

## Structure, diversity and health of Sierra Nevada red fir forests with reestablished fire regimes

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**Abstract.** The reestablishment of natural fire regimes may benefit forest ecosystems by restoring their fundamental structural, compositional or functional attributes. We examined the influence of fire on the structure, understorey diversity and health of red fir (*Abies magnifica*) forests by comparing burned and unburned stands in 22 separate, paired fires of Yosemite, Sequoia and Kings Canyon National Parks and the Giant Sequoia National Monument. Burned red fir plots were characterised by lower tree densities and canopy cover, restored spatial heterogeneity and higher understorey species richness than unburned plots. Densities of large trees and large snags and red fir regeneration were similar between burned and unburned sites. Forest health indicators were similar between burned and unburned sites, and red fir crown loss ratings were primarily associated with topographic variables indicative of increased moisture stress or reduced soil moisture availability (i.e. lower elevations, south-facing slopes). Our results suggest that fire does not improve the health of red fir trees especially in areas of greater moisture stress, but it can restore red fir forest structure, increase understorey diversity and enhance adaptive capacity in landscapes with reestablished fire regimes.

**Additional keywords:** fire effects, forest health, moisture stress, natural fire regime, wildfire.

Received 21 July 2018, accepted 7 December 2018, published online 19 February 2019

### Introduction

The management of wildfires to support natural resource objectives (i.e. wildfires with strategies other than full suppression that can promote beneficial fire effects for ecosystems) has reestablished natural fire regimes throughout several wilderness areas and other remote regions of western North America (van Wagtenonk 2007; Miller and Aplet 2016). The reestablishment of natural fire regimes has numerous benefits for forest ecosystems, including the restoration of historical stand structure and composition (Fulé and Laughlin 2007; Holden *et al.* 2007), reduction of fuel loads (Fulé and Laughlin 2007; Collins *et al.* 2016) and restoration of stand structural heterogeneity (Larson and Churchill 2012; Lydersen and North 2012), such as increased representation of large-diameter trees (i.e. greater mean tree diameter, more even tree size class

distribution) and reduction of tree clustering at small spatial scales often associated with heavily logged, fire-excluded stands (Taylor 2004; Lydersen *et al.* 2013). At a landscape scale, reestablishment of fire regimes may create greater landscape patch structural diversity (Kane *et al.* 2013, 2014), reduced fire severity and self-limiting effects to subsequent fires (Collins *et al.* 2009; Teske *et al.* 2012; van Wagtenonk *et al.* 2012; Parks *et al.* 2014). Wildland fire (i.e. prescribed fire and wildfire) may also create a greater variety of effects that support higher biodiversity in forest landscapes (Webster and Halpern 2010; Ponisio *et al.* 2016). Wildland fire can maintain or enhance the quality of wildlife habitat for a diverse array of species (Fontaine and Kennedy 2012), including habitat specialists associated with late-successional forests (e.g. Roberts *et al.* 2011). Additionally, the reestablishment of natural fire regimes may

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augment soil water availability and reduce surface water runoff (Boisramé *et al.* 2017), increase tree growth rates (Holden *et al.* 2007), stabilise forest carbon (Krofcheck *et al.* 2017) and reduce the probability or extent of drought-induced tree mortality (van Mantgem *et al.* 2016). These changes contribute to the long-term health and functioning of forest ecosystems under changing climatic conditions (Stephens *et al.* 2013).

Red fir (*Abies magnifica*) forests in the Sierra Nevada of California are a model ecosystem for the study of the reintroduction of wildland fire. These forests often dominate the upper montane zone in the region, where large managed wildfires may be common within remote landscapes with little risk to public safety and private property (van Wagtenonk and Lutz 2007; Meyer 2015). In contrast to frequent-fire-regime forests (e.g. ponderosa pine, dry mixed conifer), red fir forests have moderately long fire return intervals in California with a mean historical fire return interval of ~40 to 50 years (Van de Water and Safford 2011; Meyer and North *in press*). Moreover, their current fire severity patterns have not departed significantly from historical conditions, which are primarily dominated by low- to moderate-severity classes, with smaller proportions of high-severity fire (5 to 20% of the burned landscape) occurring in smaller ( $\leq 4$  ha) patches (Meyer and North *in press*). Consequently, most fire-excluded red fir stands exhibit only a moderate departure from their historical fire regime by 'missing' two or three fire cycles (Safford and Van de Water 2014) and relatively minor departure in fire severity patterns at a regional scale (Mallek *et al.* 2013); the potential for the reestablishment of the natural fire regime may thereby be achieved with fewer fire entries than forests with a frequent fire regime. The reintroduction of natural fire regimes may restore historical stand structure in fire-excluded Sierra Nevada red fir forests that are currently characterised by higher tree densities (especially in the smaller size classes), greater canopy cover and lower mean tree diameter than under the natural (i.e. historical) range of variation (Meyer and North *in press*). For example, fire can elicit significant changes in structural heterogeneity and canopy cover, even following low-severity fire (Kane *et al.* 2014), although it is not entirely clear whether large-tree densities significantly decline with the reintroduction of fire (Dolanc *et al.* 2014; Becker and Lutz 2016). Despite these structural effects, there does not appear to be a relationship between fire return interval and fire severity in red fir forests (Steel *et al.* 2015), suggesting that fire may be successfully reintroduced into long-fire-excluded red fir stands without the need for pretreatment activities (e.g. mechanical thinning) to mitigate excessive pre- or post-entry fuel loading.

