esa

ECOSPHERE

The fire frequency-severity relationship and the legacy of fire suppression in California forests

Zachary L. Steel,[1] Hugh D. Safford,[1,2,]† and Joshua H. Viers[3]

[1]*Department of Environmental Science and Policy, University of California, One Shields Avenue, Davis, California 95616 USA*
[2]*United States Department of Agriculture, Forest Service, Pacific Southwest Region, Vallejo, California 94592 USA*
[3]*School of Engineering, University of California, 5200 N. Lake Road, Merced, California 95343 USA*

Citation: Steel, Z. L., H. D. Safford, and J. H. Viers. 2015. The fire frequency-severity relationship and the legacy of fire suppression in California forests. Ecosphere 6(1):8. http://dx.doi.org/10.1890/ES14-00224.1

Abstract. Fire is one of the most important natural disturbance processes in the western United States and ecosystems differ markedly with respect to their ecological and evolutionary relationships with fire. Reference fire regimes in forested ecosystems can be categorized along a gradient ranging from "fuel-limited" to "climate-limited" where the former types are often characterized by frequent, lower-severity wildfires and the latter by infrequent, more severe wildfires. Using spatial data on fire severity from 1984–2011 and metrics related to fire frequency, we tested how divergence from historic (pre-Euroamerican settlement) fire frequencies due to a century of fire suppression influences rates of high-severity fire in five forest types in California. With some variation among bioregions, our results suggest that fires in forest types characterized by fuel-limited fire regimes (e.g., yellow pine and mixed conifer forest) tend to burn with greater proportions of high-severity fire as either time since last fire or the mean modern fire return interval (FRI) increases. Two intermediate fire regime types (mixed evergreen and bigcone Douglas-fir) showed a similar relationship between fire frequency and fire severity. However, red fir and redwood forests, which are characterized by more climate-limited fire regimes, did not show significant positive relationships between FRI and fire severity. This analysis provides strong evidence that for fuel-limited fire regimes, lack of fire leads to increasing rates of high-severity burning. Our study also substantiates the general validity of "fuel-limited" vs. "climate-limited" explanations of differing patterns of fire effects and response in forest types of the western US.

Key words: California, USA; fire frequency; fire regime; fire return interval; fire severity; Sierra Nevada; wildfire.

Received 25 July 2014; revised 29 September 2014; accepted 3 October 2014; final version received 15 December 2014; **published** 21 January 2015. Corresponding Editor: F. Biondi.

† **E-mail:** hughsafford@fs.fed.us

Introduction

Fire is one of the most important natural disturbance processes in ecosystems of the western United States. Fire affects ecosystems in myriad ways and ecosystems themselves strongly influence fire, primarily through feedbacks on fuel quantity, condition, and distribution. As a disturbance, fire is unique in that its intensity and frequency depend on, among other things, the accumulation rate (growth and decomposition) of the fuel (live and dead vegetation) it consumes. As a result, wildfire frequency and intensity are broadly inversely related (Pickett and White 1985, Turner et al. 1989, Huston 2003). Fire has been likened to an herbivore, as one of its principal effects is to periodically reduce biomass in the ecosystems it affects (Bond and Keeley 2005). Fire greatly influences spatial and temporal patterns of biodiversity, impacting plant and wildlife community composition and species abundance (Pickett and White 1985, Sugihara et al. 2006*a*). Ecological processes such as nutrient cycling, soil structure (Wohlgemuth et al. 2006) and carbon storage (North and Hurteau 2011) are also influenced by fire frequency and intensity. In California, the 3–6 month annual drought leads to highly propitious conditions for fire ignition and spread, and fire is a keystone ecological process in ecosystems across the State (Agee 1993, Barbour et al. 1993, Sugihara et al. 2006*b*, Keeley et al. 2012).

Ecosystems differ markedly with respect to their ecological and evolutionary relationships with fire, and useful distinctions can be made among ecosystems based on the extent to which fuel conditions and climate influence their fire regimes (Agee 1993, Noss et al. 2006, Sugihara et al. 2006*b*, Pausas and Paula 2012). At one end of the gradient are ecosystems where climatic conditions during the fire season are nearly always conducive to burning and the primary limiting factor for fire ignition and spread is the presence of sufficient fuel. California examples of ecosystems with mostly "fuel-limited" fire regimes include interior grassland, oak woodlands, yellow pine (*Pinus ponderosa* and *P. jeffreyi*) and mixed conifer forests. At the other end of the gradient are ecosystems where sufficient fuel is generally present for fire occurrence, but fuel and/or atmospheric moistures are typically too high for combustion except under extreme climatic circumstances (usually some combination of drought, heat waves, and high winds). California examples of "climate-limited" forest ecosystems are relatively rare, but include maritime forests of the coastal northwest, and moist forests at higher elevation. Many ecosystems fall in intermediate positions along this gradient (so-called "mixed-severity" fire regimes) and exhibit high spatial and temporal variability among fire effects and drivers of fire behavior (Halofsky et al. 2011; Fig. 1).

Another important factor influencing the occurrence of fire in California ecosystems is the availability of ignitions. Ecosystems in the mountains and deserts of interior California experience relatively frequent lightning strikes (van Wagtendonk and Cayan 2008), while the lowest lightning strike densities in the contiguous US are found along the California coast (Orville 2008). As a result, many coastal-proximal ecosystems in California are "ignition-limited", where non-human sources of ignition are rare during periods when fuels and climate are suitable for burning. Examples of ignition-limited ecosystems include moist coastal forests, redwood (*Sequoia sempervirens*) forests, and chaparral and related shrublands in southern California. Interestingly, many areas of redwood supported relatively high frequencies of fire in the centuries before Euroamerican settlement, but this was driven almost entirely by seasonal Native American ignitions; without this anthropogenic fire source, redwood forests would support much longer fire return intervals (Fig. 1; Greenlee and Langenheim 1990, Stuart and Stephens 2006).

Due to the presence of summer lightning and aboriginal American fire management, California forest ecosystems with principally fuel-limited fire regimes supported high fire frequencies before Euroamerican settlement (pre-1850), with mean fire return intervals (FRIs) of 10–20 years (Van de Water and Safford 2011). Because of the fuel-driven inverse correlation between frequency and intensity, such fires tended to be of low intensity, and the levels of tree mortality and woody biomass loss were also relatively low. On the other hand, principally climate-limited forest ecosystems support much less frequent fire (unless, as in the case of redwood forests, Native Americans provided high numbers of ignitions). Long FRIs in these ecosystems coupled with slow rates of fuels accumulation and the common coincidence of ignitions with extreme climatic conditions lead to infrequent fires often characterized by more "severe" effects on vegetation and other ecosystem components (Agee 1993, Sugihara et al. 2006*b*). Fire severity is a measure of the ecosystem impact of a fire, for example as a function of mortality or biomass loss to fire. Fire severity correlates (imperfectly) with intensity and, given the known inverse relationship between intensity and fire frequency, we would expect severity and frequency to be inversely related as well. Actual measurements of fire intensity—the energy output of a fire—are difficult to obtain, while severity is readily measured. Fire severity is strongly influenced by vegetation adaptations to fire and some dominant species in climate and/or ignition-limited ecosystems—for example, California red-

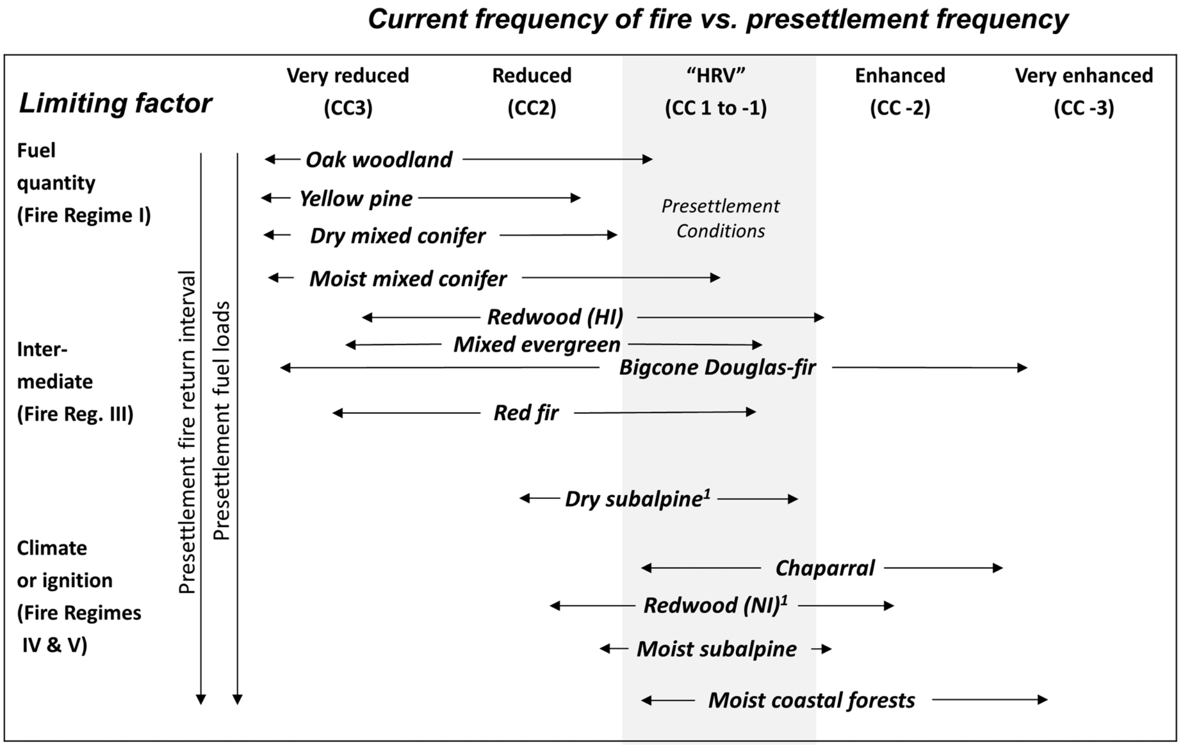

Fig. 1. Major forest ecosystems in California plus chaparral, arranged by their pre-Euroamerican settlement fire regime (y-axis; increasing from top to bottom) and the range of their current departure from presettlement fire frequencies (x-axis; departure ranges from Safford and Van de Water 2013). Locations along both axes are approximate. CC = condition class, see text and Table 1 for details. Dry subalpine and redwood NI (NI = natural ignitions, excluding human ignitions) types estimated without data from Safford and Van de Water (2013). Redwood HI = redwood forest including human ignitions. HRV = historic range of variability. Fire regime types (I, III, IV, V) from Schmidt et al. (2002).

wood—may survive all but the most intense fires.

For the last century, humans have been conducting an unwitting experiment in fuels manipulation across the western US. Suppression of wildfires on public lands began in the first decades of the 20th century and today billions of dollars and tens-of-thousands of personnel are employed annually to extinguish fires in western US ecosystems. The effectiveness of the fire exclusion policy has been tremendous, with more than 97% of all fires extinguished before they reach 120 ha (Calkin et al. 2005). However, the unintentional outcome of this success has been the long-term accumulation of fuels in those ecosystems where frequent fires once reduced them. Because a century of excluding fire has greatly reduced fire occurrence and total annual area burned in erstwhile frequent-fire ecosystems but to a lesser extent in ecosystems where fire was always rare (Mallek et al. 2013, Safford and Van de Water 2013), the ecological impacts of fire suppression should theoretically be stronger in the former than the latter. A specific hypothesis that arises from this relationship is that fire frequency and severity should be strongly inversely related for ecosystems characterized by fuel-limited fire regimes, but not closely related for ecosystems characterized by fire regimes more limited by factors other than fuel. Until recently, the data to rigorously evaluate this hypothesis were lacking, but the growing availability of remotely-sensed imagery has provided solid evidence that fire-suppressed areas dominated by more fuel-limited forest ecosystems are experiencing increases in fire severity over time, while more climate-limited forest types generally are not (Miller et al. 2009*b*, Dillon et al. 2011*b*, Miller et al. 2012*b*, Mallek et al. 2013). These analyses have shown that climate variables account for some of the observed patterns, and inference has been made connecting differences in relative fuel accumulations with these patterns, but a comprehensive and direct analysis of fire severity patterns versus fuels has remained lacking.

