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Prescribed fire and natural recovery produce similar long-term patterns of change in forest structure in the Lake Tahoe basin, California

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ABSTRACT

In the context of concerns about degrading forest health, increasing fire activity, and practical restoration alternatives, we analyzed 20 years of data on the response of mixed conifer forest stands in the Sierra Nevada, California to two distinctly different management approaches. Specifically, we used a Bayesian hierarchical modeling approach to evaluate the direction and magnitude of changes in forest structure and fuel variables in areas treated with prescribed fire as well as untreated forest stands in the Lake Tahoe basin. Counter to many regional studies, our results indicated that treated and long-unaltered, untreated areas may be moving in a similar direction. Treated and untreated areas experienced declines in tree density, increases in the size of the average individual, and losses of surface fuels in most size classes. The number of large trees increased in untreated areas, but decreased in treated areas. Our results suggested that untreated areas may be naturally recovering from the large disturbances associated with resource extraction and development in the late 1800s, and that natural recovery processes, including self thinning, are taking hold. Given the high cost and broad extent of treatment required to restore forest health, management approaches that promote naturally recovering landscapes may complement ongoing and planned fuel reduction treatments. Deliberately managing for natural processes to proceed unimpeded may also be important for maintaining or increasing forest heterogeneity, resilience, and biodiversity.

1. Introduction

Increasing wildfire frequency, size, and associated economic costs under a warming climate are growing concerns for resource managers and the public alike (Schoennagel et al., 2017). In the Sierra Nevada of California, past land disturbance and a century of fire suppression have been implicated as the principal drivers of present-day forest conditions (Dolanc et al., 2014; Knapp et al., 2013; Stephens and Ruth, 2005; Stevens et al., 2016). These factors may compound the climate-driven increase in susceptibility of mixed conifer forests in the region to disease- and drought-caused mortality (Asner et al., 2016) and fire severity (Parks et al., 2014). Accordingly, urgent action to increase the pace and scale of fuels treatment has been recommended to restore forest health and resilience, and to mitigate the risk of undesirable wildfire events over extensive areas (North et al., 2012; SNC, 2017).

Management actions that move forests towards pre-settlement structural conditions are expected to increase fire resilience, and restoration to reduce tree density is the management recommendation for large portions of the Lake Tahoe basin (Taylor et al., 2014). This view is not limited to the Lake Tahoe basin as millions of hectares of forest in the western United States may need restoration to increase resilience to fire, insects, and drought (Stephens et al., 2016). The recommended restoration methods involve fuel treatments that reduce tree density and surface fuel loads using mechanical tree removal and/or fire management (Brown et al., 2004; Agee and Skinner, 2005), and studies link these structural treatments to different measures of increased ecological resilience (Hood et al., 2016; Stevens et al., 2014; Reinhardt et al., 2008; Loudermilk et al., 2017). Although forest restoration and fuel treatments that focus on the retention of large trees and removal of small trees (i.e., 'ladder' fuels) and surface fuels can be effective in reducing overall tree mortality and fire severity in this region (Brown et al., 2004; Safford et al., 2012), treatment effectiveness decays over time and routine re-treatment is often necessary (Kalies and Yocom Kent, 2016; Reinhardt et al., 2008; Stephens et al., 2012; Vaillant et al., 2013). The combination of transient treatment effects, variability in the effectiveness of different treatment methods (Kalies and Yocom Kent,

Abbreviations: CWD, coarse woody debris; BCI, Bayesian credible interval; MCMC, Markov chain Monte Carlo

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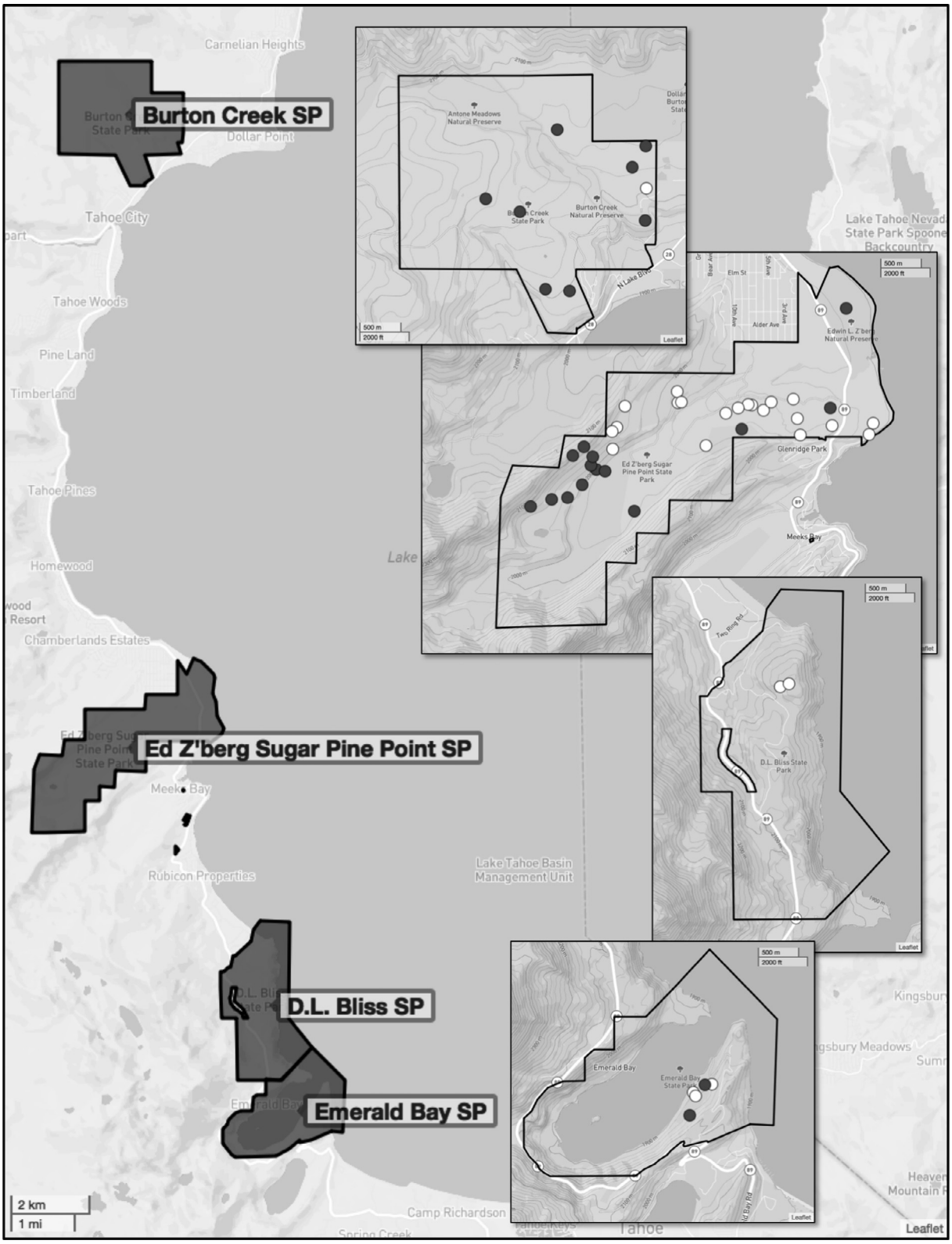

Fig. 1. Study area. The study area includes four state parks on the west shore of Lake Tahoe: Burton Creek, Ed Z'berg Sugar Pine Point, D. L. Bliss, and Emerald Bay state parks. Untreated (control) and treated (burned) plots are shown in dark gray and white circles, respectively.

2016; Martinson and Omi, 2013; Prichard et al., 2010), and operational and funding constraints (North et al., 2015) limits the practicality of frequent treatments at the landscape scale; and there is growing recognition that fuels reduction alone may not be able to effectively alter regional wildfire trends (Schoennagel et al., 2017).

