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Modern departures in fire severity and area vary by forest type, Sierra Nevada and southern Cascades, California, USA

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Abstract. Acute changes in ecological disturbance regimes can have major consequences for ecosystems and biota, including humans, living within them. Human suppression of fire in the western United States over the last century has caused notable changes to many ecosystems, especially in lower elevation, semiarid forest types dominated historically by fire tolerant taxa like *Pinus* and *Quercus*. Recent increases in fire activity in western US forests have highlighted the need for restoration of ecological structure and function, but management targets for restoration in different forest types remain uncertain. Working in the forests of eastern California, we evaluated the direction and magnitude of change in burned area and fire severity between the period prior to Euro-American settlement (~1500–1850) and the "modern" period (1984–2009). We compared total annual area burned; proportional area burned at low-moderate severity and high severity; and annual area burned at low-moderate severity and high severity between the two time periods in seven forest types. We also examined modern trends in fire area and severity. We found that modern rates of burning are far below presettlement levels for all forest types. However, there were major differences between low to middle elevation forests and high elevation forests regarding the components of this departure. Low and middle elevation forests are currently burning at much higher severities than during the presettlement period, and the departure in fire area is overwhelmingly expressed in the low to moderate severity categories; in these forest types, mean annual area of high severity fire is not notably different between the modern and presettlement periods. In higher elevation forests on the other hand, the modern departure in fire area is expressed equally across fire severity categories. Our results underline the critical need for forest and fire restoration in the study area, especially in low and middle elevation forests adapted to frequent, low severity fire. Expanded management of naturally ignited fires for resource benefit is clearly needed, but in many parts of our study area, strategic reduction of forest fuels will likely be necessary before large-scale restoration of fire becomes ecologically, politically, and financially feasible.

Key words: California, USA; ecological restoration; fire area; fire severity; Sierra Nevada.

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Introduction

Fire is an ancient and geographically widespread ecological disturbance process that influences the composition, structure and function of ecosystems at local to global scales (Harris 1958, Glasspool et al. 2004, Chuvieco et al. 2008, Krawchuk et al. 2009). These influences are best understood using the concept of fire regimes (Heinselman 1981), which describe the spatial, temporal, and magnitudinal aspects of fire that characterize different ecosystems. At local and regional scales, anthropogenic changes in fire regimes, sometimes amplified by positive fire-vegetation feedbacks, can present significant challenges to the conservation of biota, the management of natural resources, and the provision of ecosystem goods and services (D'Antonio and Vitousek 1992, Cochrane et al. 1999, Noss et al. 2006). This is an area of increasing concern because ecosystems that are already under stress from altered fire regimes are probably more vulnerable to climate-driven ecological change (Stephens et al. 2010). At the global scale, widespread changes in fire regimes driven by changes in climate and/or direct human intervention, particularly in the world's forested ecosystems, have the potential to significantly affect the terrestrial carbon sink, atmospheric carbon dioxide concentration, and global temperature (Bowman et al. 2009, Pan et al. 2011). Such changes also threaten biodiversity, the scale and speed of various biological, hydrological, pedological, and geological processes, and in some cases, human safety and security (Dale et al. 2001, Folke et al. 2004, Pausas and Keeley 2009).

Like most other regions influenced by a Mediterranean-type climate, fire has been a keystone ecological process in California ecosystems for millennia (Sugihara et al. 2006, Keeley et al. 2012). However, most California fire regimes changed abruptly with the arrival of Euro-American settlers in the middle to late 19th century. Initially, changes in forested ecosystems arose due to the effects of disease and displacement on Native American populations and their burning traditions, as well as intensive resource use, including logging and grazing, by Euro-Americans (Beesley 1996, Stephens and Sugihara 2006). Later, and more profoundly, these changes were driven by a national policy of wildland fire suppression, adopted by the U.S. government in the early 20th century and implemented with particular effectiveness following the Second World War.

The ecological consequences of the fire suppression policy are understood to differ depending on the ecosystem type and its corresponding natural fire regime (Schoennagel et al. 2004, Noss et al. 2006). In forest types characterized by relatively infrequent fires with a notable high severity component, fire exclusion is thought to have had relatively little effect on ecosystem composition, structure, and function because the period of effective fire exclusion has been comparable to or shorter than average presettlement fire-free intervals (Safford and van de Water 2013). Moreover, California forests characterized by these types of fire regimes often occur at relatively high elevations or in otherwise remote locations such that fire exclusion began later and/or has been implemented less aggressively than in forests closer to human population centers (North et al. 2009, Safford and Van de Water 2013). In contrast, in forests historically characterized by frequent, low- to moderate-severity fires, fire exclusion has resulted in significant shifts in ecosystem composition, structure, and function including, among other things, increases in tree density and forest fuels, reduction in structural heterogeneity, a shift in dominance from shade-intolerant (e.g., *Pinus* spp.) to shade-tolerant (e.g., *Abies* spp.) tree species, increased drought stress during the annual dry period, decreases in understory plant diversity, and lowered rates of nutrient cycling (Parsons and DeBenedetti 1979, Agee 1993, Barbour et al. 1993, 2007, Skinner and Chang 1996, Gruell 2001, Sugihara et al. 2006).

Critically, increases in vertical and horizontal fuel continuity and fuel load resulting from fire exclusion, together with climate change, have been implicated in recently observed increases in annual area burned and fire severity in certain forest types in the Sierra Nevada and adjacent areas (Westerling et al. 2006, Miller et al. 2009*b*, Miller and Safford 2012). Despite these documented increases over the last several decades, the western United States as a whole remains in a large "fire deficit" (Marlon et al. 2012). Marlon et al. (2012) used a reconstruction of historic fire activity from sedimentary charcoal records to show that current burning rates are anomalously low under the reigning climate. This current divergence of fire and climate is unprecedented in at least the last 1500 years, and is due to fire suppression policies (Marlon et al. 2012). Such policies are decreasingly successful however in dampening the growing inertia for fire activity being driven by increasing forest fuels and warmer and drier conditions during western US fire seasons (Westerling et al. 2006, Miller et al. 2009*b*, Miller and Safford 2012). The conservation implications of this fire-climate-vegetation feedback for California forests are considerable, particularly for already threatened species that are closely associated with late-seral forest habitat such as the California spotted owl (*Strix occidentalis occidentalis*), Pacific fisher (*Martes pennanti*), and northern goshawk (*Accipiter gentilis*) (Lawler et al. 2012, North 2012).

While there is general agreement about the need to restore fire as an ecological process in the Sierra Nevada and adjacent forested areas (Barbour et al. 1993, Skinner and Chang 1996, Sugihara et al. 2006, North et al. 2012), uncertainties remain about the amount of fire required for restoration, the extent to which different degrees of fire severity should be emphasized in these efforts, and how this may vary across the ecoregion's distinct forest types. Much has been recently made of the ecological value of high severity fire, as dead and dying trees created by intense fires are important habitat for a variety of biota (Hutto 2008, Swanson et al. 2011). However the extent of high severity burning varies dramatically among forest types and climate regions (Agee 1993, Schoennagel et al. 2004, Noss et al. 2006), and—in the absence of local studies—extrapolations of ecologically appropriate fire patterns and biotic responses from one forest type or geographic region to another are highly uncertain and problematic. An understanding of the differences between contemporary fire patterns and those of the past is important for clarifying these uncertainties (Swetnam et al. 1999, Safford et al. 2012*b*), as is an understanding of recent trends, particularly with regard to annual area burned at different levels of fire severity. Previous modern vs. presettlement comparisons and trend assessments have focused on fire frequencies, annual area burned and proportional area burned at different levels of fire severity (McKelvey et al. 1996, Skinner and Chang 1996, Miller and Safford 2008, 2012, Miller et al. 2009*b*, Safford and Van de Water 2013). However, we know of no modern-vs.-presettlement comparisons or trend assessments that focus explicitly on annual area burned while discriminating between forest types and different levels of fire severity.

The goal of this study was to aid regional resource management planning for the study area's ~6 million ha of forests by clarifying priorities for the restoration of fire as an ecological process. We did this primarily by examining contemporary patterns of burning in relation to fire regimes that are believed to have maintained biologically diverse and resilient forested ecosystems prior to widespread Euro-American intervention in the middle to late 1800s. Specifically, we ask the following questions: (1) What are the contemporary annual rates of burning at high severity and low-to-moderate severity in the forests of the Sierra Nevada and adjacent mountains? (2) To what extent do these rates differ from the rates prior to Euro-American settlement? (3) How do these modern-vs.-presettlement differences vary among forest types? (4) To what extent have recent trends exacerbated or ameliorated these differences? We also provide results of parallel analyses for annual area burned and proportional area burned at different levels of fire severity because these are the variables that completely explain variation in the annual area of high severity fire (AAHS).

Methods

Study region

Our goal was to evaluate the net direction and magnitude of change in two components of the fire regime, burned area and fire severity, between the period prior to Euro-American settlement (pre-1850, "presettlement") and the "modern" period, defined here as the 26-year period between 1984 and 2009, in mountain forests of eastern and northeastern California (Fig. 1). In order to be consistent with previous ecological assessments and management planning efforts for the area, we focused our analysis on the study area used for the Sierra Nevada Ecosystem Project (SNEP 1996), which subse-