Such an analysis is important because basic generalizations about fire behavior and fire's relationship to fuel across ecosystems underlie our ability to manage fire and fuel. Most widely-used classifications of wildland fire regimes are derived from the relationship between fire frequency and severity (e.g., Heinselman 1973, Heinselman 1981, Johnson and Vanwagner 1985, Brown and Smith 2000, Schmidt et al. 2002), and such classifications form the basis for understanding and mapping current ecosystem status, identifying departures from reference conditions, and prioritizing management actions. Synoptic considerations of fire ecology treat various components of the fire regime (e.g., Agee 1993, Bond and van Wilgen 1996, Sugihara et al. 2006*b*), but fuel and its interactions with fire frequency and severity invariably play a primary role in discussions of ecosystems and their differential relationships with fire. Nevertheless, several authors have recently called into question the role of fuel in driving fire behavior, claiming that weather conditions at the time of burning are globally more important, and declaring that decades-old generalizations about fuels, fire frequency and fire severity are unsupportable (e.g., Odion and Hanson 2006, Hanson and Odion 2013).

In this contribution, we conduct a broad-scale analysis of the relationship between fire frequency and severity across forest ecosystem types that vary in their dominant species, environment, and historical relationship with fire. Our purpose is to evaluate the hypothesis that fire frequency and fire severity should be negatively related for forest ecosystems characterized by mostly fuel-limited fire regimes (e.g., yellow pine, mixed conifer), but not closely related for forest ecosystems characterized by fire regimes more limited by other factors. The difficulty with such an analysis is the absence of wildland fuel data at the temporal and geographic scales necessary to carry out a long-term, broad-scale assessment of this hypothesis. However, because of the fire frequency-severity relationship, a useful surrogate for direct measurements of the fuel load is the modern fire frequency itself. In this contribution, we combine geospatial data on fire frequency over the last century with remotely sensed data measuring fire severity to vegetation since 1984 for five major forest types in California to evaluate the overall relationship between fire severity and two inverse metrics of fire frequency: time since last fire and fire return interval.

Methods

Study area and forest types

We were interested in the effects of fire suppression on fire severity in conifer-dominated forests, and the US Forest Service continues to suppress almost all wildland fires occurring on lands under its jurisdiction. Because the effects of fire suppression on severity patterns are likely to be most evident on Forest Service land, our analysis focused on fires that burned at least partially on these lands in California (Fig. 2).The US National Park Service on the other hand, the other major federal forest manager in California, allows many wildland fires to be managed for resource benefits (rather than immediately suppressing them), and fire suppression effects on fuels have been ameliorated in many NPS-managed landscapes, especially in the Sierra Nevada (Collins et al. 2009). Private and corporate landowners manage most of the remaining forestland in California. On these lands, dead and dying trees are usually logged within a month or two of any fire event, which makes fire severity assessment using the standard one-year post-fire comparison (as in the national Monitoring Trends in Burn Severity [MTBS] program) impossible.

California's climate is largely Mediterranean with wet, cool winters and warm, dry summers; an intra-annual dry period of 3–6 months is typical (Minnich 2006). For a given elevation and distance from the ocean, northern California is cooler and wetter than southern California. We limited our analysis to forest types that supported presettlement fire regimes characterized by mean fire return intervals (FRIs) of less than 50

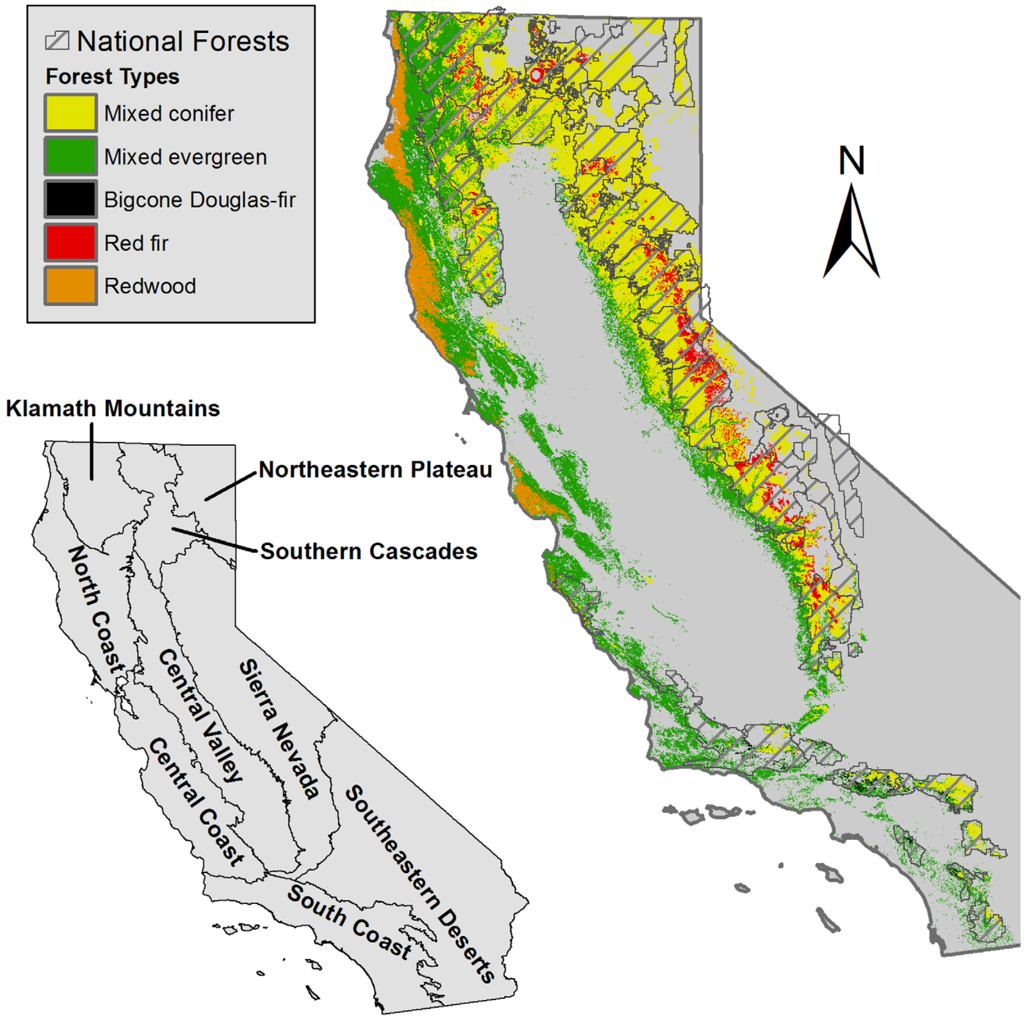

Fig. 2. Distribution of forest types across California and the bioregions used in this assessment (from Sugihara et al. 2006*b*). Forest type legend order is from shortest to longest reference fire return interval (excluding human ignitions in the case of redwood).

years and where our severity database contained at least 5000 ha of mapped fire area. Presettlement fire regimes with longer historic FRIs were excluded because our dataset does not extend far enough into the past to allow accurate assessment of the current FRIs of infrequently burning forests. Due to their similarity in fire regimes and general tree composition and also due to very similar outcomes of the statistical modeling, yellow pine, dry mixed conifer and moist mixed conifer were combined into a single "mixed conifer" category for our final analysis (as per Hessburg et al. 2005, Miller and Safford 2012). Therefore, the forest types considered in our analysis include mixed conifer, mixed evergreen, red fir, bigcone Douglas-fir (BCDF) and redwood (Fig. 2, Table 1). These forest types are largely conifer-dominated, but hardwood/broadleaf trees are present in all of them and can be locally dominant in certain phases of mixed conifer and especially mixed evergreen forests. Because our analysis was focused primarily on Forest Service lands, inland forest types like mixed conifer, mixed evergreen and red fir are best represented. The distribution of BCDF in California is largely encompassed by National Forest lands but covers a relatively small area in the South Coast bioregion. Because the distribution of redwood

Table 1. Forest type classifications, reference fire return intervals, fire regime classes and dominant woody species. Forest types are ordered from shortest to longest reference fire return interval (excluding human ignitions in the case of redwood; see Fig. 1).

Forest type	Reference fire return intervals (years)† Mean (median)	Range	Regime group‡	Dominant woody species†
Mixed conifer				
Yellow pine	11 (7)	5–40	I	*Pinus ponderosa, P. jeffreyi, P. lambertiana, Quercus kelloggii*
Dry mixed conifer	11 (9)	5–50	I	*Pinus ponderosa, P. lambertiana, Calocedrus decurrens, Abies concolor, Q. kelloggii*
Moist mixed conifer	16 (12)	5–80	I	*Abies concolor, Pseudotsuga menziesii, Calocedrus decurrens, Pinus ponderosa, P. lambertiana, P. contorta* ssp. *murrayana, Sequoiadendron giganteum*
Mixed evergreen	29 (13)	15–80	I/III§	*Pseudotsuga menziesii, Lithocarpus densiflorus, Quercus agrifolia, Q. chrysolepis, Umbellularia californica, Arbutus menziesii, Acer macrophyllum, Pinus ponderosa, P. lambertiana*
Bigcone Douglas-fir	31 (30)	5–95	I/III§	*Pseudotsuga macrocarpa, Quercus chrysolepis*
Red fir	40 (33)	15–130	III	*Abies magnifica, A. concolor, Pinus monticola, P. murrayana*
Redwood	23 (15)	10–170	I/III¶	*Sequoia sempervirens*

† From Van de Water and Safford (2011). "Reference" = the three or four centuries prior to Euroamerican settlement.
‡ The standard National Fire Plan Fire Regime Groups (Schmidt et al. 2002) are defined as: I, fire frequency between 0 and c. 35 years and fire severity mostly low (predominantly surface fires); III, fire frequency of c. 35 to c. 200 years and mixed severity (patchy distribution of low and high severity).
§ Mixed evergreen and bigcone Douglas-fir are often placed in fire regime III even though mean historical fire frequency is <35, because modern fire effects are dominated by mixed severity.
¶ Redwood presettlement fire regime almost entirely driven by anthropogenic ignitions. In the absence of these, regime would be III and the reference FRI would be longer.

forests is largely coastal and outside of Forest Service management, our data are relatively sparse for this forest type and only encompass areas within the southern part of the species' range (Fig. 2).

Spatial data

The Forest Service maintains a geodatabase of fire severity data, based on LANDSAT-TM satellite imagery, for medium and large fires (mostly >80 ha in the Sierra Nevada and NE California, >400 ha elsewhere) since 1984 that have occurred at least partially on Forest Service lands in California (available online at http://www.fs.usda.gov/wps/portal/fsinternet/main/r5/landmanagement/gis). To allow inter-fire comparisons of severity, we based our fire severity analyses on the Relativized differenced Normalized Burn Ratio (RdNBR), which takes into account different pre-fire vegetation conditions. RdNBR data were converted to units of the composite burn index (CBI; Key and Benson 2006), a field-based measure of fire severity (Miller and Thode 2007). In our severity analysis, which includes fires mapped between 1984 and 2011, we focused on the occurrence of "high-severity" fire, where a substantial proportion of the pre-fire biomass is removed or killed by fire. Our definition of high-severity follows Miller and Thode (2007), and includes all burned areas where the CBI is >2.25. In conifer-dominated forest patches, this high-severity class equates to approximately 95–100% change in canopy cover (Miller et al. 2009*a*). Thus, the high-severity category we used represents stand-replacing fire, where forest has mostly been converted to a non-forested condition. One-year post-fire extended assessments of fire severity are most common in the database, but initial assessments conducted soon after a fire is extinguished were also conducted in some cases. Where initial assessments exist and are preferred (as indicated in the database), we substituted them for data derived from extended assessments in our analysis (a little less than 10% of all fires).