Prescribed natural regeneration (Clewell and McDonald, 2009) is often ignored as a viable land-use option (Chazdon and Uriarte, 2016), but deliberately allowing natural processes to proceed unimpeded in some areas is one method employed as part of California State Parks' overall forest restoration management strategy that includes prescribed

burning and more intensive defensible space treatments to protect life and property. Forest structure develops after past disturbance in a generally predictable sequence towards increasing complexity (Oliver and Larson, 1996; Franklin and Van Pelt, 2004), the rate of which determines its resilience (Larson et al., 2008; Halpern, 1988), and self thinning results in fewer, larger trees due to the inverse relationship between plant size and frequency (Enquist and Niklas, 2001). In this context, empirical measures of how forest structure is currently changing in the absence of active treatment are necessary to weigh management tradeoffs, to make efficient use of limited resources to apply active management in the highest priority areas, and to help refine inputs to models that are used to predict future forest and fire behavior conditions.

An important driver of forest stand development dynamics is past disturbance (Oliver, 1980). Mixed conifer forests throughout the Sierra Nevada, including the Lake Tahoe basin, were substantially impacted by logging, grazing, and disruption of the natural fire regime that began in the mid-1800s, resulting in near complete landscape alteration by the early 1900s (Beesley, 2004; Elliott-Fisk et al., 1996; Leiberg, 1902; Strong, 1984) and a 95% reduction of old-growth forest in the basin (Barbour et al., 2002). Sudworth (1900) and Leiberg (1902) noted that nearly all accessible timber had been logged in the Tahoe area by the beginning of the twentieth century, that large portions of the landscape had been denuded, and that sheep grazing and annual fires set by sheep ranchers had removed a half-century of conifer regeneration. Beesley (2004) equated this impact to a glaciation event in terms of magnitude of change. Fulé et al. (2012) described similar effects of industrialized society across the range of Jeffrey pine forests starting in the mid-1800s, which resulted in a change in forest structure towards dense stands of young trees. Dense and even-aged regrowth, primarily by California white fir (*Abies concolor var. Lowiana*; hereafter white fir), characterized much of the basin after these decades-long disturbance pressures declined (Elliott-Fisk et al., 1996; Strong, 1984). These past disturbances may have contributed to currently elevated tree densities compared to the early 20th century (Dolanc et al., 2014; McIntyre et al., 2015). Given this complex history, current trajectories of forest stand development under a suite of forest management approaches is important to guide future decisions because generalizations that fire hazard in the Sierra Nevada will increase in the absence of active fuel reduction treatment (Stephens and Moghaddas, 2005; Stephens et al., 2012; Collins et al., 2013) are not adequately considering landscapes with different management histories, elevations, and moisture regimes (Rother and Veblen, 2016). Indeed, stands in some western forests may be adapting to changing ecological and climatic conditions (Rother and Veblen, 2016; Schoennagel et al., 2017). Because naturally recovering forests may be proceeding more rapidly through forest stand development due to increasing temperatures and extended growing seasons (Pretzsch et al., 2014), natural recovery may be a cost-effective approach to consider as part of large scale forest restoration (Birch et al., 2010; Chazdon and Guariguata, 2016; Nunes et al., 2017).

In this context, we evaluated the response of mixed conifer forest in the Lake Tahoe basin to two distinctly different management approaches: prescribed fire (treated) and no treatment (untreated). Specifically, we evaluated the direction and magnitude of changes in forest structure and fuel variables in treated and untreated forested areas over a 20-year period. We used data generated by the California State Parks Lake Tahoe basin long-term prescribed fire monitoring program and Bayesian hierarchical modeling to estimate parameters related to the state of these forests under the two different management approaches. The Bayesian framework requires that all unobserved quantities be treated as random variables, which allows all inference to be based on probabilities that are comparable (Hobbs and Hooten, 2015). This makes Bayesian inference much more interpretable than traditionally applied frequentist methods, for which significance tests can be difficult to interpret and easily misleading (Johnson, 1999). Our primary goal was to provide a contemporary and rigorous modeling and inferential framework for informing decisions about mixed conifer forest management.

2. Methods

2.1. Study area

This study was conducted on California State Parks lands on the west side of the Lake Tahoe basin, which have not been grazed or commercially logged for at least 50 years under California State Parks management (Fig. 1). Lake Tahoe is a large (496.2 km^2), high elevation (1897 m) lake in the Sierra Nevada. The lake sits in a basin encompassed by the Pacific Crest to the west and the Carson Range to the east. The border between California and Nevada divides the lake, which is ~30 km southwest of Reno, Nevada and 125 km northeast of Sacramento, California. Research plots included in this study were located in Burton Creek, Ed Z'berg Sugar Pine Point, D. L. Bliss, and Emerald Bay state park at elevations ranging from 1909 m to 2103 m. Tree species in the Sierran mixed conifer forest of these parks include white fir, red fir (*A. magnifica*), Jeffrey pine (*Pinus jeffreyi*), ponderosa pine (*P. ponderosa*), sugar pine (*P. lambertiana*), lodgepole pine (*P. contorta*), and incense-cedar (*Calocedrus decurrens*).

Soils in the study area are generally of the Meeks-Tallac association with a few plots in the Cagwin-Toem association (USDA, 2007). Soils in these associations are geologically young and poorly developed. These soils are generally well- or excessively-drained, have coarse texture composed of gravel or sand, and contain small amounts of organic material (Stephens et al., 2004; USDA, 2007). Slopes across the study area average less than 30%. Climate is Mediterranean with warm, dry summers and cold, wet winters, and an average annual temperature range between -2 °C in January and 16 °C in August (Beaty and Taylor, 2008). Most of the mean average annual precipitation of 799 mm falls as snow during the cold winter period between November and April; very little precipitation occurs during the growing season (WRCC, 2016).

2.2. Fuels treatment

California State Parks manages 2749 ha in the Lake Tahoe basin and has had an active prescribed fire program since 1984. A fire monitoring program to track short- and long-term fire effects was established in 1992 based on guidelines and protocols in the National Park Service Fire Monitoring Handbook (USDI, 2003). The short-term objectives of the monitoring program were to reduce fire hazard and increase the mortality of young white fir; the long-term goal was to reintroduce fire as an ecological process and to change stand structure to mimic, as closely as possible, pre-settlement fire regime and forest stand characteristics (Mandeno, 2000).

Prescribed burning was conducted on burn units between September and November from 1992-1997 under burn prescriptions that were developed individually for each unit according to topography, slope, aspect, canopy cover, fuel type, wind direction and speed, accessibility, and smoke considerations. Fire behavior for all burns was characterized as low to moderate intensity with a flaming front that rarely exceeded 0.6 m except for occasional torching in pockets of heavy fuel accumulation and where ladder fuels allowed (Mandeno, 2000). Rate of spread was typically 32–64 km/h. Burn conditions for all units ranged between 25–60% relative humidity, 0–16 km/h wind speed, 2–21 °C, 8–16% fuel moisture content for 1-h, 10-h, and 100-h fuels, and 10–20% fuel moisture for coarse woody debris (CWD). Burn preparation to prevent fire escape included limited lopping and scattering and construction of small burn piles along fire lines, snag removal along fire lines, and clearing around some legacy sugar pine trees. These pre-burn preparations were considered negligible in regards to forest structure or fire behavior within the burn units. Additional detail on the prescribed burn treatments, including

information about treatment objectives, are provided in Stanton and Pavlik (2011).

2.3. Data collection

Forest structure and surface fuel attributes were measured at 50, 50 × 20-m (0.1 ha) plots both before and repeatedly after fuels treatment occurred. Plots were randomly located within potential burn units and in control areas where no treatment was planned. Control areas included a combination of plots specifically established to track changes in the absence of treatment, as well as plots established in preparation for burning, but in which prescribed burning was never implemented. The center line and all four corners of each plot were permanently marked with rebar and labeled metal tags.