Recently, red fir forests have exhibited clear signs of declining health throughout California, including increased mortality rates, incidence of pathogens and crown loss (Mortenson *et al.* 2015). These patterns may be a consequence of the combined effects of progressive canopy moisture stress derived from recent (2012–16) exceptional drought conditions (Asner *et al.* 2015; Brodrick and Asner 2017; Paz-Kagan *et al.* 2017), increasing temperatures associated with climate change (Safford *et al.* 2012), and long-term fire exclusion, which have led to increased stand densities and biomass in upper montane forests (Dolanc *et al.* 2014; Boisramé *et al.* 2017). Increased canopy moisture stress and bark beetle pressure were

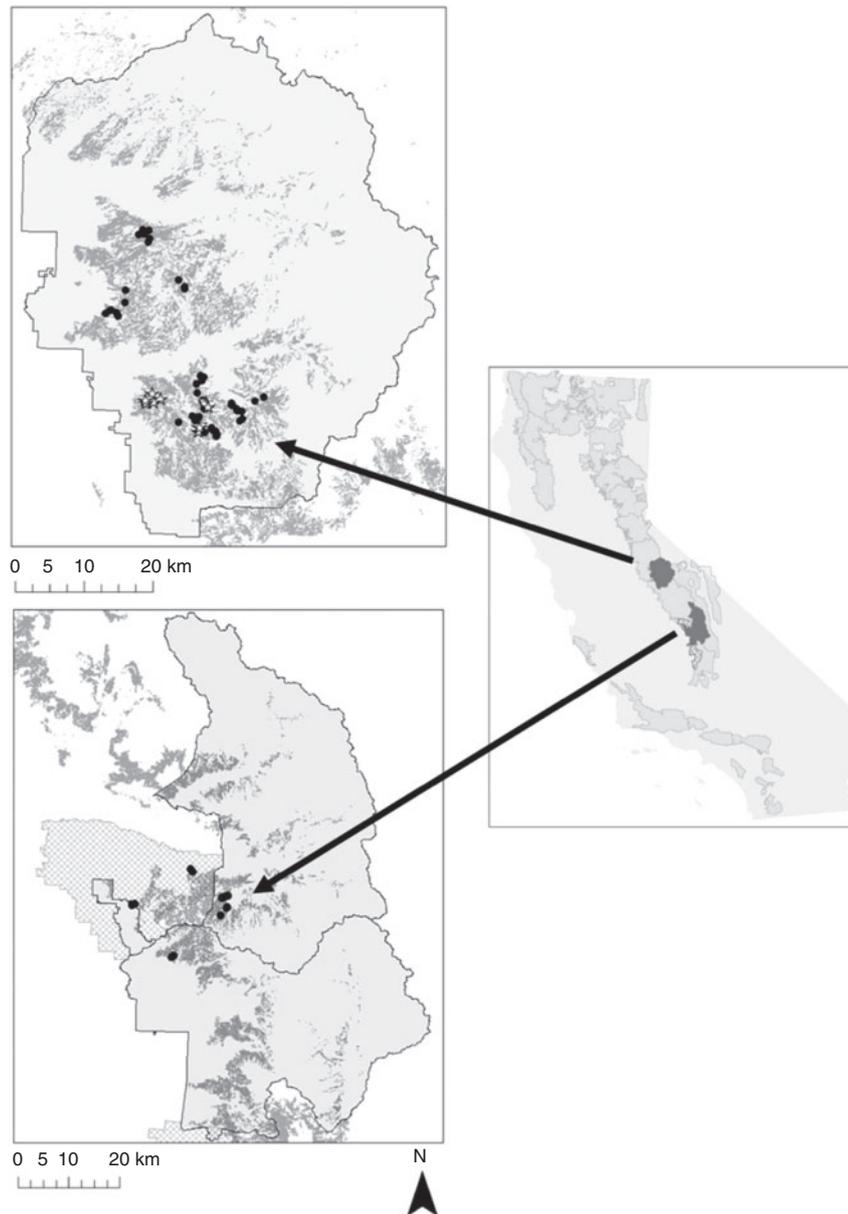
particularly evident during the middle stages of the recent drought (2015–16) compared with early (2012–13) or late (2017) drought conditions (Brodrick and Asner 2017; Preisler *et al.* 2017). Red fir forests of the Sierra Nevada are highly vulnerable to projected changes in climate during the 21st century, suggesting that these forests may be especially susceptible to increasing levels of moisture stress in the region (Meyer and North *in press*). Accordingly, red fir and other high-elevation forests that have departed from their natural fire regime (i.e. fire deficit), contain higher stand densities or biomass (and presumably density-dependent competition) and are located at lower elevations or warmer topographic positions are likely more vulnerable to the effects of increasing moisture stress in the Sierra Nevada (van Mantgem and Stephenson 2007; Asner *et al.* 2015; Mortenson *et al.* 2015; Paz-Kagan *et al.* 2017). Although it is generally assumed that the reestablishment of natural fire regimes contributes to the integrity of Sierra Nevada forest ecosystems by reinstating a key ecological process (North 2012; Meyer 2015), the potential benefit to fire to red fir forest health is largely untested, especially under recent warmer drought conditions.

The goal of our study was to evaluate whether fire restores red fir forest structure, increases diversity and enhances health by comparing stands in reestablished fire regime landscapes (i.e. twice-burned stands representing minimal to no departure in historical fire return interval) with nearby unburned stands (i.e. areas with no fires recorded over the last century, indicative of moderate departure from historical fire return interval). We hypothesised that reestablished fire regimes observed in twice-burned landscapes (hereafter 'burned' referring to areas with two documented fires over the last century) would result in: (1) lower tree densities and canopy cover similar to the natural range of variation; (2) lower surface fuel loads; (3) restored structural heterogeneity (i.e. lower percentage trees in clusters, greater mean tree diameter, and more even diameter distribution); (4) increased species diversity (herbaceous plants, shrubs and tree regeneration); (5) improved forest health conditions (lower percentage of unhealthy trees); (6) similar or increased red fir tree regeneration; and (7) the retention or promotion of large trees, snags and shrub cover that represent key habitat elements important to wildlife. Our second objective was to evaluate potential factors associated with increasing red fir moisture stress as indicated by an index of stand-level red fir crown loss. We hypothesised that red fir crown loss would increase under more stressful conditions associated with: (1) the absence of fire, (2) increasing topographic dryness (i.e. lower elevations on south-facing slopes), and (3) increasing stand biomass (i.e. live basal area).

