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# When do contemporary wildfires restore forest structures in the Sierra Nevada?

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## Abstract

**Background** Following a century of fire suppression in western North America, managers use forest restoration treatments to reduce fuel loads and reintroduce key processes like fire. However, annual area burned by wildfire frequently outpaces the application of restoration treatments. As this trend continues under climate change, it is essential that we understand the effects of contemporary wildfires on forest ecosystems and the extent to which post-fire structures are meeting common forest restoration objectives. In this study, we used airborne lidar to evaluate fire effects across yellow pine and mixed conifer (YPMC) forests of California's Sierra Nevada. We quantified the degree to which forest structures in first-entry burned areas (previously unburned since ~ 1900s) and unburned controls aligned with restoration targets derived from contemporary reference sites. We also identified environmental conditions that contributed to more restorative fire effects.

**Results** Relative to unburned controls, structural patterns in first-entry burned areas aligned more closely with reference sites. Yet, across all burn severities, first-entry wildfires were only moderately successful at meeting targets for canopy cover (48% total area) and ladder fuels (54% total area), and achieving these targets while also producing tree clump and opening patterns aligning with reference sites was less common (16% total area). Moderate-severity patches had the highest proportion of restorative fire effects (55–64% total area), while low- and high-severity patches were either too dense or too open, respectively. Our models (and publicly-available mapped predictions) indicated a higher probability of restorative effects within 1 km of previous fires, within the mid-upper climate range of the YPMC zone, and under moderate fire intensities (~ 1–2 m flame lengths).

**Conclusions** First-entry wildfires can sometimes restore structural conditions by reducing canopy cover and ladder fuels and increasing structural heterogeneity, especially within moderate-severity patches. However, these initial fires represent just one step toward restoring dry forest ecosystems. Post-fire landscapes will require additional low- to moderate-intensity fires and/or strategic management interventions to fully restore structural conditions. In yet unburned forests, managers could prioritize mechanical treatments at lower elevations, early-season burning at mid to high elevations, and resource objective wildfires in landscapes with mosaics of past wildfires.

**Keywords** Wildfire, Restoration, Natural range of variation, Sierra Nevada, Contemporary reference sites, Fire effects

## Resumen

**Antecedentes** Luego de una centuria de exclusión de fuegos en el oeste de América del Norte, los gestores usan tratamientos de restauración para reducir la carga de combustibles y reintroducir procesos clave como el fuego. Sin

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embargo, el área anual quemada por incendios de vegetación supera frecuentemente a la aplicación de tratamientos de restauración. Como esta tendencia continúa bajo los efectos del Cambio Climático, es esencial que comprendamos los efectos de incendios contemporáneos en ecosistemas boscosos, y la medida en la cual las estructuras post fuego alcanzan los objetivos de restauración de los bosques afectados. En este estudio, usamos la tecnología LIDAR para evaluar los efectos de incendios en bosques de pino amarillo y de coníferas mixtas (YPMC) en las Sierras Nevadas de California. Cuantificamos el grado al cual las estructuras forestales en áreas quemadas por primera vez (previamente no quemadas desde alrededor de 1900) y controles no quemados se alineaban con los objetivos de restauración derivados de sitios de referencia contemporáneos. Identificamos también condiciones ambientales que contribuían con efectos más restaurativos de los fuegos.

**Resultados** Relacionado con controles no quemados, los patrones estructurales en áreas quemadas por primera vez se alinearon de manera muy cercana con los sitos de referencia. Aún así, a través de todas las severidades de quemas, los incendios registrados por primera vez fueron solo moderadamente exitosos para alcanzar las metas de cobertura de doseles (48% del área total) y escaleras de combustible (54% del área total), y el alcanzar esas metas y al mismo tiempo producir agrupaciones de árboles y áreas abiertas alineadas con sitios de referencia fueron menos comunes (16% del área total). Parches de moderada severidad tuvieron la proporción más alta de efectos restaurativos del fuego (55-64% del área total), mientras que los parches de baja y alta severidad fueron o muy densos o muy abiertos, respectivamente. Nuestros modelos (y predicciones mapeadas disponibles públicamente), indicaron una alta probabilidad de efectos restaurativos dentro de 1 km de fuegos previos, dentro de un rango climático medio-alto de la zona YPMC, y bajo moderadas intensidades de fuego (~ 1-2 m de altura de llama).

**Conclusiones** Los fuegos ocurridos por vez primera pueden muchas veces restaurar las condiciones estructurales mediante la reducción los doseles y las escaleras de combustibles, e incrementar la heterogeneidad estructural, especialmente dentro de parches de moderada severidad. Sin embargo, esos fuegos iniciales representan solo un paso en la restauración de ecosistemas forestales secos. Los paisajes post fuego requerirán, además, fuegos de baja a moderada intensidad y/o intervenciones estratégicas de manejo para restaurar totalmente las condiciones estructurales de los rodales. En los bosques aún no quemados, los gestores podrían priorizar tratamientos mecánicos en elevaciones bajas, quemas prescriptas al inicio de la estación de crecimiento en elevaciones medias a altas, y fuegos orientados a los recursos en paisajes con mosaicos de incendios pasados.

## Background

Most of the dry, conifer-dominated forests of western North America adapted under a frequent, low-severity fire regime, where fires historically served to regulate vegetation dynamics and support overall ecosystem function (Falk et al. 2011; Hessburg et al. 2019; Hagmann et al. 2021). Following a century of fire suppression, eradication of Indigenous burning, and recent climate change, contemporary wildfires are increasingly distinguished by large patches of high severity effects (~ >95% basal area mortality) (Lydersen et al. 2016; Westerling 2016; Parks and Abatzoglou 2020; Cova et al. 2023), which can have widespread ecological impacts (Coop et al. 2020; Hagmann et al. 2021; Parks et al. 2023). However, while increased high-severity fire is a critical management concern, recent work suggests that area burned at low and moderate severity (~50–70% basal area mortality) has also increased considerably over recent decades (>60% total burned area in California fires 1985–2020) (Lydersen et al. 2016; Cova et al. 2023). These low- to moderate-severity effects highlight an alternate scenario in which first-entry wildfires (those burning for the first time since the start of fire exclusion) may indeed be restoring ecosystem structures and functions as they return to dry forest landscapes (Meyer 2015; Lydersen et al. 2016; Kane et al. 2019; Churchill et al. 2022).

In the fire-suppressed yellow pine and mixed conifer (YPMC) forests of California's Sierra Nevada, land managers rely on forest treatments to reduce fuel loads, restore key processes like fire, and mitigate the negative impacts of future disturbances and climate change (hereafter referred to as "restoration treatments") (Safford et al. 2012; Forest Management Task Force 2021; North et al. 2022; Hankin et al. 2023). However, annual area burned by wildfires continues to drastically outpace the implementation of restoration treatments in the region (Vaillant and Reinhardt 2017; North et al. 2021), with a documented sixfold increase in annual area burned over the past two decades (Williams et al. 2019). With trends of increasing annual area burned likely to continue under climate change (Abatzoglou et al. 2019; Williams et al. 2019), it is critical to understand how contemporary fires are impacting forest ecosystems, and the extent to which post-fire structures are aligning with common restoration objectives (North et al. 2015, 2021; Meyer et al. 2021).

Reference conditions have long been used by forest managers to design and evaluate restoration treatments (Moore et al. 1999; Safford and Stevens 2017; Bohlman et al. 2021). These conditions can be derived from historical datasets, palaeoecological reconstructions, traditional knowledge systems, simulations, or contemporary reference sites (Fulé et al. 1997; Lydersen et al. 2013; Collins et al. 2016; Lake et al. 2017). In any case, reference conditions describe ecosystems that are maintained by key processes (e.g., a frequent low-severity fire regime in YPMC forests of the Sierra Nevada) where structural and compositional attributes are expected to be more resilient (i.e., able to resist or recover) under subsequent disturbances and climate change (Landres et al. 1999; Moore et al. 1999; Collins et al. 2016; Jeronimo et al. 2019). Contemporary reference sites offer a promising approach for quantifying reference conditions. These sites are at least partially adapted to contemporary and future climates, and they enable detailed inventories of structure and composition using modern inventory techniques (e.g., remote sensing) (Collins et al. 2016; Jeronimo et al. 2019; Wiggins et al. 2019; Chamberlain et al. 2023a). These sites have limitations as well; for example, contemporary reference sites in the Sierra Nevada may still reflect some of the residual effects of twentieth century fire suppression (Lydersen et al. 2014).

Recent airborne lidar-based assessments have characterized structural conditions across contemporary reference sites in the YPMC zone of California's Sierra Nevada (Jeronimo et al. 2019; Kane et al. 2019; Chamberlain et al. 2023a, 2023b). These lidar-based characterizations may not cover all aspects of functioning ecosystems (e.g., species composition and surface fuel loading) but they do provide useful targets for key structures that contribute to overall ecosystem function (Jeronimo et al. 2019; Kane et al. 2019). Past work shows that Sierra Nevada contemporary reference sites are characterized by low total canopy cover, tree densities, and ladder fuels (Jeronimo et al. 2019; Kane et al. 2019). Fine-scale spatial patterns reflect mosaics of individual trees, small clumps of trees, and relatively high proportions of open space (i.e., an individual, clump, and opening (ICO) pattern) (Jeronimo et al. 2019; Chamberlain et al. 2023a). These neighborhood-level structural patterns can increase resilience to subsequent fires, droughts, beetle outbreaks, and other disturbances (Larson and Churchill 2012; Churchill et al. 2013; Ritter et al. 2020; Atchley et al. 2021; Steel et al. 2021; Furniss et al. 2022), while also serving as proxies for other key ecosystem services such as biodiversity and wildlife habitat (Larson and Churchill 2012; Kramer et al. 2021; Stephens et al. 2021). At broader spatial scales, tree densities and ICO patterns vary across topographic and climatic gradients (Lydersen and North 2012; Kane et al. 2015b; Jeronimo et al. 2019; Ng et al. 2020). Cooler climate zones, valleys, and north-facing slopes support more closed canopy structures, while drier climate zones, ridges, and south-facing slopes support more open structures (Jeronimo et al. 2019; Wiggins et al. 2019; Ng et al. 2020). Evaluating the extent to which contemporary wildfires are shifting forests and landscapes toward these reference conditions represents a critical management objective in the Sierra Nevada (Safford and Stevens 2017; Meyer et al. 2021).

In addition to quantifying the extent and patterns of contemporary fire effects, it is important to understand the environmental factors that influence fire effects so that managers can better plan for and manage future fires (Kane et al. 2019; Huffman et al. 2020). Past work shows that fire effects are governed by complex interactions between broad bioclimatic trends, pre-fire forest structure and composition, fire weather, and topographic factors, as well as the broader landscape context within which an area burns (Sullivan 2017; Parks et al. 2018; Jeronimo et al. 2020). While several studies have begun to quantify environment-fire effects relationships using moderate-resolution (30-m) burn severity indices (Kane et al. 2015a, b; Parks et al. 2018; Povak et al. 2020; Cansler et al. 2022), fine-resolution (~ 1-m) airborne lidar datasets support more detailed assessment and comparison of how environmental factors influence resultant post-fire structures (McCarley et al. 2017; Kane et al. 2019).

In this study, we evaluated the extent to which first-entry wildfires contributed to restoring structural patterns in Sierra Nevada YPMC forests. We classified fire effects as restorative when structure metrics aligned with a site's natural range of variation (NRV), based on measures derived from contemporary reference sites (Chamberlain et al. 2023b). We focused on three structural components that represent important attributes of functioning YPMC forests and can be measured using airborne lidar: total canopy cover, ladder fuel density, and clump complexity (an index of fine-scale ICO patterns). We also used machine learning to evaluate how various environmental factors influenced restorative fire effects, then mapped modeled predictions under mild and moderate fire weather scenarios for previously unburned areas. We sought to address four primary objectives in our study:

i) Quantify the extent to which contemporary first-entry wildfires have restored forest structural patterns.
ii) Evaluate patch size distributions of restored structures resulting from first-entry wildfires.
iii) Identify the pre-fire and active-fire (i.e., day-of-burn fire weather) conditions under which first-entry wildfires were most likely to have restorative effects.
iv) Map the probability of restorative fire effects across unburned areas in the Sierra Nevada for the year 2020.

## Methods

We used airborne lidar data to evaluate and compare structural patterns across 55 contemporary reference sites, 35 wildfires, and a set of unburned control sites in the Sierra Nevada YPMC zone (Fig. 1). We subdivided the reference sites to define topographically and climatically adjusted NRVs for each of our three structure metrics (canopy cover, ladder fuel density, and clump complexity). Post-fire structures and control sites were then assessed as below, within, or above their respective topo-climatic NRV (Objective 1). We also produced three restoration indices to define scenarios in which multiple structure metrics fell within NRV—cover restoration (canopy cover within NRV), partial restoration (canopy cover and ladder fuel density within NRV), and full restoration (all three structure metrics within NRV). We quantified the proportions (Objective 1) and patch size distributions (Objective 2) of each of these restoration indices. Next, to identify the environmental conditions that influenced restorative fire effects (Objective 3), we fit and evaluated Random Forest (RF) classification models with full restoration as the response (binary index) and a large set of bioclimatic, fire weather, topographic, pre-fire forest structure, and other metrics as predictors. Finally, to demonstrate the application of our modeling results, we mapped the probability of the full restoration index, under two weather scenarios, across all previously unburned areas within the Sierra Nevada YPMC zone in the year 2020 (Objective 4). We performed all primary analyses in R (R Core Team 2023).

### Study area

The Sierra Nevada region is characterized by a Mediterranean climate with relatively wet, cold winters and hot, dry summers. YPMC forests span the low- to mid-montane region of the Sierra Nevada, ranging in elevation from approximately 500 m in the north to 2,500 m in the south. Dominant species include Jeffrey pine (*Pinus jeffreyi* Balf.*)*, ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson*)*, Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*), sugar pine (*Pinus lambertiana* Douglas), incense-cedar (*Calocedrus decurrens* (Torr.) Florin), and white fir (*Abies concolor* (Gord. & Glend.) Lindl. Ex Hildebr.) with California black oak (*Quercus kelloggii* Newberry) intermixing at lower elevations and red fir (*Abies magnifica* A. Murray bis) and lodgepole pine (*Pinus contorta* Douglas ex Loudon var. *murrayana* (Balf.) Engelm.) intermixing at higher elevations (North et al. 2016; Safford and Stevens 2017). Prior to Euro-American colonization, YPMC forests were characterized by a frequent, low-severity fire regime, driven by natural- and human-ignited fires, with a mean fire return interval of 11–16 years (Taylor et al. 2016; Safford and Stevens 2017; Klimaszewski-Patterson et al. 2024).

