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Do repeated wildfires promote restoration of oak woodlands in mixed-conifer landscapes?

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ABSTRACT

Oak woodlands are dependent on frequent fire to maintain the low stem density and diverse understories that typify these ecosystems. Without this recurrent disturbance, fire-sensitive conifer competitors encroach on oaks, reducing their vigor, and diminishing habitat quality. In fire-excluded oak woodlands, stand-replacing wildfire can trigger shifts in canopy dominance from seed-generated conifers to oaks, which are capable of vigorous sprouting following topkill. We examined the occurrence and sprouting dynamics of California black oak (*Quercus kelloggii* Newb.) following repeated wildfires in the Lassen National Forest, California. We found that following reburn, changes in oak relative stand dominance, as well as oak sprout basal area and height, were each positively related to fire severity ($P < 0.0001$ for each analysis). While conifer regeneration suffered complete mortality at moderate and high reburn severities, 97% of topkilled oaks resprouted from surviving rootstocks, reinforcing oak dominance. Black oak resprouts that originated following topkill in the first wildfire were frequently topkilled in the second fire, including at lower burn severities survived by advance conifer regeneration. The results of this study indicate that while as individuals, black oaks are resilient to recurring wildfire, restoration of historic woodland structure and function is an unlikely outcome of these repeated disturbances. Management of post-wildfire regenerating oak stands in this region will require supplemental fuel reduction treatments, including prescribed burning.

1. Introduction

Fire-dependent ecosystems, woodlands and savannas have existed for millennia in concert with natural and anthropogenic fire (Staver et al., 2011, Swanson et al., 2011). Frequent, low-severity fires maintain the open canopy structure and diverse herbaceous understories characteristic of these ecosystems. Low-intensity fires, propagated in herbaceous fuels, eliminate the ingrowth of fire-intolerant species, and sustain open canopies of fire-tolerant savanna trees (Engber et al., 2011, Engber and Varner, 2012, Veldman et al., 2013). These frequent fires create a negative feedback, preventing the accumulation of heavy fuels, and maintain an open canopy that allows for development of the herbaceous fuels that perpetuate surface fires (Agee, 1993). Without frequent fires, open woodlands and savannas in many regions are replaced by closed-canopy forests through the normal processes of stand development (Oliver, 1980, Agee, 1993, Nowacki and Abrams, 2008, Staver et al., 2011).

More than a century of fire exclusion throughout the western U.S. has interrupted historic patterns of both natural and anthropogenic fire activity on the landscape (Agee, 1996, Sugihara et al., 2006). Dendrochronological studies indicate that frequent fire (between-fire intervals of < 20 years) was common in many low- and mid-elevation Pacific Northwest landscapes, most of which have not burned in the last century (Taylor, 2000, Skinner et al., 2006, Bekker and Taylor, 2010, Van de Water and Safford, 2011). This shift in fire regimes has resulted in the ingrowth of fire-sensitive species, resulting in denser vegetation and increased fuel loads in many western forests (van Wagtendonk, 1984, Agee, 1993, Sugihara et al., 2006). Along with the consequential increase in landscape homogeneity, these changes in the structure and composition of forests increase the risk of high-severity wildfires.

Rich in both ecological and cultural values, montane California black oak (*Quercus kelloggii* Newb.) woodlands of the Pacific Northwest have experienced a dramatic decline since the advent of large-scale fire exclusion (Scholl and Taylor, 2010, Cocking et al., 2014, Crotteau et al.,

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2014, Long et al., 2016b). Mature black oaks provide nesting cavities and platforms for a variety of birds and wildlife, and their mast supplies a critical food source for numerous species (Long et al., 2016b). Black oak woodlands were regularly burned by tribes in order to maintain and facilitate access to important dietary, medicinal, and material resources provided by this "cultural keystone" species (Anderson, 2005, Long et al., 2016a). Much of the degradation of these woodlands can be attributed to the absence of fire, and the consequent invasion of white fir (*Abies concolor* (Gord. & Glend.)), a highly pyrophobic species, and coast Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*), which is sensitive to fire prior to maturity (Ryan and Reinhardt, 1988). Continued suppression from neighboring conifers weakens oaks and ultimately causes mortality (Cocking et al., 2012). Black oak has several adaptive strategies that confer competitive advantages over conifers in fire-prone landscapes, including protective bark that permits above-ground survival of low intensity surface fires, epicormic bole and crown sprouting that enable recovery from crown injury, and vigorous basal sprouting that outpaces conifer regeneration after high-intensity fire has topkilled above-ground vegetation (McDonald, 1980, Donato et al., 2009a, Cocking et al., 2012, Collins and Roller, 2013, Crotteau et al., 2014). These advantages are lost, however, in the absence of fire. The removal of fire from the landscape has resulted in the transition of many oak woodlands and savannas to dense, mixed-conifer forests (Barnhart et al., 1996, McDonald and Tappeiner, 2002, Skinner et al., 2006).

