Lydersen et al. Fire Ecology (2019) 15:43
https://doi.org/10.1186/s42408-019-0060-x

Fire Ecology

ORIGINAL RESEARCH

Open Access

Fuel dynamics and reburn severity following high-severity fire in a Sierra Nevada, USA, mixed-conifer forest

Jamie M. Lydersen[1,2*], Brandon M. Collins[3], Michelle Coppoletta[4], Melissa R. Jaffe[1], Hudson Northrop[1] and Scott L. Stephens[1]

Abstract

Background: High-severity fire in forested landscapes often produces a post-fire condition of high shrub cover and large loads of dead wood. Given the increasing patch size of high-severity fire and the tendency for these areas to reburn at high severity in subsequent wildfires, post-fire management often targets restoration of these areas. However, these areas are challenging to manage, in part due to limited knowledge of post-fire fuel dynamics over space and time and uncertainties in how specific fuel components such as snags and logs influence future fire severity. In this study, we used high-resolution aerial imagery collected nine years after a wildfire to measure snags, logs, and shrub cover within high-severity patches, and to assess how fuel development influenced reburn severity in a subsequent wildfire.

Results: The abundance of snags, logs, and shrubs following high-severity fire varied with elevation and slope steepness; however, generalized additive models explained only 6 to 21% of their variation over the post-fire landscape. High densities of both snags and logs were associated with high reburn severity in a subsequent fire, while shrub cover had a marginally insignificant (P = 0.0515) effect on subsequent fire severity.

Conclusions: Our results demonstrate that high levels of large dead wood, which is often not considered in fire behavior modeling, corresponded with repeated high-severity fire effects. Future research should leverage the increasing availability of high-resolution imagery to improve our understanding of fuel load patterns in space and time and how they may impact landscape resilience to facilitate management planning for post-fire forest landscapes.

Keywords: coarse woody debris, fuel dynamics, high severity fire, mixed-conifer forest, repeat fire

* Correspondence: jamie.lydersen@fire.ca.gov
[1]Ecosystem Sciences Division, Department of Environmental Science, Policy, and Management, University of California, 130 Mulford Hall, Berkeley, CA 94720, USA
[2]Present Address: California Department of Forestry and Fire Protection, Fire and Resource Assessment Program, PO Box 944246, Sacramento, CA 94244, USA
Full list of author information is available at the end of the article

Resumen

Antecedentes: Los fuegos de alta severidad en paisajes forestales producen frecuentemente condiciones post-fuego en las que predominan arbustos y una alta carga de material leñoso muerto. Dado el patrón incremental en el tamaño de los parches de alta severidad y la tendencia de esas áreas a quemarse con alta severidad en fuegos subsecuentes, el manejo del post-fuego se enfoca primariamente en la restauración de esas áreas. Sin embargo, esas áreas incluyen desafíos en su manejo, en parte debido al conocimiento limitado de la dinámica de los combustibles post-fuego en el tiempo y el espacio, y las incertidumbres sobre cuáles de los componentes específicos de los combustibles como los árboles muertos en pié y troncos influencian la futura severidad del fuego. En este estudio, usamos imágenes de alta resolución colectadas nueve años después de un incendio para medir los árboles muertos en pié, troncos, y la cobertura de arbustos dentro de parches quemados con alta severidad, y determinar como el desarrollo de este combustible influencia la severidad cuando el área se quema nuevamente en otro incendio.

Resultados: La abundancia de árboles muertos en pié, troncos y arbustos luego de un fuego de alta severidad varió con la elevación y la pendiente. Sin embargo, los modelos generales aditivos explicaron sólo del 6 al 21% de su variación en el paisaje post-fuego. La alta densidad tanto de muertos en pié como de troncos caídos fue asociada con la alta severidad de áreas que se vuelven a quemar en un fuego posterior, mientras que la cobertura de arbustos tuvo un efecto marginalmente insignificante ($P = 0.0515$) en la severidad del fuego subsecuente.

Conclusiones: Nuestros resultados muestran que niveles altos de madera muerta, que no es frecuentemente considerada en el modelado del comportamiento de incendios, se corresponde con efectos repetidos de eventos de fuego de alta severidad. Investigaciones futuras deberían ponderar la disponibilidad de imágenes de alta resolución para mejorar nuestro entendimiento de los patrones de carga de combustible en el espacio y el tiempo y cómo pueden impactar en la resiliencia del paisaje, para facilitar la planificación del manejo en paisajes forestales post-fuego.

Introduction

Fire changes the quantity, type, and arrangement of fuels across a landscape. In mixed-conifer forests of the western US, surface fires generally reduce fine fuels, thereby lowering future fire activity and promoting a low- to moderate-severity fire regime (Collins et al. 2009; Larson et al. 2013; Lydersen et al. 2017). In contrast, high-severity fire that kills overstory trees can create large quantities of dead wood (Monsanto and Agee 2008) and promote rapid establishment and growth of shrubs (McGinnis et al. 2010). The combination of large woody fuels and dense shrub cover has been shown to reinforce a pattern of high-severity fire when burned in subsequent wildfire (Coppoletta et al. 2016). This pattern can lead to so-called "alternative stable states" for mid-elevation montane ecosystems, in which a fire-caused transition to shrub or herbaceous dominance is maintained over time by relatively frequent fire (Cocking et al. 2014; Coop et al. 2016; Lauvaux et al. 2016; Nemens et al. 2018).

The size and proportional area of high-severity patches within wildfires in the Sierra Nevada, USA, have been increasing in recent decades (Miller and Safford 2012; Stevens et al. 2017). This increase in stand-replacing fire is attributed to alterations in forest structure and landscape vegetation patterns that have occurred over the last century during an extended period of fire exclusion (Parsons and DeBenedetti 1979; Hessburg et al. 2007; Brown et al. 2008; Miller et al. 2009; Lydersen and Collins 2018), as well as a warming climate (Keyser and Westerling 2017). The resulting large high-severity patches are outside the historical range of variation for Sierra Nevada mixed-conifer forest (Meyer 2015; Stephens et al. 2015; Safford and Stevens 2017), leading to concerns over the resilience of these forest-dominated landscapes (Stephens et al. 2016). These concerns are centered on two trends within high-severity patches. First, large patches of high-severity fire significantly reduce the probability of natural conifer tree regeneration, especially in the interior of large patches that are very far from live seed source (Collins and Roller 2013; Crotteau et al. 2013; Welch et al. 2016; Shive et al. 2018). Second, when these areas burn in a subsequent wildfire, there is a tendency for repeated high-severity fire, thereby preventing the regrowth of mature forest. Due to these concerns, management of forests in the Sierra Nevada is often focused on reforestation following high-severity fire (Long et al. 2014). However, reforestation can be difficult given the time it takes for a tree to grow to a fire-resistant size, and managers must contend with factors such as competition with shrubs and the resulting dense stands of similarly sized trees that increase the vulnerability to future wildfire (Zald and Dunn 2018; North et al. 2019). Although they provide important habitat for wildlife, the presence of shrubs, legacy snags, and logs are a concern for both young plantations and areas with natural regeneration due to their role in promoting high-severity fire (White and Long 2018).

Understanding fuel dynamics following high-severity fire and the processes driving these patterns could provide valuable information for managing post-fire landscapes, but accurately measuring and modeling fuels is challenging. Fuels are difficult to quantify, in part due to their high variability in time and space (Keane 2013). Access to field sites can be difficult in steep or remote terrain, and in post-fire conditions where dense shrub growth impedes sampling and high densities of decaying snags pose a falling hazard (Dunn et al. 2019). Beyond these difficulties, field plots in forests burned at high severity tend to be small (0.004 to 0.01 ha; Collins and Roller 2013; Crotteau et al. 2013; Chambers et al. 2016; Welch et al. 2016). This small plot size can lead to highly variable data for phenomena that are inherently spatially heterogeneous or clumped, which may explain the modest statistical predictions for tree regeneration and coarse fuels following high-severity fire (*e.g.,* Collins and Roller 2013; Dunn and Bailey 2015b). Furthermore, these plot sizes are often several orders of magnitude smaller than the scale at which fire effects are manifested. High-resolution aerial imagery offers an alternative method to field measurements, and allows quantification of vegetation and large woody fuels over larger areas and in sites where access would be difficult. Aerial photo analysis has been widely used to categorize fuel type (Arroyo et al. 2008); however, it is limited in its ability to provide direct information on fuels in forest lands due to interference from the canopy (Keane et al. 2001).

In this study, we use high resolution (0.3 m) aerial imagery collected nine years after a wildfire to examine fuel development across a post-fire landscape, and to determine what extent fuel development influenced reburn severity. Although the present study draws from the same set of fires used in a related study (Coppoletta et al. 2016), the data used are quite distinct between the two investigations. Coppoletta et al. (2016) relied on data collected in relatively small field plots (~0.008 to 0.08 ha), while the present study used 1 ha photo plots. Our objectives were to (1) quantify standing snags, logs, and shrub cover over large aerial photo plots following high-severity fire; (2) assess how these photo-interpreted fuel levels varied by topographic setting; and (3) assess the influence of fuels on subsequent wildfire severity. We limited our analysis to areas that had burned at high severity in the initial fire to avoid areas where the forest canopy would obstruct the view of the ground.