To identify the Sierra Nevada YPMC zone, we limited our study area to the intersection of two layers: (1) the Environmental Protection Agency's Level IV Ecoregions dataset (Level IV Ecoregions 2023) and (2) the FVEG Wildlife Habitat Relationship classes (FVEG 2015). We buffered the Sierra Nevada ecoregion by 5 km to ensure inclusion of a few contemporary reference sites that fell just north of the official boundary. We then selected five FVEG Wildlife Habitat Relationship codes—Montane Hardwood-Conifer, Ponderosa Pine, Jeffrey Pine, Douglas Fir, and Sierran Mixed Conifer—to represent the YPMC zone (Fig. 1). We also restricted our analyses to three of the Sierra Nevada climate zones defined by Jeronimo et al. (2019): Warm Dry Low Montane, Warm Mesic Low Montane, and Cool Dry Mid Montane. Jeronimo et al. (2019) defined these climate classes based on measures of 1981–2010 climatic water deficit, actual evapotranspiration, and January minimum temperature. In our analyses, we used these classes to define climatically adjusted NRVs. The three climate classes used in our study spanned 54% of the total YPMC zone. Other climate classes were excluded from our analyses due to insufficient sample sizes of contemporary reference site pixels (< 500). We also excluded the Foothill Low Montane Transition zone since exploratory analyses revealed that contemporary reference site structures from this zone were questionable compared to other climate zones (Jeronimo et al. 2019; Chamberlain et al. 2023b).

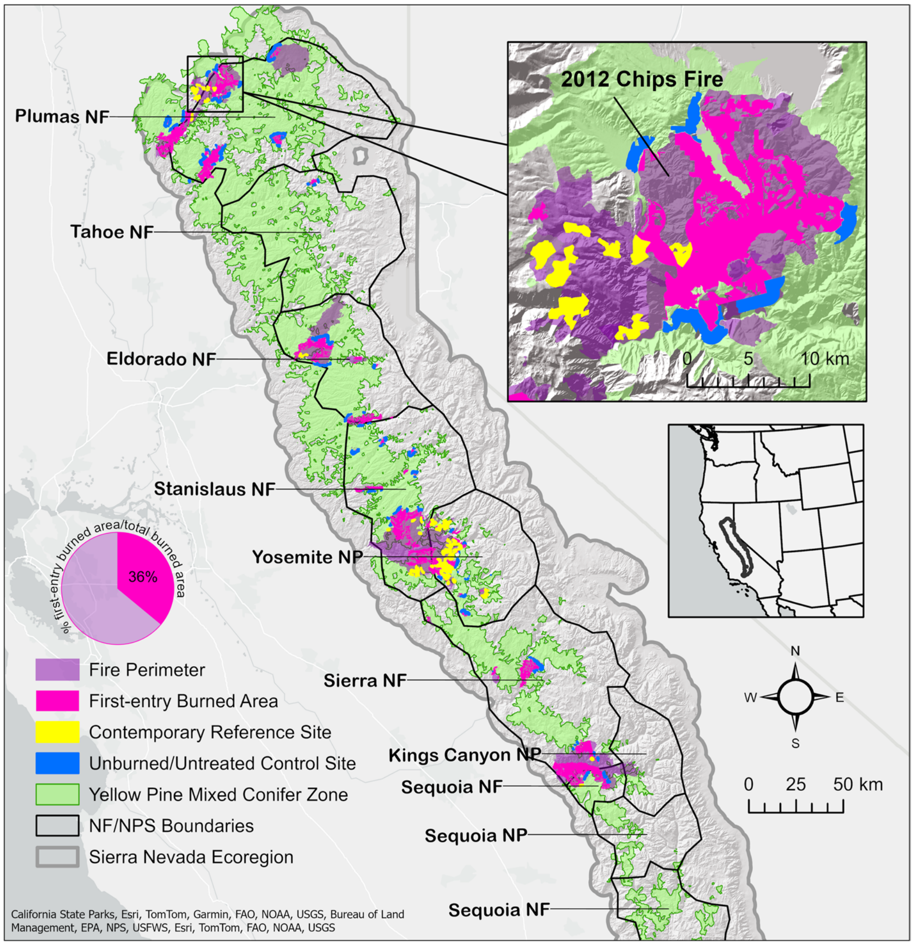


**Fig. 1** Study area showing wildfire perimeters, first-entry burned area within fire perimeters, contemporary reference sites, and unburned and untreated controls (for the year 2015) within the yellow pine and mixed conifer (YPMC) zone in the Sierra Nevada ecoregion, CA, USA. Inset shows a close-up of the 2012 Chips Fire which contains first-entry burned area and several contemporary reference sites. National Forest and National Park Service boundaries are shown for context, with polygon boundaries smoothed for visualization. The pie chart shows the percentage of first-entry burned area out of the total fire area. NF, National Forest; NP, National Park

## Datasets

### *Contemporary reference sites*

We used a dataset of contemporary reference sites to define NRVs for the three structure metrics. The reference site dataset was described in detail in Chamberlain et al. (2023a) and (2023b) and Jeronimo et al. (2019). These sites primarily cover the YPMC zone and represent areas where a frequent, low-severity fire regime has begun to reestablish after decades of fire suppression (Jeronimo et al. 2019; Chamberlain et al. 2023a). To be identified as a reference area, sites must have experienced at least 2 fires with low- or moderate-severity effects in the last 30 years, with one fire having mostly moderate-severity effects. Sites ranged in size from ~ 100 to 1,000 ha and could not have been previously harvested or treated and could only contain small (< 10-ha) patches of high severity (Chamberlain et al. 2023b). The full reference site dataset contained 119 sites. For this study, we used a subset of 55 sites (Fig. 1) that (1) were covered by airborne lidar, (2) burned 5–15 years prior to the lidar acquisition, and (3) were within one of the three Jeronimo et al. (2019) climate classes (described in the "Study area" section).

### *First-entry Wildfires*

We identified 35 first-entry wildfire polygons (121,730 ha) for our study (Fig. 1; Table S1). To do so, we first selected all fire perimeters that intersected our study area, excluding prescribed burns, from CALFIRE's Fire and Resource Assessment Program (FRAP) fire history dataset (CALFIRE Fire Perimeters 2021). We then subset these fire perimeters to ensure that airborne lidar had been collected 5–15 years post-fire. A 5-year post-fire interval was used to account for lags in post-fire mortality, while a 15-year maximum was selected so that observed forest canopy structures were less likely to be driven by post-fire regeneration (van Mantgem et al. 2011; Jeronimo et al. 2020).

From these fire perimeters, we produced a set of polygons that met two further criteria: (1) were first-entry wildfires and (2) had not previously experienced harvest, thinning, or fuel treatments. First, we masked out all areas within fire perimeters that had previously burned, and where subsequent fires had occurred between the fire date and the lidar acquisition date (CALFIRE Fire Perimeters 2021). Next, we masked out previously treated areas from this subset of fire perimeters and any areas where treatments occurred between the fire date and the lidar acquisition date. Treatment history data was derived from a dataset produced by Knight et al. (2022) for the years 1985–2020 and the Forest Service FACTS database for years prior to 1985 (see full methods for producing this dataset in Chamberlain et al. 2023b). After applying these masks to all fire perimeters, we discarded any polygons < 100 ha so that fire sizes were similar to contemporary reference sites.

#### *Unburned control sites*

We identified a set of unburned and untreated control sites in the year 2015 to serve as a proxy for pre-fire conditions (Fig. 1). We produced these control sites by creating a buffered region 100–1,000 m outside the perimeters of our analysis fires. As with our fire perimeters, we masked out any areas that had burned or been treated prior to their corresponding lidar acquisition, and we discarded any final polygons < 100 ha. Based on these criteria, not all analysis fires had a corresponding control, so the resulting dataset represents unburned conditions for the full study area.

### Measuring forest structure with airborne lidar

We used point cloud data from six airborne lidar acquisitions (Table 1) to measure forest structures within our reference sites, analysis fires, and control sites (Fig. 2). Mean pulse density ranged from 12.6 $m^{-2}$ (Tuolumne County) to 28.0 $m^{-2}$ (Eldorado National Forest), representing data suitable for vegetation-related research using airborne lidar (i.e., meeting the United States Geological Survey's Quality Level 1 (Mitchell et al. 2018)) (Table 1). We used the Forest Service's FUSION software (McGaughey 2020) to process all six airborne lidar acquisitions and produce metrics of (1) canopy cover for all vegetation ≥ 2 m (hereafter, canopy cover), (2) relative canopy cover in the 2–8 m height stratum (hereafter, ladder fuel density), and (3) canopy fractal dimension index (hereafter, clump complexity) (Table 2; Fig. 2). We produced all metrics at 90-m resolution since past research suggests that fine-scale tree clump and opening patterns generally emerge at approximately this scale in frequent-fire forests (Larson and Churchill 2012; Knapp et al. 2017). We first normalized point clouds so that $Z$ coordinates represented vegetation height above ground. We also produced 0.75-m canopy height models (CHMs) from the normalized point clouds, which were smoothed using a 3 × 3-cell mean filter.

We used established methods for quantifying canopy cover (Kane et al. 2014, 2023) and ladder fuel density (Kramer et al. 2014; Hankin and Anderson 2022). For clump complexity, we developed a modified version of the FRAGSTATS fractal dimension index (McGarigal and Marks 1995). The original index describes, on average, the degree of fragmentation of patches within an area of interest. Our modified version is more computationally efficient and describes the degree of fragmentation of the entire canopy area within a 90-m pixel. Exploratory analyses (see Fig. S1) revealed that this clump complexity index was closely related to the fine-scale tree clump and opening patterns previously identified in the contemporary reference sites (Chamberlain et al. 2023a). As shown in Fig. S1, low clump complexity values (~ < 1.3) suggest structures dominated by large contiguous tree clumps, moderate values (~ 1.3–1.6) suggest fine-scale patterns of individual trees and small clumps of trees with high proportions of open space (an ICO pattern), and high values (~ > 1.6) indicate very low canopy cover composed primarily of standing snags within high-severity burn patches (Fig. S1).

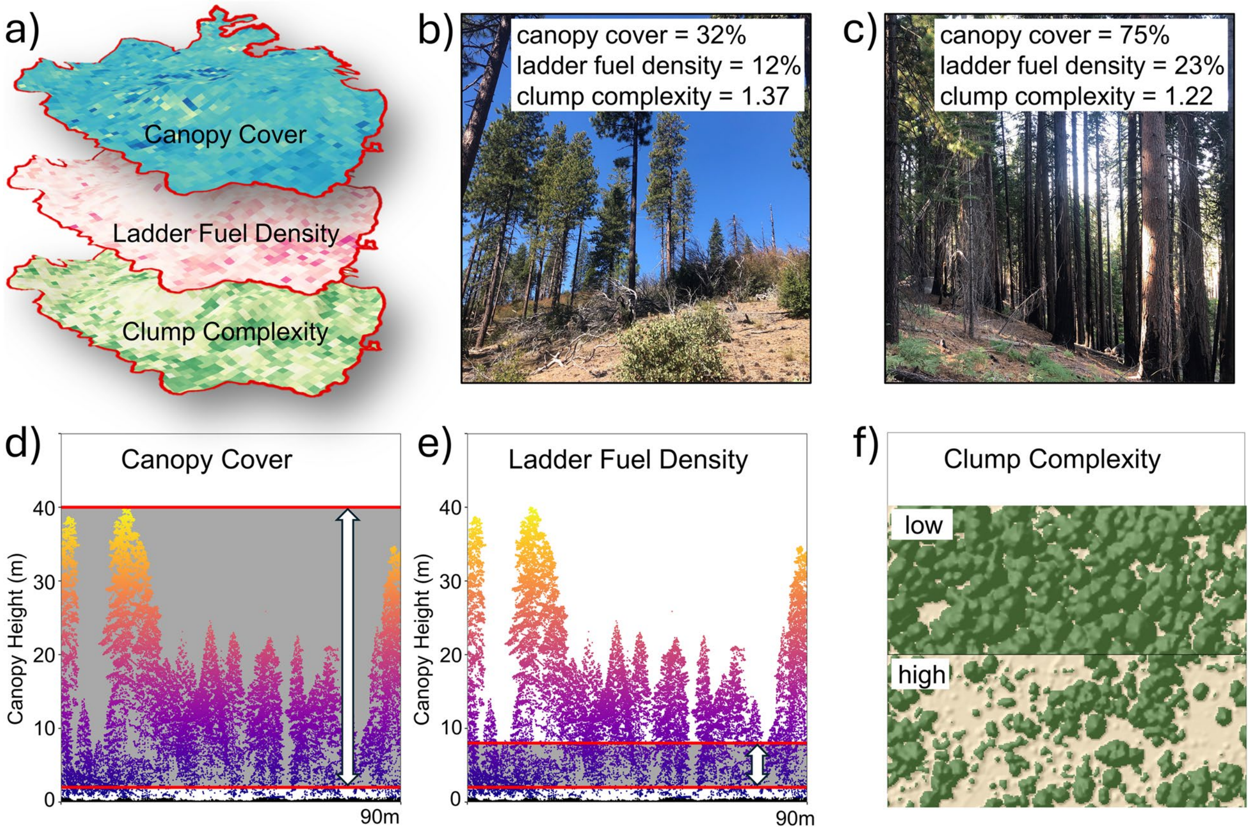


**Fig. 2** Visualizations of the three airborne lidar-derived structure metrics that represent key forest structures in yellow pine and mixed conifer forests of the Sierra Nevada, CA, USA. **a** Example 90-m resolution rasters of each metric within the 2,036-ha 2004 Meadow Fire. **b** Photo of site that met the full restoration index (canopy cover, ladder fuel density, and clump complexity all within the natural range of variation (NRV)) in the Plumas National Forest in summer 2023. **c** Photo of site that fell outside NRV for each metric on the Stanislaus National Forest in summer 2023. Cross-section of lidar point cloud shows how (**d**) canopy cover and (**e**) ladder fuel density metrics were computed from airborne lidar point clouds. **f** Illustration of low and high clump complexity values for a top-down view of a canopy height model. Photo credits: Caden Chamberlain

### Quantifying the extent of restorative fire effects (Objective 1)

We defined NRVs from the lidar-derived structure layers spanning the 55 reference sites (Fig. 3; Table S2). We subdivided the reference sites by climate and topographic classes to account for variability in forest structure across these gradients. For climate classes, we used the three Jeronimo et al. (2019) classes described in the "Study area" section. We then subdivided each climate class into four topographic classes using the land management units (LMUs) defined by Underwood et al. (2010) which include ridges, valleys, southwest-facing slopes, and northwest-facing slopes. Each NRV was then defined as the inner 68% (1 standard deviation around the mean) of the distribution of reference values for a given structure metric, within each topo-climatic class. This process resulted in 12 topo-climatic NRVs for each structure metric (Fig. 3; Table S2). Defining NRVs as ± 1 SD from the distribution mean is recommended when adequate sample sizes are possible and is similar to the "range of means" approach that has previously been used to define the historical range of variation for dry forest ecosystems (Safford and Stevens 2017; Bohlman et al. 2021).

We evaluated and compared the extent to which first-entry wildfire and control sites aligned with topographically and climatically matched NRVs for each structure metric. Specifically, we matched all first-entry wildfire and control pixels with NRVs from the same topo-climatic classes, then evaluated whether pixels fell below, within, or above NRV for each structure metric. Prior to comparing first-entry wildfire and control sites, we balanced the number of samples between first-entry and control sites in each topo-climatic class (randomly sampling from first-entry wildfire and control samples to reach the minimum sample size for a given class) to ensure similar representation of biophysical conditions.

