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Long-term effects of fire severity on oak–conifer dynamics in the southern Cascades

Matthew I. Cocking,[1,3] J. Morgan Varner,[1,4] and Eric E. Knapp[2]

[1]*Wildland Fire Laboratory, Department of Forestry and Wildland Resources, Humboldt State University, Arcata, California 95521 USA*
[2]*United States Department of Agriculture Forest Service, Pacific Southwest Research Station, Redding, California 96002 USA*

Abstract. We studied vegetation composition and structure in a mixed conifer–oak ecosystem across a range of fire severity 10 years following wildfire. Sample plots centered on focal California black oaks (*Quercus kelloggii*) were established to evaluate oak and neighboring tree and shrub recovery across a gradient of fire severity in the southern Cascade Range, USA. Shrub and oak resprouting was strongest around focal oaks where conifer mortality was greatest. Linear modeling revealed negative relationships between California black oak sprout height or basal area and residual overstory tree survival, primarily white fir (*Abies concolor*). The two dominant competing species, California black oak and white fir, showed opposite responses to fire severity. Sprouting California black oak and associated shrubs dominated in severely burned areas, while surviving, non-sprouting white fir maintained dominance by its height advantage and shading effects in areas that burned with low fire severity. Our results indicate that high-severity fire promotes persistence and restoration of ecosystems containing resprouting species, such as California black oak, that are increasingly rare due to widespread fire exclusion in landscapes that historically experienced more frequent fire. We present a conceptual model based on our results and supported by a synthesis of postfire resprouting dynamics literature. Our results and conceptual model help illuminate long-term postfire vegetation responses and the potential ability of fire to catalyze formation of alternate vegetation community structures that may not be apparent in studies that evaluate postfire effects at shorter time-since-fire intervals or at coarser scales.

Key words: alternative vegetation states; conifer encroachment; fire effects; fire exclusion; Quercus kelloggii; *resprouting; top-kill; tree mortality*.

Introduction

Fire is a catalyst for the formation and maintenance of ecosystems in many regions of the world (Abrams 1992, Agee 1993, Arseneault 2001, Bond and Keeley 2005). Plant species have evolved specific traits and life history strategies that enable their persistence across a variety of fire regimes: thick, heat-resistant bark (Jackson et al. 1999), heat-triggered seed germination (Keeley 1987), flammable litter (Fonda 2001, Kane et al. 2008, Engber and Varner 2012*a*), and a multitude of resprouting mechanisms (Bond and Midgley 2001, Hoffmann and Solbrig 2003, Vesk and Westoby 2004, Keyser et al. 2005). In fire-prone communities, species capable of resprouting are often abundant and frequently dominate the early years following fire (e.g., Bellingham and Sparrow 2000, Barton 2002, Cocking et al. 2012).

Fire has played a strong role in the success of many resprouting shrubs and trees in California ecosystems. Among them is California black oak (*Quercus kelloggii*), a moderate-statured tree with high cultural (McCarthy 1993) and ecological importance (Bowyer and Bleich 1980, Kelleyhouse 1980, Koenig et al. 2008). Early accounts in frequently burned environments in the Sierra Nevada suggest that California black oak-dominated woodlands were common (Kellogg 1882, 1889), often sharing dominance with scattered large, canopy emergent, fire-resistant pines, especially ponderosa (*Pinus ponderosa*) and sugar pine (*P. lambertiana*) (McDonald 1969, Vankat and Major 1978). The disruption of fire regimes by contemporary fire exclusion in California poses a serious threat to these ecosystems by enabling invasion and establishment of less fire-tolerant native conifers, particularly white fir (*Abies concolor*) and Douglas-fir (*Pseudotsuga menziesii*) (Barr 1946, Vankat and Major 1978, Parsons and DeBenedetti 1979, Stewman 2001, Cocking et al. 2012). Dense growth of young fir in remnant oak stands eventually leads to decline and mortality of shade-intolerant oaks (Barnhart

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[3] Present address: United States Department of Agriculture Natural Resources Conservation Service, Eureka, California 95503 USA. E-mail: micocking@gmail.com

[4] Present address: Department of Forestry, Forest and Wildlife Research Center, Mississippi State University, Mississippi 39762-9681 USA.

et al. 1996, Stewman 2001), while the developing conifers become more fire resistant as they increase in size (Ryan and Reinhardt 1988).

Conifer encroachment in Pacific West oak woodlands has become increasingly recognized in recent decades and is an important ecological restoration and management concern (Barnhart et al. 1996, Stewman 2001, Devine and Harrington 2006, Engber and Varner 2012*b*). A potential mechanism to restore oak dominance in conifer-encroached stands may involve oak species' ability to resprout following fire. Resprouting ability provides a disturbance advantage to California oaks because competing conifers must regenerate from seed. Relative growth of encroaching fir species is initially slower than oak sprouts (Hermann and Lavender 1990, Laacke 1990, Bellingham and Sparrow 2000), which utilize root reserves to enable immediate, rapid growth (e.g., Bowen and Pate 1993). This rapid and vigorous sprout response allows California black oak and other hardwoods to persist in frequently burned environments (McDonald and Tappeiner 2002), and acts as a last-resort survival mechanism in the event of severe disturbance. This important adaptation is often overshadowed by the commonplace practice of viewing high-severity fire as negative (see review in Kauffman 2004). Such events are an essential reestablishment mechanism for California black oak woodlands, especially where encroaching conifers are too large to be killed by lower intensity wildfire (Cocking et al. 2012).

Resprouting vegetation response has the potential to affect stand structure for many decades (Bellingham and Sparrow 2000, Barton 2002, Garcia et al. 2002). Despite the importance of long-term sprout responses, short-term mortality patterns dominate fire effects literature. This is due in part to a general focus on the death of stems, especially conifers, and the assumption that greater stem death (regardless of resprout ability) is an appropriate measure of harmful ecological impacts. Along this vein, most postfire research on vegetation response focuses on the first few years following fire, resulting in a constrained understanding of postfire recovery and vegetation trajectories over time (Jules et al. 2011). Postfire research in California forests containing California black oak and other hardwoods also often neglects to make a deeper analysis of resprouting, which becomes more apparent with time since fire and is a critical factor in determining long-term postfire forest structure, stand condition, and the persistence of resprouting hardwoods. This bias produces an assumption that the most important effects of fire occur relatively soon after an area burns, a finding often in contrast with longer term results (Arseneault 2001, Agee 2003, Jules et al. 2011, Stevens-Rumann et al. 2012, Crotteau et al. 2013).

