



Variability in vegetation and surface fuels across mixed-conifer-dominated landscapes with over 40 years of natural fire



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ARTICLE INFO

Article history:

Received 7 June 2016

Received in revised form 30 August 2016

Accepted 9 September 2016

Available online 19 September 2016

Keywords:

Heterogeneity

Forest restoration

Fire regime

Managed fire

Reference conditions

ABSTRACT

Studies of historical fire and vegetation conditions in dry conifer forests have demonstrated a high degree of heterogeneity across landscapes. However, there is a limit to the amount of inference that can be drawn from historical fire reconstructions. Contemporary “reference” landscapes may be able to provide information that is not available from historical reconstructions. In this study, we characterized variability in vegetation structure and composition across two Sierra Nevada landscapes with long-established fire restoration programs. We used tree, shrub, and surface fuel data from 117 initial plots, 86 of which were re-measured 8–12 years later, to identify the mechanisms driving variability in vegetation and fuel conditions. Our analyses identified nine distinct vegetation groups, with mean live tree basal area and density ranging from 0.3 to 72.7 m² ha⁻¹ and 2.5 to 620 trees ha⁻¹ for individual groups. For all plots combined, mean live tree basal area and density was 28.4 m² ha⁻¹ and 215 trees ha⁻¹, but standard deviations (SD) were 29.1 m² ha⁻¹ and 182 trees ha⁻¹, respectively. These ranges and SDs demonstrate considerable variability in vegetation structure, which was partially related to site productivity and previous fire severity. Fine surface fuel loads were generally low (overall mean, 16.1 Mg ha⁻¹), but also exhibited high variability (SD, 12.6 Mg ha⁻¹). Surprisingly, surface fuel loads based on initial measurement and change between measurements were not related to fire characteristics. The only statistical relationship found was that surface fuel loads were associated with forest structure and composition. These results capture a contemporary ‘natural’ range of variability and can be used to guide landscape-level restoration efforts. More specifically, these results can help identify distinct targets for variable forest structures across landscapes.

Published by Elsevier B.V.

1. Introduction

Landscapes dominated by dry conifer forests are a subject of particular concern for land management due to the altered fire patterns observed in recent decades (Mallek et al., 2013; Stephens et al., 2013). This concern has spawned several directives from public land management agencies in the U.S. to implement large scale restoration efforts aimed at mitigating future fire effects and ultimately improving ecosystem resilience (USDA-FS, 2011, 2012, 2013). There are a number of historical forest reconstructions based on tree-ring data (Fulé et al., 1997; Taylor, 2004;

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North et al., 2007; Brown et al., 2008) and archived historical data (Williams and Baker, 2012; Hagsmann et al., 2013, 2014; Baker, 2014; Collins et al., 2015; Stephens et al., 2015) to guide restoration efforts in these landscapes. The assumption with these reconstructions is that disturbance regimes were relatively intact for the period of reference and the forest conditions described represent the natural range of variation for these ecosystems (Hessburg et al., 2015). Furthermore, these conditions are assumed to be resilient to major ecosystem change brought about by natural disturbance and stressors (Fulé, 2008; Safford et al., 2012).

Heterogeneity in vegetation structure and composition is increasingly recognized as a salient attribute of dry forest-dominated landscapes with intact disturbance regimes (North et al., 2009; Hessburg et al., 2015). This heterogeneity appears to have existed at both the stand-level (<100 ha), with highly variable

tree spatial patterns (Stephens and Gill, 2005; Taylor, 2010; Larson and Churchill, 2012; Lydersen et al., 2013; Fry et al., 2014), and at the landscape-level (>10,000 ha), with variable forest structure and composition among stands or patches (Hessburg et al., 1999; Beaty and Taylor, 2008). However, due to limitations associated with methodologies and data availability, most historical forest reconstruction studies provide incomplete characterizations of vegetation conditions across forest-dominated landscapes (Swetnam et al., 1999; Collins et al., 2016). For example, tree-ring based reconstructions rely on extant data that “survived” 100+ years beyond the period of interest. It is difficult to know what information may be absent as a result of decomposition or consumption in subsequent fires. This makes estimates of small tree densities, snags, and coarse woody debris very difficult from tree-ring reconstructions. Furthermore, non-tree information (e.g., shrub cover, surface fuels) is often missing from historical reconstructions.

Contemporary “reference” landscapes may be able to provide information that is unavailable from historical reconstructions. These are landscapes in which vegetation conditions have been less altered by modern land use change and management (e.g., development, timber harvesting, grazing) than surrounding areas. Additionally, fire has been restored in these landscapes as an integral ecosystem process (Miller and Aplet, 2016). Advantages of using these areas as reference landscapes for current restoration over historical reconstructions include greater detail of vegetation characteristics (both from plot measurements and remote sensing), potential for repeat measurements over time, known recent history of disturbance (last 20–40 years), and they have experienced climate similar to contemporary forests in need of restoration. These advantages allow for relatively complete descriptions of “natural” vegetation conditions and they provide potential to understand the factors driving vegetation and fuel conditions across landscapes. Contemporary reference landscapes, however, tend to be in somewhat unique locations, which can limit broader inference. Furthermore, many of these areas have been impacted by many decades of fire suppression prior to the relatively recent restoration of fire (Collins and Stephens, 2007). These disadvantages emphasize that information obtained from these landscapes should be used to complement, rather than replace, information from historical forest reconstructions.

In this study, we used an extensive network of field plots with repeat measurements across two contemporary reference landscapes to: (1) identify relatively distinct vegetation groups based on overstory and understory structure and composition, (2) explore the extent to which recent fire and topographic characteristics explain the distribution of vegetation groups across the two landscapes, and (3) investigate factors influencing surface fuels, which is one of the main drivers of fire behavior and effects. Given the depth of sampling across these two areas and the level of fire activity captured in the sampling, this work can provide insight into the interaction between fire, vegetation, and fuels under a relatively intact disturbance regime.