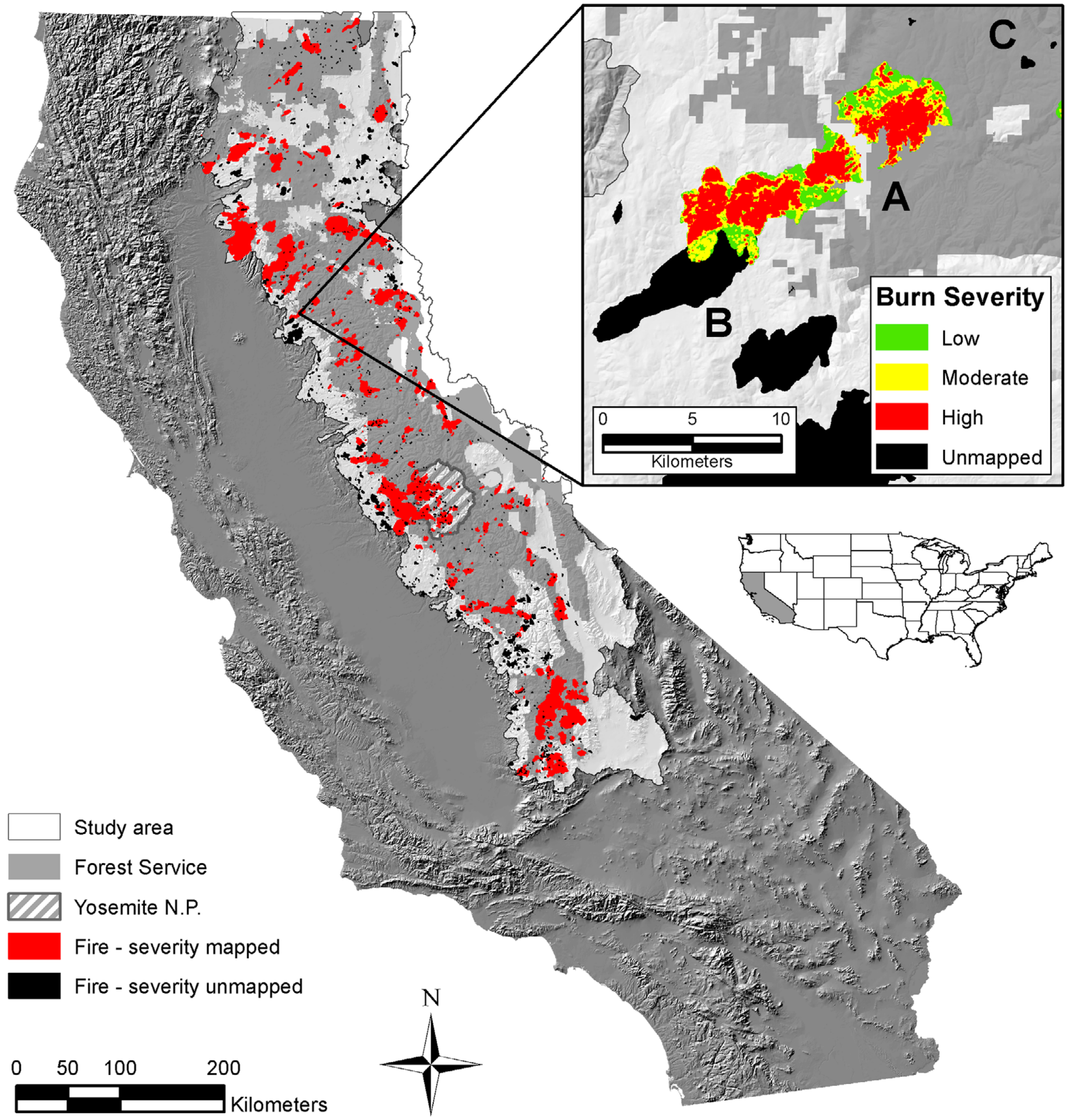

Fig. 1. Map of study area. Red polygons indicate fires that burned within the study area during the modern period (1984–2009), and were mapped for burn severity (see inset A for detail). Black polygons indicate fires within the study area that burned during the same period and were not mapped for burn severity because they (B) did not occur on lands managed by the US Forest Service or Yosemite National Park, or (C) were less than 40 ha in size.

quently formed the basis for the Sierra Nevada Forest Plan Amendment (SNFPA; USDA 2004), which in turn guides forest management on Forest Service lands throughout the study area. This area also forms the boundary for the Forest Service's bioregional assessment and science synthesis programs that are supporting the new round of Forest planning. The defining geographic feature of the area, encompassing approximately 120,000 km^2, is a north-south trending chain of mountains consisting of the Sierra Nevada in the southern and central portions of the study area, together with the southern Cascade Range, Modoc Plateau, and

Table 1. Dominant tree species and mean elevation (m) for the seven forest types used in the study, total extent (%) within the study area, total mapped area (ha) burned within the study period (1984–2009), and the total burned area (ha) mapped for fire severity from the same period.

Forest type	Dominant species†	Mean elevation	Extent‡	Burned area	Area mapped for severity§
Oak woodland (OW)	QUDO, QUWI, PISA	756	941,485 (8)	210,948	164,452 (78)
Dry mixed conifer (DMC)	PIPO, PILA, CADE, ABCO, QUKE	1,121	737,759 (6)	109,769	103,225 (94)
Moist mixed conifer (MMC)	ABCO, PSME, PILA, CADE, SEGI	1,590	1,367,706 (11)	147,607	137,746 (93)
Yellow pine (YP)	PIJE, PIPO, QUKE	1,714¶	1,540,923 (13)	231,613	218,696 (94)
Red fir (RF)	ABMA	2,335	1,037,403 (9)	88,422	78,494 (89)
Lodgepole pine (LP)	PICO	2,786	110,618 (1)	2,470	1,670 (68)
Subalpine (SA)	PIAL, PIMO, PIFL, PICO, TSME	3,163	346,709 (3)	1,686	1,180 (70)

† Dominant species abbreviations: ABCO: *Abies concolor*; ABMA: *A. magnifica*; CADE: *Calocedrus decurrens*; PIAL: *Pinus albicaulis*; PICO: *P. contorta* ssp. *murrayana*; PIFL: *P. flexilis*; PIJE: *P. jeffreyi*; PILA: *P. lambertiana*; PIMO: *P. monticola*; PIPO: *P. ponderosa*; PISA: *P. sabiniana*; PSME: *Pseudotsuga menziesii*; QUDO: *Quercus douglasii*; QUKE: *Q. kelloggii*; QUWI: *Q. wislizenii*; SEGI: *Sequoiadendron giganteum*; TSME: *Tsuga mertensiana*.

‡ Values in parentheses indicate forest type extent as a percentage of the total study area extent.

§ Values in parentheses indicate the total burned area mapped for fire severity as a percentage of the total area burned within that forest type.

¶ Elevational distribution is bimodal, with PIPO and QUKE found mostly below mixed conifer, and PIJE at higher elevations on the east slope.

Warner Mountains in the north; the White Mountains form part of the southeastern boundary of the area (Fig. 1). Elevation ranges from approximately 300 m above sea level along the western boundary to over 4000 m along the Sierra Nevada crest. The climate is Mediterranean-type with cool, wet winters and warm, dry summers. Vegetation in the region is dominated by forest and woodland. Oak (*Quercus* spp.) woodlands dominate much of the lower elevations along the western boundary, transitioning to yellow pine (*Pinus ponderosa* and/or *P. jeffreyi*) and mixed conifer forests at middle elevations (Table 1). Red fir (*Abies magnifica*) forests dominate above 1800–2000 m elevation, depending on latitude. Lodgepole pine (*Pinus contorta*) and different varieties of subalpine forest are found at the highest elevations. Pinyon pine (mostly *P. monophylla*) and juniper (*Juniperus* spp.) woodlands occur at lower elevations to the north and east (Barbour et al. 2007).

Modern-vs.-presettlement means comparisons

For all forestlands combined, and for a suite of the most common forest types, we carried out comparisons of the following wildfire statistics between the presettlement and modern periods: (1) annual area burned (AAB_{pre} vs. AAB_{mod}); (2) proportional area burned at low-to-moderate severity ($PLMS_{pre}$ vs. $PLMS_{mod}$) and high severity (PHS_{pre} vs. PHS_{mod}); and (3) annual area burned at low-to-moderate severity ($AALMS_{pre}$ vs. $AALMS_{mod}$) and high severity ($AAHS_{pre}$ vs. $AAHS_{mod}$). We began by identifying and mapping the forest types to be used in the study. For our forest classification, we used the "pre-Euro-American settlement fire regime groups" (PFRs) developed by Van de Water and Safford (2011), which organized California ecosystems into 28 broad categories on the basis of presettlement fire regime and dominant plant species. Of these, we identified 12 PFRs that were dominated by trees, and were known to occur within the study area. We then mapped the distributions of these PFR forest types in a geographic information system (GIS) by grouping and reclassifying forest types represented in the LANDFIRE Biophysical Settings layer (BpS; www.landfire.gov, accessed 14 July 2011) into PFR forest types based on similarities in fire regime and species dominance (see Appendix: Table A1). In contrast to maps depicting current vegetation distributions, the BpS layer is a modeled output of potential vegetation representing the distributions of vegetation types as they are hypothesized to have existed prior to Euro-American settlement, based on topography, climate, soils, and the presettlement disturbance regime (Rollins 2009). We used the reclassified BpS layer, as opposed to maps of existing vegetation, to stratify all of our analyses because fire regimes both influence and are influenced by vegetation, and maps representing existing vegetation may thus confound the ability to detect shifts in fire regime over time. Although

Table 2. Major forest types in the study area, estimates of fire rotation prior to Euro-American settlement, and literature used to generate estimates.

Forest type†	Fire rotation (years) Mean	Range	Literature
OW	18	12–25	McClaran and Bartolome 1989, Mensing 1988
DMC	23	11–34	Beaty and Taylor 2001, 2007, Bekker and Taylor 2001, Everett 2008, Kilgore and Taylor 1979, Scholl and Taylor 2010, Stephens 2001, Taylor and Scholl 2012
MMC	31	15–70	Agee 1991, 1993; Beaty and Taylor 2001, Bekker and Taylor 2001, Collins and Stephens 2007, Kilgore and Taylor 1979, Stephens and Collins 2004, Taylor and Skinner 1998, Swetnam et al. 2009, Taylor 2000, Taylor and Skinner 2003, Taylor and Solem 2001
YP	22	11–34	Agee 1993, Taylor 2000, Beaty and Taylor 2001, Bekker and Taylor 2001, North et al. 2009,‡ Stephens et al. 2003, Taylor 2004, 2010
RF	61	25–76	Bekker and Taylor 2001, Pitcher 1987, Scholl 1999, Skinner 2003, Stephens 2001, Taylor 2000, Taylor and Solem 2001
LP	63	46–80	Agee 1993, Bekker and Taylor 2001, Taylor and Solem 2001
SA	394	75–721	Bekker and Taylor 2001, Dickman and Cook 1989, Rourke 1988, Skinner 2003, van Wagtendonk 1995

† See Table 1 for key to forest type abbreviations.
‡ Study's authors provided fire dates.

there are some local discrepancies between the BpS product and Forest Service existing vegetation mapping, the BpS output is the only map of potential vegetation in California that is based on a transparent and peer-reviewed modeling process, incorporates the effects of fire, includes lands of all management jurisdictions, and extends across our entire study region. The final set of forest types for our analysis consisted of PFRs that individually occupied sufficient extents to allow robust statistical assessment of fire patterns for the modern period, and collectively represented the great majority of forest area in the study area. Of the 12 PFR forest types in our study region, we retained eight that each represented at least 1% of the total mapped forest area, but then removed the pinyon-juniper PFR (5% of the study area) due to insufficient presettlement fire regime information. The seven forest types included in our final analysis are listed in Table 1, in order of their mean elevation. In the text, we refer to the first four (OW, YP, DMC, MMC) as "low and middle elevation" forest types, and the last three (LP, RF, SA) as "high elevation" forest types.