Methods

Study area

Our study was conducted within the area burned by the Storrie Fire in the northern Sierra Nevada, USA (Fig. 1). The Storrie Fire was active between 17 August and 27 September 2000, burning 22 687 ha mainly on the Plumas and Lassen national forests. The area experienced several subsequent fires, including the 2012 Chips Fire, which reburned 10 166 ha (45%) of the area impacted by the Storrie Fire (Coppoletta et al. 2016). Elevation within the Storrie Fire footprint ranged from 525 to 2163 m. Prior to the fires, vegetation at the study site was a mosaic of conifer forest (68%), conifer–hardwood forest (14%), shrubland (7%), hardwood forest (5%), and herbaceous vegetation (4%; 1997 to 1999 USFS Region 5 existing vegetation type, https://data.fs.usda.gov/geodata/edw/datasets.php?xmlKeyword=Existing+vegetation%3A+Region+5). The most common forest type was mixed conifer, consisting of white fir (*Abies concolor* [Gord. & Glend.] Lindl. ex Hildebr.), Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco), ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson), Jeffrey pine (*Pinus jeffreyi* Balf.), sugar pine (*Pinus lambertiana* Douglas), incense-cedar (*Calocedrus decurrens* [Torr.] Florin), and California black oak (*Quercus kelloggii* Newberry). Above 1800 m elevation, mixed-conifer forest transitioned to white fir and red fir (*Abies magnifica* A. Murr.) forest, while shrublands, characterized by *Ceanothus* L. and *Arctostaphylos* Adans. (manzanita) species, dominated lower-elevation, drier, and southeast-facing canyon slopes. Although forests in the area experienced a frequent, low- to moderate-severity fire regime historically (mean fire return interval of 8 to 22 years; Moody et al. 2006), only 12% of the area had burned in the century prior to the Storrie Fire (California Department of Forestry and Fire Protection Fire and Resource Assessment Program fire perimeter data, available at http://frap.fire.ca.gov/mapping/gis-data/).

Imagery processing

Aerial orthoimagery covering the footprint of the Storrie Fire was collected by Quantum Spatial (Novato, California, USA) between 31 July and 11 August 2009 (nine years after the fire). The aerial imagery had a resolution of 0.3 m. We defined high-severity patches within the Storrie Fire using the extended (1 year post-fire) assessment of the relative differenced normalized burn ratio (RdNBR), with a minimum threshold of 641 (Miller and Thode 2007). This definition of high-severity fire typically represents complete or near complete basal area mortality (Lydersen et al. 2016). High severity effects accounted for approximately one third of the Storrie Fire area, 75% of which was concentrated in contiguous patches exceeding 1000 ha (Fig. 1). The largest contiguous patch (2150 ha) was entirely reburned by the 2012 Chips Fire. Circular 1 ha plots were created in ArcMap 10.3.1 (ESRI 2014) at random locations within high-severity patches in the Storrie Fire using the

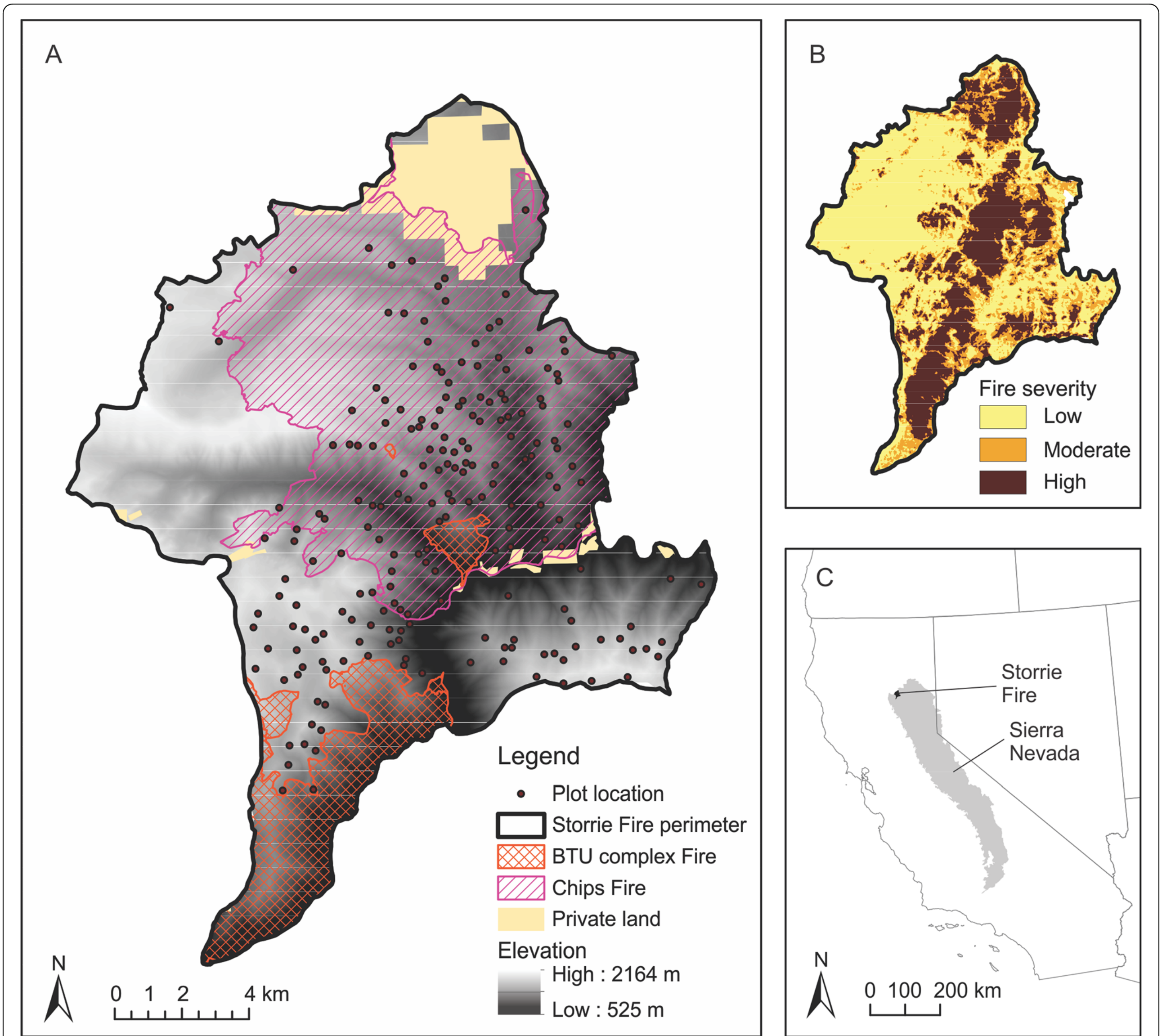

Fig. 1 (**A**) Plot locations, subsequent fire boundaries, and private land boundaries within the perimeter of the 2000 Storrie Fire. (**B**) Classified fire severity map of the Storrie Fire. (**C**) Location of Storrie Fire within the Sierra Nevada of California, USA

Create Random Points and Buffer tools with a minimum spacing of 200 m between plot centers. Plots were situated to include only pixels that burned at high severity in the Storrie Fire (RdNBR ≥ 641), rather than including a mix of pixel severities within plots. We limited our analysis to high-severity patches because the loss of overstory cover allowed for more accurate visual assessment of understory fuels conditions, including snags, logs, and shrub cover, as compared to areas with an intact tree canopy. We restricted the analysis to US Forest Service land, included all vegetation types, and excluded the area burned in the 2008 Butte Lightning (BTU) fire complex, resulting in 202 inventory plots (Fig. 1). The pre-fire vegetation in the plots was mainly forest, with 79% in conifer or mixed-conifer-hardwood forest and 7% in hardwood forest. The remaining plots were in shrubland (13%) or barren land (0.5%).

Snag density, log density, shrub cover, and live tree cover in the orthoimagery were assessed visually within the 1 ha plots by two photo analysts. All visible snags were counted for the entire plot. Visible logs were tallied by intersection along six 56.4 m radial transects (Fig. 2). Transects were spaced 60° apart with a random starting orientation. Logs that overlapped more than one transect were counted twice, similar to what would be done using the planar intersect method to measure fuels in the field (Brown 1974). To provide an estimate of the total number of logs per plot, we used simple linear