We defined two sets of summary statistics: (1) for individual structure metrics and (2) for each of the restoration indices described in the "Study area" section (cover, partial, and full restoration). For individual structure metrics, we measured the proportion of total burned area or control area that fell below, within, or above NRV. For the restoration indices, we measured the proportion of total burned area or control area that either met the criteria or did not (i.e., binary indices). We selected the three restoration indices as they represent a gradient of increasingly restored conditions, each of which may be an acceptable measure of restoration under certain circumstances. For more detailed interpretations, we also plotted raw distributions of structure metrics across each topo-climatic class and split by first-entry wildfire, reference site, and control sites in Fig. S2.

Finally, we assessed how summaries of individual structure metrics and restoration indices varied across commonly used spectral measures of burn severity classes. We produced rasters of the Composite Burn Index (CBI) for each of our analysis fires using Google Earth Engine scripts developed by Parks et al. (2019). We used the bias-corrected CBI outputs from their script, and then classified rasters as low (0.1–1.24), moderate (1.25–2.24), and high (2.25–3.0) severity.

**Spatial patterns of restorative fire effects (Objective 2)**

To understand the landscape spatial patterns of restorative fire effects, we evaluated the spatial distribution and arrangement of contiguous patches of the three restoration indices. We defined patches of each restoration index using an 8-neighbor rule based on adjacency of like-cells. Then for each restoration index, we reported total counts of different patch sizes, as well as cumulative distribution curves of total patch area across the full extent of our analysis fires.

**Drivers of restorative fire effects (Objective 3)**

To evaluate the drivers of restorative fire effects, we fit RF classification models predicting the full restoration index (as a binary response) using a set of predictor variables describing pre- and active-fire burning conditions. In other words, we evaluated how pre- and active-fire burning conditions influenced the probability that post-fire structures simultaneously met canopy cover, ladder fuel density, and clump complexity targets. We conducted all modeling using the *tidymodels* package (Kuhn and Wickham 2020).

We first compiled a large set of predictor variables spanning all areas within the perimeters of our analysis fires. These predictors captured a range of conditions that were likely to influence fire behavior and effects,

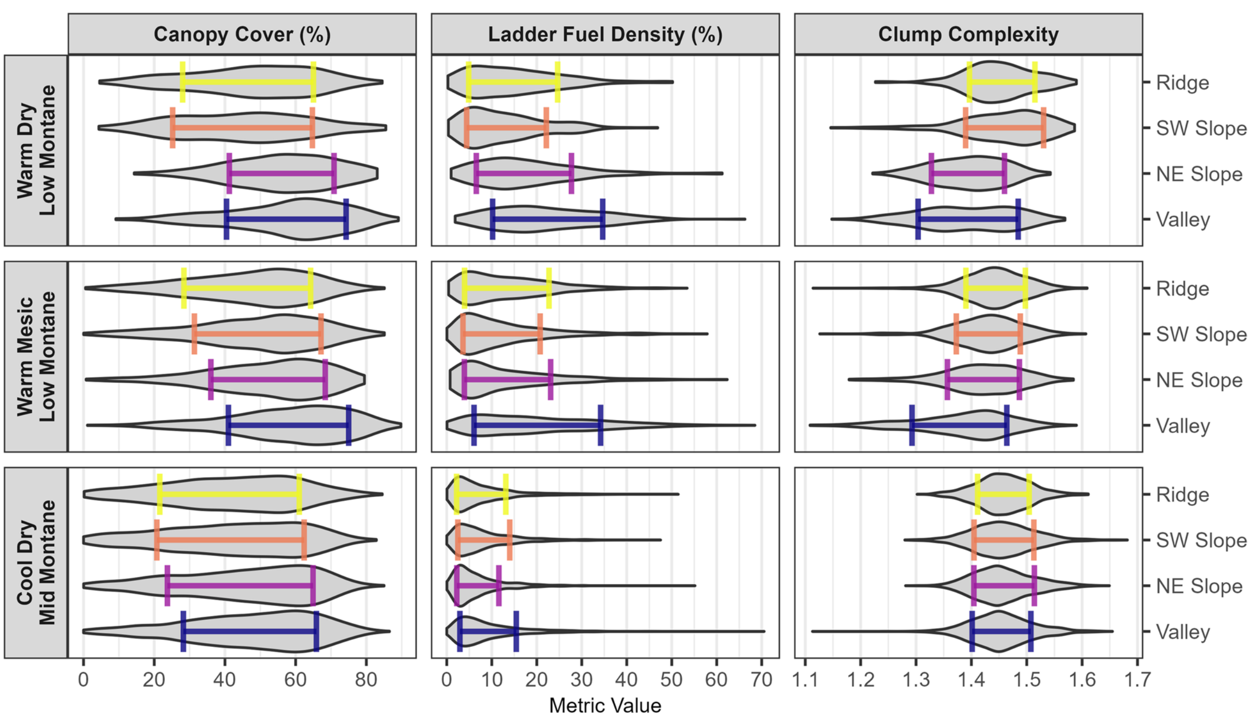


**Fig. 3** Natural Ranges of Variation (NRV) as defined from contemporary reference sites for three airborne lidar-derived structure metrics across three climate classes and four topographic classes in the Sierra Nevada ecoregion, CA, USA. We defined NRVs (colored bars) as the inner 68% of the full distribution of each metric for each unique topo-climatic class, with full distributions shown in gray violin plots. SW, southwest; NE, northeast

**Table 1** Statistics for six airborne lidar acquisitions ordered from north to south, covering portions of the Sierra Nevada ecoregion, CA, USA. *NF*, National Forest; *NP*, National Park

| Acquisition name | Years flown | Total area (ha) | Mean pulse density (pulse m$^{-2}$) |
|---|---|---|---|
| North Plumas NF | 2018 | 466,774 | 13.3 |
| South Plumas NF | 2018 | 560,370 | 12.6 |
| Eldorado NF | 2019 | 577,109 | 28.0 |
| Tuolumne County | 2018–2019 | 694,330 | 15.3 |
| Yosemite NP | 2019 | 369,824 | 23.5 |
| SSARR (Sierra NF) | 2020 | 569,810 | 22.0 |

including bioclimatic, fire weather, topographic, and pre-fire forest structure, as well as four landscape context variables (e.g., distance to past fires). Full descriptions of all 34 predictor variables are provided in Supplemental Methods 1 and Table S3, while the 13 predictors included in the final model (post-variable reduction) are described in Table 3. We describe our full variable reduction procedure in Supplemental Methods 2.

We produced a grid of sample points across our analysis fires using the centroid of each cell in the full restoration layer. We then subsampled this grid so that sample points were spaced ≥ 270 m apart to reduce the effects of spatial autocorrelation in our modeling (Kane et al. 2015a; Povak et al. 2020; Cansler et al. 2022). We also discarded all sample points that fell within a 30-m buffer of any roads or powerlines. We extracted the 13 continuous predictor variables (Table 3) to our sample points to create a final modeling dataset and balanced that dataset on the binary full restoration response. Our final modeling dataset had 1,844 observations. We used the full model dataframe to tune hyperparameters using fivefold cross-validation. We tuned all possible hyperparameters for RF models that were available from the *ranger* engine (Wright and Ziegler 2017), using the *tune_race_anova* function from the *finetune* package (Kuhn 2023). We computed overall model accuracy as the mean accuracy across all five cross-validation folds for the optimized models. Lastly, we fit a final RF model using the full modeling dataframe, and computed permutation importance for each predictor variable. We also produced partial dependence plots (PDPs) for each predictor using the *DALEXtra* package (Maksymiuk et al. 2020). We provide PDPs for the top 6 predictor variables. We provide the full set of 13 PDPs for all predictors in Fig. S3, and two-variable PDPs to show the interaction between burning index and other top predictors in Fig. S4.

#### Mapping the probability of restorative fire effects (Objective 4)

We used the final RF model to predict and map the probability of restorative fire effects (full restoration) across all previously unburned areas in the Sierra Nevada YPMC zone for the year 2020. We began by producing a polygon representing potential first-entry wildfire area for the year 2020 using the CALFIRE FRAP fire history dataset (CALFIRE Fire Perimeters 2021). This was accomplished by masking out all areas that had burned

**Table 2** Equations and ecological importance for the three airborne lidar-derived structure metrics that represent key structural conditions in Sierra Nevada YPMC forests, CA, USA

| Metric name | Computation | Ecological importance | Range | Units |
|---|---|---|---|---|
| Canopy cover | $\frac{\sum_{i=1}^{n} z_i \geq 2}{n}$<br>where *n* is the number of points in the 90-m cell and<br>$z_i$ is the height above ground of the *i* th point;<br>units in meters | Higher canopy cover leads to higher crown fire spread rates and increased water stress and competition which relate to fire and drought resistance; lower canopy cover relates to increased area gap which increases the likelihood of successful post-fire regeneration | 0–100 | Percent |
| Ladder fuel density | $\frac{\sum_{i=1}^{n} 2 \leq z_i < 8}{\sum_{i=1}^{n} z_i < 8}$<br>Symbols defined as above | Higher ladder fuel density suggests a higher density of short, sub-canopy trees, which results in a higher likelihood of crown fire initiation | 0–100 | Percent |
| Clump complexity | $\frac{2\ln\left(0.25\sum_{i=1}^{n} P_i\right)}{ln\left(\sum_{i=1}^{n} A_i\right)}$<br>where *n* is the number of canopy patches in the 90-m cell, $P_i$ is the perimeter of the *i* th patch, and $A_i$ is the area of the *i* th patch; modified version of FRAGSTATS FRAC metric which improves computational efficiency | Clump complexity provides a single-metric proxy for describing fine-scale patterns of individual trees, clumps of trees, and openings which are essential to frequent-fire forest structures; moderately high complexity (~ 1.3–1.6) leads to reduced crown fire initiation and spread rates, and increased post-fire regeneration; moderate clump complexity also suggests improved wildlife habitat and biodiversity | Approx. 1–2 | Unitless; high values = increased complexity |

**Table 3** Continuous predictor variables used in final random forest (RF) model predicting the full restoration index for first-entry burned sites in the Sierra Nevada ecoregion, CA, USA. Variables represent the subset of all predictors post-variable reduction, listed in order of importance, first by category then by variable. The full variable list is provided in Table S1. *PRECIP*, average annual precipitation; *CWD*, climatic water deficit; *TPI*, topographic position index; *DEM*, digital elevation model

| Data category | Variable name | Variable description | Resolution (m) | Units | References |
|---|---|---|---|---|---|
| Landscape context | Distance to past fire | Distance to nearest previous fire | 90 | m | CALFIRE Fire Perimters 2021; Hijmans et al. 2023 |
| | Distance to water | Distance to nearest river, stream, or lake | 90 | m | Hijmans et al. 2023 |
| | Distance to treatment | Distance to nearest prior treatment | 90 | m | Knight et al. 2022; Hijmans et al. 2023 |
| | Distance to roads | Distance to nearest national, state, or Forest Service road | 90 | m | Hijmans et al. 2023 |
| Climate | Elevation | Elevation | 10 | m | Digital Elevation Model 2022 |
| | PRECIP 1981–2010 | Mean annual total precipitation across years 1981–2010 | 270 | mm | Flint et al. 2021 |
| | Fire resistance score | Community fire resistance score | 250 | Continuous numeric | Stevens et al. 2020 |
| | CWD 1981–2010 | Mean climatic water deficit across years 1981–2010 | 270 | mm | Flint et al. 2021 |
| Topographic | Topographic position index (TPI) 510-m | Topographic position index derived from USGS 10-m DEM using a 510-m window; lower values represent moderate-scale valleys and higher values represent moderate-scale ridges | 30 | Unitless | Digital Elevation Model 2022; Evans and Murphy 2021 |
| | Topographic ruggedness | Topographic ruggedness index derived from USGS 10-m DEM using a 130-m window; 0–80 = level terrain; 81–116 = nearly level surface; 117–161 = slightly rugged surface; 162–239 = intermediately rugged surface; 240–497 = moderately rugged surface; 498 + = highly-extremely rugged surface | 30 | Unitless | Digital Elevation Model 2022; Evans and Murphy 2021 |
| | Solar radiation index | Solar radiation index derived from USGS 10-m DEM; 0 represents land oriented in north-northeast direction and 1 representss land oriented in south-southwest direction | 30 | Unitless | Digital Elevation Model 2022; Evans and Murphy 2021 |
| Fire weather | Burning index | Index of fire intensity; "combines the spread component and energy release component to relate the contribution of fire behavior to the effort of containing a fire" | 30 | Unitless | Abatzoglou 2013 |
| Forest structure | Diameter diversity index | "measure of the structural diversity of a forest stand, based on tree densities in different DBH classes" | 30 | Continuous index | GNN Structure 2023 |

prior to or during 2020 (but did not account for areas that burned after 2020). Next, we compiled all predictor variable rasters covering this potential first-entry wildfire area. We then predicted the probability of restorative fire effects (full restoration) across this region and classified it as a binary outcome using a 0.5 threshold. We made predictions under two fire weather scenarios, mild and moderate, by setting burning index at its 25th and 75th percentile, which represented burn indices of 53 and 71, respectively. Finally, to improve visualizations of mapped outputs across the full Sierra Nevada, we aggregated 90-m pixel predictions to the national NHDPlusV2 catchments dataset (NHDPlusV2 2021) using the majority class prediction within each catchment. We provide mapped predictions of the cover only and partial restoration indices in Figs. S5 and S6, respectively. We also archived raster layers of the mapped predictions in a Zenodo Digital Repository (https://doi.org/https://doi.org/10.5281/zenodo.12802224).

## Results

### Extent of restorative fire effects (Objective 1)

Across all topo-climatic classes within the contemporary reference sites, canopy cover NRVs ranged from 21.56 to 74.99%, ladder fuel density ranged from 2.18 to 34.66%, and clump complexity ranged from 1.29 to 1.53 (Fig. 3; Table S2). Generally, ridges and southwest-facing slopes had lower targets for canopy cover and ladder fuel density and higher targets for clump complexity. In contrast, valleys and northwest-facing slopes were characterized by higher canopy cover and ladder fuel densities and lower clump complexities. Additionally, canopy cover and ladder fuel density NRVs were lower and clump complexity NRVs were higher within the Cool Dry Mid Montane zone, relative to the Warm Dry Low Montane and Warm Mesic Low Montane zones (Fig. 3; Table S2).

For all three structure metrics, first-entry wildfires produced higher proportions of area within NRV relative to the unburned control sites (a proxy for pre-fire conditions) (Fig. 4a). First-entry wildfires were most successful at achieving NRV targets for ladder fuel density (54% total area; 32% more area within NRV than controls), followed by canopy cover (48% total area; 13% more area within NRV than controls), and then by canopy complexity (41% total area; 11% more area within NRV than controls). Patches of moderate severity contained considerably higher proportions of area within NRV for all three individual structure metrics (55–64%), compared to patches of low or high severity. Although 48% of low-severity patches had ladder fuel densities within NRV, canopy cover fell above NRV across 50% of sites and clump complexity fell below NRV across 58% of sites. Conversely, in high-severity patches, although ladder fuel densities were often within NRV (57% total area), canopy cover was below NRV across 68% of sites and clump complexity was above NRV across 68% of sites (i.e., loss of fine-scale heterogeneity) (Fig. 4a).