To estimate AAB_{pre}, we divided the estimated areal extent of each forest type in our reclassified BpS map (Table 1) by the presettlement fire rotation (FR_{pre}) of that forest type (Table 2), defined as the number of years required for fire to burn an area within a forest type equivalent to the forest type's total extent (Heinselman 1973). Information on FR_{pre} for each forest type was gathered and synthesized from published literature (Table 2; Appendix: Fig. A1). Fire history studies in the study region often do not produce direct estimates of FR_{pre} because fires in the forests of our study area generally fail to sufficiently alter overstory vegetation to permit simple visual delineation of past fire perimeters, and because interpolation of fire perimeters from fire scars on trees requires intensive sampling which can be relatively costly and time-consuming. In rare instances, fire-scar studies have inferred FR based on the assumption that the proportion of sample units recording fire in a given year reflects the proportion of the study area burned in that year, and we accepted these estimates (see Taylor and Skinner 2003, and Farris et al. 2010 for an example and validation, respectively). A more consistently reported metric is the mean fire interval. The relationship between mean fire interval and FR is complex (Baker and Ehle 2001, Reed 2006). However, we found that one variant, the grand mean fire interval (i.e., the mean of tree-level mean fire intervals; GMFI), reasonably identified with FR in studies that reported both metrics for identical locations and periods of time ($n = 12$, median error (%) $= -4.79$, root mean squared error (%) $= 30.02$; Appendix: Fig. A2). Therefore, with the exception of the SA forest type (explanation in Appendix), we accepted GMFI as a proxy for FR_{pre} in studies where no FR_{pre} was explicitly reported.

For five of the seven PFR forest types, estimates of PHS_{pre} were obtained by averaging estimates from two sources: the BpS modeling output documentation (http://www.landfire.gov/NationalProductDescriptions24.php), where "percent stand replacement fire" was the variable used, and Stephens et al. (2007), where "percent crown burned" was the variable used (for more details on the fire severity comparisons, see Appendix). Estimates from the BpS documentation followed the LANDFIRE vegetation classification, and were cross-walked to our forest types, as above (see Appendix: Table A1). Because each forest type in our analysis was mapped as a composite of multiple BpS forest types, we estimated PHS_{pre} for each forest type by calculating an area-weighted average PHS_{pre} across its BpS constituents. The estimates from Stephens et al. (2007) followed the forest classification of Barbour and Major (1977), and also had to be cross-walked to our forest type classification prior to averaging (Appendix: Table A2). For two of the seven PFR forest types, we used only the BpS estimate of PHS_{pre}. Specifically, in the case of oak woodland, Stephens et al. (2007) did not estimate PHS_{pre}. In the case of red fir, because of the dearth of quantitative information on fire severities in red fir forests at the time of their research, Stephens et al. were forced to make their PHS_{pre} estimate based primarily on field observations of contemporary fires and the Sugihara et al. (2006) simplification of the red fir fire regime as "bimodal" (S. Stephens, *personal communication*). Taken together, the following information sources suggest that Stephens et al.'s (2007) estimate of 50% PHS_{pre} is very high: (1) post-2007 publication of fire severity results from wildland fire use areas in Sierra Nevada red fir forests (8–13% high severity [HS]) (Miller and Safford 2008, Thode et al. 2011, Miller et al. 2012); (2) the release of the final LANDFIRE BpS models (20% HS in red fir); (3) estimates of fire severity for the Sierra Nevada made during the late 19th century (8% HS in mostly red fir forests) (Leiberg 1902); and (4) a review of red fir literature (e.g., Kilgore 1971, Kilgore and Briggs 1972, Agee 1993, Taylor 1993, Chappell and Agee 1996). In this case, rather than insert our own estimate in place of Stephens et al. (2007), we elected to use only the BpS value (20%, which itself may be an overestimate; see Discussion). $PLMS_{pre}$ estimates were calculated by subtracting PHS_{pre} from one.

We constrained all assessments of modern burning to the 26-year period from 1984 to 2009 because these were the only years for which high-quality fire severity data were continuously available for the largest geographic area within the study area. In addition, 1984 appeared to be a reasonable cutoff for the modern period given that several studies have found that the mid-1980s coincided with a marked transition toward greater fire activity in the region (Westerling et al. 2006, Miller et al. 2009*b*). AAB_{mod} in each forest type was calculated by overlaying yearly fire perimeter maps (www.frap.fire.ca.gov, accessed 14 July 2011) onto the reclassified BpS layer in a GIS. Perimeters of prescribed fires were not included. Similarly, for each forest type, $AALMS_{mod}$ and $AAHS_{mod}$ were obtained by overlaying yearly fire severity maps onto the reclassified BpS layer. $PLMS_{mod}$ and PHS_{mod} were calculated simply by dividing $AALMS_{mod}$ and $AAHS_{mod}$, respectively, by their sum. The fire severity maps were derived by comparing pre- and post-fire Landsat thematic mapper imagery to calculate the relative difference normalized burn ratio (RdNBR; Miller and Thode 2007, Miller et al. 2009*a*, *b*), and field-calibrated to reflect spatial variation in the Composite Burn Index (CBI; Key and Benson 2005). CBI breakpoints for separating low-to-moderate severity pixels from high severity pixels followed those of Miller and Thode (2007). Based on calibration to hundreds of field plots across the Sierra Nevada, the CBI boundary between moderate and high severity fire corresponds to approximately 95% first-year postfire mortality in forest canopy trees (Miller et al. 2009*a*); i.e., our definition of high severity fire is equivalent to "stand-replacing" fire. Modern fire severity data were available only for fires larger than 40 ha that occurred at least partially on land managed by either the U.S. Forest Service or Yosemite National Park. These fires accounted for 89% of the total area burned in our seven PFR forest types during the modern period. Among individual forest types, the proportion of total area burned that was mapped for fire severity ranged from 68% to 94% (Table 1). For those remaining fires which had not been mapped using RdNBR, we used $PLMS_{mod}$ and PHS_{mod} to estimate the unmapped extent of areas burned at either level of fire severity, and incorporated these extents into $AALMS_{mod}$ and $AAHS_{mod}$, respectively. We did not include fires occurring exclusively on private lands, as these fires and the lands they burn are not managed by the U.S. Forest Service or National Park Service, and because fire-killed and -damaged timber on such lands is usually harvested within weeks to months of the fire event. This greatly complicates fire severity measurements from the one-year postfire Landsat images, and also essentially removes such lands from the pool of available habitat for animals requiring high numbers of dead and dying trees.

Modern trends

To understand how recent trends may have either exacerbated or ameliorated modern-presettlement differences, we used time series regressions to examine trends in AAB_{mod}, PHS_{mod}, and $AAHS_{mod}$ over the modern period (1984–2009) for all forest types combined and for each forest type separately. We used a Bayesian, rather than frequentist, approach to inference because this allowed us to make direct probability statements about the direction and magnitude of trends, which is what land managers and policy makers are primarily interested in knowing. Candidate models consisted of three basic types, described here in order of accumulating complexity: (1) generalized linear models (GLMs) in which AAB_{mod} and $AAHS_{mod}$ were modeled using a gamma distribution with log link function, and PHS_{mod} was modeled using a binomial distribution with logit link function; (2) generalized linear mixed effects models (GLMMs) which explicitly accounted for interannual variation in excess of that expected under our GLMs through the inclusion of a random year effect; and (3) GLMMs that accounted for potential temporal autocorrelation by adding a time-ordered structure to the random year effect in the form of autoregressive (AR) and/or moving-average (MA) functions. Intercept-only models were not considered in our analyses because our stated goal was to evaluate the direction and magnitude of all trends, rather than simply address the question of whether or not trends 'exist'. In addition, no attempt was made to model (i.e., control for) spatial autocorrelation in the analyses of PHS_{mod} as our goal was to describe trends in the observations themselves, not trends in the processes underlying those observations.

Regression parameters were estimated using Markov Chain Monte Carlo (MCMC) procedures because this method simultaneously accommodated the non-Gaussian and autocorrelative features of our candidate models. Uninformative priors were used in all MCMC runs. All models were implemented in WinBUGS 1.4.3 (Lunn et al. 2000) with three chains and thinned after an initial burn-in to generate 10,000 independent samples, resulting in a total of 30,000 samples per parameter. Convergence was assessed through visual inspection of the chains and with Gelman and Rubin's diagnostic (Gelman and Rubin 1992). The resulting model fit was assessed using posterior predictive distributions (Gelman et al. 1996), Ljung-Box-modified Box-Pierce tests, and autocorrelation plots of the residuals. Final model selection was made by comparing the deviance information criterion (DIC), which penalizes for poor model fit and model complexity, and we selected the model with the lowest DIC (Spiegelhalter et al. 2002). To clarify the degree of confidence that the time series data represented upward trends over time, posterior probabilities were calculated for the hypothesis that slope coefficients in the best models were greater than zero. In addition, to facilitate interpretation of the estimated magnitude of change over time, regression parameter estimates (β) were transformed to represent annual percent change using the formula $\beta\ (\%) = (e^{\beta} - 1) \times 100$. Thus, the transformed regression parameters for the analyses of AAB_{mod} and $AAHS_{mod}$ indicate the annual percent change in area burned and area burned at high severity, respectively; and those for PHS_{mod} indicate the annual percent change in the odds that a site burned at high severity, given that it burned at all.

Results

Modern-versus-presettlement means comparisons

We obtained 43 estimates of pre-Euro-American FR from 28 published studies (Table 2). Median record length was 200 years (interquartile range = 144 to 277 years). Among the seven

Table 3. Summary of selected fire regime characteristics for modern and pre-Euro-American periods.

	AAB (ha)		PHS (%)		PLMS (%)		AAHS (ha)		AALMS (ha)	
Forest type†	mod	pre	mod	pre	mod	pre	mod	pre	mod	pre
All	30,481	215,759	29	7	71	93	8,869	16,113	21,612	199,646
OW	8,113	51,168	22	6	78	94	1,771	3,275	6,342	47,893
DMC	4,222	31,461	25	6	75	94	1,061	1,903	3,161	29,558
MMC	5,677	44,076	30	8	70	92	1,685	3,658	3,992	40,418
YP	8,908	69,411	42	5	58	95	3,727	3,349	5,182	66,062
RF	3,401	17,007	13	20	87	80	449	3,384	2,952	13,662
LP	95	1,758	33	18	67	82	31	323	64	1,435
SA	65	879	12	25	88	75	8	220	57	659

† See Table 1 for key to forest type abbreviations.

forest types considered in this study, we found the greatest number of empirical presettlement FR estimates for MMC (n = 12), DMC (n = 8), and YP (n = 8), and the fewest for OW (n = 2), LP (n = 3), and SA (n = 4).

Comparisons between AAB_{mod} and AAB_{pre} indicated that modern (1984–2009) rates of burning are far below their presettlement (pre-1850) levels throughout forests in the study area. For study area forests as a whole, AAB_{mod} was only 14% of AAB_{pre} (Table 3, Fig. 2A), representing a shift in overall fire rotation from 28 years prior to Euro-American settlement to 200 years during the modern period. This suggests that the burned-area deficit accumulated over a 33-year period would surpass the total extent of all the forest types used in our study combined. Among forest types, we found considerable variation in AAB_{mod} and AAB_{pre}. Nevertheless, AAB_{mod} values were less than 20% of their corresponding presettlement means in all cases (Fig. 2A).