We used the California Fire Return Interval Departure database (Safford and Van de Water 2013; http://www.fs.usda.gov/detail/r5/landmanagement/gis/?cid=STELPRDB5327836) to define contiguous patches of forest with the same presettlement fire regime (PFR; Van de Water and Safford 2011) and fire history. The California FRID database is comprised of a series of fire frequency-related metrics and compares

Table 2. Fire return interval departure classes and class descriptions. Negative condition classes occur where current FRIs are shorter than presettlement FRIs; positive condition classes occur where current FRIs are longer than presettlement. Adapted from Safford and Van de Water (2013).

FRID condition class	Description of current FRI relative to presettlement mean
−3	Less than 1/3 the length
−2	Between 2/3 and 1/3 the length
−1	Greater than 2/3 the length
1	Less than 1.5 times longer
2	Between 1.5 and 3 times longer
3	Greater than 3 times longer

them to pre-settlement frequencies for major ecosystem types differentiated by their fire regimes (Van de Water and Safford 2011, Safford and Van de Water 2013). Where severity data exist, fire history layers were stratified by a combination of PFR and two fire frequency-related metrics: current mean fire return interval (FRI; Eq. 1) and time since last fire (TSLF).

$$Y = A/(B+1) \tag{1}$$

where $Y =$ the current mean fire return interval, A = the number of years on record (fire year − 1908); and $B =$ the number of fires.

This created a dataset of unique polygons representing forest patches with distinct fire histories: these patches were our basic sample unit. Fire history and fire severity layers were intersected for each year from 1984 to 2011 and the proportion of high severity fire (PHS) was subsequently calculated for each forest patch. For summary purposes we also calculated fire return interval departure (FRID) using the mean percent FRID ("mean PFRID") metric. FRID measures the contemporary (since 1908) departure from mean presettlement ("reference") FRIs in percent (Safford and Van de Water 2013). Mean PFRID ranges from 100% to −100% (Eqs. 2 and 3).

$$Y_{(L)} = [1 - \left(\frac{A}{B}\right) \times 100 \tag{2}$$

$$Y_{(S)} = [1 - \left(\frac{B}{A}\right) \times 100 \tag{3}$$

where $Y_{(L)}$ is mean PFRID when current FRI is longer than reference and $Y_{(S)}$ is mean PFRID when current FRI is shorter than reference; $A =$ the mean reference FRI; and $B =$ the current mean FRI.

We subsequently reclassified mean PFRID to a scale ranging from 3 to −3, which conforms to the condition class scale of Safford and Van de Water (2013), and assigned the appropriate value to each patch. In this scale, negative and positive classes represent a shortening and lengthening of FRI respectively, as compared to presettlement FRIs (Table 2).

Statistical analysis

We treated each contiguous burned patch with distinct fire history and forest type as our sample unit. Our data are inherently nested, with multiple patches of the same forest type occurring within the boundaries of each individual fire and burning under similar weather and/or topographic conditions, so to avoid pseudoreplication we used a mixed model approach with fire ID and patch ID as obligatory random effect variables. The two fixed effects tested were current mean fire return interval (FRI; years) to account for a patch's long-term fire frequency (between 1908 and the year of the burn considered), and time since last fire (TSLF; years) to account for a patch's more recent fire history. The minimum patch size considered was 900 m^2, equal to the resolution of the LANDSAT-derived severity data. Our response variable was the proportion of area burned at high-severity (PHS) within a patch. We used a generalized linear mixed model with a binomial error structure and logit-link. TSLF and FRI predictors were centered and parameter estimates are reported on the logistic scale. Since our surrogates for fire frequency—TSLF and FRI—are inversely related to frequency, a positive relationship between PHS and TSLF or FRI is evidence of a negative relationship between severity and frequency. That is, a positive slope indicates a likely increase in PHS as TSLF increases or as FRI lengthens.

In addition to modeling the relationship between fire frequency metrics and fire severity across a forest type's state-wide range, we also assessed relationships on a bioregional basis (Fig. 2). Bioregional models were run for forest types where a minimum of 5000 hectares of fire severity data existed. This approach restricted bioregional models to mixed conifer and mixed evergreen forests in those bioregions where they

Table 3. Modeled sample size in terms of burned area, number of fires and number of patches for full and bioregion models.

Forest type	Bioregion	Total area (ha)	No. fires	No. patches
Mixed conifer	All	184,562	360	12,990
	Klamath Mountains	41,832	80	2,649
	North Coast	9,721	24	898
	Sierra Nevada	98,764	168	6,340
	South Coast	14,788	43	1,687
	Southern Cascades	14,783	26	978
Mixed evergreen	All	221,538	395	18,891
	Central Coast	50,611	26	3,216
	Klamath Mountains	84,678	78	2,175
	Sierra Nevada	26,472	126	3,055
	South Coast	51,864	134	8,930
Bigcone Douglas-fir	All	14,442	65	2,080
Red fir	All	5,577	57	574
Redwood	All	5,060	10	328

are most well represented. Although all areas mapped for fire severity are included in our summary of fire history condition, patches for which we could not calculate TSLF and FRI accurately (i.e., areas that had not previously burned since 1908) could not be included in the statistical modeling, reducing our model sample size (Table 3). The statistical package R (R Development Core Team 2011) was used for all statistical analysis, and the lme4 package (Bates et al. 2012) was used for our mixed models.

Results

We assessed the relationship between the fire frequency history of forests at the time of contemporary burns and fire severity both in aggregate for each forest type and at the patch-level. Statistical assessment of the association between fire frequency and severity was done at the patch-level, although we also present the implications of model predictions for each forest type as a whole. Due to the uneven distribution of patch size (Fig. 3), the question of how much high-severity fire is occurring across the landscape differs somewhat from how much high-severity fire is occurring in a "typical" patch of a given forest type. For all forest types combined, 87% of burned patches were <25 ha in size but only accounted for 17% of the total area burned, while patches >150 ha in size accounted for only 3% of the total number of patches but 64% of the total burned area. Thus, the small number of large patches has a disproportionate effect on the overall percentage of high-severity observed across a forest type.

Fire history condition and severity

The data show most of the forested area mapped for severity in California has experienced very infrequent fire since reliable records began in 1908, relative to pre-Euroamerican settlement norms. At the time of the mapped fires, 66% of the study area had not burned since at least 1908. Red fir and mixed conifer showed the greatest relative area without a previous fire (87% and 74%, respectively) and redwood forests showed the least (29%; Table 4). Likewise, prior to the observed burns the current mean fire return interval (FRI) was longer than presettlement means for the majority of the area of all forest types. This is especially true for mixed conifer, with 93% of its total area categorized as condition class three, indicating an especially large and consistent lengthening of the FRI for this forest type over the last century (Fig. 4). Likewise, if forests were currently burning under reference (presettlement) frequencies we would expect TSLF values to be distributed around the mean reference FRI. However, our data show that TSLF values are mostly greater than the mean reference FRI, with high proportions of the area not having experienced fire for at least 75 years (Fig. 4).

Across the five forest types assessed, 22% of the mapped area burned at high-severity. BCDF and mixed conifer forests had the most relative area burned at high-severity (35% and 26%, respectively), and redwood forests showed the least relative area (7%; Table 4). At the patch-

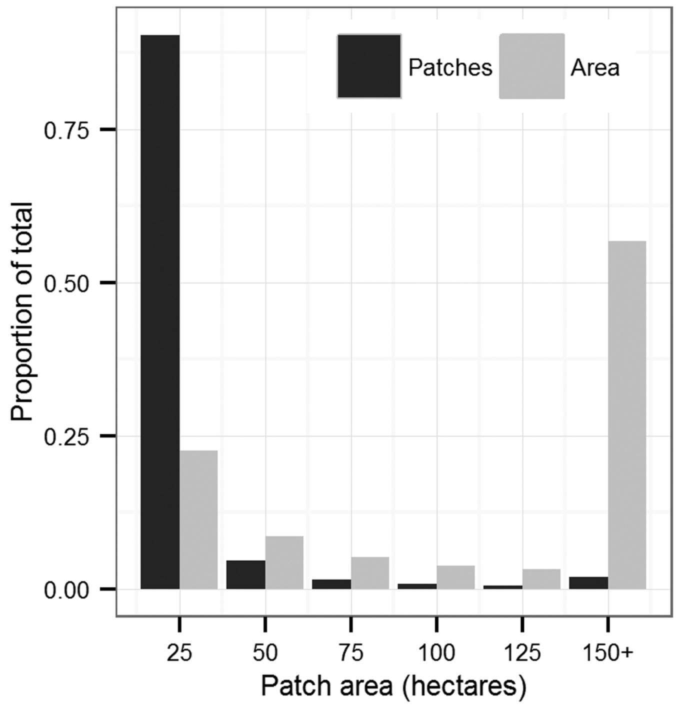

Fig. 3. Summary of patch size classes for all forests assessed as proportion of the total number of burned patches (black) and total burned area (gray).

level, BCDF also showed the highest proportional levels of high-severity fire, with mean and median values of 32% and 11%, respectively. Red fir and redwood forests showed the lowest levels of high-severity fire under current conditions. In all cases, mean patch high-severity was greater than the median due to the non-Gaussian distribution of proportional data and the tendency of large patches to burn at higher severity than small patches (Table 4). Importantly, it can be seen that proportion high-severity (PHS) in contemporary fires is much higher than the presettlement estimate for the more fuel-limited forest types (mixed conifer and mixed evergreen), but close to the presettlement estimate for the more climate- or ignition-limited types (red fir and redwood; Table 4). We have no presettlement estimate for fire severity in BCDF forests.

Table 4. Summary of fire history condition and burn severity for burned areas assessed. Areas without a previous fire record are included in this summary but not in the statistical modeling.

Forest type	Area mapped for severity (ha)	Area without previous fire record (%)	Presettlement reference high severity (% area)†	Area burned at high severity (%)	Patch mean (median) high severity (%)‡
All	1,280,482	66.23	NA	22.32	15.69 (0.00)
Mixed conifer	720,706	74.35	4–8	26.08	13.17 (0.00)
Mixed evergreen	488,476	54.53	2–5	17.35	18.17 (0.00)
Bigcone Douglas-fir	21,894	33.85	Unknown	35.22	31.57 (11.03)
Red fir	42,235	86.75	8–20	11.64	8.07 (0.00)
Redwood	7,171	29.37	0–6	6.78	6.03 (0.00)

† Estimate of mean high severity as a percent of burned area during the presettlement reference period. Mixed conifer and red fir from Mallek et al. (2013), mixed evergreen and redwood from Stephens et al. (2007) and the LANDFIRE BpS fire modeling outputs (Rollins 2009; see Mallek et al. 2013 for details).

‡ Patch-level metrics are calculated with a minimum 900-m^2 patch size.

