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Fire history and the structure and dynamics of a mixed conifer forest landscape in the northern Sierra Nevada, Lake Tahoe Basin, California, USA

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Abstract

The goal of this study was to understand how fire regimes promote fine- and coarse-grain vegetation patterns in an old-growth mixed conifer forest dominated landscape in the General Creek watershed on the west shore of Lake Tahoe, California. We quantified the structure (e.g., composition, age, and size) of old-growth mixed conifer stands located across a range of environmental settings. Fire histories were reconstructed using fire-scar dendrochronology, and the influence of regional climatic variability on fire occurrence was assessed by relating the fire record to regional climate reconstructions. Fire regimes parameters varied across topographic gradients at landscape scales promoting fine grain forest structural patterns. The timing and extent of fires was related to inter-annual and inter-decadal variation in drought which was linked to the El Niño-Southern Oscillation and the Pacific Decadal Oscillation. Coarse scale vegetation patterns where related to upper slope positions and relatively infrequent high severity fires. Fire regimes and forest structure have changed since EuroAmerican settlement with virtually no fires and structural shifts towards higher stand densities and a greater representation of fire intolerant species. At the landscape scale, fire regimes and forests patterns in mixed conifer forests are influenced by a variety of process operating at multiple spatial and temporal scales. Coarse scale heterogeneity related to topography and moderate to high severity fire is superimposed on fine scale variability related to topographic gradients and local variability in fuel and forest structural characteristics. Fire suppression has resulted in a more homogenous landscape particularly with regard to the loss of coarse scale heterogeneity.

Keywords: Fire regimes; Environmental gradients; Landscape heterogeneity; Climate

1. Introduction

Recurring fire is a keystone disturbance process that strongly influences the structure, composition, and dynamics of mixed conifer forests in the Sierra Nevada of California (Kilgore and Taylor, 1979; Skinner and Chang, 1996), and variation in fire regime characteristics is thought to promote structural heterogeneity at both stand (e.g. Bonnicksen and Stone, 1981, 1982) and landscape (e.g. Beaty and Taylor, 2001; Nagel and Taylor, 2005) scales. Most research on fire and forest structure in mixed conifer forests has focused on how frequent, low severity surface fires promote development of multi-aged or multi-sized stands that are comprised of small overlapping patches of even-aged or even-sized groups of trees (Bonnicksen and Stone, 1981, 1982; Stephens and Fry, 2005; Stephens and Gill, 2005; Beaty and Taylor, 2007). Stand structure and development is thought to be primarily controlled by the interactions between fire and forest structure where burn patterns and fire effects are constrained by the time it takes fuels to accumulate in a burned patch so it can burn again (e.g., Bonnicksen and Stone, 1981; van Wagtendonk, 1995). Widespread and/or high severity fires are thought to be uncommon because of discontinuous and low levels of fuels. Recent work, however, suggests a more complex interaction between fire and forest structure because fire regimes and fire effects are influenced by landscape and regional controls such as topography (Taylor and Skinner, 1998, 2003; Taylor, 2000; Beaty and Taylor, 2001), climate variability (Swetnam, 1993; Norman and Taylor, 2003; Taylor and Beaty, 2005), and human activities such as logging or fire suppression (Weatherspoon and Skinner, 1995).

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Identifying the influence of different controls on mixed conifer forest fire regimes and forest structure is a challenge because forests in the Sierra Nevada have been extensively altered by Euro-American land use practices. Forests have been logged, grazed, burned, or subject to fire suppression management since the mid to late 19th century (McKelvey and Johnston, 1992). These land use practices have obscured the relationships between fire and forest development. Even in protected areas such as national parks and wilderness areas mixed conifer forests have undergone change. For example, the reduction in fire occurrence caused by fire suppression has caused an increase in forest density and shifted species composition to more fire intolerant species (Vankat and Major, 1978; Parsons and DeBenedetti, 1979; Taylor, 2000; Beaty and Taylor, 2007). The influence of fire suppression on landscape scale vegetation composition and structural patterns is less well understood, but forested landscapes have been reported to become more homogenous (Skinner, 1995; Beaty and Taylor, 2001).