## Methods

### *Study area and plot selection*

Our study area included Yosemite, Sequoia and Kings Canyon National Parks, and the Giant Sequoia National Monument of the Sierra Nevada bioregion of California (Fig. 1). Within this region, red fir is commonly a dominant or codominant conifer throughout the upper montane zone (~1800–2800 m elevation; Potter 1998). At lower elevations in this zone, red fir often occurs as a codominant species mixed with white fir



**Fig. 1.** Map of red fir study areas located in Yosemite National Park (top), Sequoia and Kings Canyon National Parks (grey, bottom), and Giant Sequoia National Monument (cross-hatched, bottom) in California (right). In maps on left, plot locations are indicated by black circles, plots with understorey sampling by stars, and red fir distribution by dark grey shading.

(*Abies concolor*), Jeffrey pine (*Pinus jeffreyi*) or sugar pine (*P. lambertiana*). At higher elevations, red fir is frequently mixed with western white pine (*P. monticola*), lodgepole pine (*P. contorta*) or mountain hemlock (*Tsuga mertensiana*; Potter 1998; Meyer and North in press). We selected several landscapes in the upper montane zone with reestablished fire regimes but also included localised areas of recent fire activity. Our site selection criteria included stands that were: (1) dominated by red fir forest (typically 2000–2600-m elevation and  $\geq 10\%$  tree cover); (2) not impacted by prior logging activity;

and (3) exposed to at least two overlapping fires ('site'), with the most recent fire (since 1980 or one median fire return interval) at low to moderate severity (based on 1-year post-fire vegetation burn severity derived from relative differenced Normalized Burn Ratio (RdNBR) satellite-based imagery; Miller and Thode 2007). Our use of two recent fires to define red fir forests with a reestablished fire regime is based on mean historical fire return interval estimates for mid-elevation Sierra Nevada red fir forests (48 years; Meyer and North in press). We avoided high-severity burned areas because these sites lacked

**Table 1. List of pairs of fires used as study sites in the Sierra Nevada of California**

Study sites are listed by fire events, location, elevation range and number of burned inventory plots established in the overlapping fire perimeters (number does not include one unburned plot per site). All fires were categorised as natural ignitions (unless otherwise noted) that were primarily managed for resource benefits (e.g. 'wildland fire use') with the exception of those fire names in italics, which were human-ignited wildfires managed for suppression objectives

Second fire name and year	First fire name and year	Location <sup>A</sup>	Elevation range (m)	No. of burned plots
Grouse 2009	<i>Steamboat 1990</i>	YNP <sup>B</sup>	2054–2274	4
Harden Lake 2009	<i>Ackerson 1996</i>	YNP	2221–2345	3
Hoover 2001	Alaska 1988	YNP	2215–2274	2
Hoover 2001	Fat Head 1980	YNP	2358–2421	2
Lost Bear 1987	<i>Unnamed 1980</i>	YNP	2120–2252	3
Lost Bear Bruno 1999	Horizon 1988	YNP <sup>B</sup>	2177–2263	3
Lost Bear Bruno 1999	Lost Bear 1985	YNP	2151–2229	3
Meadow 2004	Buena Vista 1981	YNP	2106–2242	3
Slope 2010	Harden 2005	YNP	2220–2261	1
Tamarack 2011	<i>Walker 1988</i>	YNP	2122–2260	4
Unnamed 1984	Gordo 1980	YNP	2398–2437	3
Horizon 1994	Buena Vista 1981	YNP	2133–2186	3
Meadow 2004	<i>Unnamed 1980</i>	YNP <sup>B</sup>	2112–2142	3
Lost Bear Bruno 1999	Ostrander 1992	YNP	2287–2528	3
Lost Bear Bruno 1999	Twin Snake 1978	YNP	2548–2594	3
<i>Rim 2013</i>	PW-3 Gin Flat 2002 <sup>C</sup>	YNP	2034–2179	3
Dark Hole 2014	Dark 1999	YNP	2317–2375	3
Williams 2003	Sugarloaf 1985	SEKI	2371–2564	2
Williams 2003	Williams 1999	SEKI	2463–2504	3
Buena Vista 2004 <sup>C</sup>	Redwood 1974 <sup>C</sup>	SEKI	2198–2267	2
Rough 2015 <sup>D</sup>	Sheep 2010	GSNM	2478–2541	1
Dorst 1996	Halstead 3 1987	SEKI	2405–2432	1

<sup>A</sup>Locations are Yosemite National Park (YNP), Sequoia and Kings Canyon National Parks (SEKI), and the Giant Sequoia National Monument (GSNM).

<sup>B</sup>Locations that included sampling for understory plant diversity (herbs and shrubs).

<sup>C</sup>Prescribed fire.

<sup>D</sup>The Rough Fire (2015) was caused by a natural ignition and managed under suppression objectives.

the necessary  $\geq 10\%$  tree cover required for measuring red fir health and crown condition indicators ( $\leq 5\%$  of sites based on the other site selection criteria). Based on all criteria, we identified and focussed on 17 sites in Yosemite National Park, four sites in Sequoia and Kings Canyon National Parks, and one site on the Giant Sequoia National Monument (Table 1). All study sites were located on well-drained, cryic soils derived from granodiorite.

#### Field methods and site data

In July through September of 2014 to 2017, we randomly established a total of 80 (58 twice burned, 22 unburned) circular plots (12.61-m radius; 0.05 ha) based on our site selection criteria and maintained a minimum distance of 100 m between plots (mean distance between adjacent plots was 668 m) and 100 m from the fire boundary, existing roads and trails. At each site, we established between one and four (average: 2.8) plots in burned red fir stands and one plot in a nearby (mean distance was 1759 m) 'unburned' red fir stand (i.e. no record of fire occurrence for the site in fire history databases dating back to 1908–30; Fire and Resource Assessment Program (FRAP) 2017; National Park Service (NPS) 2017). We established only single plots in unburned areas, because previous studies and preliminary sampling indicated unburned red fir stands exhibit substantially less stand structural variation than burned sites (Kane *et al.* 2013, 2014; Meyer and North *in press*).