Where the decline of black oak woodlands has resulted in the loss of important regional resources, opportunities remain for oak restoration, particularly following moderate and high-severity wildfires. Previous studies (Cocking et al., 2014, Crotteau et al., 2014) found that a single high-severity wildfire can re-establish oak overstory dominance following decades of ingrowth of competing fire-sensitive conifer species. To evaluate the effects of repeated wildfires on black oak persistence, we examined sprout vigor and shifts in patterns of community structure and composition across a continuous spectrum of fire severity combinations following two mixed-severity wildfires that burned through the same area in 2000 (Storrie Fire) and again in 2012 (Chips Fire). We asked the following questions: (1) what were the effects of repeated fire on stand structure and composition across the range of fire severities? (2) were there interactive effects between the two fires on oak sprouting response? and (3) what were the effects of combined fire severity on regeneration of both oaks and conifers? Based on the results of previous studies (Cocking et al., 2014, Crotteau et al., 2014, Hammett et al., 2017), we hypothesized that successive wildfires would set oak woodlands on a trajectory of recovery, given their competitive advantages over co-occurring fire-sensitive conifers. These results have implications for the management and restoration of oak woodlands across northern California and, perhaps more broadly, across the western region of the United States

2. Methods

2.1. Study area

This study was conducted within the intersection of the Storrie (2000) and Chips (2012) Fire extents in the southern Cascade Range in the Lassen National Forest in northern California, USA. Soils of the site are typically young and of volcanic origin, but also include granitic soils in the southernmost portion of the study area, where the Cascades and Sierra Nevada intersect (Kliewer, 1994). Climatic patterns are Mediterranean, with warm dry summers, and cool, wet winters, during which 95% of the annual precipitation is received (Kliewer, 1994). Elevations range from 900 to 1800 m above sea level (asl), with steep slopes dominating the terrain. Forest cover type in the study area is classified as Sierra Nevada Mixed Conifer (McDonald, 1980). Common overstory species are ponderosa pine (*Pinus ponderosa* var. *ponderosa* C. Lawson), sugar pine (*Pinus lambertiana* Douglas), coast Douglas-fir, white fir, incense-cedar (*Calocedrus decurrens* (Torr.) Florin), and California black oak. Common shrub species are deerbrush (*Ceanothus integerrimus* Hook. & Arn.), greenleaf manzanita (*Arctostaphylos patula* Greene), snowbrush (*Ceanothus velutinus* Douglas ex Hook. var. *velutinus*), Sierra gooseberry (*Ribes roezlii* Regal var. *roezlii*), mountain whitethorn (*Ceanothus cordulatus* Kellogg), and trailing snowberry (*Symphoricarpos mollis* Nutt.).

The Storrie Fire burned approximately 23,000 ha in the Lassen and Plumas National Forests (hereafter "Lassen" and "Plumas") in August of 2000. The Chips Fire burned approximately 30,000 ha in the same area, beginning in the Feather River Canyon of the Plumas, and quickly spreading onto the Lassen in August of 2012. The Chips Fire burned into the perimeter of the Storrie Fire, creating an overlapping reburn area of approximately 9,900 ha. Both wildfires burned at a mix of severities, allowing sampling across a spectrum of combined burn severity strata. Data collection occurred in the summer of 2015, three years after the Chips Fire, and 15 years after the Storrie Fire.

2.2. Field sampling

Ninety-three plots were established inside and adjacent to the 9,900 ha reburn area, ranging in elevation from 900 to 1600 m asl. Our sampling design used Monitoring Trends in Burn Severity project (MTBS, www.mtbs.gov) classifications of burn severity in order to stratify the Storrie Fire area into categories of burn severity (unburned, low, moderate, and high), and then paired these with the same classes of Chips Fire severity, for a total of 16 possible burn severity combinations (i.e., unburned-unburned, unburned-low, unburned-moderate, etc.; Fig. 1). Within areas where California black oak was present, we selected plots randomly within the previously defined strata using ArcGIS (ESRI, Redlands, California, USA). Plots were located at least 10 m from roads and trails to avoid edge issues. We further excluded areas with evidence of subsequent post-fire management activity (e.g., post-fire salvage, fuel mastication).

To characterize stand overstory structure and composition before and after each fire, we established 0.045 ha fixed-area circular plots. Within each plot, we recorded species, diameter at breast height (DBH; 1.37 m above ground), and percent live crown for all live trees > 2.5 cm DBH. Basal diameter, snag condition class (Thomas et al., 1979), and fire history (e.g., killed in Chips Fire, topkilled the Storrie Fire, or survived both fires) were recorded for all dead stems > 1.37 m tall. Designations of Storrie Fire, Chips Fire, and other causes of mortality were made based on snag condition class and other visual cues (e.g., presence of unconsumed bark on snags, substantial consumption of snags and stumps, considerable decay of old snags). Substantially burned snags and stumps were identified to species where possible using remnant bark or wood samples, and classified to genus where field identification was unreliable due to deterioration of samples (Cocking et al., 2014, Hammett et al., 2017). Locations for all measured stems within each plot were mapped and recorded using distance and azimuth from plot center.

Oak sprout vigor was assessed using a nested "focal oak" subplot (as in Cocking et al., 2014). Within each larger plot, we located the nearest living California black oak (mature tree or sprout clump) to plot center that was ≥ 1.37 m tall, and used that individual as the locus for a single10 m radius (314 m^2 area) circular plot. All living and dead sprouts emerging from the base of this "focal oak" were counted and the fire that triggered their formation (sprouted post-Storrie Fire or sprouted post-Chips Fire) and diameter at 20 cm above ground level were recorded. Substantial size differences between 15-year old sprouts (Storrie Fire origin) and three-year old sprouts (Chips Fire origin), as well as minimal consumption of live (at the time of the Chips Fire) vegetation in the second fire made identifying each sprout generation unambiguous (Hammett et al., 2017). Live and dead oak sprout clump crown diameter and live emergent height were measured for this clump, as well as for two additional randomly selected clumps per plot.

