

ARTICLE

Vegetation Ecology

High fire frequency in California chaparral reduces postfire shrub regeneration and native plant diversity

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Handling Editor: Jonathan D. Coop**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 is adapted to high-intensity burning, with relatively long intervals between fires (30–100 years) typifying undegraded conditions. Modern fire frequencies are much higher in chaparral, driven largely by high densities of human ignitions and coincidence between ignitions and severe weather conditions. This change in the fire regime has major implications for biodiversity, leading to exotic invasion, decreased ecosystem services, and potential type conversion of shrubland to grassland dominated by exotic species. 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 California, which allowed us to investigate higher fire frequencies than previously published 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 short-interval fires significantly reduced postfire 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 one additional fire since 1985 decreased the proportion of native species cover by 12% and both richness and Shannon diversity by 4%. Consequently, areas with higher fire recurrence supported a more structurally and botanically homogeneous landscape dominated by a homogeneous group of non-native species.

KEYWORDS

chaparral, fire frequency, postfire regeneration, species diversity

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INTRODUCTION

Fire is vital for maintaining biodiversity in many fire-adapted ecosystems around the world, but interactions between rapid climate warming 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, droughts and episodes of extreme fire weather are more common, and there is an increase in human population and housing density in the wildland–urban interface (Abatzoglou & Park Williams, 2016; Keeley & Fotheringham, 2003; Molinari et al., 2018; Syphard et al., 2018). Natural fire regimes have been greatly altered across the NAMCZ, posing serious risks to ecosystem integrity, especially in lowland and coastal shrublands like chaparral (Molinari et al., 2018; Park et al., 2018; Syphard et al., 2019).

Chaparral shrubland is a widespread vegetation type in the NAMCZ that provides numerous ecosystem services and is an important biodiversity hotspot (Rundel, 2018; Underwood et al., 2018). The chaparral shrub canopy is characteristically dense and horizontally continuous, resulting in fires that typically burn at high intensities (Keeley & Safford, 2016). Chaparral is also adapted to relatively infrequent fire, with paleo- and historical data, as well as modeling studies, suggesting an optimal fire-return interval range between c. 30 and 90 years (Van de Water & Safford, 2011). Although chaparral is relatively resilient to episodic variability in fire frequencies (Allen et al., 2018; Keeley, Fotheringham, & Baer-Keeley, 2005; Minnich & Bahre, 1995), long-term and profound alteration of the natural fire regime can lead to transitions from chaparral to woodland or grassland. Very long intervals without fire can promote tree invasion (Callaway & Davis, 1993; Safford et al., 2021), but much more common today is a transition to grassland dominated by non-native species driven by increased fire frequency (Keeley & Fotheringham, 2003; Syphard et al., 2019; Zedler et al., 1983). In southern California, large areas of lowland and lower montane chaparral have been converted to exotic grassland in recent decades, driven primarily by an interaction between recurrent drought and short-interval reburning (D'Antonio & Vitousek, 1992; Keeley & Brennan, 2012; Park et al., 2018; Syphard et al., 2019).

Uncharacteristically frequent fire can eliminate chaparral species that do not have adaptations to short fire-return intervals (Keeley, 1991). Postfire plant 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 or second postfire year), obligate resprouters (which lack a dormant seed bank but regenerate vegetatively), and facultative seeders (which have postfire germination coupled with resprouting) (Keeley & Safford, 2016). Increased fire frequency may induce substantial mortality for obligate seeders because these species often require a decade or more to replenish the seed bank (Jacobsen et al., 2004; Zedler et al., 1983). Studies have shown that even resprouting chaparral species may be eliminated after more than two short-interval fires, presumably due to the depletion of stored carbohydrates (Haidinger & Keeley, 1993; Keeley & Brennan, 2012).

Shifts in species composition and type conversion to non-native grassland have large-scale implications for ecosystem resilience, as well as regional and local biodiversity (Rundel, 2018). These changes also affect ecosystem services, including primary production, carbon sequestration, nutrient cycling, pollination, erosion mitigation, and habitat provision (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 few studies have focused on the Coast Range of northern California (e.g., Safford & Harrison, 2004; Werner et al., 2022), which is becoming one of the most frequently burned regions in the state (FRAP, 2021; Safford et al., 2022).

Our study took place in the footprint of the 2020 Hennessy Fire, the largest of the fires comprising the LNU Lightning Complex. The landscape burned by the Hennessy had 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 previous 20 years (Safford et al., 2022). Some areas in the Putah and Cache Creek drainages have burned six times since 1985, including up to four times in the seven years prior to our study. This makes these areas among the most frequently burned wildlands in California and a unique natural laboratory to study landscape change and vegetation-type conversion (Guiterman et al., 2022).

To better understand how the resilience of chaparral communities is affected by the interaction between fire frequency and invasion, we asked two primary questions: (1) How does fire frequency affect the diversity and cover

of native and non-native species? (2) What are the consequences of higher burn frequency on shrub seedling establishment and resprouting success? Generally, an increase in fire frequency decreases fire intensity by replacing woody fuels with herbaceous fuels, which diminishes the heat filter that kills the non-native seed pool and promotes the germination of native species (Keeley et al., 2008; Keeley & Brennan, 2012). Based on the body of research in southern California, we formed the following hypotheses and predictions for our study area:

H1. Frequent fires occurring at intervals of less than 10 years will reduce fire intensity, diminishing the heat filter that typically kills the non-native seed pool. As a result, the diversity and cover of native species will decline, while the cover of non-native species will increase.

P1. Across all sites, the number of fires since 1985 will show a significant negative relationship with native species diversity and cover and a significant positive relationship with non-native species diversity and cover.

H2. Native chaparral species that experience repeated fires at intervals of less than 10 years on average will not have time to reach maturity and replenish the seed bank before reburning, leading to the elimination of native shrub regeneration.

P2. Across all sites, the number of fires since 1985 will show a significant negative relationship with native shrub regeneration.

H3. Resprouting shrub species will be more resilient to recurring fires due to their lack of reliance on a seed bank. However, frequent enough fire will deplete their reserves of nonstructural carbohydrates, leading to a loss of resprout growth.

P3. Across all sites, the number of fires since 1985 will show a significant negative relationship with the resprout height of native species.

METHODS

Study site

Our 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. Mixed chaparral stands occur on more mesic exposures with deeper soils and include chamise as well as other co-dominant taxa such as *Arctostaphylos* spp., *Ceanothus* spp., *Heteromeles arbutifolia*, and *Quercus berberidifolia*.

Historical mean fire-return intervals in California chaparral have been estimated to be between 30 and 90 years (Van de Water & 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 purposes (Anderson & Keeley, 2018). Lightning ignitions certainly occurred but were relatively rare in our study region, as they are today (Keeley & Syphard, 2018). Today, human ignition sources are typically due to accidents from power lines, vehicles, and campfires (Anderson & Keeley, 2018; Syphard & Keeley, 2015).