2. Methods

2.1. Study area

Our study was conducted in two designated wilderness areas in the central and southern Sierra Nevada, Illilouette Creek basin and Sugarloaf Creek basin, respectively (Fig. 1). The climate is Mediterranean with cool, moist winters, and warm, generally dry summers. Based on observations from Remote Automated Weather Stations (RAWS) near both basins, average January daily minimum temperatures ranged from -5°C to 1°C , while average July daily maximum temperatures ranged from 24°C to 25°C (2000–2015;

<http://www.wrcc.dri.edu/>; White Wolf and Crane Flat RAWS in Yosemite National Park [NP]; Sugarloaf RAWS in Sequoia-Kings Canyon NP). Average annual precipitation (Oct–Sep) ranged from 47 to 60 cm in both areas (2000–2015; <http://www.wrcc.dri.edu/>; White Wolf and Crane Flat RAWS in Yosemite NP; Cedar Grove RAWS in Sequoia-Kings Canyon NP). Elevations range from 1400 m to nearly 3000 m on the surrounding ridges. Vegetation is predominantly upper-elevation mixed-conifer forest composed of Jeffrey pine (*Pinus jeffreyi*), red fir (*Abies magnifica*), white fir (*A. concolor*), lodgepole pine (*P. contorta* var. *murrayana*), and sugar pine (*P. lambertiana*). Meadows, shrublands, and bare rock make up most of the remaining area in both basins.

Natural fire management programs were established in the NPs encompassing Illilouette Creek Basin (Yosemite NP) and Sugarloaf Creek basin (Sequoia-Kings Canyon NP) in 1972 and 1968, respectively (van Wagtenonk, 2007). These programs intended to restore fire as a dynamic ecosystem process by allowing lightning-ignited fires to burn across these landscapes. Based on watershed boundaries for Illilouette Creek and Sugarloaf Creek the basins are 16,200 and 12,300 ha, respectively. Since the onset of these programs, 27 and 10 fires >40 ha have occurred in Illilouette and Sugarloaf, respectively, burning the equivalent area of 80% (Illilouette) and 58% (Sugarloaf) of the basins. Based on tree-ring reconstructions, the historical fire regime within Jeffrey pine-dominated areas predominantly consisted of frequent low- to moderate-severity fires (Collins and Stephens, 2007). From 1700 to 1900, Collins and Stephens (2007) reported a mean fire interval of 6 and 9 years, and a fire rotation of 24 and 49 years for Illilouette and Sugarloaf, respectively. The same study also demonstrated that fire occurrence since the onset of the natural fire programs (1972–2005) did not differ noticeably from pre-settlement estimates.

2.2. Field sampling

Sampling was not conducted across the entirety of both basins due to logistical limitations. Instead, sampling was focused where the greatest range of burn frequencies (since onset of the natural fire programs) could be captured in contiguous areas (Fig. 1). Convex hull polygons around the field plot locations were approximately 1500 and 600 ha in Illilouette and Sugarloaf, respectively. Plot locations were chosen using a 200 m systematic grid overlaid on two strata: burn frequency since onset of the natural fire program (0–4) and dominant tree genus (*Pinus*, *Abies*). For two stratum combinations in Sugarloaf, however, we used a 100 m grid due to limited available area (Fig. 1). The goal was to sample a minimum of five plots in each burn frequency-dominant tree genus combination. A total of 117 field plots were established in 2002 (65 in Illilouette, 52 in Sugarloaf). Plot center coordinates were generated in GIS and navigated to using handheld GPS with 5–10 m accuracy. Plots were fixed-radius, 0.05 ha, in which the following information was collected for all trees >10 cm diameter-at-breast-height (dbh): status (live, dead), species, dbh, total height, and height to live crown base. Canopy cover was measured with a densitometer (Geographic Resource Solutions; <http://www.grsgis.com/densitometer.html>) based on 25 points per plot (5×5 grid, 3 m between points). Shrub cover for each species was visually estimated over the entire plot based on vertical projection. In each plot downed woody, litter, and duff fuels were sampled on three transects using random azimuths radiating from plot center. The planar-intercept method was used to sample downed woody fuels (Brown, 1974) with the following transect lengths: 2 m for 1- and 10-h fuels (0–0.64 and 0.65–2.54 cm), 4 m for 100-h fuels (2.55–7.62 cm), and 11 m for 1000-h fuels (>7.62 cm). Duff, litter, and overall surface fuel depths (cm) were measured at two points along each transect. Fuel loads were calculated using species-specific coefficients