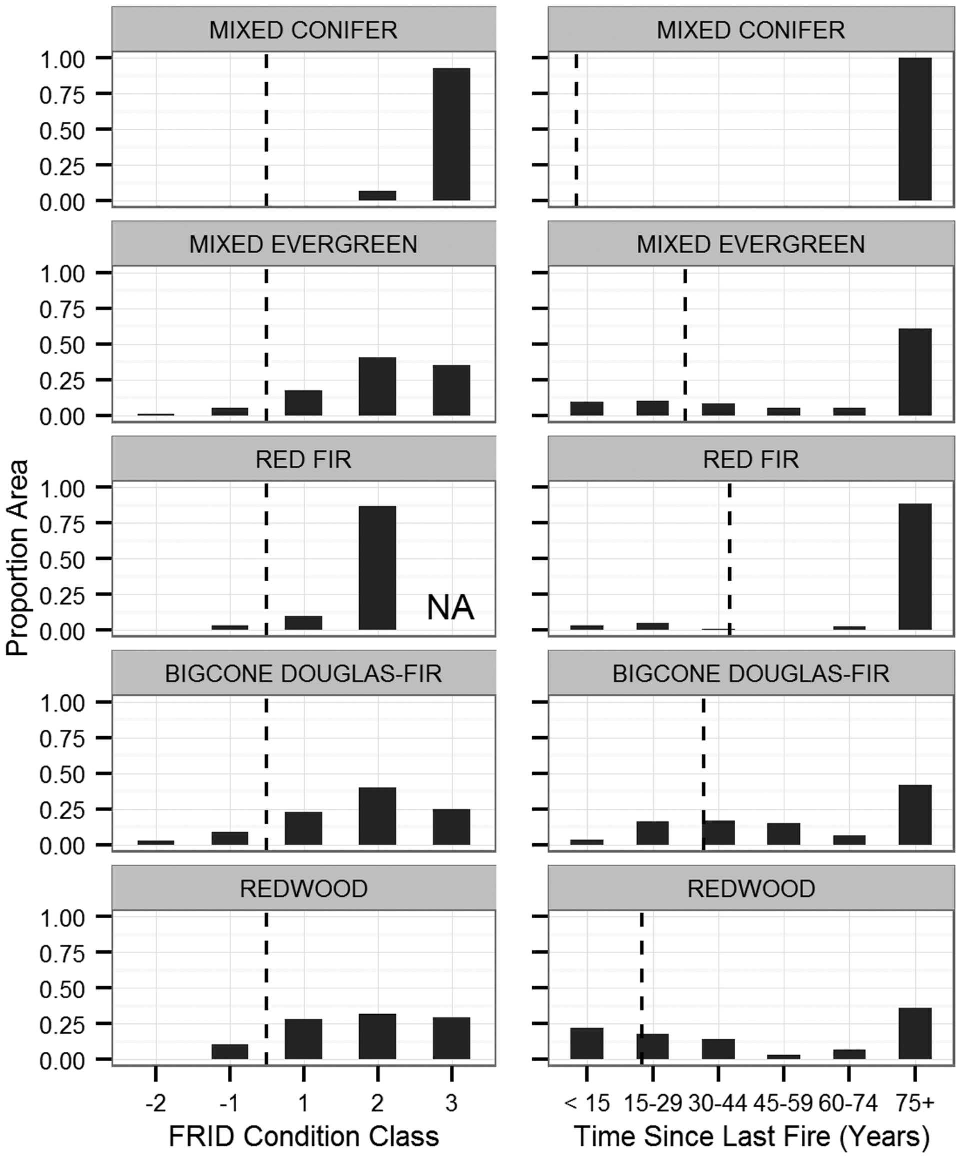

Fig. 4. Proportion of area within each fire return interval departure (FRID) condition class and time since last fire (TSLF) bin for each forest type of interest. Vertical dashed lines show the estimated mean reference conditions. Some of the area within red fir forests is likely in FRID condition class 3, but due to the relatively long reference FRI of red fir (40 years), we do not have sufficient data history to distinguish between condition class 2 and 3 (the minimum current FRI to be categorized as condition class 3 would be 121 years). Condition class −3 (representing a departure of greater than 67% toward more frequent fires) is not shown because none of the land area mapped for burn severity fell within this class.

Statistical analyses

Model estimates for all bioregions combined show that TSLF and FRI are strongly positively related to PHS in three of the five forest types (Fig. 5, Table 5). In the mixed conifer, mixed evergreen, and BCDF forest types, the longer an area has gone without fire or the less frequent fire has been since 1908, the higher the likelihood that a greater proportion will burn at high-severity during a subsequent fire. The 95% confidence interval of the estimated slopes for the associa-

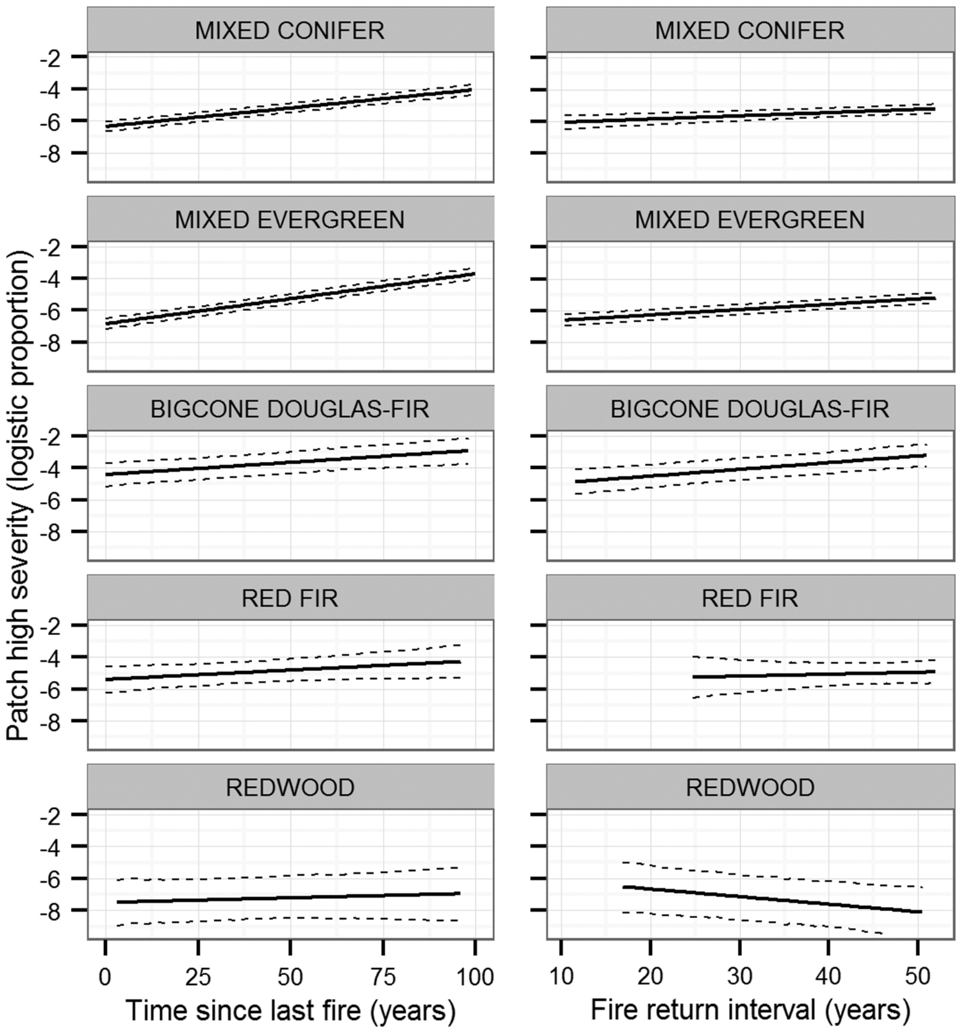

Fig. 5. Plotted estimates and 95% confidence intervals of the effect of time since last fire and mean fire return interval on proportion high severity (logistic scale) of a typical patch. Confidence intervals reflect the variation among model fixed effects but not its random effects.

tion between PHS and TSLF in red fir and redwood forests as well as PHS and FRI for red fir bracketed zero, suggesting no strong relationship between these variables. Our results indicate a negative relationship between FRI and PHS in redwood forests, suggesting in this case that high-severity fire increases with fire frequency (Fig. 5, Table 5).

Within mixed conifer and mixed evergreen forests, we observe further differentiation of these relationships when bioregions are considered separately. TSLF and PHS are strongly positively related in all of the bioregions except the Klamath Mountains, where there appears to be no statistical relationship. Assessments of the relationship between FRI and PHS by bioregion suggest weaker relationships for both forest types. Mixed conifer forests showed a strong positive relationship in the southern Cascades bioregion, as did mixed evergreen forests in the South Coast and Sierra Nevada bioregions. The other bioregion models resulted in slope estimates where the 95% confidence interval encompassed zero, suggesting that for these California regions FRI is not as strong a predictor of high-severity burning as TSLF (Fig. 6, Table 6).

Table 5. Parameter estimates (and standard errors) of the logit-linear relationship between time since last fire and fire return interval with proportion of high-severity fire of burned patches. Significant estimates (i.e., where the 95% confidence intervals do not include zero) are in boldface.

Forest type	Time since last fire model		Fire return interval model	
	Intercept	Slope	Intercept	Slope
Mixed conifer	**−5.377 (0.143)**	**0.023 (0.002)**	**−5.428 (0.143)**	**0.020 (0.005)**
Mixed evergreen	**−5.625 (0.157)**	**0.031 (0.002)**	**−5.674 (0.160)**	**0.033 (0.004)**
Bigcone Douglas-fir	**−3.772 (0.338)**	**0.015 (0.004)**	**−3.728 (0.335)**	**0.042 (0.008)**
Red fir	**−5.007 (0.342)**	0.012 (0.007)	**−5.004 (0.338)**	0.012 (0.026)
Redwood	**−7.300 (0.668)**	0.006 (0.009)	**−7.490 (0.718)**	**−0.048 (0.021)**

Figs. 5 and 6, and Tables 5 and 6 present parameter estimates in units of the logistic scale. In Fig. 7 we present the relationship between PHS and TSLF for mixed conifer forests using the untransformed response variable to facilitate interpretation. In Fig. 7, gray lines represent the aggregated predictions of all patches within each fire in our modeled dataset, and the thick blue line is the aggregated model prediction for all patches within the forest type. These curves represent model predictions for the population of patches and fires in our modeled dataset across the range of TSLF. For mixed conifer forests across California, our model predicts an approximately 2.5× increase in the aggregate PHS as TSLF moves from zero to 100 years. Tables 7 and 8 provide similar information in tabular format for each forest type and bioregion where applicable.

Discussion

Our results show that two inverse measures of fire frequency, fire return interval (FRI) and time since last fire (TSLF), are strongly positively related to fire severity in California forests and bioregions where climatic conditions during the fire season are nearly always propitious for fire activity but fuel availability may not be (e.g., yellow pine and mixed conifer). On the other hand, such inverse measures of fire frequency did not show positive relationships with fire severity in forest types (e.g., red fir and redwood) and bioregions (e.g., Klamath Mountains) where fire may be more limited by factors other than fuel loads, such as climate or ignition rates. Two intermediate forest types, mixed evergreen and bigcone Douglas-fir (BCDF), also showed a strong association between fire frequency and severity. These results support the general theoretical precept that where fuel amount is a major limiting factor to fire activity, removing that limitation (by increasing fuels due to long-term lack of fire) should result in an increase in fire intensity—and thus severity—when fire does occur.

Our results are especially robust for the more fuel-limited mixed conifer forests (yellow pine, mixed conifer) and mixed evergreen, which together comprise 94% of our study area and experienced most of the burned area we analyzed. These forest types experienced frequent fire before Euroamerican settlement, but today fire is very rare. Various studies have found increasing trends in fire severity in frequent-fire forest ecosystems that are managed under current policies of fire suppression in California and the southwestern US, and inference has been made regarding the likely role of increasing fuels in driving these patterns (e.g., Dillon et al. 2011*a*, Miller and Safford 2012, Mallek et al. 2013). To this point however, a broad scale test of the fire suppression-fire severity hypothesis has been lacking. Our results provide the first broad-scale assessment of the hypothesis—across almost three decades, hundreds of fires, and the state of California—and show that, as predicted, the dependence of fire behavior on fire frequency is strong for more fuel-limited forest types and bioregions but weak or nonexistent for forests where fire is limited more strongly by other factors.