We sampled chaparral plant communities after the 2020 LNU Lightning Complex Fire, which was one of the largest fires in California history, burning 146,990 ha in Napa, Yolo, Solano, Sonoma, and Lake Counties (FRAP, 2021; Safford et al., 2022). We focused on the area burned in the Hennessy Fire, which ignited by lightning on August 17 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), Bobcat Ranch Audubon Reserve (38°31' N, 122°04' W), Berryessa Snow Mountain National Monument (38°54' N, 122°18' W), and Valley Vista Regional Park (38°54' N, 122°16' W) (Figure 1). These plots were geographically segregated into two locations, one in the Cache Creek Canyon and one in the Putah Creek Canyon (Figure 1). The two locations are separated by 40 km, but their physical and biological characteristics are remarkably similar. Through careful site selection, we were able to sample essentially identical topographic, geographic, geological, pedological, and management sites. Both locations were 85 km NE of the coast, and plots at both sites were found between 260 and 540 m elevation (Cache Creek site: 310–540 m; Putah Creek site: 260–460 m). Approximately equal numbers of plots were sampled on warm vs. cool slopes at each location ($N = 49$, $N = 48$, respectively). In both locations, plots were arrayed on the east and west slopes of the Blue Ridge geographic feature, which is formed atop resistant beds of Cretaceous sandstone. Soils under all plots in

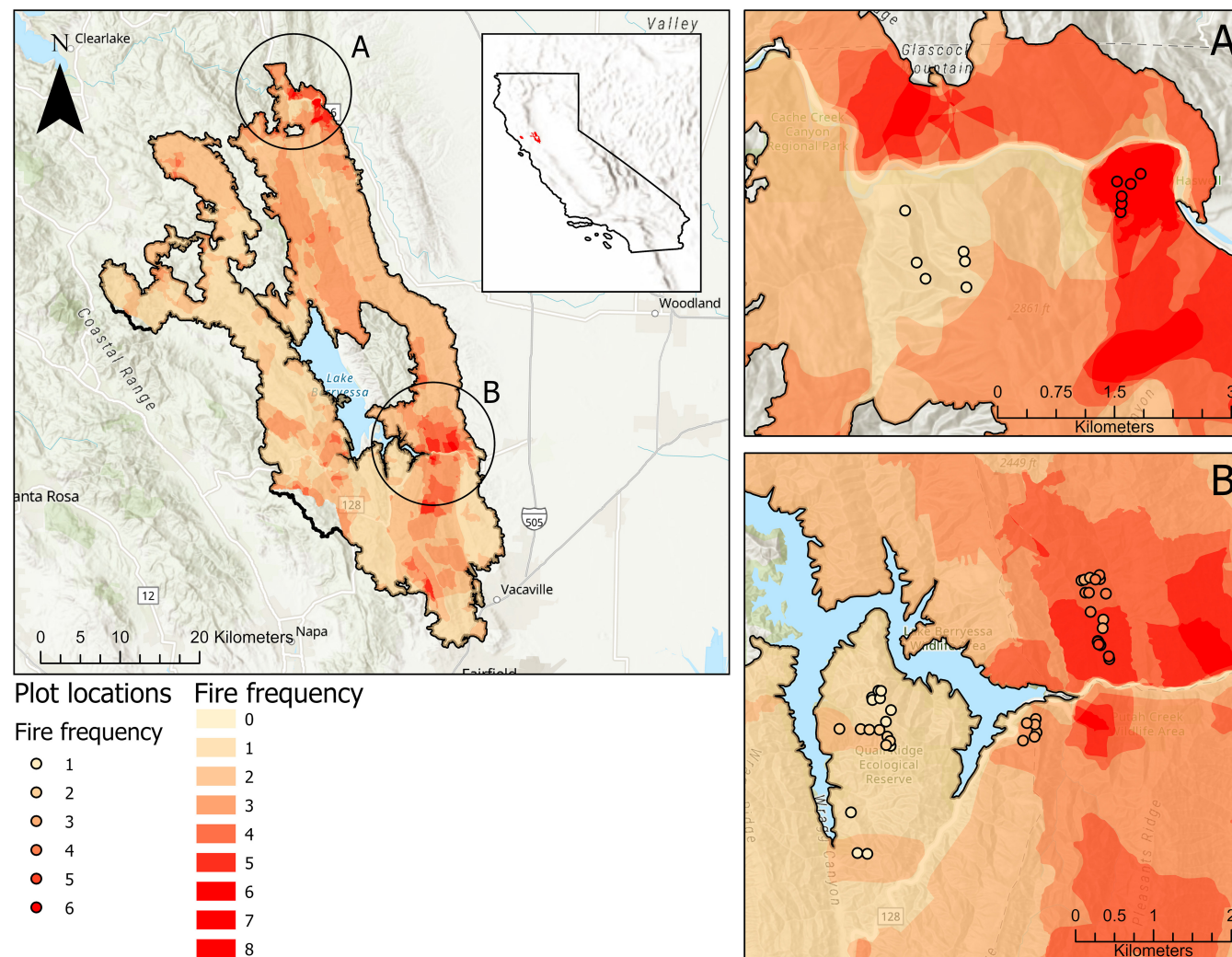


FIGURE 1 Spatial extent of the number of fires since 1985 across the Hennessey Fire perimeter (black outline), with the highest fire frequency shown in red and the lowest fire frequency shown in white. Plot locations are shown for (A) Cache Creek and (B) Quail Ridge, Bobcat Ranch, and Cold Canyon, which were distributed across a fire-frequency gradient of one total burn (tan) up to six total burns since 1985 (red). Fire-frequency data were sourced from the California Fire Return Interval Departure (FRID) database (Safford et al., 2011). Google Earth historical imagery was used to examine the landscape for unburned patches after each fire, and we adjusted the fire frequency for each plot location accordingly.

both locations are shallow inceptisols from the Maymen and Millsholm series (California Soil Web; <https://casoilresource.lawr.ucdavis.edu/gmap/>). Precipitation at both locations averages 630–760 mm, and temperatures range from a January mean minimum of about 3°C to a July mean maximum of about 34°C (30-year average, 800-m resolution; PRISM Climate Group, 2022). Natural vegetation at both locations was dominated by a similar mix of chamise chaparral in more xeric locations with thin soils and mixed chaparral in more mesic locations with somewhat deeper soils. All sites were also subject to intermittent cattle grazing, but their thin soils, steep slopes, and generally shrubby vegetation led to minor grazing impacts compared with grassland and riparian areas.

The study area had a variable fire history, ranging from never burned to six burns in the past 30 years (Table 1; Appendix S1: Table S1). 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 start date 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). As 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

TABLE 1 Description of all study sites included in the analysis.

