

ORIGINAL RESEARCH

Open Access



Drivers of fire severity in repeat fires: implications for mixed-conifer forests in the Sierra Nevada, California

Lindsey Jasperse^{1*}, Brandon M. Collins^{1,2}, Michelle Coppoletta³, Kyle Merriam³ and Scott L. Stephens¹

Abstract

Background While the reintroduction of recurring fire restores a key process in frequent-fire adapted forests, the ability to significantly shift the structure and composition of departed contemporary forests has not been clearly demonstrated. Our study utilized an extensive network of field plots across three short-interval successive fires occurring in the northern Sierra Nevada, California. We evaluated the influence of plot-level forest structure and composition, topography, and weather on fire severity in a third successive fire (i.e., second reburn). Additionally, we assessed the range of forest structural conditions that emerge following multiple low- to moderate-severity fires, whether these conditions were associated with fire severity in a third fire, and how they compare to historical estimates for these forests.

Results Across plots that burned in multiple low- to moderate-severity fires, our findings indicated that post-fire outcomes in these systems are variable, resulting in a range of structural conditions following a first reburn (i.e., second fire). Areas with high levels of dead biomass burned at significantly higher severity in the third fire compared to those with higher shrub cover. Following a second fire, many plots exceeded historical estimates of stand structure metrics for yellow pine and mixed-conifer forests of the Sierra Nevada, particularly for coarse woody debris load, with some plots exceeding historical natural range of variation (NRV) estimates for live tree density. In plots with a history of varying fire severity in the initial and second fires, we found that snag basal area was associated with higher fire severity in the third fire.

Conclusions Low- to moderate-severity fire has the ability to restore ecosystem processes and reduce future fire severity in the long term, but our results suggest that it can also create fuel conditions that drive higher fire severity in successive fires. Our study demonstrates that vegetation and fuel conditions existing prior to the initial first-entry fire can largely influence post-reburn outcomes.

Keywords Forest restoration, Reburns, Natural range of variation, Forest structure, Short-interval fire

*Correspondence: Lindsey Jasperse jaspersela@gmail.com Full list of author information is available at the end of the article



Jasperse et al. Fire Ecology (2025) 21:46 Page 2 of 19

Resumen

Antecedentes Mientras que la reintroducción de fuegos recurrentes restaura procesos claves en bosques adaptados al fuego, la habilidad para cambiar significativamente la estructura y composición de bosques contemporáneos no ha sido aun claramente demostrada. Nuestro estudio utilizó una extensa red de parcelas a campo a través de tres fuegos ocurridos sucesivamente en un corto intervalo de tiempo en el norte de la Sierra Nevada de California. Evaluamos la influencia de la estructura y composición, topografía, y el tiempo meteorológico sobre la severidad del fuego en el tercer fuego consecutivo (i.e. segunda requema). Adicionalmente, determinamos el rango de las condiciones estructurales que emergieron luego de múltiples fuegos de baja a moderada severidad, cuando esas condiciones estuvieron asociadas con la severidad del fuego en un tercer incendio, y como ellos se comparaban con estimaciones históricas para esos bosques.

Resultados A través de las parcelas que se quemaron en múltiples fuegos de severidad baja a moderada, nuestros resultados indican que los efectos en esos sistemas fue variable, resultando en un rango de condiciones estructurales posteriores a la primer requema (i. e. el segundo fuego). Áreas cubiertas por altos niveles de biomasa muerta se quemaron a severidades más altas en la segunda requema que aquellas con mayor cobertura de arbustos. Luego del segundo fuego, muchas parcelas excedieron las estimaciones históricas sobre las métricas de la estructura de los rodales para el pino amarillo y de coníferas mixtas de la Sierra Nevada, particularmente para la carga de restos leñosos gruesos, con algunas parcelas excediendo las estimaciones de los rangos naturales de variación histórica (NRV) para la densidad de de árboles vivos. En parcelas con una historia de variación en la severidad del fuego en el incendio inicial y en la primera requema, encontramos que el área basal de los árboles muertos en pié (*snags*) estuvo asociado a una severidad más alta en la segunda requema.

Conclusiones Los fuegos de baja a moderada severidad tuvieron la habilidad de restaurar los procesos ecosistémicos y reducir la severidad de fuegos futuros en el largo plazo, aunque nuestros resultados sugieren que pueden también condiciones de combustibles que lleven a severidades mayores en fuegos sucesivos. Nuestro estudio demostró que la vegetación y la condición de los combustibles existentes antes de la primera quema influencian grandemente los resultados de quemas subsiguientes.

Background

As the size and severity of wildfires continue to rise in the western US (Singleton et al. 2019; Williams et al. 2023; Parks and Abatzoglou 2020), managers are faced with a growing number of challenges that may ultimately impact the viability of long-term forest recovery. Within these large fire footprints, lower severity fire effects are generally considered ecologically beneficial and are often a lower priority for post-fire restoration and recovery actions. However, are areas that have burned at low-to moderate-severity restored in terms of forest structure, and resilient to future wildfire? This question is particularly relevant in many dry conifer forests across the western US, where forest management practices, the removal of Indigenous burning (Anderson 2005), and a century of fire exclusion have significantly altered forest structure and composition (Hagmann et al. 2021). The legacy of these practices has contributed to increased tree densities, dominance of shade-tolerant species, continuity and accumulation of fuels, and landscape homogeneity (Stephens et al. 2015; Naficy et al. 2010; Scholl and Taylor 2010; Safford and Stevens 2017; Hessburg et al. 2019). Together, the compounding effects of climatic change, shifts in fire regimes, and altered landscape conditions may trigger an increase in spatially overlapping

successive wildfires (i.e., reburns) (Coop et al. 2020; Nemens et al. 2022; Prichard et al. 2017; Harvey et al. 2023), with potential for increases in their frequency and severity.

Previous fires can modify the patterns, severity, and interactions of fire-on-fire events; the effects varying both temporally and spatially, with the interval between fires and initial fire severity influencing subsequent fire patterns (Prichard et al. 2017; Parks et al. 2014; Coppoletta et al. 2016; Van Wagtendonk, Van Wagtendonk, and Thode 2012; Collins et al. 2009). In turn, overlapping fires can facilitate feedbacks in which one fire impacts the occurrence and severity of a future fire (Harvey et al. 2023). These feedbacks are evidenced historically, where frequent low- to moderate-severity fire regimes that characterized many mixed-conifer, ponderosa pine (Pinus ponderosa Dougl. ex Laws. & C. Laws.), and Jeffrey pine (Pinus jeffreyi Grev. & Balf.) forests of the western US played an important role in disrupting fuel continuity, maintaining understory vegetation and overstory species composition, and ultimately creating landscape-level heterogeneity (Hessburg et al. 2015; Safford and Stevens 2017). Throughout time, this frequent low- to moderateseverity fire regime created a self-limiting stabilizing feedback, in which regular fires promoted future low- to Jasperse et al. Fire Ecology (2025) 21:46 Page 3 of 19

moderate-severity fire (Larson et al. 2013; Collins et al. 2009; Coppoletta et al. 2016; Murphy et al. 2021). This relationship has been demonstrated in contemporary systems in several studies, where previous fire footprints have been shown to moderate the behavior of subsequent fires, thereby minimizing fire spread, size, and severity (Teske et al. 2012; Prichard et al. 2017; Parks et al. 2014; Collins et al. 2009).

The fire-vegetation interactions of a landscape both influence and are influenced by the burn mosaics that result from previous fires (Airey Lauvaux, Skinner, and Taylor 2016; Prichard et al. 2017). Post-fire vegetation, fuel development, and forest structure, often linked to burn severity, are important factors in determining how an area reburns in one or more subsequent fires. For instance, an initial high-severity fire may result in substantial dead biomass, an accumulation of surface fuels, and a vegetation composition shift from conifers to resprouting species, which affects the severity of a future fire (Coop et al. 2020; Coppoletta et al. 2016; Lydersen et al. 2019; Airey Lauvaux, Skinner, and Taylor 2016; Coop et al. 2016). Furthermore, vegetation composition and structure following fire can influence the ability of landscapes to resist high-severity reburn and vegetative transitions, and recover towards forested states (Steel et al. 2021). Thus, in historically frequent-fire ecosystems, previous wildfire can act as both a stabilizing (i.e., selflimiting) and destabilizing (i.e., self-reinforcing) feedback process, thereby enhancing or diminishing resilience to future disturbance (Steel et al. 2021; Coop et al. 2020).

Particularly in areas that initially burn at high severity, post-fire changes can catalyze pronounced shifts in understory vegetation and forest structure. These changes have the potential to inhibit the ability of previous fires to moderate future fires and tend to drive subsequent high-severity fire, thereby contributing to a destabilizing feedback (Coppoletta et al. 2016; Van Wagtendonk, Van Wagtendonk, and Thode 2012). Shortinterval high-severity fire, in turn, can cause extensive and prolonged shifts, acting as a mechanism for vegetation-type conversion and ecological state changes in the long term (Coop et al. 2020; Johnstone et al. 2016). This reinforcing effect of wildfire, where stand-replacing fire promotes future stand-replacing fire (Thompson et al. 2007; Coop et al. 2020), has justifiably raised growing concern over the recovery and trajectory of these forest ecosystems in the future. Over time, it is possible that the adaptive mechanisms of these ecosystems are eroded to a point in which post-fire forest recovery and resiliency is compromised (Johnstone et al. 2016; Coop et al. 2020).

However, not all reburns facilitate a trajectory of transition, particularly those occurring at low-to moderate-severity. Rather, low-and moderate-severities are often

combined to uniformly characterize fire effects that restore ecosystem structure and function (Mallek et al. 2013; North et al. 2012; Williams et al. 2023). These effects have been demonstrated to reduce tree densities and fuel loads (Becker and Lutz 2016; Collins, Everett, and Stephens 2011), promoting resilience to future wildfire and thereby promoting a stabilizing feedback (Lydersen et al. 2017; Parks et al. 2014; Wu et al. 2023; Taylor et al. 2022). Previous studies also indicate that repeated low- to moderate-severity fires modify departed forest structure and composition (Prichard et al. 2017; Holden et al. 2007; Stevens-Rumann et al. 2016; Larson et al. 2013), and it has been suggested that two successive fires may promote restoration of pre-suppression stand structure in terms of stand density and gap creation in ponderosa pine (Taylor 2010; Ng et al. 2020; Lydersen and North 2012).

Despite these demonstrated effects, other studies point to the inability of low- to moderate-severity fire to substantially change forest structure to achieve restoration goals of lower tree densities, canopy gaps (Schmidt et al. 2006; Steel et al. 2021), and shifts in species composition (Paudel et al. 2022; Greenler et al. 2023) reflective of historical conditions. This is further evidenced by previous studies highlighting that prescribed fire treatments alone, even with multiple burns, had residual tree densities that greatly exceeded those described from historical or reference forests (Stephens et al. 2024; Hood et al. 2024). As such, the vulnerability in the face of enhanced forest stressors such as drought, insects, and disease is quite high relative to treatments involving mechanical tree removal (Collins et al. 2014; Hood et al. 2016).