Within each 0.05-ha plot, we recorded site attributes (e.g. slope, aspect, geographic coordinates), vegetation cover (estimates of live canopy, shrub and herb cover based on eyesight alone) and stand variables (e.g. live and dead basal area). We also recorded the attributes of all trees  $\geq 5$  cm diameter at breast height (DBH), including species, status (live or dead), DBH, number of stems per cluster (defined as  $\leq 1$  m of the base of a neighbouring stem), percentage live crown (low, 0–25%; moderate to full, 25–100%), decay class (Cline *et al.* 1980) and evidence of insects (e.g. fir engraver, *Scolytus ventralis*) and pathogens (e.g. annosus root disease, *Heterobasidion occidentale*). For all live red fir trees, we recorded a crown loss rating (CLR) derived from the Hawksworth (1977) six-class dwarf mistletoe (*Arceuthobium* spp.) rating system. CLR is based on a visual estimation of recent foliage loss (browning foliage) and localised branch death (i.e. 'flagging') in the crown that we suspected was caused by moisture stress, red fir dwarf mistletoe (*Arceuthobium abietinum magnificae*) and cytospora canker (*Cytospora abietis*), other pathogens and insects, or their interaction. We estimated CLR by visually dividing the tree crown into three sections (lower, middle, upper) and rating each section for intensity of foliage loss in one of three categories: 0 = no branch flagging or foliage loss; 1 =  $\leq 50\%$  of branches with flagging or foliage loss; and 2 =  $> 50\%$  of branches with flagging or foliage loss. We calculated crown loss rating by adding all three sections, resulting in values ranging from 0

(none) to 6 (heavy foliage loss). We also estimated the percentage of unhealthy red fir trees in each 0.1-ha plot based on the proportion that were: (1) low (<25%) percentage live crown; (2) recently dead (decay class 1); or (3) impacted by bark beetles (e.g. fir engraver) or pathogens (excluding dwarf mistletoe covered in CLR). We recorded tree regeneration by species (all seedlings and saplings >10 cm height and <5 cm DBH) in each 0.05-ha plot and categorised counts as: 0, no regeneration; 1, 1–10; 2, 11–100; 3, >100 seedlings and saplings. We also recorded the status (live, dead), species, DBH, percentage live crown, decay class (snags) and health condition of all trees  $\geq 50$  cm DBH in a 17.85-m radius plot (0.1 ha) centred on each 0.05-ha plot to provide a better estimate of large tree and snag densities.

We sampled surface fuels in one burned and one unburned plot per site (22 twice burned, 22 unburned) using the planar-intercept method (Brown 1974) based on the following transect lengths: 3.3 m for 1- and 10-h fuels (0–0.64 and 0.65–2.54 cm), 7.6 m for 100-h fuels (2.55–7.62 cm), and 11.3 m for 1000-h fuels (i.e. coarse woody debris; >7.62 cm). We estimated litter and duff depth at two points and overall surface fuel depths at three points along each transect (two transects per plot). We estimated height to live crown and bole char height with a hand-held laser range finder on four dominant or codominant trees that were located closest to plot centre. In 2015, we opportunistically sampled understorey vegetation (herbaceous plants, shrubs) in a subset of 18 plots (nine burned, nine unburned) from three sites in Yosemite National Park (Table 1, Fig. 1). For these plots, we estimated percentage cover of understorey plants by species in a 5.64-m-radius (0.01-ha) subplot centred on each 0.05-ha plot.

We calculated a Topographic Relative Moisture Index (TRMI) as an indicator of soil moisture availability ranging from 0 (xeric) to 60 (saturated) based on slope position and configuration, aspect and percentage slope (Parker 1982). We used a 30-m digital elevation model from the national elevation dataset to estimate elevation (Gesch *et al.* 2002). We used the USDA Forest Service Pacific Southwest Region vegetation burn severity database (available online at <https://www.fs.usda.gov/main/r5/landmanagement/gis>, accessed 11 July 2018) to estimate the proportion of high-severity fire for all sampled fires (excluding older or smaller fires that were not included in the database). We quantified the Fire Return Interval Departure (FRID) condition class for burned and unburned plots using the US Forest Service Region 5 FRID database (Safford *et al.* 2015).

### Analysis

We calculated the percentage of trees in clusters per plot by dividing the number of live tree stems within close proximity ( $\leq 1$  m) of neighbouring stems by the total number of trees per plot. High percentage tree cluster values (generally exceeding 25–30%) at small spatial scales ( $\leq 1$  m) represent clumped tree distributions that are common within homogenised, fire-excluded and heavily logged stands, whereas low percentage tree cluster values ( $\leq 10\%$ ) typify a regular distribution associated with tree plantations or stands burned at high severity (Taylor 2004; Lydersen *et al.* 2013; Meyer and North *in press*). We included the natural range of variation (NRV) in stand structural variables based on means and standard deviations where this information was available from Meyer and North

(*in press*) for relative comparison with burned and unburned plots sampled in our study. We used one-way analysis of variance (ANOVA) and Kruskal–Wallis tests to examine whether forest structural, understorey diversity and health variables were different between burned and unburned red fir stands. We compared tree diameter distributions between burned and unburned plots with a Kolmogorov–Smirnov two-sample test. We used Spearman's rank correlation to examine the association between the time since last fire and surface fuel loading variables (1-, 10-, 100-h fuels; coarse woody debris, fuel depth). All variables were evaluated for normality, homoscedasticity and independence of residuals. We log-transformed tree density and mean DBH and square-root-transformed coarse woody debris cover to meet the parametric assumptions of ANOVA.