For study area forests as a whole, fire effects during the modern period were qualitatively different from those during the presettlement period. For all forest types combined, the percentage of burned area that experienced high severity fire effects during the modern period (29%) was more than four times greater than the same estimate for the presettlement period (7%) (Table 3, Fig. 2B). Conversely, the percentage of burned area that experienced low to moderate severity fire effects during the modern period (71%) was approximately three-quarters of presettlement levels (93%). Low and middle elevation forest types (OW, DMC, MMC, and YP), which collectively represented the majority of the forestland in our study area (75%), exhibited values for PHS_{mod} that were consistently more than three times greater (for YP, eight times greater) than corresponding values for the presettlement period. For high elevation forest types (RF, LP, and SA), PHS_{mod} and PHS_{pre} were more alike.

Differences between the modern and presettlement periods in mean annual area burned within each of the two severity categories (i.e., $AAHS_{mod}$ vs. $AAHS_{pre}$, and $AALMS_{mod}$ vs. $AALMS_{pre}$) reflect the combined effects of changes in AAB and PHS/PLMS. For all forest types combined, although mean annual area burned during the modern period was less than the estimated presettlement mean for both categories of fire severity, the disparity was much greater for low to moderate severity than for high severity (Fig. 2C). $AAHS_{mod}$ was 55% of $AAHS_{pre}$, whereas $AALMS_{mod}$ was only 11% of $AALMS_{pre}$. This contrast between severity categories was largely a manifestation of the pattern observed across the four lower- to middle-elevation forest types which comprised more than three-quarters of the total study area. For each of these forest types (OW, DMC, MMC, and YP), $AAHS_{mod}$ was within the range of the corresponding presettlement estimates, and greater than 45% of the estimated presettlement mean. Pooling across all four low and middle elevation forest types, $AAHS_{mod}$ accounted for 68% of $AAHS_{pre}$. In contrast, $AALMS_{mod}$ for each of these low and middle elevation forest types was consistently outside and below the range of presettlement estimates, and less than 15% of the estimated presettlement mean. For the higher elevation forest types (RF, LP, SA), $AAHS_{mod}$ was 12% of $AAHS_{pre}$ (range 4–13%), while $AALMS_{mod}$ constituted 20% of $AALMS_{pre}$ (range 4–22%) (Table 3, Fig. 2B).

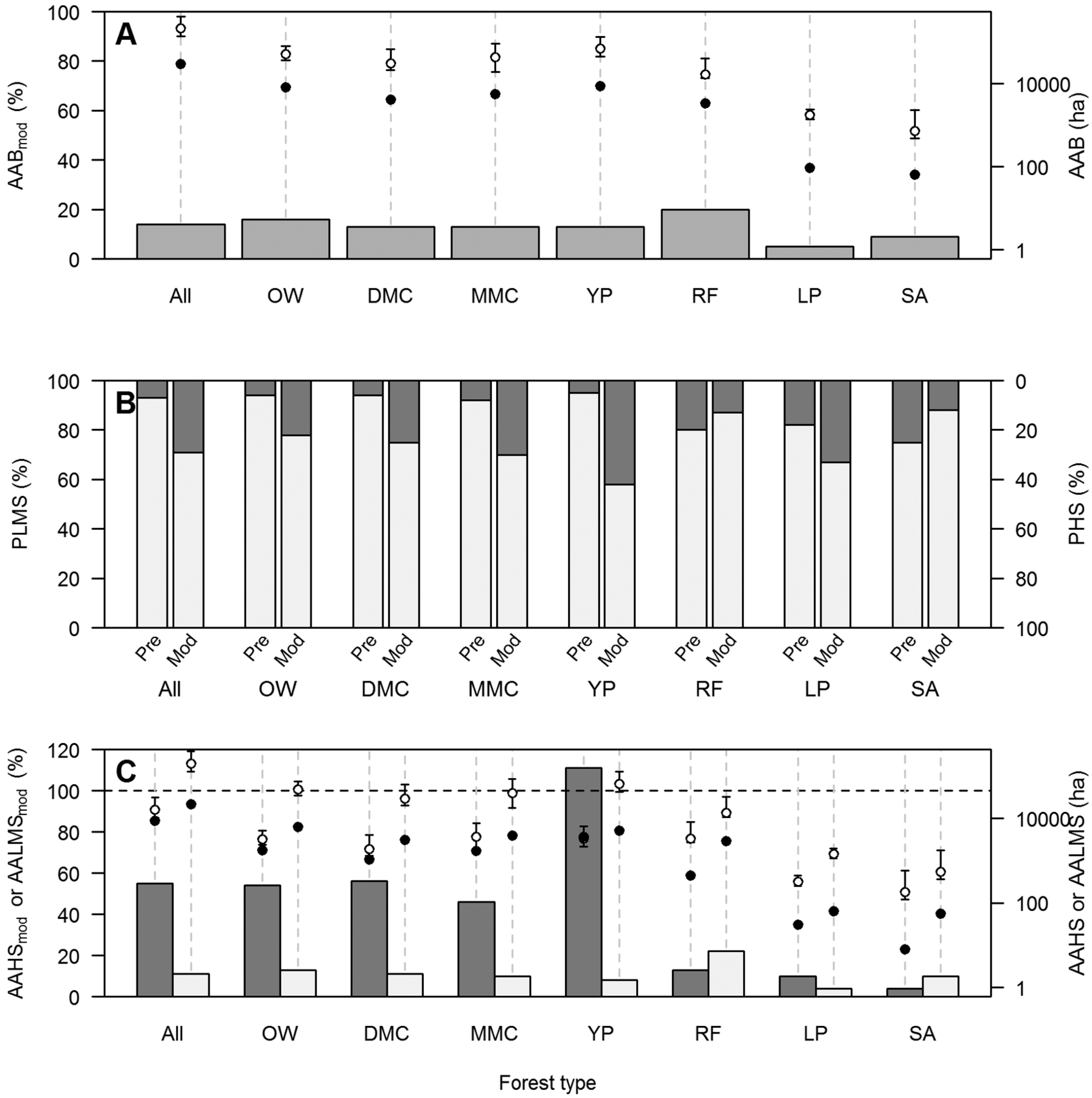

Fig. 2. Comparison of selected fire regime characteristics between time periods. Estimates shown for (A) annual area burned (all severity classes combined; AAB); (B) proportional area burned at low-to-moderate severity (PLMS) and high severity (PHS); and (C) annual area burned at low-to-moderate severity (AALMS) and high severity (AAHS) for the pre-Euro-American settlement (pre-1850) and modern (1984–2009) periods for all major forest types (combined and separately) in the study area. Bars in plots (A) and (C) show means for the modern period as percentages of presettlement means (left Y-axis). Open circles show presettlement means for AAB (A) and AAHS (C), and vertical lines show range, calculated using the range in prehistoric fire rotations (right Y-axis, log scale). Filled circles show modern means. In plots (B) and (C), dark gray represents high severity fire effects, and light gray represents low-to-moderate severity fire effects.

Modern trends

Time series regression analyses indicated that mean AAB most likely increased during the modern period for all forest types combined and for each forest type separately, with the lone exception of OW (Table 4, Fig. 3). Strong

Table 4. The direction and magnitude (median and 95% credible interval) of the rate of change (β[%]) in AAB_{mod}, PHS_{mod}, and $AAHS_{mod}$, for each forest type during the period 1984–2009, and the probability that the data indicate an upward trend (Pr[β > 0]).

	AAB_{mod}		PHS_{mod}		$AAHS_{mod}$	
Forest type	β (%)	Pr(β > 0)	β (%)	Pr(β > 0)	β (%)	Pr(β > 0)
All	4.65 (−3.00, 13.04)	0.89	0.48 (−3.60, 4.64)	0.59	5.06 (−4.78, 15.37)	0.86
OW	−2.86 (−12.13, 6.60)	0.27	1.36 (−7.00, 10.54)	0.62	−1.71 (−16.37, 14.72)	0.41
DMC	6.36 (−8.07, 20.77)	0.82	4.87 (1.81, 8.02)	>0.99	10.05 (−6.26, 27.01)	0.91
MMC	5.87 (−10.63, 23.08)	0.77	2.04 (−0.34, 4.17)	0.96	7.26 (−9.04, 24.55)	0.82
YP	7.04 (−2.50, 17.27)	0.93	−0.26 (−3.46, 2.92)	0.43	7.29 (−2.92, 17.86)	0.93
RF	8.17 (−2.18, 18.82)	0.94	2.55 (−2.23, 7.54)	0.86	10.72 (−0.19, 22.43)	0.97
LP	16.82 (1.87, 33.36)	0.99	1.73 (−8.64, 12.89)	0.63	17.99 (1.17, 36.12)	0.98
SA	21.58 (1.47, 43.71)	0.98	−0.32 (−13.96, 15.20)	0.48	19.08 (1.69, 36.85)	0.99

evidence of an increase in mean AAB (i.e., $\Pr(\beta > 0) \geq 0.95$) was found for the two highest-elevation forest types, LP and SA, where mean AAB most likely increased at rates of 16.82% $year^{-1}$ and 21.58% $year^{-1}$, respectively. In addition, modest evidence of increases in mean AAB (i.e., $\Pr(\beta > 0) \geq 0.90$) were found for the next-highest forest types, YP and RF, where mean AAB most likely increased at rates of 7.04% $year^{-1}$ and 8.17% $year^{-1}$, respectively. Evidence of an increase in mean AAB for all forestlands combined was only slightly weaker ($\Pr(\beta > 0) = 0.89$). The remaining lower-elevation forest types showed no clear evidence of trend in mean AAB during the modern period.

In contrast to the findings for AAB, strong evidence of positive trends in mean PHS were found exclusively among forest types at lower elevations, including DMC and MMC (Table 4, Fig. 3). During the modern period, the expected odds of an area burning with high severity effects, as opposed to low-to-moderate severity effects, most likely increased at a rate of 4.87% $year^{-1}$ in DMC, and 2.04% $year^{-1}$ in MMC. The remaining lower-elevation forest types showed no clear evidence of trend in mean PHS during the modern period.

Evidence of positive trends in mean AAHS followed a similar pattern to that found for AAB. Mean AAHS most likely increased during the modern period for all forest types combined and for each forest type separately, with the exception of OW (Table 4, Fig. 3). Evidence of an increase in mean AAHS was strong (i.e., $\Pr(\beta > 0) \geq 0.95$), or at least modest (i.e., $\Pr(\beta > 0) \geq 0.90$), for five of the seven forest types examined. Strong evidence of an increase was found for each of the three highest-elevation forest types, including RF, LP, and SA, where mean AAHS most likely increased at the rates of 10.72% $year^{-1}$, 17.99% $year^{-1}$, and 19.08% $year^{-1}$, respectively. Modest evidence of an increase in mean AAHS was found for DMC and YP, where mean AAHS most likely increased at the rates of 10.05% $year^{-1}$ and 7.29% $year^{-1}$, respectively.

