

The changing landscape of wildfire: burn pattern trends and implications for California's yellow pine and mixed conifer forests

Zachary L. Steel  · Michael J. Koontz  · Hugh D. Safford

Received: 19 September 2017 / Accepted: 31 May 2018 / Published online: 7 June 2018
© Springer Nature B.V. 2018

Abstract

Purpose Wildfire spatial patterns drive ecological processes including vegetation succession and wildlife community dynamics. Such patterns may be changing due to fire suppression policies and climate change, making characterization of trends in post-fire mosaics important for understanding and managing fire-prone ecosystems.

Methods For wildfires in California's yellow pine and mixed-conifer forests, spatial pattern trends of two components of the post-fire severity matrix were

assessed for 1984–2015: (1) unchanged or very low-severity and (2) high-severity, which represent remnant forest and stand-replacing fire, respectively. Trends were evaluated for metrics of total and proportional burned area, shape complexity, aggregation, and core area. Additionally, comparisons were made between management units where fire suppression is commonly practiced and those with a history of managing wildfire for ecological/resource benefits.

Results Unchanged or very low-severity area per fire decreased proportionally through time, and became increasingly fragmented. High-severity area and core area increased on average across most of California, with the high-severity component also becoming simpler in shape in the Sierra Nevada. Compared to suppression units, managed wildfire units lack an increase in high-severity area, have less aggregated post-fire mosaics, and more high-severity spatial complexity.

Conclusions Documented changes in severity patterns have cascading ecological effects including increased vegetation type conversion risk, habitat availability shifts, and remnant forest fragmentation. These changes likely benefit early-seral-associated species at the expense of mature closed-canopy forest-associated species. Managed wildfire appears to moderate some effects of fire suppression, and may help buy time for ecosystems and managers to respond to a changing climate.

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s10980-018-0665-5>) contains supplementary material, which is available to authorized users.

Z. L. Steel (✉) · H. D. Safford
Department of Environmental Science and Policy,
University of California, One Shields Avenue, Davis,
CA 95616, USA
e-mail: zlsteel@ucdavis.edu

Z. L. Steel · M. J. Koontz
Graduate Group in Ecology, University of California, One
Shields Avenue, Davis, CA 95616, USA

M. J. Koontz
Department of Plant Sciences, University of California,
One Shields Avenue, Davis, CA 95616, USA

H. D. Safford
United States Department of Agriculture, Forest Service,
Pacific Southwest Region, Vallejo, CA 94592, USA

Keywords Fire ecology · Burn severity · Landscape heterogeneity · Disturbance · Patch dynamics · Climate change

Introduction

Wildfire dramatically alters vegetation patterns and ecological processes across broad landscapes. In forested ecosystems, fire effects range widely from negligible changes in canopy structure to complete mortality of existing vegetation (Agee 1993; Sugihara et al. 2006). Within individual fires, the size, shape, and configuration of remnant and stand-replacing patches can determine post-fire ecosystem recovery, including the maintenance or reconfiguration of vegetation communities (Turner et al. 1998). Changes in habitat type and landscape heterogeneity subsequently drive other ecological processes and patterns such as future fire regimes, plant and animal colonization, community composition, and species abundance (Pickett and White 1985; Sugihara et al. 2006; van Mantgem et al. 2015). Fire-induced changes to landscapes are often immediate, but may persist in some form for decades to centuries (Turner 2010). As a consequence, directional shifts in the landscape pattern of wildfires over time, due to forest management, climate, or other factors, will have broad ecological impacts.

In most semiarid pine-dominated forests of the western United States, current fire regimes differ dramatically from those characterizing these ecosystems prior to Euro-American settlement in the second half of the nineteenth century (Agee 1993; Sugihara et al. 2006; Safford and Stevens 2017). The best-documented divergence is in fire frequency (Safford and Van de Water 2014). In California, these forest types (mostly yellow pine [*Pinus ponderosa* and *Pinus jeffreyi*], and mixed conifer) supported mean fire return intervals between 10 and 20 years over the 4–6 centuries before Euro-American settlement, but due to fire suppression policies, $\frac{3}{4}$ of these forests have not experienced a single fire over the last century (Safford and Van de Water 2011; Steel et al. 2015). Broad-scale exclusion of fire has resulted in forest densification, compositional shifts toward fire-sensitive tree species, and increased continuity of fuels (Safford and Stevens 2017). Concurrently, a warming climate has led to

longer and drier fire seasons and more extreme fire weather (Abatzoglou and Williams 2016; Westerling 2016). Since the 1980s, especially in these forests of the Southwest and California, the interaction between accumulating forest fuels and changing climate has led to increases in fire size and severity—a measure of the effect of fire on an ecosystem (Miller et al. 2009b, 2012b; Dillon et al. 2011; Dennison et al. 2014; Safford and Stevens 2017; Restaino and Safford 2018). The translation of these broad changes in fire regimes to shifts in forest process and pattern depends in part on the spatial pattern of the wildfire severity mosaic on the burned landscape.

Wildfire spatial pattern can influence ecological process by affecting the timing and trajectory of post-fire vegetation succession. The size, shape, and configuration of high-severity (stand-replacing) patches determine the distance from living seed sources and greatly influence the rate of tree regeneration for non-serotinous species (Turner et al. 1998; Welch et al. 2016). Any increases in high-severity patch size, and/or decreases in patch shape complexity can result in internal core areas increasingly isolated from seed sources, and increased risk of type conversion to other vegetation physiognomies such as hardwood forest, shrubland, or grassland. Additionally, changing fire regimes will impact the composition and abundance of plant and wildlife communities. Shifts from forested to non-forested habitats are likely to negatively affect species associated with old-growth forests (Jones et al. 2016; Stephens et al. 2016b), and positively affect early-seral and shrubland-associated species (White et al. 2016). Beyond the absolute availability of habitat types created by wildfire, our understanding of how fire-induced spatial pattern influences biota is limited (but see Roberts et al. 2008; Tingley et al. 2016). Studies of disturbances such as timber harvest and agricultural conversion have demonstrated that the resulting habitat fragmentation or heterogeneity can greatly influence habitat quality (Yahner and Scott 1988; Tews et al. 2004; Steel et al. 2017). In particular, the amount of edge versus core habitat, and the aggregation versus fragmentation of vegetation types can modify resource availability, predation pressure, and ultimately wildlife reproductive success (Andren 1994; Villard 1998).

Changes in spatial or landscape patterns of fire also depend in part on land use history. While forests with a

history of sustained fire suppression have experienced notable divergences from historic fire regimes, such shifts appear less prominent or are undetected where the natural fire regime has been partially restored (van Wageningen and Lutz 2007; Miller et al. 2012a; Meyer 2015), or where fire suppression policies were implemented only recently (Rivera-Huerta et al. 2016). Managed wildfire areas, where naturally-ignited fires are allowed to burn under certain conditions, may be buffered from some of the dramatic shifts in fire patterns observed elsewhere. Thus, the expansion of such policies has been proposed to mitigate the negative effects of past forest management, and increase forest resilience (i.e. the ability to absorb a disturbance without shifting to an alternative stable state; Holling 1973; Safford et al. 2012) in the face of climate change (North et al. 2009; Meyer 2015; Stephens et al. 2016a). By comparing landscape patterns and trends of burn severity between managed wildfire and suppression areas, we can better understand the consequences of different management approaches and inform management policy. If shifts in burn severity pattern are principally driven by management, differences between managed wildfire and wildfire suppression units may be evident, either in terms of averages across fires and/or trends over time. Alternatively, if climate warming is the principle driver of changing fire patterns, we would expect little difference between analogous forests under different management regimes.

In this contribution we address two primary questions: (1) Has the landscape pattern of burn severity changed in California yellow pine and mixed-conifer forests from 1984 to 2015?; and (2) do average severity patterns, and/or the rate at which they are changing, differ in administrative units with a history of managed wildfire as compared to units predominantly managed under a policy of fire suppression? To address these questions, we utilize remotely sensed burn severity data across California, focusing on the unchanged or very low-severity, and high-severity levels within each fire. These contrasting components of the burn mosaic represent islands of intact forest within a fire perimeter (either left unburned or so lightly burned that remote sensed imagery does not detect vegetation change), and patches of stand-replacing fire, respectively. For each of these severity levels, trends were evaluated for metrics of total area, proportion area, shape complexity, aggregation, and

core area. Landscape ecology theory links characteristics of landscape pattern to the size of a focal landscape (e.g. an individual fire) and the proportion of the landscape composed of a given cover class (e.g. severity level; Gardner et al. 1987; Gustafson and Parker 1992). Further, this theory is supported by empirical studies of wildfire pattern in the Pacific Northwest and the Northern Rocky Mountains (Cansler and McKenzie 2014; Harvey et al. 2016). These studies, plus documented increases in fire size, proportion high-severity fire, and high-severity patch size (Miller and Safford 2012; Miller et al. 2012b) within some regions of California suggest the configuration of high-severity areas may also be changing in some forests. To evaluate this potential and to expand our knowledge of the important but less-studied unchanged or very low-severity component, trends were evaluated across the yellow pine and mixed-conifer forests of California, and comparisons were made between suppression and managed wildfire areas within the Sierra Nevada bioregion.

Methods

Study area

We assessed fires that burned in predominantly yellow pine and mixed-conifer (hereafter “YPMC”) forests in the state’s Klamath Mountains, North Coast, Northeastern Plateau, Sierra Nevada, South Coast, and Southern Cascades bioregions (Fig. 1a). Common tree species found within California YPMC forests include ponderosa pine (*Pinus ponderosa*), Jeffrey pine (*P. jeffreyi*), sugar pine (*P. lambertiana*), black oak (*Quercus kelloggii*), canyon live oak (*Q. chrysolepis*), incense cedar (*Calocedrus decurrens*), white fir (*Abies concolor*), and lodgepole pine (*P. contorta*) (Fites-Kaufman et al. 2007). Historically, these forest types supported a high-frequency (mean fire return intervals of 10–20 years) and low- to moderate-severity fire regime, where large patches of stand-replacing fire were less common (Van de Water and Safford 2011; Safford and Stevens 2017).

