJE	108	Fall 2019
Sugar Pine Point	State Parks	1,920	946	-6.9	26.2	2	Mixed Conifer	PIJE, ABCO, CADE	2	Fall 2022

Table 3.2: Weather conditions during each prescribed burn. All data are from the nearest Remote Automated Weather Station (RAWS).

Site	Date	Temperature (°C)	Wind speed (m/s)	Relative Humidity (%)	Fuel moisture (%)	Days since precipitation
Bear Mountain	9/30/2019	2	3	65.8	11.3	14
Burton State Park	1/11/2020	-3.4	4	71.2	27.3	2
Calaveras State Park	5/26/2022	19	4	32.5	5.5	17
Caples Fire	10/2019	9	1	37.5	5.1	23
Drycreek, Inyo NF	6/23/2022	12	1	55.3	7.4	45
French Meadows, TNC	5/16/2021	9	3	80.1	12.0	96
Modoc NF	5/10/2021-5/11/2021	12-15	2-3	28-34	5.5 - 7.1	15-16
Odell Property	2/8/2022	14	1	29.6	7.5	32
Shaver Lake	5/19/2022	15	1	58.8	11.4	28
Slypark, SPI	1/31/2020	13	1	53.9	13.1	6
Springs Fire, Inyo NF	8/10/2019-8/20/2019	14	5	32.0	6.0	3

Table 3.3: Mean fuel loads (Mg/ha) with standard error of prefire and immediately postfire surface fuel variables.

Fuel type	Prefire	Postfire immediate
1 hour fuels	0.12 (0.02)	0.04 (0.01)
10 hour fuels	0.50 (0.05)	0.27 (0.04)
100 hour fuels	1.37 (0.17)	0.58 (0.08)
1000 hour fuels	3.59 (0.43)	1.41 (0.26)
litter load	11.61 (0.63)	3.89 (0.32)
duff load	25.23 (2.04)	6.52 (0.87)

Table 3.4: Mean tree density (stems/ha), snag density (stems/ha), basal area of live trees (m²/ha), basal area of snags (m²/ha), and canopy cover (%) before and 1 year after prescribed fire.

Forest structure characteristic	Prefire	Postfire 1 year
Tree density (stems/ha)	331 (19)	253 (16)
Snag density (stems/ha)	114 (8.5)	184 (18.5)
Live basal area (m ² /ha)	43.0 (2.24)	39.3 (2.20)
Snag basal area (m ² /ha)	15.8 (1.72)	14.3 (1.63)
Canopy cover (%)	42 (0.9)	34 (0.8)