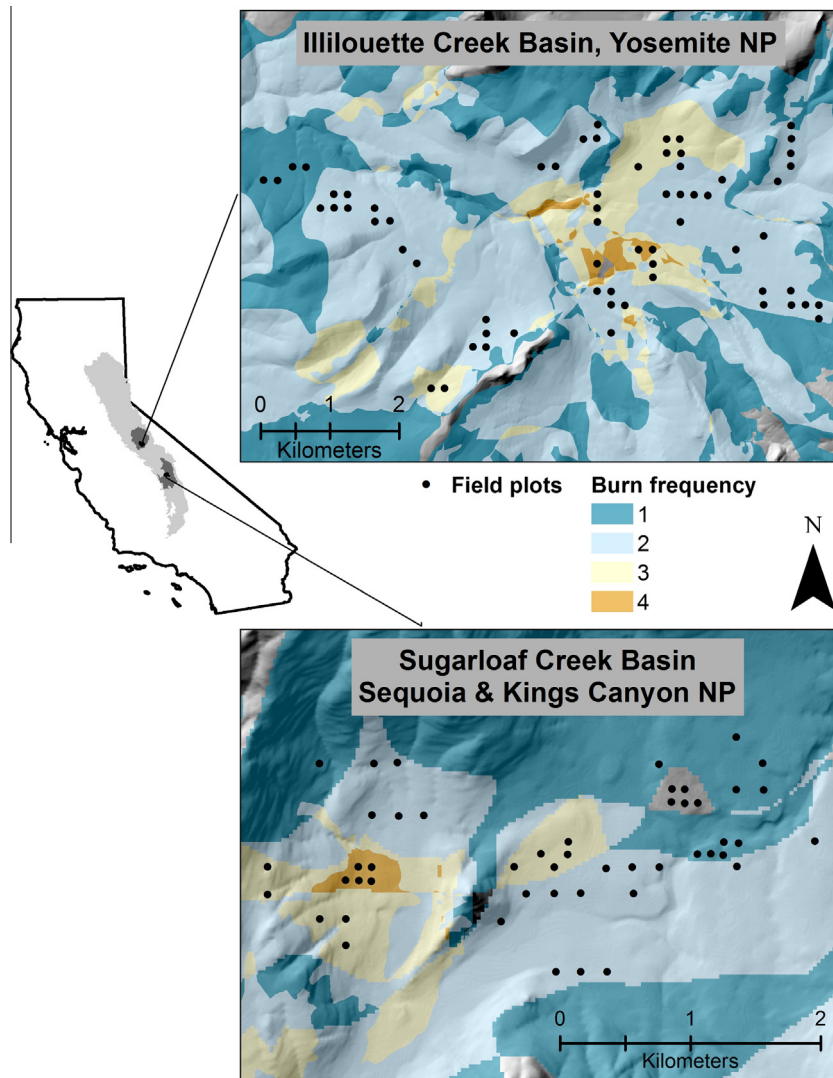


Fig. 1. Field plot locations (black dots) in two Sierra Nevada wilderness areas with long-established natural fire programs. Mapped burn frequencies include fires larger than 40 ha that occurred since the onset of the natural fire programs (1968 in Sequoia-Kings Canyon National Park [NP], 1972 in Yosemite NP). Note, there are five plots in Sugarloaf Creek Basin that have no recent fire history (gray background).

(van Wagendonk et al., 1996, 1998), weighted by the proportion of total basal area (BA) of each species (Stephens, 2001).

Between 2010 and 2014 all but three of the 117 plots established in 2002 were re-measured. The spread in years of re-measurement was due to lack of sufficient funding for a dedicated field crew. Three plots were not re-measured due to inability to re-locate plot centers. Repeat measurements were made using the same protocol as in 2002, with the exception that in 28 of the 114 re-measured plots, azimuths for the surface fuel transects were based on cardinal directions as opposed to the same random azimuths used originally. Those plots were excluded from analysis of fuel change between the two time periods, resulting in 86 total plots with repeated fuel measurements using the same transect azimuths. Opportunistically, fourteen of those plots burned between initial sampling and re-measurement.

2.3. Data analysis

The following vegetation structure and composition variables were generated for each plot: total tree BA, BA proportion by tree species, total tree density, tree density by dbh class (10–30.4 cm,

Table 1

Summary of topographic, moisture availability, and fire variables for all field plots in Illilouette Creek and Sugarloaf Creek basins, Sierra Nevada, California ($n = 117$). Note that the number of plots having fire severity values is less than those having a time since last fire. This is because fire severity, as measured by the relative differenced Normalized Burn Ratio (RdNBR), was only available for plots that burned in 1984 or later.

Variable (continuous)	Mean	Range
Elevation (m)	2237	1990–2523
Slope (%)	16.2	1.4–62.8
Aspect (classified, Parker (1982))	10.5	1–20
Topographic relative moisture index	31.4	17–45
Actual evapotranspiration (mm)	212.5	210–215
Annual climatic water deficit (mm)	207.7	203–211
Time since last fire (years), $n = 108$	12.9	1–29
Variable (categorical)		Number of plots
Topographic position	Valley bottom	2
	Gentle slope	53
	Steep slope	62
	Ridge	0
Fire severity class-RdNBR	Low	53
	Moderate	13
	High	7

30.5–61.0 cm, >61.0 cm), canopy cover, and shrub cover. These variables were used in a k-means cluster analysis (Kaufman and Rousseeuw, 2009) to identify distinct vegetation groups. Although there is no clear consensus on which clustering method (e.g., k-means vs. hierarchical) performs better, it has been suggested that k-means may be more reliable for larger datasets (Kaur and Kaur, 2013), which is why we chose it. This analysis was performed in the statistical package R using the CLUSTER package (Peeples, 2011). Input variables were z-score standardized prior to clustering to account for differences in scale. Standard practices were followed for choosing the number of clusters that corresponded with an abrupt flattening of the curve depicting within-group sum-of-squares-error as a function of number of clusters (Kaufman and Rousseeuw, 2009).

Several topographic and fire variables were generated to investigate the factors driving the distribution of the identified vegetation groups. The variables were: elevation, aspect, slope gradient, topographic position index (TPI), topographic relative moisture

index (TRMI), actual evapotranspiration (AET), annual climatic water deficit, fire severity, and time since last fire. Topographic variables were derived in GIS using a 30 m digital elevation model obtained from the National Elevation Dataset (Gesch et al., 2002). Aspect was classified so that values ranged from 0 (xeric) to 20 (mesic) using the approach outlined in Parker (1982). Four TPI classes (valley bottom, gentle slope, steep slope or ridgetop) were generated using the CorridorDesigner toolbox (Majka et al., 2007), with a neighborhood size of 200 m. The cutoff point for gentle versus steep slope was 6° (10.5%). TRMI was calculated using TPI, classified aspect, slope gradient, and slope curvature following the method of Parker (1982). We used the 2014 version of AET and annual climatic water deficit generated by Flint et al. (2013). For plots that burned between 1984 and 2014 fire severity class of the most recent fire was estimated using thresholds for the relative differenced Normalized Burn Ratio described by Miller and Thode (2007). These fire severity classes have been assessed with independent field datasets by Miller et al. (2009) and Lydersen