Discussion

Our principal finding is that while modern (1984–2009) regional rates of burning at low-to-moderate severity (AALMS) were far below their presettlement levels for all forest types we examined, departures in regional rates of burning at high severity (AAHS) were evident only for high-elevation forests (red fir, lodgepole pine, subalpine). Modern regional rates of burning at high severity exhibited comparatively little or no departure from their presettlement levels in low- and middle-elevation forests. Previous studies have documented reductions in rates of burning in forests of the Sierra Nevada and adjacent mountains (McKelvey et al. 1996, Caprio and Graber 2000, Safford and Van de Water 2013), but, to our knowledge, our findings represent the first quantitative characterization of how changes in rates of burning vary by both forest type and fire severity.

Ecologically speaking, our most notable finding is that there is a large modern deficit in low and moderate severity fire in lower and middle elevation forest types in the study area. The historically dominant tree species in these forest types—mostly from the genera *Pinus* and *Quercus*—are adapted to fire regimes dominated by

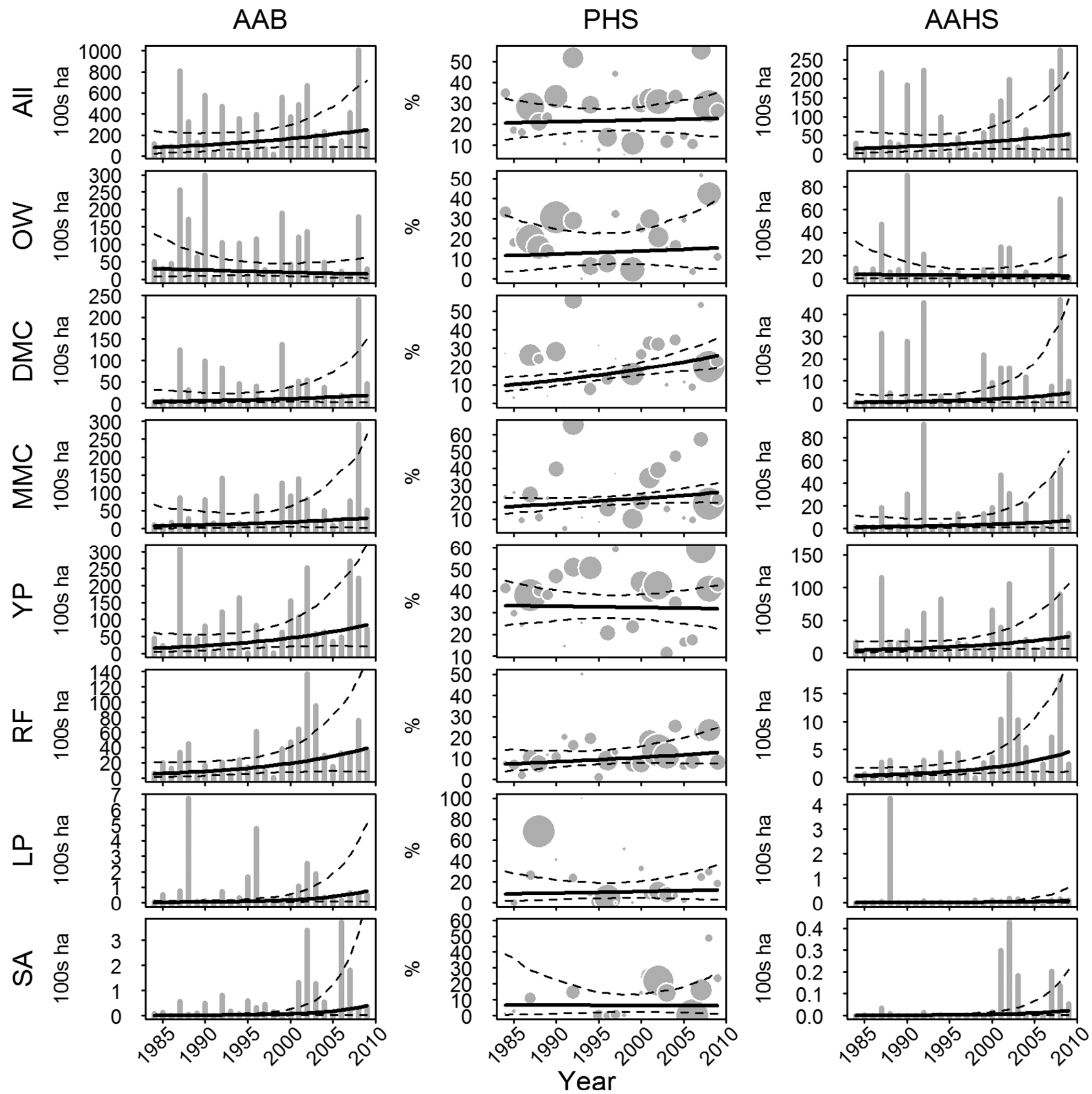

Fig. 3. Observed annual values and estimated trends in AAB_{mod}, PHS_{mod}, and $AAHS_{mod}$ for the period 1984–2009. Yearly values of AAB_{mod} and $AAHS_{mod}$ indicated by bar heights. Yearly values of PHS_{mod} indicated by circle location. Circle area is shown proportional to AAB_{mod} values because our regression models assumed that years with higher AAB_{mod} provided more information on PHS_{mod} than years with low AAB_{mod}. Predicted trends (solid lines) and 95% credible intervals (dashed lines) were derived from best-fit linear time series regressions.

low severity events burning in surface fuels, but where patches of high intensity fire occasionally kill clusters of trees (Agee 1993, Keeley and Stephenson 2000, Sugihara et al. 2006). These species tend to have thick, fire-resistant bark and highly flammable litter, which promotes rapid passage of intense surface fires that kill less fire tolerant competitors and open mineral soil for seedling recruitment; the pines additionally self-prune lower branches to enable a gap between surface and canopy fuels (Zedler 1995, Fonda et al. 1998, Keeley and Zedler 1998, Engber and

Varner 2012). Historically, topography interacted with the fire regime in these forests to create highly heterogeneous stand structures that supported a high diversity of plants and animals (North et al. 2009). Litter decomposition rates in low and middle elevation forests in the study area are extremely slow (Hart et al. 1992), and long fire-free intervals lead to accumulation of fuel and fundamental changes in soil and litter nutrient dynamics (Johnson et al. 2009). The lack of low and moderate severity fire in these forests over most of the last century has also increased tree densities and canopy cover; changed tree species dominance patterns (from fire tolerant/shade intolerant species to fire intolerant/shade tolerant species, e.g., in the genera *Abies* and *Calocedrus*); reduced soil interception of light and water; changed surface and ground water hydrology; decreased herbaceous production and diversity in the understory; reduced critical foraging habitat for animals; led to higher rates of adult tree mortality from insects, diseases and water stress; and resulted in a major fire regime transition to one dominated by infrequent, large, and highly severe fires (Agee 1993, Barbour et al. 1993, Allen et al. 2002, Bales et al. 2006, Sugihara et al. 2006, Fettig et al. 2007, Miller et al. 2009*b*, North et al. 2009, Van Mantgem et al. 2009, Miller and Safford 2012, North 2012). It is telling that the conifer types in our study region that supported the lowest severity fires during the presettlement period (YP, DMC, MMC), now support the highest severity fires (YP = 42%, area weighted mean of the three types = 34%).

Areas of high severity fire create ecologically important patches of dead and dying trees and early seral conditions (Hutto 2008, Swanson et al. 2011). At some level, areas of high severity fire have always occurred in Sierra Nevada forests of all types. Before Euro-American settlement, the relative importance of high severity fire in low and middle elevation forests in our study region was low however, and—because modern fires are burning at such high severity—our results indicate little to no departure in the average annual area of high severity fire in these ecosystems. Rather, strong evidence of modern vs. presettlement differences in the occurrence of high severity fire in these forest types exists only for its spatial configuration, not its overall spatial extent; i.e., individual fires and high severity patches within fires tend to be larger under modern than under presettlement conditions. For example, Miller et al. (2012) show that modern fires in our study region over the last quarter-century in fire-suppressed yellow pine and mixed conifer forests average over 2600 ha in size. Data from contemporary reference (i.e., unlogged and no fire suppression) forests and reconstructions of fire size from studies of presettlement landscapes suggest that average fires under presettlement conditions were at least an order of magnitude smaller (Show and Kotok 1923, Taylor and Skinner 1998, Minnich et al. 2000, Taylor 2000, Beaty and Taylor 2001, Taylor and Solem 2001, Collins and Stephens 2007; B. M. Collins, *personal communication*; A. H. Taylor, *personal communication*). In low and middle elevation forests, high severity patch size has also risen, with a dominance of small, scattered patches in presettlement and reference estimates transitioning to more contiguous, coarser-grained patchiness in modern fire-suppressed forests. High severity patches more than a few hectares in size were relatively unusual (although not unknown) in fires in Sierra Nevada yellow pine and mixed conifer forests before Euro-american settlement (Sudworth 1900, Show and Kotok 1923, Kilgore 1973, Agee 1993, Skinner 1995, Skinner and Chang 1996, Weatherspoon and Skinner 1996, Keeley and Stephenson 2000), but in recent years high severity patches >500 ha have become a regular occurrence (Miller and Safford 2008, Miller et al. 2012). Between 1984 and 2006, mean high severity patch size in Forest Service fires in the study area nearly doubled (Miller et al. 2009*b*). Comparisons between current reference yellow pine and mixed conifer forests (mean patch sizes 1.7–4.2 ha) and Forest Service forests (managed primarily under full fire suppression; mean patch sizes >12 ha) further reflect these changes (Minnich et al. 2000, Collins and Stephens 2010, Miller et al. 2012).

Our finding that high elevation and low to middle elevation forests experienced roughly similar levels of departure in overall burned area was somewhat surprising. For a variety of reasons, modern fire regimes in higher elevation forests in the western United States are generally thought to have changed little in response to human management over the last century (Agee 1993, Schoennagel et al. 2004, Noss et al. 2006,

Table 5. Comparisons of independent reference estimates of percent high severity in wildland fires with presettlement estimates used in this study. See Appendix for details.

PFR forest types	Independent sources	Estimate of percent high severity: Independent reference estimates	This study (PHS_{pre})†
YP + DMC	Minnich et al. 2000, Stephens et al. 2008; Safford et al., *unpublished manuscript*	4–8	5.3
YP + DMC + MMC	Show and Kotok 1925	5	6.1
MMC + RF + LP	Collins et al. 2009	13	12.6
RF	Leiberg 1902, Miller et al. 2009*b*, 2012	8–13	19.9
SA	Miller et al. 2009*b*	7	25
All combined	Leiberg 1902	8	7

† Presettlement high severity estimates weighted by presettlement area burned within each PFR type listed in column 1.