We used a generalised linear mixed model with a normal distribution with an identity link function to examine the relationship between mean red fir CLR per plot (hereafter 'CLR') and categorical (i.e. burn, site) and continuous predictor variables (i.e. elevation, TRMI, basal area, year sampled), with site included as a random effect to account for variation within burned sites. We included year sampled to evaluate potential progressive drought effects associated with the 2012–16 drought, with greatest CLR anticipated during earlier years of sampling that occurred during the peak of the drought period (i.e. 2014–15). We used Akaike's Information Criterion corrected for low sample size relative to the number of parameters ( $AIC_c$ ) to quantitatively compare our set of *a priori* candidate models. We considered six *a priori* candidate models including specific parameters from our three hypotheses of red fir crown loss (burning, topographic dryness based on elevation and TRMI, and live basal area), two additional hypotheses based on the additive effects of burning with topography or basal area, and a base model with three parameters (i.e. site, year sampled and intercept). We did not include parameter interactions or the additive effects of all five parameters in our *a priori* candidate models to avoid model overfitting (Burnham and Anderson 2002). To compare alternative models to the best model, we calculated evidence ratios as  $w_1/w_2$ , where  $w_1$  and  $w_2$  refer to Akaike weights for the compared models with the best model in the numerator. Evidence ratios  $\leq 2.7$  (equivalent to a  $\Delta AIC_c \leq 2$ ) indicate moderate to substantial support for the alternative model relative to the best model, whereas evidence ratios  $\geq 3$  provide little evidence in favour of the alternative model (Burnham and Anderson 2002). We examined correlations among independent factors to evaluate collinearity and removed models that included highly correlated variables (i.e.  $r \geq 0.7$ ). We conducted all statistics with *Statistica 6.1* (StatSoft Inc.) using an  $\alpha$  level of 0.05 for parametric tests.

### Results

We sampled a total of 3445 live and dead trees in 80 plots across our study area, with most plots (82.5%) located in Yosemite National Park (Table 1). All unburned plots had missed at least two fire return intervals ( $> 87$  years), and most burned plots (88%) had been burned in the past 20 years (Table 2). Topographic variables were generally similar between burned and unburned plots, and unburned plots were characterised by a longer period of fire exclusion and fire regime interval departure

(Table 2). Red fir was solely dominant on 44% of plots, a combination of red fir and white fir on 31%, red fir and lodgepole pine on 10%, red fir and Jeffery pine or sugar pine on 9%, and other species combinations (e.g. red fir–white fir–lodgepole pine) on 6%. Burned plots had significantly lower tree densities, canopy cover and percentage trees in clusters and greater mean DBH than unburned plots (Table 3). The shape of the tree size class distribution was different between burned and unburned plots ( $P < 0.001$ ), with flat and inverse J-shaped distributions evident in burned and unburned plots respectively (Fig. 2). Across burned and unburned plots, 26% of sampled red fir trees ( $n = 1758$ ) showed signs of health issues unrelated to crown loss rating.

**Table 2. Mean (±s.d.) topographic and fire characteristics of unburned and burned plots**

In this and subsequent tables, summary statistics are based on 22 unburned and 58 burned plots unless otherwise noted

Structural variable	Unburned	Burned
Elevation (m)	2292 (144)	2279 (145)
Slope (%)	15 (11)	17 (9)
Northness <sup>A</sup>	-0.28 (0.71)	-0.22 (0.69)
TRMI <sup>B</sup>	33.0 (6.6)	33.6 (6.2)
Average high-severity fire (%) <sup>C</sup>	–	5.5 (5.5)
Time since last fire (years)	>87.5 (6.4)	12.2 (7.9)
FRID condition class <sup>D</sup>	2.5 (0.5)	0.6 (1.2)

<sup>A</sup>Northness is calculated as a cosine of aspect: 1 = north-facing, 0 = east or west-facing, -1 = south-facing.

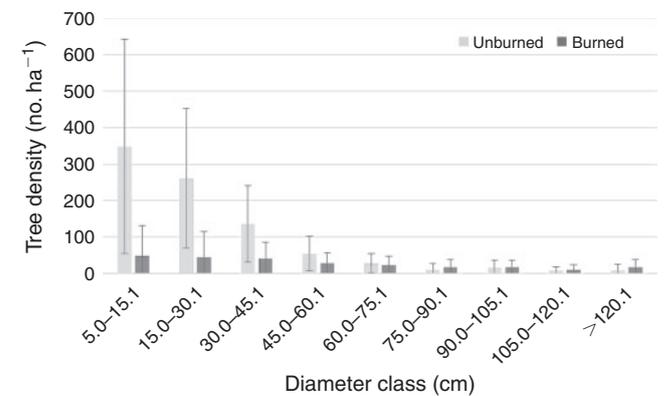
<sup>B</sup>Topographic Relative Moisture Index (TRMI) is an estimate of relative soil moisture availability based on topography that ranges from 0 (xeric) to 60 (saturated).

<sup>C</sup>Percentage high-severity fire is estimated from all sampled fires.

<sup>D</sup>Fire Return Interval Departure (FRID) condition class (range: -3 to 3) quantifies the difference between current and pre-Euroamerican settlement fire frequencies, where greater positive values (i.e. 2 to 3) indicate areas burning at lower frequencies than occurred before Euro-American settlement.

Of these trees, 44% had marginal crowns (crown class 1), 32% were recently dead (decay class 1), 12% exhibited signs of recent fire engraver activity, 6% possessed bole cankers or abnormal swelling and 6% contained other crown or bole abnormalities. Burned and unburned plots were similar in live tree and snag basal area, large tree and snag densities, number of trees per cluster, and percentage unhealthy red fir (Table 3). Fuel characteristics also were similar between burned and unburned red fir plots, although there was a tendency for less coarse woody debris and litter in burned plots (Table 4). In burned plots, there was a weak positive correlation between time since last fire and fuel depth ( $r = 0.351$ ,  $P = 0.016$ ) but no correlation between time since last fire and other fuel variables ( $P > 0.05$ ). Understorey species richness, shrub cover and density of shade-intolerant pine regeneration was greater in burned than unburned plots (Table 5). In burned and unburned plots, density of red fir regeneration was fairly high (220–2000 seedlings and saplings  $ha^{-1}$ ), and only 3 to 4% of plots contained no red fir regeneration.