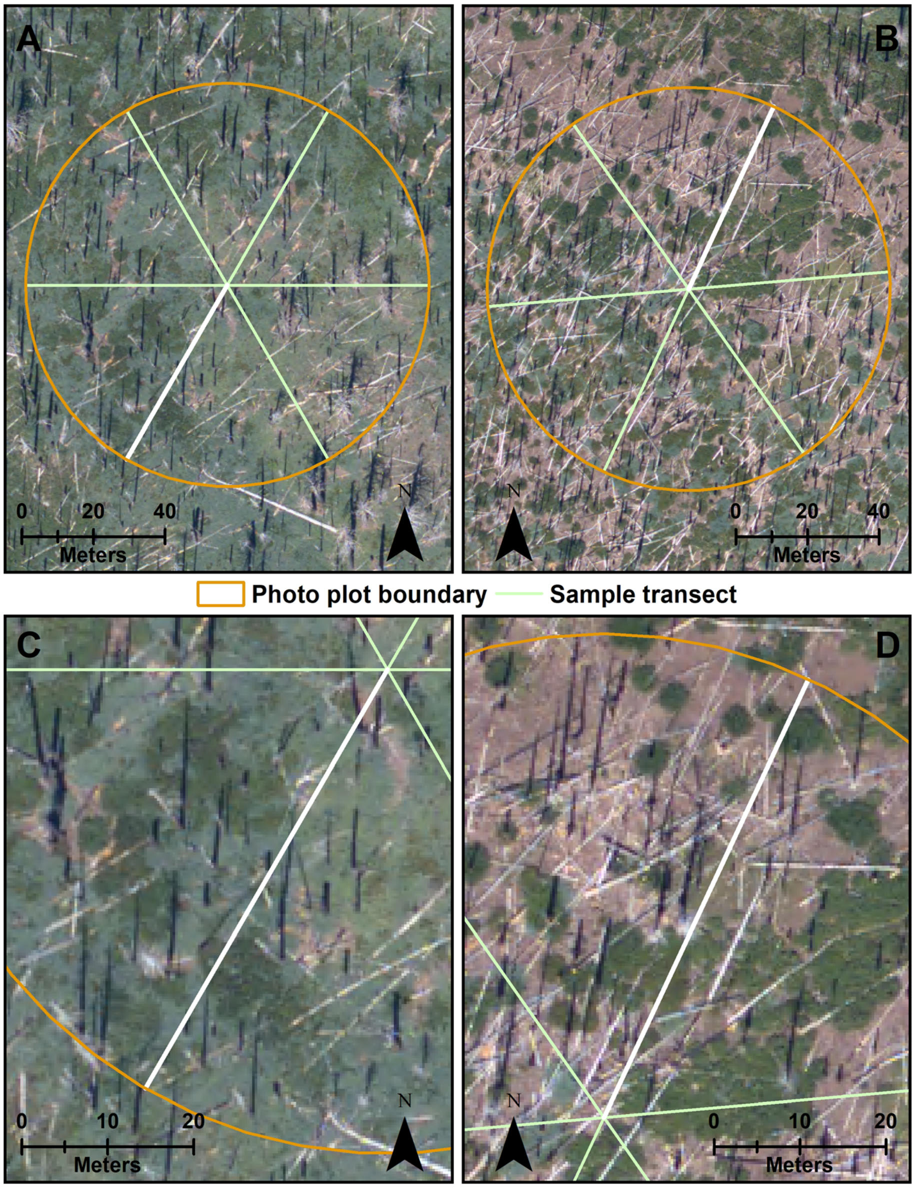

Fig. 2 Examples of two photo plots at two spatial scales within the area burned by Storrie Fire in the Sierra Nevada of California, USA, in 2009, nine years after the fire. Images in (**A**) and (**B**) are shown at 1:1200 and images in (**C**) and (**D**) are shown at 1:500. The green and white radii show the transects used in the photo analysis. Shrubs appear as green cover. Black lines are the shadows of snags, while downed logs typically appear as white lines

regression to derive the relationship between the number of logs tallied on the transects and a count of the total number of logs in the plot, using a subset (41) of the plots (Additional file 1). We reported log density using this plot-level estimate to provide a measure that is more meaningful to managers than the number of logs per transect, but we performed all statistical analyses on the raw data collected on the transects to avoid introducing error into the numbers used for inference. Cover of shrubs and live trees within each plot were estimated visually within six subsections created by the plot transects, then averaged for the plot. The two photo analysts used slightly different methods; one analyst estimated cover within each of the six 0.17 ha segments created by the radial transects, and the other analyst estimated cover along each radial transect. Plots were assigned to analysts randomly so that each analyst provided data for plots across the entire Storrie Fire footprint, covering a range of elevation, slope, and aspect. Twenty plots were measured by both photo analysts to provide a comparison of the estimates for fuel loads between operators.

Statistical analysis

We considered plots to be independent replicates due to our random sampling design and restrictive spacing between plots. Previous work had also found that spatial autocorrelation among plots within one fire is negligible due to the large variability in forest structure typical of Sierra Nevada forests (van Mantgem and Schwilk 2009). We assessed variation in three fuels variables within the Storrie Fire footprint: snag density, log density, and shrub cover. As noted above, the number of logs tallied on transects was used for the log density response variable, as opposed to the derived plot-level estimate of log density.

These response variables were used in two different analyses. We first used generalized additive models (GAMs) to assess how post-fire fuels varied with topographic and water balance variables across the Storrie Fire footprint (Table 1). Topographic variables were processed at a 10 m resolution from a digital elevation model (https://viewer.nationalmap.gov/basic/), and water balance variables were available at a 270 m resolution (Flint et al. 2013). Topographic and water balance variables for each plot were based on the values at the plot centers and extracted using bilinear interpolation. We implemented the GAMs using the `gam` function in the `mgcv` package in R version 3.5.1(R Core Team 2018) and a stepwise model selection process. The `gam` function requires user specification of the error distribution and the link function to be used in the model (Wood 2017). For snag and log density, which had continuous positive values, general additive models were defined using a Gaussian distribution and a log link. For shrub cover , which had values that ranged from 0 to 1, we specified a beta distribution and a logit link. For each fuels variable, we first ran the full model including all covariates, then sequentially removed the covariate with the highest concurvity until all covariates' concurvity estimates were <0.4. This limited the influence of correlation between covariates in the model. We then removed the covariate with the highest insignificant *P*-value until all covariates were statistically significant. Because *P*-values for smooth terms in GAMs are approximate, we used a conservative *P*-value of 0.01 to assess significance (Zuur et al. 2009). To check if GAMs provided improved fit compared to linear models, we ran a comparable model selection process for generalized linear models, also using the `gam` function in the `mgcv` package. Covariates with Pearson correlation coefficients (Sokal and Rohlf 1995) of absolute value >0.5 were removed first, followed by a stepwise selection that removed insignificant covariates. We examined residual versus predicted and quantile-quantile graphs and applied transformations to the response variables to meet model assumptions of residual homoscedasticity and normal distribution. Snag density and shrub cover were transformed with a square root function, and log density was transformed with a power function of 0.25. All models were compared using the Bayesian information criterion (BIC; Schwarz 1978), and the model with the lowest BIC was chosen as the final model for each fuels variable.

Second, we used ANOVA to detect differences in fuels between fire severity classes in a subsequent fire, the 2012 Chips Fire. We used the extended RdNBR assessment for the Chips Fire to assign a fire severity class to each plot based on thresholds developed by Miller and Thode (2007; low: <316, moderate: 316 to 640, high: ≥641). Chips Fire severity for a plot was determined using bilinear interpolation of the plot center and a 30 m grid of fire severity. We also compared fuel conditions in plots outside the Chips Fire footprint that had burned at high severity in the Storrie Fire, which we classified as unburned. Values for each of the three fuels variables (snag density, log density, and shrub cover) were compared between these four classes using `Proc GLM` in SAS version 9.4 (SAS Institute, Inc. 2014). To meet model assumptions of residual homoscedasticity and normal distribution, snag density was transformed using

Table 1 Covariates used in generalized additive models (GAMs) to assess variation in post-fire fuels nine years after the Storrie Fire

Model covariate	Mean (min–max) or class (*n*)	Source
Elevation (m)	1440 (838–1989)	US Geological Survey (2013)
Topographic position index	Canyon (21), flat slope (6), steep slope (117), ridge (58)	Derived from the digital elevation model using CorridorDesigner Toolbox (Majka et al. 2007)
Slope steepness (%)	51.1 (4.7–136.5)	Derived from the digital elevation model
Solar radiation ($WHm^{-2} \times 10^5$)	13.1 (5.7–16.8)	Derived from the digital elevation model using the Solar Radiation Toolbox in ArcGIS 10.3 (ESRI 2014)
Slope aspect (transformed)	1.03 (0–2)	Derived from the digital elevation model, transformed as $1 + \cos(45 - A)(\pi \div 180)$, where *A* is the aspect in degrees
Actual evapotranspiration	385 (293–534)	The basin characterization model downscaled climate and hydrology datasets (Flint et al. 2013)
Climatic water deficit	582 (359–703)	The basin characterization model downscaled climate and hydrology datasets (Flint et al. 2013)

a square root function, log density was transformed using a power function of 0.35, and shrub cover was transformed with an arcsin function. Significance levels were adjusted using the Tukey method (Sokal and Rohlf 1995) to account for multiple comparisons.

Results

Snag density, log density, and shrub cover were highly variable across high-severity fire plots in the Storrie Fire. Plots had an average of 54 snags ha^{-1} and 37 logs ha^{-1}. However, the distributions of snags and logs were positively skewed, so that the median snag and log density were 37 and 17 ha^{-1}, respectively, and the maximum densities were 284 and 367 ha^{-1}, respectively. Shrub cover averaged 51%, with a range of 0 to 98%. Live tree cover was low, with a median of 0%, a mean of 2%, and a maximum of 19%. Mean estimates for snag density, shrub cover, and live tree cover were fairly similar between photo analysts (Additional file 2). This was not the case for log density, for which one mean was half that of the other (Additional file 2). However, inspection of individual plot estimates for the two analysts revealed general consistency in the relative degree to which plots had high versus low density or cover (Additional file 3).

In general, the models assessing variation in fuel levels across the landscape had low explanatory power. Among the topographic and water balance variables considered in GAMs, only elevation and slope percent appeared in the final models (Fig. 3). The best model for snag density included both elevation and slope percent, and explained 19.4% of the deviance. Snag density was highest at mid elevations and on shallower slopes. The best model for log density included only slope percent, explained 20.9% of the deviance, and showed a significant decline in log density with increasingly steeper slopes. The best model for shrub cover had particularly low explanatory power, accounting for only 6.5% of the deviance. Shrub cover tended to be greater at lower elevation.

We found a significant relationship between density estimates for both snags and logs and subsequent fire severity (Fig. 4). The density of snags was significantly higher in plots that reburned at high severity compared to low and moderate severity (P = 0.0002 and 0.0007, respectively), and areas outside the Chips Fire (P < 0.0001). Snag density was also significantly higher in areas that reburned at moderate severity compared to areas outside the Chips Fire (P = 0.0028). Similarly, the density of logs was significantly higher in plots that reburned at high severity compared to low and moderate severity (P = 0.0039 and 0.0011, respectively), and areas outside the Chips Fire (P < 0.0001). There were no significant differences in shrub cover between subsequent fire severities, although the difference between plots that reburned at low severity and high severity was only marginally insignificant (P = 0.0515), with generally higher shrub cover associated with higher-severity fire (Fig. 4). Given the observed variability between analysts, we tested these same relationships for each analyst separately. The relationships were quite similar to those using the full dataset, with two exceptions: (1) snag density for plots reburned at moderate severity was indistinguishable from unburned areas for both analysts, and (2) shrub cover was greater in plots that reburned at high severity compared to low severity for one analyst (P = 0.037).