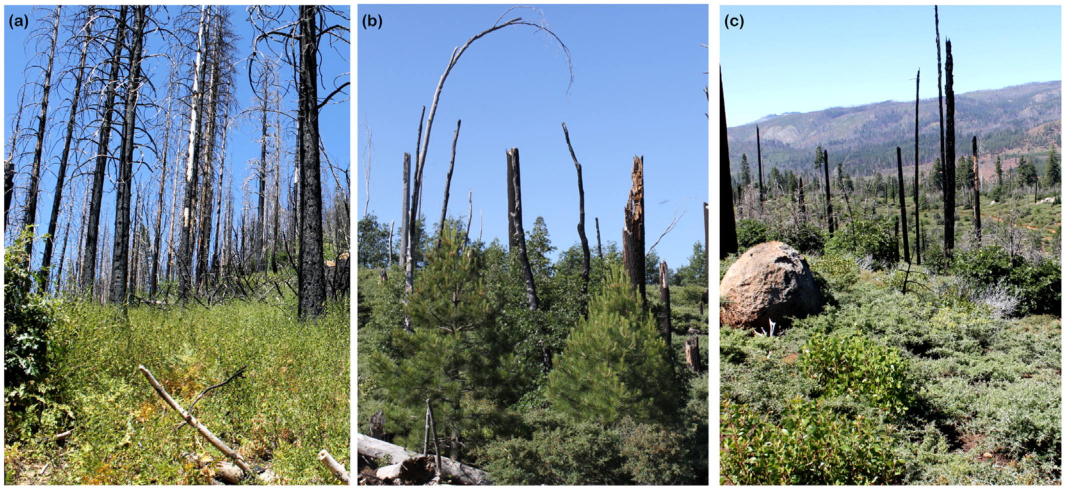

Fig. 1. Examples of burn severity combinations: (a) low severity in Storrie Fire/high severity in Chips Fire, (b) high severity in Storrie Fire/low severity in Chips Fire, and (c) high severity in both fires.

Within each circular subplot, ocular estimates of percent cover for all shrub species were recorded in two equal-sized opposing quadrants using the following modified Daubenmire cover classes: < 1%, 1–10%, 11–25%, 26–50%, 51–75%, and > 76%. Diameter, species, and cause of mortality (where possible) were recorded for all stumps within the focal oak subplot.

We examined tree regeneration in a second subplot centered in the large plot. Within this 4.2 m radius (56.48 m^2 area) circular plot, all woody plant species were mapped using distance and azimuth from plot center. Tree seedlings and saplings were recorded in the following height categories: 10–25 cm or 25–50 cm for seedlings and 50–75 cm, 75–137 cm, and > 137 cm but ≤ 2.5 cm DBH for saplings. Seedlings < 10 cm tall were considered ephemeral and excluded from sampling due to their high mortality rates (Crotteau et al., 2013). A size threshold of 50 cm in height was used to distinguish saplings from seedlings, as conifers in the study area have not been observed to reach this height in less than three growing seasons (J. Crotteau, pers. comm.), and thus were presumed to have been present at the time of the Chips Fire.

2.3. Data analysis

We used Relative differenced Normalized Burn Ratio (RdNBR) values for each fire as our predictor variable in all vegetative response analyses across the spectrum of fire severity combinations. This widely used continuous measure of burn severity has been shown to be sensitive to pre-fire stand condition and accurate in depicting burn severity across diverse vegetative types (Miller and Thode, 2007, Miller et al., 2009a).

In order to examine the effects of Chips Fire severity on overstory canopy structure and composition, changes were measured across a spectrum of fire severities. This was done by determining the species and fire history for each overstory tree (i.e., which fire caused mortality), and using these data to calculate pre- and post-fire relative dominance for living oaks and principal competing conifers (white fir and Douglas-fir) in each plot. For each species group (oak or competing conifer), post-fire relative dominance was subtracted from the pre-fire relative dominance to produce a change in relative dominance. Chips Fire severity (i.e., RdNBR value) was used as the explanatory variable, with change in relative dominance as the response, in a generalized linear regression model examining their relationship. Root mean square error (RMSE) and explained deviance were used to evaluate model fit, as these are more appropriate than R^2 values commonly reported for OLS regression (Guisan and Zimmermann, 2000).

Black oak sprouting response was quantified using sprout density for each measured oak sprout clump (number of stems per clump), sprout basal area (cm^2 per clump), maximum sprout height (m), and mean clump crown area (m^2 per clump). Due to the non-linear relationships between each sprout response metric and Chips Fire burn severity, these responses were analyzed using generalized additive models (GAM). Akaike Information Criterion (AIC) and F-tests were used to compare model performance against linear models and assess GAM fit. Potential interactive effects of the two fires on sprout vigor were assessed using generalized linear modeling.