Disturbance regimes are summaries of disturbance behavior in ecosystems over many years and across many events (Pickett and White 1985). For fire regimes, the amount of time necessary to determine descriptive statistics ranges from many decades to centuries, depending on fire

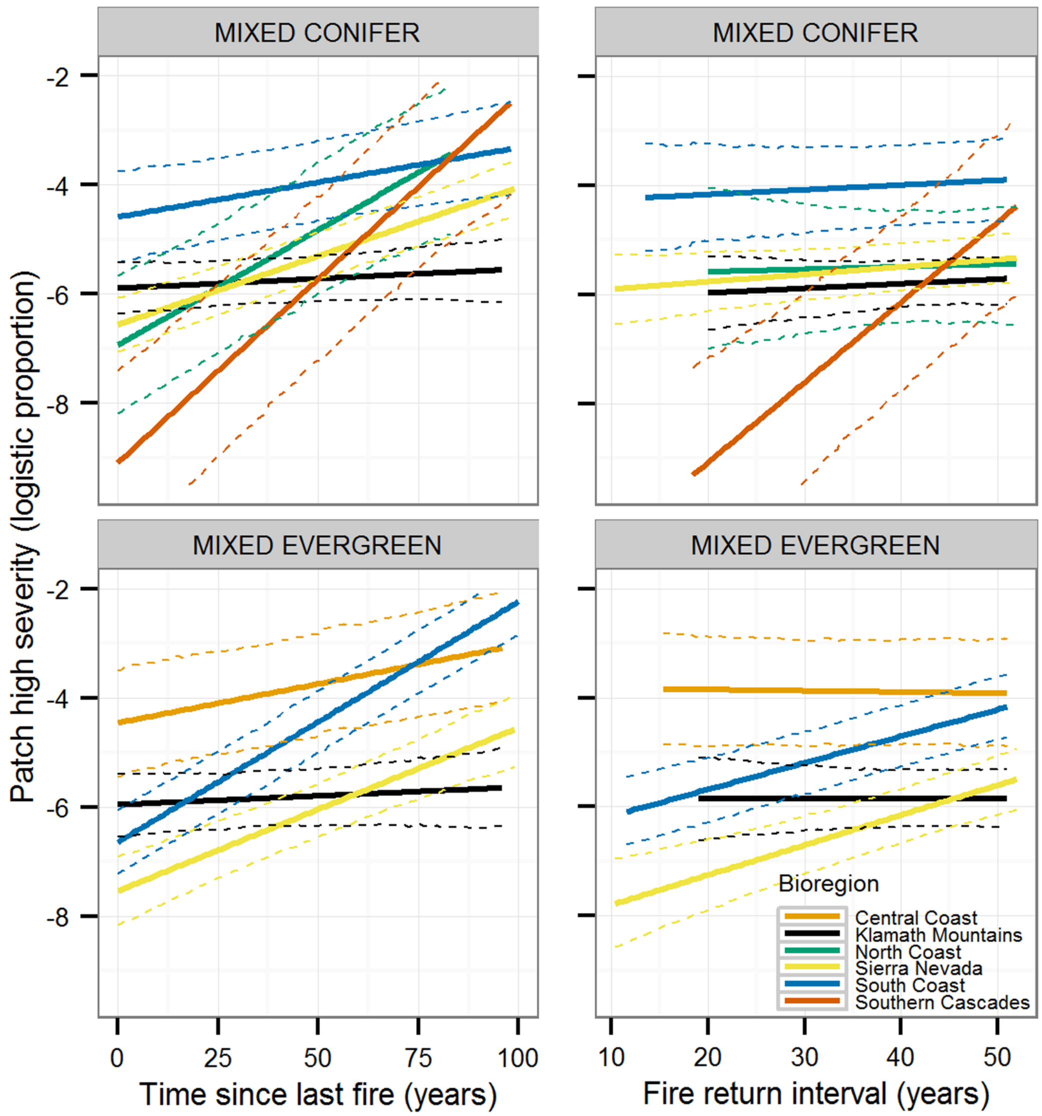

Fig. 6. Plotted estimates and 95% confidence intervals for mixed conifer and mixed evergreen bioregional models.

frequency, extent, and variability, among other things. For this reason, it is challenging to use short-term datasets like our fire severity database—which in this study includes 660 fires and less than thirty years of data—to study the nature of fire regimes. That said, we know of no other attempt to empirically validate general theory regarding the relationship between fire frequency and severity that has studied the issue across such a broad landscape and with such a comprehensive dataset. At the same time, there are a number of studies based on a few fires from a single year or a few years which have attempted to draw conclusions about the general frequency-severity relationship in ecosystems in and around California (Odion et al. 2004, Odion and Hanson 2006). Studies based on such small samples have little application to questions of departures from general fire regimes however, and caution should be used in generalizing their results (Safford et al. 2008, Miller and Safford 2012).

Our findings underline the importance of the ecosystem context in understanding the relative

Table 6. Parameter estimates (and standard errors) of the logit-linear relationship between time since last fire (TSLF) and fire return interval (FRI) with proportion of high-severity fire of burned patches. Significant estimates (i.e., where the 95% confidence intervals do not include zero) are in boldface.

Fixed effects	Bioregion					
	Central Coast	Klamath Mountains	North Coast	Sierra Nevada	South Coast	Sothern Cascades
Mixed conifer						
Intercept	...	**−5.786 (0.211)**	**−5.282 (0.598)**	**−5.420 (0.222)**	**−3.980 (0.373)**	**−6.049 (0.770)**
TSLF	...	0.004 (0.003)	**0.042 (0.007)**	**0.025 (0.003)**	**0.013 (0.004)**	**0.067 (0.008)**
Intercept	...	**−5.779 (0.209)**	**−5.489 (0.526)**	**−5.489 (0.220)**	**−3.967 (0.373)**	**−6.583 (0.830)**
FRI	...	0.008 (0.011)	0.004 (0.023)	0.014 (0.008)	0.009 (0.012)	**0.147 (0.024)**
Mixed evergreen						
Intercept	**−4.012 (0.480)**	**−5.871 (0.261)**	...	**−6.166 (0.250)**	**−4.834 (0.287)**	...
TSLF	**0.014 (0.004)**	0.003 (0.004)	...	**0.030 (0.004)**	**0.044 (0.002)**	...
Intercept	**−3.897 (0.488)**	**−5.856 (0.260)**	...	**−6.287 (0.253)**	**−4.850 (0.286)**	...
FRI	−0.002 (0.008)	0.000 (0.012)	...	**0.055 (0.011)**	**0.049 (0.005)**	...

Notes: Bioregional models were developed where at least 5000 ha of severity data were available. Where fewer data were available models were not created and cells are left blank.

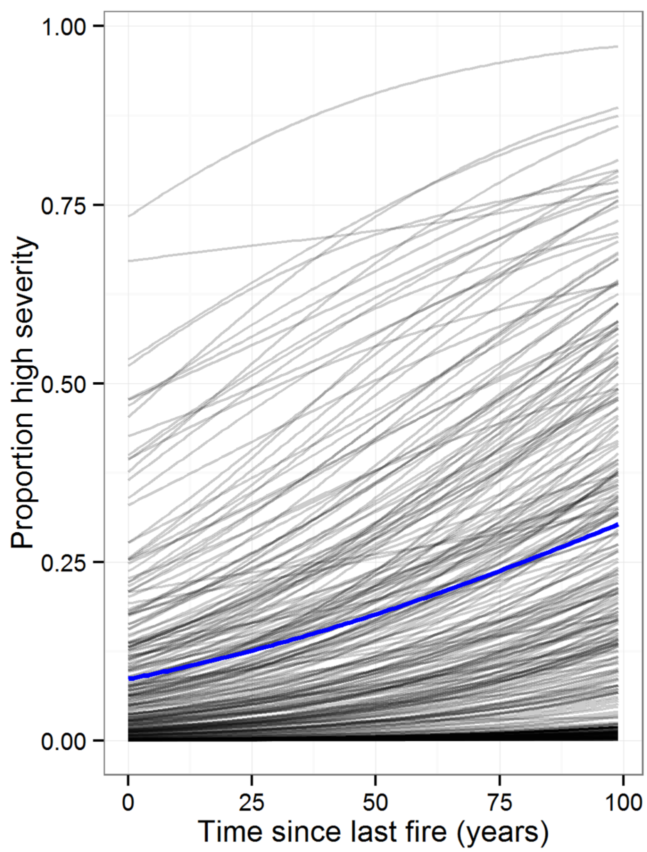

Fig. 7. Predictions of proportion high-severity fire across the range of time since last fire for mixed conifer forests. Predictions are made for each patch in our modeled dataset and aggregated by fire (gray lines) and for the forest type as a whole (blue line). Aggregations were weighted by patch area.

Table 7. Predicted proportions of high-severity fire at various levels of time since last fire. Predictions are made for each patch in our modeled dataset and aggregated for all observed burns of each forest type. Aggregations were weighted by patch area.

Forest	Time since last fire				Model prediction at ref TSLF†
	10 years	25 years	50 years	75 years	
Mixed conifer	0.12	0.13	0.17	0.20	0.13
Klamaths	*0.12*	*0.12*	*0.12*	*0.13*	0.12
North Coast	*0.08*	*0.11*	*0.18*	*0.27*	0.08
Sierra Nevada	*0.11*	*0.13*	*0.16*	*0.20*	0.11
South Coast	*0.35*	*0.37*	*0.40*	*0.43*	0.35
S. Cascades	*0.02*	*0.03*	*0.08*	*0.16*	0.02
Mixed evergreen	0.14	0.16	0.21	0.28	0.17
Central Coast	*0.26*	*0.28*	*0.31*	*0.34*	0.28
Klamaths	*0.06*	*0.06*	*0.07*	*0.07*	0.06
Sierra Nevada	*0.08*	*0.09*	*0.12*	*0.16*	0.10
South Coast	*0.21*	*0.26*	*0.35*	*0.44*	0.27
Bigcone Douglas-fir	0.36	0.38	0.41	0.45	0.35
Red fir	0.08	0.09	0.10	0.12	0.10
Redwood	0.06	0.06	0.06	0.07	0.06

† Modeled predictions of proportion of high severity if the current landscape were characterized by TSLF or FRI values equal to the presettlement mean FRIs for the given forest type (Table 2; 11 years used for mixed conifer).

roles of fuels and other factors in influencing fire regimes. Forest Service-managed landscapes in California are topographically complex and involve broad gradients of elevation and climate. Vegetation and fuels respond to these gradients, and have fundamental effects on fire occurrence and behavior. Although every fire is to some extent an idiosyncratic event, broad similarities in fire regime typify certain combinations of vegetation and fuels, and such commonalities have given rise to broad and useful generalizations relating fire and the ecosystems in which it occurs (e.g., Heinselman 1973, Agee 1993, Schoennagel et al. 2004, Noss et al. 2006, Sugihara et al. 2006*b*, Halofsky et al. 2011). Our results demonstrate that variability exists between ecosystem types and bioregions. Below we briefly treat each of the forest types we analyzed, and discuss ecological and management implications of our findings.

Table 8. Predicted proportions of high-severity fire at various levels of fire return interval. Predictions are made for each patch in our modeled dataset and aggregated for all observed burns of each forest type. Aggregations were weighted by patch area.

Forest	Fire return interval				Model prediction at ref FRI†
	10 years	15 years	30 years	45 years	
Mixed conifer	0.12	0.13	0.14	0.16	0.12
Klamaths	. . .	. . .	*0.11*	*0.12*	0.11
North Coast	. . .	. . .	*0.15*	*0.15*	0.15
Sierra Nevada	*0.13*	*0.13*	*0.14*	*0.15*	0.14
South Coast	. . .	*0.38*	*0.39*	*0.40*	0.39
S. Cascades	. . .	. . .	*0.05*	*0.13*	0.05
Mixed evergreen	. . .	0.15	0.17	0.20	0.16
Central Coast	. . .	*0.30*	*0.29*	*0.29*	0.29
Klamaths	. . .	. . .	*0.07*	*0.07*	0.07
Sierra Nevada	. . .	*0.08*	*0.11*	*0.14*	0.10
South Coast	. . .	*0.24*	*0.29*	*0.35*	0.29
Bigcone Douglas-fir	. . .	0.32	0.38	0.44	0.34
Red fir	. . .	. . .	0.08	0.09	0.09
Redwood	. . .	. . .	0.08	0.05	0.08

Note: Where predictions would extend beyond the range of the data, cells are left blank.