Fire effects on mixed conifer forest development in the Sierra Nevada before the onset of fire suppression have only been characterized at the stand scale. In these stands, periods between fires were short (i.e., 5–17 years), fires burned mainly at low- to moderate-severity, and stands were multi-aged or multi-sized (Parsons and DeBenedetti, 1979; Kilgore and Taylor, 1979; Bonnicksen and Stone, 1982; North et al., 2005; Beaty and Taylor, 2007). High-severity fires that kill most or all of the trees in a stand are thought to be rare (Bonnicksen and Stone, 1982; Kilgore, 1973). Yet, large patches (>10 ha) of even-aged forest embedded within a matrix of old-growth forest suggest that high severity fire may be an integral component of some mixed conifer forest fire regimes and forest structure and dynamics (Wilken, 1967; Beaty and Taylor, 2001; Nagel and Taylor, 2005).

Topography and climate are also important controls that are thought to contribute to variation in mixed conifer forest fire regimes and forest structure. Topography (i.e., slope pitch, slope aspect, slope position, elevation) directly and indirectly influences fire behavior and fire regimes by affecting the nature and structure of fuels, the location of barriers to fire spread, and preheating of fuels as fires spread (Rothermel, 1983; Heyerdahl et al., 2002; Taylor, 2000; Taylor and Skinner, 2003; Cocke et al., 2005). For example, fire return intervals in mixed conifer forests in some areas are shorter on south than north-facing slopes (Beaty and Taylor, 2001) because fuels are dry enough to carry fire each year for longer periods on south-facing slopes. Pre-fire suppression fires in mixed conifer forests are also more severe on upper slopes in some areas (e.g., Taylor and Skinner, 1998; Beaty and Taylor, 2001) but not others (e.g., Taylor and Skinner, 2003). Variation in fire extent in the mixed conifer zone may also be influenced by interannual variation in climate, particularly drought. In some western conifer forests, fire extent is greater during dry than wet years (e.g., Taylor and Beaty, 2005) and the timing of dry and wet years is related to interannual and multi-decadal variation in coupled ocean-atmosphere circulation patterns such at the El Niño-Southern Oscillation (ENSO) (Diaz and Markgraf, 2000) and the Pacific Decadal Oscillation (PDO) (Gershunov et al., 1999).

In this paper, we examine how topography and climate variation contribute to spatial and temporal variability in fire regimes and forest structure in an old-growth mixed conifer forest in the northern Sierra Nevada of California. We specifically address the following questions: (1) How do fire regimes vary spatially and temporally? We expected spatial variation in fire regimes in this mountainous terrain to be related to topography (i.e., slope aspect, slope position, forest composition). We also expected fire occurrence to decline with organized fire suppression. (2) How has forest structure and composition changed since Euro-American settlement? We expected forests to have increased in density and extent with the onset of change being coincident with the onset of the fire suppression period; (3) How does climate variability influence fire regimes? We expected temporal variation in fire extent to be related to dry and wet years and variation in ENSO and the PDO in the tropical and north Pacific, respectively.

2. Methods

2.1. Study area

We studied mixed conifer forests in the 2000 ha General Creek watershed (GCW) on the west shore of Lake Tahoe in California (Fig. 1). General Creek drains a formerly glaciated valley and elevations range from 1850 to 3000 m and the topography is diverse and includes flat valley bottoms to moderately steep (~ 20°) side slopes. The climate is characterized by warm dry summers and cold wet winters: most (80%) precipitation falls as snow during the winter. Mean monthly temperatures at Tahoe City (15 km north) range from −2° in January to 16 °C in August, and mean annual precipitation is 784 mm.

The forests around Lake Tahoe have a diverse history of human use. The Lake Tahoe basin was used by the Washoe,

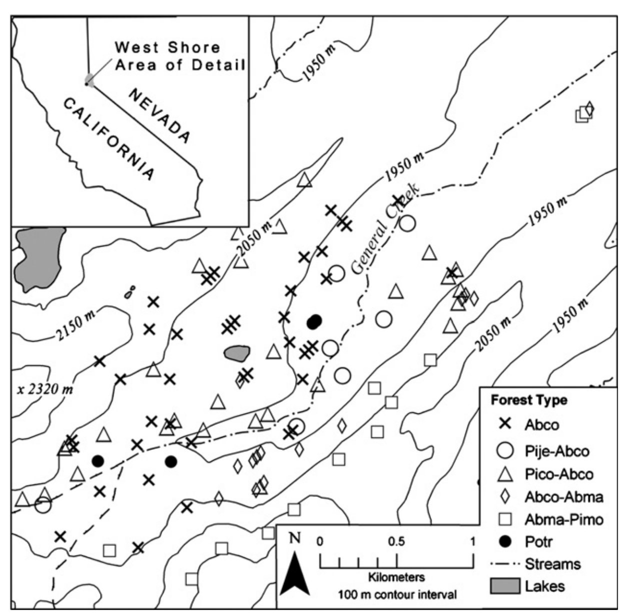

Fig. 1. Location of study area and sample sites by forest type ($n = 108$) in the General Creek Watershed, Lake Tahoe Basin, California.