Live overstory trees and snags (standing dead trees) > 15 cm diameter at breast height (DBH) were tagged and mapped. The DBH of each stem was also recorded and used to calculate both the Quadratic Mean Diameter (QMD; Curtis and Marshall, 2000) and basal area of live trees on each plot. Prior to analysis, basal area was scaled to $m^2\,ha^{-1}$ and stem counts for live trees and snags were converted to stem densities (stems ha^{-1}).

Surface fuels (i.e., litter and duff, in addition to downed woody debris) were sampled on four 22.9 m random-azimuth transects using Brown's (1974) line-intercept method. Litter (O1 horizon) and duff (O2 horizon) depths were measured every 1.5 m on each transect prior to 2010; starting in 2010, only four measurements of litter and duff depth were made on each transect (i.e., every 3.05 m in order to streamline data collection; Stanton and Pavlik, 2011). To minimize measurement error associated with determining the depth of the boundary between O1 and O2 horizons, litter and duff were combined as a single variable (see below), referred to as fuelbed depth.

Counts of 1-h (0–0.64 cm) and 10-h (0.65–2.54 cm) time-lag fuel classes were recorded over the first 1.8 m, and 100-h (2.55–7.62 cm) fuels over the first 3.7 m, of each transect. The DBH of CWD (1000-h fuels > 7.62 cm) were recorded along the entire transect. Transect-based fuel counts were pooled to the plot level prior to analysis.

Burn severity, a measure of the relative effect of fire on organic matter consumption and soil heating, was measured on treated plots according to Fire Monitoring Handbook protocols (USDI National Park Service, 2003). Severity codes were recorded every 1.5 m along each 15.24 m transect. Prior to analysis, burn severity was standardized (to mean zero, unit variance) and, to facilitate more intuitive interpretations of parameter estimates, reoriented such that values closer to 5 indicate heavily burned areas while values closer to 1 indicate unburned areas.

The initial, baseline (hereafter 'year 0') sample consisted of 24 control (hereafter 'untreated') and 26 prescribed burn (hereafter 'treated') plots (Table 1). Fire monitoring plots, such as the treated plots in this study, are typically used to monitor conditions and gauge retreatment needs at several timesteps post-treatment—e.g., years 1, 2, 5, and 10 and subsequent 10-year intervals (USDI, 2003). Control plots are often set up to measure baseline conditions but, as a result of current national policy, are not consistently revisited, especially when project funding is limited (Lutes et al., 2006). California State Parks' monitoring program was no different; however, an effort was made to resample control plots more regularly starting in years 15 and 20.

Table 1
The distribution of the sampling effort (i.e., numbers of plots visited) by group (control vs prescribed burn) at years 0 (pre-treatment) and 20.

Group[a]	Year 0[b]	20
Untreated (control)	24	12
Treated (prescribed burn)	26	19

[a] Plots in each group occupied broadly similar biophysical settings (~1990 m elevation, 9° slope; σ = 55 m and 6°, respectively).
[b] Baseline sampling began between 1992 and 2000 for plots in the treated and untreated study groups, respectively.

2.4. Fuel load calculations

We followed the calculations described in Brown (1974) to derive fuel loading information. Because slopes, and therefore slope correction factors, are specific individual transects, the computations were made at the transect level before aggregating to the plot and scaling plot means to $kg\,m^{-2}$. The species composition of downed woody debris was not recorded, so we assumed the composite values reported by Brown (1974). Only the 'nonslash' values of the parameters (i.e., for the squared average-quadratic-mean diameters of ground fuels and non-horizontal correction factors) were used. We used the bulk densities reported in FFI (Lutes et al., 2006) to compute duff and litter (and total fuelbed) loads. The fuels categories we evaluated included the mean fine fuel load, which consists of duff, litter, 1-, and 10-h fuels, as well as woody fuels, which consist of 100-h fuels and CWD (*sensu* Keifer et al., 2006). Total mean fuel loads were computed as the sum of fine- and woody-fuel loads.

We report both counts and fuel loads because we felt uneasy about including fuel loads alone. Thoroughly modeling fuel loads would require more extensive calibration data (linking counts to biomass) than exist for our specific project area and would have required adding an observation model to the full Bayesian network for fuel-related variables. Nearly all of the steps described in Brown's (1974) fuels calculations carry significant assumptions (e.g., the exact bulk density of fuels, the exact species composition and diameter of fuels, etc.). To model fuel loads, we were forced to assume that the conversion of counts to loads is perfect and has no uncertainty. Of course, this is a heroic assumption. Because we have no assessment for errors in calibrating counts to loads, the inferences associated with fuel loads are likely to be excessively optimistic.

2.5. Summary statistics

Descriptive statistics were generated to provide contextual information against which statistical inference (described below) could be made. Specifically, we generated summary statistics related to community composition, and used the correlation coefficient, r, to evaluate the linear relationship among several response variables. All data preparation and development of summary statistics (described below) were done in the R statistical environment (v3.3.1; R Development Core Team, 2008).

2.6. Bayesian hierarchical models

We used Bayesian hierarchical models for inference and to derive parameters and other quantities of interest. Importantly, baseline conditions between treated and untreated plots differed subtly, likely because fire managers—for reasons related to fire safety and goals of ecological restoration—may have selected plots to burn that were dominated by fewer and larger trees. This feature of the study design, as well as the need to control for burn severity as an additional factor on burned plots, precluded a direct comparison of treatment and control groups. As a result, models were specified and fit independently for each study group and associated dataset. Because of the sparsity of samples for untreated plots in years 1–10 (Table B.1), in addition to our focus on long-run trends, we included samples only for years 0 and 20 in this analysis.

The same general multilevel (i.e., hierarchical) model structure was applied to each dataset. Examples of the detailed derivation of specific models are provided in Appendix A. A description of each of the variables considered in this analysis and information about the probability distributions assigned to specific parameters, can be found in Table B.2

or by referring to the code developed for each dataset and variable (appended along with diagnostics in Appendix C).

We model the observations tied to a given forest structure or fuel variable as

$$g(\beta_{0jk},\boldsymbol{\beta},\mathbf{x_{ijk}}) = \beta_{\mathbf{0jk}} + \boldsymbol{\beta}\mathbf{x_{ijk}} \tag{1}$$

$$\beta_{0jk} \sim \text{normal}(\beta_{0k},\varsigma_{jk}^2) \tag{2}$$

$$\beta_{0k} \sim \text{normal}(\beta_0,\varsigma_k^2) \tag{3}$$

$$\left[\beta_{0jk},\boldsymbol{\beta},\beta_{0k},\varsigma_{jk}^2,\beta_0,\varsigma_k^2,\sigma_{ijk}^2|\mathbf{y}\right] \propto \prod_{k=1}^{n_k}\prod_{j=1}^{n_j}\prod_{i=1}^{n_i}\left[y_{ijk}|g\left(\beta_{0jk},\boldsymbol{\beta},\mathbf{x}_{ijk}\right),\sigma_{ijk}^2\right] \times \left[\beta_{0jk}|\beta_{0k},\varsigma_{jk}^2\right]\left[\beta_{0k}|\beta_0,\varsigma_k^2\right]\left[\beta_0\right]\left[\varsigma_k^2\right]\prod_{p=1}^{m}\left[\beta_p\right]\left[\sigma_{ijk}^2\right] \tag{4}$$

where y_{ijk} is the ith observation for plot j, and where plot j belongs to the collection of plots initially sampled in year k. (As noted in Table 1, baseline sampling was staggered, largely for logistical reasons over several years at the start of the study.) The y_{ijk} are modeled as a linear function (Eq. (1)) of covariates x_{ijk}. In the case of the analysis of untreated plots, the x_{ijk} consist of a single indicator variable for time (year 0 or 20). The models tied to treated plots include the same indicator variable for time and two additional variables—burn severity and the interactive effect of burn severity and time. Thus, the total number of coefficients, m, in the equations above ranges from $m = 1$ in the case of the analysis of untreated plots to $m = 3$ in the case of treated plots. Similarly, the total number of observations, plots, and baseline sampling events (n_i, n_j, and, n_k, respectively) varies according to the analysis—whether of untreated or treated plots. The nested random intercept (our group-level effect), β_{0jk}, varies among plots within initial sampling years (Eqs. (2) and (3)). The variance term σ_{ijk}^2 accounts for all the influences on y_{ijk} that are not included in the process model, $g(\beta_{0jk},\beta,x_{ijk})$, while the variance terms tied to each group-level effect (ς_{jk}^2 and ς_k^2), represent uncertainty arising as a result of variation among plots or initial sampling years, respectively. In other words, we treat the effect of plot (within initial sampling year) as random, an effect that varies randomly according to sources of variation we acknowledge exist, but do not attempt to explain. The full expression for the posterior and joint distribution is provided in Eq. (4). The link function relating the mean, μ, of the response to the linear predictors in the model depended on the nature of the response variable (e.g., log links for counts and logit links for proportions; Table B.2).