While much of the research and management emphasis has focused on the short- and long-term effects of high-severity fires and especially high-severity reburns, we were specifically interested in examining the effects of repeated low- to moderate-severity fires to understand post-fire stand structure outcomes to identify future management options. Our study leveraged a unique opportunity to use extensive field data across three successive short-interval fires occurring in the northern Sierra Nevada, California between 2000 and 2021. Specifically, we asked the following questions: (1) what are the forest structural characteristics, weather conditions, and topographic variables that drive plot-level fire severity in a third successive fire (i.e., second reburn)? and (2) focusing specifically on plots that burned previously at low-to moderate-severity (in both the first and second fire), (a) what is the range of forest structural conditions following two "restorative" fires (i.e., low-to moderate-severity), (b) how do these conditions compare with historical estimates (natural range of variation, NRV), and (c) is there an association between these conditions and fire

Jasperse *et al. Fire Ecology* (2025) 21:46 Page 4 of 19

severity in a third fire? This research aims to understand how repeated fires influence forest structure and subsequent fire severity in dry mixed-conifer forests, with the ultimate goal of identifying post-fire stand structure characteristics that managers can target to meet desired restoration objectives and promote resiliency in the face of subsequent fire.

Methods

Study area

The study area covers approximately 10,545 ha located on the Plumas and Lassen National Forests in the northern Sierra Nevada, California (Fig. 1). Between 2000 and 2021, several wildfires occurred in short succession across the study area. Two initial, non-overlapping fires, the 2000 Storrie Fire and 2008 Rich Fire, burned a total of 25,160 ha. In 2012, the Chips Fire reburned approximately 10,166 ha within the Storrie Fire footprint and 379 ha within the Rich Fire footprint. In 2021, the Dixie Fire

ignited in the southwest of the study area and reburned a majority of the previous fire footprints. Our sampling focused mostly on the area originally burned in the Storrie and Rich fires (initial) which then reburned in the Chips Fire (second) and then reburned again in the Dixie Fire (third).

Topography in the area is steep, with elevation ranging from 525 to 2160 m. The study site was predominantly mixed-conifer forest prior to the initial fires. Vegetation consisted of white fir (Abies concolor [Gordon & Glend.] Lindl. ex Hildebr.), Douglas-fir (Pseudotsuga menziesii [Mirb.] Franco var. menziesii), Jeffrey pine, sugar pine (Pinus lambertiana Dougl.), ponderosa pine, California black oak (Quercus kelloggii Newb.), and incense-cedar (Calocedrus decurrens [Torr.] Florin). Montane chaparral species, including manzanita (Arctostaphylos spp.) and wild lilac (Ceanothus spp.), were present in the study area and were dominant on lower elevation, drier canyon slopes. Red fir (Abies magnifica A. Murray bis) stands

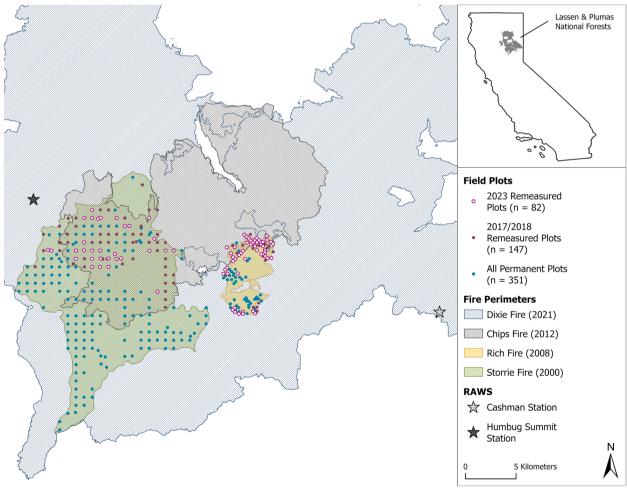


Fig. 1 Map of study area location in the Storrie, Rich, Chips, and Dixie fires in the Plumas and Lassen National Forests, California, USA. Circles represent permanent field plot locations established in 2009 to 2012 (n = 351) and field plot locations resampled in 2017 or 2018 (n = 147) and 2023 (n = 82). Stars represent Remote Automatic Weather Stations (RAWS)

Jasperse et al. Fire Ecology (2025) 21:46 Page 5 of 19

were present in moist, higher elevation sites above 1800 m. Historically, this area was characterized by a low- to moderate-severity, frequent fire regime with a mean fire return interval of 8 to 22 years (Moody et al. 2006). However, in the century prior to the initial fires, only 15% of the area had burned (Coppoletta et al. 2016). The region is characterized by a Mediterranean climate with cold, wet winters and hot, dry summers. Average annual precipitation ranges from 950 to 2290 mm, with average minimum temperatures from 1.8 to 9.4 °C and maximum temperatures from 13.8 to 22.2 °C (http://www.prism.oregonstate. edu/normals/). Prior to the Dixie Fire, California experienced a record-breaking drought from 2012 to 2016 (Bedsworth et al. 2018), exacerbated by unusual warmth (A. P. Williams et al. 2015) and low Sierra Nevada snowpack levels (Dettinger and Anderson 2015). Hotter and drier than average conditions developed again in water year 2020, with half the state in an exceptional drought by the start of water year 2021 (Abatzoglou 2021).

Field data

This study utilized permanently marked field plots that were established by the US Forest Service (USFS) between 2009 and 2012 in the 2000 Storrie and 2008 Rich Fire footprints (Coppoletta et al. 2016). Plots were established in areas that were characterized by lower montane mixed-conifer forest prior to the initial fires and were placed on the vertices of an 800-m grid in the Storrie Fire and a 200-m grid in the Rich Fire. Plots were resampled in 2017 and 2018 after the second fire (2012 Chips Fire), and again in 2023, after the third fire (2021 Dixie Fire). Forest treatment history was determined using the Forest Service Activity Tracking System (FACTS) and verified on-site, with sampling only completed at sites without visual evidence of forest treatment or activity such as salvage logging. All sampling methods followed the USFS Common Stand Exam Protocol, consisting of a plot center with two concentric circular plots, with four transects in each cardinal direction (USDA Forest Service 2007).

Within the larger 11.3 m radius plot, we collected tree data (> 12.7 cm diameter at breast height, dbh) including species, dbh, and status (live or dead). We measured fuels following a planar intersect method (Brown 1974) that included measurements for duff, litter, and fuel depth, fine woody fuels, and 1000-h fuels along the length of each 11.3-m transect. A smaller 5 m radius plot was used to measure seedlings and saplings. Within the small plot, the dbh, height, number, species, and status of saplings (> 1.7 m tall) and height class, species, and status of seedlings (< 1.7 m tall) were measured for conifers and hardwoods. Percent shrub cover was visually estimated in each quadrant of the small plot; total shrub cover was

then calculated as the average across quadrants. All data and statistical analyses were conducted with RStudio software version 2024.04.2 +764 (R Core Team 2024), using a significance level of P < 0.05 to determine statistical significance. Live and snag basal area (m² ha¹), coarse woody debris loads (Mg ha¹), and live tree density (trees ha¹) were calculated for each plot and time period (i.e., after the second and third fires) using the "BerkeleyForestAnalytics" package (Rutherford, Foster, and Battles 2024). Tree density and basal area calculations included conifer and hardwood trees > 12.7 cm dbh.

Plot selection

We used the following criteria to select plots to resample in 2023 (post-Dixie Fire): (1) plots were resampled in 2017 or 2018 after the second fire (post-Chips Fire), (2) had adequate data quality in 2017 and 2018 with consistency in data collection methods and minimal missing or suspect values, and (3) had no documented treatments after the second or third fires. To ensure sampling captured the range of conditions found across the study area, plots were stratified based on forest structure measurements taken in 2017 and 2018 after the second fire. We used both live tree and snag basal area, including conifers and hardwoods, as our primary metric to indicate forest structure and stratified plots based on basal area classes from low to high.

Spatial data

Fire severity for each fire was estimated using the Relative Differenced Normalized Burn Ratio (RdNBR) to facilitate comparisons with prior analyses (Coppoletta et al. 2016) and for its utility in comparing severity between fires throughout time and space, allowing for landscape-level analyses (Miller and Thode 2007). Thirty-meter resolution RdNBR rasters were generated for the Storrie, Rich, Chips, and Dixie fires in Google Earth Engine (Gorelick et al. 2017) from methods established by Parks et al. (2018). This methodology uses a mean compositing approach over a specified date range (June to September) pre-fire (1 year before) and postfire (1 year after) (Parks et al. 2018). RdNBR values were then categorized into unchanged (< 69), low (69 to 315), moderate (316 to 640), and highseverity (≥ 641) classes based on thresholds determined by Miller and Thode (2007). Field verification of RdNBR using methods such as Composite Burn Index (CBI) plots or other fieldbased methods were not conducted in this study. Topographic variables, including slope (%) and elevation (m), were derived for each plot from the LANDFIRE database (https://www.landfire.gov). To characterize fire severity and topography at each plot, we used the "sf" package in

Jasperse et al. Fire Ecology (2025) 21:46 Page 6 of 19

R (Pebesma and Bivand 2023; Pebesma 2018) to extract RdNBR, slope, and elevation raster values to plot points with bilinear interpolation.

To assess the importance of fire weather as a driver of fire severity in the 2021 Dixie Fire, we extracted average daily weather variables corresponding to each plot on its estimated burn day. Weather data from two Remote Automated Weather Stations (RAWS) near our study region and within the Dixie Fire perimeter were collected from the Fire and Aviation Application Information and the Desert Research Institute Program for Climate, Ecosystem, and Fire Applications portals. Distance from the RAWS to plots ranged from approximately 3 to 25 km depending on plot location. Hourly relative humidity (%), dry bulb temperature (°C), windspeed (km h⁻¹), burning index (BI), and energy release component (ERC) were extracted and processed in Fire Family Plus 5 (https:// www.firelab.org/project/firefamilyplus). Energy release component represents potential fire intensity, incorporating live and dead fuel moisture from days to weeks, while BI represents potential flame length by incorporating wind speed (Taylor et al. 2022). Hourly weather data was averaged for each day between 11:00 and 18:00 PST to represent periods of heightened weather influence on fire behavior (Stephens et al. 2022).

To estimate the burn day for each plot, we generated a daily fire perimeter map for the Dixie Fire. We utilized combined Moderate Resolution Imaging Radiometer Spectrum C6 (MODIS) and Visible Infrared Imaging Radiometer Suite (VIIRS) V1, 375 m active fire detection points generated by Estabrook (2025) to interpolate daily fire perimeters. Daily fire perimeters were interpolated using a convex hull algorithm in the "sf" package, following methodology from Briones-Herrera et al. (2020) and Stephens et al. (2022). Average daily temperature (°C), relative humidity (%), BI, and ERC were assigned to each plot based on its estimated burn date. Weather variables from each RAWS were joined to plots based on geographic proximity, assigning data from Cashman RAWS to plots located in the Rich Fire perimeter and Humbug Summit RAWS to plots within the Storrie Fire perimeter (Fig. 1).

To assess how weather conditions during the Dixie Fire deviated from average conditions preceding the Dixie Fire for the area, we compared weather conditions for the year of the Dixie Fire (2021) with those of previous years (2012 to 2017) following methodology from Stephens et al. (2022). To estimate conditions for years preceding the Dixie Fire for the region, the "boot" package (Davison and Hinkley 1997; Canty and Ripley 2024) was used to bootstrap 95% confidence intervals for each weather variable from 2012 to 2017 across RAWS. Bootstrapping was then performed for 2021 to assess if daily weather

conditions during the Dixie Fire fell outside the region's baseline average for years preceding the Dixie Fire. We focused on the months of July and August for our analysis given that the majority of our plots burned during that period.

