

RESEARCH ARTICLE

TOP-DOWN AND BOTTOM-UP CONTROLS ON FIRE REGIMES ALONG AN ELEVATIONAL GRADIENT ON THE EAST SLOPE OF THE SIERRA NEVADA, CALIFORNIA, USA

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ABSTRACT

Fire is an ecologically significant process in the fire-prone ponderosa pine and mixed conifer forests of the northern Sierra Nevada. Fire regimes are influenced by processes that operate over a range of scales that can be grouped broadly as bottom-up (e.g., topography, forest type) or top-down (e.g., climate variation, human land use) controls. To identify the bottom-up versus top-down controls on fire regimes, we quantified spatial and temporal variation in fire occurrence and extent using fire-scar dendrochronology. Inter-annual climate variability and human land use patterns strongly influenced fire regimes. Years of widespread burning and fire-free years were associated with dry and wet years, respectively. Variation in fire activity was also associated with variation in the El Niño-Southern Oscillation (ENSO) and the Pacific Decadal Oscillation (PDO). Widespread burning occurred during La Niña years (cool ENSO) and during positive conditions of the PDO (warm PDO). Fire occurrence declined with Euro-American settlement in the nineteenth century and only two fires were recorded in the study area after 1905, the date fire suppression was implemented. Fire regimes were also influenced by bottom-up controls. Fire return intervals (FRI) were shorter in pine-dominated low-elevation forests than in high-elevation fir-dominated mixed conifer forests, although FRI did not vary by slope aspect.

Keywords: climate change, dendroecology, fire history, fire scars, fire suppression, livestock grazing, mixed conifer forest, ponderosa pine

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INTRODUCTION

Wildfire is the most ecologically significant process affecting fire-prone ponderosa pine and mixed conifer forests of the Sierra Nevada (Skinner and Chang 1996). Spatial and temporal variability in fire regimes (i.e., frequency, season, extent, spatial complexity, intensity, severity and type of fire for a particular area) are thought to be important controls on the structural and compositional diversity of fire-prone vegetation communities because species response to fire varies with fire regime characteristics (Martin and Sapsis 1989, Bond and van Wilgen 1996). Fire regimes, in turn, are controlled by processes that operate over a range of spatial and temporal scales. For example, bottom-up controls such as variation in vegetation type or slope aspect (e.g., Taylor 2000, Heyerdahl *et al.* 2001), or time since last fire (e.g., Taylor and Skinner 2003, Scholl and Taylor 2010) influence the type, arrangement, moisture, and connectivity of forest fuels, and hence fire occurrence at local scales. Variation in climate or land use are large scale top-down controls that can override bottom-up control and synchronize or interrupt fire occurrence over wide areas and across ecosystems (Lertzman and Fall 1998, Heyerdahl *et al.* 2001, Taylor *et al.* 2008). Thus, determining the relative influence of bottom-up and top-down controls requires analyses of fire regimes at both fine and coarse spatial scales (Heyerdahl *et al.* 2001, Taylor and Skinner 2003, Taylor *et al.* 2008).

The eastern Sierra Nevada rise abruptly on the western side of the Great Basin in California and Nevada, USA. With the change in elevation there is an abrupt shift of vegetation from arid sagebrush-grassland at 1300 m to conifer forest at higher elevations (Barbour 1988, Riegel *et al.* 2006). Spatial variation in fire occurrence across the pine-mixed conifer forest gradient on the eastern side of the Sierra Nevada is thought to be related to the bottom-

up controls of local topography and species composition that influence variables that affect combustion and fire spread (Agee 1993, Taylor 2000). Conditions at higher elevations are cooler and wetter, and the period that fuels are dry enough each year to burn is shorter than at lower elevations. Surface fuel density also varies with forest species composition, which is related to elevation. Litter bulk density is nearly two-fold higher in white fir-mixed conifer forests than in pine forests at low elevation (van Wagtenonk *et al.* 1998). Dense litter beds inhibit fire spread and shorten fire season length because they require a longer period of drying to become flammable (van Wagtenonk *et al.* 1998, Stephens 2001). Spatial and temporal variation in fire regimes across a gradient from xeric dry pine through mixed conifer forests, however, have not been quantified on the eastern side of the Sierra Nevada.

In this study, we examined spatial and temporal variability in fire occurrence on the east side of the Sierra Nevada. Our goal was to identify the relative influence of bottom-up vs. top-down controls on fire regimes and how they varied spatially and over time. We reconstructed fire occurrence for the last three to four centuries in 34 forest stands in the Diamond Mountains in the northeastern Sierra Nevada, California (Figure 1). We assessed the bottom-up controls of topography and species composition by comparing fire frequency in different forest types and slope aspects across an elevation gradient. We expected that fire was more common in dry pine than in mixed conifer forest because conditions are warmer and drier, fuel beds are less dense, and fires can more easily spread from adjacent sagebrush grassland at the base of the mountains.

We assessed top-down controls of fire regimes by comparing temporal variability in fire occurrence and extent to changes in land use since Euro-American settlement and climate variation. We expected that fire frequen-