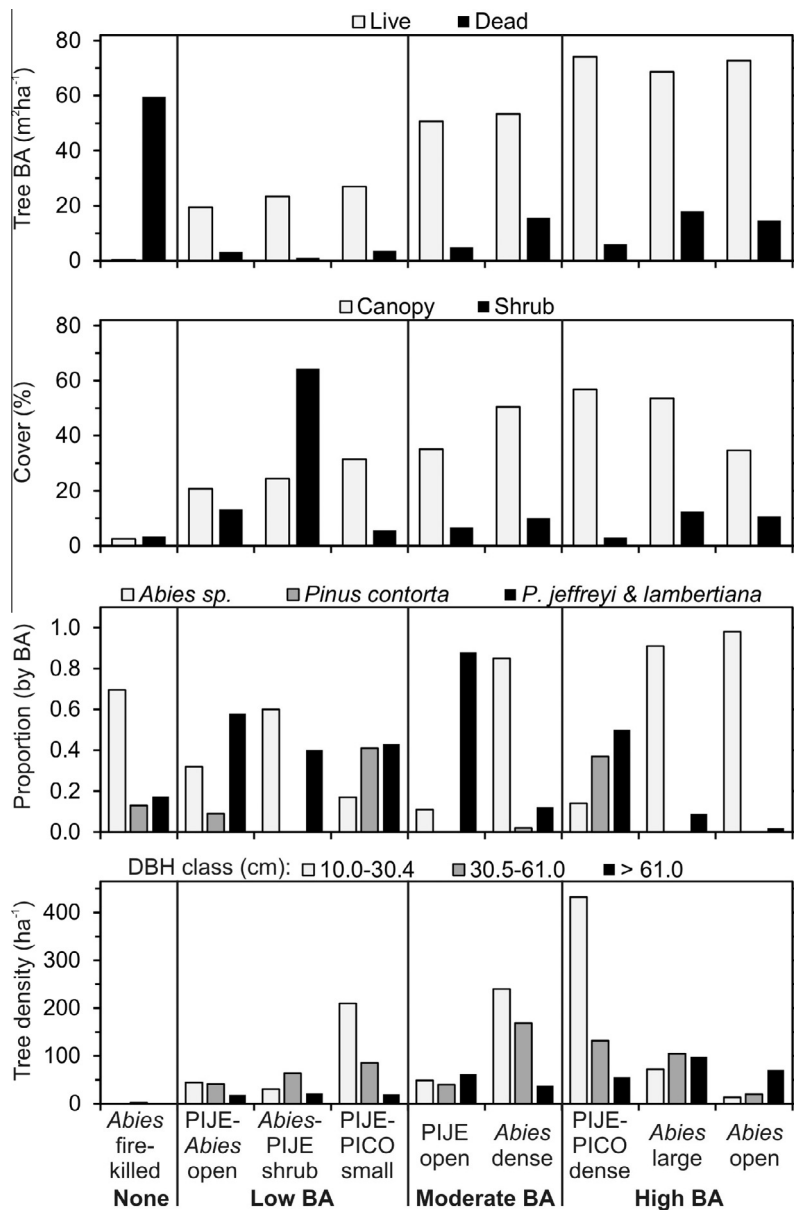


Fig. 2. Mean live forest structure characteristics and tree species composition of nine vegetation groups that were identified using a k-means cluster analysis. Vertical lines separate sets of vegetation groups based on broad live tree basal area (BA) classes (bold). Individual groups are named based on dominant tree species (PIJE-*Pinus Jeffreyi*; PICO-*P. contorta* v. *murrayana*) and the most salient structural characteristic (“small” and “large” refer to distributions of trees among size classes).

et al. (2016) and have been shown to robustly capture distinct changes in basal area and tree density caused by fire. Remotely sensed estimates of fire severity allowed for consistent estimates of fire-caused change across fires and years, and were used over field-based estimates due to the wide range in time since last fire (Table 1). Times since last fire (years) were derived using digital fire atlases for all fires that occurred since the onset of the natural fire programs (available from <https://irma.nps.gov/Portal>). Values for continuous variables were extracted for each plot using bilinear interpolation in ArcGIS (Table 1).

Conditional inference tree analysis (Hothorn et al., 2006) was used to explain the distribution of the identified vegetation groups across the two landscapes. This method was chosen over other approaches due to its ability to both capture complex, hierarchical relationships between predictor and response variables (De'ath and Fabricius, 2000) and identify potential thresholds for predictor variables (e.g., Lydersen et al., 2014). Furthermore, results from conditional inference trees are straightforward, which allows for interpretation for a wide audience. Topographic, site productivity/moisture availability, and fire variables were used as predictors. This analysis was performed using the “ctree” function in the PARTY package in R statistical computing software (Hothorn et al., 2009). This technique identifies influential explanatory variables using a partitioning algorithm that is based on the lowest statistically significant P value derived using a simple Bonferroni correction, which avoids overfitting and biased selection among covariates (Hothorn et al., 2006). A significance level of 0.05 was used in assessing all splits.

The same conditional inference tree approach was used to explore factors related to surface fuel loads calculated based on initial measurement and change between initial and re-measurement. Fine fuel loads, which included litter, 1-, 10-, and 100-h woody fuels, and coarse fuel loads (1000-h sound and rotten) were analyzed separately due to their differential influence on fire behavior and effects (van Wagtenonk, 2006). Predictors included the same topographic, site productivity/moisture availability, and fire variables, as well as the vegetation structure and composition variables described previously. Time since previous fire was re-calculated based on the re-measurement data. Additionally, fire severity was updated for the 14 plots that burned between the two measurement periods to reflect the most recent fire. Goodness-of-fit was assessed by calculating an R^2 as $1 - (\text{variance of the residuals}/\text{total variance})$. This R^2 could only be calculated for conditional inference trees predicting continuous response variables (i.e., surface fuel loads, not vegetation groups).

3. Results

The k-means analysis resulted in nine distinct vegetation groups. The groups tended to separate based on three characteristics: BA, dominant tree species composition, and tree density (Fig. 2). One group was clearly distinct from the others because it was dominated by dead white fir trees (*ABIES FIRE-KILLED*). Eight plots were in this group and they all occurred in Illilouette (Fig. 3). Three groups had low average live tree BA (19.5, 23.4, 26.9 $\text{m}^2 \text{ha}^{-1}$), but differed in tree density, tree species composition, and shrub cover: *PIJE-ABIES OPEN*, *ABIES-PIJE SHRUB*, and *PIJE-PICO SMALL* (Table S1). These three groups made up nearly half of the total plots ($n = 57$). The two *ABIES-PIJE* groups were dominated by white fir and Jeffrey pine, and had low tree density across all size classes. The *ABIES-PIJE SHRUB* had on average over 60% shrub cover (Fig. 2). The *PIJE-PICO SMALL* group was dominated by Jeffrey and lodgepole pine, had relatively high small tree density (Fig. 2) and occurred more frequently in Sugarloaf (11 out of 14 plots, Fig. 3). Two groups had moderate live tree BA (50.7, 53.4 $\text{m}^2 \text{ha}^{-1}$), but differed primarily in tree species composition and density: *PIJE OPEN* and *ABIES DENSE*. These two groups