Full suppression is the dominant management response to wildfires in California, and has been so since the early twentieth century (North et al. 2015). However, within a minority of the Sierra Nevada Mountains, natural fires (lightning-caused) are

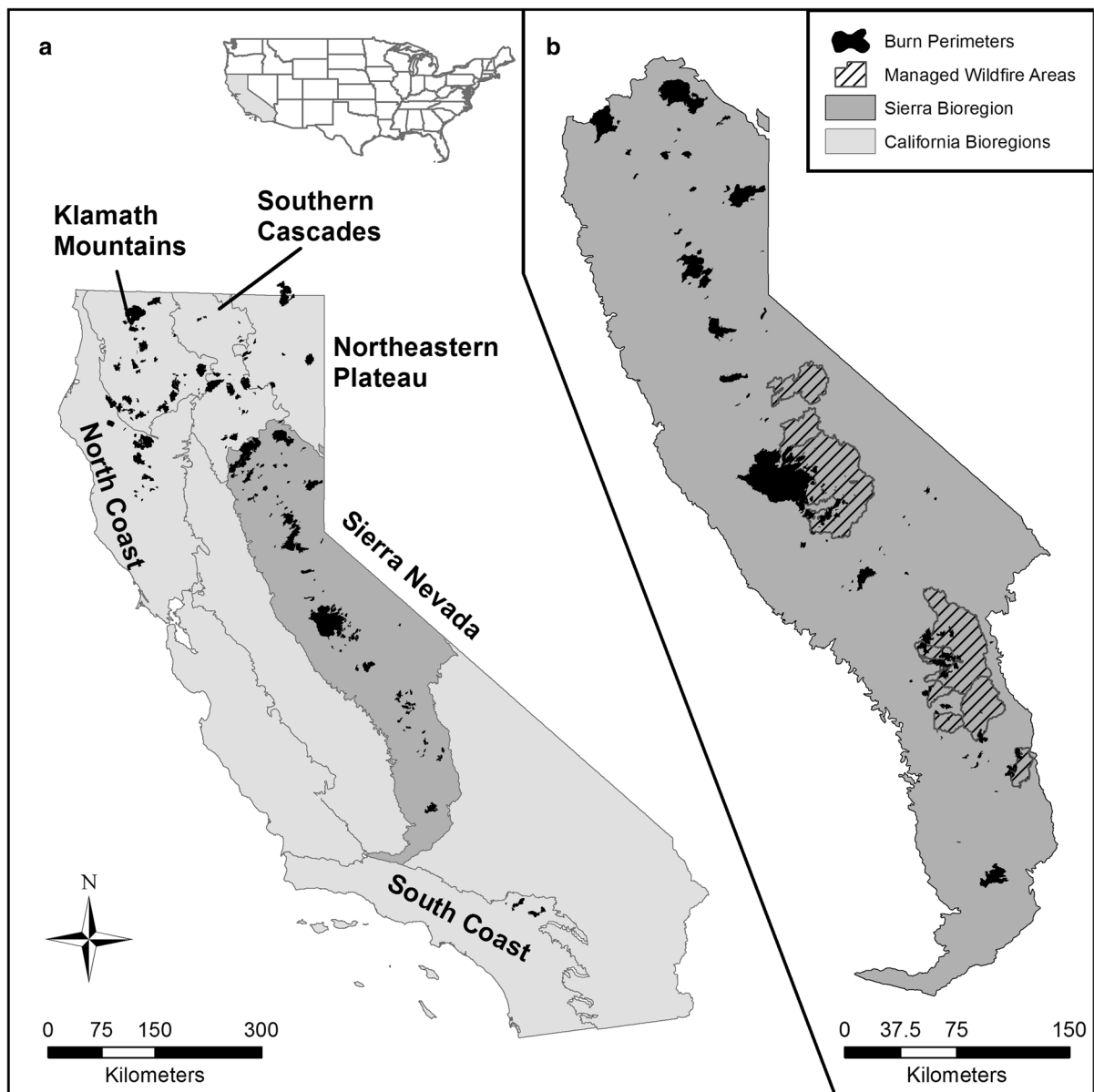


Fig. 1 Map of study region and fires. **a** The state-wide analysis includes fires ≥ 400 ha in size, distributed across six bioregions of California (from Sugihara et al. 2006). **b** The Sierra Nevada

managed wildfire analysis includes fires ≥ 80 ha in size that have mean elevations within the elevation range of managed wildfire areas

allowed to burn through a policy known as managed wildfire (previously called “wildland fire use”). Sequoia and Kings Canyon (SEKI), and Yosemite (YOSE) National Parks began managed wildfire programs in the early 1970s that now encompass much of their land area (van Wagtenonk 2007). Additionally, some Sierra Nevada Forest Service wilderness areas permit managed wildfire under

certain conditions (USDA 2004). Among these areas, YOSE has the most clearly defined managed wildfire program, where 46% of the burned area since 1973 is attributable to managed wildfire, totaling over 73,000 ha. We used the managed wildfire history of YOSE as our standard, and classified SEKI management units and Forest Service wilderness areas as managed wildfire units if greater than 46% of the area

Table 1 National Park (NPS) and US Forest Service (FS) management units classified as managed wildfire units

	Agency	Unit name	Burned area (ha)	% managed wildfire area
Management units are listed in descending order by total burned area between 1973 and 2015. Additional abbreviations: Yosemite National Park (YOSE), and Sequoia and Kings Canyon National Parks (SEKI)	NPS	YOSE—Fire Use	73,456	46.0
	NPS	SEKI—Sierra Crest	21,070	90.7
	FS	South Sierra	10,281	51.1
	FS	Monarch	9513	51.8
	NPS	SEKI—Cedar Grove	8216	57.6
	NPS	SEKI—Kern Canyon	4308	98.4
	FS	Carson-Iceberg	2996	96.5
	FS	Emigrant	1690	71.8
	NPS	SEKI—East Fork Kaweah	1187	74.0
	NPS	SEKI—Marble Fork Kaweah	768	83.7
	FS	Jennie Lakes	13	67.7

burned from 1973 to 2015 can be attributed to managed wildfire according to the California inter-agency fire perimeter database (available at http://frap.fire.ca.gov/data/frapgisdata-sw-fireperimeters_download). In total, eleven National Park management units or Forest Service wilderness areas were classified as managed wildfire units (Table 1; Fig. 1b). All Sierra Nevada forest units outside of national parks and wilderness areas are considered wildfire suppression units.

Severity data and landscape metrics

Fire severity data from 1984 to 2015 were obtained from a Forest Service maintained database, which includes all fires ≥ 400 ha that occurred at least partially on Forest Service or National Park Service land in California since 1984 (available at www.fs.usda.gov/detail/r5/landmanagement/gis). The database is more comprehensive for the Sierra Nevada region, where all fires ≥ 80 ha are included. All Sierra Nevada fires ≥ 80 ha were used to compare management units within the Sierra Nevada bioregion, but only fires ≥ 400 ha were used when assessing state-wide trends (Fig. 1). The database is derived from LANDSAT-TM satellite imagery and the Relative differenced Normalized Burn Ratio (RdNBR) is used to classify four severity levels (i.e., unchanged or very low, low, moderate and high) as defined by Miller and Thode (2007) with a minimum patch size of 900 square meters (i.e. one pixel). Comprehensive explanations of the data generation process and calibration with field data can be found in Miller and Thode (2007), Miller and Safford (2008), Miller et al.

(2009a), Miller and Quayle (2015), and Lydersen et al. (2016). We analyzed the unchanged or very low-severity (hereafter “unchanged”) and high-severity components of each fire, as they represent the extrema of the fire severity spectrum. Specifically, the unchanged component represents areas within fire perimeters that either did not burn or that experienced surface fire causing no discernable difference between pre- and post-fire satellite imagery of canopy conditions. The high-severity component represents stand replacing fire with $> 95\%$ mortality of the forest canopy (Miller et al. 2009a; Lydersen et al. 2016). The low- and moderate-severity levels that encompass the gradient of canopy mortality between remnant forest and stand-replacement were not assessed.

We classified each fire according to its dominant forest type and bioregion, using pre-settlement fire regime (PFR) groups from the California Fire Return Interval Departure database (Safford and Van de Water 2011, 2014; www.fs.usda.gov/detail/r5/landmanagement/gis/), and bioregions as defined by Sugihara et al. (2006; Fig. 1). We chose to use PFRs, which represent vegetation potential (including the role of disturbance) instead of current vegetation layers because the latter are sensitive to recent changes in vegetation, and we are interested in identifying general shifts in fire patterns over time. Fires where the majority of the burned area overlaps with the yellow pine, moist mixed-conifer, or dry mixed-conifer PFR types were used in our analysis and are referred to jointly as “YPMC forests”. Rarely, areas within burn perimeters could not be assessed remotely for burn severity due to cloud cover. Because the metrics assessed here can be biased by the existence of these

Table 2 Median (1st, 3rd quantile) values of metrics of interest for the unchanged component of fires included in analysis

Model type	Group	Composition metrics		Configuration metrics			N
		Area (HA)	Proportion Area	Shape complexity (m/m ²)	Aggregation (PLA ^a)	Core area (Ha)	
State-wide	Sierra Nevada	171 (84, 358)	0.11 (0.07, 0.22)	394 (298, 465)	0.66 (0.53, 0.76)	2.0 (0, 8)	137
	Klamath Mountains	223 (90, 380)	0.09 (0.06, 0.16)	388 (305, 490)	0.62 (0.52, 0.70)	3.4 (0, 25)	51
	Southern Cascades	139 (46, 243)	0.06 (0.03, 0.14)	444 (348, 655)	0.56 (0.42, 0.71)	0.2 (0, 5)	23
	North Coast	157 (68, 712)	0.11 (0.06, 0.18)	411 (324, 525)	0.57 (0.49, 0.74)	5.5 (0, 23)	22
	Northeastern Plateau	222 (80, 614)	0.06 (0.04, 0.13)	386 (288, 488)	0.50 (0.42, 0.59)	5.4 (0, 45)	12
	South Coast	293 (109, 601)	0.08 (0.07, 0.08)	422 (359, 484)	0.43 (0.37, 0.54)	3.3 (1, 31)	4
Sierra management	Suppression	63 (24, 137)	0.13 (0.06, 0.22)	402 (312, 534)	0.76 (0.62, 0.86)	0.1 (0, 3)	79
	Managed wildfire	123 (50, 197)	0.27 (0.18, 0.37)	336 (278, 431)	0.83 (0.77, 0.85)	1.1 (0, 8)	43
	Both	174 (95, 343)	0.12 (0.08, 0.27)	408 (348, 465)	0.68 (0.58, 0.76)	0.4 (0, 6)	33

The number of fires in each bioregion and management group are also included. Sierra Nevada managed wildfire models include proportion burned area within managed wildfire units as a predictor. However, for ease of comparison, fires are grouped here by those that fall fully within suppression units, managed wildfire units, or both (i.e. where the burn perimeter intersects the management boundary)

^aProportion like-adjacency

unmapped polygons, we removed three fires where more than 1% of the burned area was unmapped.