Site	Jurisdiction	Fire history (since 1985)	Shortest interval between fire (years)	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), 1988 (Miller)	5	3
Cache Creek	BLM, Valley Vista Regional Park	2020 (Hennessey), 2012 (sixteen complex), 2004 (Rumsey), 2002 (Sixteen), 1999 (Rumsey), 1987 (Haswell)	2	1, 6

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 & Keon, 2002). Precipitation and temperature point estimates were extracted for each transect using the 4-km resolution PRISM dataset (PRISM Climate Group, 2022).

We sought to understand how the number of wildfires in a given period of time might influence a suite of ecological response variables. Due to the idiosyncratic nature of the different wildfires that had affected our study area, sites that burned one and six times during our period of interest were found in one geographic area, and sites that burned one to five times were found in another geographic area, 40 km to the south. For an experimentalist, this study system raises the specter of potential pseudoreplication (Hurlbert, 1984). The complication is that wildfires, as unique natural disturbances, are not experimental in nature. Research on wildfires is necessarily opportunistic, where the collection of unbiased data is difficult due to inadequacies in randomization, replication, and spatial dispersion of disturbance effects (which are often the focus of research) (Davies & Grey, 2022). However, studying wildfires is crucial for several reasons, especially because their intensity and frequency in certain locations cannot be experimentally replicated. To reduce the statistical impact of nonrandomness in the spatial distribution of different numbers of fires, we selected sites that were biotically and abiotically similar (Mantgem et al., 2001).

Sampling design and processing

At each of the 54 sampling sites, 50 × 5 m belt transects (hereafter “plots”) were established following Safford and Harrison (2004) and Werner et al. (2022). Sites were visited in the spring of 2021 and 2022. All plant species were recorded within the entire 250-m² plot 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 percentage cover of all native and exotic species; number and height of shrub seedlings; resprout height; percentage cover of rock, bare soil, and litter; and litter depth. All variables collected at the 1-m² scale were averaged to give a plot-level value. Plant life history data for each species were obtained from the USDA Forest Service Fire Effects Information System (<https://www.feis-crs.org/feis/>) or the University of California Jepson Herbarium eFlora (<https://ucjeps.berkeley.edu/eflora/>). 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, species richness, and diversity were calculated at each plot for each year (2021 and 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 (Oksanen et al., 2023; R Core Team, 2021).

Fire severity was estimated in each plot by measuring the stem diameter (1 cm from the terminus) of four stems remaining on the shrub skeleton from a randomly chosen *A. fasciculatum* (chamise) individual rooted in or adjacent to each 1-m² quadrat (Perez & Moreno, 1998). A 300-mm digital caliper with LCD display and ±0.02 mm accuracy was used to measure each stem diameter (Arbor Scientific, Saline, Michigan). We used this measurement as a proxy for fire intensity, as the remaining stem diameter is inversely related to fire intensity (hotter fire results in more stem loss). We did not measure fresh stems but rather dead stems that were remaining on the

burned shrub skeleton. Five additional individuals were measured at the entire 250-m² transect scale. In the few cases when chamise was not present, we used scrub oak (*Q. berberidifolia*) individuals or toyon (*H. arbutifolia*) if both of the former were absent. Chamise and scrub oak have nearly identical wood densities (both range from 0.75 to 0.8 g/cm³) and give similar fire severity results (Pivovarov et al., 2014; Ackerly, personal communication). Toyon has a lower wood density (0.6–0.65 g/cm³) and tends to exhibit slightly more stem loss than the other two species (Pivovarov et al., 2014; Ackerly, personal communication). For the plots in which we had to use toyon (Quail Ridge, Cold Canyon, and Bobcat), we expected to slightly overestimate fire severity due to lower wood density. Due to logistical constraints, we did not collect data on fire severity at sites that burned twice prior to the Hennessey Fire. We measured heterogeneity in fire severity within each belt transect by calculating the CV for the five quadrats within a transect.

Statistical analyses

Species cover, diversity, and composition (H1)

To examine the effect of fire frequency on the proportion of native species cover, richness, and diversity for both survey years, we used a Bayesian linear regression using a beta-binomial likelihood, which accommodates values between 0 and 1. We used a Bayesian framework due to its ability to specify model distributions that fit the data and generate robust estimates of parameter values and their credible intervals, which do not depend on extremely large sample sizes (Kruschke, 2021). To unconfound the influence of fire frequency on our response variable of interest, we performed model selection on a suite of environmental predictors using the expected log pointwise predictive density (ELPD) to measure leave-one-out cross-validation for our goodness-of-fit measure. The predictors that we evaluated were 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 (Appendix S1: Figure S1). We first fit each response variable with each individual predictor separately and added significant predictors in order of ELPD to determine whether they significantly increased the ELPD of the resulting model. A second-order polynomial was applied to the number of burns for the curved pattern of the proportion of native species cover, richness, and diversity. We used ELPD to compare models with and without this second-order polynomial and used the model that maximized the

estimated ELPD. If the difference in ELPD was less than four, models were considered to be equivalent (Sivula et al., 2023). We were unable to include a random effect for site location due to the nonrandom spatial distribution of sites that have experienced a different number of fires.

Nonmetric multidimensional scaling (NMDS) was used to visualize compositional differences between areas with variable fire recurrence as a part of the vegan package in R (Oksanen et al., 2023; R Core Team, 2021). 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. The final stress of the three-dimensional solution was 0.166. This value represents model fit, in which values less than 0.20 are considered acceptable (Clarke, 1993).

Shrub regeneration (H2)

We used a similar modeling procedure to understand the effect of fire frequency on shrub regeneration. We fit seedling presence/absence using multiple Bayesian linear models with Bernoulli likelihood. Similar to species diversity, we used the ELPD as a measure of leave-one-out cross-validation for our goodness-of-fit measure to compare models. 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 the ELPD of the resulting model. The predictors that we evaluated were mean annual precipitation, mean annual temperature, heat load index, aspect, and slope. For seedling presence/absence, we also calculated the area under the receiver operating curve (AUC) using 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.

Resprout growth (H3)

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. We used the ELPD as a measure of leave-one-out cross-validation for our goodness-of-fit measure to compare models with the following predictors: mean annual precipitation, mean annual temperature, heat load index, aspect, slope, and

diameter of the largest stem. The diameter of the largest stem was added to account for prefire size, which can impact resprout vigor (Sparks & Oechel, 1993). We first fit the resprout growth with each individual predictor separately and added significant predictors in order of ELPD to determine whether they significantly increased the ELPD of the resulting model. After the 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.

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 weakly informative priors to prevent overfitting with four chains, each with 2000 iterations and a warm-up of 1000. For models that used a beta-binomial or Bernoulli likelihood, we specified a prior distribution of $\text{student_t}(3, 0, 2)$ for the intercept to allow for thicker tails and a normal

prior distribution of $\text{normal}(0,1)$ for each coefficient (Gelman et al., 2021). A $\text{normal}(0,1)$ prior distribution for the intercept and each coefficient was used for resprout growth models in which we used a Gaussian likelihood. Trace plots, Markov Chain Monte Carlo chain inspection, and R-hat values were assessed to confirm proper mixing and model convergence.