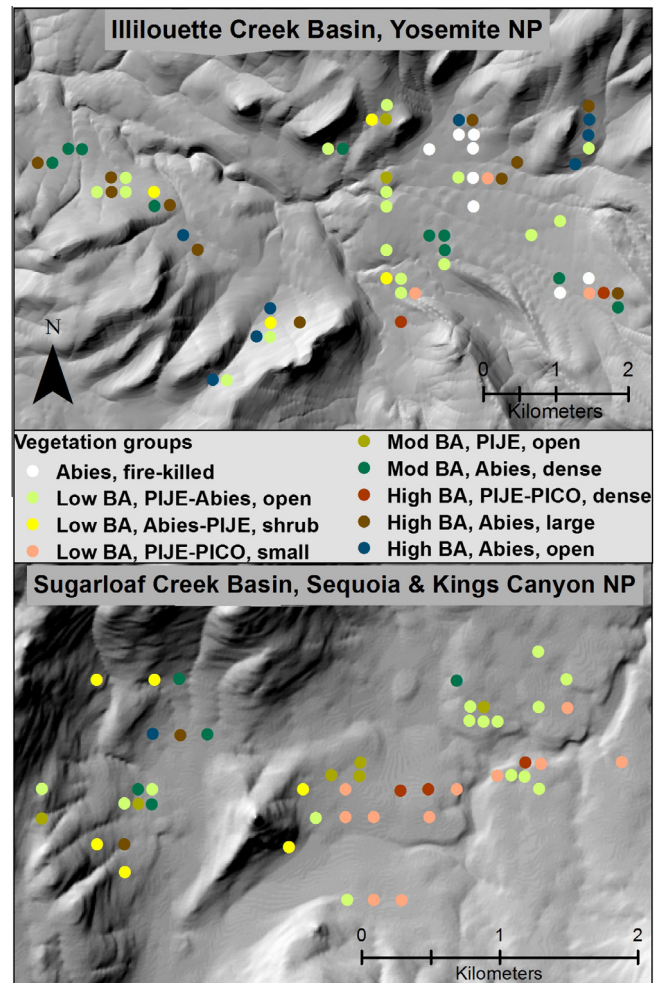


Fig. 3. Field plot locations classified by vegetation groups. Groups were identified using a k-means cluster analysis based on overstory and understory structure and composition.

accounted for 21% of the plots ($n = 25$). The *ABIES DENSE* group was dominated by white and red fir and had slightly higher canopy cover, and had 4–5 times the number of small- to mid-sized trees (Fig. 2). Also, the *ABIES DENSE* group occurred more frequently in Illilouette (10 out of 15 plots, Fig. 3). The last three groups had high average BA (68.7, 72.7, 74.1 $\text{m}^2 \text{ha}^{-1}$), but differed in tree species composition and tree density (Fig. 2, Table S1): *PIJE-PICO DENSE*, *ABIES LARGE*, and *ABIES OPEN*. These groups accounted for 23% of the plots ($n = 27$). The *PIJE-PICO DENSE* group was dominated by Jeffrey and lodgepole pine, and had very high small tree density and the highest average canopy cover (Fig. 2). The two *ABIES* groups were dominated by white and red fir and occurred more frequently in Illilouette (18 out of 21 plots, Fig. 3). The *ABIES LARGE* group had noticeably more trees in the small- and mid-size class and higher canopy cover than the *ABIES OPEN* group.

AET and fire severity influenced the distribution of vegetation groups across the two study areas (Fig. 4). Despite the identification of these two variables as important, there were only a couple of noticeable distinctions among vegetation groups. First, plots in the two PICO groups (*PIJE-PICO SMALL*, *PIJE-PICO DENSE*) were predominantly associated with greater AET (12 of 17 plots total; Fig. 4). The likely explanation for this is that PICO tends to be more tolerant of moist, and even poorly aerated soils relative to other conifers present in our study (Fites-Kaufman et al., 2007). Second, not surprisingly, plots in the *ABIES FIRE-KILLED* group were in areas that burned at high and moderate fire severity. The majority of plots

in the other six vegetation groups were associated with lower AET and either low severity fire or no available fire severity information (i.e., for plots that burned before 1984).

Conditional inference tree results explaining observed surface fuel loads differed among the various dependent variables analyzed (initial fine and coarse fuel loads; change from initial to re-measured fine and coarse fuel loads). No significant predictor variables were identified explaining coarse fuel loads either based on initial measurement or the change over time. The same was true for change in fine fuel loads over time. However, fine fuel loads based on initial measurement were related to tree canopy cover

and *Abies* sp. live BA (Fig. 5). Goodness-of-fit for the model with these two variables was moderate, with an R^2 of 0.31. Higher canopy cover and *Abies* sp. live BA were associated with greater fine fuel loads (Fig. 5). Fine fuel loads were near 30 Mg ha^{-1} for plots that exceeded 52% canopy cover. The lowest fine fuel loads occurred in plots that had $\leq 13.1 \text{ m}^2 \text{ ha}^{-1}$ of *Abies* sp. live BA, with a further distinction based on canopy cover. These plots averaged 7.7 and 11.9 Mg ha^{-1} for those with $\leq 20\%$ and $>20\%$ canopy cover, respectively (Fig. 5). Plots that had $\leq 52\%$ canopy cover and $>13.1 \text{ m}^2 \text{ ha}^{-1}$ of *Abies* sp. live BA had intermediate fine fuel loads, averaging 20.4 Mg ha^{-1} .

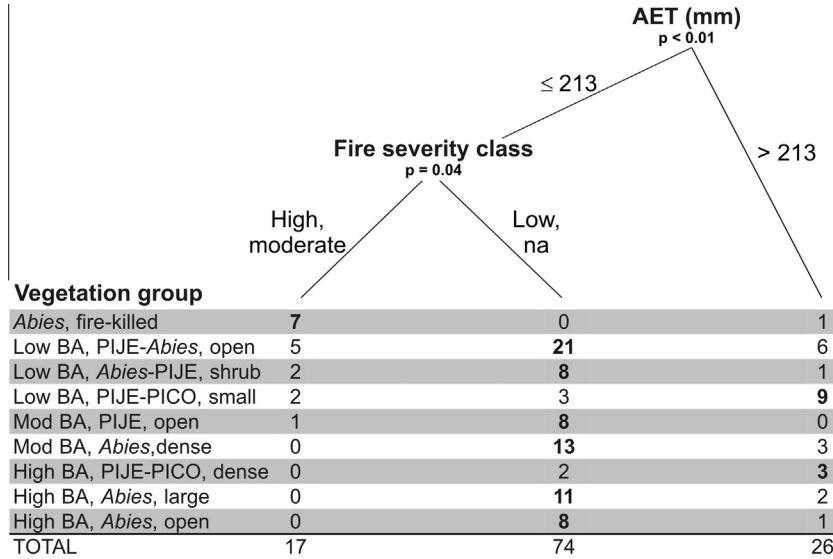


Fig. 4. Conditional inference tree output explaining the influence of identified variables on the distribution of vegetation groups. The table below identifies the number of plots in each terminal node, and their distribution among the nine vegetation groups. Individual groups are named based on live basal area (BA), dominant tree species (PIJE-*Pinus Jeffreyi*; PICO-*P. contorta v. murrayana*), and the most salient structural characteristic (“small” and “large” refer to average tree size). Numbers in bold emphasize the terminal node(s) where the majority of observations for each vegetation group lie. P-values are from a Monte Carlo test of the partial null hypothesis of independence between a single predictor variable and the response variable (vegetation group occurrence). AET stands for actual evapotranspiration. Fire severity class is defined by Miller and Thode (2007), and “na” indicates fire severity information was not available.