This study evaluates prefire community structure and postfire vegetation recovery (including overstory and understory) 10 years following fire in a mixed California black oak–conifer stand in the southern Cascade Range in northern California. Our research objective was to investigate the longer term effects of varying fire severity on California black oak and nearby competing vegetation in stands containing a mixture of California black oak, native conifers, and understory shrubs. We investigated: (1) the relationship between black oak resprouting response and fire severity, (2) whether abundance of co-occurring overstory white fir (*Abies concolor*) surrounding focal oak trees decreased with increasing fire severity, and (3) whether the response to a gradient of fire severity differed between black oak and competing conifers. We follow our results with a conceptual discussion of how short-term characterization of severe fire effects can differ substantially from longer term postfire stand development, leading to an incomplete view of fire effects. We further emphasize the importance of prefire species composition, and how the interaction between fire and species-specific traits can catalyze shifts in forest composition that can persist for many years after a single fire.

Methods

Site description

The study site was located within the northeastern extent of the Storrie Fire on the western side of the Southern Cascade mountain range in the Lassen National Forest of northern California, USA (40°05′48.25″ N, 121°14′46.18″ W). The Storrie Fire burned ~23 000 ha between 17 August and 27 September 2000 in the Plumas and Lassen National Forests. The central portion of the fire burned generally with higher severity along a southwest–northeast axis. The west and east flanks burned with more subdued fire behavior, resulting in a matrix of high-, medium-, and low-severity areas (Fig. 1; Crotteau et al. 2013; VegBurnSeverity Metadata, data *available online*).[5]

The Cascades are a relatively young volcanic range atop a plateau primarily composed of basalt with the southern reaches of the range intermixing with granite and metamorphic substrates similar to those that dominate the neighboring Klamath Mountains and Sierra Nevada. Soils in the Southern Cascades are typically formed from volcanic substrates (Miles and Goudey 1997). As in other Mediterranean climates of the region, the bulk of precipitation occurs in winter in the form of rain or snow. Summers are dry and hot with intermittent wet or dry thunderstorms, the latter contributing to the frequent fire that characterized the historical regime (Taylor and Skinner 1998, Taylor 2000). Burning by native people to promote various resources was also common prior to western settlement (Lewis 1990, Anderson 2006).

The Southern Cascades are generally conifer dominated. California black oak often occupies a secondary

[5] http://www.fs.usda.gov/detail/r5/landmanagement/gis/?cid=fsbdev3_048275

canopy among very large emergent pine trees or exists in distinct patches on drier or milder sites (Taylor 2010). Common conifers in the region are Douglas-fir, ponderosa pine, sugar pine, Jeffrey pine (*Pinus jeffreyi*), white fir, and incense-cedar (*Calocedrus decurrens*) while common hardwoods include California black oak, bigleaf maple (*Acer macrophyllum*), mountain dogwood (*Cornus nuttallii*), and canyon live oak (*Quercus chrysolepis*). Reconstructed fire return intervals in these mixed-conifer forests and woodlands were short, ranging from 9 to 42.5 years (Beaty and Taylor 2001, Skinner and Taylor 2006). Increased forest density as a result of fire exclusion is common in the region, and a large portion of compositional change is attributed to increasing presence of native, shade-tolerant tree species, particularly white fir (Beaty and Taylor 2001, Skinner and Taylor 2006).

Field sampling

Ten-year postfire sampling was focused around focal oaks between 1350 m and 1450 m above sea level (Fig. 1) across a range of postfire overstory tree mortality, here used as a fine-scale metric of fire severity. The composition of vegetation in this area was similar to vegetation found elsewhere within the Storrie Fire at that elevation, with an abundance of small to mid-sized conifers (particularly white fir) mixed with scattered large ponderosa and sugar pines and many mature California black oaks (Crotteau et al. 2013).

Plots were intentionally centered on California black oaks (>25 cm diameter at breast height [dbh]) to ensure inclusion of overstory oaks and to focus data collection on neighboring competition (as in Spector and Putz 2006, Cocking et al. 2012). Focal California black oaks were selected along transects with randomly chosen azimuths. A direct path was walked along that azimuth until intersection with the first oak greater than 25 cm dbh that was at least 50 m from the previous focal oak or 30 m from a road edge. We avoided all areas with evidence of postfire management (for example, salvage of dead trees). Both live and dead oak stems (that were alive prior to the fire) were used as plot foci, and sampling was conducted within a 10 m radius (area of 314 m^2) of each focal oak.

Within each plot, all live and dead stems greater than 10 cm dbh were identified and measured for diameter and height. Live trees and snags that were leaning or had broken off part way up the stem were categorized and measured for maximum height along the bole. Stems that appeared to have been dead prior to the fire were infrequently observed and were excluded from measurement. Characteristics used to identify and exclude prefire mortality were substantial lack of bark on lower portions of the bole and consumption of stem wood beyond outer bark. Fire consumption of stem wood is likely to only occur with dead, dry stems at the time of fire. Most dead stems were at least partially intact and standing 10 years after fire and were assumed to have died as a result of fire 10 years previous. Delayed mortality of two to four years occurs for very large trees following fire in mixed-conifer forests of the Cascades; however, mortality of smaller diameter trees (which composed the wide majority of stems in our study) is generally immediate (Agee 2003). Snag longevity of 10 years or more is common in the western United States following wildfires (Harmon et al. 1987, Morrison and Raphael 1993), particularly in unsalvaged areas (Russell et al. 2006).

California black oak stems that were top-killed (i.e., whose aboveground portion died postfire, but subsequently resprouted) were intensively measured for sprout response. Within each sprout clump (i.e., group of sprouts arising from the same parent stem), all sprouts at least 1.37 m (equal to dbh) tall were counted and their diameter measured at 0.2 m above ground level. Maximum sprout height (defined as the tallest sprout among the respective grouping) was also measured for each sprout clump.