RESULTS

Fire severity

The mean and maximum fire severity, as well as the heterogeneity of fire severity, were significantly reduced after more than one fire in 30 years (Figure 2, Table 2). Fire severity in plots that only burned once was significantly higher than all other fire-frequency classes. Subsequent fires did not significantly change fire severity (differences among fire frequency [FF] = 3, 4, 5, and 6 were not statistically different from each other).

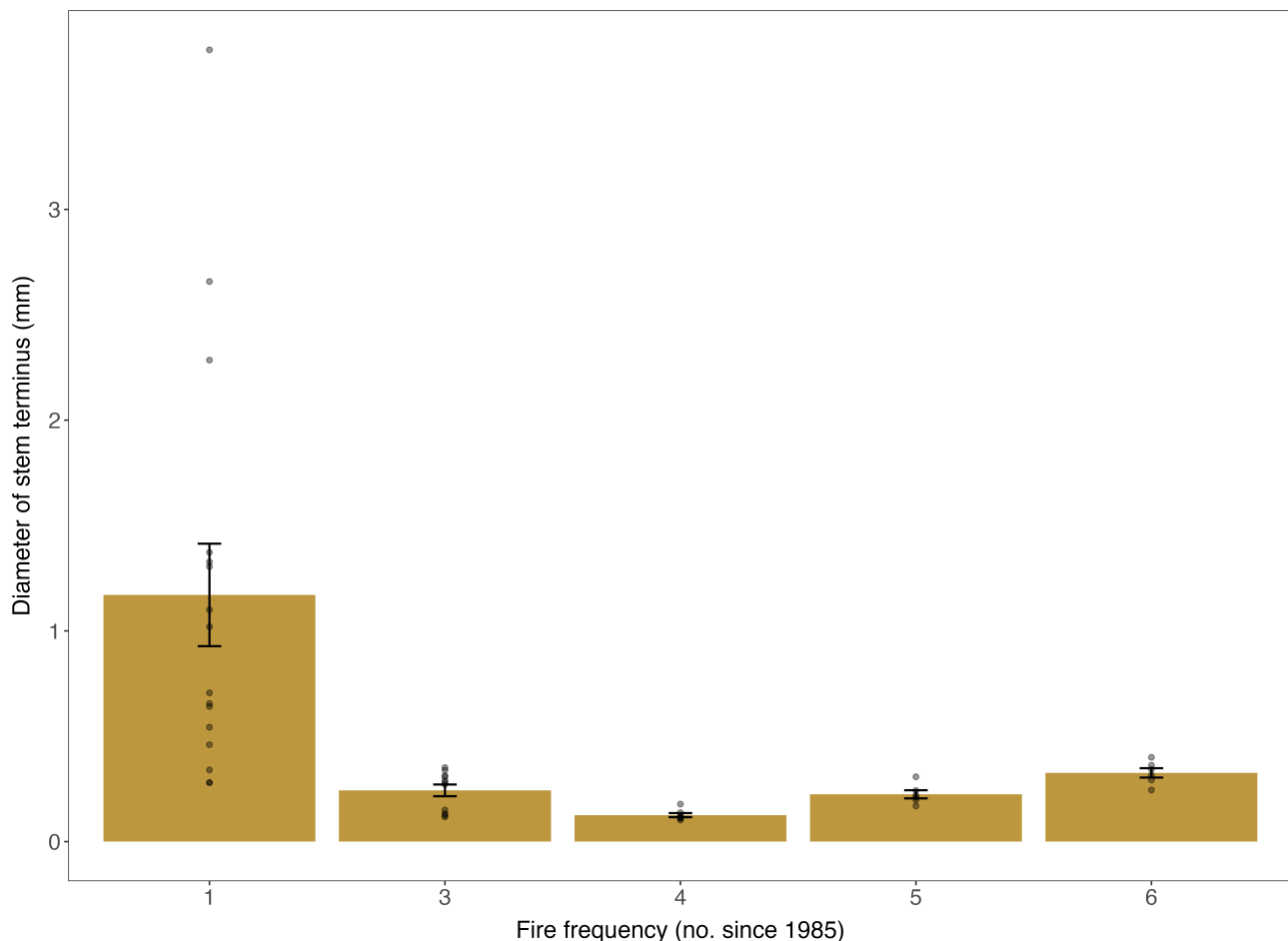


FIGURE 2 Fire severity (mean $\pm$ SE), represented by burned stem terminus diameter, significantly decreased after more than one fire in 30 years. Raw values are designated by gray points.

TABLE 2 Coefficient of variation (CV) in mean and maximum (max) fire severity (in millimeters), measured by the diameter of burned stem termini, across the fire-frequency gradient (number of fires since 1985).

Category	Fire frequency				
	1	3	4	5	6
CV in mean fire severity (%)	83.1	37.9	20.3	21.1	16.7
CV in max fire severity (%)	78.4	47.2	34.6	23.1	10.3

The heterogeneity of mean and maximum fire severity in plots with high fire frequency (FF = 6) declined by 80% and 87%, respectively, compared with plots with lower fire frequency (FF = 1).

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 (Figure 3). The effect of fire recurrence was strongest for the proportion of native cover ($\beta_{\text{firefreq}} = -1.17$; CIs = -1.67 to -0.67) and moderately strong for the proportion of native species richness ($\beta_{\text{firefreq}} = -0.50$; CIs = -0.86 to -0.15) and Shannon diversity ($\beta_{\text{firefreq}} = -0.65$; CIs = -1.14 to -0.16) (Appendix S1: Table S2). The overall average marginal effect of a 1-unit increase in fire frequency decreased the proportion of native cover by 12%, native richness by 4%, and native Shannon diversity by 4%.

This effect of fire frequency, however, varied at higher and lower levels of fire frequency for all diversity metrics (Figure 3). At lower levels of fire frequency, one additional fire since 1985 led to a significant 16% decrease in the proportion of native cover (Figure 3B). In contrast, a frequency of five fires in the past 30 years resulted in a slight 5% increase in the proportion of native cover. The patterns of native richness and Shannon diversity closely align with the findings for native cover (Figure 3D,F). For lower levels of fire frequency, one additional fire since 1985 was associated with 7% and 9% decreases in native richness and Shannon diversity, respectively. However, as fire frequency rose to higher levels, there was 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 (more than two short-interval fires) that contained more non-native

herbaceous species, while plots with lower fire recurrence (≤ 2 short-interval fires) contained more native herbaceous species and shrubs (Figure 4). Species characteristic of the high fire-frequency plots included *Avena barbata*, *Centaurea melitensis*, *Erodium cicutarium*, and *Festuca myuros* (Figure 4), all classic dominant species in the exotic annual grassland that characterizes highly disturbed sites in lowland California. Plots with higher fire recurrence showed closer clustering compared with areas with low fire recurrence, indicating a shift from a more heterogeneous postfire landscape to a more homogeneous landscape with many similar non-native species. Species assemblages also became progressively more differentiated from the one-burn assemblage as fire frequency increased (Figure 4).