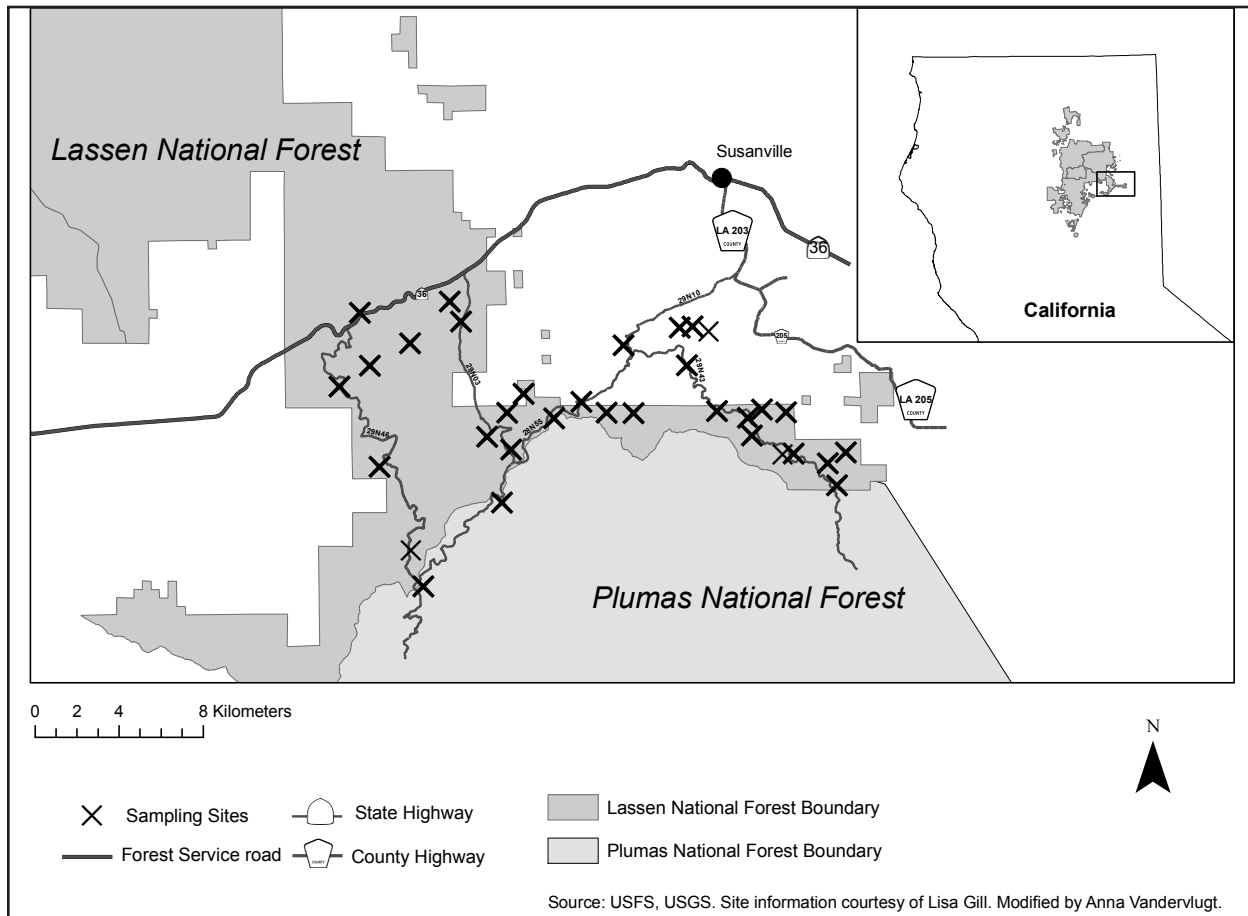


Figure 1. Location of study area and fire-scar collection sites ($n = 34$) in the Diamond Mountains, California.

cy and extent decreased after Euro-American settlement with the introduction of livestock in this region, which removed fine grass fuels (Norman and Taylor 2005). We also expected that inter-annual variability in moisture conditions (i.e., Palmer Drought Severity Index, PDSI, Palmer 1965) would influence fire extent. During wet years, the fire season is shorter, fuels are less combustible, and fires are smaller in extent compared to fires under the opposite climatic conditions (Taylor *et al.* 2008). In California, precipitation variability is influenced by variation in the El Niño Southern Oscillation (ENSO), and the Pacific Decadal Oscillation (PDO), which are coupled ocean-atmospheric processes that influence Pacific sea surface temperatures (SSTs) and climate (Cayan *et al.* 1999, Nigam *et al.* 1999). We compared our fire record to ENSO and

PDO to determine if they regulate fire regimes in the Diamond Mountains as they do in some fire-prone forests in the western United States (e.g., Swetnam and Betancourt 1990, Veblen *et al.* 2000, Taylor and Beaty 2005, Heyerdahl *et al.* 2008). This study also provides key reference data on historical variability in fire regimes important for management of Sierra Nevada forests (Weatherspoon *et al.* 1992, Skinner and Chang 1996, Stephens and Sugihara 2006).

METHODS

Study Area

We studied fire regimes in the Diamond Mountains on the east side of the Sierra Nevada (Figure 1). Elevations range from 1340

m at the base of the range to 2355 m on the summit of Diamond Peak. The climate is characterized by warm, dry summers, and cool, wet winters (Mediterranean type), and there is a steep climatic gradient from the base to the top of the Diamond Mountains. Mean monthly temperatures in Susanville, California (1300 m), at the base of the Diamond Mountains in sagebrush-grassland, range from -1°C in January to 18°C in July, and average annual precipitation is 36 cm. At Canyon Dam (1380 m), 35 km southwest of the study site, the average annual precipitation is much greater (98 cm) and most falls as snow (75%). The terrain is steep and complex and soils are developed in marine and continental sediments of volcanic and non-volcanic origin, basaltic and andesitic lava flows, and Mesozoic aged granite (Hill 1975).

Low-elevation forests at the base of the Diamond Mountains are dominated by ponderosa pine (*Pinus ponderosa* C. Lawson) and Jeffery pine (*Pinus jeffreyi* Balf.), singly or in mixture, and California black oak (*Quercus kelloggii* Newberry) is an important associate. Montane forests at higher elevation are the mixed conifer type, which are comprised of six species: ponderosa pine, Jeffery pine, incense cedar (*Calocedrus decurrens* [Torr.] Florin), sugar pine (*Pinus lambertiana* Douglas), white fir (*Abies concolor* [Gord. & Glend.] Lindl. ex Hildebr.), and California black oak. Dominance varies with stand history, elevation, and landscape position. White fir is more abundant on cooler mesic sites and slope aspects compared to species of pine (Barbour 1988, Parker 1995, van Wagtenonk and Fites-Kaufman 2006). Lodgepole pine (*Pinus contorta* Douglas ex Loudon) and quaking aspen (*Populus tremuloides* Michx.) are locally abundant on sites with high water tables or cold air drainage (Pierce and Taylor 2010). Forests above the mixed conifer forest belt are dominated by a mixture of red fir (*Abies magnifica* A. Murray) and western white pine (*Pinus monticola* Douglas ex D. Don).

People have influenced fire regimes in the study area for a long time (Strong 1973, Anderson 2005). Prior to Euro-American settlement, the Maidu actively used fire to promote production of acorns, berries, roots, and fiber; to flush game; and to collect grasshoppers (Camacho *et al.* 1997). The Maidu population declined sharply after Euro-settlement in 1848 (Camacho *et al.* 1997). Livestock grazing (primarily sheep) began in the early 1860s and peaked around 1900 (Taylor 1990, Norman and Taylor 2005). The Lassen National Forest was established in 1907, and a policy of fire suppression was implemented (Strong 1973). Small-scale logging operations began on the lower slopes in the mid- to late nineteenth century, on what are still private lands. Less accessible forests at higher elevations were not logged until a road was constructed in 1970.