Shrubs and seedlings were measured within plots to characterize the long-term response of competing vegetation associated with focal California black oaks. Percent cover for each shrub species was visually estimated within northeast and southwest quarter-wedges of each plot using a system of cover class values (1 represents <1%, 2 was 1–10%, 3 was 11–25%, 4 was 26–50%, 5 was 51–75%, and 6 was 76–100%). Maximum height of shrubs was estimated by the average of direct measurement of two representative individual plants in each plot (one in each quarter-wedge) for each shrub species. In addition, all conifer and oak seedlings (individuals between 10 and 137 cm tall) occurring within each quarter wedge were identified and grouped by height class (1 represented 10–25 cm, 2 was 25–50 cm, 3 was 50–75 cm, and 4 was 75–137 cm). Small seedlings (≤5 cm tall) are often ephemeral and less likely to contribute to the future overstory, so were excluded from sampling ("immature seedlings" as in Crotteau et al. 2013). Prefire abundance of saplings, seedlings, and shrubs was not reconstructed from field sampling because killed stems in these small size classes had degraded in the 10 years since fire, rendering accurate measurement unlikely or impossible.

Data analysis

For all broken or leaning California black oak and white fir trees on which height could not be measured in the field, prefire tree height was estimated from dbh values using regression analysis. Bark was missing on all top-killed and dead California black oaks, prompting an additional bark thickness adjustment to dbh values for those stems. Both tree height and bark thickness were estimated using equations for California black oak generated from data collected at the Challenge Experimental Forest in nearby Yuba County (~75 km away) by McDonald (1983). We developed equations to predict height from dbh for

white fir using measurements taken on 30 randomly selected trees at a nearby location (~8 km away) just outside the perimeter of the Storrie Fire (height in meters = 6.01 + 0.42 × dbh in centimeters; $R^2 = 0.97$). Values for trees where the portion of the trunk at dbh was missing or indeterminable were not estimated and excluded from analyses. This condition accounted for 9.5% of all white fir stems found in plots and was largely due to stem breakage, not stem consumption during fire.

For all vegetation response analyses, we used a continuous measure of fine-scale fire severity (with one value for each plot) as the predictor variable. Fire severity was a fine-scale measure for each plot defined as:

$$\text{plot fire severity} = \frac{\text{number of dead stems}}{\text{total stems}}$$

where the number of dead stems was defined as dead stems >10 cm dbh of all species combined (including top-killed oak stems) for each plot, and total stems was the total reconstructed number of stems >10 cm dbh of all species combined for each plot.

Using this metric, fire severity values of 1 corresponded to complete stem mortality, and fire severity of 0 corresponded to no stem mortality for stems >10 cm dbh.

Relationships between fire severity and oak sprout recovery were analyzed with general linear modeling. Analysis of California black oak sprout recovery was performed for two oak sprout growth responses summarized at the plot level: (1) the mean basal area per sprout clump (cm^2/clump) and (2) the mean maximum sprout height per sprout clump (m/clump). Absence of any top-killed oaks in three plots prompted omission of these plots from analyses of resprouting. Shrub height, shrub cover, and California black oak seedling density responses were also analyzed with general linear modeling to investigate relationships with fire severity. Plot averages of shrub cover class values were treated as a continuous response variable. When data failed to meet statistical assumptions of linear modeling, response variables were transformed (natural log or square root) prior to analysis. The predictor variable, fire severity (proportion), was also transformed where necessary using the arcsine-square root transformation (Zar 2003). Significance of $\alpha = 0.05$ was used for all tests.

The changes in relative composition (%) of California black oak and overstory firs (*Abies concolor* and *Pseudotsuga menziesii*) were also compared to overstory tree mortality to investigate shifts in species abundance. White fir and Douglas-fir were lumped together because some dead stems were not identifiable beyond "fir" and also because these two conifer species are often the most important competitors with California black oak (Barr 1946, Vankat and Major 1978, Stewman 2001, Cocking et al. 2012). Change in relative composition was defined as the prefire proportion of plot trees that were oaks or firs (>10 cm dbh) subtracted from each respective postfire proportion. The resulting continuous measure of change in relative composition for black oak and fir was tested using general linear modeling with fire severity as the independent variable. All variables were square-root transformed prior to analysis to provide an appropriate fit of the data to residual distribution, independence, and constant variance assumptions for general linear modeling.

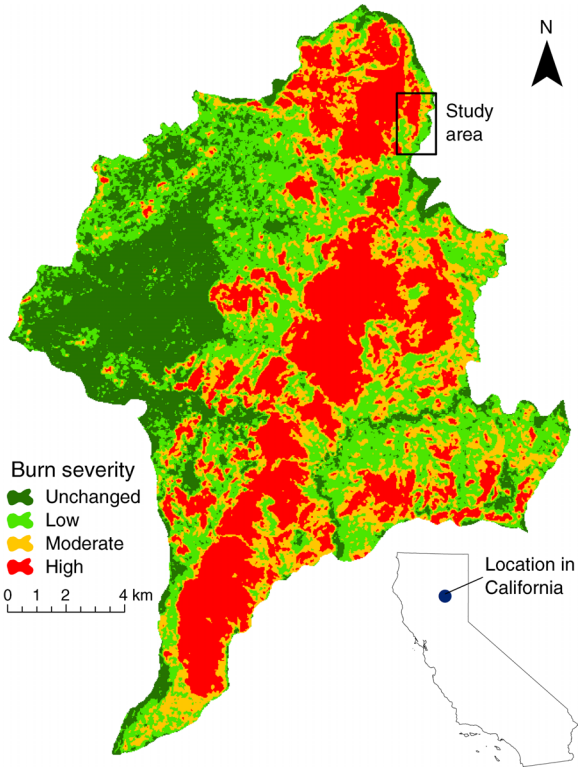

FIG. 1. The study sites were located in the region of the Storrie Fire, a mixed-severity wildfire in the southern Cascade Range of northern California, USA. Circular plots were centered on randomly selected focal California black oaks (*Quercus kelloggii*) within the study area. Vegetation burn severity is shown in four categories for the entire Storrie Fire area (data *available online*; see footnote 5).

Several measurement difficulties prompted the use of stem density (of trees >10 cm dbh) rather than basal area to characterize fire effects in our analyses. Prefire estimates for tree diameter could not be estimated for surviving trees as we lacked adequate radial growth equations, which would have allowed correction for 10 years of postfire growth. This inhibited our ability to calculate prefire basal area, as well as change in basal area as a result of the fire. Broken and fallen stems further inhibited accurate measurements of prefire dbh. We were able to accurately tally the number of trees (dead, live, and top-killed) for each plot; hence, the use of tree density rather than basal area in our analyses.

TABLE 1. Frequency and density of dead, live, and top-killed trees (>10 cm dbh) by species in plots 10 years after the Storrie Fire in the Lassen National Forest, California, USA.