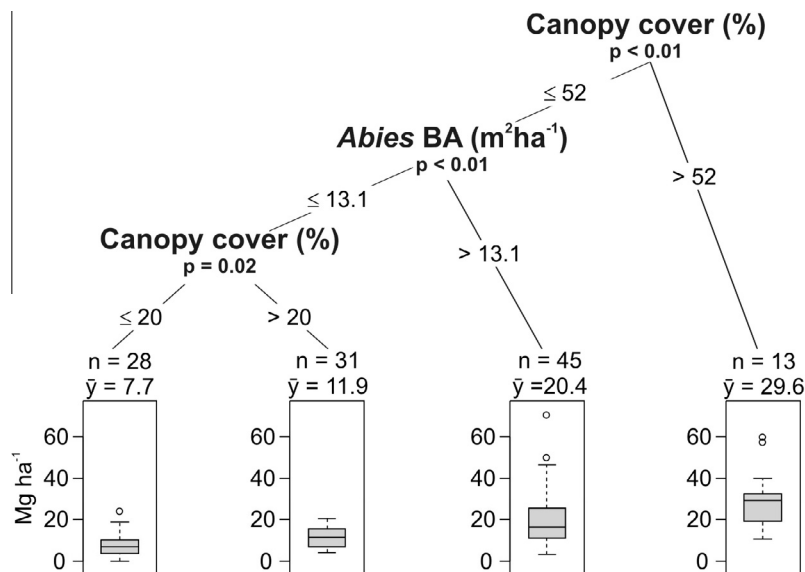


Fig. 5. Conditional inference tree output explaining the influence of identified variables on total fine surface fuel loads (sum of litter, 1, 10, and 100 h) based on initial plot measurements. The Box and Whisker plots at each terminal node show the distribution of fine surface fuel loads (Mg ha^{-1}) for field plots resulting from the preceding splits. The number of field plots (n) and mean fine surface fuel load (\bar{y}) corresponding with each terminal node is also reported. P-values are from a Monte Carlo test of the partial null hypothesis of independence between a single predictor variable and the response variable (fine fuel load).

4. Discussion

Historical reconstructions are often used to infer more natural fire-vegetation dynamics across forest-dominated landscapes (e.g., Romme, 1982; Swetnam et al., 1999). For dry forests in particular, several studies have robustly described historical vegetation patterns across landscapes (Hessburg et al., 1999, 2007; Collins et al., 2015; Stephens et al., 2015). One of the common attributes emphasized in these studies is variability in vegetation structure and composition. However, due to the incomplete nature of historical reconstructions (Swetnam et al., 1999) these studies lack sufficient detail to comprehensively characterize this variability. Furthermore, historical reconstructions offer little to no information on surface fuel conditions. These limitations make it difficult to explore links between vegetation structure/composition, fire, fuels, and landscape attributes (e.g., topography, moisture availability). The field-based vegetation and surface fuel information from our two study areas provides some of the detail that is lacking from historical studies. Given the duration of the natural fire programs in our two study areas (>40 yr) and the fire frequency experienced over this period (Fig. 1) the range in vegetation and surface fuel conditions we present can be used as a reference for landscape-level restoration in similar forest types. These conditions cannot replace those derived from historical reconstructions; instead they can be used to compliment historical reconstructions by filling information gaps.

Our assertion that Illilouette Creek and Sugarloaf Creek basins are contemporary reference sites warrants further discussion. Although both areas have experienced recent fire frequencies that were similar to historical (pre-fire suppression) frequencies (Collins and Stephens, 2007), they were impacted by a prolonged period of fire exclusion that predated the onset of the natural fire management programs. During this period there was considerable tree recruitment that exceeded recruitment levels in the previous 200 years (Collins and Stephens, 2007). This means that the vegetation structure and composition captured by our field plots likely does not approximate historical conditions. A similar argument could be made for the surface fuel load estimates from our plots. Although, given the number of plots that burned two or more times prior to our measurements (Fig. 1, Table 1), surface fuels that accumulated during the fire exclusion period were probably substantially reduced. We submit that despite being departed from historical conditions, the vegetation structure and composition in our study areas represent a functional landscape-level interaction between fire and vegetation; one in which fire effects are variable at multiple spatial scales, but fall within the range of historical fire effects for these forest types (Collins et al., 2009; Mallek et al., 2013). This is different from the range of fire effects observed in mixed-conifer forests throughout much of the Sierra Nevada, where fire suppression and exclusion practices continue to dominate. These areas have experienced much greater stand-replacing patch sizes and proportions relative to our understanding of historical fire patterns (Miller et al., 2012; Mallek et al., 2013). Beyond the “restored” fire characteristics in our study areas, independent tree mortality data associated with a multi-year drought in the Sierra Nevada indicated substantially lower tree mortality in one of our study areas (Illilouette) relative to surrounding areas (Boisramé et al., 2016). Taken together, the intact contemporary fire regime and the lower incidence of drought-related mortality suggest that our study areas exhibit the type of resilience that is often associated with reference sites (e.g., Stephens et al., 2010).

The range in vegetation structure and composition across the nine vegetation groups identified from our analysis demonstrate considerable variability across both landscapes studied (Fig. 2, Table S1). Our results suggest that site productivity, as indicated

by AET, and previous fire severity contribute to this variability (Fig. 4). Neither of these are particularly novel findings; the influence of site productivity/moisture availability on vegetation composition and structure has been shown in previous studies (Lydersen and North, 2012; Kane et al., 2015), as has the relationship between fire severity and forest structure (e.g., Miller and Urban, 1999; Kane et al., 2013). What is more interesting about our findings is: (1) the high range in vegetation conditions that occurs in areas with so much recent fire activity, and (2) the general inability to explain what is driving the occurrence of these different vegetation conditions across both landscapes.