Shrub regeneration (H2)

Increased fire frequency in chamise chaparral reduced shrub seedling regeneration, as expected (Figure 5). In plots with higher fire frequency (FF = 6), seedling regeneration for FS declined by 83% and OS regeneration declined by 99% when compared with plots with lower fire frequency (FF = 1). OS species, including *Ceanothus oliganthus* and *Ceanothus cuneatus*, were almost completely eliminated in areas with more than two fires in the past 30 years (Figure 5). We found a strong negative association between fire frequency and the presence of OS regeneration ($\beta_{\text{firefreq}} = -0.92$; CIs = -1.43 to -0.49 ; Figure 5A) and a significant, albeit less strong, negative association between fire frequency and the presence of FS regeneration ($\beta_{\text{firefreq}} = -0.33$; CIs = -0.47 to -0.19 ; Figure 6A). Fire frequency significantly reduced the presence of *C. cuneatus* ($\beta_{\text{firefreq}} = -1.10$; CIs = -1.65 to -0.64 ; Figure 5B) and *C. oliganthus* ($\beta_{\text{firefreq}} = -1.20$; CIs = -2.27 to -0.41 ; Figure 5C). The effect of fire frequency on FS regeneration was species-specific and significantly reduced the presence of *A. fasciculatum* ($\beta_{\text{firefreq}} = -0.70$; CIs = -1.02 to -0.40 ; Figure 6B) and *Lepechinia calycina* seedlings ($\beta_{\text{firefreq}} = -0.66$; CIs = -1.00 to -0.35 ; Figure 6D). Despite an overall decrease in the presence of FS regeneration due to fire frequency, we found a slight increase in *Eriodictyon californicum* seedlings ($\beta_{\text{firefreq}} = 0.05$; CIs = -0.18 to 0.28), but this effect was not significant (Figure 6C).

Shrub resprout growth (H3)

In contrast to H3, we did not see any significant decrease in *A. fasciculatum* resprout growth with increased fire frequency ($\beta_{\text{firefreq}} = 0.00$; CIs = -0.02 to 0.01 ; Figure 7).

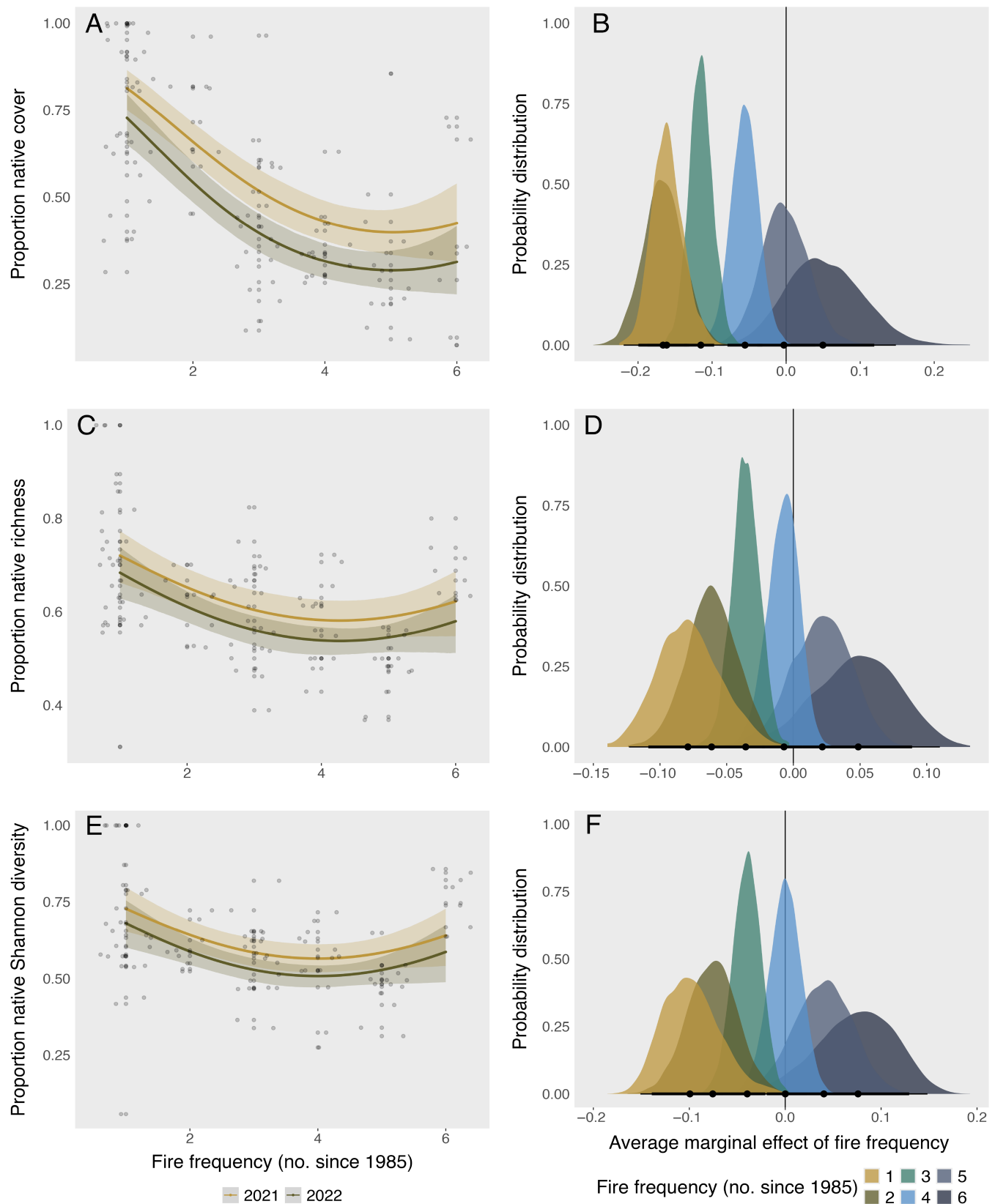


FIGURE 3 (A) Proportion of native species cover, (C) species richness, and (E) Shannon diversity at the plot level generally decline with increased fire frequency (number of fires since 1985) in both survey years (2021 and 2022). Predicted values from the top-ranked Bayesian model with 95% credible intervals, as well as raw values (gray points, $n = 103$). The overall average marginal effect of a 1-unit increase in fire frequency (number of fires since 1985) varied for high and low levels of fire frequency for (B) native species cover, (D) species richness, and (F) Shannon diversity. Black dots show the mean effect size, with 80% and 95% confidence intervals shown in black.