We calculated five landscape metrics for the unchanged and high-severity components of each fire that characterize class composition and configuration. Composition metrics include (1) total class area, and (2) class proportion of fire area. Configuration metrics include (3) edge:area ratio—a measure of shape complexity, (4) proportion like-adjacency (PLA)—a measure of aggregation, and (5) total class core area (Tables 2 and 3). High edge:area values indicate a fire is composed of irregular and/or smaller patches, whereas small values represent fires composed of compact (e.g. circular) and/or large patches. PLA is a measure of class-specific aggregation with values ranging from zero to one. A zero value signifies maximum disaggregation (fragmentation) where each patch is composed of a single pixel, and a value of one signifies maximum aggregation where all area of a severity level is composed of a single patch (McGarigal et al. 2012). PLA is calculated using a 4-neighbor rule where pixels of the same class arranged along a diagonal are considered distinct patches (Turner and Gardner 2015). The concept of patch core area is important for a number of ecological processes, including habitat for edge-sensitive wildlife species, and succession of disturbed areas (Turner et al. 1998;

Villard 1998). Here, core areas are defined by an internal buffer of 100 m, which was chosen as the approximate distance from live conifer seed-trees beyond which non-serotinous conifer regeneration is expected to be very low (Welch et al. 2016). Thus, within high-severity core area, type-conversion to a non-forested state is more likely. Within unchanged core area, edge effects resulting from adjacent burned areas are likely to be minimal. When considering conifer regeneration, the appropriate distance threshold depends on tree species and dispersal mechanism (Collins et al. 2017), and various studies in the western US have defined thresholds ranging from approximately 70–400 m (Donato et al. 2009; Cansler and McKenzie 2014; Harvey et al. 2016; Kemp et al. 2016). An analysis varying the distance threshold between 50 and 400 m showed model slope estimates to be insensitive to the threshold used, although estimates of model intercepts varied predictably (Online Resource 1). Core area is a function of both patch size and shape, and thus co-varies with the metrics of class area and edge:area ratio. The five metrics assessed were selected to describe different aspects of landscape composition and configuration but are not completely orthogonal (Online Resource 2), and in some cases are best interpreted collectively.

Table 3 Median (1st, 3rd quantile) values of metrics of interest for the high-severity component of fires included in analysis

Model type	Group	Composition metrics		Configuration metrics		N
		Area (HA)	Proportion area	Shape complexity (m/m ²)	Aggregation (PLA ¹)	
State-wide	Sierra Nevada	175 (36, 708)	0.14 (0.04, 0.30)	222 (131, 333)	0.77 (0.70, 0.85)	137
	Klamath Mountains	258 (115, 613)	0.18 (0.07, 0.30)	202 (147, 269)	0.77 (0.66, 0.86)	51
	Southern Cascades	405 (143, 898)	0.25 (0.18, 0.48)	133 (97, 192)	0.85 (0.81, 0.91)	23
	North Coast	244 (53, 887)	0.13 (0.07, 0.23)	174 (143, 324)	0.77 (0.73, 0.84)	22
	Northeastern Plateau	1605 (806, 2910)	0.46 (0.33, 0.58)	98 (90, 131)	0.85 (0.79, 0.92)	12
	South Coast	2408 (1217, 4123)	0.42 (0.28, 0.54)	126 (93, 174)	0.83 (0.79, 0.86)	4
Sierra management	Suppression	50 (14, 367)	0.18 (0.05, 0.32)	190 (127, 305)	0.86 (0.80, 0.92)	79
	Managed wildfire	11 (2, 42)	0.02 (0.00, 0.07)	387 (308, 599)	0.75 (0.69, 0.81)	43
	Both	75 (4, 305)	0.05 (0.01, 0.14)	281 (225, 395)	0.71 (0.64, 0.78)	33

The number of fires in each bioregion and management group are also included. Sierra Nevada managed wildfire models include proportion burned area within managed wildfire units as a predictor. However, for ease of comparison, fires are grouped here by those that fall fully within suppression units, managed wildfire units, or both (i.e. where the burn perimeter intersects with management boundary)

Statistical analysis

We used multilevel linear regression models to estimate trends in fire metrics from 1984 to 2015, with the individual fire as our sample unit. We built two groups of models: (1) state-wide models and, (2) Sierra Nevada-specific managed wildfire models.

$$y_i = \alpha + \alpha_{brj} + (\beta_{yr} + \beta_{brj}) * year_i \quad (1)$$

$$y_i = \alpha + \beta_{pmw} * PMW_i + (\beta_{yr} + \beta_{yr:pmw} * PMW_i) * year_i + \beta_{ele} * ele_i + \beta_{rough} * rough_i + \beta_{fm} * fm_i \quad (2)$$

For both model groups, response variables y were total area, proportion area, shape complexity (edge:area ratio), aggregation (PLA), and core area for the unchanged and high-severity components of each fire i (Tables 2 and 3). Predictor variables for state-wide models included year (β_{yr}) as the sole fixed effect, and bioregion j as a random effect on both the intercept (α_{br}) and slope of year (β_{br}). By modeling bioregion as a random effect we allowed partial pooling across categories, which improves estimates (McElreath 2016), and makes explicit the assumption that fire regimes in neighboring geographic regions are not wholly independent. The managed wildfire models are specific to the Sierra Nevada bioregion as the practice has yet to be widely implemented elsewhere in the state. Predictor variables for managed wildfire models included the proportion of the burned area in managed wildfire units (PMW ; β_{pmw}), year (β_{yr}), an interaction of year and PMW ($\beta_{yr:pmw}$), elevation (β_{ele}), topographic roughness (β_{rough}), and fuel moisture (β_{fm} ; Table 4). Elevation, topographic roughness, and fuel moisture were included as covariates to account for local climate, topography, and fire weather differences between management groups, which are known to influence fire effects (Sugihara et al. 2006).

Fire size can also drive burn patterns (Cansler and McKenzie 2014; Harvey et al. 2016), but is not included as a model covariate because it is confounded with time (Miller et al. 2009b) and not strongly correlated with PMW (r [95% CI] = − 0.05 [− 0.21, 0.10]). Elevation data were sourced from the USGS National Elevation Dataset, a 1/3-arc second digital elevation model (available at nationalmap.gov/elevation.html). Per-pixel topographic roughness was calculated as the standard deviation of elevation values

Table 4 Median (1st, 3rd quantile) values of mean elevation, topographic roughness and fuel moisture of fires used in managed wildfire models

Management group	Elevation (m)	Roughness (m)	100-h fuel moisture (%)
Suppression	1749 (1581, 2006)	830 (654, 954)	7.4 (6.4, 8.7)
Managed wildfire	2270 (2171, 2402)	997 (964, 1032)	8.8 (8.0, 9.6)
Both	2128 (1957, 2349)	1025 (957, 1055)	8.2 (7.4, 9.3)

Elevation and roughness represent average pixel values within a fire perimeter. One hundred-hour fuel moisture values represent the average pixel value within a fire perimeter for reported burn days

within a 55×55 pixel moving window (approximately 550 m on each side). This measure of terrain ruggedness has been shown to be an important predictor of wildfire severity (Holden et al. 2009). The 100-h fuel moisture data were sourced from the GRIDMET gridded product (Abatzoglou 2013) and were calculated per pixel as the mean value during the reported burning period. Elevation, topographic roughness, and 100-h fuel moisture were calculated using Google Earth Engine (Gorelick et al. 2017) and per-fire values of these variables represent the mean of all pixels within the fire perimeter. Fires included in the managed wildfire models were limited to the elevational range (1437–2700 m) of fires burning at least partially across managed wildfire units. Additionally, 19 fires for which we could not calculate mean fuel moisture (i.e. fires without documented beginning and ending dates) were excluded. Unlike the state-wide models which estimate absolute temporal trends, trend estimates for the managed wildfire models should be interpreted as marginal changes over time after accounting for the influence of elevation, topography, weather, and management strategy. For most metrics, 249 total fires were included for the California-wide models and 155 fires for the managed wildfire models (Fig. 1, Tables 2 and 3). Metrics of shape complexity and aggregation cannot be calculated when no patches exist of the cover class of interest, which was the case for high-severity in five fires from the California dataset, and 14 in the managed wildfire dataset. These fires were removed when modeling high-severity shape complexity and aggregation, resulting in slightly smaller sample sizes.