Sugihara et al. 2006). Presettlement fire return intervals in these forest types were much longer than in lower elevation forests, and a century of fire suppression has only resulted in zero to two missed fire cycles on most of the landscape (Safford and Van de Water 2013). In California, high elevation forests are much more likely than low and middle elevation forests to be found in wilderness areas and National Parks, where timber extraction was minimal or nonexistent and where modern fire suppression policies are often relaxed. Additionally, road densities in these forests are relatively low, which inhibits easy fire fighter access. Very low ecosystem productivity in high elevation forests also leads to slower plant growth and lower rates of fuel accumulation between fires (Barbour et al. 2007).

There are a number of sources of possible error in our high elevation estimates that must be taken into account before we develop an ecological explanation of the high elevation results. These include: (1) the possibility that the LANDFIRE vegetation map may be relatively less accurate at higher elevations, due to lower numbers of high elevation field samples supporting the vegetation modeling; (2) the relatively short temporal window of our analysis for high elevation ecosystems that are naturally characterized by infrequent fire events (this may be compensated for by the very large size of our study area); and (3) the higher proportion of small (<40 ha) fires at high elevations, which could lead to underreporting of modern area burned in red fir and subalpine forests and subsequent inflation of our measures of departure.

Another factor that influences our estimate of departure in high elevation forests is the set of values we used for presettlement PHS. Our PHS_{pre} approximations derive from two sources: estimates made from literature sources and field observations (Stephens et al. 2007) and estimates derived from state-and-transition modeling carried out by fire and forest ecology experts (LANDFIRE BpS models; Rollins 2009). Table 5 compares our PHS_{pre} estimates for a set of forest types and forest type combinations against independent estimates made from reference areas (both current and presettlement; see Appendix). In Table 5, our estimates of PHS_{pre} for lower and middle elevation forest types (YP, DMC, MMC plus some LP and RF) are closely corroborated by the independent sources. In contrast, our estimates for PHS_{pre} in the highest elevation forest types (RF and SA) seem high (Table 5). Most estimates of fire severity in these forest types, whether from contemporary or presettlement sources, suggest that natural severities of fire are probably below the 20–25% PHS_{pre} values we used in our study (Kilgore 1971, Kilgore and Briggs 1972, Weaver 1974, Agee 1993, 2005, Taylor 1993, Chappell and Agee 1996, Miller et al. 2009*b*, 2012; M. D. Meyer, *personal communication*). The implications of our probable overestimate of PHS_{pre} in red fir and subalpine forest are that the real differences between presettlement and current annual area burned at high severity (AAHS) for high elevation forests are likely less than our analysis suggests. Substituting the independent reference estimates (Table 5) for PHS_{pre} in Table 3 results in an $AAHS_{pre}$ of 1871 ha for red fir and 62 ha for subalpine forest. Using these values, the departures in high elevation forest between modern and presettlement AAB in the high severity and low + moderate severity classes become more similar: combining RF and SA, $AAHS_{mod}$ is 23.3% of presettlement, $AALMS_{mod}$ is 18.9% of presettlement.

Therefore, assuming that the departure we measured in overall burned area in the high elevation forest types is real—if slightly exaggerated—then it is not due to a general change in fire behavior, but rather to a change in overall burned area. In other words, higher elevation fires do not appear to be burning in a qualitatively different manner today than before Euroamerican settlement, there are just fewer of them. High elevation fires are relatively easy to put out. The needles of high elevation conifers tend to be short and highly compact, and they form moist, dense litter layers that are difficult to ignite and slow to burn. The fire season is short, and summer daytime temperatures are low and relative humidities high. Soils are rocky and forest stands are often open and separated by areas of low flammability (Fonda et al. 1998, Sugihara et al. 2006, Barbour et al. 2007). All of these factors lead to a high success rate when a suppression decision is made on a high elevation fire. Most fires in our study area are still subject to fire suppression, especially on Forest Service and private lands. Although high elevation fires are not as zealously suppressed as low elevation fires (and there are a number of high elevation wilderness areas where fires are often managed rather than suppressed), natural fire rotations for the higher elevation forest types are 3–20 times longer than lower elevation types (Table 2). This suggests that, all else being equal, fire suppression can cause departures at higher elevations similar to those at lower elevations even when effective suppression is only 1/3 to 1/20 as intense. In other words, the intensity of effective fire suppression necessary to produce a given modern-vs.-presettlement departure declines rapidly with elevation, and this could potentially compensate for any elevation gradient in fire suppression effort.

Our trend analyses indicate that the strongest increases in annual area burned (and AABHS) in our modern study period occurred in the high elevation forest types (Table 4). A number of factors could help to explain this trend. First of all, since the late 1970s fire management policies in progressively larger areas of high elevation wilderness in the Sierra Nevada have been converted from a fire suppression focus to a fire management focus. This is especially the case in Yosemite and Sequoia-Kings Canyon National Parks (van Wagtendonk 2007). Second, climate warming in the study area has led to drier and longer fire seasons, rain replacing snow in many precipitation events, declining snowpack, and an upward migration of the elevation of the freezing line (Safford et al. 2012*a*). These changes are having major impacts on higher elevation ecosystems, especially red fir forests, which occur at the elevation of greatest snowpack and just above the freezing line in winter storms (Safford and Van de Water 2013). The loss of snow is increasing tree regeneration and leading to the filling of canopy gaps and formerly perennial snowpatches with small trees in subalpine forests (Dolanc et al. 2012). These dynamics are gradually leading to higher fuel continuity, but the system remains patchy, with generally thinner soils and low productivity. Overall, general behavior of fire in high elevation forests has not changed dramatically from presettlement times, but as climate warming proceeds, climatic conditions appropriate for burning are becoming more common and the length of the fire season is increasing (Westerling et al. 2006). As snowpack continues to decrease, summers warm, and forest densification accelerates (Dolanc et al. 2012, Safford et al. 2012*a*), we would predict that fire behavior in high elevation forests will become more extreme.

Miller and Safford (2012) recently found that the area of high severity fire in yellow pine and mixed conifer forest types had increased significantly between 1984 and 2010 ($P < 0.01$). This differs somewhat from our finding that yellow pine high severity fire area only increased marginally (posterior probability = 0.92), and mixed conifer (posterior probability < 0.90) even less, but dissimilarities in the time period, study area, and analysis help to explain the difference. Miller and Safford (2012) studied only Forest Service managed lands in the study area, included an extra year of fire data (2010), combined the yellow pine and mixed conifer types in their analysis, and employed ARIMA time-series regression modeling. To see to what extent the combination of yellow pine and mixed conifer forest types accounted for the difference, we reran our analysis combining the yellow pine and mixed conifer types and obtained a posterior probability of 0.92 for the combination. We then removed the National Park fires from our dataset and reran the same analysis, which resulted in a posterior probability of >0.94. Other reasons for the differences include the extra year of fire data, and the use of a fourth-order autoregressive function in Miller and Safford (2012; ARIMA models using only the first-order autoregressive function were not statistically significant). Under the Bayesian framework, our Forest Service only, yellow pine-mixed conifer combined analysis suggests a greater than 94% chance (put another way, >15:1 odds) that the area of high severity fire increased between 1984 and 2009. We should also note that we chose to remain conservative in our analysis and employed "naïve" (uninformed) priors. Since previous work had shown increases in the percent of high severity fire in the same study region between 1984 and 2006 (Miller et al. 2009*b*), we might have incorporated informative priors in our analysis, which would have resulted in posterior probabilities well over 0.95.

As with the yellow pine and mixed conifer forest types, our trend results for $AAHS_{mod}$ in red fir were also slightly different from Miller and Safford (2012). We found a posterior probability of 0.96 for an increasing trend between 1984 and 2009, Miller and Safford (2012) found a traditional statistical probability of $P = 0.06$ (equivalent to a posterior probability of 0.94) for the same trend. As above, these minor differences find their roots in the different areas and years of analysis.

Implications for management

Our results have important implications for the management of fire, forests, and wildlife in the study area and surrounding regions. The ecological consequences of fire suppression and the subsequent fire deficit in frequent-fire forest types in the western US have been understood for many years (see Introduction; Weaver 1943, Biswell 1972, Parsons and Debenedetti 1979, Agee 1993, Sugihara et al. 2006). Nonetheless, under current federal policies almost all fires, whether naturally ignited or not, are put out within days of ignition. The exception in our study area is National Park Service lands (Yosemite, Sequoia-Kings Canyon, and Lassen National Parks), where many fires are managed for resource benefits, and a few Forest Service wilderness areas, where some fires are managed in similar fashion. Outside of these limited areas, nearly the only fires that reach any size are those that escape control under severe climatological conditions, in heavy fuels, and/or in inaccessible topography (Calkin et al. 2005). Since almost all fires occurring under moderate conditions are put out, areas burned by wildfire in the contemporary study area suffer a statistical predisposition to burn at higher severity. This is especially evident in lower and middle elevation forests like yellow pine and mixed conifer, where steadily increasing levels of forest fuels due to a century-and-counting of fire suppression, and the effects of warming climates, decreasing snowpack, and drier late summer days on fire behavior are accelerating forest biomass loss to fire (Miller et al. 2009*b*, Miller and Safford 2012).

To a great extent, current forest management practices in the study area are responding to these trends by focusing on protection of human lives and infrastructure from wildfire. Such work is critical, but the intense emphasis on short-term, small-scale and stop-gap measures leaves vast areas of forest ecosystems in the study area increasingly vulnerable to threshold-type ecological events ("type conversions") caused by interactions between severe fires, drought, climate warming, insects and diseases, and other stressors (Barbour et al. 1993, Dale et al. 2001, Allen et al. 2010). In addition, almost all fuels management in the western US is focused on creating conditions where fires can be more easily suppressed, not creating conditions where forests will be more resilient if wildfire arrives (Reinhardt et al. 2008). It is important to remember that in California's climate and ignition environment, the question in many forest types is not "if" fire will arrive, but rather "when".

Our results show that departures in area burned in the study area are proportionally similar in low/middle and high elevation forests, but the areal signature of the fire deficit is an order of magnitude greater in the former (c. 170,000 ha per year vs. c. 16,000 ha). In high elevation forest types like red fir and subalpine, fire severities of all types are lacking in nearly equal measure, and restoration of fire through expanded use of managed (versus suppressed) wildfire is likely to rapidly realize ecological benefits. In low and middle elevation forests like yellow pine and mixed conifer however, the critical deficit is in low and moderate severity fire, and the management focus must be not only on increasing the area burned, but also replacing high severity hectares with low and moderate severity hectares. As Pyne (2009) put it, we need to replace the "wrong kind of fire" with the "right kind of fire." In these lower and middle elevation forests, expanded use of managed wildfire is also called for under moderate weather and fuels conditions, but the latter are relatively rare on the modern landscape. Our results support the notion that forest fuels will need to be strategically reduced in many areas of yellow pine and mixed conifer forest before restoration of fire as a beneficial ecological process becomes ecologically, politically, and financially feasible (Allen et al. 2002, Arno and Fiedler 2005, Moghaddas et al. 2010, Stephens et al. 2010, North et al. 2012).