We used logistic regression to analyze the impact of the response variable sprout topkill. Goodness-of-fit was evaluated using a likelihood ratio test, and predictive ability of the model by calculating the area under the Receiver Operating Characteristic curve (AUC) for the model. An AUC value of 0.5 represents no improved model accuracy over random, and a value of 1 indicates prefect predictive ability of the model (Egan, 1975). Density of conifer regeneration was compared across Chips burn severity categories using ANOVA. All analyses were conducted using the R statistical program, version 3.3.2 (The R Core Development Team 2014).

3. Results

Following the second wildfire, overstory composition shifted toward a greater relative dominance by California black oak with increasing burn severity when compared with white fir and Douglas-fir ($P < 0.0001$, RMSE = 17.8, deviance explained = 55%; Fig. 2). Competing conifers were killed at higher burn severities, while the majority of oaks resprouted following the fire. Relative dominance was unchanged after the Chips Fire in plots where all overstory conifers were killed in the Storrie Fire: in these plots, no conifers had been added to the overstory since that event, and extant oaks survived or resprouted following topkill. This phenomenon was observed across a range of Chips Fire severity values, and occurred in 20 of our 93 plots. These plots were excluded from this analysis, due to the potential for misinterpretation of these null values.

Ninety seven percent of oaks that sprouted after the Storrie Fire resprouted after being topkilled in the Chips Fire. Sprouts of Chips Fire origin were more abundant, but smaller in stature, than those that sprouted following the Storrie Fire (demonstrating their propensity to self-thin over time, as documented by McDonald (1969)), and sprouts generated from both fires were more abundant than saplings of competing conifer species (Table 1). Post-Chips Fire sprout vigor was positively related to Chips Fire burn severity. Both emergent sprout height ($P < 0.0001$, RMSE = 0.79, deviance explained = 56.5%) and sprout basal area ($P < 0.0001$, RMSE = 44.7, deviance explained = 69.1%)

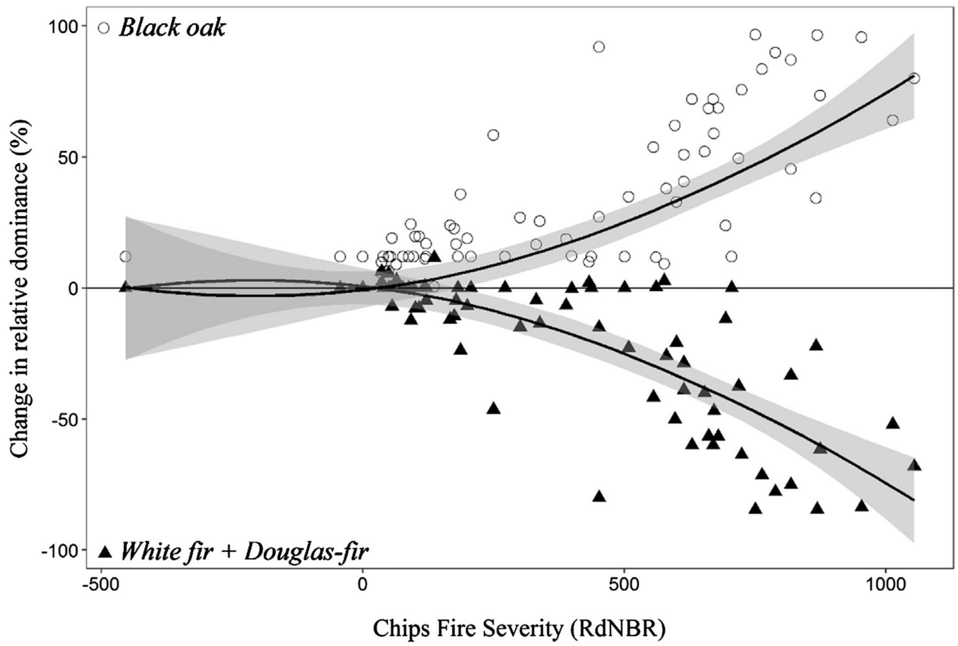

Fig. 2. Change in relative dominance of overstory species after Chips Fire by Relative differenced Normalized Burn Ratio (RdNBR). Circles represent oaks, triangles represent conifer competitors (*A. concolor and P. menziesii*).

increased with fire severity (Fig. 3). Results of F-tests (P = 0.016 and P < 0.0001), and AIC values indicated that GAMs performed well, and demonstrated significant improvement over linear models utilizing the same link functions. Surviving post-Storrie Fire sprout clumps (n = 20 plots) had a maximum emergent height of 7.9 m after 12 seasons of growth, while post-Chips Fire sprouts (n = 58 plots) reached a maximum of 4.2 m tall in three growing seasons after the fire.

Generalized linear modeling of post-Chips Fire sprout metrics stratified by categorized Storrie Fire RdNBR values yielded no significant interactive effects between burn severities in the two fires. Two measurements of sprout vigor, sprout basal area and emergent sprout height, were modeled; neither model revealed significant interactions (P = 0.24 and P = 0.62, respectively).