Site Selection

Potential sample sites were identified by first stratifying the study area by elevation (low < 1600 m; middle from 1600 m to 1800 m; or high > 1800 m) and slope aspect (north 315° to 44° ; east 45° to 134° ; south 135° to 224° ; and west 225° to 314°) using a topographic map. Strata were surveyed for fire scar samples, and the location (GPS), environmental setting (elevation, slope aspect, slope configuration), forest type (pine-oak, pine-mixed conifer, fir-mixed conifer), and number of scars on each potential sample were recorded. Thirty-four sites were chosen for sampling after considering the spatial distribution of potential sites among strata, land ownership, condition of samples, distance from roads, and the number of visible fire scars (Figure 1). Partial wood cross-sections were extracted from trees, logs, or stumps using a chainsaw (Arno and Sneek 1977). The average size of a fire scar collection site was 20 ha (range, 9 ha to 36 ha) and the average number of samples collected on a site was five (range, 1 to 11).

Reconstructing Fire Regimes

Fire frequency, return interval, season of fire, and fire extent were reconstructed from the dates of fires recorded in wood samples from each site. Fire dates were identified by first sanding each wood sample to a high polish and then cross dating the sample's tree rings using standard dendrochronological techniques (Stokes and Smiley 1968). The calendar year of each annual ring with a fire scar in it was then recorded as the fire year.

Season of fire. The season of burn was inferred from the relative position of a fire scar within an annual growth ring (*cf.*, Baisan and Swetnam 1990). Season of burn was identified using the following scar position categories: (1) early (first third of earlywood); (2) middle (second third of earlywood); (3) late (last third of earlywood); (4) latewood (in latewood); and (5) dormant (at ring boundary). In this winter-wet, summer-dry climate, dormant season fires are most likely to represent late summer or fall burns after radial growth has ceased for the year, rather than winter or early spring burns (Caprio and Swetnam 1995). The winter snowpack and high fuel moisture during spring reduces the likelihood of early season burns.

Temporal patterns. Temporal variation in fire return intervals (FRI) that may be related to changes in land use was identified by comparing composite fire return intervals (CFRI) for the pre-Euro-American (prior to 1850), settlement (1850 to 1904), and fire exclusion (since 1905) periods using a Student's *t*-test. A composite record of all sites was used for temporal comparisons for fires that burned any of our sites, 10% or more of our sites, or 25% or more of our sites. This analysis distinguishes how land use changes affected the frequency of fires of different extent (Dieterich 1980).

Spatial patterns. Spatial variation in FRI was determined by comparing sites in different slope aspect and forest composition groups using a Kruskal-Wallis H-test (Sokal and Rohlf 1995). Each FRI measure provides different information on the variability of FRI with elevation. Composite records were derived from all samples on a site and then grouped for comparison (i.e., slope aspect, forest type). Site CFRI provides a more complete inventory of fire dates than PFRI (Dieterich 1980). Site CFRI's shorten as more samples from a wider area are combined into a single fire chronology because the number of recorded events increases with sampling area (Arno and Peterson 1983; Falk and Swetnam 2003). The PFRI's, on the other hand, reflect the time dependence of fire occurrence associated with fuel accumulation at a single point (Dieterich 1980, Kitzberger and Veblen 1997). For this study, an average PFRI was calculated for each site using sample PFRI values and then site PFRI's were grouped for comparison (i.e., slope aspect, forest type). We used linear regression to determine the relationship between elevation and both site PFRI and site CFRI. We also used partial correlation coefficients to reassess the strength of the association between FRI and elevation with the effect of number of samples per site held constant.

Fire extent. It was not possible to calculate area burned by each fire in the study area using fire dates at each site because the site network was too sparse to estimate fire perimeters (e.g., Taylor 2000, Hessl *et al.* 2007). Instead, we used two measures of relative fire extent based on fire years at each site. First we calculated FRI for fires that burned any site, 10% or more, or 25% or more of our sites. This measure distinguishes how frequent ($\geq 25\%$), intermediate ($\geq 10\%$), or relatively widespread small (any site scarred) fires were in the study area. Second, we counted the number of sites that recorded a fire each year. We assume that

burning was more or less widespread in years when more or fewer sites recorded a fire. We used SPSS 13.0 (SPSS Inc., Chicago, Illinois, USA) and FHX2 software (Grissino-Mayer 2001) for our FRI analysis.

Fire-Climate Relationships

Climate records. We used four tree-ring proxy records of climate to identify fire-climate relationships. First, we used PDSI as a measure of moisture availability (data from gridpoint 5 [41° N, 122.5° W], Cook *et al.* 1999). The PDSI integrates temperature and precipitation from both the current and previous months plus a measure of soil water holding capacity to estimate drought severity (Palmer 1965). Negative values indicate dry conditions and positive values indicate wet conditions. Second, we used the NIÑO3 reconstruction of winter (December to February) sea surface temperatures (SST) in the equatorial Pacific as an index of ENSO (Cook 2000). El Niño (warm) conditions prevail when the NIÑO3 index is positive and La Niña (cold) conditions prevail when the index is negative. Finally, we used two tree-ring reconstructions of the PDO as measures of variability of northern Pacific SST. The PDO_G reconstruction by Gedalof and Smith (2001) is based on temperature sensitive tree-ring series from coastal Alaska, British Columbia, and Oregon. The D'Arrigo *et al.* (2001) reconstruction, PDO_D, is based on temperature sensitive tree rings in the same region but also includes moisture sensitive series in northern Mexico. Index values are positive during a warm phase PDO and negative during a cool phase PDO.

Climate reconstructions vs. local climate. The proxy climatic indices represent climate variation over large spatial scales that may not be reflected in our smaller study area. To identify how the indices are related to local climate, we calculated Pearson product moment

correlations between the instrumental record for each index (winter values) and instrumental climate data for annual time scales. We used average annual temperature and average total precipitation from four nearby climate stations (Susanville, Canyon Dam, Mineral, and Manzanita Lake) with long instrumental records as a measure of local climate.

Fire-climate analysis. The relationships between fire occurrence and extent and climate were determined using two methods: (1) superposed epoch analysis (SEA) (Baisan and Swetnam 1990), and (2) correlation analysis (Taylor *et al.* 2008). We only analyzed fire-climate relationships between 1700 and 1900, the period of overlap for all proxy climate records and before likely changes in fire-climate relations caused by fire suppression.