who annually migrated from the Great Basin during the summer. Ethnographic accounts indicate that the Washoe used the forests for hunting and gathering of forage and fiber (Lindström, 2000). EuroAmericans first traversed the Tahoe region in 1844 but large numbers of EuroAmericans did not settle in the Lake Tahoe basin until the 1860s. Beginning in the 1870s, nearly 70% of the Lake Tahoe watershed was logged to provide wood for silver mines in Virginia City, Nevada (Eliott-Fisk et al., 1996). Some areas on the west shore of Lake Tahoe were not logged or were only selectively logged (Lindström, 2000). The GCW was not logged and the watershed became part of the California State Park System in, 1965. A program of prescribed burning has been implemented in the park, but none of the sites used in this study were burned by prescribed fire.

2.2. Forest composition and structure

Forest composition and structure was sampled across a range of environmental settings in GCW (Table 1; Fig. 1). Sites for sampling were chosen after first stratifying the study area by elevation, slope aspect, and topographic position and then strata were sampled using 400 m^2 plots (20 m $\times$ 20 m). The diameter at breast height (dbh) of all live trees (>5.0 cm dbh) was measured, and seedlings (0.2–1.4 m tall) and saplings (>1.4 m tall; <4 cm dbh) were counted in each sample plot. The age structure of trees in each plot was determined by coring 15–25 trees (mean = 16; coring height = 30 cm) across the range of tree species and size classes in each plot and cross-dating the annual growth rings beneath a binocular microscope (e.g., Stokes and Smiley, 1968). The date of the center ring was used as the tree age estimate.

The location (GPS), elevation, slope aspect, slope pitch, topographic position, and slope configuration for each plot were also recorded. The last four variables were used to calculate the Topographic Relative Moisture Index (TRMI; Parker, 1982), which is a measure of potential soil moisture that varies from 0 for xeric sites to 60 for mesic sites. Groups of plots with similar species composition were identified by first calculating importance values (IV = sum of relative frequency and relative density) for each species in each plot and then clustering IVs using relative Euclidean distance and Ward's method. Ward's clustering method minimizes within group variance relative to between group variance (Gauch, 1982; van Tongeren, 1995). Differences in environmental conditions among forest IV groups were identified by comparing environmental variables using distribution free Kruskal–Wallis *H*-test (Sokal and Rohlf, 1995).

Forest compositional changes within each compositional group were inferred by ordinating the relative density of tree species in three diameter classes (under-story stems (trees <15 cm dbh), intermediate stems (Trees 15.0–40.0 cm dbh), and canopy stems (trees >40.0 cm dbh)) using detrended correspondence analysis (DCA; Gauch, 1982). This approach assumes that under-story tree abundance is an indicator of future forest composition in the absence of disturbance.

2.3. Fire history and fire regimes

Fire regimes (i.e., return interval, season, extent, severity) in GCW were reconstructed using three types of data. First, written fire records were used to identify the frequency, extent, and season of fires in the twentieth century. Second, fires that occurred before ca. 1900 were identified in fire scarred trees and in radial growth changes in tree cores (e.g., Arno and Sneck, 1977; Barrett and Arno, 1988). Finally, tree population age-structure data was used to infer the severity of the most recent burns.

Partial wood cross-sections were collected from live and dead fire-scarred trees throughout the study area with a chain saw. Cross-sections were collected from small groups of trees using the following criteria: (1) the geographic location of samples in the watershed to ensure adequate coverage of the study area, (2) the observed number of external fire scars, and (3) sample integrity. Fire dates were identified by first sanding wood samples to a high polish and then cross-dating (Stokes and Smiley, 1968) the tree-rings with a nearby tree-ring chronology (e.g., Holmes et al., 1986). The calendar year of the ring with a fire scar in it was then recorded as the fire date.