Discussion

With an increase in both the scale and severity of wildfires over the last few decades, there is a growing need to understand the development of post-fire fuels and their influence on future fire behavior. In forested areas where high-severity wildfire has the ability to create a pulse of coarse woody debris, understanding the influence of standing snags and downed logs on subsequent fire severity is often critical to the development of long-term post-fire management strategies. Yet, the effect of coarse woody debris on fire behavior is not well understood, in particular when large quantities of snags and logs are present (Westerling 2018). Given this gap in knowledge, large logs are not factored into most fire behavior models, which may hinder planning for fuels management and expected fire severity (Hyde et al. 2011; Keane et al. 2001). Difficulty in obtaining accurate measurements that adequately represent fuel load variability using small field plots is a further limitation to understanding the role of coarse woody debris on fire behavior and effects (Sikkink and Keane 2008; Keane et al. 2012; Stephens et al. 2018). Our use of large (1 ha) plots allowed for better matching of the scale between fuels data and fire behavior as compared to field plots that are usually smaller in size due to sampling constraints. At this larger scale, we found that high densities of both snags and logs were associated with high severity in a subsequent fire, while shrub cover had less of an effect.

The direct role of snags on fire behavior is not well studied (Donato et al. 2013). Although not measured in our study, high loads of fine fuels co-occur locally with snags (Lydersen et al. 2015), and presumably logs. This is due to the deposition of branches as dead trees progress through stages of decay (Peterson et al. 2015). If snag density is high, these local jackpots of surface fuels accumulating over time would be expected to contribute to exacerbated fire behavior. This could explain the positive association we found between snag density and subsequent fire severity. Additionally, snags and logs are local sources of long-burning fuel, which are readily available to burn at 12 years old. These burning snags

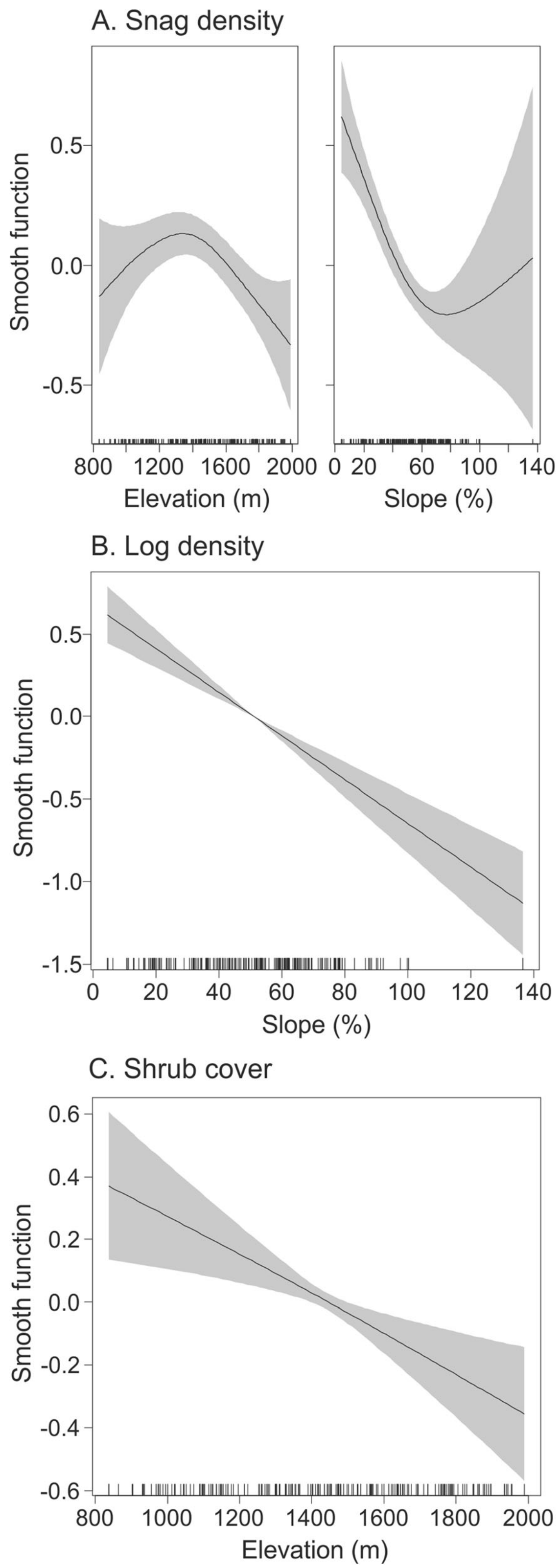

Fig. 3 Fitted smooth functions showing relationships between post-fire fuels in 2009 and topographic and water balance variables in high-severity burn areas within the 2000 Storrie Fire, California, USA. Shaded areas show the 95% confidence interval. Tick marks at the bottom of the graphs show the plot distribution. Relationships shown are for (**A**) snag density, (**B**) log density, and (**C**) shrub cover

and logs can create localized pockets of long-duration heating that can ignite adjacent live fuels or adjacent snags and logs (Monsanto and Agee 2008). Again, at high snag or log densities, this local long-burning effect could contribute to larger-scale high-severity effects (Buma and Wessman 2011).

In our study, 33% of the plots that reburned in the Chips Fire burned at high severity, while the majority (56%) reburned at moderate severity. Although relatively few plots (11%) reburned at low severity, the proportion of high-severity fire is somewhat lower than that found by other studies demonstrating a positive relationship between initial and subsequent high-severity fire. For example, Lydersen et al. (2017) found that 49% of pixels that burned in a previous high-severity fire burned at high severity in the Rim Fire in the central Sierra Nevada. The scale of the data used in the present analysis may have affected the lower amount of subsequent high-severity fire observed in this study. Our 1 ha plots were situated so that all pixels within the plots were high-severity fire in the Storrie Fire, but plots could include a mixture of pixel severities in the Chips Fire, leading to a lower overall average when assessing the subsequent fire severity. In addition, many shrub- and hardwood-dominated areas resprouted quickly after the Chips Fire (Nemens et al. 2018), which may have led to a lower estimate of fire severity based on imagery collected one year after the fire (Lydersen et al. 2016). It is worth noting that remotely sensed assessments of fire severity in areas that have experienced multiple fires can be confounded by the differences in structure and composition of pre-fire vegetation. For example, in a forested area that develops into lower-stature vegetation (*e.g.,* young trees or shrubs) following an initial fire, the absolute amount of vegetation consumed is greater in the initial fire than in a subsequent fire. Because RdNBR reflects the relative change in pre- and post-fire vegetation, fire is classified as high severity when most of the green vegetation is consumed by the fire, regardless of the vegetation present when the fire occurs (Miller and Thode 2007). The lower-stature vegetation present following a high-severity fire may be more susceptible to a higher degree of consumption and mortality (*i.e.,* repeat high severity) at a lower fire intensity (Thompson and Spies 2010; van Wagtendonk et al. 2012; Parks et al. 2014). Field studies validating satellite-based measures of fire severity such as RdNBR in young, low-stature

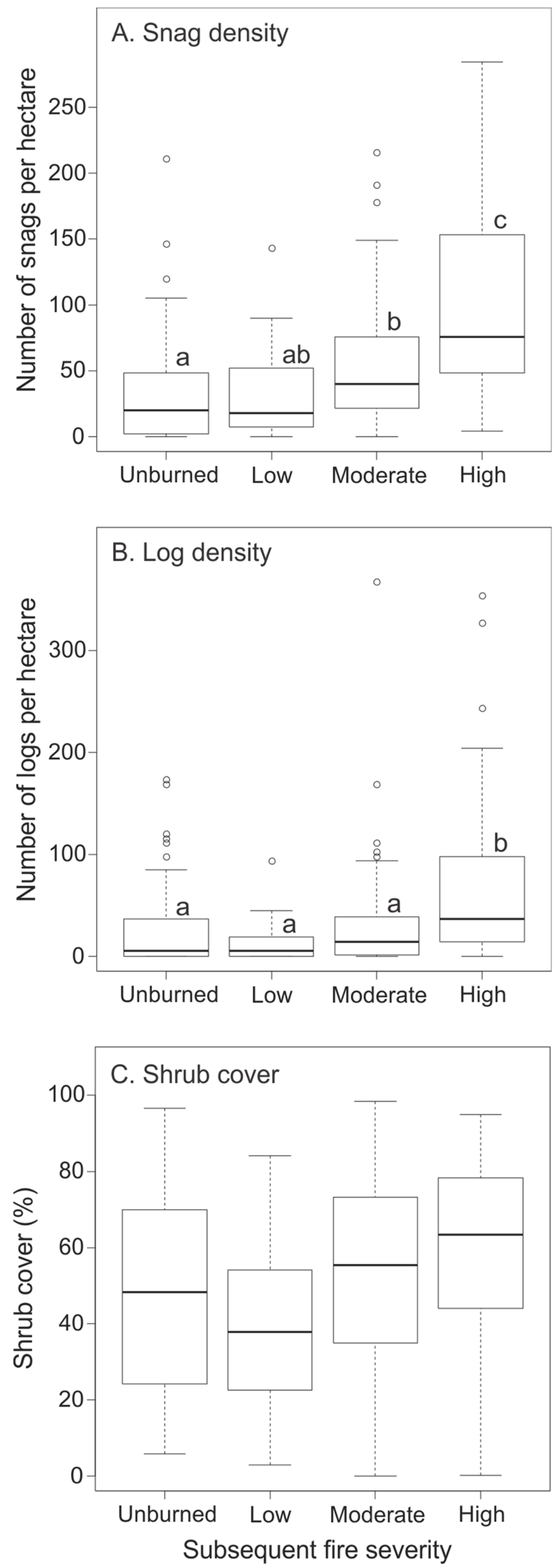

Fig. 4 Fuel loads in 2009 by fire severity class in the 2012 Chips Fire, for areas initially burned at high severity in the 2000 Storrie Fire in the Sierra Nevada of California, USA. Unburned plots were outside of the Chips Fire. Different lower-case letters indicate significant differences between subsequent fire severity classes. Box and whisker plots depict median (horizontal band), interquartile range (white bar), range of data within 1.5 interquartile range of the lower and upper quartiles (vertical dashed lines), and outliers (open circles). Data shown are for (**A**) snag density, (**B**) log density, and (**C**) shrub cover

vegetation are needed to support research on the effects of multiple fires (Harvey et al. 2016; Harvey et al. 2019).