The SEA was used to identify the relationship between inter-annual variability in climate and fire. The analysis tests the hypothesis of no relationship between fire years and climate preceding, during, and following the fire year. The SEA compares mean climate (PDSI, NIÑO3, PDO) in fire years to climate in an eight-year window (i.e., five years before, the fire event year, and two years after the fire event year). We used autocorrelation functions (ACF) and auto-regressive moving average (ARMA) models to identify and remove serial autocorrelation in PDSI, NIÑO3, and PDO (Box *et al.* 2008). The SEAs were conducted with the model residuals for those time series that exhibited serial autocorrelation. Monte Carlo simulations (1000 runs) were used to calculate confidence intervals for average climate conditions for years in the window and then compare them to randomly selected years in the record (Mooney and Duval 1993, Grissino-Mayer 2001). The analysis was performed for fires of different extent (any site, $\geq 10\%$, and $\geq 25\%$ of sites burned), and for non-fire years.

We also used correlation analysis to identify the relationships between fire extent and climate to complement the SEA. An index of variability in fire extent was calculated by first determining the percentage of samples that recorded a fire in each year at each site. We then summed the site percentages as an index of annual variability in fire extent (Taylor *et al.* 2008). We made no assumptions about the number or extent of individual fires that may be represented by the index. Pearson product moment correlation coefficients were then calculated between the fire extent index and each climate variable.

RESULTS

Fire Record

A total of 301 fires were identified in the 180 cross-dated wood samples from live ($n =$

25) and dead ($n = 155$) trees. Fires were recorded between 1476 and 1984. However, the period 1525 to 1900 was selected for the fire regime analyses to ensure that $\geq 50\%$ of the sample sites were recording fires. There were 293 fires recorded during this period (Figure 2).

Season of Fire Occurrence

We determined the season of fire occurrence for 1345 (68% of total) fire scars. Fire scars were found mainly in latewood (47%) and at the ring boundary (32%) and they were much less frequent in early wood (late = 15.6%; middle = 5.8%; early = 0.2%).

Fire Return Intervals

The statistical description of point and composite FRI for the 34 sites include the mean, median, and Weibull median probability

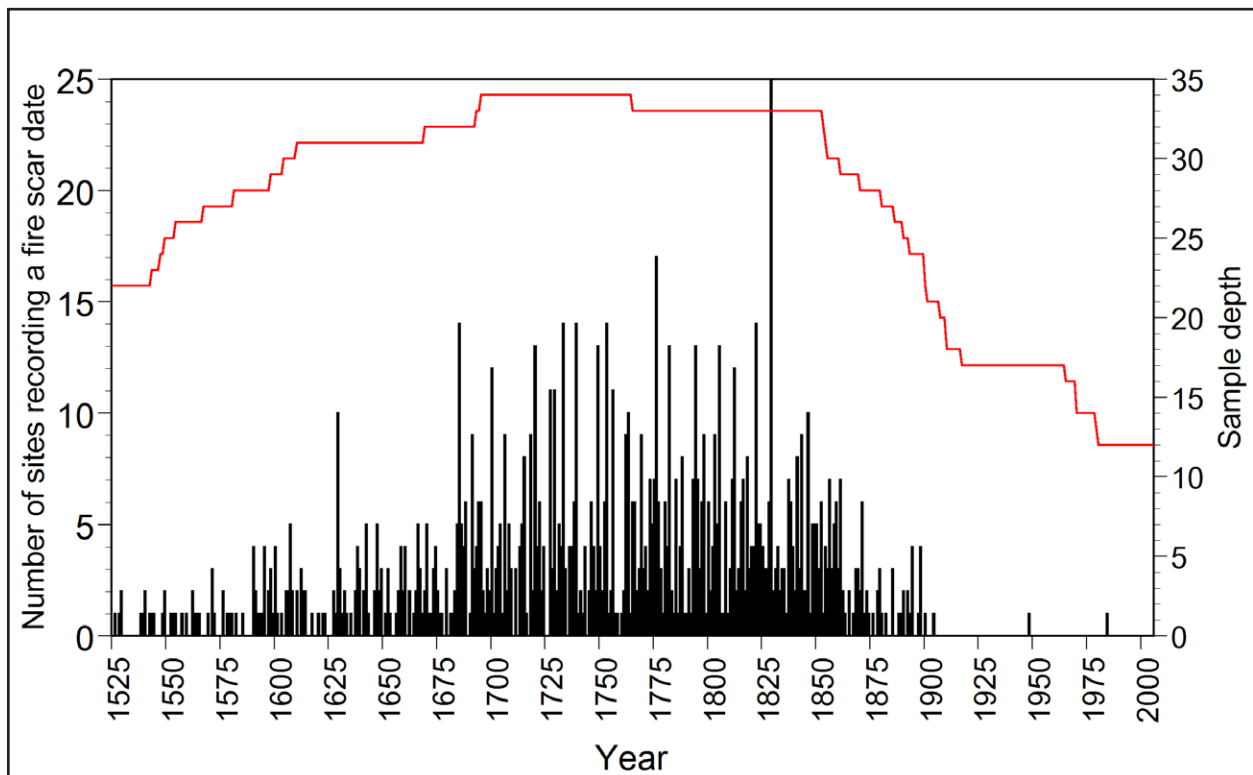


Figure 2. Number of sites recording a fire scar date (bars on the primary y-axis) and sample depth (line on the secondary y-axis) in the Diamond Mountains, California. Sample depth is the number of sites with dated tree-ring material each year that had at least one fire scar and was susceptible to recording additional fires.

interval (WMPI) as measures of central tendency. The FRI distributions are often skewed and WMPI is a measure of central tendency for skewed distributions (Grissino-Mayer 2001). The measures of central tendency for FRI of all sites were similar. The grand mean and grand median CFRI for all sites were 12.1 years and 10.4 years, respectively (Table 1). The PFRI were longer than the CFRI. The grand mean PFRI was 19.8 years and the grand median PFRI was 17.7 years. The mean and median CFRI for all fires in the study area were 1.3 years and 1 year, respectively.