Fire can also injure trees and cause a sudden decrease in radial growth (i.e., growth suppression) and the onset of the growth suppression can corresponds to the date of the fire (Arno and Sneck, 1977; Barrett and Arno, 1988; Means, 1989; Brown and Swetnam, 1994). Alternately, a fire may enhance growing conditions for a tree by eliminating competitors (Agee, 1993), causing a sudden increase in radial growth (i.e., growth release; Brown and Swetnam, 1994). Releases and suppressions were identified as fire related if their dates corresponded with the date of a fire scar in a nearby sample. Fire related growth responses were identified in the plots by radial growth releases or suppressions in each tree core. Cores were sanded to a high polish and their tree-rings were cross-dated. Growth releases or suppression were defined as an abrupt 200% increase or decrease in ring-width that was sustained for at least 5 years (Barrett and Arno, 1988).

The season of each fire was inferred from the position of fire scars within annual growth rings (e.g., Baison and Swetnam, 1990). Scar positions were classified as: (1) early (first one-third of earlywood); (2) middle (second one-third); (3) late (last one-third); (4) latewood (in latewood); or (5) dormant (at ring boundary). In the northern Sierra Nevada, dormant season fires represent fires that burn in late summer or fall after trees stop growing for the year (e.g., Caprio and Swetnam, 1995).

Composite and point fire return intervals (FRI) were calculated for the entire study area and for major topographic divisions. Differences in fire frequency among topographic divisions were identified by comparing FRIs using a Kruskal–Wallis *H*-test (Sokal and Rohlf, 1995).

Variation in fire occurrence that may be related to land-use changes after EuroAmerican settlement were identified by comparing fire return intervals for three periods; (1) the pre-settlement period (1700–1849), (2) the settlement period (1850–1900), (3) and fire suppression period (1900–2000) using a *t*-test. Composite FRIs for the entire watershed were

Table 1
Mean importance value (IV; maximum 200), basal area ($m^2\ ha^{-1}$), density (stems ha^{-1}), age structure, and site characteristics for forest compositional groups identified by cluster analysis of species importance values in the General Creek Watershed, Lake Tahoe Basin, California

	Forest compositional group																	
	White fir ($n = 42$)			Jeffrey pine-white fir ($n = 28$)			Lodgepole pine-white fir ($n = 7$)			White fir-red fir ($n = 14$)			Red fir-western white pine ($n = 13$)			Quaking aspen ($n = 4$)		
Species	IV	BA	Den.	IV	BA	Den.	IV	BA	Den.	IV	BA	Den.	IV	BA	Den.	IV	BA	Den.
White fir* (*Abies concolor*)	147	60	1148	90	26	571	85	26	2471	109	37	1323	25	5	350	24	6	181
Red fir* (*Abies magnifica*)	3	<1	26	7	2	55	6	1	289	62	24	580	115	50	648			
Incense cedar* (*Calocedrus decurrens*)	6	5	27	<1		1												
Lodgepole pine* (*Pinus contorta*)	4	2	28	<1		1	91	31	675	<1	<1	2	1	<1	2	6	4	38
Jeffrey pine* (*Pinus jeffreyi*)	35	32	93	100	63	219	14	1	14	15	9	25	21	13	35			
Sugar pine (*Pinus lambertiana*)	3	3	4	3	2	4				4	1	9	7	6	15			
Western white pine* (*Pinus monticola*)	2	1	7	<1		6				11	2	95	28	11	119			
Mountain hemlock* (Tsuga mertensiana)	<1		2										2	2	12			
Quaking aspen (Populus tremuloides)*																170	44	2788
Mean age*	112			127			79			158			190			73		
S.D. age	54.6			93.6			41.5			78.5			93.8			39.7		
Min. age	34			5			16			60			46			14		
Max. age	533			500			201			444			484			140		
Percent even aged	46%			20%			50%			0%			18%			100%		
Elevation (m)*	2058			2054			1985			2049			2150			2030		
Slope aspect (deg.)*	111			120			57			37			34			49		
Slope aspect (direction)	SE			SE			NE			N			N			NE		
Slope pitch (deg.)*	13			16			2			19			23			2		
Topographic position*	Middle slope			Middle slope			Valley bottom			Middle slope			Upper slope			Valley bottom		
Mean TRMI (range 0–60)*	31			27			45			28			24			46		

n is the number of samples in each group. Variables with an (*) were significantly different among forest compositional groups ($P < 0.05$, Kruskal–Wallis H-test).

used for the temporal comparisons because composite FRIs are more sensitive to subtle changes in fire occurrence and burning pattern than samples from a single site or a single tree (Dietrich, 1980).