Regarding point (1) above, a common assertion often made about dry forests under intact frequent fire regimes is that they were predominately low tree density, dominated by large trees and very few small trees (e.g., HFRA, 2003). This has been demonstrated in numerous studies using robust historical datasets (e.g., Brown et al., 2008; Scholl and Taylor, 2010; Taylor, 2010; Collins et al., 2015). We certainly found evidence of this in four of the nine vegetation groups (PIJE-ABIES OPEN, ABIES-PIJE SHRUB, PIJE OPEN, and ABIES OPEN), which collectively averaged 113 trees ha⁻¹ and 25% canopy cover, and accounted for just over half of all plots. It is intriguing that the other five vegetation groups have such disparate vegetation structures, ranging from no live trees (ABIES FIRE-KILLED) to on average over 600 trees ha⁻¹ (PIJE-PICO DENSE; Fig. 2), and occur in close proximity (Fig. 3). The ranges in tree density, basal area, and canopy cover across our study areas were even greater than those reported in mid-elevation mixed conifer forests across a wide range of sites with relatively restored recent fire activity (Lydersen and North, 2012). This suggests that vegetation composition and structure in upper elevation mixed-conifer forests with intact fire regimes are incredibly complex, which also been demonstrated in the northern U.S. Rocky Mountains (Belote et al., 2015).

Regarding point (2) above, anecdotal observations from these areas and findings from previous work (Lydersen and North, 2012; Kane et al., 2013, 2015) indicate that vegetation composition and structure in areas with relatively intact fire regimes is driven by complex interactions between fire characteristics (severity, time since, frequency), topography, and moisture availability. Despite having included these variables in our statistical analysis, we only found modest explanation of observed variability in vegetation composition and structure. Perhaps the scale of our analysis, which consisted of discrete, relatively small footprint plots (500 m²) and 30 or 270 m derived topographic and fire variables, is not the most appropriate scale for investigating drivers of variability at the scales studied (1500 and 600 ha for Illilouette and Sugarloaf, respectively). This may be particularly relevant for AET and climatic water deficit, which given their reliance on coarse soil maps do not exhibit a large range in values across our study areas (Table 1). Another possibility is the interactions between vegetation, fire, topography, and moisture availability, combined with stochastic factors such as seed availability and favorable climate for tree establishment (Collins and Roller, 2013), are too complex to capture in approximately 120 plots spread across two study areas. More plots, or an explicit coupling of existing plots with small footprint remote sensing (e.g., Light Detection and Ranging), may be necessary to better explain what is driving observed variability across these landscapes (Kane et al., 2014).

There are a couple concerns related to our study areas and our sampling within them that potentially limit the applicability of our findings to broader restoration efforts in dry forests. First, these areas are somewhat unique relative to much of the montane forests throughout the Sierra Nevada (North et al., 2015). The elevational range of our field plots (Table 1) is generally considered transitional between lower and upper montane forests (Fites-Kaufman et al., 2007). As a result, vegetation in Illilouette and

Sugarloaf basins contains attributes of both zones, which likely influenced the high degree of compositional variability observed (Fig. 2). Given that a majority of restoration needs tend to be in the lower montane zone (North et al., 2012) one could question how informative our vegetation and surface fuel characteristics are for forest restoration. Our response to this is that while the specific values for vegetation structure/composition and fuel loads we report may not be directly applicable, the range in vegetation structure and surface fuel conditions can be used as bounds for landscape-level forest restoration.

A second concern related to applicability of this work is the use of relatively small footprint plots (500 m²) to represent vegetation and surface fuel conditions across large landscapes. Despite having a relatively large number of field plots (n = 117) the spatial coverage across our two study areas is incomplete. Deriving more complete vegetation and surface fuel information across these areas would require coupling our field observations with remotely sensed vegetation and/or biophysical information (e.g., Ohmann and Gregory, 2002; Su et al., 2016). This type of analysis is beyond the scope of the present study. That said, a comparison of total versus sampled proportions in different mapped vegetation classes across our study areas indicated that our sampling was reasonably representative (Table 2). Note, this comparison was based on detailed current vegetation maps (0.5 ha minimum mapping unit, available from <https://irma.nps.gov/Portal>) generated for each National Park and excluded the following vegetation classes from the calculation of total proportions: meadow/wetland, barren/primary vegetation, sparse subalpine conifer, and water. The rationale for removing these classes is that fire is not a major driver of vegetation dynamics, which is also why our sampling intentionally excluded these areas. Given that our field sampling captured the major vegetation classes fairly well our findings can be scaled-up to the landscape with reasonable confidence.

On average fine surface fuel loads for all of our vegetation groups: 16.1 Mg ha⁻¹ (Table S1), were clearly lower than those reported for untreated mixed-conifer forests in the Sierra Nevada: 35–50 Mg ha⁻¹ (Stephens and Finney, 2002; Knapp et al., 2005; Stephens and Moghaddas, 2005; Lydersen et al., 2015). This suggests a uniform reduction in surface fuels associated with the re-establishment of the natural fire regime in our study areas. Given this, it was rather surprising that no fire variables were identified as having a significant influence on initial fuel loads or their change over time. Our initial fuel measurements included 31 plots that burned the previous year, and these were re-measured 8–10 years later. Additionally, recall that 14 plots burned between initial and re-measurement. re-measurement of these plots was conducted 6–7 years post-fire. Given the range of times since fire and measurement sequences (Table 1), we expected that time since fire would have been identified as a strong predictor of change in surface fuel loads. Clearly fire has an immediate impact on surface fuels via

consumption; however, what is apparent from our findings is the signal of the initial reduction may not be predictable or consistent over time. We also expected fire severity to be a predictor of surface fuel loads. This expectation is based on the assumption that higher fire severity would generate greater relative amounts of both fine and coarse dead material as fire-killed trees lose branches and ultimately fall. In fact, average coarse fuel loads for the *ABIES* FIRE-KILLED group more than doubled between initial and re-measurement (Table S1). However, the large range of change in coarse fuels for this and other vegetation groups (Table S1) likely contributed to the lack of statistical importance in the regression tree analysis. It is possible that our sampling approach, which inventoried fine fuels on a total of 6–12 m and coarse fuels on 33 m per plot, was not intensive enough to capture actual surface fuel conditions (Sikkink and Keane, 2008). However, this sampling intensity has been used previously to accurately capture surface fuel changes following forest restoration treatments across a wide geographic gradient (Stephens et al., 2009). Furthermore, it is not clear that at the scale of our plots (0.05 ha) simply adding more transects within the plot footprint would result in more accurate estimates. Another, more process-based explanation for why fire severity and time since fire were not identified as significant predictors of surface fuel loads is that surface fuels may be characterized as a dynamic equilibrium in an intact fire regime (sensu Bonnicksen and Stone, 1982); one in which fire not only consumes fuel, but it continually changes fuel characteristics as fire-killed material moves from the live to the dead fuel pool and ultimately gets deposited on the surface.