Measured oaks in a total of 48 plots (52%) had live post-Storrie Fire sprouts at the time of the Chips Fire. Of these plots, approximately 60% (29 plots) experienced complete oak sprout mortality in the Chips Fire (Fig. 4a). Post-Storrie Fire sprout survival rates were binomially distributed, with nearly all plots experiencing either 0 or 100% mortality of measured post-Storrie fire sprouts. A threshold value of 70% stem mortality within each clump was used to categorize "live" and "dead" status for remaining (n = 3) plots. Post Storrie-Fire sprouts were topkilled at low burn severities in the Chips Fire (excepting a single outlier, sprout clumps experienced complete or near-complete aboveground mortality at values ≥ 167 RdNBR). Fire severity alone explained oak sprout survival with a high level of accuracy (P < 0.0001, AUC = 0.95). All measured sprout clumps that were topkilled in the Chips Fire had resprouted by the time of measurement.

Regeneration dynamics of competing conifer species was compared across Chips Fire severities. The majority of conifer regeneration was in the form of small-statured seedlings (< 50 cm tall), which constituted 80% of white fir and 55% of Douglas-fir in our plots. Sapling (> 50 cm < 137 cm tall) density per plot was considered to be of particular importance, since these had presumably established before the Chips Fire occurred, and could be used to measure the effects of fire severity on conifer regeneration. Survival of competing conifer saplings (*A. concolor* or *P. menziesii*) was observed exclusively below RdNBR values of approximately 250 in the Chips Fire (Fig. 4b). Conifer sapling density was significantly greater at lower burn severities (P < 0.0001).

4. Discussion

4.1. California black oak response to repeated wildfire

In the montane forests of northern California, where conifers are otherwise dominant, a single high-severity wildfire can shift the competitive environment to favor California black oak dominance, releasing oaks from suppression due to overtopping conifers (McDonald and Tappeiner, 2002, Cocking et al., 2014, Hammett et al., 2017). We found that after a second wildfire, this trajectory toward oak dominance is reinforced in multiple strata, as higher severities in the Chips Fire

Table 1
Metrics for living Storrie Fire-origin and Chips Fire-origin black oak sprouts and competing conifer (excluding pines) saplings (> 50 cm tall) and seedlings (< 50 cm tall). All measurements were made following the Chips Fire. Mean and (standard error) values are given for each measure.

	Frequency	Basal area (cm^2/clump)	Height (m)	Density (stems/clump)	Density (stems/ha)
Q. kelloggii sprout (Storrie Fire origin)	20	241(57.4)	4.1(1.6)	10.9(1.8)	1733.3(3 8 6)
Q. kelloggii sprout (Chips Fire origin)	58	77.4(8.1)	2.2(0.6)	40.5(3.1)	6062.8(826.5)
Q. kelloggii seedling	27	…	…	…	1088(3 1 9)
A. concolor sapling	12	…	…	…	572(1 6 2)
P. menziesii sapling	2	…	…	…	123(1 0 9)
A. concolor seedling	17	…	…	…	1575(8 3 9)
P. menziesii seedling	8	…	…	…	97(33)

Note: Plots that did not have measurable oak sprouts resulting from each wildfire event are excluded from calculations. Basal area and individual height data (outside of height class) were not measured for conifer species, missing data indicated by ellipses.