The spatial extent of fires was not directly measured since the spatial coverage of fire-scar samples was not sufficient to develop fire perimeter maps (e.g., Taylor, 2000). Instead relative fire extent was estimated using the number of trees scarred by fire: (1) local fires where two or more sites burned, (2) intermediate fires where five or more sites burned, and (3) widespread fires where nine or more sites burned ($\geq$45% of sites). Intermediate and widespread fires may have been contiguous burns or smaller, separate fires resulting from multiple ignitions.

Fire severity was inferred using stand structure data in plots (age, size) and forest structure patterns evident on historical aerial photograph pairs (1941 and 2000) (Taylor and Skinner, 1998; Russel et al., 1998). This approach assumes that stands with mainly older and taller trees experienced low to moderate severity fires while stands dominated by populations of trees with similar age and size, or brushfields (Wilken, 1967; Bolsinger, 1989; Nagel and Taylor, 2005), established after high severity fires. Stands were mapped in 1 ha^{-1} grid cells on each aerial photograph and grouped into three severity classes (low, moderate, and high) based on the density of trees in different height classes evident on historic aerial photographs: (1) low severity >20 emergent stems ha^{-1}, (2) moderate severity 10–20 emergent stems ha^{-1}, and (3) high severity <10 emergent stems ha^{-1}. Plot age- and size-class data was used to confirm severity class membership identified from the air photos. Spatial variation in fire severity was then determined by calculating the percentage of high, moderate, and low severity burns by topographic position (low, middle, high) and slope aspect. Areas occupied by montane chaparral were placed in the high severity class because montane chaparral establishes primarily after high severity fire (Nagel and Taylor, 2005). This severity map represents the cumulative pattern of fire severity generated by the most recent fires; evidence of earlier fires is erased by subsequent fires (Taylor and Skinner, 1998; Beaty and Taylor, 2001). A potential shortcoming of this approach is that some areas with poor soils (e.g., valley bottom and ridge tops) may have a low number of trees unrelated to fire history. However, to account for this, we used tree age data to determine if stands were even- or multi-aged as evidence of high and low to moderate severity, respectively.

Relationships between fire and climate were determined by comparing climatic conditions in years with different size fires. First, a Palmer Drought Severity Index (PDSI) reconstruction (Cook et al., 1999; GP-47) was used to evaluate the influence of drought on fire. PDSI integrates current and lagged monthly temperature and precipitation values to estimate drought severity (Palmer, 1965; Alley, 1984). Negative PDSI values represent drought and positive PDSI values represent moist conditions. The PDSI reconstruction we used explains 50–70% of the variation in instrumental PDSI (Cook et al., 1999).

Next, we compared fire occurrence and extent to a reconstruction of the NINO3 index, a measure of tropical Pacific SST temperature variation (Cook, 2000). Positive NINO3 values indicate El Niño conditions and negative values indicate La Niña conditions. This NINO3 reconstruction explains 53% of the variation in the instrumental NINO3 (Cook, 2000).

Temporal variation in fire occurrence and extent was also compared to variation in the Pacific Decadal Oscillation (PDO). We used the Biondi et al. (2001) reconstruction of the PDO index for the fire climate comparison. Index values are positive when the PDO is in its warm phase and negative when in its cool phase. The PDO reconstruction captures 41% of the variance in the instrumental PDO (Biondi et al., 2001).

We used superposed epoch analysis (SEA) (Haurwitz and Brier, 1981) to identify relationships between reconstructed fire and climate variables. SEA involves calculating the average value of a climate proxy for the years during, before, and after fire events (i.e., the ‘‘epoch’’ surrounding an event). Statistical significance was determined by comparing the epoch surrounding a fire event with bootstrapped confidence intervals based on randomly selected epochs from 1000 Monte Carlo simulations (Mooney and Duval, 1993). Analyses were performed separately on local, intermediate, and widespread fire years, as well as for non-fire years to identify climatic conditions that are not conducive to fire.