For the proportion area and aggregation models, we used generalized linear models with a beta error structure and a logit link. All other models used a Gaussian error structure and a log transformation on the response variable. To avoid transforming zero

values, the equivalent of one map pixel was added to area, proportion area, and core area metrics (i.e., 0.09 ha). Predictor variables were standardized prior to model fit. Models were fit using Hamiltonian Monte Carlo estimation and weakly regularizing priors via the Statistical Rethinking and RStan packages (McElreath 2016; Stan Development Team 2016) in program R (R Development Core Team 2011). Model convergence was assessed by examining Rhat values, Gelman plots, and trace plots. Managed wildfire models were fit using fires that burned exclusively within management units as well as those that burned across management boundaries. However, when comparing central tendencies and trends over time between management strategies we make model predictions for an average fire burning completely within suppression (PMW equivalent to 0 prior to standardization) and managed wildfire units (PMW equivalent to 1 prior to standardization). For simplicity, when making probability statements regarding model uncertainty we utilize the abbreviations of $\text{Pr}(+)$, $\text{Pr}(-)$, and $\text{Pr}(d)$ to describe the probability of an increase, decline or difference between management types, respectively. For example, $\text{Pr}(+) = 0.91$ indicates there is a 91% probability that a given metric is increasing over time, given the data and specified model.

Results

Changing fire patterns in California

Our assessment of fire landscape patterns generally showed opposite temporal trends for the unchanged and high-severity components of California fires. Models of the unchanged component within fire perimeters suggest absolute area is static over the 32-year time-period (Fig. 2a), but the mean proportion

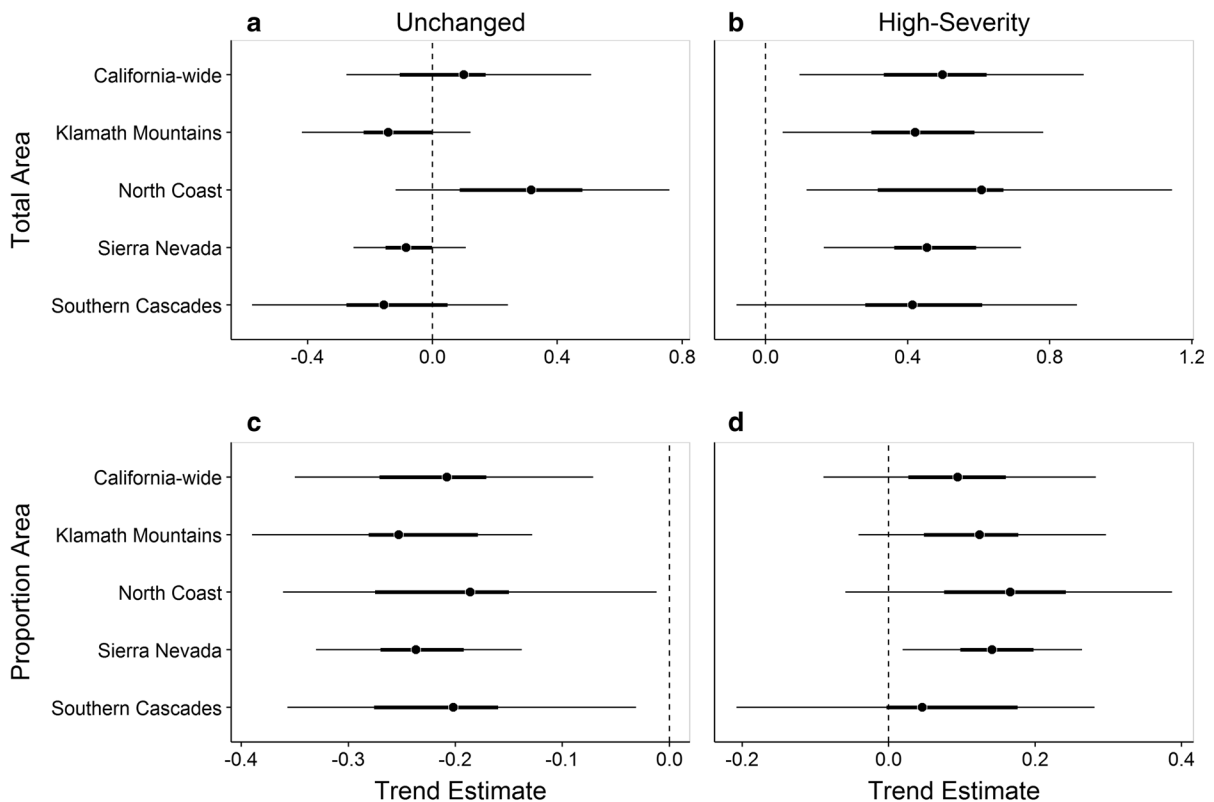


Fig. 2 Standardized trend estimates for total area (**a** and **b**) and proportion area (**c** and **d**) of each severity component. Each subplot displays results for a single model with estimates for California, and those bioregions with a minimum sample size of 20 fires (estimates for all bioregions provided in Online Resource 3). Subplots are organized by the metric assessed

(rows) and level of burn severity (columns). Dotplots show mean estimates along with the 50th and 90th percentile credible intervals. Estimates to the left and right of the dotted line represent declines and increases over time, respectively. Parameter estimates, uncertainty measures, and probability that trends are directional, are tabulated in Online Resource 3

of wildfire area left unchanged has declined across California and its bioregions with a greater than 95% probability in all cases (Fig. 2c). Conversely, within the high-severity component, we observed increases in the amount of area burned per fire over time, with a greater than 95% probability in all cases except for the Southern Cascades, which had a 92% probability of a positive trend (Fig. 2b). We also observed increases in the proportion of high-severity per fire for most bioregions, but with more uncertainty in model estimates. Increasing proportion high-severity was likely in the case of California as a whole ($\text{Pr}(+) = 0.82$), the Klamath Mountains ($\text{Pr}(+) = 0.89$), the North Coast ($\text{Pr}(+) = 0.91$), and most clear for the Sierra Nevada, where the model estimates a 98% chance of a positive trend (Fig. 2d; Online Resource 3).

For the unchanged component, models of configuration metrics estimate increasing shape complexity (edge:area ratio; $\text{Pr}(+) > 0.95$), and declining core area for both the Klamath Mountains and Sierra Nevada bioregions ($\text{Pr}(-) > 0.95$; Fig. 3a, e). The aggregation metric (proportion like-adjacency) of unchanged patches declined over time across California and all bioregions ($\text{Pr}(-) > 0.95$; Fig. 3c). These results indicate unchanged areas have become increasingly fragmented across the state and, at least for the Klamath Mountains and Sierra Nevada, unchanged patches have also become smaller and/or more complex in shape. For the high-severity component, the shape complexity model estimates a decline within the Sierra Nevada ($\text{Pr}(-) = 0.98$), but no clear trends elsewhere in the state (Fig. 3b). Aggregation of high-severity patches does not appear to have changed in the assessed areas (Fig. 3d), but high-severity core

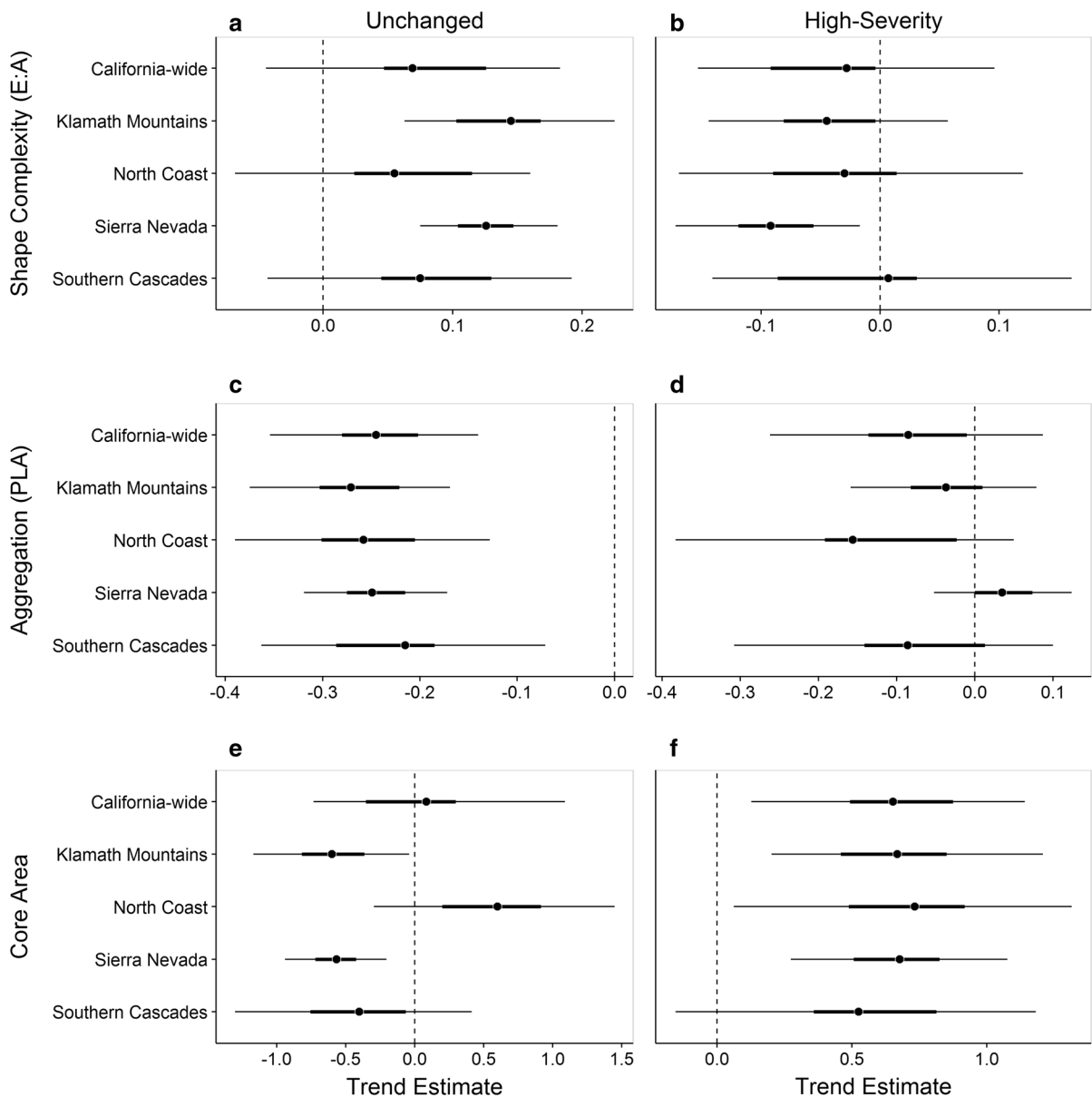


Fig. 3 Standardized trend parameter estimates for shape complexity (edge:area; **a** and **b**), aggregation (proportion like-adjacency; PLA; **c** and **d**), and core area (**e** and **f**) of each severity component. Each subplot displays results for a single model with estimates for California, and those bioregions with a minimum sample size of 20 fires (estimates for all bioregions provided in Online Resource 3). Subplots are organized by the