We generally followed the recommendations of the Stan Development Team (2016) regarding choice of priors. Models were set up hierarchically such that clusters of parameters had shared prior distributions. For example, we used weakly informative half-Cauchy priors for variance parameters (Gelman, 2006). Though we found some prior information regarding forest structure and fuel conditions (e.g., McIntyre et al., 2015; Stephens, 2000), incompatibilities between forest types, land-use legacies, and time-periods hampered our ability to assign informative priors consistently. As a result, we used non-informative flat priors for population intercept terms and vague priors (the Cauchy) for the remaining regression coefficients (Gelman et al., 2008).

Posterior distributions of parameters were estimated using the No-U-Turn sampler (NUTS, Hoffman and Gelman, 2011) implemented in R via RStan (Stan Development Team, 2016). Control parameters (an initial step-size of 0.01 and a target acceptance rate of 0.99) were provided to avoid divergence of numerical simulations during warmup. A total of four Markov chains were computed for each parameter, with random initial values for all parameters. Each chain ran for 30,000 iterations, with 15,000 warmup samples being used for adaptation and subsequently discarded to produce the final sample – a total of 60,000 draws.

2.7. Model evaluation and inference

Model convergence was confirmed by visual inspection of trace plots, and by the $\hat{R}$ statistic (Gelman et al., 2013). We conducted posterior predictive checks to evaluate the fit of each model to the data (Gelman et al., 2003). Bayesian P values (P_B; Gelman et al., 2003) for two test statistics (the mean and standard deviation) were calculated from the observed data and from replicated data sets simulated from the posteriors. A model shows lack of fit if P_B is close to 0 or 1.

The posterior distribution of the mean, μ, for a given x (e.g., a scenario involving year 0 and untreated plots) was approximated by calculating

$$\mu^z = \beta_0^z + \sum_{p=1}^{m}\beta_p^z x_{p,ijk} \tag{5}$$

at each iteration (indexed by superscript$z$) of the Markov chain Monte Carlo (MCMC) algorithm. Group-level effects (the random intercepts) were dropped from predictions, so the vector μ^z reflects only the fixed effect portion of the model. For reporting purposes, the vector μ^z was transformed back to the response scale using the inverse logit for binomial variables and the exponential function for lognormal and Poisson variables. The distribution of μ^z was evaluated at year 0 and 20 for each model and forms the basis of the inference made from each dataset. In the case of models of forest structure and fuels on treated plots, specifically, we had to choose a fixed value for burn severity at which μ^z could be evaluated. We chose to use the mean burn severity value (approximately zero, after standardization) across all treated plots. The equivariance property of MCMC algorithm means that any quantity calculated from random variables becomes a random variable with its own probability distribution (Hobbs and Hooten, 2015). As such, inference can be made on quantities derived from parameters in addition to the parameters themselves. Because we were interested in the net effect of time on the response of forest structure and fuel variables, we also computed the difference between μ^z's between year 20 and year 0 for each group (again on the response scale).

Finally, the posterior distributions of all parameters and derived quantities were characterized using the median and 50% and 95% Bayesian credible interval (BCI). If the 95% BCI for a given parameter estimate did not include zero, we interpreted this as evidence that the parameter had a statistically significant correlation with a given response variable. Similarly, if the 95% BCI for year 20 vs year 0 differences did not overlap zero, we inferred evidence of a statistically significant shift in the mean.

3. Results

3.1. Species composition

The species composition of trees was broadly similar on untreated and treated plots and over time. With minor exceptions, plots in both groups were dominated by white fir (69–73% of all trees), followed by Jeffrey pine (16–22%). Less dominant constituents of the community included incense-cedar, red fir, lodgepole pine, and sugar pine (with relative abundances in the range of 2–5%; Table 2). Because shade-tolerant tree (white fir, red fir, and incense-cedar) and total tree counts were highly correlated ($r = 0.88$; Figs. B.1–2), we did not evaluate shade-tolerant tree density independently of total tree density. While total tree density and tree densities within individual size class categories (small, medium, large; see Table 3 for specific size-class breaks) were also correlated, we decided to retain these results because fuel treatments focus on reduction of small trees which act as ladder fuels, and retention of large, fire resistant trees (Agee and Skinner, 2005; Safford et al., 2012), and because recent research reports that small trees may be increasing and large trees may be declining across other forested lands in the Sierra Nevada (Dolanc et al., 2014; McIntyre et al.,

Table 2
The (mean) relative abundance of live trees for the five most abundant species at the baseline measurement event and 20 years post-treatment (sorted according to baseline abundance).

Group	Species	Baseline	20 years post-treatment
Untreated	*Abies concolor*	0.69	0.73
	Pinus jeffreyi	0.22	0.16
	Abies magnifica	0.03	0.04
	Pinus contorta	0.03	0.02
	Calocedrus decurrens	0.03	0.05
Treated	*Abies concolor*	0.69	0.69
	Pinus jeffreyi	0.18	0.22
	Abies magnifica	0.05	0.03
	Calocedrus decurrens	0.03	0.02
	Pinus lambertiana	0.03	0.04

2015).

3.2. Model evaluation

Diagnostics for all models indicated convergence. Trace plots showed that the parameters mixed well after warmup (Fig. C.2), which also lead to generally high numbers of effective samples (n_{eff}) relative to the number of iterations and a mixing diagnostic ($\hat{R}$) close to 1 (Fig. C.4). Posterior predictive checks involving Bayesian *P* values (Fig. C.5) did not indicate a lack of fit between model estimates and data. With the exception of the basal area model for treated plots, Bayesian *P* values were between 0.38 and 0.88 for all of the models. In cases in which the test statistics exceeded 0.8, the lack of fit entailed only the variance test statistic, in which the simulated data exhibited higher variance than the observed data.

3.3. Parameter estimates, the posterior distribution of the mean, and derived quantities

Parameters were generally estimated with reasonably narrow credible intervals (see the 'Parameter estimates' section and Figs. C.1 in the diagnostics for each model in Appendix C). With the sole exception of 100-h fuel counts, parameter estimates related to the effect of time on untreated plots were all statistically significant. On treated plots, the interactive influence of burn severity and time was significant for 8 of the 12 variables. The four variables for which this was not the case include snag density and 1-, 10-, and 100-h fuels. However, with the exception of 100-h fuels, the main effects of burn severity and time were statistically significant for these four variables.

The posterior distributions of the mean for each year, as well as year 20 vs year 0 differences are shown for untreated plots in Fig. 2 and treated plots in Fig. 3. Model estimates of the posterior distributions of each forest condition variable indicated that forest structure changes were occurring and, with just one exception (large tree densities), in the same direction in both treated and untreated plots (Figs. 2 and 3). Irrespective of management over a 20 year period, the density of trees (including small- and medium-sized trees) and snags declined, while QMD increased. 1- and 10-h fuel counts declined, and fuelbed depth declined, which are reflected in declining fine fuel load estimates. CWD increased and 100-h fuels were unchanged from baseline condition

Table 3
Medians and 95% Bayesian credible intervals (indicated parenthetically) for the posterior distribution of the mean at each year as well as other derived quantities (i.e., year 0 vs year 20 differences).