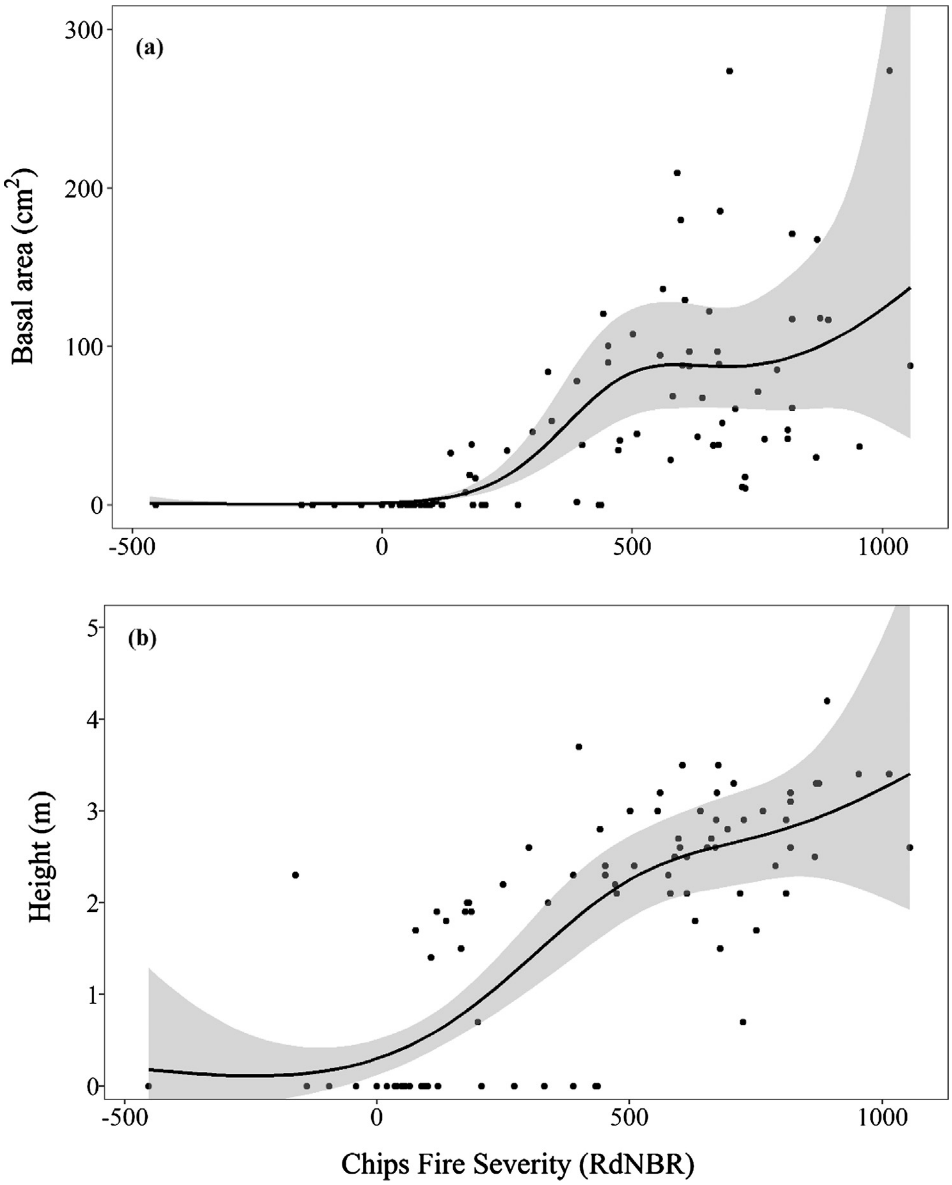

Fig. 3. California black oak basal area per sprout clump (a) and maximum height (b) of post-Chips Fire sprouts by Chips Fire severity.

eliminated post-Storrie Fire conifer regeneration and killed remaining overstory conifers, while oaks continued to resprout. This outcome aligns with the conceptual model by Cocking et al. (2014) wherein severe fire is the catalyst for resurgent oak dominance in previously suppressed stands. Following high-severity fire, height growth of resprouting oaks outpaces seed-origin conifer regeneration, garnering a substantial competitive advantage. This advantage is only temporary, however, as oaks will eventually be overcome by the faster-growing conifers as their vertical growth slows in maturity (McDonald, 1969) The significant conifer regeneration that occurred after both the Storrie (Crotteau et al., 2013) and Chips fires demonstrates the need for low-severity fire at frequent intervals (such as the fire regime maintained by tribal practices in the past) in order for oak dominance to be maintained.

Twelve years after the initial fire, oaks in previously burned areas underwent vigorous regrowth after a second fire, with a more robust response in higher-severity plots. Surprisingly, this response was unrelated to previous burn severity in the Storrie Fire, indicating that underground carbohydrate storage was either not substantially depleted after a single resprouting event, or that the 12-year interval between fires was sufficient for oaks to rebuild these reserves (Donato et al., 2009b). These results provide further support for the finding that California black oaks are resilient in the face of multiple fires (Hammett et al., 2017). Further study is needed to determine if black oak's capacity to regenerate is interval-dependent. In some species of oaks, shorter-interval fires have been shown to diminish regeneration (Delitti et al., 2005, Hutchinson et al., 2005), while others have proved resilient over multiple burns (Barton, 2002, Coop et al., 2016). Predicted regional increases in fire frequency will likely provide further opportunities to study this species' capacity for repeated regeneration over shorter fire return intervals.

McDonald (1980) suggests that California black oak needs approximately 60 years to attain bark thickness sufficient to withstand cambial injury in low-intensity fires. This delay in fire-resistance presents a challenge for oak woodlands recovering from high-severity fire in conifer-dominated regions. In this study, oak resprouts did not survive a second fire, except at the lowest burn severities (Fig. 4a). This pattern supports a "goldilocks principle" referred to by (Long et al., 2016a): California black oak is highly dependent on fire to maintain early seral stand conditions, but its above-ground growth is paradoxically sensitive to fire. While oaks made gains in relative dominance post-fire (Fig. 2), this was at the expense of overstory recruitment, as