metric assessed (rows) and level of burn severity (columns). Dotplots show mean estimates along with the 50th and 90th percentile credible intervals. Estimates to the left and right of the dotted line represent declines and increases over time, respectively. Parameter estimates, uncertainty measures, and probability that trends are directional, are tabulated in Online Resource 3

area has clearly increased across California ($\text{Pr}(+) = 0.97$), including the Klamath Mountains ($\text{Pr}(+) = 0.98$), North Coast ($\text{Pr}(+) = 0.97$), and the Sierra Nevada ($\text{Pr}(+) > 0.99$; Fig. 3f; Online Resource 3).

Managed wildfire

The direction of temporal trends among the managed wildfire models were similar in some respects to those

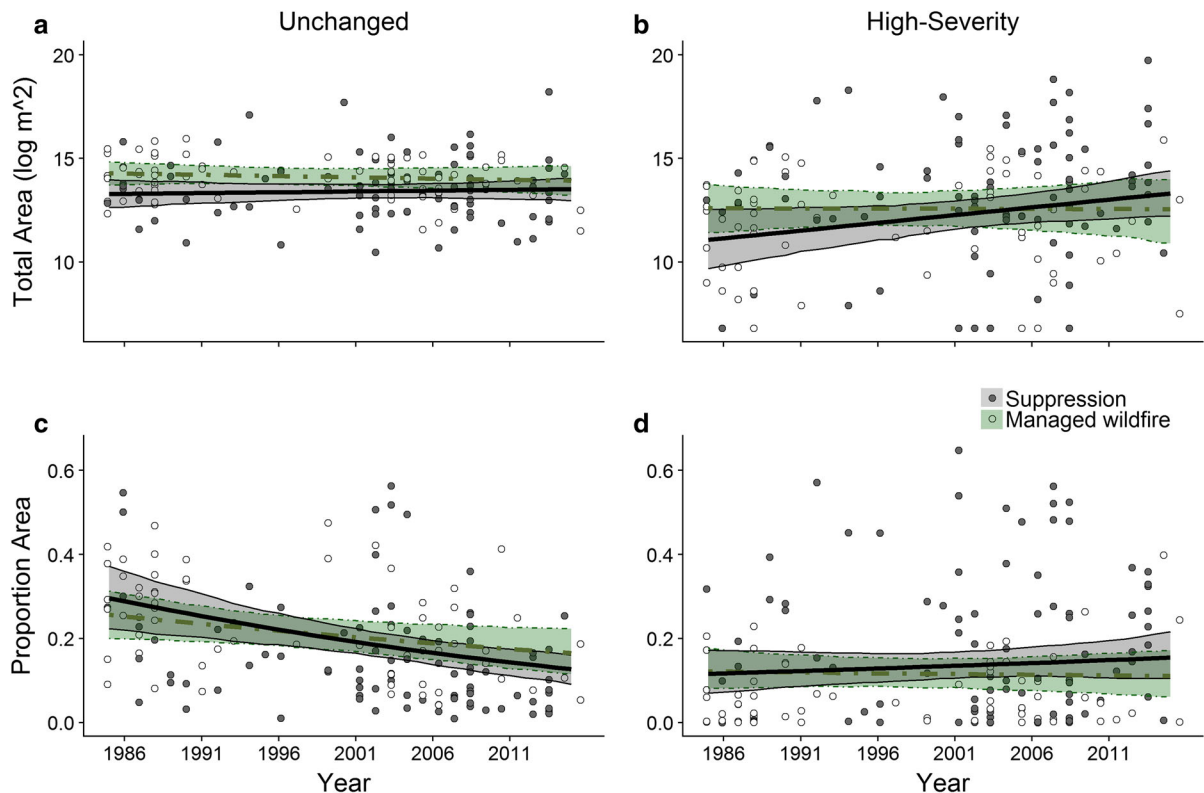


Fig. 4 Managed wildfire model predictions of change over time and 90% credible intervals for total area (**a** and **b**) and proportion area (**c** and **d**) of the unchanged and high-severity fire components. Predictions are made for fires burning completely within suppression units (PMW = 0) and managed wildfire units (PMW = 1), with other model covariates held at their mean values. Predictions for suppression units are illustrated by solid lines and grey shading, and those for

managed wildfire units are illustrated by dashed lines and green shading (online version in color). Values for individual fires with a majority of their area burning in suppression and managed wildfire units are shown as filled and open points respectively. Some extreme points were removed from the plot to better illustrate model fit, but all points were included in the analysis

estimated for the Sierra Nevada bioregion in the state-wide models. However, the effect of burn area proportion within managed wildfire units (PMW) was strong for many metrics, indicating fires burning in suppressed versus managed wildfire units produce different severity patterns in some respects independent of temporal trends. There is no apparent trend in the total amount of unchanged area for fires in either suppressed ($\text{Pr}(+) = 0.68$) or managed wildfire units ($\text{Pr}(+) = 0.24$), but the proportion of unchanged area declined in both cases ($\text{Pr}(-) > 0.99$), with fires in suppression units likely declining at a faster rate ($\text{Pr}(d) = 0.90$). Fires burning in managed wildfire units contained greater total unchanged area than those in suppression units ($\text{Pr}(d) = 0.99$; Fig. 4a; Table 2). Our model of total high-severity area shows a clear increase among fires in suppression units ($\text{Pr}(+) =$

0.98), but no corresponding trend for fires in managed wildfire units (Fig. 4b). There is limited evidence that the proportion of high-severity area among fires in suppression units is increasing ($\text{Pr}(+) = 0.80$), and is greater on average than fires in managed wildfire units ($\text{Pr}(d) = 0.76$); Fig. 4d; Table 2; Online Resource 4).

The shape complexity model showed clear increases ($\text{Pr}(+) > 0.99$) in the unchanged component for fires in both suppression and managed wildfire units with no apparent difference in estimated intercept or slopes (Fig. 5a). At the same time the aggregation model showed a clear and declining temporal trend among unchanged patches for both management types ($\text{Pr}(-) > 0.99$). The estimated intercept of fires within suppression units was greater ($\text{Pr}(d) = 0.97$) but likely declining at a faster rate ($\text{Pr}(d) = 0.89$), effectively reducing the mean

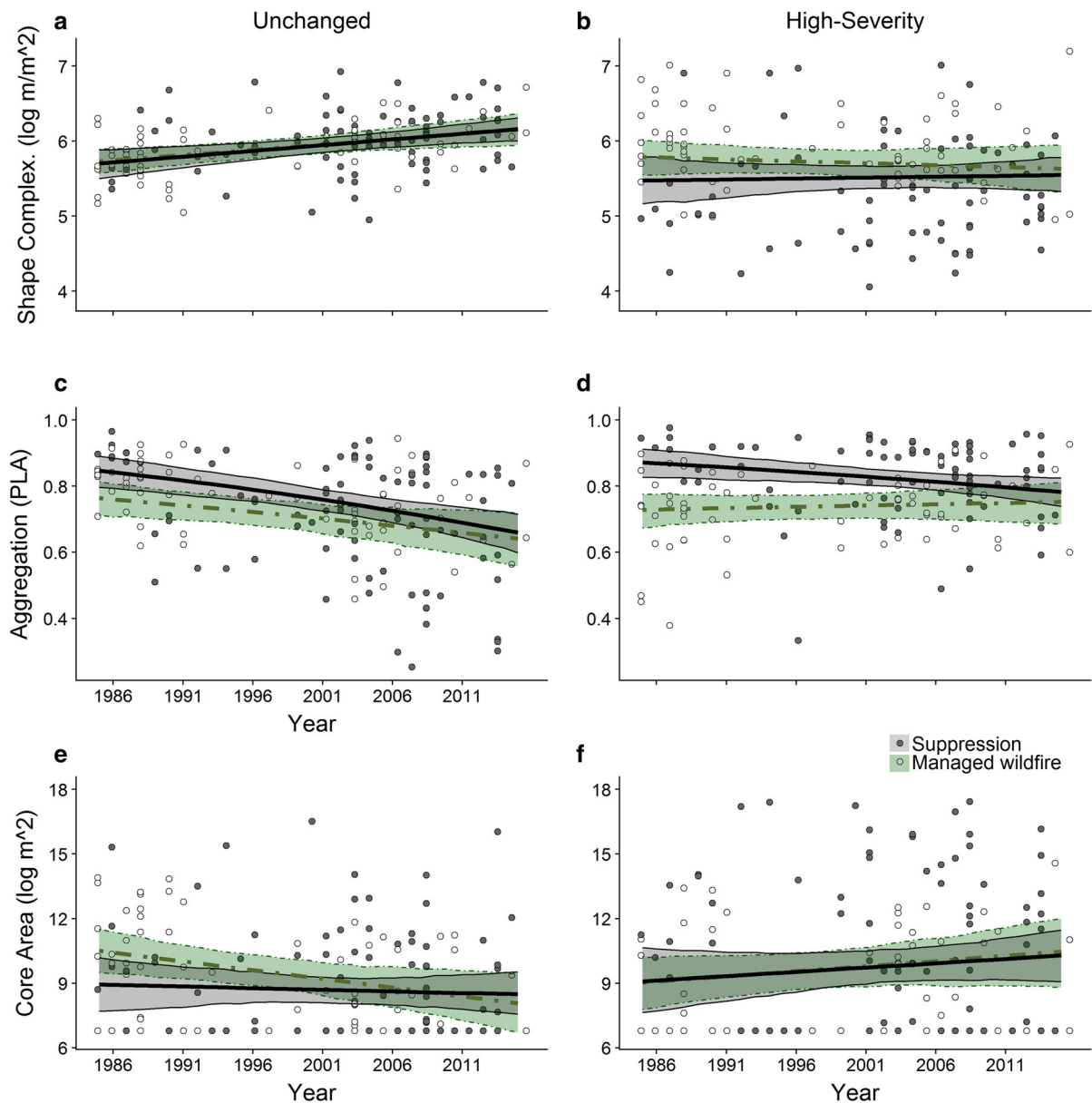


Fig. 5 Managed wildfire model predictions of change over time and 90% credible intervals for shape complexity (edge:area ratio; **a** and **b**), aggregation (proportion like-adjacency; **c** and **d**), and core area (**e** and **f**) of the unchanged and high-severity fire components. Predictions are made for fires burning completely within suppression units (PMW = 0) and managed wildfire units (PMW = 1), with other model covariates held at their mean values. Predictions for suppression units are illustrated by solid