Fire Extent

Fire extent varied among years and most fires were relatively small and recorded only in a few sites (Figure 2). For the period 1700 to 1900, when 90% of sites were recording fires, half of the fires ($n = 90$) burned three or fewer sites, and 78% burned six or fewer sites (Figure 2). Only three fires burned 50% or more of the sites. For the 1700 to 1900 period, a fire of any extent occurred somewhere in the study area every 1.1 years, while intermediate extent (10%), and widespread (25%) fires burned every 2.2 years and 12.6 years, respectively.

Spatial Variation

Slope aspect. The site composite FRI for any (small), intermediate, and widespread fires were similar ($P > 0.05$) on all slope aspects (Table 2). Similarly, there was no difference in site point FRI ($P > 0.05$) by slope aspect (Table 2).

Forest composition. The site point and site composite FRI varied by forest type ($P < 0.05$). Mean PFIs were longest in fir-mixed conifer (24.9 years), shortest in pine-oak (11.9 years), and intermediate in pine mixed-conifer (17.7 years) (Table 3). The length of mean CFRI for each cover type followed the same pattern as for mean PFI ($P < 0.05$).

Elevation. The length of PFRI and CFRI increased with elevation. Forty-four percent of the variance in mean PFRI is explained by elevation ($P < 0.0001$) (Figure 3a). The relationship was weaker for CFRI but still highly significant ($P < 0.0001$) (Figure 3b). The relationship between site PFRI and elevation ($r = 0.66$, $P < 0.001$) remained strong with the effect of sample size per site held constant (partial $r = 0.55$, $P < 0.001$). However, the association between elevation and CFRI ($r = 0.57$, $P < 0.010$) was substantially influenced by the number of fire scar samples per site (partial $r = 0.34$, $P < 0.05$).

Temporal Variation

Fire frequency varied by land-use period (Table 4). The mean CFRI for all fires in the pre-Euro-American settlement period was 1.2 years (range = 1 yr to 4 yr), and it was longer (CFRI = 1.4 years; range = 1 yr to 4 yr) during the settlement era ($P < 0.05$). Fire frequency declined dramatically after the onset of fire suppression in 1905. Only two fires were recorded in the twentieth century. The length of CRFI for intermediate sized fires had the same temporal pattern of variation ($P < 0.05$); wide-

Table 1. Fire return interval (years) summary for 34 sites in the Diamond Mountains, California.

	Grand mean \pm SD	Grand median \pm SD	Grand mean WMPI \pm SD	Range of medians
Composite FRI	12.1 \pm 7.4	10.4 \pm 7.9	10.2 \pm 7.2	4 to 30.5
Point FRI	19.8 \pm 8.0	17.7 \pm 9.0	18.3 \pm 7.7	8 to 49.5

Table 2. Composite and point fire return interval (years) statistics by slope aspect for small (any site scarred), intermediate (10% or more sites burned), and widespread fires (25% or more sites burned). There was no difference in FRI (Kruskal Wallis H-test, $P > 0.05$) by slope aspect for any size burn or for point fire return interval; n is the number of sites.

Composite fire return intervals, any scarred (yr)				
Slope aspect	Mean	Median	Range	SD
North ($n = 6$)	7.2	5.6	4.7 to 12.8	2.9
East ($n = 9$)	10.8	9.2	4.0 to 22.3	6.9
West ($n = 10$)	14.0	11.3	4.9 to 29.8	8.4
South ($n = 9$)	14.5	12.5	6.1 to 32	8.1
Composite fire return intervals, 10% scarred (yr)				
Slope aspect	Mean	Median	Range	SD
North ($n = 6$)	7.2	5.8	4.7 to 12.8	2.9
East ($n = 9$)	10.8	9.3	4.0 to 22.3	6.9
West ($n = 10$)	14.0	12.4	4.9 to 29.8	8.4
South ($n = 9$)	14.5	12.6	6.1 to 32	8.1
Composite fire return intervals, 25% scarred (yr)				
Slope aspect	Mean	Median	Range	SD
North ($n = 6$)	10.0	8.3	2.7 to 6.5	2.8
East ($n = 9$)	11.8	10.1	6.3 to 22.3	6.2
West ($n = 10$)	17.4	16.6	17.9 to 29.8	6.7
South ($n = 9$)	16.4	15	1 0.2 to 32	6.8
Point fire return intervals (yr)				
Slope aspect	Mean	Median	Range	SD
North ($n = 6$)	14.5	10.5	11.2 to 20.4	3.8
East ($n = 9$)	18.4	17.8	8.7 to 23.8	11.7
West ($n = 10$)	22.4	18.3	10.4 to 30.2	6.2
South ($n = 9$)	21.6	20	11.8 to 32	6.4

spread burns were only recorded during the pre-settlement period (mean CFI = 8.2 years; range = 1 yr to 56 yr).

Fire-Climate Relationships

Variation in the local temperature and precipitation was related to the climatic indices at annual time-scales. Current year PDO was correlated with average annual temperature ($r = 0.45$, $P < 0.001$) but not annual precipitation or annual PDSI. Current year NIÑO3 was not correlated ($P > 0.05$) with annual temperature, annual precipitation, or annual PDSI.

The SEA and the correlation analysis of fire and PDSI ($r = -0.26$, $P < 0.001$) indicate that fire years and fire extent were associated ($P < 0.05$) with drought, except for any site scarred (Figure 4a). The opposite was true for non-fire years that were associated with wet conditions. There was no association between antecedent moisture conditions and fire in the study area. The PDSI and NIÑO3 exhibited no serial autocorrelation, so these analyses were conducted with the reconstructed series values.

Fire and non-fire years were associated with variation in ENSO ($P < 0.05$) (Figure 4b).

Table 3. Mean composite fire return interval (years) for small (any site scarred), intermediate (10% or more sites burned), and widespread fires (25% or more sites burned and point fire return interval) by forest type. Composite and point fire return intervals varied by forest type (Kruskal Wallis H-test, $P < 0.05$) and were longest in fir-mixed conifer and shortest in pine oak forests ($P < 0.05$, Tukey post-hoc test); n is the number of sites.