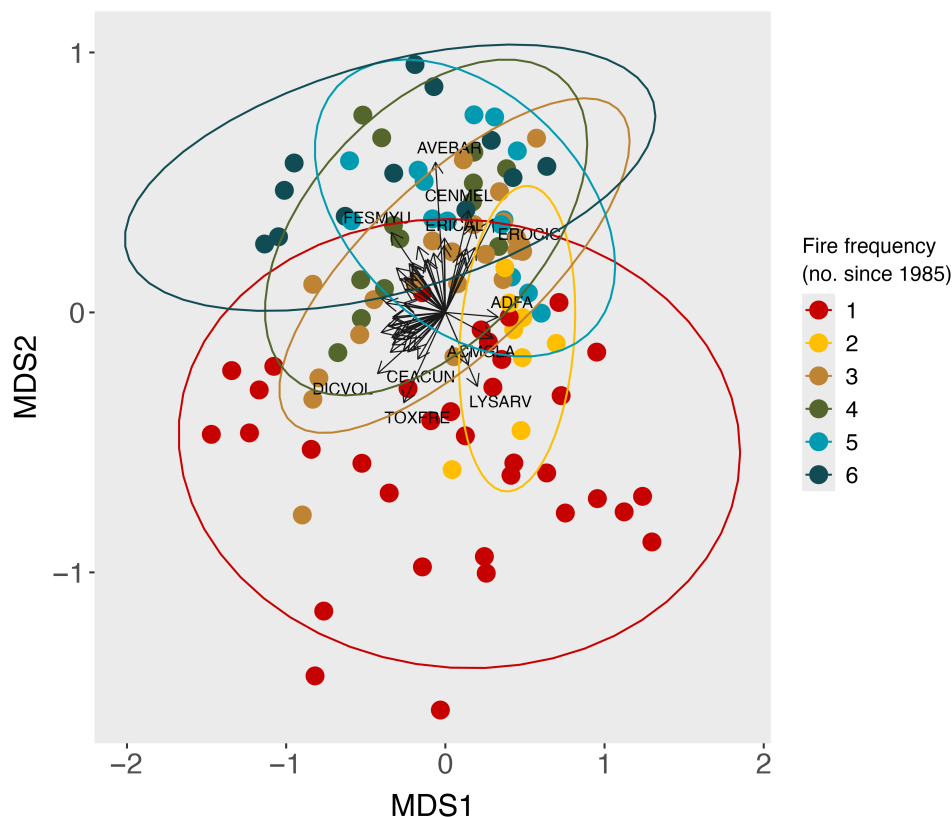


FIGURE 4 Nonmetric multidimensional scaling plot (NMDS) of Bray–Curtis dissimilarity matrix across fire-frequency gradient. Each point represents a survey point. Plots with high fire recurrence (green, light blue, dark blue) are more clustered together, indicating that they have a more similar species composition than plots with lower fire recurrence (red, yellow, brown). Labeling priority was given to more abundant and frequent species. Species codes: ACMGLA, *Acmispon glaber*; ACMWRA, *Acmispon wrangelianus*; ADFA, *Adenostoma fasciculatum*; ASTGAM, *Astragalus gambelianus*; AVEBAR, *Avena barbata*; CEACUN, *Ceanothus cuneatus*; CENMEL, *Centaurea melitensis*; CLAUNG, *Clarkia unguiculata*; DICVOL, *Dichelostemma volubile*; ERICAL, *Eriodictyon californicum*; EROCIC, *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.

Despite a reduction in live individuals, postfire height was around 0.4 m one year after fire for all levels of fire frequency. Heat load index (hli) 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 ; $\beta_{\text{diamlargeststem}} = -0.01$; 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 (Enright et al., 2011; Haidinger & Keeley, 1993; Jacobsen et al., 2004; Keeley & Brennan, 2012; Kraaij et al., 2013; Santana et al., 2014; Zedler et al., 1983). 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 (more than two short-interval fires in 30 years) in chaparral results 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 is 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, more than fire frequency per se, is a key component of type conversion (Jacobsen et al., 2004; Syphard et al., 2019). Our study examines the effect of fire frequency over a fixed period of time, and

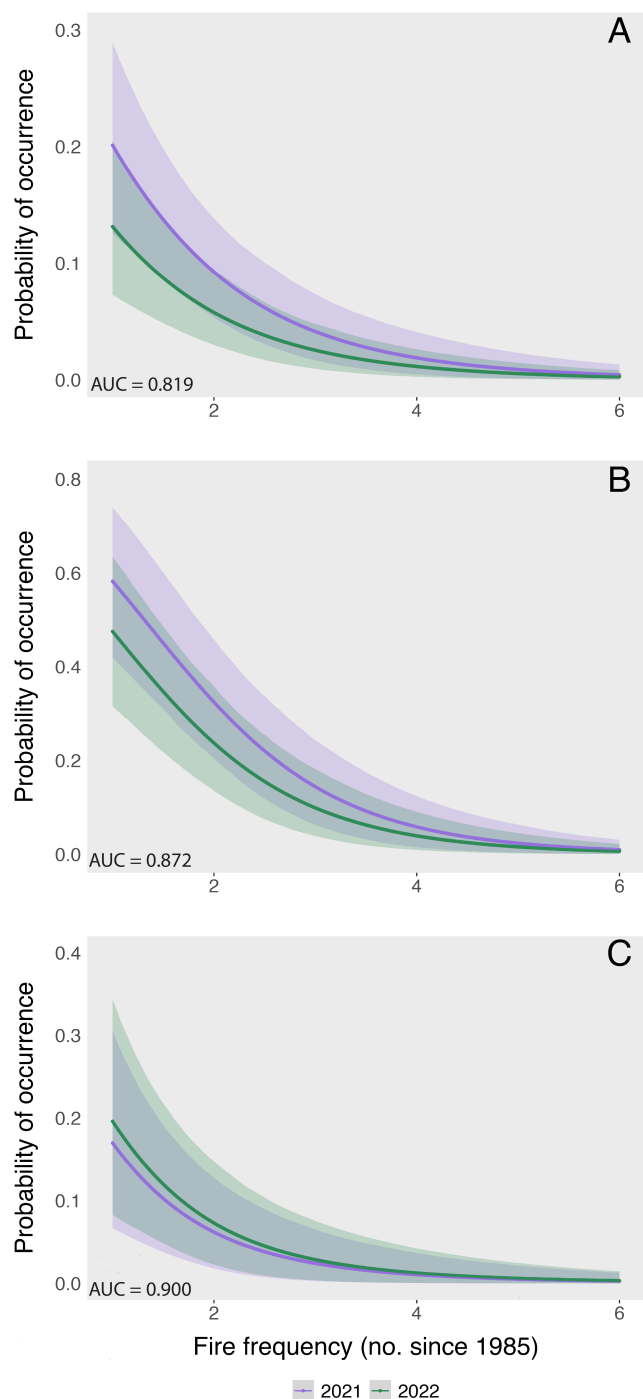


FIGURE 5 The probability of occurrence of a seedling from (A) an obligate seeding shrub species, including (B) *Ceanothus cuneatus* and (C) *Ceanothus oliganthus*, declined with increased fire frequency in both survey years (2021 and 2022). The probability of occurrence is the presence of at least one seedling in the 250-m² plot. Error bars show 95% CIs. The area under the receiver operating curve (AUC), a measure of model accuracy ranging from 0 to 1, is noted in the bottom left.