lines and grey shading, and those for managed wildfire units are illustrated by dashed lines and green shading (online version in color). Values for individual fires with a majority of their area burning in suppression and managed wildfire units are shown as filled and open points respectively. Some extreme points were removed from the plot to better illustrate model fit, but all points were included in the analysis

difference in unchanged aggregation between management types over time (Fig. 5c). Mean core area of the unchanged component is estimated to be similar between fires in the two management types, but has

declined for fires in managed wildfire units ($\text{Pr}(-) = 0.99$) over the study period and at a faster rate than the suppression group ($\text{Pr}(d) = 0.93$; Fig. 5e). Among configuration metrics, the only apparent trend was a

decline in aggregation for fires in suppression units ($\text{Pr}(-) = 0.99$; Fig. 5d), although there is also some evidence that high-severity core areas are increasing jointly for fires in both the managed wildfire units ($\text{Pr}(+) = 0.89$) and suppression units ($\text{Pr}(+) = 0.85$). Importantly, high-severity proportion and core area is negatively correlated with elevation (Online Resources 2 and 4). This relationship may explain why trends for both metrics were stronger within our statewide dataset (Fig. 3f), which includes additional fires below the elevation range of managed wildfires units. The differences in management group central tendencies were more apparent in the high-severity configuration metrics (Table 2), with fires in managed wildfire units showing higher shape complexity ($\text{Pr}(d) = 0.93$), and lower aggregation ($\text{Pr}(d) > 0.99$) (Fig. 5).

Discussion

Burn pattern trends and implications

We observed some clear trends in burn severity metrics, with the direction of apparent changes often opposite for the unchanged (i.e., unburned or very lightly burned), and high-severity (i.e. near-complete canopy mortality) components of yellow pine and mixed conifer (YPMC) wildfires in California. Specifically, the relative amount of unchanged area within fires has declined and unchanged patches are becoming more fragmented (less aggregated) across the state. Additionally, for the unchanged component of the Klamath Mountains and Sierra Nevada fires, shape complexity (edge:area) increased and core area decreased since 1984 (Figs. 2 and 3). Conversely, we observed an increase in the area burning at high-severity in many bioregions of California and a corresponding increase in the amount of high-severity core area; linked to previously reported increases in fire size (Miller et al. 2009b). The proportion of high-severity in individual fires may also be increasing in many areas of the state, but such a shift is most clear in the Sierra Nevada, in agreement with previous assessments at the region-level, which incorporated fewer years (Miller et al. 2009b; Miller and Safford 2012). Likewise, high-severity areas in the Sierra Nevada have shown declining shape complexity (Figs. 2 and 3). Such changes in these two contrasting

levels of fire effects are likely to influence ecological process, as well as the composition of post-fire floral and faunal communities.

Observed increases in high-severity fire in YPMC forests have led to concerns about forest resilience (Stephens et al. 2016a; Welch et al. 2016). Serotiny is uncommon in our study area, and regeneration of most California conifer species depends on the availability of seeds from surviving trees. Conifer seed dispersal decays exponentially with distance to source, with regeneration of heavy seeded pine species especially sensitive to live tree proximity (Shive et al. in press; Welch et al. 2016). In these forests, an additional challenge is water and light competition from fire-stimulated shrub species, especially from the genus *Ceanothus*, and hardwoods (e.g., *Quercus*), which resprout after even relatively severe fires (Tepley et al. 2017; Welch et al. 2016). In large high-severity patches, type conversion to shrub fields can ensue, and may be prolonged to a quasi-permanent state if areas are reburned at high-severity before conifer species can reestablish and become resistant to fire (Coppoletta et al. 2016; Tepley et al. 2017). Thus, larger and geometrically simpler patches of stand-replacing fire create more areas isolated from conifer seed sources and more core area at risk of conversion to other vegetation types (Collins et al. 2017; Stevens et al. 2017). Our findings that mean high-severity area and high-severity core area are both increasing over the last 32 years across most of our study area are evidence that conifer forest resilience is increasingly at risk in some areas. Our state-wide model, which includes fires from the full elevational range of YPMC, provides evidence that this risk of type conversion may be especially high in the Sierra Nevada.

Between 1984 and 2015, our models of per-fire high-severity area and high-severity core area predict mean increases of 12, and 19% on the log scale respectively (Fig. 6a; Online Resource 3). The prediction that high-severity core area is increasing at a faster rate than high-severity area is in part attributable to the fact that high-severity patches do not contain core areas until they reach a certain size (at least π ha or $10.4 \log \text{m}^2$, when the distance to edge threshold is 100 m). Thus, high-severity core area only increases with high-severity area once relatively large patches of stand-replacing fire are created (Fig. 6b). As high-severity patches surpass this size threshold,

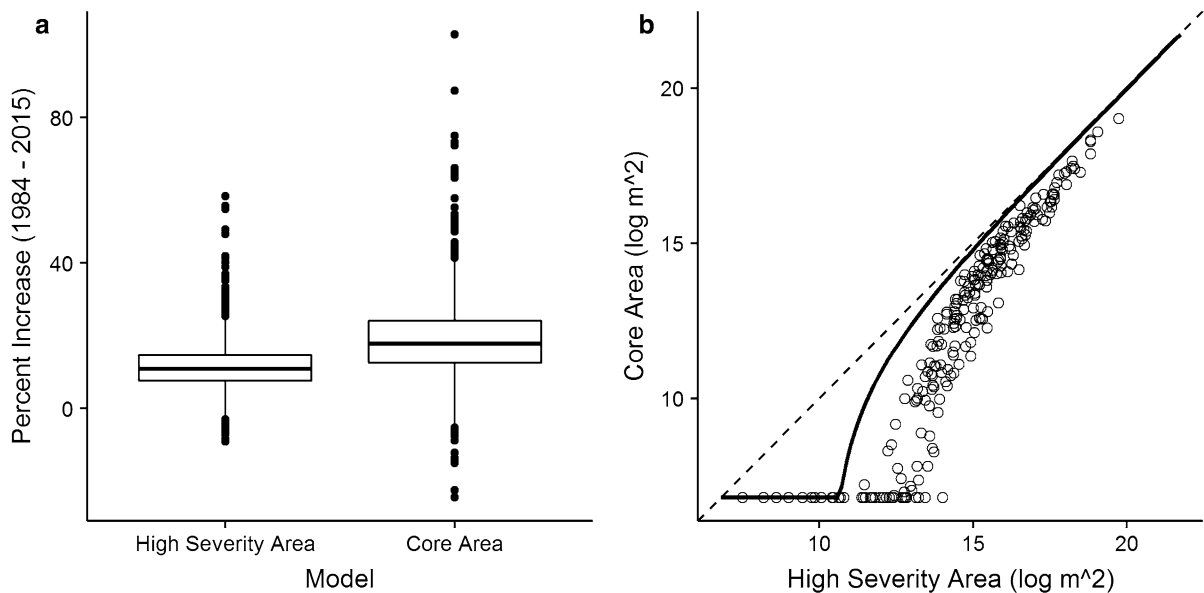


Fig. 6 A comparison of **a** predicted change in high-severity area and high-severity core area between 1984 and 2015, and **b** correlations between observed high-severity area and high-severity core area for all California fires. The latter plot also includes a dashed line of perfect correlation, and a solid line representing the geometric relationship between the variables if

the high-severity area of each fire was aggregated in a single circular patch. When using a 100 m distance threshold, such patches can only contain core area when it is at least π ha or 10.4 log m² in size. Departures from this relationship are due to patch fragmentation and shape complexity

the amount of high-severity core area rapidly increases from zero. Indeed, 75% of the fires in our dataset in the 16 years before 2000 contained at least some high-severity core area, whereas 88% of fires in our dataset burning in the 16 years after 2000 contained high-severity core areas. Additionally, where high-severity patches are becoming simpler (i.e. more circular), core areas will rise more rapidly relative to the absolute amount of high-severity area. This is evident in the Sierra Nevada, where shape complexity of high-severity areas has declined, and the increasing rates of high-severity area (10%) versus core area (22%) have diverged even more than the state as a whole (Online Resource 3). The imperfect relationship between changes in total area and core area illustrates the importance of burn severity spatial pattern in addition to commonly reported metrics of fire size and severity proportion when understanding how forest processes may be changing with altered fire regimes.