Variable	Untreated plots			Treated plots		
	Year 0	Year 20	Difference	Year 0	Year 20	Difference
Tree density (trees × ha^{-1})	538	421	−118	504	268	−235
	(453, 644)	(352, 504)	(−147, −94)	(399, 618)	(212, 330)	(−290, −185)
Quadratic mean diameter (cm)	34	38	3.9	39	47	7.6
	(30, 38)	(34, 42)	(2.9, 5.2)	(30, 54)	(36, 64)	(4.1, 12)
Basal area (m^2 × ha^{-1})	48	47	−1.2	59	38	−20
	(36, 65)	(35, 65)	(−8.2, 6.1)	(34, 111)	(22, 72)	(−52, −0.38)
Cover of understory vegetation	0.19	0.28	0.09	0.081	0.19	0.1
	(0.054, 0.47)	(0.087, 0.6)	(0.031, 0.15)	(0.028, 0.25)	(0.07, 0.46)	(0.041, 0.21)
Small trees ($15 \geq DBH \leq 30$ cm; trees × ha^{-1})	314	204	−109	261	69	−192
	(253, 400)	(165, 262)	(−141, −86)	(127, 451)	(33, 119)	(−333, −93)
Medium trees ($30 \geq DBH \leq 60$ cm; trees × ha^{-1})	186	168	−18	147	136	−11
	(134, 256)	(121, 231)	(−31, −8.6)	(97, 235)	(90, 217)	(−22, −3.2)
Large trees ($DBH \geq 60$; trees × ha^{-1})	13	17	4	37	30	−6.4
	(4, 40)	(5.3, 53)	(0.99, 14)	(18, 73)	(15, 60)	(−14, −2.5)
Snags × ha^{-1}	161	108	−53	115	56	−59
	(98, 280)	(66, 188)	(−94, −32)	(30, 379)	(15, 185)	(−194, −15)
Fine fuels (kg × m^{-2})[a]	9.1	5.4	−3.7	9.3	3.7	−5.6
	(6.5, 13)	(3.8, 7.8)	(−5.8, −2.2)	(7.5, 12)	(2.9, 4.6)	(−7.4, −4.1)
1-h fuel counts	112	48	−64	129	50	−79
	(76, 173)	(32, 74)	(−100, −43)	(79, 196)	(31, 77)	(−120, −48)
10-h fuel counts	32	17	−16	32	24	−8.1
	(23, 50)	(11, 26)	(−25, −10)	(24, 44)	(17, 33)	(−13, −4.6)
Fuelbed depth (cm)	13	7.6	−5	13	5.4	−7.9
	(8.7, 19)	(5.1, 11)	(−8.4, −2.7)	(11, 16)	(4.3, 6.8)	(−11, −5.7)
Woody fuels (kg × m^{-2})[b]	3.1	9.9	6.8	2.5	9	6.4
	(1.8, 5.5)	(5.3, 19)	(3, 15)	(1.3, 4.6)	(4.7, 17)	(2.9, 13)
100-h fuel counts	7.9	9.2	1.3	7.6	8.1	0.45
	(5.3, 12)	(6, 15)	(−0.87, 4.1)	(4.6, 14)	(4.8, 14)	(−1.3, 2.4)
Counts of coarse woody debris	9.6	24	14	7	23	16
	(6.4, 15)	(16, 38)	(8.9, 23)	(4, 13)	(13, 40)	(8.9, 28)
Total fuels (kg × m^{-2})[c]	13	15	2.3	13	15	1.9
	(9.2, 20)	(11, 23)	(0.52, 4.9)	(8.9, 17)	(10, 19)	(−0.41, 4.5)

[a] Fine fuel loads consists of duff, litter, 1-, and 10-h fuels.
[b] Woody fuels consist of 100-h fuels and CWD.
[c] Total mean fuel loads were computed as the sum of fine- and woody-fuel loads.

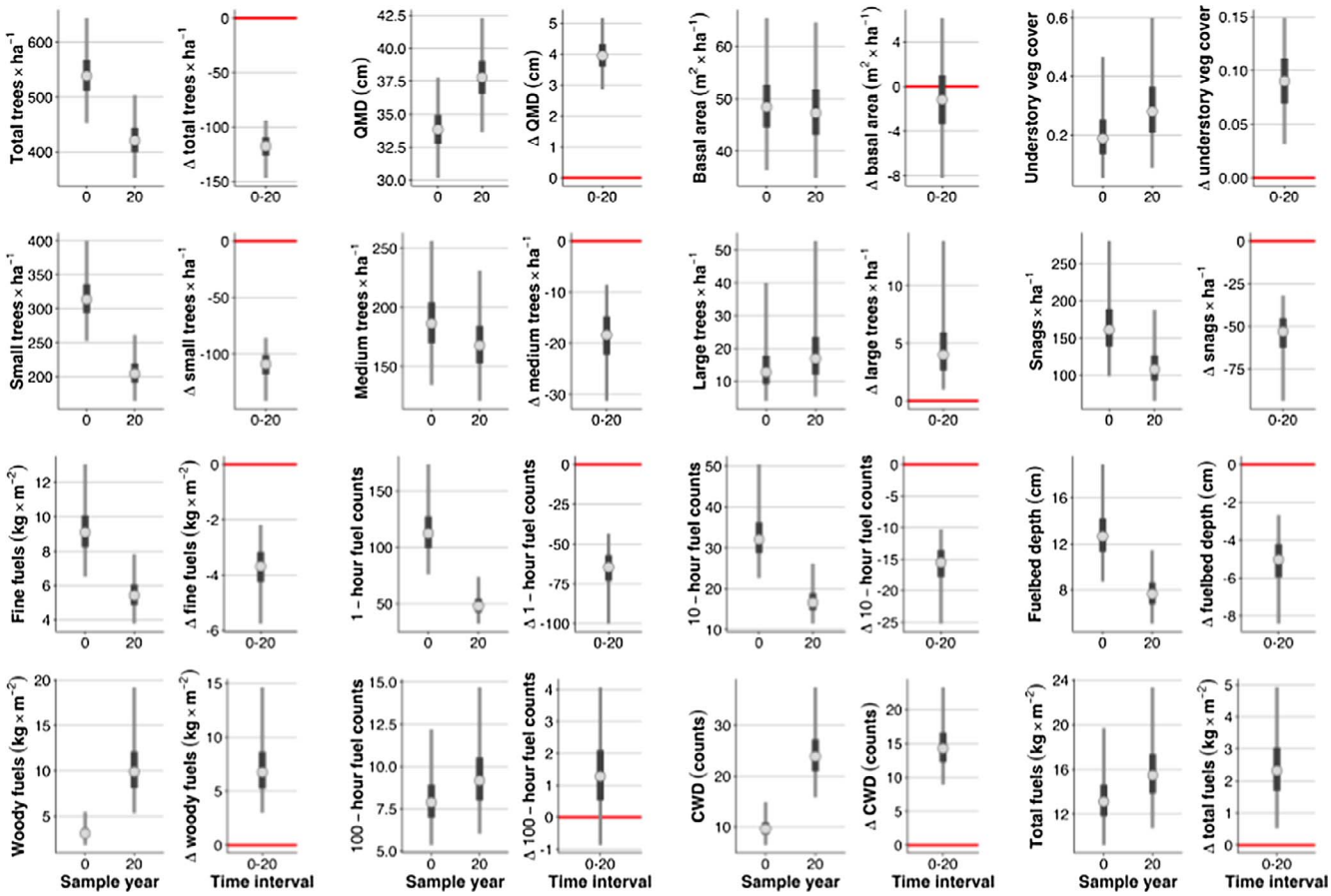

Fig. 2. Status and trends of forest structure and fuels variables in untreated areas. For each variable, the median (grey point) and 50% and 95% Bayesian credible intervals (the thick inner and thinner outer lines, respectively) of the posterior predictive distribution is shown for the mean at years 0 and 20, as well as the difference between year 0 and year 20 means (the left- and right-most panels for a given variable, respectively). The red horizontal line in the right-most panel corresponds to zero (no change). If the uncertainty interval associated with the difference between year 0 and year 20 means does not overlap zero, then— conditional on the data and model—there is a 95% chance that the mean of a given variable changed. All interval estimates were computed using quantiles of the posterior draws with all chains merged. Fine fuel loads consist of duff, litter, 1-, and 10-h fuels, while woody fuels consist of 100- and 1000-h fuels (sensu Keifer et al., 2006). Total mean fuel loads were computed as the sum of fine- and woody-fuel loads. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