Data analysis

Drivers of fire severity in a second reburn

To determine the key drivers of reburn severity in a third fire, we utilized plot-level data collected in 2017 and 2018 (n= 83), in addition to topographic and weather data. This part of the analysis considered plots across all fire severity classes (i.e., including high-severity) and did not utilize 2023 field data.

We utilized a two-stage approach to assess the effect of weather, topography, and plot-level variables on fire severity in the third fire. First, a random forest (RF) analysis was performed to identify potential influential variables and to rank their relative importance in explaining the dependent variable, Dixie Fire severity (RdNBR). The RF generates multiple regression trees, randomly selecting a subsample from the data for each tree. Along with slope, elevation, BI, temperature, wind, relative humidity, and ERC, five plot-level variables were selected for the RF to represent structural conditions post-second fire and pre-third fire, including live basal area, snag basal area, live tree density, coarse woody debris load (1000-h fuels), and shrub cover. Variables were selected given their importance for forest structure and fire severity. We generated three replicate conditional inference trees, each with 5000 regression trees, using the "party" package (Hothorn et al. 2006; Zeileis et al. 2008; Strobl et al. 2007, 2008). The number of predictor variables used to assemble each tree was set to the square root of the total number of variables. Conditional permutation measures were used to rank and indicate predictor variables with importance values greater than the absolute value of the lowest negative score. Variables ranked greater than this value in the three replicates were thus considered influential and used in the second step, a regression tree (RT) analysis. The RT analysis was used to identify the predictor variable thresholds that best explained the observed variation in the Dixie Fire RdNBR values. All variables identified as influential were included in the RT. The RT used a conditional inference tree approach and a partitioning algorithm with an alpha level of 0.05 from Monte Carlo simulations.

Forest conditions following two "restorative" fires and how they fared in a third fire

To evaluate forest conditions following "restorative fires," plots that had previously burned at high severity prior to the 2021 Dixie Fire were excluded for this part of the

Jasperse et al. Fire Ecology (2025) 21:46 Page 7 of 19

analysis. We limited our analysis to plots that burned at low-to moderate-severity (< 641 RdNBR) in the first and second fires (n = 52). Field observations indicated a range of structural characteristics across these plots after the second and third fires, likely reflecting the variability in structural outcomes resulting from the interaction between initial conditions and fire severity. Rather than representing each plot-level variable individually, we used a clustering approach to simplify data across the diverse suite of conditions within our plots. We used the same five plot-level variables from our first research question to represent structural conditions post-second fire and pre-third fire, including live basal area, snag basal area, live tree density, coarse woody debris load, and shrub cover. A principal component analysis (PCA) was used as a dimension reduction measure to simplify the plot-level data. We used the "vegan" package (Oksanen et al. 2023) to reduce our five plot-level structure metrics into principal components (PC), which represent a composite of variables and characterize variation in the data (Gotelli and Ellison 2013). Contributions to the overall PCA were assessed by examining percent of variance explained by each PC, ensuring optimal dimension reduction to PCs explaining the majority of variation in the data (Gotelli and Ellison 2013).

We performed a K-means clustering on the retained PCs, with 25 randomly generated initial configurations, using the "stats" package (R Core Team 2024). The K-means clustering algorithm utilizes a distance measure minimizing the sums of squares of distances from each object to its assigned cluster (Gotelli and Ellison 2013). A cluster size of k = 3 was determined as the optimal number of clusters based on results from an elbow plot generated with the "NbClust" package (Charrad et al. 2014). We investigated how fire severity patterns in the third fire varied among the three resulting clusters by testing for differences in Dixie Fire severity with a one-way analysis of variance (ANOVA) using the "stats" package (R Core Team 2024) with a significance level of P < 0.05. Dixie Fire RdNBR and ANOVA residuals were tested for normality using Shapiro-Wilk tests and variances were assessed using Levene's tests using the "stats" package (Shapiro and Wilk 1965; Whitlock and Schluter 2015; R Core Team 2024).

Comparisons of forest structure pre- and post-third fire to historical estimates

To understand the trajectory of plots throughout time, we compared forest structural metrics before and after the third fire (second reburn) across each cluster. Although 52 plots were used in the K-means analysis, only 30 of those plots were remeasured in 2023. We compared how metrics in these 30 plots changed pre- and

post-third fire across all plots and within each cluster. We evaluated significant differences using the two-sided Wilcoxon signed-rank test with Bonferroni correction (Wilcoxon 1945; Whitlock and Schluter 2015); R Core Team 2024), a non-parametric alternative to the paired t-test, to account for non-normal distributions of some variables and multiple comparisons within the data. Variables were evaluated for normality utilizing Shapiro-Wilk tests using the "stats" package (Shapiro and Wilk 1965); R Core Team 2024) and differences from the Wilcoxon signedrank tests were considered significant when P < 0.05. To evaluate if a third fire moved forest conditions closer to historical conditions, we used average estimates of presettlement natural range of variation (NRV) for tree density (60 to 328 trees ha⁻¹) and basal area (21 to 54 m² ha⁻¹), and estimates of historical average coarse woody debris from reference studies (1-1000-h fuels; 17.7 Mg ha⁻¹) for yellow pine and mixed-conifer forests of the Sierra Nevada (Safford and Stevens 2017).

Results

Drivers of fire severity in a third fire

The RF analysis identified five potential influential predictor variables of Dixie Fire severity (Fig. 2a). Snag basal area was identified as the most important predictor in all three RF replicates. Coarse woody debris was ranked moderately associated, while elevation, slope, and ERC were identified as marginally associated. Live tree density, relative humidity, BI, wind, temperature, shrub cover, and live basal area were not identified as predictor variables given they did not meet the conditional permutation conditions for each replicate, and thus were not included in the RT. The RT produced a tree with two terminal nodes (Fig. 2b), with snag basal area as the only significant explanatory variable (P = 0.001). Predicted Dixie Fire severity was on average highest in plots with a snag basal area greater than $11.62 \text{ m}^2 \text{ ha}^{-1}$ (n = 40) and lowest in plots with a snag basal area of 11.62 m² ha⁻¹ or below (n = 43).

Results from the 95% confidence interval bootstrapping analysis indicated that ERC and relative humidity had the greatest number of days deviating from baseline conditions for July and August 2021 during the Dixie Fire (Fig. 3a and d). Across the days in which plots included in the RF and RT analysis burned (n=83 plots over 7 days), relative humidity was below baseline conditions for 3 days, while ERC and BI exceeded baseline conditions for 5 and 2 days, respectively (Fig. 3a and c). Notably, relative humidity and ERC were departed from estimated baseline conditions on the day of Dixie Fire ignition (July 13), and relative humidity, ERC, and BI were all departed on the day in which the majority of our plots burned (July 20). Temperature remained within the normal range for most of July and August (Fig. 3b).

Jasperse *et al. Fire Ecology* (2025) 21:46 Page 8 of 19

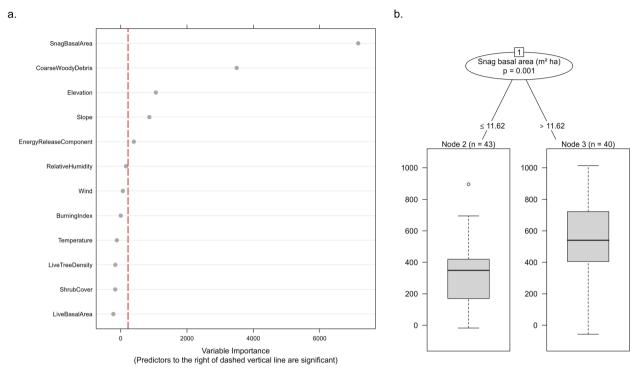


Fig. 2 Variable importance plot (a) for the 12 variables included in the random forest (RF) analysis for Dixie Fire reburn severity (relativized dNBR; RdNBR). The Y-axis indicates predictor variables included in each variable importance replicate. The x-axis indicates the median conditional variable importance value, where variables with importance values higher than the absolute value of the lowest negative score were considered potentially important. Pre-Dixie Fire plot measurements were taken in 2017 and 2018 (n = 83) and weather measurements are from Remote Automatic Weather Stations (RAWS) in the Plumas and Lassen National Forests, California, USA. Regression tree (RT; **b**) for Dixie Fire reburn severity (RdNBR) using the significant predictor variables identified in the RF analysis. The top node displays significant explanatory variables with their associated splitting threshold values and the number of plots in each group. The Y-axis of each terminal node represents fire severity (RdNBR), where RdNBR ≥ 641 indicates high severity. Horizontal black lines within each boxplot show the median RdNBR value for the respective group. *P* values were derived from Monte Carlo randomization tests with an alpha level of 0.05 to determine statistical significance

Forest conditions following two "restorative" fires and how they fared in a third fire

PC1 and PC2 were retained from the PCA for the K-means analysis, cumulatively explaining approximately 74.2% of the variance in our data. PC1 explained 45.1% of the variance, with highest contributions from live basal area and live tree density, respectively. PC2 explained 29.1% of the variance, with highest contributions from coarse woody debris and snag basal area, respectively. The K-means clustering on PC1 and PC2 resulted in three distinct structural clusters (Fig. 4d), with varying numbers of plots in each group (n = 13, 29, and 10). Median structural metrics that indicated different salient characteristics were identified for each cluster (Table 1; Fig. 4a-c). Cluster 1 was associated with relatively high shrub cover (48.8%), cluster 2 with relatively high live basal area $(38.3 \text{ m}^2 \text{ ha}^{-1})$ and live tree density (175.0 trees)ha⁻¹), and cluster 3 with relatively high coarse woody debris (120.3 Mg ha⁻¹) and snag basal area (61.5 m² ha⁻¹). We found a significant difference in Dixie Fire severity among clusters ($F_{2,49}$ = 3.622, P = 0.034; Fig. 5). Among the clusters, the highest average RdNBR (i.e., higher fire severity) was associated with the cluster with highest coarse woody debris and snag basal area (cluster 3) post-second fire. Plots in this cluster burned at significantly higher severity (P= 0.029) compared to plots with high shrub cover (cluster 1; Fig. 5). They did not burn significantly higher than plots characterized by high live tree density and basal area (cluster 2; Fig. 5).