A conversion from forest- to shrub-dominated vegetation is thought to contribute to the positive association between past and subsequent high-severity fire (Parks et al. 2014; Coop et al. 2016; Prichard et al. 2017). Contrary to other studies (*e.g.,* van Wagtendonk et al. 2012; Coppoletta et al. 2016), we found no significant effect of shrub cover on subsequent fire severity, although there was a marginally insignificant (P = 0.0515) trend for increasing shrub cover with increasing subsequent fire severity (Fig. 4). The lack of significance may have been due to the fact that our plots were only located in areas that burned at high severity in the initial fire. As a result, we likely censored the distribution of shrub cover encountered by the second fire towards more shrub-dominated areas. Our overall high estimates of shrub cover for these areas (mean 53%, median 55%) support this assertion, particularly when considering that our plots covered an entire hectare. For example, Coppoletta et al. (2016) analyzed field plots (0.008 ha) from the same study area that were distributed across a range of initial fire severities and found a wider range of shrub cover values (0 to 100%) and a mean of 25%. In a study conducted 15 years after the Storrie Fire, Nemens et al. (2018) also documented a wide range of shrub cover values across a gradient of fire severity, with cover values ranging from 33.8% in areas burned at low severity to 63.5% in high-severity patches. Coppoletta et al. (2016) also found that a threshold of 60% shrub cover was associated with reburning at high severity in the Chips Fire, which is very similar to the median shrub cover of 63% found among plots in the present study that reburned at high severity (Fig. 4).

We found little effect of topography or water balance variables on the landscape patterns of fuel level following high-severity fire. Again, this may be an artifact of constraining our samples to areas initially burned at high severity, in that we only captured a limited range of biophysical conditions across the landscape. Fire exclusion has increased tree densities and favored establishment of shade-tolerant species that are less fire resistant, resulting in a more homogeneous forest structure with greater vulnerability to high-severity fire (Lydersen et al.

2013). Given these changes and the observed fire patterns in these altered forests (*e.g.,* Stevens et al. 2017; Steel et al. 2018), it is reasonable to assume that homogeneity in forest and fuel structure contributes to more homogeneous fire effects, particularly under more reactive fire-weather conditions (Lydersen et al. 2014; Coppoletta et al. 2016; Lydersen et al. 2017; Parsons et al. 2017). Similarly, more homogenous fire effects can be expected to contribute to more homogenous post-fire fuel trajectories. Slope steepness and elevation both had some effect on fuel variability. Snags and logs both tended to be more numerous on gentler slopes, which may have supported greater pre-fire tree densities due to deeper soils with greater water-holding potential (Meyer et al. 2007). Greater snag density also occurred at mid-level elevation (approximately 1400 m). We also found that shrub cover decreased with increasing elevation, although the GAM only accounted for 6% of the variation in shrub cover. These results are consistent with the effect of elevation on productivity, in which lower elevation sites are often too dry to support greater forest cover and higher elevation sites may be more limited due to colder temperatures. The lower elevations at our study site also tended to occur in steep canyons where soil depth may limit productivity.

Although their impacts on future fire severity and forest resilience are a concern, there are many ecological benefits to coarse woody debris including snags and logs (Stevens-Rumann et al. 2015). Many avian species rely on snags for nesting and foraging habitat (Raphael and White 1984), and others depend on the shrub habitat that often co-occurs in areas with high coarse woody debris loads (Raphael et al. 1987). Large downed logs provide food resources such as fungi and arthropods for some species of small mammals (Kelt et al. 2017) and provide cover for fish in streams (Berg et al. 1998). While the benefits of coarse wood to wildlife is well studied, the effect of scale of post-fire forest habitat patches on wildlife is not well understood. Different sized patches may vary in habitat characteristics such as microclimate and amount of edge shared with green forest (Andrén 1994; Stephens et al. 2013). It is an important goal to balance management objectives on a landscape to increase resilience by reducing future likelihood of high-severity fire while also leaving areas with high densities of snags, logs, and shrubs that can provide important habitat that has been lacking in fire-suppressed areas (Peterson et al. 2015; White et al. 2016; Tarbill et al. 2018). Conserving these habitat features at the appropriate scale may help to balance management objectives within large stand-replacing patches.

The high-resolution imagery allowed for large sample plots and unrestricted areal coverage, but relying on imagery alone generates a few key limitations. We were not able to ground truth our imagery plots because comparable field data collected near the image acquisition date (2009) were not available, particularly at the 1 ha scale of our imagery plots. Given the large size and limited accessibility of many of our imagery plots, it would be difficult to collect representative field data. Therefore, it is possible that our log density estimates are lower than the actual numbers due to shrubs obscuring or fully covering their view. Similarly, our ability to detect smaller-diameter logs is likely poor and we do not actually know the size threshold for detection. However, it is also possible that shadows or other small distortions in the imagery led to an overestimate of log density on some plots. This difficulty in acquiring accurate counts of logs is reflected in the higher relative difference in log counts compared to snag and shrub measurements between the two photo analysts (Additional files 1 and 2). Our detection of snags is subject to the same limitations imposed by tree size and presence of shadows or other distortions, which also likely contributed to error in our reported density estimates. Our estimates of shrub cover may also have error, but the magnitude is probably lower than that for log and snag density. Regardless of these sources of potential error, our findings generally align with observations from studies of both fuel development following high-severity fire (*e.g.,* Ritchie et al. 2013; Dunn and Bailey 2015b), and factors driving reburn severity (*e.g.,* Coppoletta et al. 2016; Collins et al. 2018).

It is difficult to know how applicable our results are to other fires or geographic regions. The fact that we only assessed large woody fuels and shrub cover nine years after a single fire would suggest limited broader applicability. However, the general progression of high-severity fire in long-fire-excluded forests resulting in a shrub-dominated community with large but variable levels of coarse woody fuel has been demonstrated elsewhere in western North America (Prichard et al. 2017). Collins et al. (2018) found that standing dead biomass had a positive relationship with subsequent fire severity in a mixed-conifer forest in the central Sierra Nevada, which reburned 17 years after the initial fire. The effect of coarse woody debris on future fire behavior may change over time, since a greater level of decay increases combustibility and consumption (Uzoh and Skinner 2009; Hyde et al. 2012; Eskelson and Monleon 2018). The amount of standing versus fallen coarse wood also changes over time (Dunn and Bailey 2012; Dunn and Bailey 2015a). For example, Dunn and Bailey (2015b) found that 1000-hour fuels measured in high-severity fire sites within dry mixed-conifer forests in eastern Oregon, USA, reached a peak at 20 years post fire when approximately 90% of snags had fallen. Although we only found a marginally insignificant relationship between shrub cover and subsequent fire severity (P = 0.0515), other work has identified shrubs as an important predictor of subsequent fire severity (Lydersen et al. 2014; Coppoletta et al. 2016). Shrub loads, which are a product of species composition, cover, and height, also vary with time since fire (Dunn and Bailey 2015b), and their combustibility varies depending on live fuel moisture at the time of the burn (Weise et al. 2016), leading to further complexity in subsequent fire severity.

It is still unclear what the effect of large volumes of coarse woody debris produced from insect outbreaks, such as occurred following the 2012 to 2015 drought in California, will have on severity of future fires. In areas where few trees remain, the fuel trajectory may be similar to what was observed in the high-severity burn areas measured in this study area. However, high loads of coarse woody debris intermingled with live trees may have a different effect since canopy shading may keep temperatures lower and fuel moistures higher, as well as limit the growth of shrubs that can lead to increased wildfire intensity (Stephens et al. 2018). The effect of coarse woody debris produced by drought-related mortality on fire severity will likely differ depending on the size of the dead trees, which can vary by species and elevation (Fettig et al. 2019; Lydersen et al. 2019). Given the high levels of mortality occurring in the Sierra Nevada due to both drought and fire, it will be important to monitor how fuels are changing over time and interacting with subsequent forest stressors so that management actions can be taken to mitigate these risks.