3. Results

3.1. Forest composition and structure

Six forest types were identified from cluster analysis of species importance values: (1) White fir (*Abies concolor* Gord. & Glend.); (2) lodgepole pine (*Pinus contorta* Dougl. ex Loud.)-white fir; (3) Jeffrey pine (*Pinus jeffreyi* Grev. & Balf. in A. Murr.)-white fir; (4) white fir-red fir (*Abies magnifica* A. Murr.); (5) red fir-western white pine (*Pinus monticola* Dougl. ex. D. Don.); and (6) quaking aspen (*Populus tremuloides* Michx.) (Table 1). Forest types were segregated by elevation, slope aspect, topographic position, and potential soil moisture (TRMI) (Table 1; Fig. 1). The mean values for each of these variables were significantly different among forest types (Kruskal–Wallis *H*-test, $P < 0.05$).

The white fir group ($n = 42$) is the most widespread forest type and is dominated by white fir (Table 1). White fir stems are 12-fold more abundant than Jeffrey pine, the next most abundant species. The high stem density is due mainly to small diameter (i.e., dbh <35 cm) white fir that are <110 years old (Fig. 2). Trees in white fir plots are multi-sized and multi-aged but most white fir are <40 cm dbh (Fig. 2) and most old (>200 years) trees in this group are Jeffrey pine (Fig. 3). White fir plots are most common on lower slopes and valley bottoms and on south-facing slopes interspersed with Jeffrey pine-white fir plots (Fig. 1). White fir plots also occur near ridge tops that were once montane chaparral. These stands have a uni-modal age and size structure with trees <120 years old.

The Jeffrey pine-white fir group ($n = 28$) is co-dominated by Jeffrey pine and white fir. Jeffrey pine has a higher basal area but a lower density than white fir (Table 1). Jeffrey pine-white