† Modeled predictions of proportion of high severity if the current landscape were characterized by TSLF or FRI values equal to the presettlement mean FRIs for the given forest type (Table 2; 11 years used for mixed conifer).

Mixed conifer and mixed evergreen

For California as a whole, in mixed conifer and mixed evergreen forests predominantly managed by the Forest Service, we found a strongly positive relationship between PHS and both TSLF and the length of the current mean FRI (Table 5, Fig. 5). Across the population of fires and burned patches in our dataset there is wide variation in fire severity, but our analysis shows that for a given fire, and for the forest types as a whole, PHS is most likely to increase as TSLF or FRI rise (Figs. 5–7; Tables 5–8). The area burned at high-severity in mixed conifer and mixed evergreen forests is much higher today than before Euroamerican settlement: c. 26% and 17%, respectively, versus 2–8% historically (Table 4; Stephens et al. 2007, Mallek et al. 2013). For these forest types, our results strongly suggest that modern increases in fire severity are related to augmented fuels stemming from the general lack of fire over the last century.

Yellow pine and mixed conifer forests in California were historically characterized by frequent, mostly low-severity fires (Agee 1993, Sugihara et al. 2006*b*). Today, almost 75% of the area occupied by these forest types has not experienced fire since at least 1908. On Forest Service lands, where full fire suppression is still practiced in most areas, this is leading to an increase in both the area and the proportion of high-severity fire (Miller et al. 2009*b*, Miller and Safford 2012, Mallek et al. 2013). Most recently, the 2013 Rim Fire in the central Sierra Nevada burned 105,000 ha across a landscape dominated by logged and fire-suppressed mixed conifer forest. Early estimates show approximately 40% of the fire area burned at high-severity, with some patches of stand-replacing fire exceeding 5000 ha (J. Miller, *personal communication*). Patches of this size are normal in fires occurring in climate-limited forest types like Rocky Mountain lodgepole pine (*P. contorta* ssp. *latifolia*; e.g., in the 1988 Yellowstone fires) or ignition limited vegetation types like chaparral, but they were all but unheard of in mixed conifer forests until the relatively recent past (Miller et al. 2009*b*, Miller et al. 2012*a*). Natural regeneration of such severely burned forests can be markedly delayed as seed sources become increasingly distant from the interiors of large stand-replacing patches (Hobbs and Huenneke 1992, Chappell and Agee 1996, Pierce and Taylor 2011). Reduced conifer regeneration, coupled with changing climate and other anthropogenic stressors like air pollution and invasive species, increases the likelihood of ecosystem conversions in areas subject to severe fire (Lenihan et al. 2003).

Mixed evergreen forests in California also burned relatively frequently before Euroamerican settlement, with the principal difference that a higher proportion of ignitions—especially in the Coast Ranges and foothills of the Sierra Nevada—was by Native Americans, who used fire as a management tool (Stuart and Stephens 2006). In the absence of Native American ignitions, mixed evergreen forests occupy an intermediate position along the fuel quantity-fuel quality gradient (Fig. 1), and fires tend to burn with more mixed severity effects than mixed conifer forests (Agee 1993, Stuart and Stephens 2006, Halofsky et al. 2011). Halofsky et al. (2011) noted that forest types with mixed-severity fire regimes experience a more even-mix of fuel- and climate-limitation, with the two factors overlain on burned landscapes as a function of fine- and medium-scale variation in vegetation, topography, weather, and productivity. We were frankly surprised to find that fire severity scaled so strongly with fire frequency in mixed evergreen forests, where we expected higher productivity and decomposition rates plus the well-represented hardwood component to dampen the effects of fire suppression relative to mixed conifer forests.

When analyzing the fire frequency-severity connection by bioregion we see strong positive relationships between TSLF and PHS for both mixed conifer and mixed evergreen forests. On the other hand, models assessing the relationship between FRI and severity at the bioregion level show a weaker connection, suggesting that TSLF and recent fire history is a more consistent predictor of PHS than the mean FRI over the past century. The notable exception within our findings is the apparent lack of a relationship between either fire frequency metric and severity in the Klamath Mountains bioregion (Table 6, Fig. 6). Other studies have also noted divergent fire patterns in the Klamath Mountains. For example, Miller et al. (2009*b*) found increasing rates of high-severity fire over time in the Sierra Nevada and Southern Cascades, but Miller et al.

(2012*b*) found no such trend in the Klamath Mountains over approximately the same time period. The Klamath Mountains show attributes of intermediate ("mixed-severity") fire regimes (Halofsky et al. 2011) even among those forest types that would typically burn frequently at mostly low severities in other parts of the state (Mallek et al. 2013, Safford and Van de Water 2013). Most of the fires from the Klamath Mountains in our study occurred in the Marble Mountains and Trinity Alps regions. Historically in these regions, severity was lowest on lower slopes and north- and east-facing aspects, and greater on mid- and upper-slope positions, especially on south- and west-facing aspects, where higher temperatures and afternoon winds promote drier conditions (Taylor and Skinner 1998). These areas are also characterized by higher precipitation relative to other California mixed conifer forests, and high topographic variability that produces summertime inversions in valleys (Robock 1988, Skinner et al. 2006). Such inversions reduce fire intensity and promote the occurrence of surface fir (Robock 1988, 1991). When the inversions dissipate, large areas of high-severity fire can occur due to higher temperatures and increased winds. This high geographic heterogeneity coupled with relatively high ecosystem productivity and abundance of resprouting hardwoods may allow for repeated high-severity burns even when FRI is low (Halofsky et al. 2011).

The concept of a "mixed severity" fire regime is scale-dependent and while there is evidence that this regime type is not simply a conglomeration of high- and low-severity types (Halofsky et al. 2011), the relatively course scale of our analysis and use of broadly defined forest types may be inadequate for differentiating between fuel- and climate-limited forests in a region where there is great spatial heterogeneity in ecosystems and where a single fire event is likely to burn through a highly heterogeneous landscape. Intermediate fire regimes such as those observed in the Klamath Mountains are driven by a variety of interacting factors and levels of fire severity may be sensitive to thresholds in fire weather and/or topography (Taylor and Skinner 2003, Schoennagel et al. 2004, Halofsky et al. 2011). Intermediate, mixed-severity fire regimes in general—and those of the Klamath Mountains in particular—are poorly defined and poorly understood and further research is needed.

For yellow pine and mixed conifer forests, our results paint a picture corroborated by a vast number of published and unpublished scientific studies (summarized in e.g., Agee 1993, Noss et al. 2006, Sugihara et al. 2006*b*, Keeley et al. 2012). However, a recent paper by Baker (2014) based on witness tree data from 19th century land surveys (the so-called "GLO" data), suggests instead that such forests in the Sierra Nevada of California were actually relatively dense and characterized by high levels of stand-replacing fire. This would imply that mixed conifer forests in this part of California were historically more climate- than fuel-limited, and that fire frequency and severity could not have been strongly related, which runs counter to our results. Baker and colleagues (e.g., Baker 2012, Williams and Baker 2012) have made such claims about other areas of yellow pine and mixed conifer forest across the western US as well and these studies have spurred renewed interest in questions related to fire severity, historical ranges of variation, and forest restoration. This work can be fairly characterized as controversial, however, and a number of subsequent studies of the same areas have come to very different conclusions. For example, Hagmann et al. (2013, 2014) used extensive early 20th century belt transect data from areas in Oregon analyzed by Baker (2012) to show that Baker's estimates of stand density were 2.5–4 times higher than the belt transect-based estimates, which had sampled from 140 to 375 times more trees per unit area than Baker's GLO data. Fulé et al. (2014) brought attention to other problematic aspects of Baker and colleagues' GLO analyses, including assumptions that smaller trees are always younger trees, and that areas with small trees encountered at GLO sampling points were necessarily evidence of high-severity fire. Other issues include the generally poor performance of plotless density estimators like the point-center-quarter based method used by Baker and colleagues in forest types like mixed conifer characterized by highly aggregated spatial structure (Engeman et al. 1994, Larson and Churchill 2012), and the very strong contrast between the putative historical fire regime as described by Baker and colleagues (with much high-severity fire) and the fire regime and resulting forest structure described by almost all of the other available evidence (e.g., Agee 1993, Noss et al. 2006, Sugihara et al. 2006*b*, Keeley et al. 2012).

Bigcone Douglas-fir

Bigcone Douglas-fir (BCDF) forest is essentially a middle- to high-elevation variant of mixed evergreen forest in southern California. BCDF supports thick bark and can survive relatively intense fires; it is also one of few conifer species in California that can resprout after mortality of the aboveground tree (McDonald 1990, Keeley 2006). Postfire sprouting of BCDF is rare after crown torching (Minnich 1980), so we may infer that the species is best-adapted to surface fires intense enough to provoke crown scorching. BCDF's close relative Douglas-fir—which dominates mid- and late-seral mixed evergreen forests in central and northern California—is tolerant of surface fire as an adult and is well-known to have supported relatively frequent low- and moderate-severity fire in drier sites throughout the western US (Agee 1993, Sugihara et al. 2006*b*).

Beyond such inference, we know next to nothing about the severity of fires in BCDF forest under presettlement conditions. Lombardo et al. (2009) estimated mean presettlement FRIs of about 30 years in BCDF stands in the Los Padres National Forest. Given the geographic location, most of this fire must have been set by Native Americans. Lombardo et al. (2009) assumed that their BCDF fire scar record was recording the chaparral fire regime from the surrounding landscape, but over the four centuries of their study the median FRI at their sites was 20.6 years, with some sites as low as 9–12 years. Most woody species comprising chaparral cannot survive sustained periods where FRIs drop below 15–20 years (Keeley 2006). It seems likely that a notable portion of their study landscape before the 19th century was dominated by flashier surface fuels that would be found in grasslands, oak woodland, and possibly in the understories of expanded stands of mixed evergreen forest and BCDF.

Today, BCDF stands are often small chaparral-surrounded enclaves of trees on steep, rocky slopes, but distribution of BCDF was much more widespread before extensive logging occurred between the late 19th and mid-20th centuries (Keeley 2006). Notable human-driven increases in fire frequency in southern California chaparral stands over the last 30–50 years have further reduced BCDF populations (Keeley 2006). Chaparral fires are high-intensity events often driven by wind, and many modern BCDF stands interfinger with chaparral at their edges or host chaparral species in their understories. This leads to the high levels of fire severity we see in modern stands (Tables 4, 7, and 8). In these forests, fire season conditions (which now last 6–9 months) are always ripe for burning, and encroaching chaparral creates a tall layer of highly flammable fuel that can carry flames into the forest canopy. It seems likely that current rates of high-severity fire in BCDF forests are somewhat higher than under pre-Euroamerican settlement conditions, but we cannot currently assess this hypothesis.

Red fir

Because of its intermediate fire regime (Fig. 1), we did not expect to observe a significant relationship between fire frequency and burn severity for red fir forest, and our results supported this hypothesis. Of the forest types we assessed, red fir experienced the longest mean FRI historically (when we include Native American ignitions) and although total annual burned area has decreased due to fire suppression (Mallek et al. 2013), relative fire frequency departure is likely not as great as in lower-elevation forests like mixed conifer and mixed evergreen (Table 4, Fig. 4). Even where fire has been completely absent, the average red fir forest has missed only one or two fires over the last century (Safford and Van de Water 2013). Low ecosystem productivity and plant growth in high-elevation forests leads to slow fuel accumulation, fuel beds in red fir forests are dense and difficult to ignite, and fire spread is largely dependent on extreme weather conditions (van Wagtendonk and Fites-Kaufman 2006, Barbour et al. 2007). These factors lead to a more intermediate fire regime (Fig. 1) that does not differ as greatly from presettlement conditions in either fire frequency or severity as the more fuel-limited fire regimes of mixed conifer and mixed evergreen forests (Table 4; Mallek et al. 2013).