Species	Freq	Stem condition	Density (stems/ha)	SE
Abies concolor	0.92	killed	266	43.5
		live	96	29.3
Quercus kelloggii	1.00	killed	22	8.6
		top-killed	209	32.8
		live	59	18.7
Unidentified fir	0.24	killed	78	35.6
		live	3	1.8
Pseudotsuga menziesii	0.16	killed	26	25.5
		live	5	2.4
Pinus lambertiana	0.28	killed	5	2.4
		live	6	2.6
Calocedrus decurrens	0.24	killed	5	3.0
		live	6	3.2
Pinus ponderosa	0.20	killed	5	4.0
		live	5	3.0
All species		killed	795	72.2
		top-killed	209	32.8
		live	180	43.8

Notes: All trees were presumed to have been alive prior to the fire. Frequency (Freq) is the proportion of the 25 plots where each species was present (California black oak was present in all plots due to the study design). An additional row is included for top-killed California black oak trees. For top-killed stem density calculations each clump of resprouting stems was counted as one individual. Because there were no other respouting species present at the site, the total top-killed values are equivalent to those for California black oak alone.

RESULTS

Reconstructed pre-wildfire tree composition

Based on stand reconstruction, the most abundant tree species surrounding focal California black oaks prior to the fire were white fir and other California black oaks. Douglas-fir, sugar pine, incense cedar, and ponderosa pine were present at much lower densities (collectively accounting for approximately 12% of prefire stems; Table 1). White fir >10 cm dbh was particularly abundant with dead or live stems found in 23 of 25 plots and at densities generally higher than other conifers. Ponderosa pine and sugar pine were found in only five plots each. Despite their low density, some of the largest and tallest trees were ponderosa and sugar pines. Values for dbh and height of California black oak and incense-cedar were relatively low when compared to other species within study plots (Table 2).

Post-wildfire vegetation composition and structure

Aboveground stem mortality (10 years postfire) was highly variable, ranging from 0% to 100% for most species (Table 3), with 19 of 25 plots having greater than 75% stem kill of trees greater than 10 cm dbh. Only 17 of the 227 California black oaks (7.5%) measured across all plots were completely killed (i.e., no vegetative sprouts), and only three of 25 plots had complete oak mortality greater than 25%. In 36% of plots, California black oak was the only tree that survived, and all of the surviving California black oaks in those plots resprouted. Because the conifer species in this study are incapable of resprouting, complete mortality for these species was more common with 100% mortality recorded in 36% of plots. Mortality was particularly high for white fir, for which greater than 90% mortality was recorded in 48% of plots where it was present. Fire severity was highly variable, however, as high white fir survival (greater than 75%) was also observed in 26% of plots in which it was present.

Although California black oak stems were often killed aboveground, 90% of stem-killed individuals had live vegetative sprouts 10 years following the wildfire. Stature of postfire oak sprouts varied substantially across the sampled fire severity gradient. High-severity

TABLE 2. Mean and range for diameter at breast height (dbh) and height of dead, live, and top-killed stems (≥10 cm dbh) of all species across Storrie Fire plots.

Species	Stem condition	dbh (cm)			Height (m)		
		Mean	Min	Max	Mean	Min	Max
Abies concolor	dead	24.8	14.5	66.5	16.6	12.1	34.1
	live	41.0	22.0	77.9	23.3	15.3	38.9
Quercus kelloggii	dead	24.2	11.9	54.1	19.5	14.6	27.8
	live	28.8	22.6	44.1	14.7	11.2	18.6
	top-killed	20.4	14.8	35.7	15.9	8.0	19.9
Unidentified fir	dead	30.2	16.2	58.0	13.7	9.3	20.0
	live	18.3	16.5	20.1	11.5	11.5	11.5
Pseudotsuga menziesii	dead	21.0	21.0	21.0	...	...	...
	live	67.3	42.0	109.3	31.3	24.4	46.7
Pinus lambertiana	dead	45.6	12.6	110.5	...	...	...
	live	45.5	26.5	78.9	24.4	18.1	39.3
Calocedrus decurrens	dead	17.1	13.0	25.1	15.4	15.4	15.4
	live	27.9	15.2	45.2	12.7	6.6	21.8
Pinus ponderosa	dead	44.5	31.2	57.7	...	...	...
	live	37.5	22.9	62.3	25.6	19.0	37.3

Notes: Values for broken and leaning California black oak and white fir snags were adjusted prior to data summation using equations from McDonald (1983) for black oak and from data gathered on randomly chosen white firs at a site just outside the Storrie Fire perimeter ($R^2 = 0.97$). Ellipses show cases where height values for broken and leaning snags of all other species were not calculated, leading to missing height estimates for some species.

TABLE 3. Mean, standard deviation (SD), and range of mortality of species across plots.

Species	N	Mortality (%)		
		Range	Mean	SD
Abies concolor	23	0–100	71	35
Quercus kelloggii	25	0–100	79	29
Quercus kelloggii†	25	0–50	8	15
Unidentified fir	6	89–100	97	5
Pseudotsuga menziesii	4	0–95	24	48
Pinus lambertiana	7	0–100	43	45
Calocedrus decurrens	6	0–100	44	50
Pinus ponderosa	5	0–100	40	55

Note: *N* is the number of plots in which each species occurred.

† The second row for *Quercus kelloggii* represents mortality after top-killed stems had been accounted for. Note that when top-kill is considered, actual mortality of oaks is much lower.

plots had the greatest growth with sprouts at least 1.37 m tall numbering as many as 31 per top-killed individual (i.e., per sprout clump) and reaching heights as tall as 8.5 m. Sprout density was also highly variable, and averaged 1080 ± 894 sprouts/ha (mean ± SD unless otherwise noted). Sprout clumps averaged 9 ± 5 sprouts per clump within plots where top-kill was present ($n = 22$).

Tree seedling densities varied tremendously within plots surrounding focal oaks. Across all tree species, density averaged 5096 seedling/ha, but ranged from as many as 15 279 seedlings/ha to none. The four plots with the lowest number of seedlings (0–446 seedlings/ha) all experienced complete overstory stem mortality. California black oak and white fir seedlings occurred at a far higher density on average than other species. Although California black oak seedlings were the most abundant compared to other tree species, they were often shorter than seedlings of competing conifers. In contrast, oak resprouts were generally much taller than conifer and oak seedlings (Table 4).