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, 2006). This has especially negative consequences for obligate seeding shrubs that require 10–15 years to mature before replenishing the seed bank (Jacobsen et al., 2004; Zedler et al., 1983), and in particular for the genus *Ceanothus*, which tends to germinate best under higher fire intensities that are only possible in the presence of high woody fuel loads that are characteristic of infrequently burned sites (Danielle & Thomas Parker, 2005; Moreno & Oechel, 1992). 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 the close linkage between the two variables.

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, species richness, and Shannon diversity. Consequently, plots with higher fire recurrence exhibit a more homogeneous landscape, dominated by a smaller set of non-native species. This result corroborates research from 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, low levels of 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 & Kark, 2002; Keeley, Baer-Keeley, & Fotheringham, 2005). Non-native annuals provide highly flammable flashy fuels that have a higher probability of ignition and lower burn residence time, and spread fire more easily than shrubs. We observed a decrease in fire intensity—measured by the diameter of the burned stem termini—with an increase in fire frequency. This lower intensity fire diminishes the heat filter that promotes native germination and kills the non-native seed pool (Keeley et al., 2008; Keeley & Brennan, 2012).

Prior studies in California chaparral have examined the impacts of a maximum of three short-interval fires. Our study is the first to show the effect of up to six fires in the past 30 years. At the most frequently burned sites (FF = 6), there was a slight increase in the proportion of

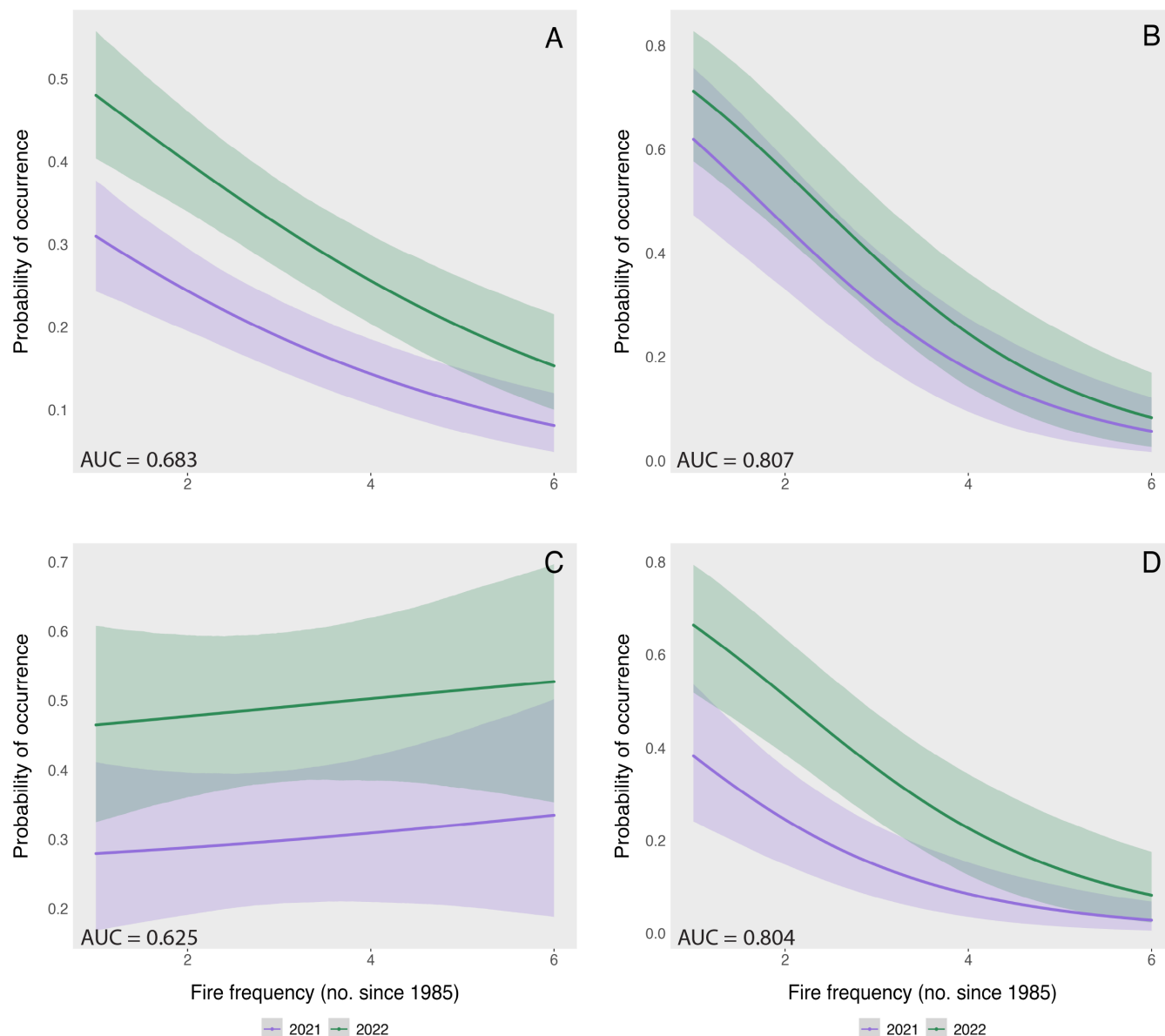


FIGURE 6 The probability of occurrence of a seedling from (A) a facultative seedling shrub species declined with increased fire frequency in both survey years (2021 and 2022). This relationship was species dependent. Fire frequency had little change on the probability of occurrence of (C) an *Eriodictyon californicum* seedling but decreased the probability of occurrence for (B) *Adenostoma fasciculatum* and (D) *Lepechinia calycina* seedlings. The probability of occurrence is the presence of at least one seedling in the 250-m² plot. Error bars show 95% CIs. The area under the receiver operating curve (AUC), a measure of model accuracy ranging from 0 to 1, is noted in the bottom left.

native diversity and richness. This was an unexpected result and we hypothesize that it may represent an ecosystem conversion to a grassland vegetation type. Frequently burned sites are primarily dominated by non-native grasses and forbs (e.g., *A. barbata*, *Bromus madritensis*, *Erodium* spp.), but 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 forbs that are common in California grassland systems (e.g., *Acmispon* spp., *Madia* spp., *Dichelostemma* spp.). Overall, these plots exhibited

lower native plant diversity than sites with low fire frequency (less than two fires in the past 30 years) that continue to be dominated by chaparral. Potentially permanent loss of chaparral on these sites could have important ecosystem service impacts in the study region. Chaparral ecosystems provide numerous services, including crop pollination by native bees that depend on shrubland flowers, carbon sequestration, erosion reduction, and beneficial influences on surface and groundwater (Kremen et al., 2004; Rundel, 2018; Underwood et al., 2018). Under Native American-influenced fire regimes, some landscapes