Although the available data suggest modest impacts of past fire suppression on fire behavior in red fir forests, today we are observing decreased snowpack and drier late season conditions associated with climate warming, as well as warming-driven increases in tree regeneration and continuity of fuels in higher elevation forests in California (Dolanc et al. 2013). As the annual fire season continues to lengthen and red fir forests become denser, we may see more extreme fire behavior and a stronger link between fire frequency and severity (Safford and Van de Water 2013).

Redwood

Redwood forests appear unique among the forest types in this analysis. Like red fir, there appears to be little to no relationship between TSLF and the proportion of high-severity fire, but unlike all of the other forest types, we found a negative relationship between FRI and the level of high-severity fire (Fig. 5, Table 5). Redwood forests grow in the area of California with the lowest occurrence of lightning, indicating that records of frequent fire before Euroamerican settlement were almost entirely due to Native American ignitions (Stuart and Stephens 2006, Orville 2008). Redwood forests are extremely productive, and redwood itself is one of the fastest growing trees in the world (Barbour et al. 2007). Young thin-barked individuals are susceptible to fire damage and top-kill, but the thick bark of adults acts as an effective buffer from fire (Stuart and Stephens 2006). Production of woody biomass/fuel is prodigious, but equilibrium between litter input and decomposition is achieved in <25 years on most sites (Pillers 1989).

Taking these factors into account, fire suppression has likely not had the same effect on contemporary fire behavior in redwood forests as in the more fuels-limited systems discussed above. Our observation that fire severity decreases as FRIs lengthen may be indicative of a reduced number of fires allowing trees to reach more fire-resistant sizes, while coastal climates and high decomposition rates maintain modest levels of moist surface fuels. Importantly, the redwood forest data used in this study encompass relatively few fires concentrated along the central coast of California (Table 3, Fig. 2), where conditions are typically drier than those found in the northern part of the state (Davis and Borchert 2006). Due to the limited geographic range of our data, we caution against generalization of our results to redwood forests managed by other landowners in other areas.

While 20th century fire suppression does not appear to have increased the risk of high severity fire in central California redwood forests, the emergence of sudden oak death (SOD; *Phytophthora ramorum*) may be contributing to increasing redwood mortality in recent wildfires. Studying redwood forests in the central coast, Metz et al. (2013) assessed the rates of tree mortality associated with SOD and wildfire. They found that when SOD was present in a stand prior to a wildfire, the effects on mortality were synergistic and showed an approximately 200% greater fire-mediated loss of basal area than would be expected if loss was simply an additive function of SOD and wildfire. Fuel loads in SOD-infected stands increase and fuel moisture decreases relative to unaffected stands, which may lead to elevated fire intensities and greater rates of crown scorch and redwood mortality when a wildfire occurs (Valachovic et al. 2011, Metz et al. 2013).

Conclusions

Our most fundamental finding is that widely-used generalizations about fire frequency and severity in western US ecosystems hold true across the major forest ecosystems of California. Fuel-limited forest types characterized by the highest fire frequencies before Euroamerican settlement of California show strong negative relationships between fire frequency and severity (i.e., positive relationships between our metrics and severity), while more climate- or ignition-limited forest types with longer presettlement FRIs show weak, or in the case of redwood, even positive relationships. Our work substantiates the general validity and usefulness of "fuel-limited" vs. "climate-limited" explanations of differing patterns of fire effects and response in forest types of the western US (Agee 1993, Schoennagel et al. 2004, Noss et al. 2006, Sugihara et al. 2006*b*, Pausas and Paula 2012).

It seems clear that recent major changes in fire severity in fuels-limited forest types like yellow pine and mixed conifer across the southwestern US and California are in large part due to the dramatic reduction in fire frequency caused by the past century of fire suppression and subsequent increase in forest fuels. This is interacting with warming climates, drier fire seasons, less aggressive fire-fighting tactics and the legacies of past resource management actions (past timber harvest practices, for example) to result in increasing frequencies of large, severe wildfires. Over this large region of the western US, the number of large and destructive forest fires is rising quickly: in only the last three years, Arizona and New Mexico have both experienced their largest wildfires ever, with New Mexico eclipsing its record twice in the period, and the Sierra Nevada range in California experiencing its largest forest fire ever in 2013 (Rim Fire); of the ten largest fires recorded in the Sierra Nevada, nine have occurred since 1990 and eight since 2000. These fires have mostly occurred in mixed conifer and related forest types, where fire season conditions are nearly always primed for burning but frequent fire used to limit the availability of fuel. Our results underline the strong relationship between fire frequency and severity in these types of forests, even after a century of human interventions has greatly modified forest structure and fuel loads.

Given the strong influence of fuel on fire activity and behavior in these forests, the strong focus by management agencies on reducing fuels seems well justified, especially since climates continue to warm and science shows that fuel reduction has strong positive effects on forest resilience to severe wildfire and the environmental effects of fuel treatments in mixed conifer forests are mostly neutral to beneficial (Safford et al. 2012, Stephens et al. 2012, Martinson and Omi 2013). The difficulty is that the scale of the problem dwarfs the capacity of active management to solve it (North et al. 2012). This is not only a simple scalar issue however. Wilderness areas, inventoried roadless areas, areas far from roads, and areas with steep slopes are essentially "off-limits" to mechanical fuel reduction, and many western National Forests contain limited land outside of these areas. It seems evident that meaningfully restoring fire- and climate-resilient structure to western yellow pine and mixed conifer forests will only be accomplished through a major expansion in the managed use of wildland fire under moderate weather conditions, which fortuitously are the most common weather conditions during the fire season. Strategic employment of active fuel reduction will be a necessary precursor in many landscapes, but it will take low and moderate severity fire to ameliorate the ecological consequences of the absence of low and moderate severity fire (Mallek et al. 2013).

Acknowledgments

We thank our anonymous reviewers and the editor for constructive comments on the original submission. Jay Miller and Malcolm North provided critiques of early drafts. Authors' division of labor: Z. Steel carried out analyses and wrote the paper; H. Safford initiated and funded the study and wrote the paper; J. Viers assisted with analyses and wrote the paper.

Literature Cited

Agee, J. K. 1993. Fire ecology of Pacific Northwest forests. Island Press, Washington, D.C., USA.

Baker, W. L. 2012. Implications of spatially extensive historical data from surveys for restoring dry forests of Oregon's eastern Cascades. Ecosphere 3:23.

Baker, W. L. 2014. Historical forest structure and fire in Sierran mixed-conifer forests reconstructed from General Land Office survey data. Ecosphere 5:79.

Barbour, M. G., T. Keeler-Wolf, and A. A. Schoenherr. 2007. Terrestrial vegetation of California. Third edition. University of California Press, Berkeley, California, USA.

Barbour, M. G., B. Pavlik, F. Drysdale, and S. Lindstrom. 1993. California's changing landscapes: diversity and conservatoin of California vegetation. California Native Plant Society, Sacramento, California, USA.

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2012. lme4: Linear mixed-effects models using Eigen and S4 classes. R package version 1.0-4. https://github.com/lme4/lme4/ http://lme4.r-forge.r-project.org/

Bond, W. J., and J. E. Keeley. 2005. Fire as a global 'herbivore': the ecology and evolution of flammable ecosystems. Trends in Ecology & Evolution 20:387–394.

Bond, W. J., and B. W. van Wilgen. 1996. Fire and plants. Chapman & Hall, London, UK.

Brown, J. K., and J. K. Smith. 2000. Wildland fire in ecosystems: effects of fire on flora. General Technical Report RMRS-GTR-42. USDA Forest Service, Rocky Mountain Research Station, Ogden, Utah, USA.

Calkin, D. E., K. M. Gebert, J. G. Jones, and R. P. Neilson. 2005. Forest Service large fire area burned and suppression expenditure trends, 1970-2002. Journal of Forestry 103:179–183.

Chappell, C. B., and J. K. Agee. 1996. Fire severity and tree seedling establishment in Abies magnifica forests, southern Cascades, Oregon. Ecological Applications 6:628–640.

Collins, B. M., J. D. Miller, A. E. Thode, M. Kelly, J. W. van Wagtendonk, and S. L. Stephens. 2009. Interactions among wildland fires in a long-established Sierra Nevada Natural Fire Area. Ecosystems 12:114–128.

Davis, F. W., and M. I. Borchert. 2006. Central Coast Bioregion. Pages 321–349 *in* N. G. Sugihara, J. W. van Wagtendonk, K. E. Shaffer, J. Fites-Kaufman, A. E. Thode, editors. Fire in California's ecosystems. University of California Press, Berkeley, California, USA.

Dillon, G. K., Z. A. Holden, P. Morgan, M. A. Crimmins, E. K. Heyerdahl, and C. H. Luce. 2011*a*. Both topography and climate affected forest and woodland burn severity in two regions of the western US, 1984 to 2006. Ecosphere 2:33.

Dillon, G. K., Z. A. Holdon, P. Morgan, M. A. Crimmins, E. K. Heyerdahl, and C. H. Luce. 2011*b*. Both topography and climate affected forest and woodland burn severity in two regions of the western US, 1984 to 2006. Ecosphere 2:130.

Dolanc, C. R., J. H. Thorne, and H. D. Safford. 2013. Widespread shifts in the demographic structure of subalpine forests in the Sierra Nevada, California, 1934 to 2007. Global Ecology and Biogeography 22:264–276.

Engeman, R. M., R. T. Sugihara, L. F. Pank, and W. E. Dusenberry. 1994. A comparison of plotless density estimators using monte-carlo simulation. Ecology 75:1769–1779.

Fulé, P. Z., et al. 2014. Unsupported inferences of high-severity fire in historical dry forests of the western United States: response to Williams and Baker. Global Ecology and Biogeography 23:825–830.

Greenlee, J. M., and J. H. Langenheim. 1990. Historic fire regimes and their relation to vegetation patterns in the Monterey Bay area of California. American Midland Naturalist 124:239–253.

Hagmann, R. K., J. F. Franklin, and K. N. Johnson. 2013. Historical structure and composition of ponderosa pine and mixed-conifer forests in south-central Oregon. Forest Ecology and Management 304:492–504.

Hagmann, R. K., J. F. Franklin, and K. N. Johnson. 2014. Historical conditions in mixed-conifer forests on the eastern slopes of the northern Oregon Cascade Range, USA. Forest Ecology and Management 330:158–170.

Halofsky, J. E., et al. 2011. Mixed-severity fire regimes: lessons and hypotheses from the Klamath-Siskiyou Ecoregion. Ecosphere 2:40.

Hanson, C. T., and D. C. Odion. 2013. Is fire severity increasing in the Sierra Nevada, California, USA? International Journal of Wildland Fire 23:1–8.

Heinselman, M. L. 1973. Fire in the virgin forests of the Boundary Waters Canoe Area, Minnesota. Quaternary Research 3:329–382.

Heinselman, M. L. 1981. Fire intensity and frequency as factors in the distribution and structure of northern ecosystems. *In* H. A. Mooney, J. M. Bonniksen, N. L. Christensen, H. A. Mooney, J. M. Bonniksen, and N. L. Christensen, editors. Fire regimes and ecosystem properties. General Technical Report WO-26. USDA Forest Service, Washington, D.C., USA.

Hessburg, P. F., J. K. Agee, and J. F. Franklin. 2005. Dry forests and wildland fires of the inland Northwest USA: Contrasting the landscape ecology of the pre-settlement and modem eras. Forest Ecology and Management 211:117–139.

Hobbs, R. J., and L. F. Huenneke. 1992. Disturbance, diversity, and invasion - implications for conservation. Conservation Biology 6:324–337.

Huston, M. A. 2003. Understanding the effects of fire and other mortality-causing disturbances on species diversity. Pages 51–84 *in* N. C. Burrows and I. Abbott, editors. Fire in south-western Australian forests: impacts and management. Backhuys, Leiden, The Netherlands.