Comparisons of forest structure pre- and post-third fire to historical estimates

After the third fire, we found a decrease in median live tree density (P= 0.003) and median live basal area (P= 0.017) overall across plots compared to after the second fire (Fig. 6a, b), and in plots with the highest live tree density and live basal area post-second fire (cluster 2; P= 0.014, P= 0.015, respectively). After the second fire (first reburn), 81% of plots in this cluster were within the NRV for live tree density (60 to 328 trees $^{-1}$) and 13% were

Jasperse *et al. Fire Ecology* (2025) 21:46 Page 9 of 19

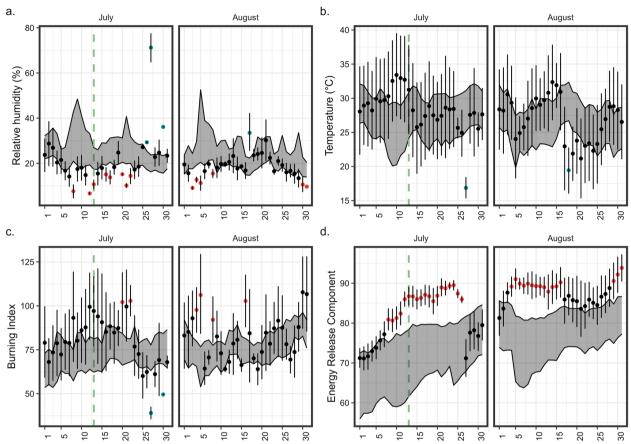


Fig. 3 Departure of Dixie Fire weather from baseline conditions preceding the Dixie Fire (2012 to 2017) for relative humidity (**a**), temperature (**b**), burning index (Bl; **c**), and energy release component (ERC; **d**) generated using 95% confidence interval bootstrapping based on methodology from Stephens et al. (2022). The vertical dashed green line indicates the start of the Dixie Fire (July 13, 2021). Error bars are confidence intervals for 2021 and gray shaded areas are bootstrapped 95% confidence intervals for baseline weather conditions. Black dots denote observations within the normal range of baseline conditions, red dots indicate observations above, and green dots indicate observations below. For relative humidity, red dots indicate observations below the baseline and green dots indicate observations above. Weather measurements are from Remote Automatic Weather Stations (RAWS) located in the Plumas and Lassen National Forests, California, USA

above, while 69% were within the NRV for live basal area (21 to $54 \text{ m}^2 \text{ ha}^{-1}$) and 25% were above.

After the third fire, 31% of plots in this cluster were within the NRV for live tree density, while 13% of plots were within the NRV for live basal area and 13% above. In plots with high shrub cover after the second fire (cluster 1), 38% of twice-burned plots were within the NRV for live tree density, while 25% were within the NRV for live basal area. After the third fire, 13% of plots in this cluster had a live tree density within the NRV, while 25% were within the NRV for live basal area. In plots with high coarse woody debris and snag basal area after the second fire (cluster 3), 33% of twice-burned plots were within the NRV for live tree density, while 17% of plots were within the NRV for live basal area. After the third fire, 17% of plots in this cluster were within the NRV for live tree density and live basal area.

Overall, we found no significant change in median shrub cover (Fig. 6c), coarse woody debris load, or snag basal area (Fig. 7a, b) after the third fire after Bonferroni correction. In plots with high shrub cover after the second fire (cluster 1), 63% of twice-burned plots had a coarse woody debris load above the historical estimate (17.7 Mg ha⁻¹), while 38% of thrice-burned plots were above. For plots with high live tree density and live basal area after the second fire (cluster 2), 44% of twiceburned plots had a coarse woody debris load above the historical estimate, while 31% of thrice-burned plots were above. For plots with high coarse woody debris load and snag basal area after the second fire, 100% of twice-burned plots had a coarse woody debris load above the historical estimate, while 67% of thriceburned plots were above.

Jasperse *et al. Fire Ecology* (2025) 21:46 Page 10 of 19

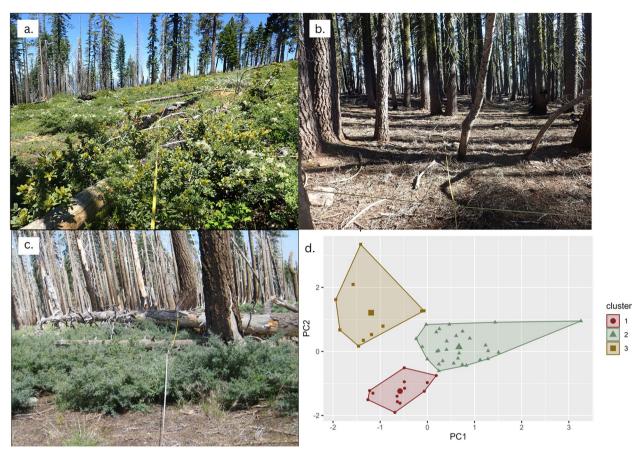


Fig. 4 Plot photos representing structural conditions after the second fire (measurements taken in 2017 or 2018) across K-means clusters (**a–c**), where cluster 1 (**a**) represents plots with relatively high shrub cover, cluster 2 (**b**) represents plots with relatively high live tree density and basal area, and cluster 3 (**c**) represents plots with relatively high coarse woody debris and snag basal area. K-means clusters (*n* = 52; **d**) with principal component analysis (PCA) reduction, where axes represent principal component 1 (PC1) and principal component 2 (PC2) scores, indicating the position of each plot in the PCA reduced dimensional space. Photo credit: USDA Forest Service, 2017 and 2018

Discussion

In the era of contemporary fire suppression, wild-fires that burn the same area in short succession (< 15 years) are a relatively new phenomenon (Prichard et al. 2017; Buma et al. 2020). Yet under historical fire regimes, many western forests routinely experienced short-interval reburns, which were a key regulating

process that limited severe fire effects and large-scale conversions to non-forest vegetation states (Hessburg et al. 2019). The reintroduction of low- to moderate-severity fire in long fire-excluded forests (so-called first-entry fires) has been shown to reduce surface fuels (Cansler et al. 2019), tree densities, and ladder fuels (e.g., Chamberlain et al. 2024), which collectively

Table 1 Structural characteristic medians for plots (n = 52) after the second fire (2012 Chips Fire; measurements taken in 2017 and 2018) by K-means clusters and the number of plots used in the K-means analysis resampled after the third fire (2021 Dixie Fire; measurements taken in 2023). Bold indicates key structural metrics characterizing the corresponding cluster. Plot measurements completed in the Plumas and Lassen National Forests, California, USA

Cluster	Coarse woody debris (Mg ha ⁻¹)	Live tree density (trees ha ⁻¹)	Shrub cover (%)	Snag basal area (m² ha ⁻¹)	Live basal area (m² ha ⁻¹)	Plots resampled in 2023 (n = 30)
1	13.0	25.0	48.8	4.2	8.2	8
2	19.0	175.0	3.0	11.4	38.3	16
3	120.3	0.0	15.4	61.5	0.0	6

Jasperse et al. Fire Ecology (2025) 21:46 Page 11 of 19

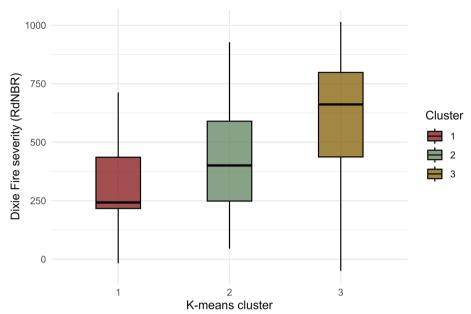


Fig. 5 Dixie Fire severity (relativized dNBR; RdNBR) by K-means cluster (n = 52). Higher RdNBR values indicate increased severity, where values ≥ 641 represent high severity (Miller and Thode 2007). Plot structural data is based on plot measurements taken in 2017 or 2018 pre-Dixie Fire in the Plumas and Lassen National Forests, California, USA

moderate subsequent wildfire effects (Tortorelli et al. 2024). Therefore, in forests that historically experienced relatively frequent fire, it is often assumed that reburning at less than high severity is largely restorative. It has been argued that this type of process-based restoration can be effective at restoring historical forest conditions on its own, without the need for structural restoration (i.e., mechanical treatment; Stephenson 1999). Our results add some nuance to this argument. In particular, the influence of dead wood, as both snags and heavy fuels, in contributing to higher-severity fire effects in a third fire (i.e., second reburn) suggests that the long legacy of fire exclusion may persist even after two lowto moderate-severity fires. Therefore, the assumption that forests will be restored after two low- to moderateseverity fires may not be accurate; it may take three or more fires to achieve forest overstory, understory, and fuel restoration objectives.

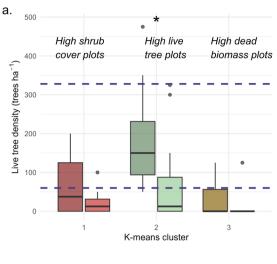
Drivers of fire severity in a third fire (second reburn)

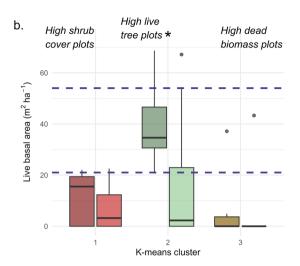
Snag basal area was positively associated with higher fire severity in the third fire. Interestingly, coarse woody debris was not identified as a significant contributor in the RT for reburn severity despite findings from the RF and K-means analyses. We presume this result reflects the high degree of correlation between the two variables, where snags contribute to corresponding coarse woody surface fuels accumulations over time. It is likely that the variation in snag fall and coarse woody debris

accumulation after fire varies temporally and with prefire stand structure and species composition (Peterson et al. 2023). It is important to note that the interval and timing of measurements in our study may have impacted the observed levels of coarse woody debris and snags. Measurements collected in 2017 and 2018 (i.e., after the second fire) used in this analysis were taken 3 to 4 years prior to the third fire (i.e., second reburn). It is possible that snags measured at this time further degraded into coarse woody debris in the 3 to 4 years leading up to the 2021 Dixie Fire. As a result, our estimated snag basal area could be over-representative and coarse woody debris loads under-representative of actual conditions prior to the third fire. Despite potential limitations in our measurements, our results overall indicate the important role that dead biomass (whether snags or coarse woody debris) resulting from one fire has in contributing to subsequent fire severity, as also demonstrated by Stephens et al. (2022) and in studies within our study area (Coppoletta et al. 2016; Lydersen et al. 2019).

Among the weather variables measured, ERC and relative humidity departed from the baseline (2012 to 2017) for more days during July and August 2021 than other weather indices measured. This finding corresponds with results from the RF, where ERC was identified as potentially important for predicting Dixie Fire severity. These departures also indicate significantly drier than average conditions across the fire area both in the near

Jasperse et al. Fire Ecology (2025) 21:46 Page 12 of 19





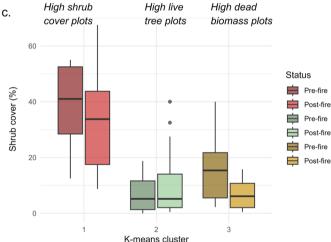


Fig. 6 Change in (a) live tree density, (b) live basal area, and (c) shrub cover pre- and post-Dixie Fire by K-means cluster (n = 30). Dashed blue lines represent the natural range of variation (NRV) for Sierra Nevada yellow pine and mixed-conifer forest, including tree density ranging from 60 to 328 trees ha⁻¹ and live basal area ranging from 21 to 54 m² ha⁻¹. Circles represent outliers. Clusters denoted with an asterisk indicate a significant result. Pre-Dixie Fire measurements were taken in 2017 or 2018 and post-Dixie Fire measurements were taken in 2023, in the Plumas and Lassen National Forests, California, USA

term (relative humidity) and long term (ERC). These dry conditions leading up to the Dixie Fire, combined with potential antecedent drought-induced aridity, likely had a considerable effect on pre-conditioning fuels across the landscape. While it is surprising that weather was not identified as significant in predicting Dixie Fire severity in our RT analysis, this lack of observed significance of weather conditions on fire severity in our plots may also point to the potential role of fuels, specifically the observed high levels of dead biomass created from prior fires in our study, coupled with dry conditions, in driving fire behavior and severity.