Model selection results for CLR indicated strong support for two candidate models that included elevation and TRMI



**Fig. 2.** Mean (±s.d.) tree density across diameter classes in burned and unburned red fir plots.

**Table 3. Mean (±s.d.) forest structure and health characteristics of unburned plots, burned plots, and the Natural Range of Variation (NRV)**

Values in the same row with the same letter are significantly different (\*\* $P < 0.001$ )

Structural variable	Unburned	Burned	NRV <sup>A</sup>
Tree density (no. $ha^{-1}$ )	873 (498)***	252 (159)***	260 (92)
Small tree density (no. $ha^{-1}$ ) <sup>B</sup>	612 (469)***	92 (135)***	80 (49)
% Red fir (by density)	72 (25)	71 (21)	72 (13)
Live tree basal area ( $m^2 ha^{-1}$ )	90.9 (31.4)	82.6 (37.6)	58 (76)
Snag basal area ( $m^2 ha^{-1}$ )	20.3 (13.2)	24.7 (22.9)	4.5
Canopy cover (%)	62 (18)***	37 (17)***	43 (15)
Mean DBH (cm)	31 (9)***	60 (22)***	70 (10)
Trees in clusters (%)	36 (20)***	15 (17)***	19 (7)
Number of trees per cluster	2.6 (1.0)	2.2 (0.9)	–
Large tree density (no. $ha^{-1}$ ) <sup>C</sup>	41 (26)	45 (25)	49 (8)
Large snag density (no. $ha^{-1}$ ) <sup>C</sup>	9 (9)	13 (12)	–
Unhealthy red fir trees (%)	26 (22)	26 (21)	–

<sup>A</sup>Based on studies summarised in Meyer and North (in press).

<sup>B</sup>Includes trees  $\leq 30$  cm DBH (diameter at breast height).

<sup>C</sup>Includes trees or snags  $>76.2$  cm DBH; NRV estimate based on late successional stands only.

(Table 6), including the top model based on topography and burn status (CLR ~elevation + TRMI + burn + site + year sampled) with an Akaike weight ( $w_i$ ) of 0.446 and the second-best model based on topography (CLR ~elevation + TRMI + site + year sampled) with  $w_i$  of 0.422 and evidence ratio of 1.06. The third-best model was the base model (CLR ~site + year sampled) with  $w_i$  of 0.061 and an evidence ratio of 7.26 indicating a lack of support. There was little evidence in support of the burn model (CLR ~burn + site + year sampled) that distinguished CLR between burned and unburned plots (evidence ratio = 12.36), the biomass model (CLR ~biomass + site + year sampled; evidence ratio = 19.78), and fire and biomass model (CLR ~biomass + burn + site + year sampled; evidence ratio = 37.54) (Table 6). In the best model, CLR is negatively related to elevation, TRMI, burn and year sampled (i.e. lower red fir crown loss in burned stands located at higher elevations, with greater soil moisture availability and sampled in later years), but only elevation, TRMI and year sampled have confidence intervals that do not overlap with 0 (Table 7).

## Discussion

The reintroduction of wildland fire resulted in numerous structural changes to red fir forests by reducing tree densities, canopy cover and some surface fuels, and restoring spatial heterogeneity

**Table 4. Mean ( $\pm$ s.d.) fuel characteristics of unburned and burned plots**

Values in the same row with the same letter are significantly different ( $*P < 0.05$ )

Structural variable	Unburned	Burned
1-h fuels (Mg ha <sup>-1</sup> )	0.9 (0.7)	0.9 (0.5)
10-h fuels (Mg ha <sup>-1</sup> )	6.4 (5.2)	5.2 (3.6)
100-h fuels (Mg ha <sup>-1</sup> )	8.3 (6.0)	6.0 (5.5)
Coarse woody debris (Mg ha <sup>-1</sup> )	214 (270)	85 (111)
Fuel depth (cm)	10 (8)	6 (7)
Litter depth (cm)	3 (2)*	2 (1)*
Coarse woody debris cover (%)	21 (21)*	11 (12)*
Height to live crown (m)	13.3 (4.4)	13.3 (4.3)
Char height (m)	–	1.9 (1.8)

**Table 5. Mean ( $\pm$ s.d.) understorey characteristics of unburned and burned plots**

Values in the same row with the same letter are significantly different ( $*P < 0.05$ ;  $**P < 0.01$ ;  $***P < 0.001$ )

Structural variable	Unburned	Burned
Shrub cover (%)	2 (7)***	9 (15)***
Herb cover (%)	5 (7)	10 (19)
Shrub species richness	1.1 (1.6)***	2.7 (1.8)***
Understorey species richness <sup>A</sup>	6.9 (3.1)*	10.7 (3.8)*
Understorey species evenness <sup>A</sup>	0.37 (0.25)	0.49 (0.15)
Tree regeneration richness	2.0 (0.9)**	2.7 (1.1)**
Red fir regeneration density (rank <sup>B</sup> )	2.0 (0.7)	2.1 (0.8)
Jeffrey pine and sugar pine regeneration density (rank <sup>B</sup> )	<0.1 (0.3)**	0.6 (0.8)**

<sup>A</sup>Includes all herb and shrub species sampled within a subset of plots located in three burned and three unburned areas in Yosemite National Park only ( $n = 9$ ).