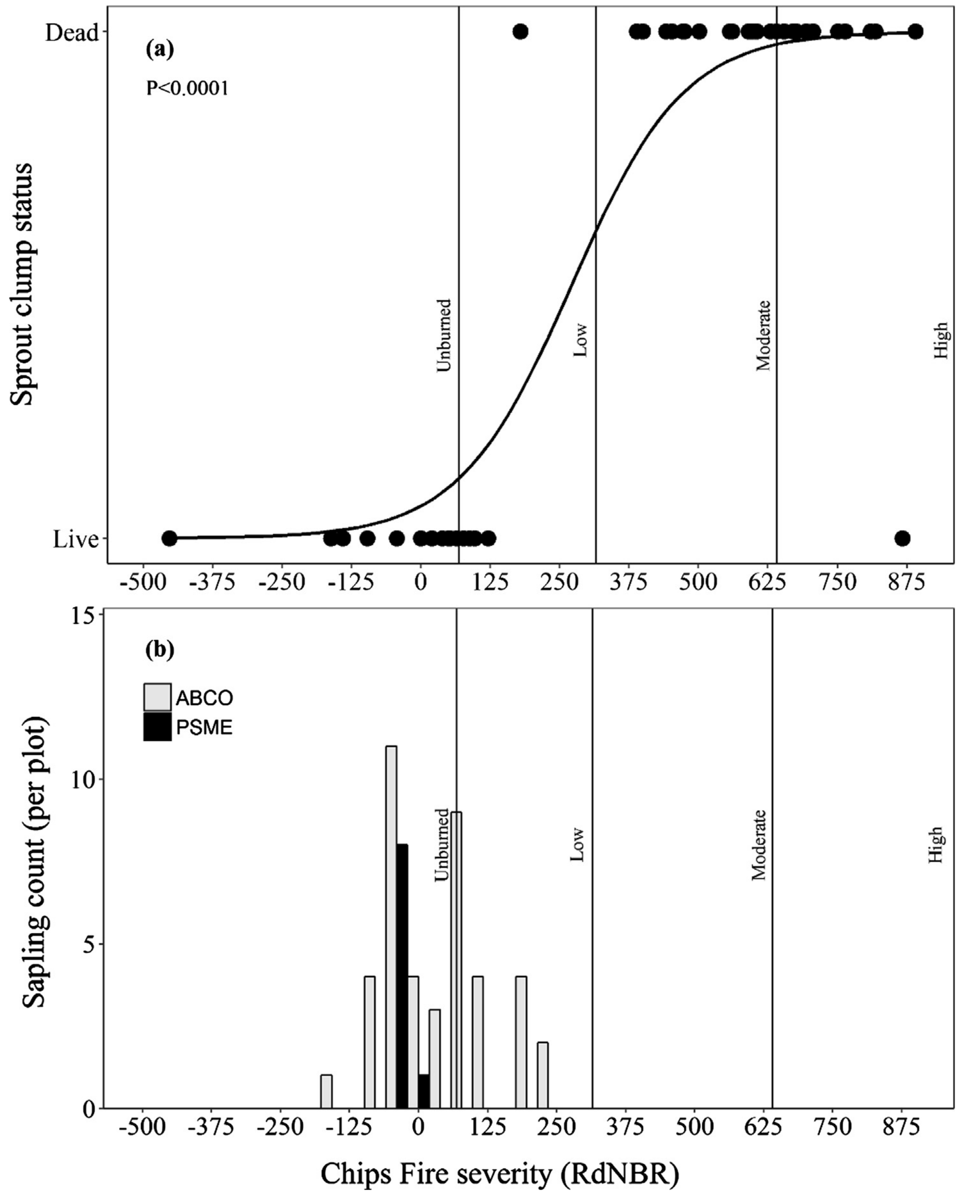

Fig. 4. Observed survival of Storrie-Fire origin California black oak sprout clumps (a) and competing conifer saplings (b) in response to Chips Fire severity (RdNBR). Burn severity thresholds from Miller and Thode (2007).

recurrent oak topkill preserved oaks in a shrub form.

4.2. Black oak woodland restoration in an altered landscape

Shifts in surface fuel structure and composition, driven by changing vegetative states, have substantial implications for the persistence of western oak woodlands. In a region dominated by conifers, California's historic montane black oak woodlands were likely the benefactors of a mixed-severity fire regime that created large gaps in the continuity of forest cover (Parsons and DeBenedetti, 1979, Scholl and Taylor, 2010). In these openings, this shade-intolerant sprouter could prevail over its competitors. This region has experienced a severe departure from historic fire return intervals, with repercussions made evident by vegetative changes. Evidence from historical accounts (Stewart et al., 2002, Anderson, 2005), as well as dendrochronological studies (Taylor, 2000, Bekker and Taylor, 2010), substantiates the existence of a formerly heterogeneous landscape with high beta-diversity. This structural and vegetative diversity likely prevented widespread, severe wildfires (Hessburg et al., 2005, Perry et al., 2011), allowing oak woodlands to persist in some of these gaps. Decades of fire exclusion have caused dramatic changes in fuel loads and arrangement, and increased the homogeneity of northern Californian forests (Kilgore and Taylor, 1979, Bekker and Taylor, 2010). This has greatly increased the risk of large-scale, stand-replacing wildfires that were likely uncharacteristic in these historically frequent-fire landscapes (Miller et al., 2009b, Perry et al., 2011, Mallek et al., 2013).

This departure from historic conditions at the stand- as well as landscape-level sets the stage for further vegetative change, as the consequences of the catastrophic wildfires that result are exhibited on the landscape. Studies of high-severity reburns in California have found that dry forests are experiencing dramatic post-fire state-shifts (Collins and Roller, 2013, Coppoletta et al., 2016, Lauvaux et al., 2016). In this region's dry mixed-conifer forests, prolific regeneration of flammable montane chaparral shrublands often occurs following stand-replacing fire (Nagel and Taylor, 2005, Collins and Roller, 2013, Lauvaux et al., 2016). Common chaparral species at our sites (deerbrush, greenleaf manzanita, snowbrush, and mountain whitethorn) are well adapted to high severity fire, often regenerating vegetatively (as in the case of

Table 2
Mean shrub cover (%) by categorized severity rating of two wildfires in the Southern Cascades in northern California.