It is important to note that there are limitations in using RAWS data to characterize fire weather in our study. For

example, RAWS data do not capture the high degree of spatial variability across our study area because stations are few and far between. While these weather stations do provide an approximation of conditions, finer spatial and temporal resolution are needed to better explain variability in conditions and provide more localized context. Furthermore, bootstrapped 95% confidence interval estimates may reflect a range of conditions between the two RAWS, given varying site locations and conditions (i.e., topographic differences) that in turn affect weather measurements. Given gaps in data availability for each RAWS, our analysis period was limited to 2012 to 2017 and thus does not capture longer-term conditions for the region or years immediately preceding the Dixie Fire. Additionally,

Jasperse et al. Fire Ecology (2025) 21:46 Page 13 of 19

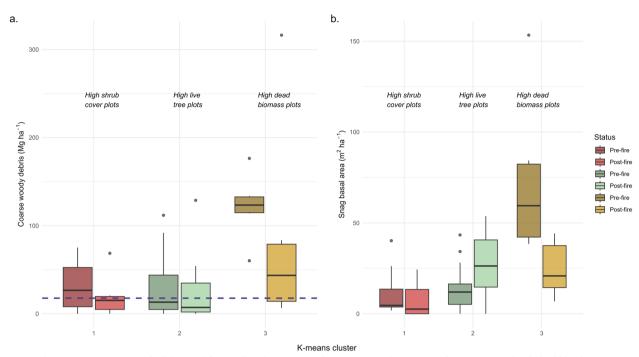


Fig. 7 Change in (a) coarse woody debris and (b) snag basal area pre- and post-Dixie Fire by K-means cluster (n = 30). The dashed blue line represents the estimated historical average coarse woody debris load (17.7 Mg ha⁻¹) for Sierra Nevada yellow pine and mixed-conifer forest. Circles represent outliers. Pre-Dixie Fire measurements were taken in 2017 or 2018 and post-Dixie Fire measurements were taken in 2023, in the Plumas and Lassen National Forests, California, USA

it is possible that because many of our plots burned on the same days and thus had similar weather inputs in our RF and RT analyses, a lack of variability could have contributed to the observed insignificance.

It is also important to note that although RdNBR is a widely used measure of fire severity, the method used to assign severity indices in this study produces an estimated RdNBR that benefits from field-verification methods such as CBI plots. However, in our study, RdNBR values were not field-verified using CBI plots or other validation methods, which may limit the assessment and accuracy of these remotely sensed severity estimates. Despite this limitation, Saberi and Harvey (2023) found that when short-interval reburns are preceded by lower severity (i.e., non-stand replacing) fires, RdNBR tends to align more closely with its interpretation for single fires. Given that many of the plots in our analysis burned at low-to moderate- severity prior to the third fire, RdNBR estimates likely provide a reasonable approximation of fire severity.

Forest conditions following two "restorative" fires and how they fared in a third fire

Snag basal area and coarse woody debris have been identified as significant predictors of severity in a second fire (Lydersen et al. 2019; Coppoletta et al. 2016; Collins et al.

2018). Our finding that, even in areas burned twice at low-to moderate-severity, high snag basal area and coarse woody debris loads were associated with significantly higher severities than plots with high shrub cover indicates that these variables are important in a third fire as well. These results also highlight that the contribution of these structural characteristics in driving reburn severity was evident in plots across the full range of past fire severity, including those with a history of low- to moderate-severity fire. How snags directly impact fire behavior is not well understood (Donato et al. 2013). However, the presence of snags can result in high heat generation during combustion (Brown, Reinhardt, and Kramer 2003; Stephens 2004). Consequently, snags and associated heavy fuel accumulation can act as mechanisms for increased smoldering combustion, ember production, crowning and torching, and spot fire ignition, thereby facilitating fire spread and rate of growth (Ritchie et al. 2013; Stephens 2004; Van Wagtendonk 2006; Stephens and Moghaddas 2005).

The succession of dead biomass post-fire can be a reinforcing mechanism for reburns, given the long residence time and smoldering characteristics of coarse woody debris (Brown, Reinhardt, and Kramer 2003; Johnson et al. 2020; Van Wagtendonk 2006). This relationship, understood as the "reburn hypothesis," suggests that

Jasperse et al. Fire Ecology (2025) 21:46 Page 14 of 19

extensive areas of post-fire snags are prone to reburn at higher severity with the accumulation of coarse woody debris and regeneration of shrubs over time (Johnson et al. 2020; McIver and Starr 2001). In such instances, the likelihood of long-term conversion from forest to either shrub- or grass-dominated can be quite high (Coop et al. 2020). Among plots resampled post-Dixie Fire (n = 30), seven plots had no live trees or saplings after the second fire, and 13 plots had no live trees or saplings after the third fire, potentially indicating a shift towards nonforested conditions following successive reburns in our study. Multiple reburns can further impact the dynamics of dead biomass, influencing snag recruitment, fall rates, decomposition, and surface fuel accumulation post-reburn, while contributing to future fire effects. These dynamics were exemplified in our study, in which dead biomass produced following the second fire was likely influenced by a third fire through consumption of available material and possible impacts to standing snags during reburn. Furthermore, we found that these same structural characteristics after the second fire also drove fire severity in the subsequent reburn.

Shrub cover was not identified as a significant driver of severity in the third fire in our study. The lack of significant influence of shrub cover on reburn severity aligns with findings of previous studies (e.g., Collins et al. 2018), where shrub cover in areas burned at moderate severity had little influence on the severity of a subsequent fire. Similarly, Brodie et al. (2024) demonstrated generally lower fire severity in areas with higher pre-fire shrub cover. Collectively, it appears that shrubs in stands with live overstory trees may ameliorate fire effects, which is generally counter to findings on the influence of shrubs where overstory trees were largely fire-killed (Coppoletta et al. 2016). The effect of shrub cover on fire intensity can vary depending on age and live fuel moisture. Young shrubs with high fuel moisture can act as heat sinks reducing fire intensity (Stephens et al. 2018) but can burn at increased intensity as they mature and live fuel moisture decreases. The presence of substantial coarse woody debris intermixed with shrubs may also exacerbate fire intensity as the combustion of long-burning woody fuels pre-heat and ultimately reduce the live fuel moisture of shrubs.

Management implications

Our results indicating a range of live basal area and live tree densities after both a second and third fire suggest that fire effects to stand structure, and particularly tree density, can vary significantly within the low- to moderate-severity class as highlighted in previous studies (Collins et al. 2018). In the cluster with the most live trees remaining after the second fire (cluster 2), a third

fire reduced live tree density and live basal area below the NRV in over half of plots (69% and 75%, respectively). In contrast, for plots with few live trees after the second fire and high levels of coarse woody debris and snags (cluster 3), a third fire resulted in only one plot within the NRV for live tree density and live basal area. These results suggest that the influence of highly departed forest conditions (i.e., too many trees, too much surface fuel) can manifest itself even after experiencing "restorative" burns due to the lasting legacy of fire-killed trees. The fact that high coarse woody fuel accumulations and stand densities in some plots persisted not only after a first fire but also after the second fire is further evidence of this legacy. Particularly in the current context of extremely large wildfires (Safford et al. 2022) with significant areas experiencing short-interval reburns, our findings suggest that a diverse set of management tools, including mechanical thinning, will be needed to achieve desired restoration outcomes.

Mechanical thinning treatments can be effective in reducing canopy bulk density and limiting fire spread (Brodie et al. 2024). However, these treatments may be limited in their ability to achieve adequate surface fuel reduction, which can result in more variable wildfire outcomes (Knapp et al. 2004; Stephens et al. 2024). In contrast, prescribed fire can significantly reduce fuel loads (Stephens and Moghaddas 2005) that contribute to scorching, crown fire behavior, and associated tree mortality (Brodie et al. 2024). Numerous studies suggest the efficacy of combined mechanical treatment with low- to moderate-severity fire in reducing future fire severity (Davis et al. 2024). Studies have shown that forests that are treated with a combination of mechanical treatments and prescribed fire are able to largely resist burning at high severity (Shive et al. 2024), and significantly reduce modeled fire behavior and predicted mortality (Stephens et al. 2009), even during extreme weather and fire growth conditions (Lydersen et al. 2017; Brodie et al. 2024). Prioritizing treatments prior to an initial fire that reduce stand density have the potential to also reduce post-fire standing snags, coarse woody debris, and ultimately the severity of a subsequent fire (Coppoletta et al. 2016).

In addition to buffering future fire severity, previous studies have shown the effectiveness of tailored mechanical and prescribed fire treatments in promoting ecosystem structure and processes that are more aligned with historical conditions. Thinning and fuel treatments can reduce forest vulnerability to climate extremes such as drought by reducing tree competition for water and promoting more drought-tolerant species (Low et al. 2021; North et al. 2022), where repeat fire alone may not be able to (Paudel et al. 2022). Findings from a 20-year forest

Jasperse et al. Fire Ecology (2025) 21:46 Page 15 of 19

restoration study in the northern Sierra Nevada demonstrate the utility of combined mechanical treatments and prescribed fire in reducing stand density index (SDI) to within the partial competition range (25 to 34%), indicating reduced inter-tree competition comparable to historical mixed-conifer forests (Stephens et al. 2024). This notion of combined treatments facilitating stand structure that is more aligned with historical conditions is further supported by North et al. (2007), where a combination of understory thinning and prescribed fire were able to significantly reduce stand density and promote spatial heterogeneity reflective of historical conditions. Results from these studies highlight that effective treatments in contemporary stands should substantially reduce small- to moderate-sized tree densities, minimize stem clustering, and decrease the percentage of shadetolerant species (North et al. 2007). While not directly addressed in our study, it is relevant to note that field observations across our plots indicated prolific resprouting of California black oak (Quercus kelloggii) despite areas of high conifer mortality. These observations coincide with previous studies within our study region (Stephens et al. 2023; Nemens et al. 2022) and underscore an opportunity for California black oak to reestablish dominance in many of these landscapes post-Dixie Fire particularly in areas where conifers may be less likely to persist under current, post-fire, or future climatic conditions (Stephens et al. 2023).

It is also critical that management in these systems focus not only on targeting conditions prior to the initial fire, but also consider the heterogeneous post-fire conditions following subsequent reburns that in turn influence future fire severity. Our results demonstrate that some areas retained relatively high live tree densities and basal area after the second fire (i.e., cluster 2), indicating a need for proactive restoration actions. In areas with high dead biomass post-fire (i.e., cluster 3), selective removal of standing snags could also reduce the accumulation of coarse woody debris over time (Stevens-Rumann et al. 2012), potentially buffering subsequent fire severity. Uniform prescriptions of snag retention and downed woody material contrast with the historically patchy distribution of biomass across dry conifer forests (Holden et al. 2007; North et al. 2009; Stephens and Fulé 2005; Stephens et al. 2007). Retaining the largest post-fire snags, coupled with flexible retention guidelines, could enable conditions more characteristic of frequent-fire forests (Hessburg et al. 2015). However, the degree to which managers should plan for retention and removal of snags and coarse woody debris is an important question; management approaches will need to balance both fire hazard reduction while ensuring the ecological function that they support.