Given the observed variability in vegetation conditions in our plots, it should not be surprising that vegetation structure and composition variables explained the observed surface fuel loads (Fig. 5). This assertion is based on the potential for different fuel inputs depending on vegetation structure and composition, irrespective of fire effects or time since fire. The two variables identified in our analysis both have distinct, but related contributions for surface fuel inputs. Greater canopy cover being associated with higher fine surface fuel loads is likely related to greater potential for deposition of needles and fine branches. Similarly, in areas with moderate or low canopy cover, the association of *Abies* sp. BA with higher surface fuel loads is likely related to the generally denser branching patterns and finer branch structures of *Abies* species relative to the pines present (Fry and Stephens, 2010; van Wagtenonk and Moore, 2010; Lydersen et al., 2015).

5. Summary and management implications

Increasing heterogeneity in vegetation structure and composition is a common objective for restoration programs in dry conifer-dominated landscapes in the western U.S (North et al., 2009; Hessburg et al., 2016). There is guidance for restoring heterogeneity at the stand-level, which involves varying tree spacing and clumpiness (e.g., Churchill et al., 2013). There is less clarity, however, with regard to restoring landscape-scale vegetation conditions. This is largely due to the limited available information on vegetation across landscapes with intact disturbance regimes. Our results quantify vegetation structure and composition for nine distinct vegetation groups. The range of vegetation conditions across these groups demonstrates that these areas with restored fire regimes are highly heterogeneous landscapes. Four of the vegetation groups, containing over 50% of the total plots, fit the open, low tree density model described by many dry forest historical reconstructions. However, two groups (*ABIES* DENSE, *PIJE*-*PICO* DENSE) were much denser and these groups comprised nearly 20% of the plots. Another group was comprised of nearly all dead trees that were killed in small patches of stand-replacing fire (Collins and

Table 2

Total proportion of area and proportion sampled (as represented the number of field plots) by aerial-photo-interpreted vegetation classes. Total area is based on the entire extent of both Illilouette Creek and Sugarloaf Creek basins combined, minus meadow/wetland, barren/primary vegetation, sparse subalpine conifer, and water classes. Naming of vegetation classes is based on dominant species (*PIJE*-*Pinus jeffreyi*; *PICO*-*P. contorta v. murrayana*) or species groups.

Vegetation class	Total	Sampled
<i>PIJE</i> woodland	0.02	0
Hardwood/riparian	0.05	0
Shrub	0.08	0.02
<i>PIJE</i> -shrub	0.11	0.07
<i>PIJE</i> - <i>Abies</i>	0.12	0.15
<i>Abies</i> - <i>Pinus</i>	0.16	0.09
<i>PICO</i>	0.16	0.25
<i>Abies</i>	0.30	0.42

Stephens, 2010), which made up 7% of all plots. The remaining 23% had intermediate tree densities. These proportions are quite similar to those described in a large-scale (>10,000 ha) Sierra Nevada lower montane forest reconstruction (Stephens et al., 2015), in which over 70% of the area was open, low density forests, 15% dense forests, 10% intermediate density forests, and 3–6% of the area affected by stand-replacing fire. The occurrence and distribution of these distinct groups across the two landscapes suggest that vegetation conditions under intact fire regimes may be even more heterogeneous than commonly represented in current restoration strategies (e.g., USDA-FS, 2013). The range in conditions we described potentially provides a suite of habitat features for several wildlife species requiring distinct and often conflicting structures and compositions (e.g., White et al., 2013). Rather than restoring currently departed dry forest conditions to any one of these vegetation conditions, our results suggest a restoration strategy could seek to develop several distinct conditions, using roughly approximate proportions similar to those we present. This is not to suggest that the convergence of two different studies on the approximate proportions in different forest structural classes (50–70% low density, open; 15–20% high density, closed canopy; 5–10% early seral in small patches) is a blueprint for designing landscape restoration projects in dry forests. Rather, these proportions could be a starting point from which to apply and monitor different landscape restoration strategies.

Fine surface fuel loads in our study sites were positively associated with canopy cover and proportion of shade-tolerant tree species. These are the same variables that were connected to greater fine fuel loads in a long-fire suppressed mixed-conifer forest in the central Sierra Nevada (Lydersen et al., 2015), as well as in an old-growth Jeffrey pine-mixed-conifer forest in Baja California, Mexico (Fry and Stephens, 2010). Interestingly, these two characteristics have also increased considerably in many dry forests as a result of fire suppression and exclusion (Parsons and Debenedetti, 1979; Hessburg et al., 2005; Collins et al., 2011). Collectively, these findings suggest that there is potential for increased surface fire behavior as dry forests infill with greater proportions of shade-tolerant tree species, independent of the exacerbated vertical (ladder fuel) and horizontal arrangement of canopy fuels associated with infilling (Agee and Skinner, 2005). As such, in areas on the landscape where open forest structure is the desired condition for restoration, shifting species composition towards pine species and reducing canopy cover is prudent not only for achieving forest structural objectives, but also for modifying subsequent surface fuel inputs.

Acknowledgements

We sincerely thank the follow people for their assistance collecting field data: Christal Niederer, Zev Balsen, Gary Roller, Chris Dow, Keith Arnold, Shane Fairchild, Amy Foo, Carolyn Richter, and Megan Seymour. Shane Fairchild helped with data compilation and error checking. Jay Miller provided much of the fire severity data used in our analysis. This project was funded by the USDA/USDI Joint Fire Sciences Program. We thank the staff at Yosemite and Sequoia-Kings Canyon National Parks for their continued support of this research.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2016.09.010>.

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