Fire severity category	Storrie fire	Chips fire
Unchanged	29.4	37.1
Low	33.8	37.7
Moderate	40.3	35.1
High	63.5	57.7

greenleaf manzanita and snowbrush), from prolific fire-stimulated seed banks (such as deerbrush), or employing both strategies (mountain whitethorn) (Keeley, 1991, Howard, 1997, Anderson, 2001, Reeves, 2006, Hauser, 2007). In our study, dense shrub regrowth was common three years after the Chips Fire, with mean cover exceeding 50% in plots that burned at high severity (Table 2). As a wildland fuel, chaparral is often self-perpetuating, as it is highly flammable under dry conditions, has many strategies for repopulating severely burned areas, and most commonly burns at high intensities (Anderson, 1982, Barro and Conard, 1991, Nagel and Taylor, 2005, Collins and Roller, 2013). While chaparral can convert to forest along normal successional pathways in the absence of fire (Conard and Radosevich, 1982a, Nagel and Taylor, 2005, Airey, 2012), predicted future increases in fire frequency and severity may maintain chaparral stands long into the future (Steel et al., 2015, Coppoletta et al., 2016, Lauvaux et al., 2016). When coupled with forecasted climatic changes, future high-severity fire regimes may cause California black oak to increase in cover (Liang et al., 2017). This increased dominance may come at the expense of mature woodland development, however, as oaks will be continually topkilled in these events, and may persist solely as a small-statured mid-story component, as has been observed in other regions (Barton and Poulos, 2018).

The results of our study, when placed within the context of others' work, suggest that in California's fire-excluded oak woodlands, a single wildfire, or two recurring wildfires, may be insufficient to restore pre-European settlement conditions. Large, mature oaks are an important source of nesting cavities and platforms, and critical to the production of large acorn crops that support wildlife and are favored by local tribes for harvest (Long et al., 2016b). Currently regenerating black oak stands, may need a substantial fire-free period in order reach a stature that confers fire-resistance and engenders the return of these lost ecological functions and cultural values. Indeed, the presence of even-aged stands of mature California black oak is evidence that woodlands have reestablished after stand-replacing fires in the past (McDonald, 1969). Additionally, extant multi-aged black oak stands provide evidence that overstory oak survival in fires is possible (Garrison et al., 2002, Cocking et al., 2012). It is likely that regular anthropogenic burning aided in the development of these woodlands by promoting a self-limiting regime of low-severity fire. However, it may be the case that current fuel conditions (and the high-severity fires which they foster) preclude the processes that allowed the development of oak woodlands in this landscape.

The legacy of long-term fire exclusion in dry forests and woodlands, coupled with a changing climate, confounds efforts to restore historic landscapes. An increasing body of evidence indicates that changing patterns of disturbance are having lasting impacts on vegetation and fire regimes in many western US ecosystems (Coppoletta et al., 2016, Donato et al., 2016, Johnstone et al., 2016, Stevens-Rumann and Morgan, 2016, Guiterman et al., 2017). While a hotter and drier future may favor oaks over less drought-tolerant species (McIntyre et al., 2015), the altered fire regimes that are increasingly replacing disturbance regimes of the past may hinder the development of mature oak woodlands. Oaks could thus be caught in a "fire trap" (Grady and Hoffmann, 2012): despite their resilience to high-severity fire, the sprouts produced following these fires are highly vulnerable in reburns. Future frequent fire, instead of maintaining mature oaks woodlands as in the past, may suppress oaks in a shrub form that lacks the characteristics important for wildlife habitat and cultural practices (Long et al., 2016b). Both Cocking et al. (2014) and Hammett et al. (2017) surmised that the return of "historically normal fire return intervals" subsequent to high-severity fire events may aid in the restoration of mature black oak woodlands. This predicted outcome presupposes a fuel-limited, low-severity fire regime, the return of which appears unlikely under current conditions. As the repercussions of long-term fire exclusion and recent climate change are expressed in current wildfire activity ecological ramifications remain uncertain. Future study of these ecosystems should help to clarify the long-term consequences of these disruptions to the processes that shaped western forests.

4.3. Management implications

Our research suggests that while severe wildfires are highly effective in reversing the impacts of long-term fire exclusion on oaks, these events may fail to promote the future recovery of mature California black oak woodlands. Additional study is needed to determine if additional burns in these resurgent woodlands yield different results. If not, additional post-fire treatments may be necessary in order to break the cycle of resprouting and topkill observed in this study. Managers can take advantage of post-wildfire oak recovery by protecting regenerating oaks from both conifer encroachment and high-severity wildfire. The reintroduction of fire will likely be essential to the success and longevity of restoration actions. Before prescribed fire is applied, careful site preparation designed to reduce oak mortality should be conducted. For example, it may be necessary to use methods such as herbicide treatment, mastication, or manual removal (Conard and Radosevich, 1982b, Potts et al., 2010), in order to interrupt the continuity of shrub fuels around resprouting oaks. Restoration of historic fuel beds via seeding of native herbaceous species may also be necessary before burns can be safely conducted. Restoration efforts may be most effective in large patches of high-severity reburn, as these are less likely to experience substantial natural conifer regeneration due to lack of nearby seed sources (Donato et al., 2009b, Pierce and Taylor, 2010, Crotteau et al., 2013).

Supplemental restoration and management practices have the added benefit of promoting forest resilience to future wildfire, by reducing shrub fuel loads, encouraging rapid post-fire regeneration, and increasing landscape heterogeneity. A species that is highly resilience to fire and drought, California black oak can play an important role in post-fire forest recovery, as it is not dependent on unreliable seed sources or seedling survival for regeneration. Management interventions will be of increasing importance in the context of predicted and on-going increases in fire size, frequency, and severity in California and the western United States (Abatzoglou and Williams, 2016, Westerling, 2016).

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