Across all three restoration indices (representing a gradient of restored structures), first-entry burned areas consistently had higher proportions within NRV relative to unburned controls—13%, 18%, and 11% higher proportion within NRV for cover, partial, and full restoration, respectively (Fig. 4b). However, it remained relatively uncommon for first-entry wildfires to simultaneously produce two, and especially three, structural characteristics within NRV. For example, only 27% of first-entry burned area met the partial restoration target (i.e., restoring both canopy cover and ladder fuels) and only 16% met the full restoration target (i.e., restoring all three structure metrics) (Fig. 4b). Patches of moderate severity had the highest proportion of total area within NRV across all three levels of restoration, with 37% and 24% of total area meeting the partial and full restoration targets, respectively (Fig. 4b).

### Spatial patterns of restorative fire effects (Objective 2)

Across all analysis fires in our study, first-entry wildfires produced relatively small patches of restored structures, which were interspersed within larger patches where post-fire structural conditions were either above or below NRV targets (Fig. 5). For all three restoration indices, patches of restorative effects were dominated by small (< 10-ha) patches, with low total counts of 10–500-ha patches. Patches of the cover restoration index were larger compared to patches of the partial and full restoration indices (Fig. 5a). For the cover only index, patches > 100 ha contributed to 55.8% of the total patch area, suggesting a high proportion of large, contiguously restored areas. Conversely for the partial and full restoration indices, patches > 100 ha contributed to only 25.2% and 5.2% total patch area (Fig. 5b), respectively, indicating that first-entry wildfires were dominated by small, interspersed patches of partially and fully restored sites, as shown in Fig. 5c.

### Drivers of restorative fire effects (Objective 3)

Our models had an overall prediction accuracy of 62.1%, indicating that pre- and active-fire conditions had a moderate influence on the probability of full restoration. Distance to past fire, a measure of the landscape context within which an area burned, had the strongest influence on the probability of restorative fire effects. Important bioclimatic and fire weather influences included elevation, long-term (1981–2010) mean annual precipitation, and day-of-burn burning index, representing top-down

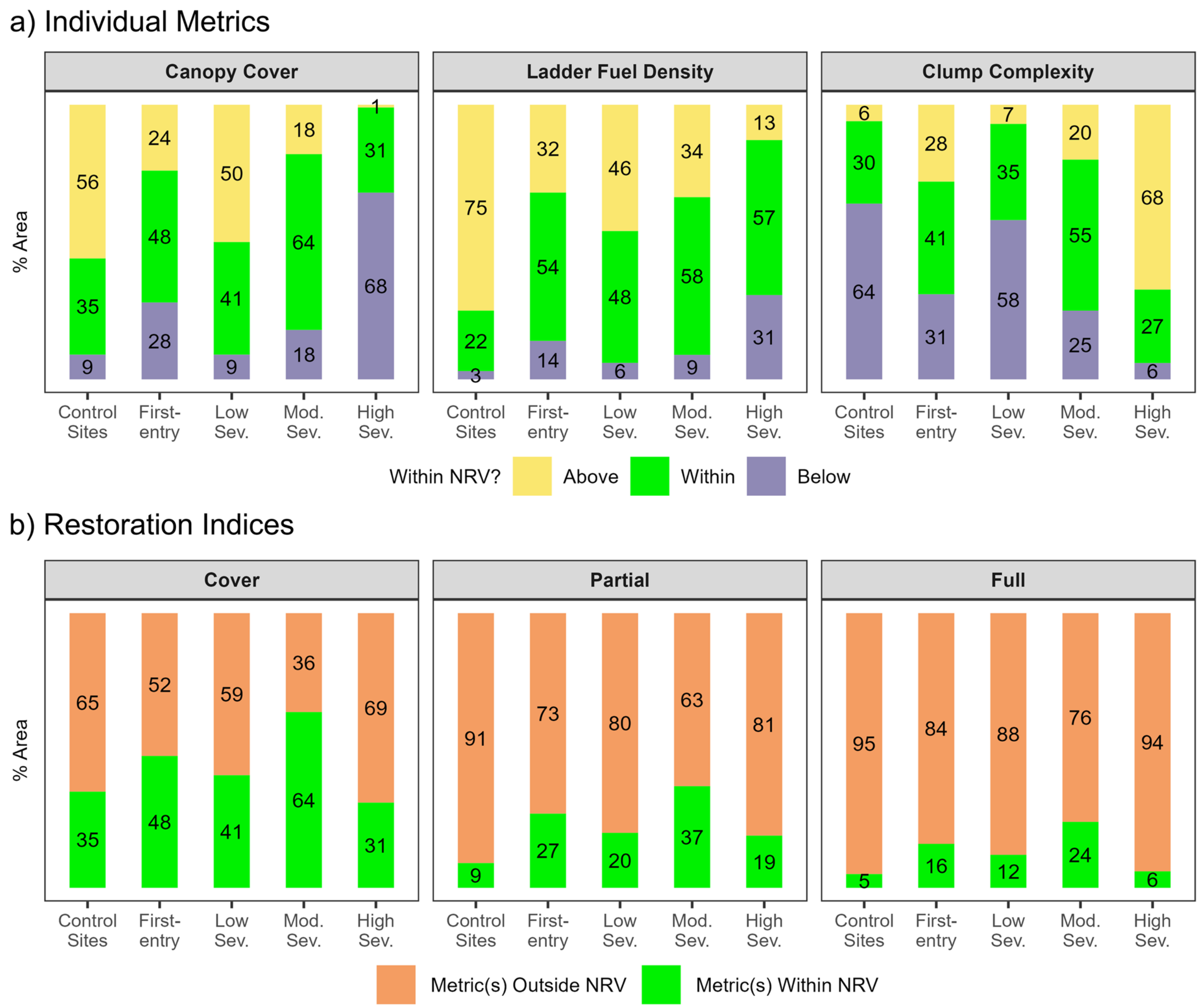


**Fig. 4** **a** Percent of total area above, within, or below the topographically and climatically adjusted natural range of variation (NRV) for individual metrics and **b** percent of total area meeting each of the restoration indices for sites in the Sierra Nevada ecoregion, CA, USA. Cover index signifies only cover within NRV, partial index signifies canopy cover and ladder fuel density within NRV, and full index signifies canopy cover, ladder fuel density, and clump complexity within NRV. *X*-axes show proportions by control area (a proxy for pre-fire conditions), all first-entry burned areas, and patches of low- (0.1–1.24), moderate- (1.25–2.24), and high- (2.25–3) severity effects as defined using Composite Burn Index (CBI). Burn severity patches were defined using an 8-neighbor rule; proportions are only representative of the first-entry area completely within burn severity patches. Mod: moderate; NRV: natural range of variation

influences. Important bottom-up drivers included topographic position index and pre-fire diameter diversity index (Fig. 6a).

We observed a mix of both linear and non-linear relationships between restorative fire effects and the top landscape context, bioclimatic, fire weather, topographic, and forest structure metrics (Fig. 6b). We found that the probability of restorative fire effects declined as distance to past fire increased (with a distinct threshold at ~ 1 km) and as fire weather became moderate to extreme (burning index > 60). We also found that higher elevations (~ > 1,500 m) and sites within the mid-range of long-term annual precipitation had the highest probability of restorative effects. Finally, we observed that valleys tended to support more restorative fire effects compared to ridges and slopes, as well as sites with higher (> 5) pre-fire diameter diversity index (Fig. 6b).

### Mapped probability of restorative fire effects (Objective 4)

We found that 48% of previously unburned areas in the year 2020 would be likely to experience restorative fire effects under moderate fire weather conditions (burning index = 71; flame lengths ~ 2 m), and 58% under mild fire weather conditions (burning index = 53;

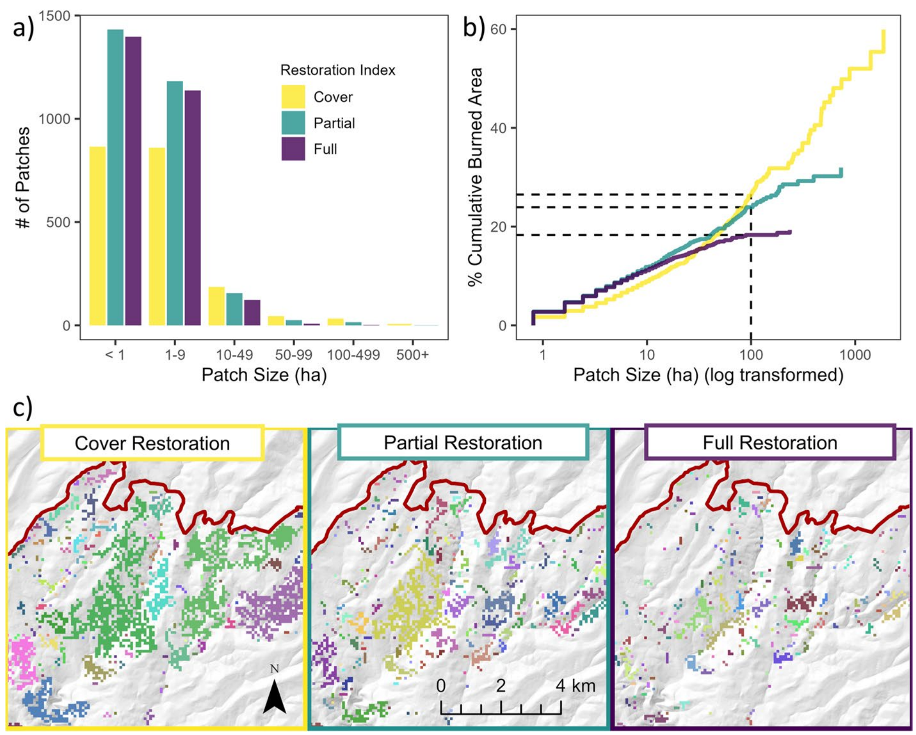


**Fig. 5** **a** Patch size distributions and (**b**) cumulative patch area distributions for patches of restorative fire effects under three restoration indices—cover restoration (canopy cover only), partial restoration (canopy cover plus ladder fuel density), and full restoration (canopy cover plus ladder fuel density plus clump complexity), for sites in the Sierra Nevada ecoregion, CA, USA. **c** Visualizations of patch sizes and spatial distributions under each restoration index within the northern portion of the 2013 Rim Fire, where each color represents a distinct patch. We transformed patch sizes on the *y*-axis in plot b for visualization. We defined contiguous patches using the 8-neighbor rule for adjacent pixels of like-classes. Dashed lines mark the cumulative proportion of the total burned area for each restoration index at a patch size of 100 ha to assist in interpretation

flame lengths ~ 1.5 m). The remaining 42% would be unlikely to experience restorative first-entry wildfire effects, regardless of fire weather conditions. Mapping the probability of restorative fire effects across the Sierra Nevada YPMC zone revealed clear geographic and spatial patterns (Fig. 7). For example, most of the previously unburned area within Yosemite National Park and Sequoia and Kings Canyon National Parks would be likely to experience restorative fire effects even under moderate fire weather conditions. In Stanislaus, Eldorado, Tahoe, and Plumas National Forests, relatively large portions of the mid- to upper-elevation sites showed a high probability of full restoration under a mild fire weather scenario. Across the Sierra Nevada, lower elevation sites, especially in the northern portions of the region, had a low probability of restorative effects, even under mild fire weather conditions (Fig. 7).

## Discussion

As wildfires make their return to fire-suppressed YPMC forests of the Sierra Nevada, it is essential to understand how these contemporary fires are affecting forest structural patterns, the extent to which these patterns align with common restoration objectives, and the factors that contribute to more restorative fire effects (Williams et al. 2019; Kane et al. 2019; Meyer et al. 2021; North et al. 2021). Our results suggest that contemporary, first-entry wildfires were moderately successful at shifting canopy cover and ladder fuel density toward NRVs, but less successful at producing the complex tree clump and opening patterns that characterize contemporary reference sites. Additional wildfires and, in some instances, post-fire management will be required to fully shift structural patterns toward those associated with fire-intact ecosystems. We found that the probability of restorative fire effects was primarily influenced by landscape disturbance history (i.e., sites located within mosaics of past wildfires) along with a suite of bioclimatic, fire weather, topographic, and pre-fire structural conditions. The bounds of these relationships may inform managers regarding when and where future fires could be successfully managed for resource objectives (North et al. 2024). Achieving conditions associated with fire-intact ecosystems, which are likely to exhibit increased resilience under future disturbances and climates, will require land

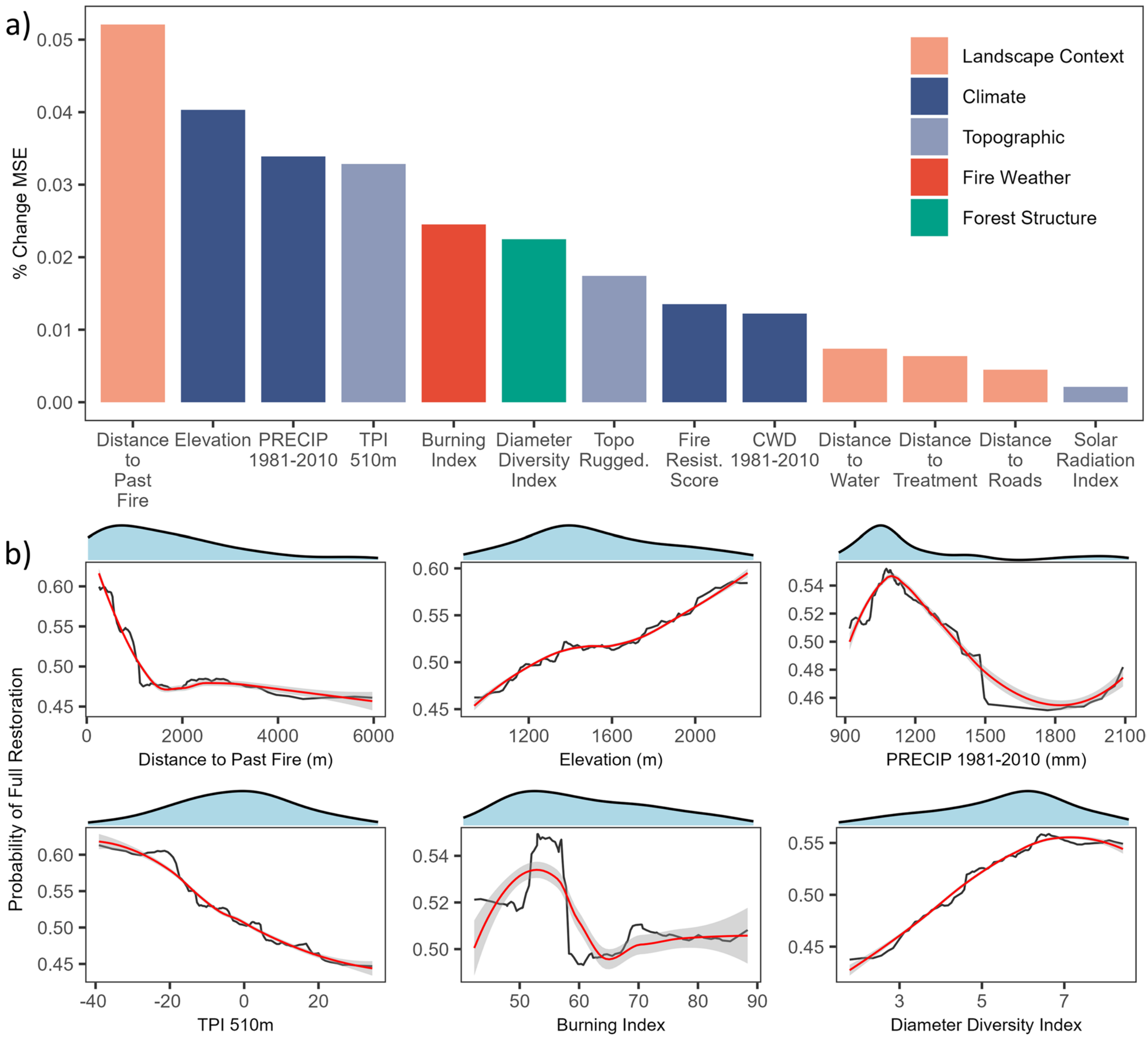


**Fig. 6** **a** Variable importance and (**b**) partial dependence plots (PDPs) from the final Random Forest model predicting the full restoration index (i.e., canopy cover, ladder fuel density, and clump complexity all within the natural range of variation (NRV)) as a binary response. Models represent conditions in the Sierra Nevada ecoregion, CA, USA. Variable importance plots colored by variable categories. We only show PDPs for the top six most important predictors (PDPs for all predictor variables are provided in Fig. S3). Black line shows predictions, while the red line shows loess smooth with standard error in gray. Density plots in blue show counts of observations across the range of values for each variable. PRECIP, average annual precipitation; TPI, topographic position index; CWD, average annual climatic water deficit

management plans that encourage beneficial low- and moderate-severity wildfires, strategic and proactive post-fire management strategies that leverage restorative fire effects, and continued efforts to increase the pace and scale of restoration treatments in high-risk areas (Hessburg et al. 2021; Meyers et al. 2021; North et al. 2024).