Conclusions

Given the uncertainties and inherent tradeoffs in managing forests with a substantial dead wood component, there is a strong need for more research to aid in management decisions. Post-fire management can pose as an opportunity to design and monitor treatments in such a way that the ecological impacts can be assessed and integrated into future management planning. For example, Tarbill et al. (2018) examined how patterns and timing of salvage logging affected wildlife when remnant "islands" of snag habitat were preserved. Several studies have opportunistically analyzed how fuels treatments influenced subsequent fire spread and severity (*e.g.*, Lydersen et al. 2017; Johnson and Kennedy 2019; Kennedy et al. 2019), but specific information on how the amount of large, dead wood on a landscape contributes to fire behavior is not well understood, and the dynamics of these fuels following treatments and wildfire are often not quantified or tracked over time due to limited resources. Using high-resolution aerial imagery, the present study demonstrates a significant effect of large dead-wood levels on subsequent high-severity fire. The increasing availability of high-resolution imagery, along with the growing feasibility of using unmanned aerial vehicles to collect accurate fuels data at scales that are meaningful for fire behavior, could be leveraged in the future to improve our knowledge of fuel patterns and processes. Given the limited resources for conducting fuel treatments, it is important to increase our understanding of how treatment methods could be optimized to meet multiple goals, such as reducing expected fire severity and promoting successful reforestation while avoiding detrimental effects to wildlife populations.

Supplementary information

Supplementary information accompanies this paper at https://doi.org/10.1186/s42408-019-0060-x.

Additional file 1: Linear regression of log density counted along transects (x-axis) and total logs counted within the 1 ha plot (y-axis) for 41 plots within the area burned by the Storrie Fire in the Sierra Nevada of California, USA. The derived relationship was $y = 4.41x - 3.58$. Plots for which the derived log density was <0 ha^{-1} were set to 0. This regression was performed to provide a more interpretable estimate of log density (logs ha^{-1}), but all statistical analyses were done using raw counts of logs per total transect length (see Methods). Error DF is the error degrees of freedom, MSE is the mean square error, R-square is the coefficient of determination, and Adj R-square is the adjusted coefficient of determination.

Additional file 2: Mean fuel levels as assessed by the two photo analysts for 20 plots using imagery collected in 2009 within the area burned by the 2000 Storrie Fire in the Sierra Nevada of California, USA. Snags were counted in the entire 1 ha plot and logs were tallied along six 56.4 m transects. The percentage shrub and live tree cover were estimated along six 56.4 m transects by Analyst 1, and within six 0.17 ha segments by Analyst 2 (see Methods).

Additional file 3: Cross comparison of (**A**) snag count, (**B**) log count, and (**C**) shrub cover for two photo analysts (represented by different shades of gray) collected on a subset of the study plots of imagery collected in 2009 within the area burned by the 2000 Storrie Fire in the Sierra Nevada of California, USA. Snags were counted within the entire 1 ha plot, and logs were counted along six 56.4 m radial transects. The first photo analyst visually assessed shrub cover along the six transects, and the second photo analyst visually assessed shrub cover within six plot sections (area of 0.17 ha each) bounded by the same six transects.

Authors' contributions

JML conceived of and designed the study, analyzed data, and wrote the paper. BMC and MC designed the study and wrote the paper. MRJ and HN analyzed the aerial imagery and wrote the paper. SLS designed the study and wrote the paper. All authors read and approved the final manuscript.

Funding

This project was supported by the USDA–USDI Joint Fire Sciences Program (project 16-1-05-13), as well as through a research partnership between the US Forest Service Pacific Southwest Research Station and UC Berkeley College of Natural Resources (project no. 16-JV-11272167-063).

Availability of data and materials

The datasets used or analyzed during the current study are available from the corresponding author on reasonable request.

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests
The authors declare that they have no competing interests.

Author details
[1]Ecosystem Sciences Division, Department of Environmental Science, Policy, and Management, University of California, 130 Mulford Hall, Berkeley, CA 94720, USA. [2]Present Address: California Department of Forestry and Fire Protection, Fire and Resource Assessment Program, PO Box 944246, Sacramento, CA 94244, USA. [3]Center for Fire Research and Outreach, University of California, 130 Mulford Hall, Berkeley, CA 94720-3114, USA. [4]USDA Forest Service, Sierra Cascade Province Ecology Program, 159 Lawrence Street, Quincy, CA 95971, USA.

Received: 3 May 2019 Accepted: 25 October 2019
Published online: 09 December 2019

References
Andrén, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos* 71 (3): 35–366 https://doi.org/10.2307/3545823.

Arroyo, L.A., C. Pascual, and J.A. Manzanera. 2008. Fire models and methods to map fuel types: the role of remote sensing. *Forest Ecology and Management* 256 (6): 1239–1252 https://doi.org/10.1016/j.foreco.2008.06.048.

Berg, N., A. Carlson, and D. Azuma. 1998. Function and dynamics of woody debris in stream reaches in the central Sierra Nevada, California. *Canadian Journal of Fisheries and Aquatic Sciences* 55 (8): 1807–1820 https://doi.org/10.1139/f98-064.

Brown, J.K. 1974. Handbook for inventorying downed woody material. USDA Forest Service General Technical Report INT-16. Ogden: USDA Forest Service, Intermountain Forest and Range Experiment Station.

Brown, P.M., C.L. Wienk, and A.J. Symstad. 2008. Fire and forest history at Mount Rushmore. *Ecological Applications* 18 (8): 1984–1999 https://doi.org/10.1890/07-1337.1.

Buma, B., and C. Wessman. 2011. Disturbance interactions can impact resilience mechanisms of forests. *Ecosphere* 2 (5): 1–13 https://doi.org/10.1890/ES11-00038.1.

Chambers, M.E., P.J. Fornwalt, S.L. Malone, and M.A. Battaglia. 2016. Patterns of conifer regeneration following high severity wildfire in ponderosa pine-dominated forests of the Colorado Front Range. *Forest Ecology and Management* 378: 57–67 https://doi.org/10.1016/j.foreco.2016.07.001.

Cocking, M.I., J.M. Varner, and E.E. Knapp. 2014. Long-term effects of fire severity on oak–conifer dynamics in the southern Cascades. *Ecological Applications* 24 (1): 94–107 https://doi.org/10.1890/13-0473.1.

Collins, B.M., J.M. Lydersen, R.G. Everett, and S.L. Stephens. 2018. How does forest recovery following moderate-severity fire influence effects of subsequent wildfire in mixed-conifer forests? *Fire Ecology* 14: 3 https://doi.org/10.1186/s42408-018-0004-x.

Collins, B.M., J.D. Miller, A.E. Thode, M. Kelly, J.W. van Wagtendonk, and S.L. Stephens. 2009. Interactions among wildland fires in a long-established Sierra Nevada natural fire area. *Ecosystems* 12 (1): 114–128 https://doi.org/10.1007/s10021-008-9211-7.

Collins, B.M., and G.B. Roller. 2013. Early forest dynamics in stand-replacing fire patches in the northern Sierra Nevada, California, USA. *Landscape Ecology* 28 (9): 1801–1813 https://doi.org/10.1007/s10980-013-9923-8.

Coop, J.D., S.A. Parks, S.R. McClernan, and L.M. Holsinger. 2016. Influences of prior wildfires on vegetation response to subsequent fire in a reburned Southwestern landscape. *Ecological Applications* 26 (2): 346–354 https://doi.org/10.1890/15-0775.

Coppoletta, M., K.E. Merriam, and B.M. Collins. 2016. Post-fire vegetation and fuel development influences fire severity patterns in reburns. *Ecological Applications* 26 (3): 686–699 https://doi.org/10.1890/15-0225.

Crotteau, J.S., J.M. Varner III, and M.W. Ritchie. 2013. Post-fire regeneration across a fire severity gradient in the southern Cascades. *Forest Ecology and Management* 287: 103–112 https://doi.org/10.1016/j.foreco.2012.09.022.

Donato, D.C., J.B. Fontaine, J.B. Kauffman, W.D. Robinson, and B.E. Law. 2013. Fuel mass and forest structure following stand-replacement fire and post-fire logging in a mixed-evergreen forest. *International Journal of Wildland Fire* 22 (5): 652–666 https://doi.org/10.1071/WF12109.

Dunn, C.J., and J.D. Bailey. 2012. Temporal dynamics and decay of coarse wood in early seral habitats of dry-mixed conifer forests in Oregon's Eastern Cascades. *Forest Ecology and Management* 276: 71–81 https://doi.org/10.1016/j.foreco.2012.03.013.

Dunn, C.J., and J.D. Bailey. 2015a. Modeling the direct effects of salvage logging on long-term temporal fuel dynamics in dry-mixed conifer forests. *Forest Ecology and Management* 341: 93-109 https://doi.org/10.1016/j.foreco.2015.01.002.

Dunn, C.J., and J.D. Bailey. 2015b. Temporal fuel dynamics following high-severity fire in dry mixed conifer forests of the eastern Cascades, Oregon, USA. *International Journal of Wildland Fire* 24 (4): 470–483 https://doi.org/10.1071/WF13139.

Dunn, C.J., C.D. O'Connor, M.J. Reilly, D.E. Calkin, and M.P. Thompson. 2019. Spatial and temporal assessment of responder exposure to snag hazards in post-fire environments. *Forest Ecology and Management* 441: 202–214 https://doi.org/10.1016/j.foreco.2019.03.035.

Eskelson, B.N.I., and V.J. Monleon. 2018. Post-fire surface fuel dynamics in California forests across three burn severity classes. *International Journal of Wildland Fire* 27 (2): 114–124 https://doi.org/10.1071/WF17148.

ESRI [Environmental Systems Research Institute]. 2014. ArcGIS release 10.3. Redlands: Environmental Systems Research Institute.

Fettig, C.J., L.A. Mortenson, B.M. Bulaon, and P.B. Foulk. 2019. Tree mortality following drought in the central and southern Sierra Nevada, California, US. *Forest Ecology and Management* 432: 164–178 https://doi.org/10.1016/j.foreco.2018.09.006.

Flint, L.E., A.L. Flint, J.H. Thorne, and R. Boynton. 2013. Fine-scale hydrologic modeling for regional landscape applications: the California Basin Characterization Model development and performance. *Ecological Processes* 2: 25 https://doi.org/10.1186/2192-1709-2-25.