Composite fire return intervals, any scarred (yr)				
Forest type	Mean	Median	Range	SD
Pine-oak ($n = 8$)	6.0	4.6	4.7 to 7.8	1.2
Pine-mixed conifer ($n = 11$)	10.8	9.3	4.0 to 32	8.0
Fir-mixed conifer ($n = 15$)	15.9	14.0	6.1 to 29.8	6.8
Composite fire return intervals, 10% scarred (yr)				
Forest type	Mean	Median	Range	SD
Pine-oak ($n = 8$)	5.9	4.7	4.7 to 7.8	1.2
Pine-mixed conifer ($n = 11$)	10.9	9.4	4 to 32	8.0
Fir-mixed conifer ($n = 15$)	15.9	14	6.1 to 29.8	6.8
Composite fire return intervals, 25% scarred (yr)				
Forest type	Mean	Median	Range	SD
Pine-oak ($n = 8$)	8.3	6.8	6.3 to 12.2	1.8
Pine-mixed conifer ($n = 11$)	13.4	12.3	7.2 to 32	7.0
Fir-mixed conifer ($n = 15$)	18.0	16.4	12.0 to 29.8	5.3
Point fire return intervals (yr)				
Forest type	Mean	Median	Range	SD
Pine-oak ($n = 8$)	11.9	11.6	10.4 to 14.6	1.3
Pine-mixed conifer ($n = 11$)	17.7	17.8	8.7 to 32	6.9
Fir-mixed conifer ($n = 15$)	24.9	23.9	15.1 to 43.8	7.0

In the SEA, the year after fires of any extent was associated with La Niña conditions, and the year following non-fire years was associated with El Niño conditions. Similarly, there was a negative correlation ($r = -0.23$, $P < 0.001$) between NIÑO3 and the fire extent index.

The SEA identified a relationship between PDO_G and fire activity (Figure 4c). A positive PDO_G was associated with the year of intermediate and widespread fires, and the year before any sized fire. In contrast, non-fire years were associated with negative PDO conditions in the preceding year. There was also a positive correlation ($r = 0.19$, $P < 0.01$) between PDO_G and the fire extent index. The SEA with PDO_D ,

in contrast, did not identify an association between fire activity and PDO (Figure 4d).

DISCUSSION

Fire return intervals varied with elevation and forest type in the Diamond Mountains. Both point and composite FRI were shorter in low-elevation pine-oak forests, longer in upper-elevation fir-mixed conifer forests, and intermediate in mid-elevation pine-mixed conifer forests. The inverse relationship between fire frequency and elevation has previously been noted in the central Sierra Nevada (Caprio and Swetnam 1995), the Cascade Range (Taylor 2000, Bekker and Taylor 2001), and the

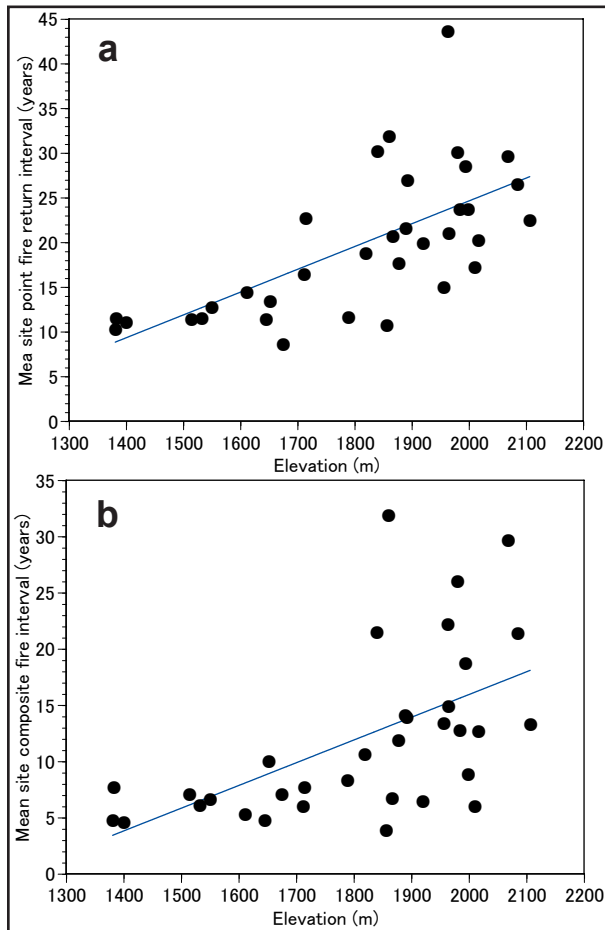


Figure 3. Scatter plot and fit of linear regression to elevation (m) and (a) mean site composite fire return interval (years); and (b) mean site point fire return interval (years) for 34 sample sites in the Diamond Mountains.

Blue Mountains in Oregon (Heyerdahl *et al.* 2001). The increase in length of FRI with elevation is attributable to several factors that influence the flammability of forest fuels, and the behavior and spread of fire. First, the density of litter mats varies with forest composition. Forests dominated by short-needled species of fir have dense litter mats that retain more moisture and have low packing ratios, which results in lower rates of spread and fire line intensity (Albini 1976, Rothermel 1983, van Wagtenonk *et al.* 1998). Second, rates of fine fuel production are higher in warm low-elevation pine-dominated forest so fuel recovery after a fire occurs more rapidly and stands

Table 4. Mean composite fire return interval (years) for the presettlement (1600 to 1849), settlement (1850 to 1904), and the fire suppression period (1905 to present) for 34 sites in the Diamond Mountains, California. The mean fire return intervals (years) were longer ($P < 0.05$) during the settlement period than pre-Euro-American period and no fires burned in the fire suppression period.

Period	Mean composite fire return interval (yr)		
	Mean	Median	Range
Presettlement			
Any scarred	1.2	1	1 - 4
10% scarred	2.1	2	1 - 13
25% scarred	8.2	6	1 - 56
Settlement			
Any scarred*	1.4	1	1 - 4
10% scarred*	5.3	2	2 - 27
25% scarred	-	-	-
Fire suppression			
Any scarred	-	-	-
10% scarred	-	-	-
25% scarred	-	-	-

can burn sooner (Agee *et al.* 1978, Strohlgen 1988). Finally, longer snow-free periods in low-elevation stands lengthen the period that fuels are dry enough to burn each year compared to upper-elevation stands with later lying snowpacks (Agee 1993, Lutz *et al.* 2009).