Shrub composition and cover varied around focal oaks 10 years following the Storrie Fire. Mountain whitethorn (*Ceanothus cordulatus*) had the highest frequency (found in 22 of 25 plots), followed by greenleaf manzanita (*Arctostaphylos patula*), which occurred in many plots (13), but with lower average cover. Mountain whitethorn cover was greater than 75% in one-fifth of all plots, forming a dense shrub stratum characteristic of severely burned areas across the post-Storrie Fire landscape (Crotteau et al. 2013). Mountain whitethorn and greenleaf manzanita were also taller, on average, than other shrubs in plots surrounding focal oaks (Table 5).

Fire severity and vegetation development

Fine-scale fire severity (as measured by stem mortality) was significantly related to many postfire vegetation characteristics. Higher fire severity (as approximated by the percentage of stem mortality) corresponded with an increasing presence of California black oak ($R^2 = 0.70$, $P < 0.001$) and decreasing presence of white fir and Douglas-fir ($R^2 = 0.44$, $P < 0.001$) (Fig. 2).

General linear modeling revealed strong linear and nonlinear, positive relationships between fire severity and stature of oak sprouts (Fig. 3). Plots with the least overstory tree mortality had maximum sprout height responses that averaged only 1 to 2 m, whereas plots with complete overstory mortality had average maximum sprout heights generally greater than 3 m and as tall as 5.5 m. In the highest severity plots (>80% stem mortality, $n = 16$), sprout clump basal area averaged 290.4 ± 164.6 cm^2/clump with a maximum of 563.2 cm^2/clump. In contrast, average sprout clump basal area never exceeded 89.4 cm^2/clump for the nine plots where overstory stem mortality was ≤80%.

TABLE 4. Mean postfire density and height of seedlings (between 10 and 137 cm tall) and sprout clumps.

Species	Freq	Density (seedlings/ha)	SE	Height (cm)	SE
Quercus kelloggii					
Seedlings	0.84	3005	772	41.5	7.7
Resprout stems	0.92	1080	191	...	...
Resprout clumps†	0.92	209	33	382.9	27.6
Abies concolor	0.92	1576	397	41.8	4.4
Pinus lambertiana	0.84	303	65	48.5	6.3
Pinus ponderosa	0.44	107	63	84.0	12.3
Pseudotsuga menziesii	0.24	59	24	39.1	7.3
Calocedrus decurrens	0.32	46	16	33.3	5.0

Notes: Resprout clumps were treated as single organisms where height was calculated from single maximum height values for each individual clump, and density was the density of individual clumps rather than individual sprouts. Height of resprout stems is not available (shown with ellipses) because height was measured only once for each sprout clump rather than for each individual sprout. Frequency (Freq) is the proportion of plots in which each species and regenerating form occurred.

† Resprout clump was defined as one individual with multiple stems sprouting from the same root collar. Resprout clumps contained an average of 9 ± 5 stems that were more than 1.37 m tall per clump.

TABLE 5. Frequency (Freq), percent cover, and average height of shrubs within 10 m of focal California black oaks.

Species	Freq	Cover (%)†		Height (m)	
		Mean	SE	Mean	SE
Ceanothus cordulatus	0.88	30.62	6.32	0.98	0.07
Arctostaphylos patula	0.52	1.58	0.89	0.97	0.10
Ceanothus prostratus	0.16	0.56	0.32	0.22	0.13
Ribes roezlii	0.36	0.18	0.05	0.35	0.07
Symphoricarpos mollis	0.36	0.18	0.05	0.18	0.02
Prunus emarginata	0.12	0.06	0.03	0.83	0.43
Chrysolepis sempervirens	0.08	0.04	0.03	0.70	0.50
Rhamnus rubra	0.04	0.02	0.02	0.30	···

Note: Only one *Rhamnus rubra* individual was found across the entire site, which prevented the calculation of standard error (shown with an ellipsis).

† Percent cover values were calculated using the midpoint for respective cover class value ranges (1 represented <1%, 2 was 1–10%, 3 was 11–25%, 4 was 26–50%, 5 was 51–75%, and 6 was 76–100%).

Both shrub cover ($R^2 = 0.55$, $P < 0.001$) and shrub height ($R^2 = 0.59$, $P < 0.001$) were also significantly related to fire severity (Fig. 3). Shrubs were more dominant, covering greater area around focal oaks where stem mortality was higher. Shrubs were also tallest (generally between 0.8 and 1.5 m) in plots with 100% stem mortality. Shrubs were generally shorter than 0.8 m in plots with <100% stem mortality.

California black oak seedling density appeared to be negatively related to fire severity ($R^2 = 0.45$, $P < 0.001$); however, assumptions of residual normality and constant error variance were not met, even following data transformation. This is not surprising, given numerous complications involved in estimating highly variable seedling densities in postfire environments (Turner et al. 1997, 1999, Shatford et al. 2007, Crotteau et al. 2013, *in press*). The greatest numbers of California black oak seedlings occurred where there was at least some overstory tree survival around focal oaks. In the 10 plots where >80% of California black oak stems survived, the density of California black oak seedlings, all of which apparently established after the fire, exceeded 2500 seedlings/ha. In the 12 plots where no overstory oak stems survived, the density of California black oak seedlings was lower, but occasionally substantial, numbering up to 1592 seedlings/ha. Conifer seedling density appeared unrelated to overstory stem mortality ($P = 0.27$). As with the oak seedling analysis, assumptions of residual normality and constant error variance were not met for this analysis.

DISCUSSION

Fire severity as a driver of vegetation change

Ten years after wildfire, tree and shrub responses varied strongly across a fine-scale fire severity gradient. Patches of high conifer mortality led to development of vigorously resprouting shrubs and California black oak structure absent in areas that burned with lowest fire severity (Fig. 4). Shrubs proliferated in these high-severity areas, contributing substantially to the vegetation surrounding focal oaks. The vegetation response found in high-severity areas of the Storrie Fire corroborates other findings that California black oak has tremendous ability to recover via vegetative resprouting and after severe wildfire (McDonald 1990, Taylor 2010, Cocking et al. 2012). This trait contrasts starkly with co-occurring conifers, for which mortality was generally high and recovery much slower in plots that burned at high severity and elsewhere in the Storrie Fire (Crotteau et al. 2013). In 10 years following fire, oak resprouts were, on average, at least nine times taller than the average height of non-pine conifer seedlings and at least four times taller than the average height of