<sup>B</sup>Rank abundance classes are: 0, none; 1 = 20–200 seedlings and saplings per ha; 2 = 220–2000 seedlings and saplings per ha; 3 = >2000 seedlings and saplings per ha.

through the reduction of tree clusters and increase in mean tree diameter (and increased evenness in size class distribution) relative to unburned red fir forests. Repeated burning also increased understorey plant species richness, including shrubs,

**Table 6. Summary of model selection statistics from generalised linear mixed model of crown loss rating (CLR) in burned and unburned plots**  $K$  is the number of model parameters,  $-2 \text{Log}(L)$  is the log<sub>e</sub> likelihood,  $\text{AIC}_c$  is Akaike's Information Criterion corrected for small sample sizes,  $\Delta\text{AIC}_c$  is the relative difference in  $\text{AIC}_c$  from the top model, and  $w_i$  is the Akaike model weight

Model <sup>A</sup>	$K$	$-2 \text{Log}(L)$	$\text{AIC}_c$	$\Delta\text{AIC}_c$	$w_i$
Burn + elevation + TRMI	7	187.19	245.34	0.00	0.446
Elevation + TRMI	6	190.73	245.44	0.11	0.422
Site + year (base)	4	203.96	249.30	3.97	0.061
Burn	5	202.90	250.36	5.03	0.036
Live basal area	5	203.63	251.31	5.97	0.022
Burn + live basal area	6	202.81	252.59	7.25	0.012

<sup>A</sup>Topographic Relative Moisture Index (TRMI) is an estimate of relative soil moisture availability and ranges from 0 (xeric) to 60 (saturated). 'Burn' refers to sites that are burned twice (burn) or unburned for two or more historical fire return intervals (no burn). Live basal area is the total basal area of all trees  $\geq 5$  cm DBH. Site and year sampled were included as parameters in all models.

**Table 7. Results of generalised linear mixed model for red fir crown loss rating (CLR) based on the top two models in Table 6**

Parameter	Top model estimate (s.e.) <sup>A</sup>	Second best model estimate (s.e.) <sup>A</sup>
Elevation	-0.007 (0.002) <sup>B</sup>	-0.004 (0.002) <sup>B</sup>
TRMI	-0.053 (0.023) <sup>B</sup>	-0.051 (0.022) <sup>B</sup>
Burn	-0.154 (0.079)	Not included
Year sampled	-1.469 (0.515) <sup>B</sup>	-0.859 (0.580) <sup>B</sup>

<sup>A</sup>Site is specified as a random effect. Model is CLR = Elevation + TRMI + Burn (top model only) + year sampled + (1 | site). All coefficients are on a linear scale (TRMI, Topographic Relative Moisture Index).

<sup>B</sup>95% confidence interval does not overlap with zero.

herbaceous plants and tree regeneration. Burning increased the densities of drought-tolerant pine regeneration but also retained a fairly high density of red fir regeneration important for recruitment. Additionally, burning increased shrub cover and maintained similar large tree and snag densities compared with unburned sites, providing key habitat structures for a variety of wildlife species associated with Sierra Nevada upper montane forests (Roberts *et al.* 2011, 2015; van Riper *et al.* 2013; White *et al.* 2016). These results largely support our first hypothesis that the reestablishment of the natural fire regime results in significant, positive changes to red fir forest structure and diversity in the Sierra Nevada.

Post-fire changes in red fir forest structure are largely consistent with similar studies conducted in frequent-fire forests of western North America (e.g. ponderosa pine, Jeffrey pine). In these studies, repeated burning generally reduced tree densities and canopy cover (especially in the smallest size classes), increased mean tree diameter, promoted flatter size class distributions, and did not substantially decrease basal area or large tree densities (Fulé and Laughlin 2007; Holden *et al.* 2007; North *et al.* 2007; Kane *et al.* 2013; Dunbar-Irwin and Safford 2016). Tree densities in our burned red fir stands were 3.5 times lower than in unburned locations, a finding almost identical in the comparison of burned and unburned stands from mixed-conifer forests of Sequoia and Kings Canyon National Parks (Webster and Halpern 2010) and ponderosa pine forests in wilderness areas of the south-western United States (Holden *et al.* 2007). Tree densities in burned stands of our study were remarkably similar to historical forest inventory estimates of red fir stands in the Sierra Nevada, including the density of large trees (Table 3; Meyer and North *in press*). This last result suggests that low- to moderate-severity fire may have a neutral or slightly positive effect on large-tree survivorship in red fir forests similar to that observed in mixed conifer (van Mantgem *et al.* 2016) following initial marginal (<5%) reductions in larger-diameter red fir trees observed with burning (Mutch and Parsons 1998).

Surface fuel loading was highly variable and largely similar between burned and unburned areas, but litter depth was marginally lower in burned areas and coarse woody debris tended to be twice as abundant in unburned than burned plots. Similarly, height to live crown was similar between burned and unburned sites, but burning significantly reduced the density of the smallest size class ( $\leq 30$  cm DBH; Table 1) that comprises the majority of ladder fuels. Our results are only partially consistent with studies conducted in frequent-fire forests, which document a clear reduction in surface and lower-strata crown fuels following the reintroduction of fire, especially following multiple fire entries (Fulé and Laughlin 2007; Webster and Halpern 2010; Kane *et al.* 2013). Additionally, although surface fuel loading increases with time since last fire in many Sierra Nevada forest ecosystems (Safford and Van de Water 2014), we found little correlation between surface fuel loading variables and time since last fire in red fir stands. The shorter growing season, lower productivity and more limited surface fuel flammability of red fir forests may result in lower levels of fuel accumulation and post-fire consumption compared with lower-elevation, frequent-fire forests (Safford and Van de Water 2014). Interestingly, these patterns may partially contribute to

the lack of a positive relationship between fire severity and fire return interval departure in red fir forests of California (Steel *et al.* 2015).

Understorey species diversity was greater in burned than unburned red fir forests of our study, a pattern similarly observed in frequent-fire forests in western North America. In Sequoia and Kings Canyon National Parks, species richness of native plants (i.e. herbaceous plants, shrubs, trees) was greater in singly or repeatedly burned mixed-conifer forests than in unburned forest stands (Keeley *et al.* 2003; Webster and Halpern 2010). Ponisio *et al.* (2016) found flowering plant diversity was positively related to pyrodiversity (i.e. diversity in fire characteristics such as extent, severity and frequency) in upper montane forests of the Illilouette Creek Basin of Yosemite National Park, resulting in greater flowering plant diversity in burned stands with variable fire effects and history. In the Grand Canyon National Park of northern Arizona, understorey plant species richness, especially native forbs, was greater in prescribed burned than unburned mixed-conifer stands (Huisinga *et al.* 2005). Chappell (1991) found a higher diversity of understorey plants in burned than unburned red fir stands in Crater Lake National Park.