Johnson, E. A., and C. E. Vanwagner. 1985. The theory and use of 2 fire history models. Canadian Journal of Forest Research 15:214–220.

Keeley, J. D., W. J. Bond, R. A. Bradstock, J. G. Pausas, and P. W. Rundel. 2012. Fire in mediterranean ecosystems. Cambridge University Press, Cambridge, UK.

Keeley, J. E. 2006. South coast bioregion. Pages 350–390 *in* N. G. Sugihara, J. W. van Wagtendonk, K. E. Shaffer, J. Fites-Kaufman, and A. E. Thode, editors. Fire in California's ecosystems. University of California Press, Berkeley, California, USA.

Key, C. H., and N. C. Benson. 2006. Landscape assessment: ground measure of severity, the Composite Burn Indes. *In* D. C. Lutes, editor. FIREMON: Fire Effects Monitoring and Inventory System. General Technical Report. USDA Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, USA.

Larson, A. J., and D. Churchill. 2012. Tree spatial patterns in fire-frequent forests of western North America, including mechanisms of pattern formation and implications for designing fuel reduction and restoration treatments. Forest Ecology and Management 267:74–92.

Lenihan, J. M., R. Drapek, D. Bachelet, and R. P. Neilson. 2003. Climate change effects on vegetation distribution, carbon, and fire in California. Ecological Applications 13:1667–1681.

Lombardo, K. J., T. W. Swetnam, C. H. Baisan, and M. I. Borchert. 2009. Using bigcone Douglas-fir fire scars and tree rings to reconstruct interior chaparral fire history. Fire Ecology 5:35–56.

Mallek, C., H. Safford, J. Viers, and J. Miller. 2013. Modern departures in fire severity and area vary by forest type, Sierra Nevada and southern Cascades, California, USA. Ecosphere 4:153.

Martinson, E., and P. Omi. 2013. Fuel treatments and fire severity: A meta-analysis. Rocky Mountain Rearch Station, Ft. Collins, Colorado, USA.

McDonald, P. M. 1990. *Pseudotsuga macrocarpa* (Vasey) Mayr bigcone Douglas-fir. Pages 520–526 *in* R. M. Burns and B. H. Honkala, editors. Silvics of North America. Volume 1. Conifers. Agricultural Handbook 654. USDA Forest Service, Washington, D.C., USA.

Metz, M. R., J. M. Varner, K. M. Frangioso, R. K. Meentemeyer, and D. M. Rizzo. 2013. Unexpected redwood mortality from synergies between wildfire and an emerging infectious disease. Ecology 94:2152–2159.

Miller, J. D., B. M. Collins, J. A. Lutz, S. L. Stephens, J. W. van Wagtendonk, and D. A. Yasuda. 2012*a*. Differences in wildfires among ecoregions and land management agencies in the Sierra Nevada region, California, USA. Ecosphere 3:20.

Miller, J. D., E. E. Knapp, C. H. Key, C. N. Skinner, C. J. Isbell, R. M. Creasy, and J. W. Sherlock. 2009*a*. 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 Sensing of Environment 113:645–656.

Miller, J. D., and H. Safford. 2012. Trends in wildfire severity: 1984 to 2010 in the Sierra Nevada, Modoc Plateau, and southern Cascades, California, USA. Fire Ecology 8:41–57.

Miller, J. D., H. D. Safford, M. Crimmins, and A. E. Thode. 2009*b*. Quantitative evidence for increasing forest fire severity in the Sierra Nevada and Southern Cascade Mountains, California and Nevada, USA. Ecosystems 12:16–32.

Miller, J. D., C. N. Skinner, H. D. Safford, E. E. Knapp, and C. M. Ramirez. 2012*b*. Trends and causes of severity, size, and number of fires in northwestern California, USA. Ecological Applications 22:184–203.

Miller, J. D., and A. E. Thode. 2007. Quantifying burn severity in a heterogeneous landscape with a relative version of the delta Normalized Burn Ratio (dNBR). Remote Sensing of Environment 109:66–80.

Minnich, R. A. 1980. Wildfire and the geographic relationships between canyon live oak, Coulter pine, and bigcone Douglas-fir forests. *In* T. R. Plumb, editor. Proceedings of the symposium on ecology, management, and utilization of California oaks. USDA Forest Service, Pacific Soutwest Forest and Range Experiment Station, Claremont, California, USA.

Minnich, R. A. 2006. California climate and fire weather. *In* N. G. Sugihara, J. W. van Wagtendonk, K. E. Shaffer, J. Fites-Kaufman, and A. E. Thode, editors. Fire in California's ecosystems. University of California Press, Los Angeles, California, USA.

North, M., B. M. Collins, and S. Stephens. 2012. Using fire to increase the scale, benefits, and future maintenance of fuels treatments. Journal of Forestry 110:392–401.

North, M. P., and M. D. Hurteau. 2011. High-severity wildfire effects on carbon stocks and emissions in fuels treated and untreated forest. Forest Ecology and Management 261:1115–1120.

Noss, R. J., J. F. Franklin, W. L. Baker, T. Schoennagel, and P. B. Moyle. 2006. Managing fire-prone forests in the western United States. Frontiers in Ecology and the Environment 4:481–487.

Odion, D. C., E. J. Frost, J. R. Strittholt, H. Jiang, D. A. Dellasala, and M. A. Moritz. 2004. Patterns of fire severity and forest conditions in the western Klamath Mountains, California. Conservation Biology 18:927–936.

Odion, D. C., and C. T. Hanson. 2006. Fire severity in conifer forests of the Sierra Nevada, California. Ecosystems 9:1177–1189.

Orville, R. E. 2008. Development of the national lightning detection network. Bulletin of the American Meteorological Society 89:180–190.

Pausas, J. G., and S. Paula. 2012. Fuel shapes the fire-climate relationship: evidence from Mediterranean ecosystems. Global Ecology and Biogeography 21:1074–1082.

Pickett, S. T. A., and P. S. White. 1985. The ecology of natural disturbance and patch dynamics. Academic Press, Orlando, Florida, USA.

Pierce, A. D., and A. H. Taylor. 2011. Fire severity and seed source influence lodgepole pine (*Pinus contorta* var. *murrayana*) regeneration in the southern cascades, Lassen volcanic National Park, California. Landscape Ecology 26:225–237.

Pillers, M. D. 1989. Fine fuel dynamics of old growth redwood forests. Humbolt State University, Arcata, California, USA.

R Development Core Team. 2011. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Robock, A. 1988. Enhancement of surface cooling due to forest fire smoke. Science 242:911–913.

Robock, A. 1991. Surface cooling due to forest-fire smoke. Journal of Geophysical Research-Atmospheres 96:20869–20878.

Rollins, M. G. 2009. LANDFIRE: a nationally consistent vegetation, wildland fire, and fuel assessment. International Journal of Wildland Fire 18:235–249.

Safford, H. D., J. Miller, D. Schmidt, B. Roath, and A.

Parsons. 2008. BAER soil burn severity maps do not measure fire effects to vegetation: A comment on Odion and Hanson (2006). Ecosystems 11:1–11.

Safford, H. D., J. T. Stevens, K. Merriam, M. D. Meyer, and A. M. Latimer. 2012. Fuel treatment effectiveness in California yellow pine and mixed conifer forests. Forest Ecology and Management 274:17–28.

Safford, H. D., and K. M. Van de Water. 2013. Using Fire Return Interval Departure (FRID) analysis to map spatial and temporal changes in fire frequency on National Forest lands in California. Research Paper PSW-RP-266. USDA Forest Service, Pacific Southwest Research Station, Albany, California, USA.

Schmidt, K. M., J. P. Menakis, C. C. Hardy, W. J. Hann, and D. L. Bunnell. 2002. Development of course-sclae spatial data for wildland fire and fuel management. General Technical Report RMRS-GTR-87. USDA Forest Service, Rocky Mountain Research Station, Ft. Collins, Colorado, USA.

Schoennagel, T., T. T. Veblen, and W. H. Romme. 2004. The interaction of fire, fuels, and climate across rocky mountain forests. BioScience 54:661–676.

Skinner, C. N., A. H. Taylor, and J.k. Agee. 2006. Klamath Mountains bioregion. Pages 170–194 *in* N. G. Sugihara, J. W. van Wagtendonk, K. E. Shaffer, J. Fites-Kaufman, and A. E. Thode, editors. Fire in California's ecosystems. University of California Press, Berkeley, California, USA.

Stephens, S. L., R. E. Martin, and N. E. Clinton. 2007. Prehistoric fire area and emissions from California's forests, woodlands, shrublands, and grasslands. Forest Ecology and Management 251:205–216.

Stephens, S. L., J. D. McIver, R. E. J. Boerner, C. J. Fettig, J. B. Fontaine, B. R. Hartsough, P. L. Kennedy, and D. W. Schwilk. 2012. The effects of forest fuel-reduction treatments in the United States. BioScience 62:549–560.

Stuart, J. D., and S. L. Stephens. 2006. North Coast bioregion. Pages 147–169 *in* N. G. Sugihara, J. W. van Wagtendonk, K. E. Shaffer, J. Fites-Kaufman, and A. E. Thode, editors. Fire in California's ecosystems. University of California Press, Berkeley, California, USA.

Sugihara, N. G., J. W. Van Wagtendonk, and J. Fites-Kaufman. 2006*a*. Fire as an ecological process. Pages 58–74 *in* N. G. Sugihara, J. W. van Wagtendonk, K. E. Shaffer, J. Fites-Kaufman, and A. E. Thode, editors. Fire in California's ecosystems. University of California Press, Berkeley, California, USA.

Sugihara, N. G., J. W. Van Wagtendonk, K. E. Shaffer, J. Fites-Kaufman, and A. E. Thode. 2006*b*. Fire in California's ecosystems. University of California Press, Berkeley, California, USA.

Taylor, A. H., and C. N. Skinner. 1998. Fire history and landscape dynamics in a late-successional reserve, Klamath Mountains, California, USA. Forest Ecology and Management 111:285–301.

Taylor, A. H., and C. N. Skinner. 2003. Spatial patterns and controls on historical fire regimes and forest structure in the Klamath Mountains. Ecological Applications 13:704–719.

Turner, M. G., R. H. Gardner, V. H. Dale, and R. V. O'Neill. 1989. Predicting the spread of disturbance across heterogeneous landscapes. Oikos 55:121–129.

Valachovic, Y. S., C. A. Lee, H. Scanlon, J. M. Varner, R. Glebocki, B. D. Graham, and D. M. Rizzo. 2011. Sudden oak death-caused changes to surface fuel loading and potential fire behavior in Douglas-fir-tanoak forests. Forest Ecology and Management 261:1973–1986.

Van de Water, K. M., and H. D. Safford. 2011. A summary of fire frequency estimates for California vegetation before Euro-American settlement. Fire Ecology 7:26–58.

van Wagtendonk, J. W., and D. R. Cayan. 2008. Temporal and spatial distribution of lighting strikes in California in relation to large-scale weather patterns. Fire Ecology 4(1):34–56.

van Wagtendonk, J. W., and J. Fites-Kaufman. 2006. Sierra Nevada bioregion. Pages 264–294 *in* N. G. Sugihara, J. W. van Wagtendonk, K. E. Shaffer, J. Fites-Kaufman, and A. E. Thode, editors. Fire in California's ecosystems. University of California Press, Berkeley, California, USA.

Williams, M. A., and W. L. Baker. 2012. Spatially extensive reconstructions show variable-severity fire and heterogeneous structure in historical western United States dry forests. Global Ecology and Biogeography 21:1042–1052.

Wohlgemuth, P. M., K. Hubbert, and M. J. Arbaugh. 2006. Fire and physical environment interactions. Pages 75–93 *in* N. G. Sugihara, J. W. van Wagtendonk, K. E. Shaffer, J. Fites-Kaufman, and A. E. Thode, editors. Fire in California's ecosystems. University of California Press, Berkeley, California, USA.