Through their management of vegetation and fire, federal agencies like the Forest Service, Bureau of Land Management, and National Park Service have significant effects on wildlife habitat. For the Forest Service and BLM, the population status of a handful of wildlife species has become the principal arbiter of management policies and practices across northern California and the Pacific Northwest. In the study area, the California spotted owl (*Strix occidentalis occidentalis*), northern goshawk (*Accipiter gentilis*), and California populations of fisher (*Martes pennanti*) are carnivores whose life histories include a close association with old forest and complex forest structure, primarily in mixed conifer forests. Current population sizes of these species are small and population growth rates are near zero or negative (Blakesley et al. 2010, Spencer et al. 2011). These conditions have led to controversy, litigation, and a resultant agency "hands off" policy towards these species that is focused on avoiding the short term putative threats of active forest management. Forest conditions have changed drastically since Euroamerican settlement however, and current trends in climate, fuel loads, forest density, and fire size and severity suggest that long term sustainability of habitat for these species is uncertain (McKenzie et al. 2004, Miller et al. 2009*b*, Scheller et al. 2011, Lawler et al. 2012, Miller and Safford 2012, Safford et al. 2012*a*). Indeed, over the last 15 years, a wave of large and severe fires in eastern Oregon and northern California has substantially reduced the number of high value habitat areas for spotted owl (Courtney et al. 2004, Spies et al. 2006, Healey et al. 2008, Keane et al. 2010, Clark et al. 2011). Likewise, demographic and habitat suitability modeling of the isolated southern Sierra Nevada fisher population indicate that large and severe fires in the absence of strategic forest management approaches could substantially reduce long-term habitat quality and population size for this species (Scheller et al. 2011, Thompson et al. 2011). Long-term retention of old forest in the study area will require substantially more integration of forest, fuels, and fire management than is currently the case, as well as a longer-term view of the costs and benefits of current fire management policies (Stephens and Ruth 2005). On the other hand, under current and projected future trends, early seral habitats in the study area are likely to expand greatly in area (McKenzie et al. 2004, Lenihan et al. 2008, Cole 2010, Gedalof 2011, Miller and Safford 2012, Safford et al. 2012*a*). Study area species with demonstrated dependence on high severity fire (e.g., black-backed woodpecker [*Picoides arcticus*]) will likely benefit from these trends.

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Supplemental Material

Appendix

We refrained from using GMFI for estimating FR_{pre} in the subalpine (SA) forest type for three reasons. First, because fires in SA are generally smaller than those in forests at lower elevations (Skinner 2003, van Wagtendonk and Fites-Kaufman 2006), we would expect spatial autocorrelation in GMFI to be comparatively low such that greater sampling intensities (i.e., number of trees sampled per unit area) may be required to achieve comparable levels of confidence when estimating the GMFI of the population (Parsons et al. 2007). Second, most studies use a targeted sampling approach, and while this is appropriate in relatively homogenous landscapes where the probability of fire occurrence is spatially uniform (van Horne and Fulé 2006), the heterogeneous fuel structure (van Wagtendonk and Fites-Kaufman 2006) and high incidence of lightning (van Wagtendonk and Cayan 2008) in SA suggests a relatively fine-grain spatial patterning in fire frequency. As a consequence, studies based on preferential sampling of fire-scarred trees are more likely to underestimate the GMFI of the population. Third, fires in SA are generally less frequent than in forests at lower elevations (van Wagtendonk and Fites-Kaufman 2006), which means that the preferential loss of long fire intervals from the tree-ring record produces a more severe downward bias in estimates of the population GMFI than is the case for forests where intervals between fires are much shorter relative to tree-ring record (Parsons et al. 2007).

Further details regarding the fire severity comparisons

1. The LANDFIRE Biophysical Settings (BpS) vegetation models are summarized at (http://www.landfire.gov/NationalProductDescriptions24.php) and described in Pratt et al. (2006). For our presettlement high fire severity estimate we used the percent of fires occurring as "stand replacement fires" in the fire interval table provided at the end of each BpS model description at the website above. The BpS modeling project defined stand replacement fires to be those with >90% mortality of canopy trees (Pratt et al. 2006). The BpS estimates of percent high fire severity thus include somewhat more tree mortality than our RdNBR-based metric, which includes areas with greater than ~95% mortality (Miller et al. 2009*a*). Put another way, a more exact comparison between the BpS-based presettlement estimates of high severity fire and our modern estimates would require that the BpS estimates be reduced somewhat. We chose to remain conservative in our comparisons and did not adjust the BpS estimates.
2. The presettlement high fire severity estimates from Stephens et al. (2007) are based on percent consumption of canopy fuels ("percent crown burned"). This is a very similar measure to our measure, since both focus on biomass lost in the canopy trees, however our measurements are made one year after fire and thus include some delayed mortality, whereas Stephens et al. (2007) refer only to the immediate effects of fire. We would thus expect Stephens et al.'s (2007) estimate to be low by some degree. Hood et al. (2007) modeled mortality probability curves for the dominant tree species in most of our conifer forest types, including models based on percent crown length killed (this was a better predictor than crown volume killed). Hood et al.'s (2007) models are for two years after fire, and show the following approximate mortality probabilities for 5% crown length killed (ignoring insect interactions, which tend to become a major mortality driver more than a year after fire, especially when fires occur in the dormant season, which is the dominant season burning in the study area [Fettig et al. 2007]): red fir, range 0–0.25, mean 0.05; incense cedar, range 0–0.03, mean 0.02; white fir, range 0.2–0.22, mean 0.075; ponderosa and Jeffrey pine, range 0.02–0.08, mean 0.04. These values suggest that, on average, Stephens et al.'s (2007) severity metric (percent consumption of crown) is actually a relatively accurate measure of crown mortality one or two years after fire, and lend us confidence in our comparisons with the Stephens et al. (2007) values.
3. Our low-to-moderate fire severity class included areas classified as "unchanged" by the RdNBR measure. "Unchanged" means that the spectral differences between pre and postfire LANDSAT-TM images were not sufficient to be recognized, and such areas may or may not have burned (Miller and Thode 2007). Given this uncertainty, we chose to remain conservative and combined unchanged and low-moderate severity into a single class. Since some of the unchanged areas did not burn, this practice systematically overestimates the area actually burned at low-to-moderate severity. The mathematical ramification of this is that our estimates of the percentage of fire area burning at high severity are underestimates of the actual percentage, to the same degree.
4. Actual fire-caused mortality is much higher than the percent of high severity fire, which in most RdNBR-based studies indicates the percent of fire area where mortality was

greater than ~95% (Miller et al. 2009*a*). As an example, Miller and Safford (2008) measured fire severity by low, moderate, and high severity classes forest wildfires on Forest Service lands in the study area for the period 2000–2004, and found that the percentages of unchanged vs. low vs. moderate vs. high severity averaged 12:30:30:28. Low severity fire was defined as <25% mortality (of canopy trees), and moderate would be 25–95%. Therefore, in this case a rough estimate of expected tree mortality would be $30 \times 0.125 + 30 \times 0.60 + 28 \times 0.975 = 49.1\%$ overall canopy tree mortality. Also, satellite imagery can only measure what it sees, thus understory trees are strongly underrepresented in our results. Finally, trees continue to die for years after fire, depending on such factors as insect populations, climate, and so on. Considering these factors, our modern measures of high severity fire notably underplay the actual underlying rates of tree mortality.

Details regarding Table 5

Collins et al. (2010) studied fire severity in a large area of Yosemite National Park dominated by moist mixed conifer (MMC), red fir (RF) and lodgepole pine (LP) where naturally ignited fires have been allowed to burn since the 1970s. They found that a total of 13% of the fire areas they assessed over a 31-year period had burned at high (stand replacing) severity. Our area-weighted PHS_{pre} for the MMC, RF, and LP forest types in the Sierra Nevada is 12.6%. Another contemporary source of reference fire regime information is the Sierra San Pedro Mártir National Park in northern Baja California, Mexico. This area is in the southernmost part of the North American Mediterranean climate zone and supports yellow pine (YP) and dry mixed conifer (DMC) forests that are very similar to those of drier portions of the Sierra Nevada (Stephens and Fulé 2005). Unlike the Sierra Nevada, most of the Sierra San Pedro Mártir was not logged and fire suppression has only been in effect for the last few decades, so the forests are much closer to pre-Euroamerican settlement conditions. Minnich et al. (2000) reported results from aerial photo interpretation of two fires that burned in the Sierra San Pedro Mártir in 1989. Using photos from 1991, they estimated that 16% of the analyzed fire area had experienced >90% mortality, thus perhaps 8% or so experienced stand replacing fire effects (>95% mortality). Aerial photo analysis is known to underestimate the area of low severity fire, as fire extent is primarily mapped based on fire effects to canopy trees, so surface fires are difficult to pick out, especially when a number of years have passed since the fire event. Consequently, we view Minnich et al.'s (2000) numbers as an upper estimate of fire severity. Stephens et al. (2008) used field plots to measure severity in a fire area in the Sierra San Pedro Mártir. Only one of their 27 plots (4% of their sample area) experienced high severity effects (>95% mortality). We are also currently carrying out an RdNBR-based assessment of 25 years of fire severity patterns in the Sierra San Pedro Mártir; our preliminary results similarly suggest an average of <10% high severity fire in YP and DMC forests. In comparison with these reference site results, our area weighted PHS_{pre} for the YP and DMC forest types in the Sierra Nevada is 5.3%.

Show and Kotok (1925) stated that fires in the "California pine region", which equates to yellow pine-mixed conifer forest, rarely burned the forest canopy, but killed canopy trees through heat from surface fires and successive scarring and hollowing out of the trunk, which resulted in typical fire-caused losses of about 5% of the "merchantable forest" (mature trees). Our area-weighted PHS_{pre} for YP, DMC, and MMC forests in the study area is 6.1%.

Leiberg (1902) carried out a field inventory of forestlands in the northern Sierra Nevada at the beginning of the 20th century and made estimates of the amount and severity of burning that had occurred in his study region over the previous century. Euroamerican presence in the Sierra Nevada was minimal until after 1850, and exclusion of fire from most Sierra Nevada forests is not noticed in the fire scar record until at least the 1870s or 1880s (Sugihara et al. 2006), so Leiberg's (1902) results at least partly reflect presettlement conditions. Leiberg tallied burned area by watershed for the northern Sierra Nevada and estimated that 8% of the 19th century fire area had experienced "total destruction", i.e., stand replacement. Leiberg's (1902) assessment did not quantitatively discern among forest types (athough most of the fires he visited had taken place in upper elevation mixed conifer and red fir forests). In comparison, our independent PHS_{pre} estimate for all forest types combined is 7%.