Harvey, B.J., R.A. Andrus, and S.C. Anderson. 2019. Incorporating biophysical gradients and uncertainty into burn severity maps in a temperate fire-prone forested region. *Ecosphere* 10 (2): e02600 https://doi.org/10.1002/ecs2.2600.

Harvey, B.J., D.C. Donato, and M.G. Turner. 2016. Burn me twice, shame on who? Interactions between successive forest fires across a temperate mountain region. *Ecology* 97 (9): 2272–2282 https://doi.org/10.1002/ecy.1439.

Hessburg, P.F., R.B. Salter, and K.M. James. 2007. Re-examining fire severity relations in pre-management era mixed conifer forests: inferences from landscape patterns of forest structure. *Landscape Ecology* 22 (Supplement 1): 5–24 https://doi.org/10.1007/s10980-007-9098-2.

Hyde, J.C., A.M. Smith, and R.D. Ottmar. 2012. Properties affecting the consumption of sound and rotten coarse woody debris in northern Idaho: a preliminary investigation using laboratory fires. *International Journal of Wildland Fire* 21 (5): 596–608 https://doi.org/10.1071/WF11016.

Hyde, J.C., A.M. Smith, R.D. Ottmar, E.C. Alvarado, and P. Morgan. 2011. The combustion of sound and rotten coarse woody debris: a review. *International Journal of Wildland Fire* 20 (2): 163–174 https://doi.org/10.1071/WF09113.

Johnson, M.C., and M.C. Kennedy. 2019. Altered vegetation structure from mechanical thinning treatments changed wildfire behaviour in the wildland–urban interface on the 2011 Wallow Fire, Arizona, USA. *International Journal of Wildland Fire* 28 (3): 216–229 https://doi.org/10.1071/WF18062.

Keane, R.E. 2013. Describing wildland surface fuel loading for fire management: a review of approaches, methods and systems. *International Journal of Wildland Fire* 22 (1): 51–62 https://doi.org/10.1071/WF11139.

Keane, R.E., R. Burgan, and J. van Wagtendonk. 2001. Mapping wildland fuels for fire management across multiple scales: integrating remote sensing, GIS, and biophysical modeling. *International Journal of Wildland Fire* 10 (4): 301–319 https://doi.org/10.1071/WF01028.

Keane, R.E., K. Gray, V. Bacciu, and S. Leirfallom. 2012. Spatial scaling of wildland fuels for six forest and rangeland ecosystems of the northern Rocky Mountains, USA. *Landscape Ecology* 27 (8): 1213–1234 https://doi.org/10.1007/s10980-012-9773-9.

Kelt, D.A., R. Sollmann, A.M. White, S.L. Roberts, and D.H. Van Vuren. 2017. Diversity of small mammals in the Sierra Nevada: filtering by natural selection or by anthropogenic activities? *Journal of Mammalogy* 98 (1): 85–93 https://doi.org/10.1093/jmammal/gyw158.

Kennedy, M.C., M.C. Johnson, K. Fallon, and D. Mayer. 2019. How big is enough? Vegetation structure impacts effective fuel treatment width and forest resiliency. *Ecosphere* 10 (2): e02573 https://doi.org/10.1002/ecs2.2573.

Keyser, A., and A.L. Westerling. 2017. Climate drives inter-annual variability in probability of high severity fire occurrence in the western United States. *Environmental Research Letters* 12: 065003 https://doi.org/10.1088/1748-9326/aa6b10.

Larson, A.J., R.T. Belote, C.A. Cansler, S.A. Parks, and M.S. Dietz. 2013. Latent resilience in ponderosa pine forest: effects of resumed frequent fire. *Ecological Applications* 23 (6): 1243–1249 https://doi.org/10.1890/13-0066.1.

Lauvaux, C.A., C.N. Skinner, and A.H. Taylor. 2016. High severity fire and mixed conifer forest–chaparral dynamics in the southern Cascade Range, USA. *Forest Ecology and Management* 363: 74–85 https://doi.org/10.1016/j.foreco.2015.12.016.

Long, J.W., C. Skinner, S. Charnley, K. Hubbert, L. Quinn-Davidson, and M. Meyer. 2014. Chapter 4.3—post-wildfire management. In *Science synthesis to support socioecological resilience in the Sierra Nevada and southern Cascade Range. USDA Forest Service General Technical Report PSW-GTR-247*, ed. J.W. Long, L. Quinn-Davidson, and C.N. Skinner, 187–220. Albany: USDA Forest Service, Pacific Southwest Research Station.

Lydersen, J.M., and B.M. Collins. 2018. Change in vegetation patterns over a large forested landscape based on historical and contemporary aerial photography. *Ecosystems* 21 (7): 1348–1363 https://doi.org/10.1007/s10021-018-0225-5.

Lydersen, J.M., B.M. Collins, M.L. Brooks, J.R. Matchett, K.L. Shive, N.A. Povak, V.R. Kane, and D.F. Smith. 2017. Evidence of fuels management and fire weather influencing fire severity in an extreme fire event. *Ecological Applications* 27 (7): 2013–2030 https://doi.org/10.1002/eap.1586.

Lydersen, J.M., B.M. Collins, and C.T. Hunsaker. 2019. Implementation constraints limit benefits of restoration treatments in mixed-conifer forests. *International Journal of Wildland Fire* 28 (7): 495–511 https://doi.org/10.1071/WF18141.

Lydersen, J.M., B.M. Collins, E.E. Knapp, G.B. Roller, and S. Stephens. 2015. Relating fuel loads to overstorey structure and composition in a fire-excluded Sierra Nevada mixed conifer forest. *International Journal of Wildland Fire* 24 (4): 484–494 https://doi.org/10.1071/WF13066.

Lydersen, J.M., B.M. Collins, J.D. Miller, D.L. Fry, and S.L. Stephens. 2016. Relating fire-caused change in forest structure to remotely sensed estimates of fire severity. *Fire Ecology* 12 (3): 99–116 https://doi.org/10.4996/fireecology.1203099.

Lydersen, J.M., M.P. North, and B.M. Collins. 2014. Severity of an uncharacteristically large wildfire, the Rim Fire, in forests with relatively restored frequent fire regimes. *Forest Ecology and Management* 328: 326–334 https://doi.org/10.1016/j.foreco.2014.06.005.

Lydersen, J.M., M.P. North, E.E. Knapp, and B.M. Collins. 2013. Quantifying spatial patterns of tree groups and gaps in mixed-conifer forests: reference conditions and long-term changes following fire suppression and logging. *Forest Ecology and Management* 304: 370-382 https://doi.org/10.1016/j.foreco.2013.05.023.

Majka, D., J. Jenness, and P. Beier. 2007. CorridorDesigner: ArcGIS tools for designing and evaluating corridors. http://corridordesign.org. Accessed 30 Nov 2015.

McGinnis, T.W., J.E. Keeley, S.L. Stephens, and G.B. Roller. 2010. Fuel buildup and potential fire behavior after stand-replacing fires, logging fire-killed trees and herbicide shrub removal in Sierra Nevada forests. *Forest Ecology and Management* 260 (1): 22–35 https://doi.org/10.1016/j.foreco.2010.03.026.

Meyer, M.D. 2015. Forest fire severity patterns of resource objective wildfires in the southern Sierra Nevada. *Journal of Forestry* 113 (1): 49–56 https://doi.org/10.5849/jof.14-084.

Meyer, M.D., M.P. North, A.N. Gray, and H.S. Zald. 2007. Influence of soil thickness on stand characteristics in a Sierra Nevada mixed-conifer forest. *Plant and Soil* 294 (1–2): 113–123 https://doi.org/10.1007/s11104-007-9235-3.

Miller, J.D., and H. Safford. 2012. Trends in wildfire severity: 1984 to 2010 in the Sierra Nevada, Modoc Plateau, and southern Cascades, California, USA. *Fire Ecology* 8 (3): 41–57 https://doi.org/10.4996/fireecology.0803041.

Miller, J.D., H.D. Safford, M. Crimmins, and A.E. Thode. 2009. Quantitative evidence for increasing forest fire severity in the Sierra Nevada and southern Cascade Mountains, California and Nevada, USA. *Ecosystems* 12 (1): 16–32 https://doi.org/10.1007/s10021-008-9201-9.

Miller, J.D., and A.E. Thode. 2007. Quantifying burn severity in a heterogeneous landscape with a relative version of the delta Normalized Burn Ratio (dNBR). *Remote Sensing of Environment* 109 (1): 66–80 https://doi.org/10.1016/j.rse.2006.12.006.

Monsanto, P.G., and J.K. Agee. 2008. Long-term post-wildfire dynamics of coarse woody debris after salvage logging and implications for soil heating in dry forests of the eastern Cascades, Washington. *Forest Ecology and Management* 255 (12): 3952–3961 https://doi.org/10.1016/j.foreco.2008.03.048.

Moody, T.J., J. Fites-Kaufman, and S.L. Stephens. 2006. Fire history and climate influences from forests in the Northern Sierra Nevada, USA. *Fire Ecology* 2 (1): 115–141 https://doi.org/10.4996/fireecology.0201115.

Nemens, D.G., J.M. Varner, K.R. Kidd, and B. Wing. 2018. Do repeated wildfires promote restoration of oak woodlands in mixed-conifer landscapes? *Forest Ecology and Management* 427: 143–151 https://doi.org/10.1016/j.foreco.2018.05.023.