Conclusion

As wildfires continue to increase in size and severity, many forests across the western US are experiencing an overlap of successive fires. How repeated fires influence future fire severity, when pre-fire stand conditions are fundamentally departed, raises critical questions for management of these systems. Furthermore, while reburns have the potential to act as a mechanism for reintroducing reoccurring fire that was historically a critical component of these frequent-fire forests, the ability of repeat low- to moderate-severity fire to restore forest structure is an important management consideration. Low- to moderate-severity fire has been previously demonstrated to restore ecosystem processes and reduce future fire severity long-term, but our results indicate that it can also create fuel conditions that can drive higher fire severity in successive fires. Post-fire outcomes in these structurally and compositionally departed forests are nuanced. In our study, successive low- to moderateseverity fires resulted in distinct structural groups representing a range of conditions characterized by high dead biomass, high live tree density and basal area, and high shrub cover. We found that following a second fire, many plots still exceeded historical estimates of stand structure metrics for yellow pine and mixed-conifer forests of the Sierra Nevada, particularly for coarse woody debris load, with some plots also exceeding historical natural range of variation (NRV) estimates for live tree density (Safford and Stevens 2017). Collectively, our study demonstrates that the structural conditions (i.e., dead biomass) resulting from a previous fire can consequently drive severity in a subsequent fire, particularly when combined with weather influences. The growing concerns regarding the proportion and area burned at high severity in the western US bring to light the management challenges for ensuring forest conservation and recovery across these systems in the years to come. However, our findings demonstrate that particularly in areas where fire has been long excluded, the impacts of past management on forest structure may persist even after repeat low- to moderate-severity fire. Although successive fires may act to restore the frequency of fire associated with historical fire regimes of these forests, our study underscores that fire alone may not be able to achieve desired management outcomes where forest restoration is the goal. In these areas, forest restoration will require on-going management efforts to enhance landscape resilience amidst changing climate conditions and inevitable future fire.

Acknowledgements

We would like to thank the California Department of Forestry and Fire Protection for funding this work and seasonal field crews from the Stephens Lab at UC Berkeley, US Forest Service, Florida Atlantic University, and Feather River College for providing assistance with field data collection.

Jasperse et al. Fire Ecology (2025) 21:46 Page 16 of 19

Authors' contributions

LJ: methodology, formal analysis, investigation, data collection, visualization, data curation, writing—original draft, writing—review and editing. BC: conceptualization, supervision, methodology, funding acquisition, writing—review and editing. MC: conceptualization, data collection, data curation, methodology, writing—review and editing. SS: conceptualization, funding acquisition, writing—review and editing. KM: conceptualization, writing—review and editing.

Funding

This work was funded by The California Department of Forestry and Fire Protection (Agreement #8CA05327).

Data availability

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

Declarations

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

¹Department of Environmental Science, Policy, and Management, University of California, Berkeley, 130 Mulford Hall, Berkeley, CA 94720, USA. ²Pacific Southwest Region, USDA Forest Service, 1323 Club Dr, Vallejo, CA 94592, USA. ³Sierra Cascade Province Ecology Program, USDA Forest Service, 159 Lawrence Street, Quincy, CA 95971, USA.

Received: 5 February 2025 Accepted: 7 May 2025 Published online: 13 August 2025

References

- Abatzoglou, John. 2021. Climatological Context for California's Ongoing Drought. ARE Update. *University of California, Giannini Foundation of Agricultural Economics*. 25 (1): 2–5. https://s.giannini.ucop.edu/uploads/pub/2021/10/28/v25n1_2.pdf.
- Anderson, M. Kat. 2005. *Tending the Wild: Native American Knowledge and the Management of California's Natural Resources*. Berkeley: University of California Press.
- Airey Lauvaux, Catherine, Carl N. Skinner, and Alan H. Taylor. 2016. High Severity Fire and Mixed Conifer Forest-Chaparral Dynamics in the Southern Cascade Range, USA. Forest Ecology and Management 363 (March):74–85. https://doi.org/10.1016/j.foreco.2015.12.016.
- Becker, Kendall M. L., and James A. Lutz. 2016. Can Low-Severity Fire Reverse Compositional Change in Montane Forests of the Sierra Nevada, California, USA? *Ecosphere* 7 (12): e01484. https://doi.org/10.1002/ecs2.1484.
- Bedsworth, Louis, Dan Cayan, Franco Guido, Leah Fisher, and Sonja Ziaja. 2018. *California's Fourth Climate Change Assessment Statewide Summary Report*. Sacramento, CA: California Energy Commission. Publication Number: SUM-CCCA4–2018–013. https://www.energy.ca.gov/sites/default/files/2019-11/Statewide_Reports-SUM-CCCA4-2018-013_Statewide_Summary_Report_ADA.pdf.
- Briones-Herrera, Carlos Ivan, Daniel José Vega-Nieva, Norma Angélica Monjarás-Vega, Jaime Briseño-Reyes, Pablito Marcelo López-Serrano, José Javier. Corral-Rivas, Ernesto Alvarado-Celestino, et al. 2020. Near Real-Time Automated Early Mapping of the Perimeter of Large Forest Fires from the Aggregation of VIIRS and MODIS Active Fires in Mexico. Remote Sensing 12 (12): 2061. https://doi.org/10.3390/rs12122061.
- Brodie, Emily G., Eric E. Knapp, Wesley R. Brooks, Stacy A. Drury, and Martin W. Ritchie. 2024. Forest Thinning and Prescribed Burning Treatments

- Reduce Wildfire Severity and Buffer the Impacts of Severe Fire Weather. *Fire Ecology* 20 (1): 17. https://doi.org/10.1186/s42408-023-00241-z.
- Brown, James K. 1974. Handbook for Inventorying Downed Woody Material. General Technical Report INT-16. Ogden, UT: USDA Forest Service, Intermountain Forest and Range Experiment Station. https://www.fs.usda.gov/treesearch/pubs/6143.
- Brown, James K., Elizabeth D. Reinhardt, and Kylie A. Kramer. 2003. Coarse Woody Debris: Managing Benefits and Fire Hazard in the Recovering Forest. RMRS-GTR-105. Ft. Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. https://doi.org/10.2737/RMRS-GTR-105.
- Buma, B., S. Weiss, K. Hayes, and M. Lucash. 2020. Wildland Fire Reburning Trends Across the US West Suggest Only Short-Term Negative Feedback and Differing Climatic Effects. *Environmental Research Letters* 15 (3): 034026. https://doi.org/10.1088/1748-9326/ab6c70.
- Cansler, C. Alina., Mark E. Swanson, Tucker J. Furniss, Andrew J. Larson, and James A. Lutz. 2019. Fuel Dynamics After Reintroduced Fire in an Old-Growth Sierra Nevada Mixed-Conifer Forest. *Fire Ecology* 15 (1): 16. https://doi.org/10.1186/s42408-019-0035-y.
- Canty, Angelo, and Brian D. Ripley. 2024. boot: Bootstrap R (S-Plus) Functions. R package version 1.3–28. https://CRAN.R-project.org/package=boot.
- Chamberlain, Caden P., Bryce N. Bartl-Geller, C. Alina Cansler, Malcolm P. North, Marc D. Meyer, Liz Van Wagtendonk, Hannah E. Redford, and Van R. Kane. 2024. When Do Contemporary Wildfires Restore Forest Structures in the Sierra Nevada? *Fire Ecology* 20 (1): 91. https://doi.org/10.1186/s42408-024-00324-5
- Charrad, Malika, Nadia Ghazzali, Véronique Boiteau, and Azam Niknafs. 2014. NbClust: An R Package for Determining the Relevant Number of Clusters in a Data Set. *Journal of Statistical Software* 61 (6). https://doi.org/10.
- Collins, Brandon M., Adrian J. Das, John J. Battles, Danny L. Fry, Kevin D. Krasnow, and Scott L. Stephens. 2014. Beyond Reducing Fire Hazard: Fuel Treatment Impacts on Overstory Tree Survival. *Ecological Applications* 24 (8): 1879–1886. https://doi.org/10.1890/14-0971.1.
- Collins, Brandon M., Richard G. Everett, and Scott L. Stephens. 2011. Impacts of Fire Exclusion and Recent Managed Fire on Forest Structure in Old Growth Sierra Nevada Mixed-Conifer Forests. *Ecosphere* 2 (4): art51. https://doi.org/10.1890/ES11-00026.1.
- Collins, Brandon M., Jamie M. Lydersen, Richard G. Everett, and Scott L. Stephens. 2018. How Does Forest Recovery Following Moderate-Severity Fire Influence Effects of Subsequent Wildfire in Mixed-Conifer Forests? Fire Ecology 14 (2): 3. https://doi.org/10.1186/s42408-018-0004-x.
- Collins, Brandon M., Jay D. Miller, Andrea E. Thode, Maggi Kelly, Jan W. Van Wagtendonk, and Scott 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.
- Coop, Jonathan D., Sean A. Parks, Sarah R. McClernan, and Lisa 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.
- Coop, Jonathan D., Sean A. Parks, Camille S. Stevens-Rumann, Shelley D. Crausbay, Philip E. Higuera, Matthew D. Hurteau, Alan Tepley, et al. 2020. Wildfire-Driven Forest Conversion in Western North American Landscapes. *BioScience* 70 (8): 659–673. https://doi.org/10.1093/biosci/biaa061.
- Coppoletta, Michelle, Kyle E. Merriam, and Brandon 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.
- Davis, Kimberley T., Jamie Peeler, Joseph Fargione, Ryan D. Haugo, Kerry L. Metlen, Marcos D. Robles, and Travis Woolley. 2024. Tamm Review: A Meta-Analysis of Thinning, Prescribed Fire, and Wildfire Effects on Subsequent Wildfire Severity in Conifer Dominated Forests of the Western US. Forest Ecology and Management 561 (June): 121885. https://doi.org/10.1016/j.foreco.2024.121885.
- Davison, A.C., and D.V. Hinkley. 1997. *Bootstrap Methods and Their Application*. Cambridge New York, NY, USA: Cambridge University Press.
- Dettinger, Michael D., and Michael L. Anderson. 2015. "Storage in California's Reservoirs and Snowpack in This Time of Drought." San Francisco Estuary and Watershed Science 13 (2). https://doi.org/10.15447/sfews.2015v13iss 2art1.