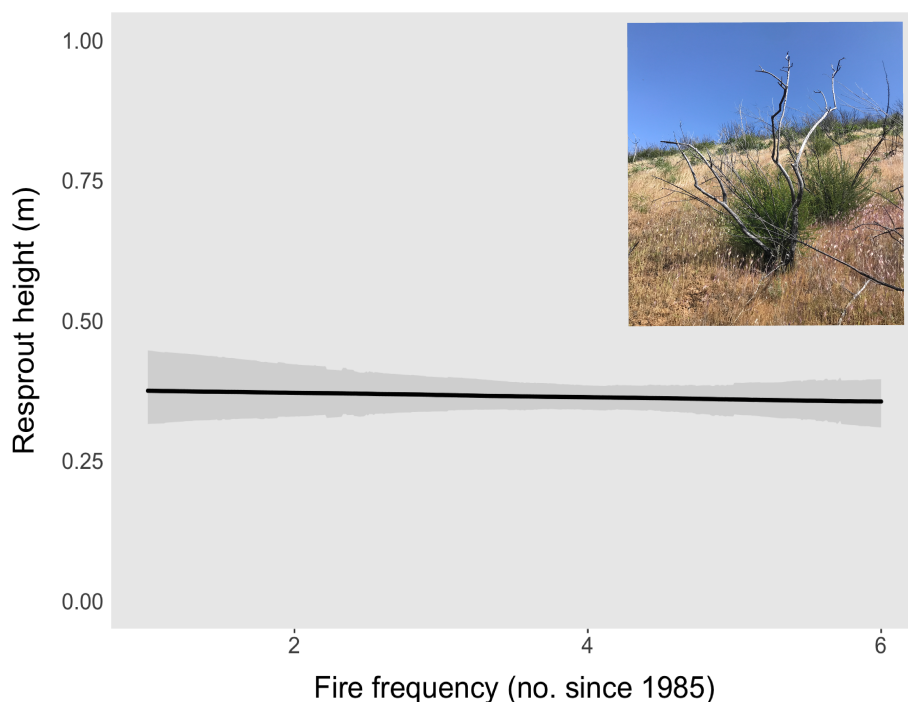


FIGURE 7 Resprout height of *Adenostoma fasciculatum* did not significantly change with increased fire frequency. Error bars show 95% CIs. Inset photo shows *A. fasciculatum* individual that has experienced three short-interval fires in the past 30 years. Photo credit: A. Grupenhoff.

currently dominated by chaparral were likely characterized by more grassland than they are today (Keeley, 2002; Timbrook et al., 1982). However, those grasslands were populated by native species, many of which were perennial geophytes or deep-rooted grasses and herbs. Coast Range and Central Valley grasslands today are heavily dominated by non-native annual species that provide a fraction of the ecosystem services provided by either chaparral or native grassland (Underwood et al., 2018).

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

As predicted, we found reductions in both OS and FS regeneration. OS species, such as *C. oliganthus* and *C. cuneatus*, were almost completely eliminated in areas with more than two fires in the past 30 years (99% reduction). These results are consistent with studies from southern California, showing that obligate seeding shrubs often require a decade or more between fires in order to reach maturity and replenish the seedbank (Jacobsen et al., 2004; Keeley & Brennan, 2012; Zedler et al., 1983). Our observed reduction in fire severity with short-interval fires confirms 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, and which also act as a filter against most non-native annuals (Park & Jenerette, 2019).

While all obligate seeding species declined with higher fire frequencies, 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 fire up to a frequency of three fires in the past 30 years. However seedling regeneration declined and was almost completely eliminated in areas with fire frequency ≥ 5 . This result contrasts slightly with research in southern California, reporting a drastic reduction in *A. fasciculatum* seedlings after just two short-interval fires (Keeley & Brennan, 2012; Zedler et al., 1983). Despite our prediction that all facultative seeding species regeneration would be eliminated after two short-interval fires, there was little effect on *E. californicum* regeneration. In fact, we found a slight increase in seedling regeneration at the most frequently burned sites. This is not necessarily surprising, considering *Eriodictyon* is a principal invader in many disturbed sites (Mooney & Hobbs, 1986). While grouping regeneration by functional type (OS, FS) can be useful, species-specific responses are vital to consider (Keeley et al., 2006).

Contrary to our expectations, and findings from research in southern California (Keeley & Brennan, 2012; Zedler et al., 1983), we found no reduction in resprout growth with increased fire frequency. While resprouting species exhibit strong adaptation to recurrent fires, they may face extirpation over time (Keeley & Brennan, 2012; Zedler et al., 1983). In this study, we saw no change in resprout growth; however, this does not equate to no mortality. Our study did not collect data on mortality rates of resprouting shrubs; however, the reduced cover and biomass of shrubs in our high fire-frequency plots are clearly a result of increased mortality among resprouting shrubs, which dominate the chaparral sites we studied. Resprouting growth has been shown to be affected by prefire drought conditions, which can exacerbate the effect of short-interval fire (Werner et al., 2022). Untangling the effects of fire frequency combined with drought conditions is important for fully understanding the dynamics of type conversion in northern California chaparral. Future studies that look to investigate the ecological implications of altered fire regimes should account for both shrub mortality and resprout success.

CONCLUSION

Much of the species diversity in the NAMCZ—a global biodiversity hotspot—is centered in chaparral and associated shrublands (Rundel, 2018). There is a rich diversity of endemic species restricted to chaparral and loss of this habitat type has major implications for 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 precipitates a notable shift in the local vegetation. Initially characterized by a distinctive assemblage of native woody and herbaceous species, chaparral shifts under frequent fire to a much more homogeneous community dominated by a smaller set of non-native annual herbs. Areas dominated by non-native grasses increase fine fuel loads, leading to more frequent fires that burn at lower intensity. The shift in fire behavior allows the non-native seedbank to persist, leading to a repeating “grass-fire cycle” (D’Antonio & Vitousek, 1992). Once a community has undergone type conversion, it has a greatly reduced probability of reverting to its previous state (Allen et al., 2018; Dewees et al., 2022). Thus, identifying and appropriately managing areas that remain largely

undisturbed but face imminent risk of conversion should be a priority for preventative management (Allen et al., 2018).

AUTHOR CONTRIBUTIONS

Hugh D. Safford and Ashley R. Grupenhoff were involved in conceptualization, methodology, and data collection. Ashley R. Grupenhoff conducted the data analysis and wrote the first draft, while both Hugh D. Safford and Ashley R. Grupenhoff contributed to the review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Grupenhoff & Safford, 2024) are available from Dryad: <https://doi.org/10.5061/dryad.7pvmcvf2h>.

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SUPPORTING INFORMATION

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

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