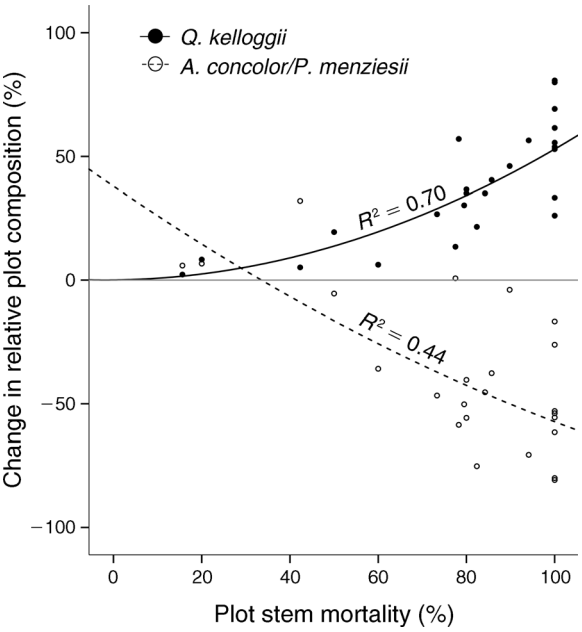

FIG. 2. Change in composition of overstory California black oak and white fir (*Abies concolor*) and Douglas-fir (*Pseudotsuga menziesii*) 10 years following wildfire in plots of varying fire severity. Fire severity for each plot is approximated by the percentage of tree stem mortality.

ponderosa and sugar pine seedlings. Oak sprouts also grew at much faster rates in areas of higher fire severity compared to sprouts in areas of lower fire severity. The sprout-to-seedling height difference illustrates the advantage gained by oaks through high-severity fire. Lower severity fire had a much different effect, resulting in subdued development of black oak sprouts and shrubs.

In areas of low fire severity, competition between oaks and conifers was still present as fewer conifer stems were killed. Although overstory oak survival was somewhat greater in low severity areas, top-kill still occurred. Oak sprouts in these areas were much less vigorous than those found in high severity, and surviving overstory oaks were not released from canopy competition with taller, shade-tolerant conifers. This finding supports the premise proposed by Cocking et al. (2012) that when competing fir trees survive fire, shade-intolerant oak sprouts and associated vegetation are unlikely to sprout vigorously. This effect is more likely attributed to lack of light than a direct effect of fire, although the two potential mechanisms were not differentiated in the methodology used in this study. This fire-catalyzed response pattern has been noted in other resprouting species adapted to frequent fire environments (Bowen and Pate 1993, Barton 2002, Hoffmann and Solbrig 2003, Hoffmann et al. 2009).

The high density of California black oak seedlings observed in plots in this study (Table 4) differs from the lack of regeneration observed following prescribed fire by Moghaddas et al. (2008) and is more consistent with Taylor (2010), who reported abundant California black oak seedlings following wildfire. Intermittent mast years (Koenig et al. 1994, Garrison et al. 2008) and slow regeneration rates for oaks throughout California have been a cause of concern for managers and scientists for decades (e.g., Griffin 1971, 1976). Of particular interest at this site is the occurrence of many California black oak seedlings in plots that experienced low fire severity. This pattern, coinciding with greater observed overstory oak survival, suggests that either the emergence of seedlings is improved because of higher acorn densities resulting from higher numbers of surviving mature oak trees, or that the open environment created by high-severity fire may be inhospitable for seedling establishment, even if it is conducive to vigorous oak sprout growth. The latter theoretical mechanism contrasts somewhat from the results from Taylor (2010), who found seedlings in intermediate to open canopy cover conditions; but is more consistent with earlier research by McDonald and Tappeiner (2002), who found oak seedlings to be far more abundant beneath existing oak crowns than elsewhere. The relative shade intolerance of California black oak saplings (McDonald 1969, 1978), coupled with the greater initial height of conifer seedlings found in our study, suggests it would be unlikely for many oak seedlings to survive to maturity in shaded areas unless competition from both conifer seedlings and overstory trees was removed. The seedling results of this study, while intriguing, should be interpreted with caution as our sampling design (plots centered on overstory oaks) did not enable unbiased analysis of dispersal mechanisms and spatial relationships to surviving plot trees.

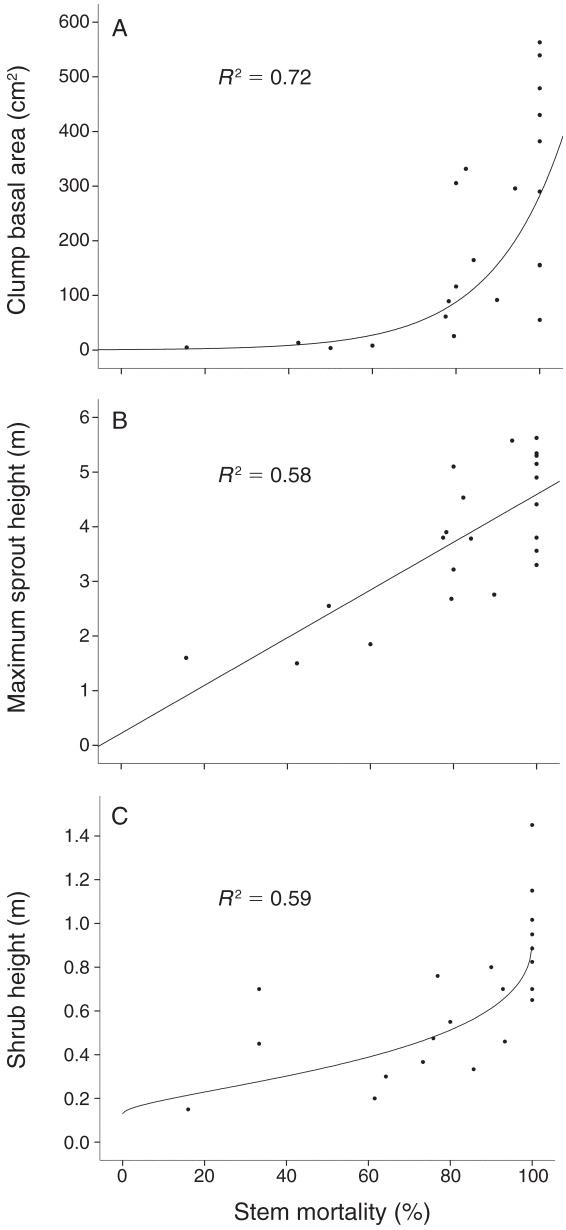

FIG. 3. Relationship between overstory tree mortality and (A) *Q. kelloggii* sprout clump basal area, (B) sprout height, and (C) shrub height 10 years after the Storrie Fire.