The percentage of unhealthy red fir trees was similar between burned and unburned plots, and there was little support for the effect of burn status on red fir CLR. Although our best model included burning in combination with topographic predictors, which suggests a possible additive effect of fire with topography, the estimate confidence intervals for burning overlapped with zero in this model (i.e. weak support for burn status as an influential predictor of CLR). In combination, these results do not strongly support our first hypothesis that the reestablishment of the natural fire regime would improve the health of red fir stands. Rather, topography was a more important predictor of red fir CLR, as the top two models included topographic parameters (i.e. elevation, TRMI). This provides support to our second hypothesis of increased CLR associated with areas of increased topographic dryness, which corroborates results from remote sensing studies documenting increased canopy water loss associations with decreasing elevation and other topographic variables (Asner *et al.* 2015; Brodrick and Asner 2017; Paz-Kagan *et al.* 2017). There was limited support for our stand biomass model, suggesting that basal area has a negligible effect on red fir CLR. However, our data collection was conducted during a severe drought event in California, which could outweigh local effects of stand biomass or fire history on red fir mortality. Notably, the negative relationship between CLR and year sampled indicates that the highest levels of red fir CLR occurred during years of greatest drought stress and lowest canopy water content in Sierra Nevada red fir forests (2014–15; Brodrick and Asner 2017). Studies conducted before this drought suggest that the local effects of stand biomass and fire history are evident in red fir forests during ‘normal’ precipitation years (e.g. Mortenson *et al.* 2015).

A primary limitation of our study is the absence of pre-fire data, which restricts insights into temporal changes in red fir forest ecosystems. However, our sampling did cover a wide array of fires (Table 1) and geographic areas, including 22 paired wildfires in a total of 11 watersheds or fireheds. Additionally, although we sampled a range of fire severities (i.e. unburned,

unchanged, low and moderate), we did not sample high-severity burned sites and other deforested areas that did not meet our minimum forest cover criteria ( $\geq 10\%$  tree cover) that could contribute to fire severity variation in our samples. However, we considered this to be of minor importance, because high-severity fire occurred in only a small proportion of our total potential sampling area ( $\leq 5\%$  of sites based on the remaining site selection criteria). Additionally, even if we had included high-severity samples in our analysis, this would only serve to further emphasise the differences in most stand structure variables (decreased stand densities and canopy cover in high-severity burned plots) and understorey diversity (increased understorey species richness when high-severity burned plots were included) between burned and unburned sites (M. D. Meyer, unpubl. data). Lastly, our results for understorey diversity were based on a limited subset of plots, which may limit the robustness of our conclusions for herbaceous plants (shrub and tree regeneration diversity analyses were based on the full complement of study plots).

Our study has several implications for forest and fire management in the Sierra Nevada. First, we observed that the repeated use of low- to moderate-severity fire, including wild-fire managed for resource objectives, may restore red fir forest structure and diversity despite long-term fire exclusion and moderate fire return interval departure (Table 1) preceding fire reintroduction efforts. This suggests that fire may be effectively managed in many red fir forests without the need for mechanical pretreatment, especially in areas outside the wildland–urban interface (e.g. Meyer 2015). Even first-entry, low-severity fire can be effective at reducing the density of small-diameter trees and restoring structural heterogeneity in Sierra Nevada red fir forests (Kane *et al.* 2014; Becker and Lutz 2016), although it is unclear to what degree a second entry burn is needed to ‘clean up’ surface fuels generated from the initial burn. In comparison, long-term fire exclusion in frequent-fire forests (e.g. ponderosa pine forests characterised by high fire return interval departure) or forest stands adjacent to human infrastructure may warrant the mitigation of high surface and ladder fuels with mechanical treatments before the application of wildland fire to achieve management objectives (Stephens *et al.* 2009; Ryan *et al.* 2013). Second, fire can facilitate structural restoration, but it may not alleviate moisture stress or enhance the health of red fir forests under warming climate or the exceptional drought conditions recently observed in the Sierra Nevada (Safford *et al.* 2012; Meyer and North *in press*). Nevertheless, repeated burning did restore red fir forest structural heterogeneity, retain large trees and abundant red fir regeneration, and increase the density of more drought- and fire-tolerant tree regeneration (i.e. Jeffrey pine and sugar pine). This suggests that wildland fire may enhance the adaptive capacity of red fir forests to projected increases in temperature and uncharacteristically severe wildfires that threaten coniferous forests regionally (Safford *et al.* 2012) and globally (Stephens *et al.* 2013). Lastly, most of our study results were observed in the national parks of the Sierra Nevada, where managed wildfires (i.e. those not managed under a full suppression strategy) and prescribed fires have resulted in beneficial fire effects supporting natural resource management objectives (e.g. van Wagtenonk and Lutz 2007; Webster and Halpern 2010; Roberts *et al.* 2011; Becker and Lutz 2016). We suspect that these patterns observed in the national parks are

broadly applicable to the neighbouring national forests, where fire effects patterns derived from remote sensing imagery suggest the use of wildland fire can support these and other resource objectives in red fir, mixed-conifer and other montane coniferous forests (Meyer 2015). Future research and monitoring will be critical in evaluating the potential benefits of managed wildfires to coniferous forests throughout western North America (Miller and Aplet 2016).

### Conflict of Interest

The authors declare that they have no conflicts of interest.

### Acknowledgements

We thank US Forest Service Region 5 Ecology Program field crews for assistance with data collection and M. MacKenzie for tree pathogen identification. Three anonymous reviewers provided helpful comments on the manuscript. The National Science Foundation (NSF) Research Experience for Undergraduates (REU) Program supported A. Stucy during this project. We acknowledge the Sierra Nevada Research Station’s Yosemite Field Station for logistic support. This research was conducted under National Park Service research study numbers YOSE-00619 and SEKI-00455.

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