### Structural targets from contemporary reference sites

Our characterizations of structural patterns from contemporary reference sites generally aligned with previous assessments from contemporary and historical reference datasets in Sierra Nevada YPMC forests. The frequent low-severity fire regime that historically characterized these forests, and the reestablishment of this regime in the modern era, tends to produce relatively low canopy covers (21–75% in our study), low ladder fuel densities (2–35% in our study), and fine-scale heterogeneity in tree spatial patterns (reflected in this study by moderate values (1.3–1.5) of the clump complexity index) (Knapp et al. 2013; Lydersen et al. 2013; Jeronimo et al. 2019;

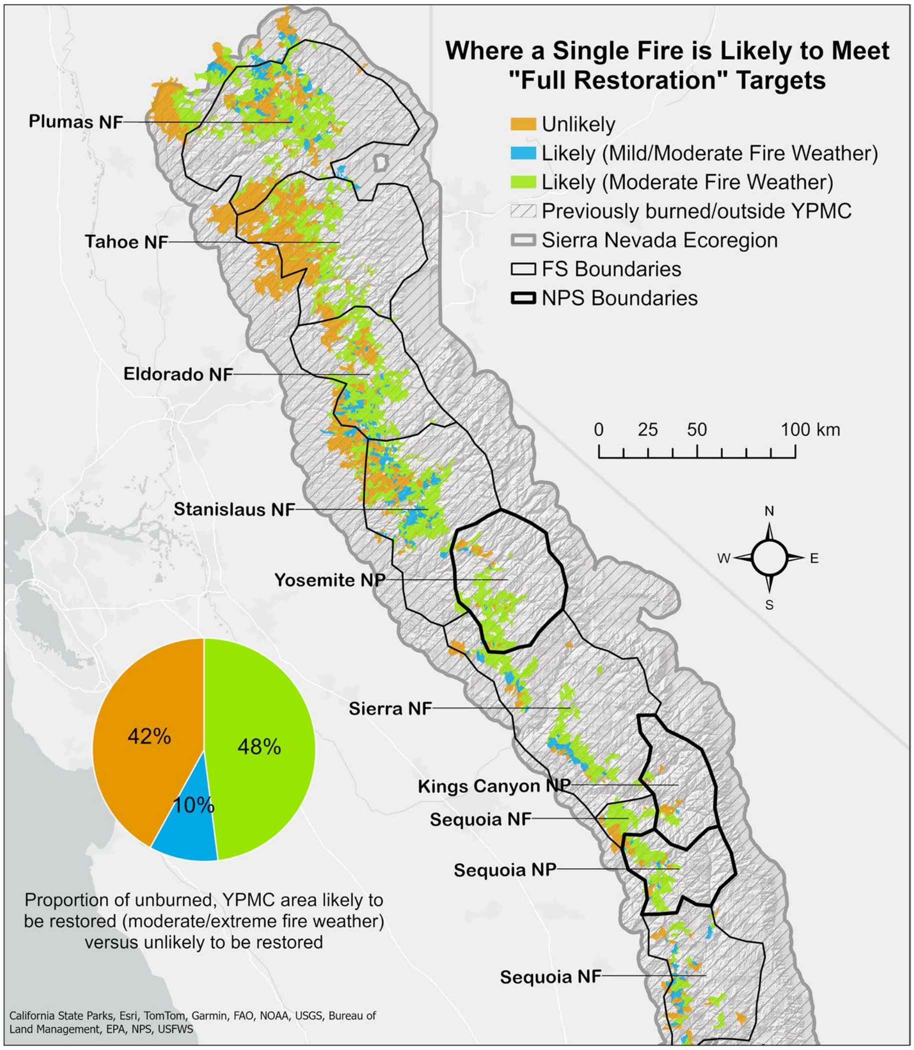


**Fig. 7** Mapped predictions of the full restoration index (i.e., canopy cover, ladder fuel density, and clump complexity all within the natural range of variation (NRV)) for the previously unburned area in the year 2020 in the Sierra Nevada yellow pine and mixed conifer (YPMC) zone, CA, USA. Blue and green sites represent a probability of full restoration > 0.5 under a mild (burning index = 53) and moderate (burning index = 71) fire weather scenario, respectively. Orange represents a probability of full restoration < 0.5 under both weather scenarios. For visualization, 90-m pixel predictions were aggregated to the catchment level using the majority class prediction within each catchment. NF, National Forest; NP, National Park; YPMC, yellow pine mixed conifer

Hankin and Andersen 2022; Chamberlain et al. 2023a). Similar to the work by Ng et al. (2020) and Jeronimo et al. (2019), we found that structural patterns indeed varied by topographic gradients and, to a lesser extent, climatic gradients, such that increased topographic and climatic variability begets site- to landscape-level structural heterogeneity. This among-site variation has also been observed in historical datasets in the Sierra Nevada (Collins et al. 2015; Knapp et al. 2017), underscoring that landscape-level heterogeneity is a key structural component produced by a frequent low-severity fire regime, and that capturing these multi-scaled structural components is critical when evaluating the restorative work of wildfires (Wiggins et al. 2019; Chamberlain et al. 2023a).

#### First-entry wildfire effects

Relative to unburned controls (which were characterized by high canopy cover (> 61–75%), dense ladder fuels (> 12–35%), and low clump complexity (< 1.3–1.4)), we found that first-entry wildfires were indeed effective at restoring structural characteristics, especially in moderate-severity patches. In this sense, our results support recent work by Kane et al. (2019) who found that first-entry wildfires in Yosemite National Park tended to realign tree clump and opening patterns with those found in contemporary reference sites. Our results also align with other remote sensing and field-based studies showing that structural patterns in moderate-severity sites were most similar to historical reference conditions (Collins et al. 2011a; Kane et al. 2013; Lydersen et al. 2016). However, while our results suggest that first-entry wildfires improved conditions relative to unburned controls, sites in which NRV was achieved for all three structure targets were relatively rare across our study fires (16% of total area and 24% of moderate-severity patches). This suggests that a large portion of first-entry burned areas, even within moderate-severity patches, may still require additional low- to moderate-intensity wildfires or other forms of post-fire management (Coppoletta et al. 2016; Meyer et al. 2021; Steel et al. 2021). First-entry burn sites where canopy cover and ladder fuel densities remained above NRV may require additional fire entries or post-fire mechanical thinning to further consume and disaggregate overstory structures (Collins et al. 2011b; Meyer et al. 2021; Ziegler et al. 2021), whereas sites with excessive overstory consumption will likely require strategic post-fire planting to promote the recovery of low-density ICO patterns (North et al. 2019; Meyer et al. 2021).

We found that first-entry wildfires were least likely to meet targets related to clump complexity relative to other structure metrics, suggesting that the complex clump patterns characteristic of fire-intact ecosystems may only be achieved after multiple, moderate-intensity fires, rather than just a single fire event. Low- to moderate-intensity surface fires produce fine-scale tree clump and opening patterns as a function of fine-scale patterns of fuel moisture, wind patterns, soil moisture gradients, existing vegetation, and fine-scale variations in past disturbances (Collins et al. 2015; Kane et al. 2015b; Hessburg et al. 2019a; Jeronimo et al. 2020). A single fire may produce some degree of fine-scale heterogeneity (Kane et al. 2019), but it is the interplay among these factors across multiple fire events that ultimately leads to the characteristic tree clump and opening patterns observed in fire-intact ecosystems (Larson and Churchill 2012; Kane et al. 2015b; Churchill et al. 2017; Greenler et al. 2023).

First-entry burn areas frequently produced large (> 100-ha) patches of cover only restoration, with smaller, dispersed patches of partial and full restoration embedded within those larger patches. This suggests that first-entry wildfires are beginning to increase stand- and landscape-level heterogeneity (i.e., increased diversity in 90-m structures across a site). Heterogeneity contributes to improved wildlife habitat and increased biodiversity while also increasing resilience to future disturbances and climate change (Stephens et al. 2016; Koontz et al. 2020; Kramer et al. 2021; Francis et al. 2023). Heterogeneity begets heterogeneity (Harvey et al. 2023); thus, we expect future, low-intensity fires to further increase stand-level heterogeneity within these large patches of cover only restoration (Kane et al. 2015a; Koontz et al. 2020). After several fires, these sites may begin to resemble the highly heterogeneous patch mosaics that characterize historical and contemporary fire-intact ecosystems (Collins et al. 2015; Jeronimo et al. 2019; Chamberlain et al. 2023a).

Species composition and surface fuel loading represent critical components of fire-intact ecosystems. Yet, methods for measuring these components using airborne lidar are not fully developed, especially at regional scales (Akay et al. 2009; Beland et al. 2019). Recent field-based studies have found that repeated fire entries (and mechanical thinning) in Sierra Nevada forests have failed to shift species composition toward historical densities of fire-resistant pines (May et al. 2023; Zald et al. 2024). Additionally, other field-based studies have found that surface fuels are unlikely to be reduced following first-entry wildfires (Cansler et al. 2019; Lutz et al. 2020; Larson et al. 2022), especially following the 2012–2016 drought in the southern Sierra Nevada which contributed substantially to surface fuel loading (Reed et al. 2023; Vilanova et al. 2023; Northrop et al. 2024). Ultimately, we suspect that the fully restored post-fire structures observed in our study, characterized by lower canopy cover, reduced ladder fuels, and increased clump complexity, represent improved structural conditions compared to their unburned counterparts (i.e., control sites) (Agee and Skinner 2005; Larson and Churchill 2012; Ritter et al. 2020). However, additional work may be needed to evaluate the extent to which first-entry wildfires have shifted species distributions and surface fuel loads toward desired conditions (Knapp and Keeley 2006; Cansler et al. 2019; Lutz et al. 2020; Hankin et al. 2024).

#### Drivers of restorative fire effects

Our results suggest that landscapes characterized by a mosaic of past wildfires were most likely to experience restorative fire effects across the entirety of the landscape during subsequent fires. Past work has demonstrated that fires occurring *within* recently burned areas tend to have low- to moderate-severity effects (Parks et al. 2015; Stevens-Rumann et al. 2016; Prichard et al. 2017). Our results suggest that these beneficial effects of past fires (i.e., mostly low- to moderate-severity effects) may extend *beyond* an individual fire's footprint, for upwards of 1 km. The effect of past fire proximity may also indicate that fire boundaries were often located at places on the landscape where fuels were already sparse (e.g., rocky ridgetops) or where fire suppression operations were more likely to be successful (e.g., major roads) (O'Connor et al. 2017; Gannon et al. 2023). It is also likely that National Parks (representing 14% of our sample) had higher densities of past fires, considering their long-standing prescribed and natural fire programs (van Wagtendonk 2007; Hankin et al. 2024). Forests within National Parks are often characterized by higher proportions of older, more fire-resistant trees due to the relative lack of early century logging, which likely contributed to increased probability of restorative fire effects (Kane et al. 2023).

Modeled flame lengths of approximately 1–2 m (burning index 50–55) were most successful at producing post-fire structures within NRV in our analyses, suggesting that moderate-intensity wildfire is necessary to produce desired structural conditions in fire-suppressed YPMC forests. Our results were similar to Schmidt et al. (2006) who found that late-season prescribed burns in the Sierra Nevada with flame lengths of ~ 1–2.5 m were most successful at producing tree density and clumping patterns matching historical conditions. Lydersen et al. (2016) also found that flame lengths < 2.4 m (burning index < 75) were most likely to produce moderate-severity fire effects within the 2013 Rim Fire, yet higher flame lengths generally resulted in high severity effects. As such, our results provide additional evidence, spanning a broad geographic extent and biophysical setting in Sierra Nevada YPMC forests, that relatively specific fire intensities may be required in fire-suppressed forests to have the best chances of achieving restored post-fire structures (Knapp and Keeley 2006; Schmidt et al. 2006; Greenler et al. 2023). Importantly, while areas that burned under less intense fire weather may have failed to fully restore canopy structures, lower severity effects are always favorable over high severity; once overstory trees are lost, reestablishing forest cover becomes far more costly and challenging (North et al. 2019; Larson et al. 2022).

We observed complex (and likely interacting) relationships between several environmental factors and the probability of restorative fire effects. For example, we found that sites at lower elevations and with higher mean annual precipitation (i.e., lower elevations in the northern Sierra Nevada), and sites with more exposed topographic positions tended to exhibit less restorative effects. To an extent, these trends may be driven by variations in species composition across the YPMC zone, in which lower elevation sites and ridges would support higher proportions of oak and incense cedar, which may have contributed to increased pre-fire ladder fuel densities and thus less restorative fire effects (Zald et al. 2008; Collins et al. 2015; Stevens et al. 2020; Cansler et al. 2020). It is also possible that underlying edaphic conditions may have contributed to increased restorative fire effects in the southern Sierra Nevada, which is generally characterized by steeper terrain and more exposed bedrock compared to the northern parts of the range (Safford and Stevens 2017). These edaphic conditions may have served as physical barriers to extreme fire spread at the landscape scale (Safford and Stevens 2017), facilitating more beneficial fire effects. Edaphic conditions in the southern Sierra Nevada may have also supported more complex pre-fire structures (i.e., higher diameter diversity index) which were associated with a higher probability of restored post-fire structures in our analyses (Meyer et al. 2007; Fry et al. 2014). Lastly, it is possible that the lower elevations in the northern Sierra Nevada represented sites within closer proximity to industrially managed forests, which can increase the incidence of high-severity fire effects on adjacent public lands (Levine et al. 2022).