In most cases, our models estimate relatively consistent trends across the bioregions of California, albeit with varying levels of uncertainty. Likewise, a study in the Northern Rockies found a similar

increase in the proportion of high-severity fire, along with non-significant declines in shape complexity and increases in high-severity core area (Harvey et al. 2016). Given the differences in forest types, fire regimes and climates of the Northern Rockies and California, differences in trend magnitude between the regions might be expected. The apparent consistency in trend direction may suggest the ultimate drivers of fire suppression (Steel et al. 2015) and climate change (Abatzoglou and Williams 2016) are acting upon distinct regions in similar ways, with local dynamics modifying the relative importance of the drivers and strength of observed trends. Studies in other systems have found strong associations between fire size and high-severity configuration metrics analogous to those assessed here (Cansler and McKenzie 2014; Harvey et al. 2016). Evaluation of such associations is beyond the scope of this study, but we expect an increase in fire size in some parts of California (Miller et al. 2009b) to be similarly linked to the high-severity trends reported here. Such relationships with the unchanged component remain less well understood.

Managed wildfire

The major factors driving fire behavior are fuels, climate/weather, and topography (Sugihara et al. 2006). In order to contrast fire management history and consequently fuel patterns, we limited fires of both management types to the same bioregion, forest types and elevational range, and accounted for variation of elevation, fire weather, and topographic complexity between fires. Thus, we interpret differences in slope estimates for fires in managed and suppression units as evidence of the ongoing influence of fire management policy on burn severity patterns. We observed such differences where fires in suppression units experienced increasing total high-severity area without corresponding changes for fires in managed wildfire units (Fig. 4b). This result is consistent with literature demonstrating the utility of managed wildfire to moderate rates of high-severity fire (van Wagtenonk and Lutz 2007; Miller et al. 2012a; Meyer 2015). Perhaps more surprising are declines in aggregation of the high-severity component among fires in suppression units and declines in the unchanged core area of fires in managed wildfire units, without similar trends found in the contrasting management type (Fig. 4d and e). Declining high-severity aggregation among fires in suppression units suggests that the observed greater high-severity area in recent fires is resulting in greater high-severity patch density (patches/area) with an increase in distinct high-severity patches rather than the merging of patches. We speculate that the declining unchanged core area among managed wildfire group is at least partially attributable to an increased willingness of National Park fire managers to manage wildfire under more challenging conditions in recent years (J. van Wagtenonk, retired USGS, Personal Communication), where unchanged patches are more likely to be broken up by low- or moderate-severity fire.

In contrast to diverging trends, parallel trends between fires within the management types would be consistent with the hypothesis that shifts in climate/weather are driving trends in severity pattern. These patterns were observed among some metrics for the unchanged component, with declines in the proportion area and aggregation, and increases in shape complexity for both managed and suppressed areas, as well as potential increases in high-severity core area. A third pattern was observed when considering total unchanged

area and shape complexity of the high-severity component, where mean values differed between fires in the two groups without corresponding divergence in trends. Such contrasts between management types may indicate some of the effects of managed wildfire were realized relatively rapidly during the years following initiation of the policy in the 1970s, and prior to the availability of LANDSAT-TM imagery in 1984. Such a pattern was also hypothesized for Yosemite National Park by Collins et al. (2009).

The habitat heterogeneity created by fire, sometimes referred to as “pyrodiversity” (Martin and Sapsis 1992), can promote species diversity at some scales, and a complex burn mosaic is beneficial to many species (Roberts et al. 2008; Fontaine and Kennedy 2012; Buchalski et al. 2013; Tingley et al. 2016; Eyes et al. 2017). Restoration of natural fire regimes (full or partial) through managed wildfire has the potential to benefit biotic diversity generally, especially where the composition and configuration of the burn severity matrix promotes a heterogeneous mix of post-fire habitat types. Further, by reducing fuel loading and continuity, and by decreasing the probability that subsequent burning will occur at high-severity, managed wildfire can be used to compensate for a century-long deficit of low- and moderate-severity fire (van Wagtenonk and Lutz 2007; North et al. 2015). Since both suppressed and managed wildfires support higher levels of severe burning than was likely common before Euro-American settlement in California (Mallek et al. 2013; Safford and Stevens 2017), both management strategies likely support post-fire specialist species at rates equal to or greater than historical conditions. With high-severity area and high-severity core area increasing across much of California, and with the impacts of climate on fire projected to intensify over the next century (Restaino and Safford 2018), post-fire specialists and chaparral-associated species are the biotic groups most likely to benefit in the coming decades.

Conclusion

We draw three main conclusions from this study of burn severity patterns in California’s YPMC forests. First, across the state, unchanged areas have decreased as a proportion of the burn severity mosaic and these remnant forest patches have also become more

fragmented. At least within the Klamath Mountains and the Sierra Nevada, forest remnant patches are also becoming more complex in shape with greater edge and less core habitat available for edge-sensitive species. Second, the amount of high-severity area and the amount of high-severity core area—the area most at risk of type conversion from conifer forest to other vegetation—have both increased across much of California, with high-severity areas in the Sierra Nevada also becoming simpler in shape. Observed shifts in burn severity composition and landscape pattern likely have cascading effects on forest ecology including the floral and faunal communities of California's YPMC forests. Third, for some metrics assessed there was little difference between management types or apparent convergence in the case of unchanged core area and high-severity aggregation. However, compared to wildfires in suppression units, in managed wildfire units high-severity area appears more stable over time, with higher post-fire heterogeneity, as indicated by less aggregation of both the unchanged and high-severity patches, as well as higher shape complexity among the high-severity component. Thus, managing wildfire for ecological benefits appears to moderate some but not all of the deleterious effects of fire suppression, and should be considered an important component of the toolbox that managers use (Peterson et al. 2011) to increase forest resistance and resilience to the ecological shifts that will come with a warming climate.

Acknowledgements We thank two anonymous reviewers, along with Mark Schwartz and Malcolm North for providing critiques of early versions of this article, and Jay Miller for assistance in accessing burn severity data. Funding was provided by the United States Forest Service Pacific Southwest Region, and the University of California, Davis.

References

- Abatzoglou JT (2013) Development of gridded surface meteorological data for ecological applications and modelling. *Int J Climatol* 33:121–131
- Abatzoglou JT, Williams AP (2016) Impact of anthropogenic climate change on wildfire across western US forests. *Proc Natl Acad Sci* 113:11770–11775
- Agee JK (1993) Fire ecology of pacific northwest forests. Island Press, Washington, DC
- Andren H (1994) Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos* 71:355–366
- Buchalski MR, Fontaine JB, Heady PA, Hayes JP, Frick WF (2013) Bat response to differing fire severity in mixed-conifer forest California, USA. *PLoS ONE* 8:7
- Cansler CA, McKenzie D (2014) Climate, fire size, and biophysical setting control fire severity and spatial pattern in the northern cascade range, USA. *Ecol Appl* 24:1037–1056
- Collins BM, Miller JD, Thode AE, Kelly M, van Wagendonk JW, Stephens SL (2009) Interactions among wildland fires in a long-established sierra nevada natural fire area. *Ecosystems* 12:114–128
- Collins BM, Stevens JT, Miller JD, Stephens SL, Brown PM, North MP (2017) Alternative characterization of forest fire regimes: incorporating spatial patterns. *Landscape Ecol* 32:1543–1552
- Coppoletta M, Merriam KE, Collins BM (2016) Post-fire vegetation and fuel development influences fire severity patterns in reburns. *Ecol Appl* 26:686–699
- Dennison PE, Brewer SC, Arnold JD, Moritz MA (2014) Large wildfire trends in the western united states, 1984–2011. *Geophys Res Lett* 41:2928–2933
- Dillon GK, Holden ZA, Morgan P, Crimmins MA, Heyerdahl EK, Luce CH (2011) Both topography and climate affected forest and woodland burn severity in two regions of the western US, 1984 to 2006. *Ecosphere* 2:33
- Donato DC, Fontaine JB, Campbell JL, Robinson WD, Kauffman JB, Law BE (2009) Conifer regeneration in stand-replacement portions of a large mixed-severity wildfire in the Klamath-Siskiyou mountains. *Can J For Res-Rev Can Rech For* 39:823–838
- Eyes SA, Roberts SL, Johnson MD (2017) California spotted owl (*Strix occidentalis occidentalis*) habitat use patterns in a burned landscape. *Condor*. <https://doi.org/10.1650/condor-16-184.1>
- Fites-Kaufman JP, Rundel PW, Stephenson N, Weixelman DA (2007) Montane and subalpine vegetation of the Sierra Nevada and Cascade ranges. In: Barbour MG, Keeler-Wolf T, Schoenherr AA (eds) *Terrestrial vegetation of California*, 3rd edn. University of California Press, Berkeley
- Fontaine JB, Kennedy PL (2012) Meta-analysis of avian and small-mammal response to fire severity and fire surrogate treatments in U.S. fire-prone forests. *Ecol Appl* 22:1547–1561
- Gardner RH, Milne BT, Turner MG, O'Neill RV (1987) Neutral models for the analysis of broad-scale landscape pattern. *Landscape Ecol* 1:19–28
- Gorelick N, Hancher M, Dixon M, Ilyushchenko S, Thau D, Moore R (2017) Google earth engine: planetary-scale geospatial analysis for everyone. *Remote Sens Environ* 202:18–27
- Gustafson EJ, Parker GR (1992) Relationships between land-cover proportion and indices of landscape spatial pattern. *Landscape Ecol* 7:101–110
- Harvey BJ, Donato DC, Turner MG (2016) Drivers and trends in landscape patterns of stand-replacing fire in forests of the US Northern Rocky Mountains (1984–2010). *Landscape Ecol* 31:2367–2383
- Holden ZA, Morgan P, Evans JS (2009) A predictive model of burn severity based on 20-year satellite-inferred burn severity data in a large southwestern us wilderness area. *For Ecol Manag* 258:2399–2406