- Donato, Daniel C., Joseph B. Fontaine, J. Boone Kauffman, W. Douglas Robinson, and Beverly 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. https://doi.org/10.1071/WF12109.
- Estabrook, Thomas. 2025. *Dixie Fire Progression Maps*. U.S. Forest Service, Pacific Northwest Research Station. https://github.com/tgestabrook/Dixie-Fire-perimeter-interpolation.
- Gorelick, Noel, Matt Hancher, Mike Dixon, Simon Ilyushchenko, David Thau, and Rebecca Moore. 2017. Google Earth Engine: Planetary-Scale Geospatial Analysis for Everyone. *Remote Sensing of Environment* 202 (December): 18–27. https://doi.org/10.1016/j.rse.2017.06.031.
- Greenler, Skye M., Christopher J. Dunn, James D. Johnston, Matthew J. Reilly, Andrew G. Merschel, R. Keala Hagmann, and John D. Bailey. 2023. Too Hot, Too Cold, or Just Right: Can Wildfire Restore Dry Forests of the Interior Pacific Northwest? *PLoS ONE* 18 (2): e0281927. https://doi.org/10.1371/journal.pone.0281927.
- Gotelli, Nicholas J., and Aaron M. Ellison. 2013. A Primer of Ecological Statistics, 2nd ed. Sunderland, MA: Sinauer Associates Inc., Publishers.
- Hagmann, R. K., P. F. Hessburg, S. J. Prichard, N. A. Povak, P. M. Brown, P. Z. Fulé, R. E. Keane, et al. 2021. Evidence for Widespread Changes in the Structure, Composition, and Fire Regimes of Western North American Forests. *Ecological Applications* 31 (8): e02431. https://doi.org/10.1002/ eap.2431.
- Harvey, Brian J., Michele S. Buonanduci, and Monica G. Turner. 2023. Spatial Interactions Among Short-Interval Fires Reshape Forest Landscapes. *Global Ecology and Biogeography* 32 (4): 586–602. https://doi.org/10. 1111/geb.13634.
- Hessburg, Paul F., Derek J. Churchill, Andrew J. Larson, Ryan D. Haugo, Carol Miller, Thomas A. Spies, Malcolm P. North, et al. 2015. Restoring Fire-Prone Inland Pacific Landscapes: Seven Core Principles. *Landscape Ecology* 30 (10): 1805–1835. https://doi.org/10.1007/s10980-015-0218-0.
- Hessburg, Paul F., Carol L. Miller, Sean A. Parks, Nicholas A. Povak, Alan H. Taylor, Philip E. Higuera, Susan J. Prichard, et al. 2019. Climate, Environment, and Disturbance History Govern Resilience of Western North American Forests. Frontiers in Ecology and Evolution 7 (July): 239. https://doi.org/10. 3389/fevo.2019.00239.
- Holden, Zachary A., Penelope Morgan, Matthew G. Rollins, and Kathleen Kavanagh. 2007. Effects of Multiple Wildland Fires on Ponderosa Pine Stand Structure in Two Southwestern Wilderness Areas, USA. Fire Ecology 3 (2): 18–33. https://doi.org/10.4996/fireecology.0302018.
- Hood, Sharon M., Stephen Baker, and Anna Sala. 2016. Fortifying the Forest: Thinning and Burning Increase Resistance to a Bark Beetle Outbreak and Promote Forest Resilience. *Ecological Applications* 26 (7): 1984–2000. https://doi.org/10.1002/eap.1363.
- Hood, Sharon M., Justin S. Crotteau, and Cory C. Cleveland. 2024. Long-Term Efficacy of Fuel Reduction and Restoration Treatments in Northern Rockies Dry Forests. *Ecological Applications* 34 (2): e2940. https://doi.org/10.1002/eap.2940.
- Hothorn, Torsten, Kurt Hornik, and Achim Zeileis. 2006. Unbiased Recursive Partitioning: A Conditional Inference Framework. *Journal of Computational and Graphical Statistics* 15 (3): 651–674. https://doi.org/10.1198/106186006X133933.
- Johnson, Morris C., Maureen C. Kennedy, Sarah C. Harrison, Derek Churchill, James Pass, and Paul W. Fischer. 2020. Effects of Post-Fire Management on Dead Woody Fuel Dynamics and Stand Structure in a Severely Burned Mixed-Conifer Forest, in Northeastern Washington State, USA. Forest Ecology and Management 470–471 (August): 118190. https://doi. org/10.1016/j.foreco.2020.118190.
- Johnstone, Jill F., Craig D. Allen, Jerry F. Franklin, Lee E. Frelich, Brian J. Harvey, Philip E. Higuera, Michelle C. Mack, et al. 2016. Changing Disturbance Regimes, Ecological Memory, and Forest Resilience. Frontiers in Ecology and the Environment 14 (7): 369–378. https://doi.org/10.1002/fee.1311.
- Knapp, Eric E, Scott L Stephens, James D McIver, Jason J Moghaddas, and Jon E Keeley. 2004. "Fire and Fire Surrogate Study in the Sierra Nevada: Evaluating Restoration Treatments at Blodgett Forest and Sequoia National Park. Proceedings of the Sierra Nevada Science Symposium: Science for Management and Conservation, edited by D. D. Murphy and P. A. Stine, 79–85. General Technical Report PSW-GTR-193. Albany, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station.

Larson, Andrew J., R. Travis Belote, C. Alina Cansler, Sean A. Parks, and Matthew 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.

Page 17 of 19

- Low, Kathryn E., Brandon M. Collins, Alexis Bernal, John E. Sanders, Dylan Pastor, Patricia Manley, Angela M. White, and Scott L. Stephens. 2021. Longer-Term Impacts of Fuel Reduction Treatments on Forest Structure, Fuels, and Drought Resistance in the Lake Tahoe Basin. Forest Ecology and Management 479 (January): 118609. https://doi.org/10.1016/j.foreco.2020.118609.
- Lydersen, Jamie M., Brandon M. Collins, Matthew L. Brooks, John R. Matchett, Kristen L. Shive, Nicholas A. Povak, Van R. Kane, and Douglas 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, Jamie M., Brandon M. Collins, Michelle Coppoletta, Melissa R. Jaffe, Hudson Northrop, and Scott L. Stephens. 2019. Fuel Dynamics and Reburn Severity Following High-Severity Fire in a Sierra Nevada, USA, Mixed-Conifer Forest. *Fire Ecology* 15 (1): 43. https://doi.org/10.1186/s42408-019-0060-y
- Lydersen, Jamie, and Malcolm North. 2012. Topographic Variation in Structure of Mixed-Conifer Forests Under an Active-Fire Regime. *Ecosystems* 15 (7): 1134–1146. https://doi.org/10.1007/s10021-012-9573-8.
- Mallek, Chris, Hugh Safford, Joshua Viers, and Jay Miller. 2013. Modern Departures in Fire Severity and Area Vary by Forest Type, Sierra Nevada and Southern Cascades, California, USA. *Ecosphere* 4 (12): 1–28. https://doi.org/10.1890/ES13-00217.1.
- McIver, James D., and Lynn Starr. 2001. A Literature Review on the Environmental Effects of Postfire Logging. *Western Journal of Applied Forestry* 16 (4): 159–168. https://doi.org/10.1093/wjaf/16.4.159.
- Miller, Jay D., and Andrea 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.
- Moody, Tadashi J., JoAnn Fites-Kaufman, and Scott 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.
- Murphy, Julia S., Robert York, Hiram Rivera Huerta, and Scott L. Stephens. 2021. Characteristics and Metrics of Resilient Forests in the Sierra de San Pedro Martír, Mexico. Forest Ecology and Management 482 (February): 118864. https://doi.org/10.1016/j.foreco.2020.118864.
- Naficy, Cameron, Anna Sala, Éric G. Keeling, Jon Graham, and Thomas H. DeLuca. 2010. Interactive Effects of Historical Logging and Fire Exclusion on Ponderosa Pine Forest Structure in the Northern Rockies. Ecological Applications 20 (7): 1851–1864. https://doi.org/10.1890/09-0217.1.
- Nemens, Deborah G., Kathryn R. Kidd, J. Morgan Varner, and Brian Wing. 2022. Recurring Wildfires Provoke Type Conversion in Dry Western Forests. *Ecosphere* 13 (8): e4184. https://doi.org/10.1002/ecs2.4184.
- Ng, Jan, Malcolm P. North, Alec J. Arditti, Monica R. Cooper, and James A. Lutz. 2020. Topographic Variation in Tree Group and Gap Structure in Sierra Nevada Mixed-Conifer Forests with Active Fire Regimes. Forest Ecology and Management 472 (September): 118220. https://doi.org/10.1016/j. foreco.2020.118220.
- North, Malcolm, Brandon M. Collins, and Scott Stephens. 2012. Using Fire to Increase the Scale, Benefits, and Future Maintenance of Fuels Treatments. Journal of Forestry 110 (7): 392–401. https://doi.org/10.5849/jof.12-021.
- North, Malcolm, Jim Innes, and Harold Zald. 2007. Comparison of Thinning and Prescribed Fire Restoration Treatments to Sierran Mixed-Conifer Historic Conditions. *Canadian Journal of Forest Research* 37 (2): 331–342. https://doi.org/10.1139/X06-236.
- North, Malcolm P., Ryan E. Tompkins, Alexis A. Bernal, Brandon M. Collins, Scott L. Stephens, and Robert A. York. 2022. Operational Resilience in Western US Frequent-Fire Forests. Forest Ecology and Management 507 (March): 120004. https://doi.org/10.1016/j.foreco.2021.120004.
- North, Malcolm, Peter Stine, Kevin O'Hara, William Zielinski, and Scott Stephens. 2009. *An Ecosystem Management Strategy for Sierran Mixed-Conifer Forests. PSW-GTR-220*. Albany, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station. https://doi.org/10.2737/PSW-GTR-220.

- Oksanen, Jari, F. Guillaume Blanchet, Michael Friendly, Roeland Kindt, Pierre Legendre, Dan McGlinn, Peter R. Minchin, et al. 2023. _vegan: Community Ecology Package. R package version 2.6–4. https://CRAN.R-project.org/package=vegan.
- Parks, Sean A., and John T. Abatzoglou. 2020. "Warmer and Drier Fire Seasons Contribute to Increases in Area Burned at High Severity in Western US Forests from 1985 to 2017." *Geophysical Research Letters* 47 (22): e2020GL
- Parks, Sean A., Carol Miller, Cara R. Nelson, and Zachary 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.
- Parks, Sean A., Lisa Holsinger, Morgan Voss, Rachel Loehman, and Nathaniel Robinson. 2018. Mean Composite Fire Severity Metrics Computed with Google Earth Engine Offer Improved Accuracy and Expanded Mapping Potential. *Remote Sensing* 10 (6): 879. https://doi.org/10.3390/rs100 60879.
- Paudel, Asha, Michelle Coppoletta, Kyle Merriam, and Scott H. Markwith. 2022.

 Persistent Composition Legacy and Rapid Structural Change Following
 Successive Fires in Sierra Nevada Mixed Conifer Forests. Forest Ecology and
 Management 509 (April): 120079. https://doi.org/10.1016/j.foreco.2022.
 120079.
- Pebesma, Edzer. 2018. Simple Features for R: Standardized Support for Spatial Vector Data. *The R Journal* 10 (1): 439. https://doi.org/10.32614/RI-2018-009.
- Pebesma, Edzer, and Roger Bivand. 2023. Spatial Data Science: With Applications in R, 1st ed. New York: Chapman and Hall/CRC. https://doi.org/10.1201/9780429459016.
- Peterson, David W., Erich K. Dodson, and Richy J. Harrod. 2023. Snag Decomposition Following Stand-Replacing Wildfires Alters Wildlife Habitat Use and Surface Woody Fuels Through Time. *Ecosphere* 14 (8): e4635. https://doi.org/10.1002/ecs2.4635.
- Prichard, Susan J., Camille S. Stevens-Rumann, and Paul F. Hessburg. 2017.

 Tamm Review: Shifting Global Fire Regimes: Lessons from Reburns and Research Needs. Forest Ecology and Management 396 (July): 217–233. https://doi.org/10.1016/j.foreco.2017.03.035.
- R Core Team. 2024. _R: A Language and Environment for Statistical Computing.