We found that a relatively high portion (58%) of the Sierra Nevada YPMC zone would be likely to benefit from future first-entry wildfires that burn under mild fire weather conditions (~ 1 m flame lengths), and a reasonable proportion (48%) could even benefit under moderate fire weather conditions (~ 2 m flame lengths). Regions with large, contiguous areas of likely restorative effects under both weather scenarios were observed primarily in Yosemite National Park, Sequoia National Park, and the upper elevation regions of several National Forests (Eldorado National Forest in particular). In Yosemite and Sequoia National Parks, this was likely due to their long-established prescribed and natural fire program which, over the past several decades, have created extensive patchworks of previously burned areas (Collins and Stephens 2007; van Wagtendonk 2007; Hankin et al. 2024). Our maps also show a large contiguous region that was unlikely to experience restorative effects across the lower elevations of Stanislaus, Eldorado, and Tahoe National Forests. In these sites, increased incense cedar and oak presence, lack of topographic barriers to fire spread, and closer proximity to industrial forests lands may contribute to less restorative fire effects. Importantly, we note that several large fires burned within the Sierra Nevada in 2021 and 2022; future research can evaluate the extent to which our predictions of restorative effects held true during these large fires.

## Management implications

The lidar-based restoration indices described in this study (or the raw topo-climatic NRV ranges provided in Table S2) could greatly inform post-fire management assessments and decision-making (Meyer et al. 2021; Stevens et al. 2021; Larson et al. 2022). Managers could delineate areas that met the full restoration target and deprioritize these sites for immediate intervention. In areas of partial restoration, additional fires will likely be necessary; but, since these sites already exhibit reduced canopy and ladder fuel loads, they may be fairly resistant to even moderate-intensity summer-season fires in the near future (Knapp et al. 2005; Knapp and Keeley 2006; Schwilk et al. 2006). Additionally, areas that only met canopy cover targets, where ladder fuel densities remained relatively high, could be considered for more careful application of fire, perhaps via prescribed burning or beneficial wildfire use during cooler months (Knapp et al. 2005; Knapp and Keeley 2006; Schwilk et al. 2006). Lastly, first-entry burned areas that failed to meet any of the restoration targets may require mechanical thinning, prescribed burning, or planting, depending on whether post-fire structures fell above or below NRV (North et al. 2019, 2021; Meyer et al. 2021). Some post-fire sites with high residual canopy cover and ladder fuel densities may be delineated for lower intensity treatments that focus on improving wildlife habitat for key species like California spotted owl (*Strix occidentalis occidentalis*) and fisher (*Pekania pennanti*) (North et al. 2017; Kramer et al. 2021; Steel et al. 2023). Importantly, while our restoration indices can provide useful guidance for post-fire management, we note that these indices only quantify upper canopy structural conditions. As discussed above, many of these first-entry burn areas likely exhibit increased surface fuel loads and potentially misaligned species distributions (May et al. 2023; Zald et al. 2024; Cansler et al. 2019; Lutz et al. 2020), which may require field-based assessments and/or more careful application, or management, of subsequent fires and treatments (Hankin et al. 2024).

Managers can use our modeling results to better define the envelope of conditions within which restorative fire effects will be most likely to occur in future fires in the Sierra Nevada YPMC zone. To aid in this process, mapped predictions of restorative fire effects have been archived as raster layers in a publicly available Zenodo Digital Repository (https://doi.org/https://doi.org/10.5281/zenodo.12802224). Notably, landscapes currently characterized by a mosaic of past fires (i.e., National Parks and portions of several National Forests) are likely to support mostly restorative fire effects in the future (Meyer 2015). We also found a higher likelihood of restorative effects at higher elevations, especially in the northern portion of the YPMC zone. Considering the operational challenges of treating higher elevation sites in the Sierra Nevada, and their relative distance from the wildland urban interface, these areas may be particularly suitable for resource objective wildfires and/or designation as Strategic Fire Zones (North et al. 2021, 2024). In contrast, lower elevation sites within Stanislaus, Eldorado, and Tahoe National Forests are less likely to experience restorative first-entry effects and may best be prioritized for mechanical treatment or prescribed burning (Krofcheck et al. 2018), particularly since such areas are closer to the wildland urban interface (North et al. 2021). Lastly, we note a distinct range of flame lengths during which restorative fire effects will be most probable (~ 1–2 m). This range of fire intensity can provide general guidance for conducting prescribed burns or for considering naturally ignited fires for resource objectives (North et al. 2021).

## Conclusion

Climate change is expected to cause major shifts in vegetation dynamics and disturbance regimes across forested landscapes of western North America (Fettig et al. 2013; Schoennagel et al. 2017). If recent trends are a harbinger for the future, wildfires will continue to increase in size, frequency, and severity, especially in fire-suppressed forests that are most susceptible to extreme fire behavior (Abatzoglou et al. 2019; Williams et al. 2019; Safford et al. 2020). Fire-intact ecosystems, for which historical datasets and contemporary reference sites offer reliable proxies, are those in which fire plays a critical role in regulating vegetation dynamics and increasing resilience to future disturbances and climate change (Collins et al. 2016; Hagmann et al. 2021; Chamberlain et al. 2023a). If our goal is to ensure the persistence of dry forest ecosystems and the values they provide, increasing the extent of fire-intact, rather than fire-suppressed, forest ecosystems will be imperative over the next few decades (Prichard et al. 2021; Hessburg et al. 2021; North et al. 2024). Achieving the structural and compositional conditions associated with fire-intact ecosystems will require (1) access to datasets and knowledge that support comprehensive and ecologically-based post-fire planning and operations (North et al. 2019; Meyer et al. 2021; Stevens et al. 2021; Larson et al. 2022) and (2) more nuanced pre- and active-fire management strategies that integrate both western science and Indigenous knowledge sources to encourage restorative and beneficial fire effects (Hessburg et al. 2021; North et al. 2021;2024; Lake et al. 2017). We believe that the results from our study, and the maps and data layers provided, will assist managers and policy makers in moving contemporary dry forest landscapes toward these desired conditions associated with fire-intact ecosystems.

**Abbreviations**

| | |
|---|---|
| NRV | Natural range of variation |
| YPMC | Yellow pine mixed conifer |
| FRAP | Fire and Resource Assessment Program |
| ICO | Individual trees, clumps, and openings |
| CBI | Composite Burn Index |
| RF | Random forest |
| PDP | Partial dependence plot |

## Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s42408-024-00324-5.

Additional file 1: Table S1. Statistics for 35 analysis fires in the Sierra Nevada ecoregion, California, USA. FE/U: first-entry, untreated. Figure S1. Comparing fractal dimension index to structure classes. We show the distribution of fractal dimension index values (our measure of clump complexity) within each of the four structure classes defined in Chamberlain et al. (2023a, b). These structure classes represent statistically distinct clusters of 90-m structure metrics (identified using a hierarchical clustering approach) spanning the contemporary reference sites. Structure classes were defined using five structure metrics including % area gap, % canopy cover of individual tree approximate objects (TAOs), % canopy cover 2–4 TAO clumps, % canopy cover 5–9 TAO clumps, and % canopy cover 10 + TAO clumps. ICO refers to individual TAOs, clumps of TAOs, and open space. TAOs refer to airborne lidar segmented trees. Chamberlain et al. 2023a, b found that contemporary reference sites were characterized primarily by intermediate ICO and open ICO structure classes, which represent fractal dimension values of approximately 1.3–1.6. TAO: tree approximate object; ICO: individual TAOs, clumps of TAOs, open space. Table S2. Natural range of variation (NRV), defined as the inner 68% of the distribution of values spanning the contemporary reference sites for each structure metric, split by climate class and topography (land management unit, LMU). Figure S2. Raw distributions of each forest structure metric split by climate and topographic classes for first-entry wildfire sites (red), contemporary reference sites (purple), and unburned control sites (blue). Black error bar over the reference site distribution represents the natural range of variation (NRV), defined as the inner 68% of the distribution. Table S3. Continuous predictor variables, prior to variable reduction, used to model restorative fire effects. DBH: diameter at breast height; AET: average annual actual evapotranspiration; AFSP: April first snow pack; CWD: average annual climatic water deficit; PET: average annual potential evapotranspiration; PPT: average annual precipitation; TMIN: average minimum annual temperature; TMAX: average maximum annual temperature; TPI: topographic position index; DEM: digital elevation model; USGS: United States Geological Survey. Figure S3. The full set of partial dependence plots (PDPs) for all 13 predictor variables included in the final random forest model predicting the full restoration index. Black line shows predictions, while red line shows loess smooth with standard error in gray. Density plots in blue show counts of observations across the range of values for each variable. PDPs were produced using the DALEXtra package (Maksymiuk et al. 2020) in R (R Core Team 2023). PRECIP: mean annual precipitation; TPI: topographic position index; CWD: average annual climatic water deficit. Figure S4. Two-variable partial dependence plots. We produced two-variable partial dependence plots from the final random forest model predicting the full restoration index. We show the interaction between burning index and the other top five predictors. Burning index is the variable that can best be controlled for during fire management (i.e., deciding to suppress or allow a fire to burn under given weather scenario); thus, it is valuable to show how the probability of restorative effects varies across this index in relation to other variables. We produced two-variable partial dependence plots using the pdp package (Greenwell 2017) in R (R Core Team 2023). TMIN: average minimum annual temperature; TPI: topographic position index. Figure S5. Model performance metrics and mapped predictions of the cover only restoration index. We used the same set of 13 predictors as described in the main text. The cover restoration model had an overall accuracy of 63.3%. When applied to yet unburned areas in the Sierra Nevada YPMC zone for year 2020, we found that 26% of total area was likely to experience restorative effects under moderate fire weather (burn index = 71), 23% under mild fire weather (burning index = 53), and 51% was not likely to experience restorative effects. Figure S6. Model performance metrics and mapped predictions of the partial restoration index. We used the same set of 13 predictors as described in the main text. The partial restoration model had an overall accuracy of 61.8%. When applied to yet unburned areas in the Sierra Nevada YPMC zone for year 2020, we found that 31% total area was likely to experience restorative effects under moderate fire weather (burning index = 71), 15% under mild fire weather (burning index = 53), and 54% was not likely to experience restorative effects.

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**Authors' contributions**
CPC: conceptualization, methodology, formal analysis, investigation, writing—original draft, visualization, funding acquisition; BBG: conceptualization, methodology, writing—review and editing; CAC: conceptualization, methodology, supervision, writing—review and editing; MPN: conceptualization, methodology, writing—review and editing, funding acquisition; MDM: conceptualization, methodology, writing—review and editing; LvW: conceptualization, methodology, supervision, writing—review and editing; HER: conceptualization, methodology, writing—review and editing; VRK: conceptualization, methodology, resources, writing—review and editing, supervision, funding acquisition.

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**Availability of data and materials**
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 there are no competing interests that could have influenced the work reported in this paper.

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### References

Abatzoglou, J. T. 2013. Development of gridded surface meteorological data for Ecol Appl and modelling. *International Journal of Climatology* 33:121–131. https://doi.org/10.1002/joc.3413.

Abatzoglou, J. T., A. P. Williams, and R. Barbero. 2019. Global emergence of anthropogenic climate change in fire weather indices. *Geophysical Research Letters* 46:326–336. https://doi.org/10.1029/2018GL080959.

Agee, J. K., and C. N. Skinner. 2005. Basic principles of forest fuel reduction treatments. *Forest Ecology and Management* 211:83–96. https://doi.org/10.1016/j.foreco.2005.01.034.

Akay, A. E., H. Oğuz, I. R. Karas, et al. 2009. Using LiDAR technology in forestry activities. *Environmental Monitoring and Assessment* 151:117–125. https://doi.org/10.1007/s10661-008-0254-1.

Atchley, A. L., R. Linn, A. Jonko, et al. 2021. Effects of fuel spatial distribution on wildland fire behaviour. *International Journal of Wildland Fire* 30:179–189. https://doi.org/10.1071/WF20096.

Beland, M., G. Parker, B. Sparrow, et al. 2019. On promoting the use of lidar systems in forest ecosystem research. *Forest Ecology and Management* 450:117484. https://doi.org/10.1016/j.foreco.2019.117484.

Bohlman G. N., Safford H. D., Skinner C. N. 2021. Natural range of variation for yellow pine and mixed-conifer forests in northwestern California and southwestern Oregon. U.S. Department of Agriculture, Forest Service