- Holling CS (1973) Resilience and stability of ecological systems. *Annu Rev Ecol Syst* 4:1–23
- Jones GM, Gutierrez RJ, Tempel DJ, Whitmore SA, Berigan WJ, Peery MZ (2016) Megafires: an emerging threat to old-forest species. *Front Ecol Environ* 14:300–306
- Kemp KB, Higuera PE, Morgan P (2016) Fire legacies impact conifer regeneration across environmental gradients in the US Northern Rockies. *Landscape Ecol* 31:619–636
- Lydersen JM, Collins BM, Miller JD, Fry DL, Stephens SL (2016) Relating fire-caused change in forest structure to remotely sensed estimates of fire severity. *Fire Ecol* 12:99–116
- Mallek C, Safford H, Viers J, Miller J (2013) Modern departures in fire severity and area vary by forest type, Sierra Nevada and Southern Cascades, California, USA. *Ecosphere*. <https://doi.org/10.1890/es13-00217>
- Martin RE, Sapsis DB (1992) Fires as agents of biodiversity: pyrodiversity promotes biodiversity. In: *Proceedings of the conference on biodiversity of northwest California ecosystems*. Cooperative Extension, University of California, Berkeley
- McElreath R (2016) *Statistical rethinking: a Bayesian course with examples in R and Stan*. CRC Press, Boca Raton
- McGarigal K, Cushman SA, Ene E (2012) *Fragstats v4: spatial pattern analysis program for categorical and continuous maps*. University of Massachusetts, Amherst
- Meyer MD (2015) Forest fire severity patterns of resource objective wildfires in the southern Sierra Nevada. *J For* 113:49–56
- Miller JD, Collins BM, Lutz JA, Stephens SL, van Wagtenonk JW, Yasuda DA (2012a) Differences in wildfires among ecoregions and land management agencies in the Sierra Nevada region, California, USA. *Ecosphere* 3:20
- Miller JD, Knapp EE, Key CH, Skinner CN, Isbell CJ, Creasy RM, Sherlock JW (2009a) Calibration and validation of the relative differenced normalized burn ratio (RdNBR) to three measures of fire severity in the Sierra Nevada and Klamath Mountains, California, USA. *Remote Sens Environ* 113:645–656
- Miller JD, Quayle B (2015) Calibration and validation of immediate post-fire satellite-derived data to three severity metrics. *Fire Ecol* 11:12–30
- Miller JD, Safford H (2012) Trends in wildfire severity: 1984 to 2010 in the Sierra Nevada, Modoc Plateau, and Southern Cascades, California, USA. *Fire Ecol* 8:41–57
- Miller JD, Safford HD (2008) *Sierra Nevada fire severity monitoring 1984–2004*. USDA-Forest Service, Pacific Southwest Region, Vallejo
- Miller JD, Safford HD, Crimmins M, Thode AE (2009b) Quantitative evidence for increasing forest fire severity in the Sierra Nevada and Southern Cascade mountains, California and Nevada, USA. *Ecosystems* 12:16–32
- Miller JD, Skinner CN, Safford HD, Knapp EE, Ramirez CM (2012b) Trends and causes of severity, size, and number of fires in northwestern California, USA. *Ecol Appl* 22:184–203
- Miller JD, Thode AE (2007) Quantifying burn severity in a heterogeneous landscape with a relative version of the delta normalized burn ratio (dNBR). *Remote Sens Environ* 109:66–80
- North M, Stine P, O'Hara K, Zielinski W, Stephens S (2009) *An ecosystem management strategy for sierran mixed-conifer forests*. U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station Albany
- North MP, Stephens SL, Collins BM, Agee JK, Aplet G, Franklin JF, Fulé PZ (2015) Reform forest fire management. *Science* 349:1280–1281
- Peterson DL, Millar CI, Joyce LA, Furniss MJ, Halofsky JE, Neilson RP, Morelli TL (2011) *Responding to climate change in national forests: a guidebook for developing adaptation options*. Pacific Northwest Research Station Portland
- Pickett STA, White PS (1985) *The ecology of natural disturbance and patch dynamics*. Academic Press, Orlando
- R Development Core Team (2011) *R: a language and environment for statistical computing* vol 2.14. Vienna, Austria
- Restaino CR, Safford H (2018) Fire and climate change. Chapter 26. In: van Wagtenonk JW, Sugihara NG, Stephens SL, Thode AE, Shaffer KE, Fites-Kaufman J (eds) *Fire in California's ecosystems*, 2nd edn. University of California Press, Berkeley
- Rivera-Huerta H, Safford HD, Miller JD (2016) Patterns and trends in burned area and fire severity from 1984 to 2010 in the Sierra de San Pedro Martir, Baja California, Mexico. *Fire Ecol*. <https://doi.org/10.4996/fireecology.1201052>
- Roberts SL, Van Wagtenonk JW, Miles AK, Kelt DA, Lutz JA (2008) Modeling the effects of fire severity and spatial complexity on small mammals in yosemite national park, California. *Fire Ecol* 4:83–104
- Safford H, Stevens JT (2017) Natural range of variation (NRV) for yellow pine and mixed conifer forests in the Sierra Nevada, Southern Cascades, and Modoc and Inyo National Forests, California. Pacific Southwest Research Station, Albany
- Safford HD, Hayward GD, Heller NE, Wiens JA (2012) Historical ecology, climate change, and resource management: can the past still inform the future? In: Wiens JA, Hayward GD, Safford HD, Giffen CM (eds) *Historical environmental variation in conservation and natural resource management*. Wiley, Hoboken
- Safford HD, Van de Water KM (2011) *California fire return interval departure (FRID) map metadata: description of purpose, data sources, database fields, and their calculations*. USDA Forest Service, Pacific Southwest Region, Vallejo
- Safford HD, Van de Water KM (2014) Using fire return interval departure (FRID) analysis to map spatial and temporal changes in fire frequency on national forest lands in California. USDA Forest Service, Pacific Southwest Research Station, Albany
- Shive K, Preisler H, Welch KR, Safford HD, Butz RJ, O'Hara K, Stephens SL (in press) Scaling stand-scale measurements to landscape-scale predictions of forest regeneration after disturbance: the importance of spatial pattern. *Ecol Appl*
- Stan Development Team (2016) *Rstan: the R interface to Stan*, 2.10.1 edn.
- Steel ZL, Safford HD, Viers JH (2015) The fire frequency-severity relationship and the legacy of fire suppression in California forests. *Ecosphere*. <https://doi.org/10.1890/es14-00224.1>

- Steel ZL, Steel AE, Williams JN, Viers JH, Marquet PA, Barbosa O (2017) Patterns of bird diversity and habitat use in mixed vineyard-matorral landscapes of central Chile. *Ecol Ind* 73:345–357
- Stephens SL, Collins BM, Biber E, Fulé PZ (2016a) US Federal fire and forest policy: emphasizing resilience in dry forests. *Ecosphere*. <https://doi.org/10.1002/ecs2.1584>
- Stephens SL, Miller JD, Collins BM, North MP, Keane JJ, Roberts SL (2016b) Wildfire impacts on California spotted owl nesting habitat in the Sierra Nevada. *Ecosphere*. <https://doi.org/10.1002/ecs2.1478>
- Stevens JT, Collins BM, Miller JD, North MP, Stephens SL (2017) Changing spatial patterns of stand-replacing fire in California conifer forests. *For Ecol Manag* 406:28–36
- Sugihara NG, Van Wagtenonk JW, Shaffer KE, Fites-Kaufman J, Thode AE (2006) *Fire in California's ecosystems*. University of California Press, Berkeley
- Tepley AJ, Thompson JR, Epstein HE, Anderson-Teixeira KJ (2017) Vulnerability to forest loss through altered postfire recovery dynamics in a warming climate in the Klamath Mountains. *Global Change Biol*. <https://doi.org/10.1111/gcb.13704>
- Tews J, Brose U, Grimm V, Tielborger K, Wichmann MC, Schwager M, Jeltsch F (2004) Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *J Biogeogr* 31:79–92
- Tingley MW, Ruiz-Gutiérrez V, Wilkerson RL, Howell CA, Siegel RB (2016) Pyrodiversity promotes avian diversity over the decade following forest fire. *Proc R Soc B*. <https://doi.org/10.1098/rspb.2016.1703>
- Turner MG (2010) Disturbance and landscape dynamics in a changing world. *Ecology* 91:2833–2849
- Turner MG, Baker WL, Peterson CJ, Peet RK (1998) Factors influencing succession: lessons from large, infrequent natural disturbances. *Ecosystems* 1:511–523
- Turner MG, Gardner RH (2015) *Landscape ecology in theory and practice: pattern and process*, 2nd edn. Springer, New York
- USDA (2004) *Sierra Nevada forest plan amendment*. Forest Service Pacific Southwest Region, Vallejo
- Van de Water KM, Safford HD (2011) A summary of fire frequency estimates for California vegetation before Euro-American settlement. *Fire Ecol* 7:26–58
- van Mantgem EF, Keeley JD, Witter M (2015) Faunal responses to fire in chaparral and sage scrub in California. *Fire Ecol*, USA, p 11
- van Wagtenonk JW (2007) The history and evolution of wildland fire use. *Fire Ecol* 3:3–17
- van Wagtenonk JW, Lutz JA (2007) Fire regime attributes of wildland fires in Yosemite National Park, USA. *Fire Ecol* 3:34–52
- Villard MA (1998) On forest-interior species, edge avoidance, area sensitivity, and dogmas in avian conservation. *Auk* 115:801–805
- Welch KR, Safford HD, Young TP (2016) Predicting conifer establishment post wildfire in mixed conifer forests of the North American Mediterranean-climate zone. *Ecosphere*. <https://doi.org/10.1002/ecs2.1609>
- Westerling AL (2016) Increasing western US forest wildfire activity: sensitivity to changes in the timing of spring. *Philos Trans R Soc B: Biol Sci* 371(1696):20150178
- White AM, Manley PN, Tarbill GL, Richardson TW, Russell RE, Safford HD, Dobrowski SZ (2016) Avian community responses to post-fire forest structure: implications for fire management in mixed conifer forests. *Anim Conserv* 19:256–264
- Yahner RH, Scott DP (1988) Effects of forest fragmentation on depredation of artificial nests. *J Wildl Manag* 52:158–161