Vigorous vegetative resprouting is often omitted or downplayed in assessments of fire severity that focus more on short-term measures of aboveground stem mortality (such as reduction of basal area or total stems). Thus, postfire research in the western United States often fails to incorporate the effects of alternative

FIG. 4. California black oak resprouts 10 years following the Storrie Fire in (A) areas where fire severity was high, and (B) areas where fire severity was lower. Note size difference.

regeneration and persistence strategies on mid- to long-term vegetation trajectories. As a result, stand-replacing fires in areas with California black oak and other resprouting species may appear severe in the short term, but instead, lead to the rapid recovery of tree and associated shrub cover, with the potential for restoration of forest composition that was more common historically, when fires were frequent. The results of this study, and work on other California hardwoods (Roy 1962, McDonald 1978, Plumb 1980), demonstrates that many North American species such as California black oak are acutely adapted to coexist with high-severity fire. Depending on the reference fire regime, the formation of this vegetation structure illustrates a potential paradox when using the term "fire *severity*" to connote unnatural or harmful effects (sensu Kaufmann 2004). In many cases, such as those in which resprouting species play an important role, fire severity should be evaluated more thoughtfully with respect to long-term vegetation recovery and the development of greater structural or compositional diversity.

Structure and composition persistence

These differing vegetation structural responses (oak and associated resprouters vs. fir dominance) form two ends of a continuous gradient, with fire frequency and intensity shifting the balance towards one or the other. Fire-catalyzed dynamics that result in the formation of alternative structural states have been described for many disturbance-prone ecosystems, most of which harbor a significant component of resprouting species (Abrams 1992, Tveten and Fonda 1999, Bellingham and Sparrow 2000, Keyser et al. 2005, Hoffmann et al. 2009). Odion et al. (2010) likened vegetation assemblages in the nearby Klamath Mountains to multiple "alternative community states" dependent on contrasting fire regimes. Skinner et al. (2006) described the potential for alternative outcomes of low- and high-intensity fire for California black oak woodlands in the same region. Alternative states enter a transition phase only through the occurrence of a unique destabilization event or temporal processes such as severe fire or fire exclusion (Odion et al. 2010). Many other studies have identified similar differential vegetation responses in frequently burned ecosystems (Trabaud and Lepart 1982, Bond and Midgley 1995, Barton 2002, Garcia et al. 2002, Hoffmann and Solbrig 2003, Keyser et al. 2005, Engber et al. 2011, Murphy and Bowman 2012, Trauernicht et al. 2012). This nuanced view of fire's effects on vegetation deserves more attention in oak woodlands in northern California and more generally where resprouters persist in fire-prone environments (Abrams 1992, Peterson et al. 2007).

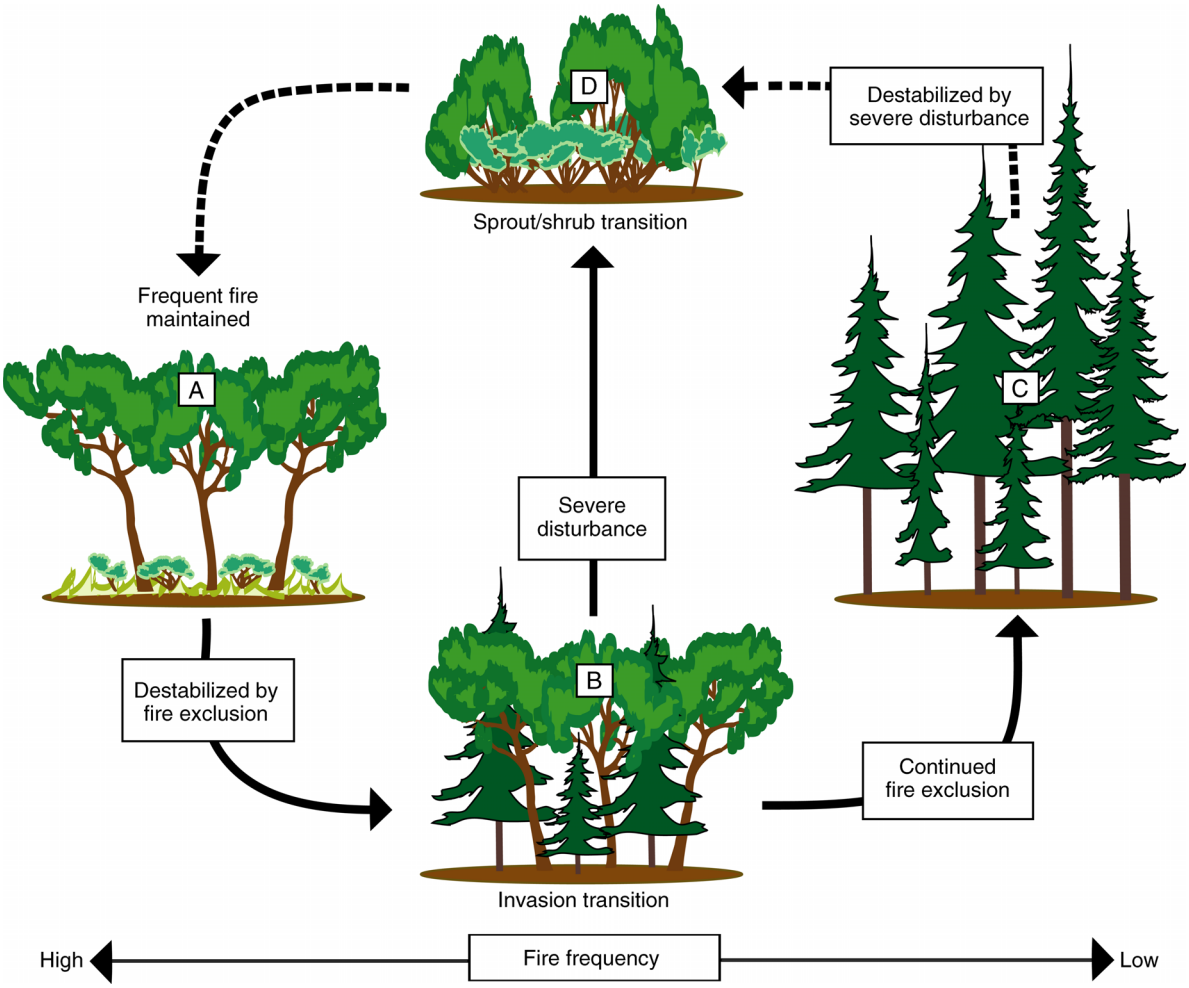

FIG. 5. A conceptual model for the destabilizing effects of fire severity across a gradient of oak–fir community states. Without repeated disturbance, the tendency of structures maintained by frequent fire, such as oak savanna/woodland (A), is toward encroachment (B). In order to destabilize and revert back to oak abundance, encroached and converted stands (C) must be subjected to increasingly greater disturbance severity. Sprout stands (D) and encroached stands occupy unstable transitional phases where the primary mechanism for destabilization changes from fire exclusion to severe disturbance. Dashed arrows indicate uncertain transitions.