– General Technical Report PSW-GTR, no. 273. 1–146. https://www.fs.usda.gov/psw/publications/documents/psw_gtr273/psw_gtr273.pdf.
CALFIRE Fire Perimeters. 2021. California Department of Forestry and Fire Protection's Fire and Resource Assessment Program (FRAP). https://frap.fire.ca.gov/mapping/gis-data/. Accessed July 2022.
Cansler, C. A., M. E. Swanson, T. J. Furniss, et al. 2019. Fuel dynamics after reintroduced fire in an old-growth Sierra Nevada mixed-conifer forest. *Fire Ecology* 15:16. https://doi.org/10.1186/s42408-019-0035-y.
Cansler, C. A., S. M. Hood, P. J. van Mantgem, and J. M. Varner. 2020. A large database supports the use of simple models of post-fire tree mortality for thick-barked conifers, with less support for other species. *Fire Ecology* 16:25. https://doi.org/10.1186/s42408-020-00082-0.
Cansler, C. A., V. R. Kane, P. F. Hessburg, et al. 2022. Previous wildfires and management treatments moderate subsequent fire severity. *Forest Ecology and Management* 504:119764. https://doi.org/10.1016/j.foreco.2021.119764.
Chamberlain, C. P., G. R. Cova, C. A. Cansler, et al. 2023a. Consistently heterogeneous structures observed at multiple spatial scales across fire-intact reference sites. *Forest Ecology and Management* 550:121478. https://doi.org/10.1016/j.foreco.2023.121478.
Chamberlain, C. P., G. R. Cova, V. R. Kane, et al. 2023b. Sierra Nevada reference conditions: A dataset of contemporary reference sites and corresponding remote sensing-derived forest structure metrics for yellow pine and mixed-conifer forests. *Data in Brief* 51:109807. https://doi.org/10.1016/j.dib.2023.109807.
Churchill, D. J., A. J. Larson, M. C. Dahlgreen, et al. 2013. Restoring forest resilience: From reference spatial patterns to silvicultural prescriptions and monitoring. *Forest Ecology and Management* 291:442–457. https://doi.org/10.1016/j.foreco.2012.11.007.
Churchill D. J., Carnwath G. C., Larson A. J., Jeronimo S. A. 2017. Historical forest structure, composition, and spatial pattern in dry conifer forests of the western Blue Mountains, Oregon. U.S. Department of Agriculture, Forest Service – General Technical Report PNW-GTR, no. 956. 1–93. https://doi.org/10.2737/PNW-GTR-956.
Churchill, D. J., S. M. A. Jeronimo, P. F. Hessburg, et al. 2022. Post-fire landscape evaluations in Eastern Washington, USA: Assessing the work of contemporary wildfires. *Forest Ecology and Management* 504:119796. https://doi.org/10.1016/j.foreco.2021.119796.
Collins, B. M., and S. L. Stephens. 2007. Managing natural wildfires in Sierra Nevada wilderness areas. *Frontiers in Ecology and the Environment* 5:523–527. https://doi.org/10.1890/070007.
Collins, B. M., R. G. Everett, and S. L. Stephens. 2011. Impacts of fire exclusion and recent managed fire on forest structure in old growth Sierra Nevada mixed-conifer forests. *Ecosphere* 2:51. https://doi.org/10.1890/ES11-00026.1.
Collins, B. M., S. L. Stephens, G. B. Roller, and J. J. Battles. 2011. Simulating fire and forest dynamics for a landscape fuel treatment project in the Sierra Nevada. *Food Research International* 57:77–88. https://doi.org/10.1093/forestscience/57.2.77.
Collins, B. M., J. M. Lydersen, R. G. Everett, et al. 2015. Novel characterization of landscape-level variability in historical vegetation structure. *Ecological Applications* 25:1167–1174. https://doi.org/10.1890/14-1797.1.
Collins, B. M., J. M. Lydersen, D. L. Fry, et al. 2016. Variability in vegetation and surface fuels across mixed-conifer-dominated landscapes with over 40 years of natural fire. *Forest Ecology and Management* 381:74–83. https://doi.org/10.1016/j.foreco.2016.09.010.
Coop, J. D., S. A. Parks, C. S. Stevens-Rumann, et al. 2020. Wildfire-driven forest conversion in western North American landscapes. *BioScience* 70:659–673. https://doi.org/10.1093/biosci/biaa061.
Coppoletta, M., K. E. Merriam, and B. M. Collins. 2016. Post-fire vegetation and fuel development influences fire severity patterns in reburns. *Ecological Applications* 26:686–699. https://doi.org/10.1890/15-0225.
Cova, G., V. R. Kane, S. Prichard, et al. 2023. The outsized role of California's largest wildfires in changing forest burn patterns and coarsening ecosystem scale. *Forest Ecology and Management* 528:120620. https://doi.org/10.1016/j.foreco.2022.120620.
Digital Elevation Model. 2022. 1/3rd Arc Second. United States Geological Survey National Map Viewer. https://www.usgs.gov/tools/national-map-viewer Accessed August 2022.
Evans J. S., Murphy M. A. 2021. "spatialEco." R package version 1.3–6, https://github.com/jeffreyevans/spatialEco.
Falk, D. A., E. K. Heyerdahl, P. M. Brown, et al. 2011. Multi-scale controls of historical forest-fire regimes: New insights from fire-scar networks. *Frontiers in Ecology and the Environment* 9:446–454. https://doi.org/10.1890/100052.
Fettig, C. J., M. L. Reid, B. J. Bentz, et al. 2013. Changing climates, changing forests: A western North American perspective. *Journal of Forestry* 111:214–228. https://doi.org/10.5849/jof.12-085.
Flint, L.E., A.L. Flint, and M.A. Stern. 2021. *The basin characterization model—A regional water balance software package*. U.S. Geological Survey Techniques and Methods 6–H1, 85pp. https://doi.org/10.3133/tm6H1.
Forest Management Task Force. 2021. California's Wildfire and Forest Resilience Action Plan. https://wildfiretaskforce.org/action-plan/.
Francis, E. J., P. Pourmohammadi, Z. L. Steel, et al. 2023. Proportion of forest area burned at high-severity increases with increasing forest cover and connectivity in western US watersheds. *Landscape Ecology* 10:2501–2518. https://doi.org/10.1007/s10980-023-01710-1.
Fry, D. L., S. L. Stephens, B. M. Collins, et al. 2014. Contrasting spatial patterns in active-fire and fire-suppressed Mediterranean climate old-growth mixed conifer forests. *PLoS ONE* 9:e88985. https://doi.org/10.1371/journal.pone.0088985.
Fulé, P. Z., W. W. Covington, and M. M. Moore. 1997. Determining reference conditions for ecosystem management of southwestern ponderosa pine forests. *Ecological Applications* 7:895–908. https://doi.org/10.1890/1051-0761(1997)007[0895:DRCFEM]2.0.CO;2.
Furniss, T. J., A. J. Das, P. J. van Mantgem, et al. 2022. Crowding, climate, and the case for social distancing among trees. *Ecological Applications* 32:e2507. https://doi.org/10.1002/eap.2507.
FVEG. 2015. California Department of Forestry and Fire Protection's Fire and Resource Assessment Program (FRAP). https://map.dfg.ca.gov/metadata/ds1327.html. Accessed July 2021.
Gannon, B., Y. Wei, E. Belval, et al. 2023. A quantitative analysis of fuel break effectiveness drivers in southern California National Forests. *Fire* 6:104. https://doi.org/10.3390/fire6030104.
GNN Structure. 2023. Landscape Ecology, Modeling, Mapping & Analysis. https://lemma.forestry.oregonstate.edu/data/structure-maps. Accessed September 2023.
Greenler, S. M., C. J. Dunn, J. D. Johnston, et al. 2023. Too hot, too cold, or just right: Can wildfire restore dry forests of the interior Pacific Northwest? *PLoS ONE* 18:e0281927. https://doi.org/10.1371/journal.pone.0281927.
Greenwell, B.M. 2017. pdp: an R package for constructing partial dependence plots. *R J* 9 (1): 421.
Hagmann R. K, Hessburg P. F., Prichard S.J, et al. 2021. Evidence for widespread changes in the structure, composition, and fire regimes of western North American forests. *Ecological Applications* 31(8): 24- 31:1–34. https://doi.org/10.1002/eap.2431.
Hankin, L. E., and C. T. Anderson. 2022. Second-entry burns reduce mid-canopy fuels and create resilient forest structure in Yosemite National Park. *California Forests* 13:1512. https://doi.org/10.3390/f13091512.
Hankin, L. E., C. T. Anderson, G. J. Dickman, et al. 2023. How forest management changed the course of the Washburn fire and the fate of Yosemite's giant sequoias (Sequoiadendron giganteum). *Fire Ecology* 19:40. https://doi.org/10.1186/s42408-023-00202-6.
Hankin, L. E., S. A. Crumrine, and C. T. Anderson. 2024. Impacts of mega drought in fire-prone montane forests and implications for forest management. *Forest Ecology and Management* 564:122010. https://doi.org/10.1016/j.foreco.2024.122010.
Harvey, B. J., M. S. Buonanduci, and M. G. Turner. 2023. Spatial interactions among short-interval fires reshape forest landscapes. *Global Ecology and Biogeography* 32:586–602. https://doi.org/10.1111/geb.13634.
Hessburg, P. F., C. L. Miller, S. A. Parks, et al. 2019. Climate, environment, and disturbance history govern resilience of western North American forests. *Frontiers in Ecology and Evolution* 7:239. https://doi.org/10.3389/fevo.2019.00239.
Hessburg, P. F., S. J. Prichard, R. K. Hagmann, et al. 2021. Wildfire and climate change adaptation of western North American forests: A case for intentional management. *Ecological Applications* 31:e02432. https://doi.org/10.1002/eap.2432.
Hijmans R. J, Bivand R, Pebesma E, Sumner M. 2023. "terra: Spatial Data Analysis" R package version 1.6.7. https://rspatial.org/index.html.
Huffman, D. W., J. P. Roccaforte, J. D. Springer, and J. E. Crouse. 2020. Restoration applications of resource objective wildfires in western US forests: A

status of knowledge review. *Fire Ecology* 16:18. https://doi.org/10.1186/s42408-020-00077-x.
Jeronimo, S. M. A., V. R. Kane, D. J. Churchill, et al. 2019. Forest structure and pattern vary by climate and landform across active-fire landscapes in the montane Sierra Nevada. *Forest Ecology and Management* 437:70–86. https://doi.org/10.1016/j.foreco.2019.01.033.
Jeronimo, S. M. A., J. A. Lutz, R. Kane V, et al. 2020. Burn weather and three-dimensional fuel structure determine post-fire tree mortality. *Landscape Ecology* 35:859–878. https://doi.org/10.1007/s10980-020-00983-0.
Kane, V. R., J. A. Lutz, S. L. Roberts, et al. 2013. Landscape-scale effects of fire severity on mixed-conifer and red fir forest structure in Yosemite National Park. *Forest Ecology and Managemnet* 287:17–31. https://doi.org/10.1016/j.foreco.2012.08.044.
Kane, V. R., M. P. North, J. A. Lutz, et al. 2014. Assessing fire effects on forest spatial structure using a fusion of Landsat and airborne LiDAR data in Yosemite National Park. *Remote Sensing of Environment* 151:89–101. https://doi.org/10.1016/j.rse.2013.07.041.
Kane, V. R., C. A. Cansler, N. A. Povak, et al. 2015. Mixed severity fire effects within the Rim fire: Relative importance of local climate, fire weather, topography, and forest structure. *Forest Ecology and Management* 358:62–79. https://doi.org/10.1016/j.foreco.2015.09.001.
Kane, V. R., J. A. Lutz, C. A. Cansler, et al. 2015. Water balance and topography predict fire and forest structure patterns. *Forest Ecology and Management* 338:1–13. https://doi.org/10.1016/j.foreco.2014.10.038.
Kane, V. R., B. N. Bartl-Geller, M. P. North, et al. 2019. First-entry wildfires can create opening and tree clump patterns characteristic of resilient forests. *Forest Ecology and Management* 454:117659. https://doi.org/10.1016/j.foreco.2019.01.033.
Kane, V. R., B. N. Bartl-Geller, G. R. Cova, et al. 2023. Where are the large trees? A census of Sierra Nevada large trees to determine their frequency and spatial distribution across three large landscapes. *Forest Ecology and Management* 546:121351. https://doi.org/10.1016/j.foreco.2023.121351.
Klimaszewski-Patterson, A., T. Dingemans, C. T. Morgan, and S. A. Mensing. 2024. Human influence on late Holocene fire history in a mixed-conifer forest, Sierra National Forest California. *Fire Ecology* 20:3. https://doi.org/10.1186/s42408-023-00245-9.
Knapp, E. E., and J. E. Keeley. 2006. Heterogeneity in fire severity within early season and late season prescribed burns in a mixed-conifer forest. *International Journal of Wildland Fire* 15:37–45. https://doi.org/10.1071/WF04068.
Knapp, E. E., J. E. Keeley, E. A. Ballenger, and T. J. Brennan. 2005. Fuel reduction and coarse woody debris dynamics with early season and late season prescribed fire in a Sierra Nevada mixed conifer forest. *Forest Ecology and Management* 208:383–397. https://doi.org/10.1016/j.foreco.2005.01.016.
Knapp, E. E., C. N. Skinner, M. P. North, and B. L. Estes. 2013. Long-term overstory and understory change following logging and fire exclusion in a Sierra Nevada mixed-conifer forest. *Forest Ecology and Management* 310:903–914. https://doi.org/10.1016/j.foreco.2013.09.041.
Knapp, E. E., J. M. Lydersen, M. P. North, and B. M. Collins. 2017. Efficacy of variable density thinning and prescribed fire for restoring forest heterogeneity to mixed-conifer forest in the central Sierra Nevada, CA. *Forest Ecology and Management* 406:228–241. https://doi.org/10.1016/j.foreco.2017.08.028.
Knight, C. A., R. E. Tompkins, J. A. Wang, et al. 2022. Accurate tracking of forest activity key to multi-jurisdictional management goals: A case study in California. *Journal of Environmental Management* 302:114083. https://doi.org/10.1016/j.jenvman.2021.114083.
Koontz, M. J., M. P. North, C. M. Werner, et al. 2020. Local forest structure variability increases resilience to wildfire in dry western U.S. coniferous forests. *Ecology Letters* 23:483–494. https://doi.org/10.1111/ele.13447.
Kramer, H. A., B. M. Collins, M. Kelly, and S. L. Stephens. 2014. Quantifying ladder fuels: A new approach using LiDAR. *Forests* 5:1432–1453. https://doi.org/10.3390/f5061432.
Kramer, H. A., G. M. Jones, V. R. Kane, et al. 2021. Elevational gradients strongly mediate habitat selection patterns in a nocturnal predator. *Ecosphere* 12:e03500. https://doi.org/10.1002/ecs2.3500.
Krofcheck, D. J., M. D. Hurteau, R. M. Scheller, and E. L. Loudermilk. 2018. Prioritizing forest fuels treatments based on the probability of high-severity fire restores adaptive capacity in Sierran forests. *Global Change Biology* 24:729–737. https://doi.org/10.1111/gcb.13913.
Kuhn, M. 2023. "finetune: Additional Functions for Model Tuning." R package version 1.1.0, https://CRAN.R-project.org/package=finetune.
Kuhn M., and Wickham H. 2020. "tidymodels: a collection of packages for modeling and machine learning using tidyverse principles." https://www.tidymodels.org.
Lake, F. K., V. Wright, P. Morgan, et al. 2017. Returning fire to the land: Celebrating traditional knowledge and fire. *Journal of Forestry* 115:343–353. https://doi.org/10.5849/jof.2016-043R2.
Landres, P. B., P. Morgan, and F. J. Swanson. 1999. Overview of the use of natural variability concepts in managing ecological systems. *Ecological Applications* 9:1179–1188. https://doi.org/10.1890/1051-0761(1999)009[1179:OOTUON]2.0.CO;2.
Larson, A. J., and D. Churchill. 2012. Tree spatial patterns in fire-frequent forests of western North America, including mechanisms of pattern formation and implications for designing fuel reduction and restoration treatments. *Forest Ecology and Management* 267:74–92. https://doi.org/10.1016/j.foreco.2011.11.038.
Larson, A. J., S. M. A. Jeronimo, P. F. Hessburg, et al. 2022. Tamm Review: Ecological principles to guide post-fire forest landscape management in the Inland Pacific and Northern Rocky Mountain regions. *Forest Ecology and Management* 504:119680. https://doi.org/10.1016/j.foreco.2021.119680.
Level IV Ecoregions. 2023. Environmental Protection Agency. https://www.epa.gov/eco-research/ecoregion-download-files-state-region-9#pane-04. Accessed March 2023.
Levine, J. I., B. M. Collins, Z. L. Steel, et al. 2022. Higher incidence of high-severity fire in and near industrially managed forests. *Frontiers in Ecology and the Environment* 20:397–404. https://doi.org/10.1002/fee.2499.
Lutz, J. A., S. Struckman, T. J. Furniss, et al. 2020. Large-diameter trees dominate snag and surface biomass following reintroduced fire. *Ecological Processes* 9:41. https://doi.org/10.1186/s13717-020-00243-8.
Lydersen, J., and M. North. 2012. Topographic variation in structure of mixed-conifer forests under an active-fire regime. *Ecosystems* 15:1134–1146. https://doi.org/10.1007/s10021-012-9573-8.
Lydersen, J. M., M. P. North, E. E. Knapp, and B. M. Collins. 2013. Quantifying spatial patterns of tree groups and gaps in mixed-conifer forests: Feference conditions and long-term changes following fire suppression and logging. *Forest Ecology and Management* 304:370–382. https://doi.org/10.1016/j.foreco.2013.05.023.
Lydersen, J. M., M. P. North, and B. M. Collins. 2014. Severity of an uncharacteristically large wildfire, the Rim Fire, in forests with relatively restored frequent fire regimes. *Forest Ecology and Management* 328:326–334. https://doi.org/10.1016/j.foreco.2014.06.005.
Lydersen, J. M., B. M. Collins, J. D. Miller, et al. 2016. Relating fire-caused change in forest structure to remotely sensed estimates of fire severity. *Fire Ecology* 12:99–116. https://doi.org/10.4996/fireecology.1203099.
Maksymiuk, S, Alicja G, and Przemyslaw B. 2020. "DALEXtra: Landscape of R packages for eXplainable Artificial Intelligence." https://arxiv.org/abs/2009.13248.
Marvin N. W, and Ziegler A. 2017. "ranger: A Fast Implementation of Random Forests for High Dimensional Data in C++ and R." *Journal of Statistical Software* 77:1–17. https://doi.org/10.18637/jss.v077.i01.
May C. J., Zald H. S. J, North M. P., et al. 2023. Repeated burns fail to restore pine regeneration to the natural range of variability in a Sierra Nevada mixed-conifer forest, U.S.A. *Restoration Ecology* 31:e13863. https://doi.org/10.1111/rec.13863.
McCarley, T. R., C. A. Kolden, N. M. Vaillant, et al. 2017. Multi-temporal LiDAR and Landsat quantification of fire-induced changes to forest structure. *Remote Sensing of Environment* 191:419–432. https://doi.org/10.1016/j.rse.2016.12.022.
McGarigal K, and B. J. Marks. 1995. *FRAGSTATS: Spatial Pattern Analysis Program for Quantifying Landscape Structure*. U.S. Department of Agriculture, Forest Service – General Technical Report PNW-GTR, no. 351. 1–122. https://doi.org/10.2737/PNW-GTR-351.
McGaughey R. J. 2020. FUSION/LDV: software for LIDAR data analysis and visualization: Version 4.00. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Seattle, WA. http://forsys.cfr.washington.edu/FUSION/fusion_overview.html.
Meyer, M. D. 2015. Forest fire severity patterns of resource objective wildfires in the southern Sierra Nevada. *Journal of Forestry* 113:49–56. https://doi.org/10.5849/jof.14-084.