under both management approaches. These changes are reflected in woody fuel load estimates that increased under both management practices. The combination of increasing woody fuel loads and declining fine fuel loads resulted in total fuel load estimates that were moving in the same direction but only statistically higher in untreated plots. Basal area was only statistically lower in treated plots. The magnitude of reduction in small trees and overall tree density was greater in treated plots. The only case in which treated and untreated plots appear to be moving in different directions entails large trees: although the changes are relatively modest, untreated plots experienced an increase in large trees while treated plots experienced a decrease. Additional statistics, including medians and 0.025 and 0.975 quantiles for the posterior distributions of each outcome are reported in Table 3.

4. Discussion

Our results add to a growing body of evidence that tree density and fine surface fuel loads are not increasing across all untreated forest land in the Sierra Nevada. Webster and Halpern (2010) also reported a long-term decline in tree density attributed to suppression-related mortality of small white fir trees in untreated plots in Sequoia Kings Canyon National Park (SEKI) that had not experienced fire since the end of the 19th century. Untreated forest plots in SEKI and Yosemite National Park (YNP) experienced a long-term, statistically significant decline in tree density that was attributed to increased mortality of small trees (van Mantgem and Stephenson, 2007). Keifer et al., (2006) observed that surface fuel loads were not accumulating in untreated areas of YNP that had not burned for 40–90 years, and suggested that these areas may have reached a steady state between accumulation and decomposition. Within mixed conifer stands, Keifer et al., (2006) report a long-term decline in litter load in untreated forest stands from 4.6 kg/m^2 to 1.9 kg/m^2. Indeed, recent research in Sierra Nevada forests showed that wildfires resulted in lower percentage and patch size of high severity fire on National Parks as compared to US Forest Service lands (Miller et al., 2012) and forests in the western US with higher levels of protection had lower fire severity ratings (Bradley et al., 2016). Miller et al., (2012) attributed their findings to differences in land management and fire management between US Forest Service and National Park lands. Within National Park lands alone, they found no difference in fire severity between fire management zones where natural ignitions are allowed to burn, and areas where fire is actively suppressed. This suggests land management histories and differences beyond fire management alone should be investigated because disturbed, fire-excluded forests may be more prone to severe wildfires and insect outbreaks than undisturbed fire-excluded forests (Naficy et al., 2010).

These observations are not limited to mixed conifer forest in the Sierra Nevada. Research in second growth coast redwood (*Sequoia sempervirens*) forest under California State Parks management exhibited rapid recovery towards old growth condition through natural regeneration, with declining tree density, increasing species richness, and increasing understory cover (Russell et al., 2014). In a study of forest restoration need across eastern Washington and Oregon, over 25% of

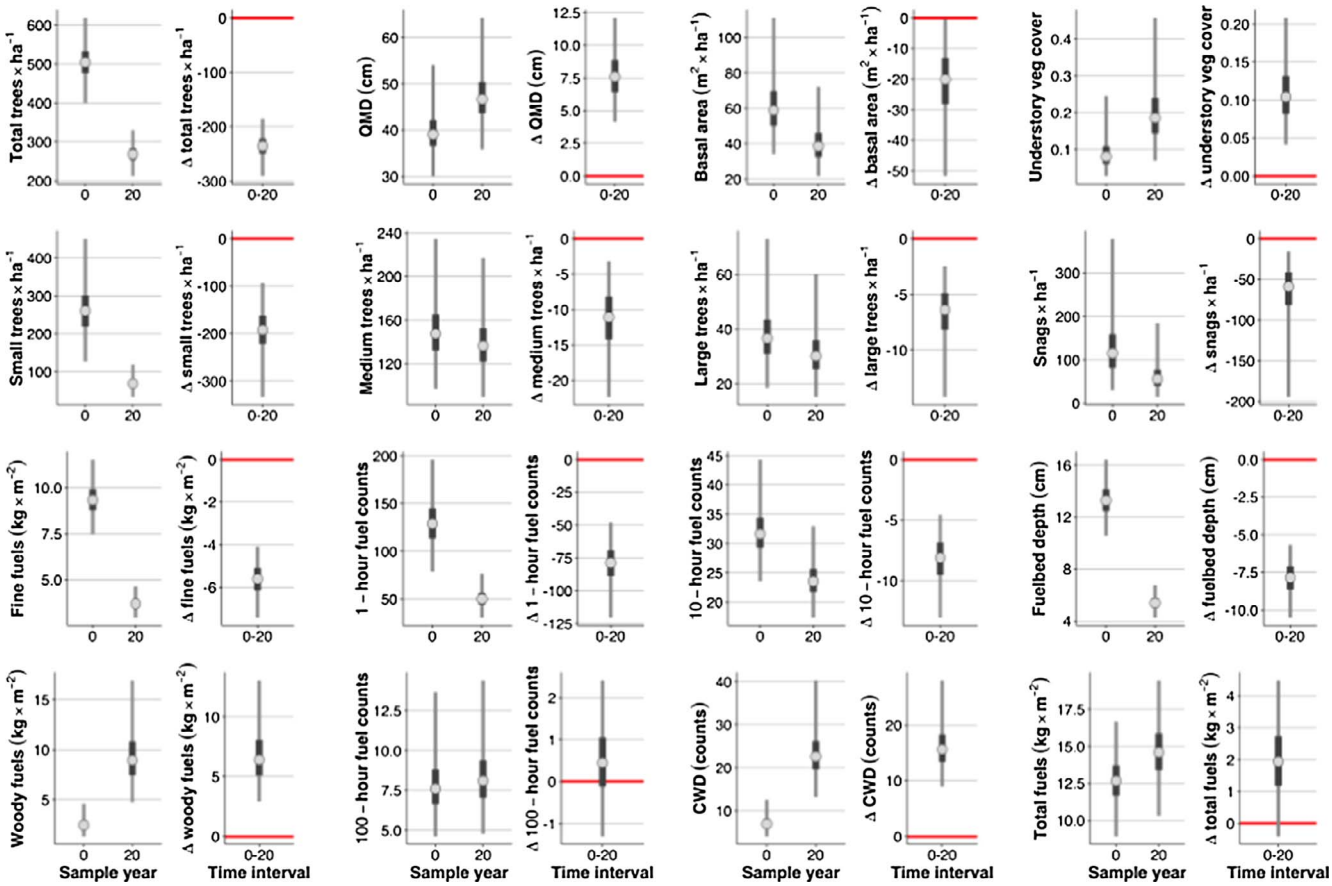

Fig. 3. Status and trends of forest structure variables in treated areas. See the caption for Fig. 2 for a complete description of the contents of each plot.

required restoration could be achieved through transition to later stages of forest stand development through successional processes as western landscapes recover from widespread historic degradation (Haugo et al., 2015). Naturally recovering forests in Central Europe are following allometric rules of declining density with increasing tree size and the pace of recovery has increased since 1960, potentially due to a rise in temperature and an extended growing season (Pretzsch et al., 2014). A global review of forest recovery indicates that simply removing the land disturbance (e.g., decades of logging, grazing, and annual burning to promote livestock forage) is often sufficient for some forestlands to recover on their own, and that more studies are needed that compare the value added of active versus naturally recovering restoration strategies in the same system (Meli et al., 2017).