The divergence of fir and oak/shrub dominance observed in this study for areas surrounding mature California black oaks (although analyzed across a fire severity gradient) may indicate a transition between alternative states with severe fire acting as a destabilizing event. This divergence of forest composition can be conceptualized across a structural gradient in which fire frequency and severity affect composition over time (Fig. 5). In the absence of fire, the natural tendency of ecosystems dominated by California black oak and formerly maintained by frequent disturbance is toward conversion to shade-tolerant conifers (Stewman 2001, Odion et al. 2010, Cocking et al. 2012). As the vegetation shifts toward fir, increasing amounts of energy (i.e., increases in fire intensity and severity) are needed to destabilize fir dominance and allow recovery of oaks. Thereafter, repeated fire, regardless of intensity, may continue to promote sprouting and early growth advantage of California black oak, while conversely impeding conifer establishment. However, the response of California black oak sprout stands to repeated, short-interval fires is uncertain, as is the fate of many existing oak stands that are declining due to effects of fire exclusion. Further research investigating these questions will help clarify the complex relationship between fire and California black oak, and determine if fire is not only a catalyst in these ecosystems, but essential to the maintenance and survival of this species within largely coniferous landscapes.

When California black oak woodlands shift toward fir dominance, treatments to restore remnant oaks are increasingly energy intensive as fir trees become large and more fire resistant. Removal of relatively large diameter fir has been successfully used to restore the

structure and vigor of encroached Oregon white oak (*Quercus garryana*) woodlands (Devine and Harrington 2006, 2013), but has yet to be intensively evaluated in California black oak ecosystems. Prescribed fire is also a possibility, but as encroaching conifers mature, prescribed fire may become increasingly ineffective (Cocking et al. 2012, Engber and Varner 2012*b*). Most prescribed fire is of lower intensity (e.g., due to liability, prevention of escapes, or fear of inducing tree mortality), and achieving sufficient intensity during prescribed fires to kill larger conifers is operationally difficult. In the Sierra Nevada, low-intensity fires often do not restore historic stand structure because high densities of younger trees that have encroached in the absence of fire are infrequently killed (Collins et al. 2011). In the current landscape, localized areas of high severity in increasingly larger fires (Miller et al. 2012) may be serendipitously restoring some structurally altered oak woodlands by creating early-seral conditions that favor oak sprouts. Mechanical restoration of these conifer-encroached stands would conversely require intensive and costly mechanical treatment in lieu of allowing high-severity fire to reduce conifer density.

Inconsistencies in related fire effects research

Despite growing evidence for California black oak decline and conversion to fir forests as a result of fire exclusion (Stewman 2001, Skinner et al. 2006, Cocking et al. 2012), there remain conflicting perceptions of this species' relationship with fire, and a poor understanding of specific reference fire regimes and pre-settlement stand structures. McDonald (1969) hypothesized that most of the California black oak stands in California established following stand-replacing fires. However, uneven-aged stands are also common (Garrison et al. 2002, Taylor 2010, Cocking et al. 2012). Further, spatial analysis by Taylor (2010) revealed a lack of groupings of similarly sized stems, a contrary pattern to what would be expected as a result of widespread resprouting following high-severity fire. The historic practice of frequent fire-aided cultivation by California tribes (Lewis 1990, McCarthy 1993, Anderson 2006) and the common occurrence of oaks older than 200 years (McDonald 1969, Garrison et al. 2002, Taylor 2010, Cocking et al. 2012) in a region with historically frequent fire (Taylor and Skinner 1998, Taylor 2000) is further evidence that California black oak stems once survived multiple fires. More frequent fire would have historically kept surface fuel loads lower relative to many stands today; thus, fires may have lacked the intensity to kill large swaths of mature oak stems, except under the most unusual weather or forest fuel conditions. Frequent fire would have also profoundly affected fire-sensitive conifer seedlings, limiting their establishment in fire-prone areas like oak or oak–pine woodlands. However, as illustrated by our model, a period of fire absence long enough to allow greater conifer recruitment would initiate a change in forest structure that requires more substantial intervention to restore oak dominance.

Although California black oak is known to survive fire by two methods (stem survival and resprouting; McDonald 1969, Taylor 2010, Cocking et al. 2012) it has been, and still is, described to a certain degree as fire susceptible (McDonald 1969, Skinner et al. 2006). Tree mortality studies often add to this confusing story when substantial resprouting is observed immediately following fire (Regelbrugge and Conard 1993, Stephens and Finney 2002, Kobziar et al. 2006, Fry 2008), but subsequent analyses of tree mortality seldom separate California black oak response into complete kill vs. top-kill only categories. When this distinction is not made, patterns of *true* tree mortality and fire severity become blurred, making the longer term effect of fire on forest stands difficult to discern.

The sprout and associated shrub success following high-severity fire described in this study is crucial to understanding persistence of species in fire-prone environments. Oak sprout response to fire severity offers a view of the potentially stimulating effect of severe fire as opposed to conventional negative views of high severity. Whether these responses persist over longer time scales is likely dependent on the repeated occurrence of fire. Research on savanna and woodland development in other regions of North America asserts that repeated fires over time are critical to develop and sustain grassland and scattered woodlands, and that the length of fire return interval is correlated strongly with species composition and vegetation type across landscapes (Abrams 1992, Peterson et al. 2007). Many oak forest and woodland types in the Midwest and eastern United States (Nowacki and Abrams 2008) have developed similar conversion issues to those only more recently described for the western United States. Whether future fires occur at intervals sufficient to maintain sprouts and other oak type structures in the western United States is dependent on management of prescribed and wild fires. Continued widespread fire suppression is likely to perpetuate altered conditions with greater abundance of fire-intolerant species and rarity of frequent fire environments where California black oak and other species can persist. Future work that investigates the persistence of resprouting species across gradients and varying frequency of disturbance will greatly improve our understanding of the dynamics of these and other fire-prone ecosystems.

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