Quantitative estimates of reference fire severities in higher elevation forests include Miller et al. (2012), who estimated 8% high severity fire in red fir forests in wildland fire use areas in Yosemite National Park over a recent 26 year period, and Leiberg (1902), whose 19th century estimate of 8% HS was predominantly measured in forests with a red fir component. Because of the minor impacts of fire suppression on high elevation forests, Miller et al.'s (2009*b*) estimates of RF (13%) and SA (7%) high fire severity on Forest Service lands are also germane. Qualitative considerations of fire severity in unmanaged red fir stands also substantiate a predominantly low and moderate severity fire regime (Kilgore 1971, Kilgore and Briggs 1972, Weaver 1974, Agee 1993, 2005, Taylor 1993, Chappell and Agee 1996).

Table A1. LANDFIRE Biophysical Settings (BpS) units grouped by the seven forest types used in this study.

BpS	BpS code	Area (ha)
Oak woodland (OW)		
California Central Valley Mixed Oak Savanna	11120	37
California Lower Montane Blue Oak-Foothill Pine Woodland and Savanna	11140	659,597
East Cascades Oak-Ponderosa Pine Forest and Woodland	10600	1,491
Mediterranean California Mixed Oak Woodland	10290	280,029
North Pacific Oak Woodland	10080	332
Dry Mixed Conifer (DMC)		
Mediterranean California Dry-Mesic Mixed Conifer Forest and Woodland	10270	737,721
Northern Rocky Mountain Dry-Mesic Montane Mixed Conifer Forest	10450	39
Moist Mixed Conifer (MMC)		
Southern Rocky Mountain Mesic Montane Mixed Conifer Forest and Woodland	10520	440
Klamath-Siskiyou Lower Montane Serpentine Mixed Conifer Woodland	10210	80
Mediterranean California Mesic Mixed Conifer Forest and Woodland	10280	1,360,819
Northern Rocky Mountain Dry-Mesic Montane Mixed Conifer Forest	10450	103
Northern Rocky Mountain Foothill Conifer Wooded Steppe	11650	2
Southern Rocky Mountain Dry-Mesic Montane Mixed Conifer Forest and Woodland	10510	2
Northern Rocky Mountain Foothill Conifer Wooded Steppe	11650	5,854
Southern Rocky Mountain Ponderosa Pine Woodland	10540	90
Klamath-Siskiyou Upper Montane Serpentine Mixed Conifer Woodland	10220	315
Yellow Pine (YP)		
Southern Rocky Mountain Ponderosa Pine Savanna	11170	1
California Montane Jeffrey Pine(-Ponderosa Pine) Woodland	10310	1,295,623
Mediterranean California Lower Montane Black Oak-Conifer Forest and Woodland	10300	209,389
Northern Rocky Mountain Ponderosa Pine Woodland and Savanna, Mesic	10531	1
Northern Rocky Mountain Ponderosa Pine Woodland and Savanna, Xeric	10532	21,064
Red Fir (RF)		
Mediterranean California Red Fir Forest	10320	45,715
Mediterranean California Red Fir Forest, Cascades	10321	429,617
Mediterranean California Red Fir Forest, Southern Sierra	10322	562,071
Lodgepole Pine (LP)		
Rocky Mountain Poor-Site Lodgepole Pine Forest	11670	7,958
Sierra Nevada Subalpine Lodgepole Pine Forest and Woodland	10580	7,644
Sierra Nevada Subalpine Lodgepole Pine Forest and Woodland, Dry	10582	30,301
Sierra Nevada Subalpine Lodgepole Pine Forest and Woodland, Wet	10581	64,714
Subalpine (SA)		
Inter-Mountain Basins Subalpine Limber-Bristlecone Pine Woodland	10200	1,029
Mediterranean California Subalpine Woodland	10330	312,753
North Pacific Dry-Mesic Silver Fir-Western Hemlock-Douglas-fir Forest	11740	2
North Pacific Maritime Dry-Mesic Douglas-fir-Western Hemlock Forest	10370	544
North Pacific Maritime Mesic-Wet Douglas-fir-Western Hemlock Forest	10390	27
North Pacific Mountain Hemlock Forest, Xeric	10412	6,005
North Pacific Wooded Volcanic Flowage	11730	432
Northern California Mesic Subalpine Woodland	10440	4,302
Rocky Mountain Subalpine-Montane Limber-Bristlecone Pine Woodland	10570	2,286

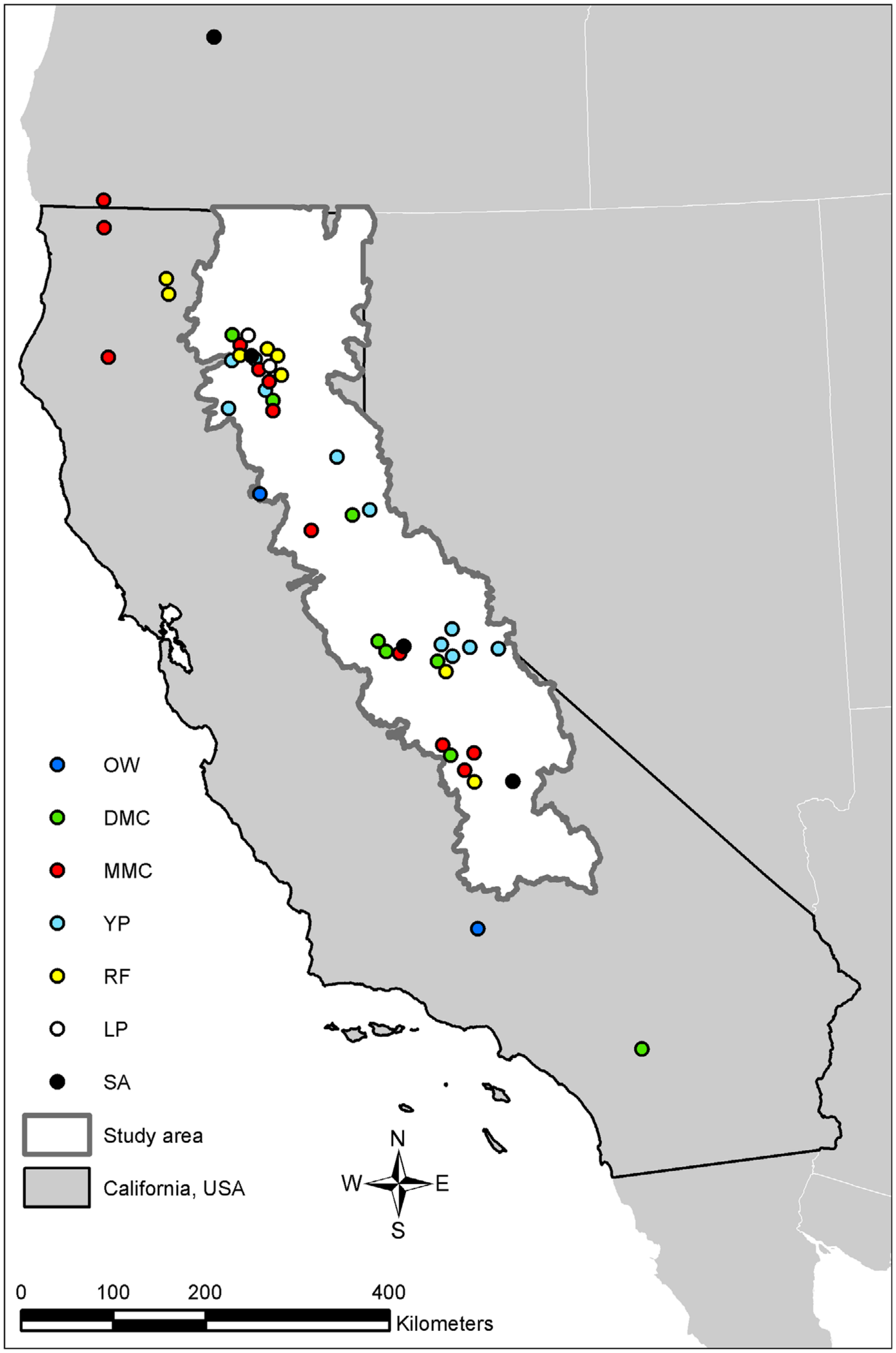

Fig. A1. Sampling locations for fire history studies used to estimate pre-Euro-American fire rotations. Symbols for nearby sampling locations slightly offset to permit visibility.

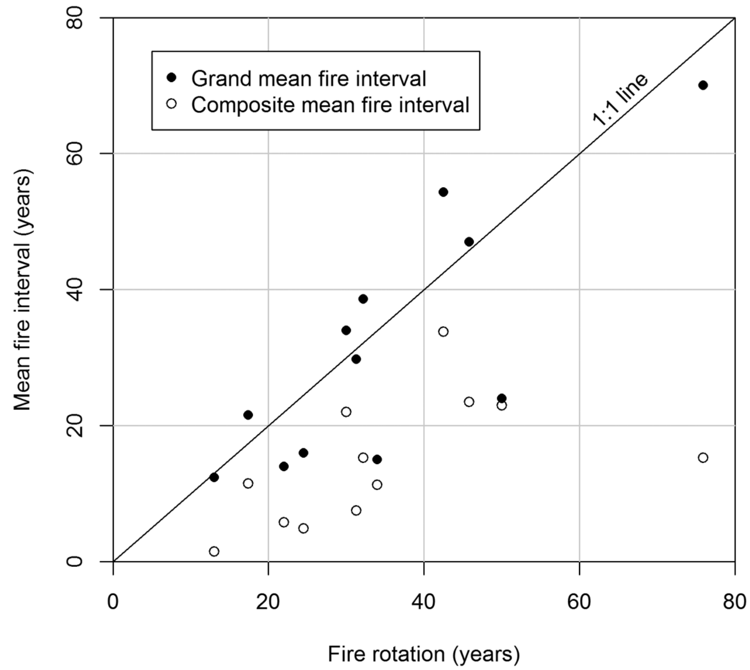

Fig. A2. Grand mean fire intervals (GMFI) and composite mean fire intervals (CMFI) plotted against fire rotation. Estimates obtained from fire-scar-based fire history studies in western North American that reported all three metrics for the same study location and period. Median error (%) and root mean square error (%) for GMFI were −4.79 and 30.02, respectively. The same statistics for CMFI were −66.76 and 63.25, respectively. Data were obtained from the following studies: Taylor (2000), Beaty and Taylor (2001), Bekker and Taylor (2001), Brown et al. (2008), and Scholl and Taylor (2010).

Table A2. Crosswalk table between forest types used in this study and forest types for which Stephens et al. (2007) estimated presettlement fire severity (originally from Barbour and Major 1977).

This study	Barbour and Major (1988) and Stephens et al. (2007)
Oak Woodland (OW)	Oak woodland
Yellow Pine (YP)	Ponderosa/shrub, Great Basin pine
Dry Mixed Conifer (DMC)	Mixed conifer
Moist Mixed Conifer (MMC)	Mixed conifer
Red Fir (RF)	Red fir
Lodgepole Pine (LP)	Lodgepole/subalpine
Subalpine (SA)	Lodgepole/subalpine