 R Foundation for Statistical Computing: Vienna, Austria. https://www.R-project.org/.
- Ritchie, Martin W., Eric E. Knapp, and Carl N. Skinner. 2013. Snag Longevity and Surface Fuel Accumulation Following Post-Fire Logging in a Ponderosa Pine Dominated Forest. *Forest Ecology and Management* 287 (January): 113–122. https://doi.org/10.1016/j.foreco.2012.09.001.
- Rutherford, Kea, Danny Foster, and John Battles. 2024. *BerkeleyForestAnalytics, Version* 2.0.1. Battles Lab: Forest Ecology and Ecosystem Dynamics, University of California, Berkeley. https://github.com/kearutherford/BerkeleyForestsAnalytics.
- Saberi, S. J., and B. J. Harvey. 2023. What Is the Color When Black Is Burned? Quantifying (Re)burn Severity Using Field and Satellite Remote Sensing Indices. *Fire Ecology* 19 (1): 24. https://doi.org/10.1186/ s42408-023-00181-8.
- Safford, Hugh D., Alison K. Paulson, Zachary L. Steel, Derek J. N. Young, and Rebecca B. Wayman. 2022. The 2020 California Fire Season: A Year like No Other, a Return to the Past or a Harbinger of the Future? *Global Ecology and Biogeography* 31 (10): 2005–2025. https://doi.org/10.1111/geb.13498.
- Safford, Hugh D., and Jens 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. PSW-GTR-256. Albany, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station. https://doi.org/10.2737/PSW-GTR-256.
- Schmidt, Lars, Marco G. Hille, and Scott L. Stephens. 2006. Restoring Northern Sierra Nevada Mixed Conifer Forest Composition and Structure with Prescribed Fires of Varying Intensities. *Fire Ecology* 2 (2): 20–33. https://doi.org/10.4996/fireecology.0202020.
- Scholl, Andrew E., and Alan H. Taylor. 2010. Fire Regimes, Forest Change, and Self-Organization in an Old-Growth Mixed-Conifer Forest, Yosemite National Park, USA. *Ecological Applications* 20 (2): 362–380. https://doi.org/10.1890/08-2324.1.

- Shapiro, Samuel S., and Martin B. Wilk. 1965. An Analysis of Variance Test for Normality (Complete Samples). *Biometrika* 52 (3–4): 591–611. https://doi.org/10.1093/biomet/52.3-4.591.
- Shive, Kristen L., Michelle Coppoletta, Rebecca Bewley Wayman, Alison K. Paulson, Kristen N. Wilson, John T. Abatzaglou, Saba J. Saberi, Becky Estes, and Hugh D. Safford. 2024. Thinning with Follow-up Burning Treatments Have Increased Effectiveness at Reducing Severity in California's Largest Wildfire. Forest Ecology and Management 572 (November): 122171. https://doi.org/10.1016/j.foreco.2024.122171.
- Singleton, Megan P., Andrea E. Thode, Andrew J. Sánchez Meador, and Jose M. Iniguez. 2019. Increasing Trends in High-Severity Fire in the Southwestern USA from 1984 to 2015. Forest Ecology and Management 433 (February):709–19. https://doi.org/10.1016/j.foreco.2018.11.039.
- Steel, Zachary L., Daniel Foster, Michelle Coppoletta, Jamie M. Lydersen, Scott L. Stephens, Asha Paudel, Scott H. Markwith, Kyle Merriam, and Brandon M. Collins. 2021. Ecological Resilience and Vegetation Transition in the Face of Two Successive Large Wildfires. *Journal of Ecology* 109 (9): 3340–3355. https://doi.org/10.1111/1365-2745.13764.
- Stephens, Scott L. 2004. Fuel Loads, Snag Abundance, and Snag Recruitment in an Unmanaged Jeffrey Pine-Mixed Conifer Forest in Northwestern Mexico. Forest Ecology and Management 199 (1): 103–113. https://doi.org/10.1016/j.foreco.2004.04.017.
- Stephens, Scott L., Alexis A. Bernal, Brandon M. Collins, Mark A. Finney, Chris Lautenberger, and David Saah. 2022. Mass Fire Behavior Created by Extensive Tree Mortality and High Tree Density Not Predicted by Operational Fire Behavior Models in the Southern Sierra Nevada. Forest Ecology and Management 518 (August): 120258. https://doi.org/10.1016/j.foreco.2022.120258.
- Stephens, Scott L., Brandon M. Collins, Christopher J. Fettig, Mark A. Finney, Chad M. Hoffman, Eric E. Knapp, Malcolm P. North, Hugh Safford, and Rebecca 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, Scott L., Daniel E. Foster, John J. Battles, Alexis A. Bernal, Brandon M. Collins, Rachelle Hedges, Jason J. Moghaddas, Ariel T. Roughton, and Robert A. York. 2024. Forest Restoration and Fuels Reduction Work: Different Pathways for Achieving Success in the Sierra Nevada. *Ecological Applications* 34 (2): e2932. https://doi.org/10.1002/eap.2932.
- Stephens, Scott L., Danny L. Fry, Ernesto Franco-Vizcaíno, Brandon M. Collins, and Jason M. Moghaddas. 2007. Coarse Woody Debris and Canopy Cover in an Old-Growth Jeffrey Pine-Mixed Conifer Forest from the Sierra San Pedro Martir, Mexico. Forest Ecology and Management 240 (1–3): 87–95. https://doi.org/10.1016/j.foreco.2006.12.012.
- Stephens, Scott L., and Peter Z. Fulé. 2005. Western Pine Forests with Continuing Frequent Fire Regimes: Possible Reference Sites for Management. *Journal of Forestry* 103 (7): 357–362. https://doi.org/10.1093/jof/103.7. 357.
- Stephens, Scott L., Les Hall, Connor W. Stephens, Alexis A. Bernal, and Brandon M. Collins. 2023. Degradation and Restoration of Indigenous California Black Oak (Quercus kelloggii) Stands in the Northern Sierra Nevada. *Fire Ecology* 19 (1): 12. https://doi.org/10.1186/s42408-023-00172-9.
- Stephens, Scott L., Jamie M. Lydersen, Brandon M. Collins, Danny L. Fry, and Marc 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.
- Stephens, Scott L., and Jason J. Moghaddas. 2005. Fuel Treatment Effects on Snags and Coarse Woody Debris in a Sierra Nevada Mixed Conifer Forest. Forest Ecology and Management 214 (1–3): 53–64. https://doi.org/10.1016/j.foreco.2005.03.055.
- Stephens, Scott L., Jason J. Moghaddas, Carl Edminster, Carl E. Fiedler, Sally Haase, Michael Harrington, Jon E. Keeley, et al. 2009. Fire Treatment Effects on Vegetation Structure, Fuels, and Potential Fire Severity in Western U.S. Forests. *Ecological Applications* 19 (2): 305–320. https://doi.org/10.1890/07-1755.1.
- Stephenson, Nathan L. 1999. Reference Conditions for Giant Sequoia Forest Restoration: Structure, Process, and Precision. *Ecological Applications* 9 (4): 1253–1265. https://doi.org/10.1890/1051-0761(1999)009[1253: RCFGSFI2.0.CO:2.
- Stevens-Rumann, Camille S., Susan J. Prichard, Eva K. Strand, and Penelope Morgan. 2016. Prior Wildfires Influence Burn Severity of Subsequent

Jasperse et al. Fire Ecology (2025) 21:46 Page 19 of 19

- Large Fires. Canadian Journal of Forest Research 46 (11): 1375–1385. https://doi.org/10.1139/cifr-2016-0185.
- Stevens-Rumann, Camille S., Carolyn H. Sieg, and Molly E. Hunter. 2012. Ten Years After Wildfires: How Does Varying Tree Mortality Impact Fire Hazard and Forest Resiliency? Forest Ecology and Management 267 (March): 199–208. https://doi.org/10.1016/j.foreco.2011.12.003.
- Strobl, Carolin, Anne-Laure. Boulesteix, Thomas Kneib, Thomas Augustin, and Achim Zeileis. 2008. Conditional Variable Importance for Random Forests. *BMC Bioinformatics* 9 (1): 307. https://doi.org/10.1186/1471-2105-9-307.
- Strobl, Carolin, Anne-Laure. Boulesteix, Achim Zeileis, and Torsten Hothorn. 2007. Bias in Random Forest Variable Importance Measures: Illustrations, Sources and a Solution. *BMC Bioinformatics* 8 (1): 25. https://doi.org/10. 1186/1471-2105-8-25.
- Taylor, Alan H. 2010. Fire Disturbance and Forest Structure in an Old-Growth *Pinus ponderosa* Forest, Southern Cascades, USA. *Journal of Vegetation Science* 21 (3): 561–572. https://doi.org/10.1111/j.1654-1103.2009. 01164.x.
- Taylor, Alan H., Lucas B. Harris, and Carl N. Skinner. 2022. Severity Patterns of the 2021 Dixie Fire Exemplify the Need to Increase Low-Severity Fire Treatments in California's Forests. *Environmental Research Letters* 17 (7): 071002. https://doi.org/10.1088/1748-9326/ac7735.
- Teske, Casey C., Carl A. Seielstad, and Lloyd P. Queen. 2012. Characterizing Fire-on-Fire Interactions in Three Large Wilderness Areas. *Fire Ecology* 8 (2): 82–106. https://doi.org/10.4996/fireecology.0802082.
- Thompson, Jonathan R., Thomas A. Spies, and Lisa M. Ganio. 2007. Reburn Severity in Managed and Unmanaged Vegetation in a Large Wildfire. *Proceedings of the National Academy of Sciences* 104 (25): 10743–10748. https://doi.org/10.1073/pnas.0700229104.
- Tortorelli, Claire M., Andrew M. Latimer, and Derek J. N. Young. 2024. Moderating Effects of Past Wildfire on Reburn Severity Depend on Climate and Initial Severity in Western U S Forests. *Ecological Applications* 34 (7): e3023. https://doi.org/10.1002/eap.3023.
- USDA Forest Service. 2007. Common Stand Exam Field Guide. Natural Resource Information System: Washington, DC. http://www.fs.fed.us/nrm/fsveg/.
- Van Wagtendonk, Jan W. 2006. Fire as a Physical Process. In *Fire in California's Ecosystems*, edited by Neil Sugihara. 38–57. University of California Press. https://doi.org/10.1525/california/9780520246058.003.0003.
- Wagtendonk, Van, W. Jan, Kent A. Van Wagtendonk, and Andrea 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.
- Whitlock, Michael C., and Dolph Schluter. 2015. *The Analysis of Biological Data*, 2nd ed. Greenwood Village, CO: Roberts and Company Publishers.
- Wilcoxon, Frank. 1945. Individual Comparisons by Ranking Methods. *Biometrics Bulletin* 1 (6): 80–83. https://doi.org/10.2307/3001968.
- Williams, A. Park., Richard Seager, John T. Abatzoglou, Benjamin I. Cook, Jason E. Smerdon, and Edward R. Cook. 2015. Contribution of Anthropogenic Warming to California Drought During 2012–2014. *Geophysical Research Letters* 42 (16): 6819–6828. https://doi.org/10.1002/2015GL064924.
- Williams, J. N., H. D. Safford, N. Enstice, Z. L. Steel, and A. K. Paulson. 2023. High-Severity Burned Area and Proportion Exceed Historic Conditions in Sierra Nevada, California, and Adjacent Ranges. *Ecosphere* 14 (1): e4397. https://doi.org/10.1002/ecs2.4397.
- Wu, Xiao, Erik Sverdrup, Michael D. Mastrandrea, Michael W. Wara, and Stefan Wager. 2023. Low-Intensity Fires Mitigate the Risk of High-Intensity Wildfires in California's Forests. Science Advances 9 (45): eadi4123. https://doi.org/10.1126/sciadv.adi4123.
- Zeileis, Achim, Torsten Hothorn, and Kurt Hornik. 2008. Model-Based Recursive Partitioning. *Journal of Computational and Graphical Statistics* 17 (2): 492–514. https://doi.org/10.1198/106186008X319331.

Publisher's Note

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