Site differences related to variation in slope aspect create forest composition differences similar to variation in elevation. In mixed conifer forests in the Sierra Nevada and Cascades, south-facing slopes are dominated by pines while white fir is predominant on north-facing slopes (e.g., Beaty and Taylor 2001, 2008; Scholl and Taylor 2010). Vegetation and environmental differences on different slope aspects in turn can influence variation in FRI. For example, FRI are longer on north- than on south-facing slopes in mixed conifer forests in the Lake Tahoe Basin (Beaty and Taylor 2008), on the western slope of the southern Cascades (Beaty and Taylor 2001), and in the Klamath

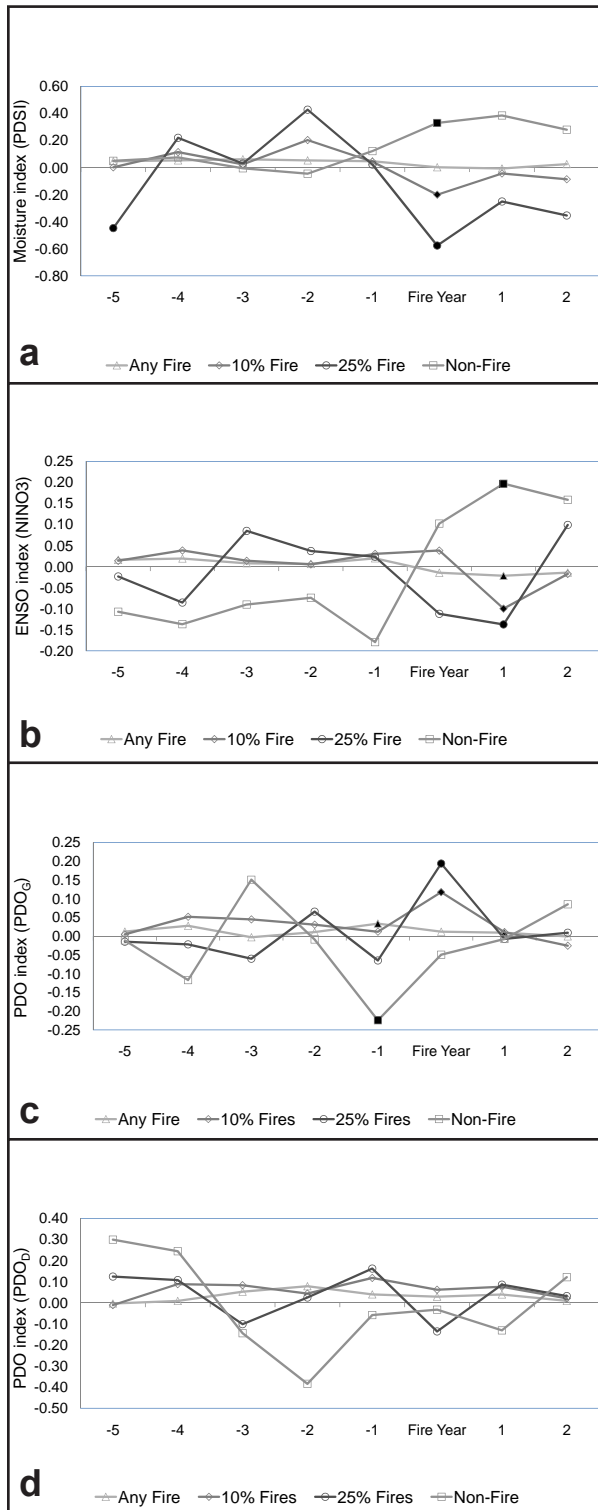


Figure 4. Superposed epoch analysis (SEA) of reconstructed a) PDSI b) NIÑO3 (ENSO) c) PDO_G (Gedalof and Smith 2001), d) PDO_D (D'Arrigo *et al.* 2001) with non-fire years and fire years of different extent for the period 1700-1900. Values with filled symbols were statistically significant ($P < 0.05$).

Mountains (Taylor and Skinner 2003). In mixed conifer forests in the Blue Mountains of Oregon, FRI varied with slope aspect in watersheds with incised complex terrain but not in more gentle terrain (Heyerdahl *et al.* 2001). Greater variation in fuel beds in the complex terrain apparently acted as fuel breaks to impede spread of fire among slope aspects creating spatially fixed patterns of FRI (Heyerdahl *et al.* 2001). Yet, FRI in our study area did not vary by slope aspect. Greater fuel connectivity and less complex terrain probably reduced slope aspect effects on FRI in the Diamond Mountains compared to these other geographic locations. Similarly, FRI did not vary with slope aspect in a mixed conifer forest landscape in Yosemite National Park (Scholl and Taylor 2010). Topographic control on spatial patterns of fire frequency may only emerge when terrain complexity exceeds a certain threshold (Taylor and Skinner 2003, Scholl and Taylor 2010).

The season of fire occurrence strongly influences fire effects and species response to burning (Kauffman 1990, Agee 1993). The position of fire-caused lesions within tree rings indicate that fires occurred in the Diamond Mountains late in the growing season or after trees became dormant for the year. This suggests that most burns occurred in the late summer to fall period. In the Sierra Nevada, fire ignitions are most frequent in July and August when lightning activity peaks (van Wagtendonk and Fites-Kaufmann 2006). The seasonality of burns in the Diamond Mountains is quite similar to the season of burns reported for other mixed conifer forests in the northern Sierra Nevada (Moody *et al.* 2006, Beaty and Taylor 2008). There is variation, however, in the predominant season of burn at different locations in the mixed conifer zone in California. In the central Sierra Nevada, growing season burns recorded in latewood are more abundant than dormant season burns (Caprio and Swetnam 1995), while in the Klamath Mountains

most fires occur during the dormant season (Taylor and Skinner 2003, Fry and Stephens 2006). In contrast, early season burns are most common in mixed conifer forests in northern Mexico in the Sierra San Pedro Martir (Stephens *et al.* 2003), suggesting that there is a latitudinal gradient in season of burn in the mixed conifer zone.