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

Meyer M. D., Long J. W, Safford H. D 2021. Postfire restoration framework for national forests in California. U.S. Department of Agriculture, Forest Service – General Technical Report PSW-GTR, no. 270. 1–204. https://www.fs.usda.gov/research/treesearch/61909.

Mitchell, B., H. Fisk, J. Clark, et al. 2018. *Lidar acquisition specifications for forestry applications*. Salt Lake City: U.S. Department of Agriculture, Forest Service, Geospatial Technology & Applications Centre. https://fsapps.nwcg.gov/gtac/CourseDownloads/Reimbursables/FY20/National_Lidar/Acquisition_Specifications/Lidar_Acquisition_Specifications.pdf.

Moore, M. M., W. W. Covington, and P. Z. Fulé. 1999. Reference conditions and ecological restoration: A southwestern ponderosa pine perspective. *Ecological Applications* 9:1266–1277. https://doi.org/10.1890/1051-0761(1999)009[1266:RCAERA]2.0.CO;2.

Ng, J., M. P. North, A. J. Arditti, et al. 2020. Topographic variation in tree group and gap structure in Sierra Nevada mixed-conifer forests with active fire regimes. *Forest Ecology and Management* 472:118220. https://doi.org/10.1016/j.foreco.2020.118220.

NHDPlusV2. 2021. Environmental Protection Agency National Hydrography Dataset Plus. https://www.epa.gov/waterdata/nhdplus-national-data. Accessed July 2021.

North, M., A. Brough, J. Long, et al. 2015. Constraints on mechanized treatment significantly limit mechanical fuels reduction extent in the Sierra Nevada. *Journal of Forestry* 113:40–48. https://doi.org/10.5849/jof.14-058.

North, M., B.M. Collins, H. Safford, and N.L. Stephenson. 2016. Montane forests. In *Ecosystems of California*, ed. H. Mooney and E. Zavaleta, 553–577. Berkeley: University of California Press. https://northlab.faculty.ucdavis.edu/wp-content/uploads/sites/195/2016/02/Montane-Forests-North-2016.pdf.

North, M. P., J. T. Kane, V. R. Kane, et al. 2017. Cover of tall trees best predicts California spotted owl habitat. *Forest Ecology and Management* 405:166–178. https://doi.org/10.1016/j.foreco.2017.09.019.

North, M. P., J. T. Stevens, D. F. Greene, et al. 2019. Tamm Review: Reforestation for resilience in dry western U.S. forests. *Forest Ecology and Management* 432:209–224. https://doi.org/10.1016/j.foreco.2018.09.007.

North, M. P., R. A. York, B. M. Collins, et al. 2021. Pyrosilviculture needed for landscape resilience of dry western United States forests. *Journal of Forestry* 119:520–544. https://doi.org/10.1093/jofore/fvab026.

North, M. P., R. E., Tompkins, A. A. Bernal, et al. 2022. Operational resilience in western US frequent-fire forests. *Forest Ecology and Management* 507:120004. https://doi.org/10.1016/j.foreco.2021.120004.

North, M. P., S. M. Bisbing, D. L. Hankins, et al. 2024. Strategic fire zones are essential to wildfire risk reduction in the western United States. *Fire Ecology* 20:50. https://doi.org/10.1186/s42408-024-00282-y.

Northrop, H., J. N. Axelson, A. J. Das, et al. 2024. Snag dynamics and surface fuel loads in the Sierra Nevada: Predicting the impact of the 2012–2016 drought. *Forest Ecology and Management* 551:121521. https://doi.org/10.1016/j.foreco.2023.121521.

O'Connor, C. D., D. E. Calkin, M. P. Thompson, et al. 2017. An empirical machine learning method for predicting potential fire control locations for pre-fire planning and operational fire management. *International Journal of Wildland Fire* 26:587–597. https://doi.org/10.1071/WF16135.

Parks S. A., Abatzoglou J. T. 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:e2020GL089858. https://doi.org/10.1029/2020GL089858.

Parks, S. A., L. M. Holsinger, C. Miller, and C. R. Nelson. 2015. Wildland fire as a self-regulating mechanism: The role of previous burns and weather in limiting fire progression. *Ecological Applications* 25:1478–1492. https://doi.org/10.1890/14-1430.1.

Parks, S. A., L. M. Holsinger, M. H. Panunto, et al. 2018. High-severity fire: Evaluating its key drivers and mapping its probability across western US forests. *Environmental Research Letters* 13:044037. https://doi.org/10.1088/1748-9326/aab791.

Parks, S. A., L. M. Holsinger, M. J. Koontz, et al. 2019. Giving ecological meaning to satellite-derived fire severity metrics across North American forests. *Remote Sensing* 11:1735. https://doi.org/10.3390/rs11141735.

Parks, S. A., L. M. Holsinger, K. Blankenship, et al. 2023. Contemporary wildfires are more severe compared to the historical reference period in western US dry conifer forests. *Forest Ecology and Management* 544:121232. https://doi.org/10.1016/j.foreco.2023.121232.

Povak, N. A., V. R. Kane, B. M. Collins, et al. 2020. Multi-scaled drivers of severity patterns vary across land ownerships for the 2013 Rim Fire, California. *Landscape Ecology* 35:293–318. https://doi.org/10.1007/s10980-019-00947-z.

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

Prichard, S. J., P. F. Hessburg, R. K. Hagmann, et al. 2021. Adapting western North American forests to climate change and wildfires: 10 common questions. *Ecological Applications* 31 (8): e02433. https://doi.org/10.1002/eap.2433.

R Core Team. 2023. R version 4.2.2. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. www.R-project.org.

Reed, C.C., S.M. Hood, D.R. Cluck, and S.L. Smith. 2023. Fuels change quickly after California drought and bark beetle outbreaks with implications for potential fire behavior and emissions. *Fire Ecol* 19: 16. https://doi.org/10.1186/s42408-023-00175-6.

Ritter S. M., Hoffman C. M., Battaglia M..A, et al. 2020. Fine-scale fire patterns mediate forest structure in frequent-fire ecosystems. *Ecosphere* 11. https://doi.org/10.1002/ecs2.3177.

Safford H. D., Stevens J. T. 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. U.S. Department of Agriculture, Forest Service – General Technical Report PSW-GTR, no. 256. 1–229. https://doi.org/10.2737/PSW-GTR-256.

Safford, H. D., J. T. Stevens, K. Merriam, et al. 2012. Fuel treatment effectiveness in California yellow pine and mixed conifer forests. *Forest Ecology and Management* 274:17–28. https://doi.org/10.1016/j.foreco.2012.02.013.

Safford, H. D., A. K. Paulson, Z. L. Steel, et al. 2020. 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. https://doi.org/10.1111/geb.13498.

Schmidt, L., M. G. Hille, and S. L. Stephens. 2006. Restoring northern Sierra Nevada mixed conifer forest composition and structure with prescribed fires of varying intensities. *Fire Ecology* 2:20–33. https://doi.org/10.4996/fireecology.0202020.

Schoennagel, T., J. K. Balch, H. Brenkert-Smith, et al. 2017. Adapt to more wildfire in western North American forests as climate changes. *Proceedings of the National Academy of Sciences* 114:4582–4590. https://doi.org/10.1073/pnas.1617464114.

Schwilk, D. W., E. E. Knapp, S. M. Ferrenberg, et al. 2006. Tree mortality from fire and bark beetles following early and late season prescribed fires in a Sierra Nevada mixed-conifer forest. *Forest Ecology and Management* 232:36–45. https://doi.org/10.1016/j.foreco.2006.05.036.

Steel, Z. L., D. Foster, M. Coppoletta, et al. 2021. Ecological resilience and vegetation transition in the face of two successive large wildfires. *Journal of Ecology* 109:3340–3355. https://doi.org/10.1111/1365-2745.13764.

Steel, Z. L., G. M. Jones, B. M. Collins, et al. 2023. Mega-disturbances cause rapid decline of mature conifer forest habitat in California. *Ecological Applications* 33:e2763. https://doi.org/10.1002/eap.2763.

Stephens, S. L., J. D. Miller, B. M. Collins, et al. 2016. Wildfire impacts on California spotted owl nesting habitat in the Sierra Nevada. *Ecosphere* 7:e01478. https://doi.org/10.1002/ecs2.1478.

Stephens, S.L., S. Thompson, G. Boisramé, B.M. Collins, L.C. Ponisio, E. Rakhmatulina, Z.L. Steel, J.T. Stevens, J.W. van Wagtendonk, and K. Wilkin. 2021. Fire, water, and biodiversity in the Sierra Nevada: a possible triple win. *Environmental Research Communications* 3 (8): 081004.

Stevens, J. T., M. M. Kling, D. W. Schwilk, et al. 2020. Biogeography of fire regimes in western U.S. conifer forests: A trait-based approach. *Global Ecology and Biogeography* 29:944–955. https://doi.org/10.1111/geb.13079.

Stevens, J. T., C. M. Haffey, J. D. Coop, et al. 2021. Tamm Review: Postfire landscape management in frequent-fire conifer forests of the southwestern United States. *Forest Ecology and Management* 502:119678. https://doi.org/10.1016/j.foreco.2021.119678.

Stevens-Rumann, C. S., S. J. Prichard, E. K. Strand, and P. Morgan. 2016. Prior wildfires influence burn severity of subsequent large fires. *Canadian Journal of Forest Research* 46:1375–1385. https://doi.org/10.1139/cjfr-2016-0185.

Sullivan, A. L. 2017. Inside the Inferno: Fundamental processes of wildland fire behaviour. *Current Forestry Reports* 3:132–149. https://doi.org/10.1007/s40725-017-0057-0.

Taylor, A. H., V. Trouet, C. N. Skinner, and S. Stephens. 2016. Socioecological transitions trigger fire regime shifts and modulate fire–climate interactions in the Sierra Nevada, USA, 1600–2015 CE. *Proceedings of the National Academy of Sciences* 113:13684–13689. https://doi.org/10.1073/pnas.1609775113.

Underwood, E. C., J. H. Viers, J. F. Quinn, and M. North. 2010. Using topography to meet wildlife and fuels treatment objectives in fire-suppressed landscapes. *Environmental Management* 46:809–819. https://doi.org/10.1007/s00267-010-9556-5.

Vaillant, N. M., and E. D. Reinhardt. 2017. An evaluation of the forest service hazardous fuels treatment program—are we treating enough to promote resiliency or reduce hazard? *Journal of Forestry* 115:300–308. https://doi.org/10.5849/jof.16-067.

van Wagtendonk, J. W. 2007. The history and evolution of wildland fire use. *Fire Ecology* 3:3–17. https://doi.org/10.4996/fireecology.0302003.

van Mantgem, P. J., N. L. Stephenson, E. Knapp, et al. 2011. Long-term effects of prescribed fire on mixed conifer forest structure in the Sierra Nevada, California. *Forest Ecology and Management* 261:989–994. https://doi.org/10.1016/j.foreco.2010.12.013.

Vilanova, E., L. A. Mortenson, L. E. Cox, et al. 2023. Characterizing ground and surface fuels across Sierra Nevada forests shortly after the 2012–2016 drought. *Forest Ecology and Management* 537:120945. https://doi.org/10.1016/j.foreco.2023.120945.

Westerling, A. L. 2016. Increasing western US forest wildfire activity: Sensitivity to changes in the timing of spring. *Philosophical Transactions of the Royal Society B: Biological Sciences* 371:20150178. https://doi.org/10.1098/rstb.2015.0178.

Wiggin, H. L., C. R. Nelson, A. J. Larson, and H. D. Safford. 2019. Using LiDAR to develop high-resolution reference models of forest structure and spatial pattern. *Forest Ecology and Management* 434:318–330. https://doi.org/10.1016/j.foreco.2018.12.012.

Williams, A. P., J. T. Abatzoglou, A. Gershunov, et al. 2019. Observed impacts of anthropogenic climate change on wildfire in California. *Earth's Future* 7:892–910. https://doi.org/10.1029/2019EF001210.

Zald, H. S .J., A. N. Gray, M. North, and R. A. Kern. 2008. Initial tree regeneration responses to fire and thinning treatments in a Sierra Nevada mixed-conifer forest, USA. *Forest Ecology and Management* 256:168–179. https://doi.org/10.1016/j.foreco.2008.04.022.

Zald H. S. J., May C. J., Gray A. N, et al. 2024. Thinning and prescribed burning increase shade-tolerant conifer regeneration in a fire excluded mixed-conifer forest. *Forest Ecology and Management* 121531. https://doi.org/10.1016/j.foreco.2023.121531.

Ziegler, J. P., C. M. Hoffman, B. M. Collins, et al. 2021. Pyric tree spatial patterning interactions in historical and contemporary mixed conifer forests, California, USA. *Ecology and Evolution* 11:820–834. https://doi.org/10.1002/ece3.7084.

## Publisher's Note