Structural forest restoration targets based on historic conditions continue to be a valuable tool for land managers (Keane et al., 2009), but changing future conditions may affect the outcomes of management based on these approaches (Flatley and Fulé, 2016; Diggins et al., 2010; Schoennagel et al., 2017), and some researchers now recommend consideration of approaches focused on saving important ecosystem components and processes that might be lost, rather than trying to fit forest structure or fire hazard rating within a specific target range (Reinhardt et al., 2008). Historic forest condition references exist for the Lake Tahoe basin, but estimates vary and there are limitations, especially in regards to small trees. Field-based measurements by George Sudworth in 1899 found tree density ranged from an average of 229 to 235 trees/ha in northern and central Sierra Nevada mixed conifer forests, but these measurements included only trees larger than 30 cm DBH (Stephens, 2000). Estimates based on forest reconstruction for mixed conifer forest in the Lake Tahoe basin ranged from 132 trees/ha (Taylor et al., 2014) to 204 trees/ha (Maxwell et al., 2014). These studies are limited in that trees that died and decomposed completely after the late 1800s would not have been available for the reconstruction, and evidence of small trees in particular may have been missed.

The last fire recorded using fire scars in reconstruction studies in the Lake Tahoe basin is from the 1870s or 1880s (Beaty and Taylor, 2008; Taylor et al., 2014). This conflicts with eye-witness accounts from the turn of the 20th century that describe near complete forest floor impacts from burning and grazing such that the ground was entirely denuded (Leiberg, 1902; Sudworth, 1900). Sudworth (1900) observed that decades of frequent fires started by livestock interests and logging operations resulted in low ground fires because there was so little humus or ground vegetation to carry the fires, and that the fires mainly burned off annual needle fall (Sudworth, 1900). These surface fires may not have been intense enough to be recorded in fire scar studies, and this frequent burning would have also removed materials available for reconstruction studies in the same way that decomposition would. While historic accounts of small tree and total tree density remain uncertain, it is clear that there was greater coverage of older forest stands dominated by large trees than contemporary conditions (Barbour et al., 2002; Stephens, 2000; Taylor et al., 2014). Movement towards fewer, but larger trees and more understory ground cover as forest stands open up is a desirable trend for California State Parks, recognizing there is no immediate landscape level fix, and that the process of forest restoration from near complete historic disturbance will take time.

In our study, both prescribed fire management and natural recovery on untreated plots resulted in long-term promotion of forest restoration goals recommended to managers in the scientific literature (Brown et al., 2004; Agee and Skinner, 2005; Taylor et al., 2014; Stephens et al., 2016) by reducing tree density, small tree numbers, fuelbed depth, fine 1-h and 10-h fuel counts, and fine fuel loading. While the reduction in small trees and fine fuels with prescribed fire management has

previously been reported for the Sierra Nevada (Safford et al., 2012; Stephens et al., 2012), long-term declines in tree density and fine fuels in untreated forest lands in the Lake Tahoe basin has not.

4.1. Trends on treated plots

Fuel treatment effectiveness decays over time and managers need to assess treatment longevity to inform long term management strategies (Kalies and Yocom Kent, 2016). Our research adds to the relatively few long-term assessments of prescribed fire management longevity (Safford et al., 2012; Stephens et al., 2012; van Mantgem et al., 2016) and extends the period of investigation to 20 years post-treatment for mixed-conifer forest in the Tahoe basin. Similar to previous investigations (Stephens et al., 2012; van Mantgem et al., 2016), we evaluated just a snapshot in time. If the data are available, future research may benefit by considering the trajectory and persistence of changes during the intervening years. Our results indicated that fuel treatment effectiveness from prescribed fire may persist more towards the longer range of the current rule of thumb that anticipates effectiveness in the range of 5–20 years (Safford et al., 2012). However, it is important to understand in this case that forests in our study area are changing in the absence of active treatment, and an understanding of the trajectory and magnitude of these changes needs to be considered in light of comparisons between pre- and post-treatment condition.

Tree density remained below baseline conditions for total, small, medium, and large tree classes and basal area was lower in treated plots 20 years after initial entry prescribed burning. The magnitude of change was much larger in the small tree size class and reductions in small trees, which can act as ladder fuels, was a primary goal of California State Parks's prescribed fire management program. Changes in densities within each size class (small, medium, large) can result from mortality, but also through graduation of trees as they mature from one class into the next, or from unrecorded saplings into the small size class (> 15 cm). The fact that small tree densities remain well below baseline conditions even 20 years after treatment indicates that it can take longer than 20 years for a new tree cohort to enter the small tree size class in high elevation mixed conifer forests of the Lake Tahoe basin. The decline in tree density that was primarily realized in the small tree size class was accompanied by an increase in QMD, even though the number of medium and large trees declined. This large tree mortality warrants further investigation as introducing prescribed fire to long-unburned forest may present a potential concern for managers interested in retaining large trees (Hood, 2010).

Live stand structure, snags, and surface fuels are intimately intertwined (Harmon, 2001). Accompanying the observed changes in overstory tree density and basal area, surface fuel changes were also present in comparisons between baseline and 20 years post-treatment. Fuelbed depth, 1- and 10-h fuel counts and fine fuel loads remained below baseline; 100-h fuels were comparable, and CWD and wood loads were higher. The combination of declining fine fuel loads with increasing wood loads resulted in a total fuel load estimate that was relatively unchanged from baseline conditions, even though the composition of surface fuels changed substantially. Existing snags felled by prescribed fire, as well as those trees killed by prescribed fire that later fell to the ground, resulted in a decline in snags, which may explain the increase in CWD.

Webster and Halpern (2010) found a long-term increase in understory vegetation in burned plots within Sequoia Kings Canyon National Park. We also found higher understory cover in treated compared to baseline conditions, indicating that application of fire and a reduction in tree density is likely promoting understory plant species.

We expect conditions in treated plots to warrant reburning based on local conditions and regrowth, but measurements important for evaluating fire hazard remain lower than baseline conditions 20 years after initial entry with prescribed fire. Prescribed fire management appears to have successfully moved treated forest stands towards short- and long-term goals established at the onset of this fire monitoring program. Indeed, there are indications that long-term effectiveness of prescribed fire management could last longer than currently assumed (Vaillant et al., 2013; van Mantgem et al., 2011), and could be temporally variable based on pulsed contributions of fuels resulting from treatment-induced mortality that may decline over time. Research that accounts for a changing climate suggests that burning intervals should be lengthened because production of forest fuels may decline in the future (Diggins et al., 2010) and disturbance that is too frequent could result in forest type conversion (Flatley and Fulé, 2016). Continued empirical monitoring is important to investigate appropriate burn rotations.

4.2. Trends on untreated plots

Structural changes on untreated plots followed the same general pattern as we observed on the treated plots. Tree density declined over the 20-year period in untreated forest plots by an average of over 100 trees/ha and the decline was mostly comprised of small white fir trees. This contradicts recent reports of increasing numbers of small trees in the Sierra Nevada (Dolanc et al., 2014; McIntyre et al., 2015). These investigations assessed change in forest structure between the 1930s and the 2000s and included areas that have been actively logged, using the 1930s data to represent a historical baseline of forest structure. Our research investigates more contemporary trajectories in small tree density over the past 20 years for forested areas that have been allowed to recover from past landscape disturbance for at least a half-century, and highlights the landscape-scale alterations to the Tahoe basin that would preclude the use of 1930s data as representative of a historic baseline because nearly all accessible timber in the Tahoe basin was logged between the 1850s and 1930s (Beesley, 1996). Recent investigations into contemporary changes in tree density in YNP and SEKI also report declining trajectories in numbers of trees for untreated forest and those declines have been concentrated in the small tree size class (Webster and Halpern, 2010; van Mantgem and Stephenson, 2007). While McIntyre et al. (2015) report a 19% decline in basal area with increased small tree density, the contemporary trends we found were similar to Webster and Halpern (2010), in that basal area remained unchanged with declining numbers of small trees. These current trends in tree size structure reported for YNP and SEKI suggest that the differences reported between the 1930s and 2000s do not necessarily reflect a continuing trend for these untreated forest plots.