Land use had a profound influence on fire regimes in the Diamond Mountains, and fire frequency varied by time period. In the Diamond Mountains, fire occurrence and extent declined dramatically following initial Euro-American settlement (circa 1850), which was then followed by implementation of a fire suppression policy on National Forest lands in 1905. The initial decline in fire frequency in about 1850 was probably related to a reduction in Native American ignitions caused by the decimation of the Maidu population (Burrill 1988, Camacho *et al.* 1997). A brief gold rush between 1856 and 1860 in Gold Run (located within the study area) brought an influx of settlers (McDow 1965). Livestock grazing in the grasslands at the base of the mountains became significant by the early 1860s. Grazing would have reduced fuels, limiting spread of fire from meadows into the forests. A similar early reduction of fire frequency has been identified in some meadow-edge forests 75 km west of the Diamond Mountains where large flocks of sheep grazed in the 1860s (Norman and Taylor 2005). More importantly, fire extent declined in all meadow-edge forests at this time, suggesting that grazing reduced fuel continuity and spread of fire across the landscape (Norman and Taylor 2005). Similar mid- to late nineteenth century declines in fire occurrence have been identified in mixed conifer forests in the central Sierra Nevada (Caprio and Swetnam 1995, Swetnam and Baisan 2003), in the north Coast Range (Skinner *et al.* 2009), and on the edge of the Sacramento Valley in the Klamath Mountains (Fry and Stephens 2006) and southern Cascades (Taylor 2010). At each

of these locations, the combination of the decline in Native American populations followed by livestock grazing is presumed to have reduced fuel continuity, leading to reduction in fire frequency and extent. Not all sites in the mixed conifer zone record a nineteenth century decline in fire frequency, suggesting that the effects of livestock grazing and Native American ignitions on fire regimes were spatially variable. For example, declines in fire frequency and extent did not occur in mixed conifer forests in some areas in the Klamath Mountains (Taylor and Skinner 1998, 2003), the southern Cascade Range (Taylor 2000, Beaty and Taylor 2001, Bekker and Taylor 2001), and the northern Sierra Nevada until after 1905 when a policy of fire suppression was implemented (Stephens and Collins 2004).

In the Diamond Mountains, most fires were small and burned less than 10% of sites (i.e., 3 to 4 sites). However, years of widespread burning did occur and they were associated with low moisture availability and drought (Cook *et al.* 1996). In contrast, non-fire years were associated with wet conditions, but wet antecedent conditions were not associated with fire years. This suggests that increased fine fuel growth during wet years was not a precondition for widespread burning in dry years. Interestingly, years of widespread burning in the Diamond Mountains (e.g., 1729, 1733, 1762, 1776, 1794, 1812, 1822, 1829, 1841) are identical to years of widespread burning in other mixed conifer forests in the northern Sierra Nevada (Stephens and Collins 2004, Taylor and Beaty 2005, Beaty and Taylor 2008), the southern Cascades (Taylor *et al.* 2008), the northern Coast Range (Skinner *et al.* 2009) and the Klamath Mountains (Taylor and Skinner 2003). This indicates that climate variation, specifically drought, was an important regional driver of wildfire activity in both the Diamond Mountains and in northern California.

Inter-annual variation in ENSO is strongly related to variation in fire frequency and extent

in fire-prone pine forests in the American southwest (e.g., Swetnam and Betancourt 1990) and Rocky Mountains regions (e.g., Veblen *et al.* 2000). Years of high fire frequency and extent in each region corresponds with the ENSO phase that brings drier and warmer conditions. In the Diamond Mountains, fire years were weakly associated with La Niña conditions, similar to the pattern for fires in pine-dominated forests in the American southwest. Years of more widespread burning in mixed conifer forests in the Lake Tahoe Basin were also associated with La Niña conditions (Beaty and Taylor 2008). However, inter-annual fire activity is not consistently associated with variation in ENSO in northern California (e.g., Taylor and Beaty 2005, Fry and Stephens 2006, Moody *et al.* 2006, Taylor *et al.* 2008, Skinner *et al.* 2009). The inconsistent relationship between variation in ENSO and fire activity may be related to high spatial variability in inter-annual temperature and precipitation in this geographic location. The Diamond Mountains are located in the transition zone that separates the southwest and northwest centers of action in ENSO influence on climate (Dettinger *et al.* 1998). Shifts in the location of ENSO affects in the transition zone from year to year may mask ENSO climatic effects on fire regimes in this region.

Variation in SSTs in the north Pacific (PDO) has been linked to variability in fire activity in several parts of the western United States including the Rocky Mountains (Schoennagel *et al.* 2004, Sibold and Veblen 2006), the southern Cascades (Norman and Taylor 2003) and other parts of the northern Sierra Nevada (Taylor and Beaty 2005, 2008; Moody *et al.* 2006). In the Diamond Mountains, years of high fire activity prior to 1900 were associated with positive values of PDO_G, and this same association has been identified between widespread forest fires and the PDO_G in the inland Pacific northwest (Hessl *et al.* 2004). In the Diamond Mountains, PDO_D was

not associated with wildfire activity, suggesting that some caution should be used in interpreting the influence of PDO on past fire activity. Nevertheless, the association between PDO_G and fire identified in the Diamond Mountains is consistent with associations between instrumental PDO and fire in the post-fire suppression period in several parts of the western United States. Area burned in the northern Rocky Mountains (Heyerdahl *et al.* 2008) and Pacific coast states (Trouet *et al.* 2006) are associated with a positive PDO. In these regions, and in the Diamond Mountains, warmer temperatures during positive PDO conditions may influence fire activity by increasing the length of the fire season because of earlier snowmelt.

Fine-scale variation in topographic variables (slope aspect, elevation, and forest type) have been identified as an important bottom-up control on fire regimes in several mixed conifer forest types in the western United States (Caprio and Swetnam 1995, Taylor 2000, Beaty and Taylor 2001, Stephens 2001, Coker *et al.* 2007). In the Diamond Mountains, local variation in fire occurrence was controlled by elevation and forest type. Fire return intervals were shorter in low-elevation pine-dominated forests and longer in upper-elevation fir-dominated forests. At broad spatial scales, pre-fire exclusion fire regimes were influenced by the top-down control of climate. Inter-annual variability in drought, ENSO, and the PDO created conditions that synchronized years of both widespread burning and no fire activity throughout the study area. Human land use also exerted strong top-down control on fire activity. Fire occurrence and extent declined dramatically after Euro-American settlement and implementation of fire suppression on federal forest lands in 1905. During that time, only two fires were recorded in the study area, by far the lowest fire frequency for a 100 year period in our 300 year fire record. In other mixed conifer and pine-dominated forests in

the Sierra Nevada (e.g., Taylor 2004; Beaty and Taylor 2007, 2008; Scholl and Taylor 2010) and the southern Cascades (e.g., Taylor 2000), exclusion of frequent surface fires that thinned mixed conifer forests has caused an increase in forest density and unprecedented accumulations of surface and canopy fuels, in-

creasing the risk of high-severity fire. The high severity of five recent wildfires that burned 30940 ha in the Diamond Mountains and threatened communities is related, in part, to this extended period of fuel accumulation caused by fire suppression.

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