North, M.P., J.T. Stevens, D.F. Greene, M. Coppoletta, E.E. Knapp, A.M. Latimer, C.M. Restaino, R.E. Tompkins, K.R. Welch, R.A. York, D.J.N. Young, J.N. Axelson, T.N. Buckley, B.L. Estes, R.N. Hager, J.W. Long, M.D. Meyer, S.M. Ostoja, H.D. Safford, K.L. Shive, C.L. Tubbesing, H. Vice, D. Walsh, C.M. Werner, and P. Wyrsc. 2019. Tamm review: reforestation for resilience in dry western US forests. *Forest Ecology and Management* 432: 209–224 https://doi.org/10.1016/j.foreco.2018.09.007.

Parks, S.A., C. Miller, C.R. Nelson, and Z.A. Holden. 2014. Previous fires moderate burn severity of subsequent wildland fires in two large western US wilderness areas. *Ecosystems* 17 (1): 29–42 https://doi.org/10.1007/s10021-013-9704-x.

Parsons, D.J., and S.H. DeBenedetti. 1979. Impact of fire suppression on a mixed-conifer forest. *Forest Ecology and Management* 2: 21–33 https://doi.org/10.1016/0378-1127(79)90034-3.

Parsons, R., R.R. Linn, F. Pimont, C. Hoffman, J. Sauer, J. Winterkamp, C.H. Sieg, and W.M. Jolly. 2017. Numerical investigation of aggregated fuel spatial pattern impacts on fire behavior. *Land* 6 (2): 43 https://doi.org/10.3390/land6020043.

Peterson, D.W., E.K. Dodson, and R.J. Harrod. 2015. Post-fire logging reduces surface woody fuels up to four decades following wildfire. *Forest Ecology and Management* 338: 84–91 https://doi.org/10.1016/j.foreco.2014.11.016.

Prichard, S.J., C.S. Stevens-Rumann, and P.F. Hessburg. 2017. Tamm review: shifting global fire regimes: lessons from reburns and research needs. *Forest Ecology and Management* 396: 217–233 https://doi.org/10.1016/j.foreco.2017.03.035.

R Core Team. 2018. *R: a language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing.

Raphael, M.G., M.L. Morrison, and M.P. Yoder-Williams. 1987. Breeding bird populations during twenty-five years of postfire succession in the Sierra Nevada. *The Condor* 89 (3): 614–626 https://doi.org/10.2307/1368651.

Raphael, M.G., and M. White. 1984. Use of snags by cavity-nesting birds in the Sierra Nevada. *Wildlife Monographs* 86: 3–66.

Ritchie, M.W., E.E. Knapp, and C.N. Skinner. 2013. Snag longevity and surface fuel accumulation following post-fire logging in a ponderosa pine dominated forest. *Forest Ecology and Management* 287: 113–122 https://doi.org/10.1016/j.foreco.2012.09.001.

Safford, H.D., and J.T. Stevens. 2017. Natural range of variation for yellow pine and mixed-conifer forests in the Sierra Nevada, southern Cascades, and Modoc and Inyo national forests, California, USA. USDA Forest Service General Technical Report PSW-GTR-256. Albany: USDA Forest Service, Pacific Southwest Research Station.

SAS Institute, Inc. 2014. *SAS 9.4*. Cary: SAS Institute, Inc.

Schwarz, G. 1978. Estimating the dimension of a model. *The Annals of Statistics* 6 (2): 461–464 https://doi.org/10.1214/aos/1176344136.

Shive, K.L., H.K. Preisler, K.R. Welch, H.D. Safford, R.J. Butz, K.L. O'Hara, and S.L. Stephens. 2018. From the stand scale to the landscape scale: predicting the spatial patterns of forest regeneration after disturbance. *Ecological Applications* 28 (6): 1626–1639 https://doi.org/10.1002/eap.1756.

Sikkink, P.G., and R.E. Keane. 2008. A comparison of five sampling techniques to estimate surface fuel loading in montane forests. *International Journal of Wildland Fire* 17 (3): 363–379 https://doi.org/10.1071/WF07003.

Sokal, R.R., and F.J. Rohlf. 1995. *Biometry the principles and practice of statistics in biological research*. New York: W.H. Freeman and Company.

Steel, Z.L., M.J. Koontz, and H.D. Safford. 2018. The changing landscape of wildfire: burn pattern trends and implications for California's yellow pine and mixed conifer forests. *Landscape Ecology* 33 (7): 1159–1176 https://doi.org/10.1007/s10980-018-0665-5.

Stephens, S.L., J.K. Agee, P.Z. Fulé, M.P. North, W.H. Romme, T.W. Swetnam, and M.G. Turner. 2013. Managing forests and fire in changing climates. *Science* 342 (6154): 41–42 https://doi.org/10.1126/science.1240294.

Stephens, S.L., B.M. Collins, E. Biber, and P.Z. Fulé. 2016. US federal fire and forest policy: emphasizing resilience in dry forests. *Ecosphere* 7 (11): e01584 https://doi.org/10.1002/ecs2.1584.

Stephens, S.L., B.M. Collins, C.J. Fettig, M.A. Finney, C.M. Hoffman, E.E. Knapp, M.P. North, H. Safford, and R.B. Wayman. 2018. Drought, tree mortality, and wildfire in forests adapted to frequent fire. *BioScience* 68 (2): 77–88 https://doi.org/10.1093/biosci/bix146.

Stephens, S.L., J.M. Lydersen, B.M. Collins, D.L. Fry, and M.D. Meyer. 2015. Historical and current landscape-scale ponderosa pine and mixed conifer forest structure in the southern Sierra Nevada. *Ecosphere* 6 (5): 1–63 https://doi.org/10.1890/ES14-00379.1.

Stevens, J.T., B.M. Collins, J.D. Miller, M.P. North, and S.L. Stephens. 2017. Changing spatial patterns of stand-replacing fire in California conifer forests. *Forest Ecology and Management* 406: 28–36 https://doi.org/10.1016/j.foreco.2017.08.051.
Stevens-Rumann, C., P. Morgan, and C. Hoffman. 2015. Bark beetles and wildfires: how does forest recovery change with repeated disturbances in mixed conifer forests? *Ecosphere* 6 (6): 1–17 https://doi.org/10.1890/ES14-00443.1.
Tarbill, G., A.M. White, and P.N. Manley. 2018. The persistence of black-backed woodpeckers following delayed salvage logging in the Sierra Nevada. *Avian Conservation and Ecology* 13 (1): 16 https://doi.org/10.5751/ACE-01206-130116.
Thompson, J.R., and T.A. Spies. 2010. Factors associated with crown damage following recurring mixed-severity wildfires and post-fire management in southwestern Oregon. *Landscape Ecology* 25 (5): 775–789 https://doi.org/10.1007/s10980-010-9456-3.
US Geological Survey. 2013. USGS NED n41w121 1/3 arc-second 2013 1 x 1 degree ArcGrid: US Geological Survey. https://viewer.nationalmap.gov/basic/. Accessed 28 Jan 2019.
Uzoh, F.C., and C.N. Skinner. 2009. Effects of creating two forest structures and using prescribed fire on coarse woody debris in northeastern California, USA. *Fire Ecology* 5 (2): 1–13 https://doi.org/10.4996/fireecology.0502001.
van Mantgem, P.J., and D.W. Schwilk. 2009. Negligible influence of spatial autocorrelation in the assessment of fire effects in a mixed conifer forest. *Fire Ecology* 5 (2): 116–125 https://doi.org/10.4996/fireecology.0502116.
van Wagtendonk, J.W., K.A. van Wagtendonk, and A.E. Thode. 2012. Factors associated with the severity of intersecting fires in Yosemite National Park, California, USA. *Fire Ecology* 8 (1): 11–31 https://doi.org/10.4996/fireecology.0801011.
Weise, D.R., E. Koo, X. Zhou, S. Mahalingam, F. Morandini, and J.-H. Balbi. 2016. Fire spread in chaparral—a comparison of laboratory data and model predictions in burning live fuels. *International Journal of Wildland Fire* 25 (9): 980–994 https://doi.org/10.1071/WF15177.
Welch, K.R., H.D. Safford, and T.P. Young. 2016. Predicting conifer establishment post wildfire in mixed conifer forests of the North American mediterranean-climate zone. *Ecosphere* 7 (12): e01609 https://doi.org/10.1002/ecs2.1609.
Westerling, A.L. 2018. Wildfire simulations for California's fourth climate change assessment: projecting changes in extreme wildfire events with a warming climate. California's fourth climate change assessment, California Energy Commission Publication Number: CCCA4-CEC-2018-014. https://www.energy.ca.gov/sites/default/files/2019-07/Projections_CCCA4-CEC-2018-014.pdf. Accessed 11 Apr 2019.
White, A.M., and J.W. Long. 2018. Understanding ecological contexts for active reforestation following wildfires. *New Forests* 50 (1): 41–56 https://doi.org/10.1007/s11056-018-9675-z.
White, A.M., P.N. Manley, G.L. Tarbill, T.W. Richardson, R.E. Russell, H.D. Safford, and S.Z. Dobrowski. 2016. Avian community responses to post-fire forest structure: implications for fire management in mixed conifer forests. *Animal Conservation* 19 (3): 256–264 https://doi.org/10.1111/acv.12237.
Wood, S.N. 2017. *Generalized additive models: an introduction with R. Second edition*. New York: Chapman and Hall/CRC.
Zald, H.S.J., and C.J. Dunn. 2018. Severe fire weather and intensive forest management increase fire severity in a multi-ownership landscape. *Ecological Applications* 28 (4): 1068–1080 https://doi.org/10.1002/eap.1710.
Zuur, A., E.N. Ieno, N. Walker, A.A. Saveliev, and G.M. Smith. 2009. Mixed effects models and extensions in ecology with R. New York: Springer-Verlag https://doi.org/10.1007/978-0-387-87458-6.

Publisher's Note

Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.