The dampening effect of frequent fires on conifer regeneration started by mining and logging activities, and in support of grazing interests, is well documented in the historic record (Leiberg, 1902, Sudworth, 1900, Show and Kotok, 1924). Decades of heavy grazing pressure also suppressed conifer regeneration (Leiberg, 1902; Sudworth, 1900). These foresters describe rapid and dense regeneration in areas where these disturbances were removed and believed these pressures were maintaining artificially low stocking levels. Widespread human disturbance pressures that suppressed conifer regeneration were followed by a policy of fire suppression that started in California around 1930 with the first suppression crews mobilized in the late 1920s (Safford and Stevens, 2016). Release of these forest stands from anthropogenic disturbance pressures, coupled with fire suppression, resulted in predictably dense regrowth of seedlings and saplings (Fulé et al., 2012), but this regrowth may self-thin over time as forest stand development advances. We observed that the number of large trees increased in untreated plots, which is contrary to research elsewhere indicating declining numbers of large trees between the 1930s and 2000s in areas of the Sierra Nevada that experienced logging (McIntyre et al., 2015) and also within YNP (Lutz et al., 2009). Lutz et al. (2009) discussed the possibility that declines in large diameter trees in YNP could be due to a declining tree cohort that established after a historical stand-initiating event that affected large portions of the park. Historical landscape-scale disturbance events resulting in a lack of small and intermediate sized trees from decades of grazing and repeated

anthropogenic burning could have altered forest structure such that the remaining cohort (as opposed to a 'stand-initiating' event as discussed by Lutz et al. (2009)) would have been largely represented by large trees with little representation of an intermediate sized cohort to fill in as the older cohort started to decline (McKelvy and Johnston, 1992; Show and Kotok, 1924).

The self-thinning rule describes a relationship between tree size and density such that, as average tree size increases in a forest stand, the density of trees would be expected to decline (Zhang et al., 2013). This maturation includes processes such as death and pruning of lower branch systems (Franklin et al., 2002) which results in increased crown rise (Valentine et al., 2013) and reduced ladder fuels. Forest stands are expected to increase in structural diversity over time, as a result of the heterogeneity introduced by disturbances such as managed or natural low-intensity fire, but also as a result of wind, insects, disease, drought, and competitive exclusion, which act throughout the development process (Franklin et al., 2002; Franklin and Van Pelt, 2004; Oliver and Larson, 1996; Zhang et al., 2013). Such increased structural diversity could result in increased forest resilience (Larson et al., 2008). Our empirical measurements showed not only a steady decline in tree density—primarily through loss of small diameter white fir trees, which is a restoration priority in the Lake Tahoe basin (Taylor et al., 2014)—but also increases in the number of large trees and QMD over the 20 year study period.

Collins et al., (2013) project a steep future decline in conditional burn probability in untreated Sierra Nevada forest stands that are subjected to low ingrowth rates, such as in this study where declining numbers of small trees were observed. In addition, cut stumps of many of the small trees in recently thinned stands of similar age and history on Parks land adjacent to our study plots are greater than 50 years old, even though they may only be 5–10 cm DBH in size (Appendix B; Figs. B.4–B.6). There is a long history of researchers remarking on the ability of true fir to persist as small trees in the understory for decades (Sudworth, 1916; Maul, 1958; Gordon, 1973). This suggests that not all of the small trees in these long-undisturbed forest plots are a result of continuing ingrowth. These changes in long-recovering, untreated forest under California State Parks management show movement towards old forest conditions as defined and quantified for the Lake Tahoe basin (Barbour et al., 2002) and suggest that stewardship of natural recovery processes should be considered as one forest restoration tool in the managers' toolbox.

Our results indicated that cover of understory vegetation increased and that some of the untreated plots have experienced enough self-thinning for reinitiation of the understory. We did not analyze differences in species richness but this bears further investigation, as Webster and Halpern (2010) found potentially increasing species richness for some understory components in long-protected untreated forest in SEKI, and few studies have examined long term change in understory dynamics and composition of burned forest relative to untreated control areas (Abella and Springer, 2015).

Changes in overstory, as measured by declining tree density and increasing numbers of large trees in our untreated forest plots, may alter fuel inputs and accumulation over time (Lydersen et al., 2015). As forest stands develop from a past stand initiating event through the stem exclusion stage, density dependent self-thinning results in an acceleration of self-pruning of lower branches, lifting of the live crown, and crown class differentiation (Jack and Long, 1996); and then into advanced stages of succession and maturity where density dependent drivers resulting in mortality of small trees and self-pruning are replaced by density independent drivers (Oliver and Larson, 1996). Stand density was positively correlated with fine fuel loads and litter loads were negatively correlated with time since last fire in mature, untreated forest in central Oregon (Stanton and Arabas, 2009). Litter loading in mixed conifer forest in YNP and SEKI declined over time in untreated plots from 4.6 kg/m^2 to 1.9 kg/m^2 (Keifer et al., 2006). Swim et al., (2016) report declining fine surface fuel loads in the Lake Tahoe basin on untreated forest plots. Other researchers have also reported that some fine fuel loads are declining in western forest control plots (Youngblood et al., 2008; Stephens et al., 2012). As small tree mortality and self-pruning rates slow with forest stand development, surface fuel composition may change.

The use of pre- and post-treatment fuel measurements is recommended to allow managers to quantify the results of completed fuel treatments in terms of altering potential fire behavior metrics and informing theoretical fire behavior models and simulations (USDI, 2003; Vaillant et al., 2009). Post-treatment fuel measurements that are collected at periodic intervals to track the recovery of fuel loads after the steep initial treatment effect are important because they allow managers to assess required maintenance treatment needs. However, assuming that untreated forests would maintain pre-treatment baseline conditions in the absence of treatment, or simulating ingrowth into all untreated forest stands in comparative assessments of treated vs untreated forest, may miss changes associated with structural development as forests recover from past anthropogenic disturbance. In addition, lumping forest lands in the Sierra Nevada into a common category of 'untreated' for comparisons with recently treated forest disregards the differences in forest structure between different stages of forest development, as well as the different land-use legacies. Additional empirical measurement of how forests at different stages of development are adapting to current stressors is needed.

5. Conclusions

Both prescribed fire management and natural recovery resulted in movement—acknowledging that the movement rates are different—towards recommended forest restoration goals of fewer small trees (ladder fuels) and lower fine surface fuel loading. Substantial changes observed in our untreated plots indicated that some long-protected forest lands in the Lake Tahoe basin are continuing to recover from the well-documented chronic, landscape level logging, grazing, and other anthropogenic impacts during the latter half of the 19th and into the early 20th century, even while exposed to a changing climate and long-term fire suppression. A combination of management approaches that includes prescribed burning and stewardship of natural recovery could increase landscape heterogeneity (Chazdon and Guariguata, 2016). Additional benefits might entail decreasing stream delivery of nitrates and increasing water quality (Coats et al., 2016), as well as the maintenance of important wildlife habitat components, such as snags and CWD (Stephens and Moghaddas, 2005). Moreover, incorporation of natural regeneration into forest management planning can greatly reduce the cost and resource requirements of large-scale restoration efforts (Chazdon and Guariguata, 2016; Nunes et al., 2017), while also providing habitat for fire-dependent and undisturbed old forest dependent species (Roberts et al., 2015).

Supplementary material

All of the code for both data preparation and the statistical analysis are available via a Bitbucket repository (access available upon request): https://bitbucket.org/nau-lci/ca-forest-structure-and-fuels-analysis. Additional supplementary material is organized into the following three appendices.

Appendix A: specific model specifications. (File format: HTML, viewable via any modern web browser.)

Appendix B: miscellaneous descriptive statistics and results. (File format: Google Doc.)

Appendix C: model diagnostics. (File format: Zip file containing a set of HTML files, one for each model.)

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