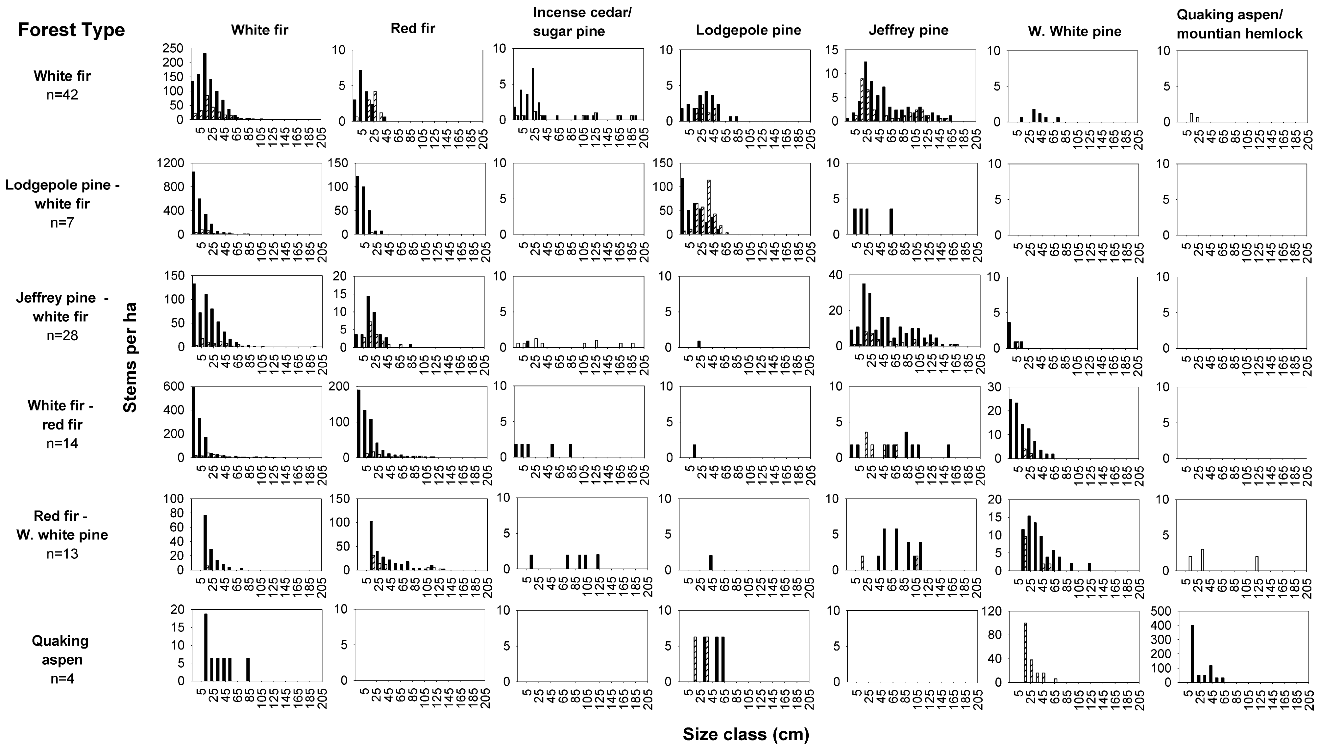

Fig. 2. Average size distributions for mixed conifer forest types in the General Creek Watershed, Lake Tahoe Basin, California. Filled bars in size-class graphs represent live trees and open bars represent dead trees. Note that only every other age-class is labeled and that the scaled of the vertical axis is difference for each graph Species acronyms are given in Table 1.

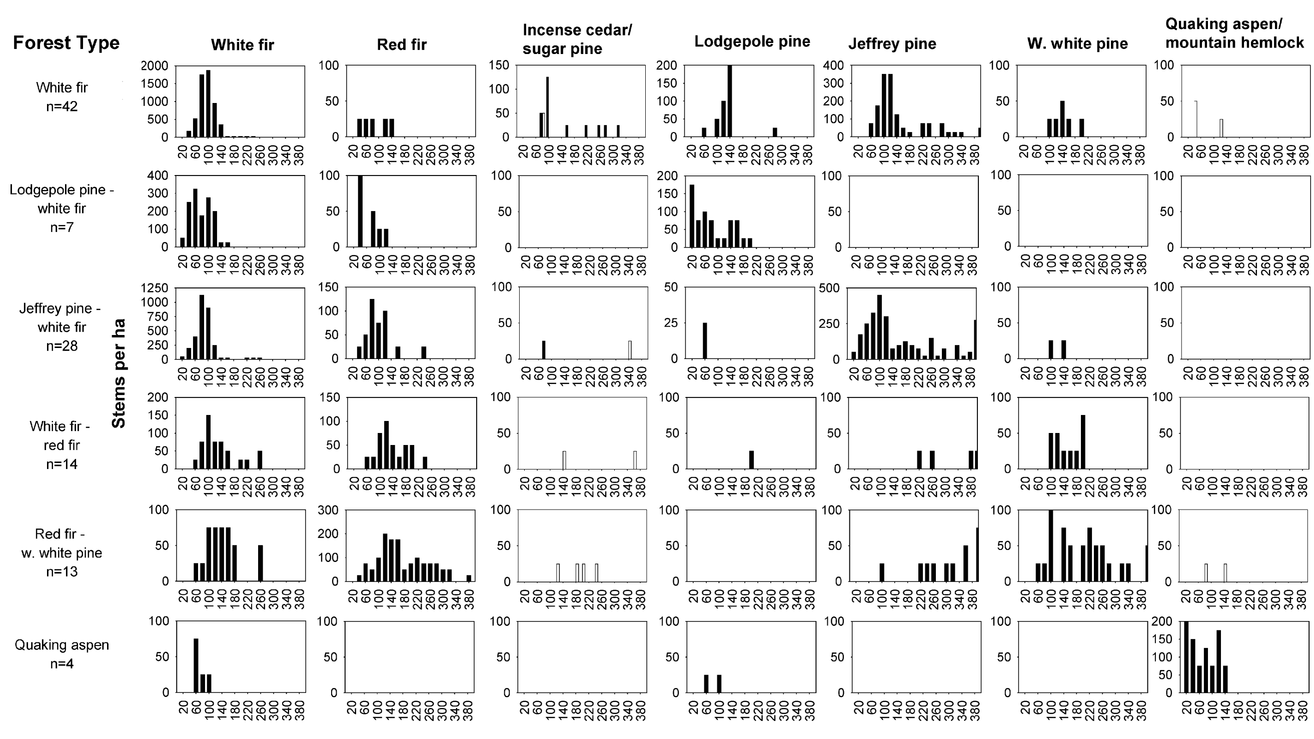

Fig. 3. Average age distributions for mixed conifer forest types in the General Creek Watershed, Lake Tahoe Basin, California. Note that only every other age-class is labeled and that the scaled of the vertical axis is difference for each graph. Species acronyms are given in Table 1.

fir stands are multi-sized and multi-aged but most white fir are small (<40 cm dbh) and <120 years old (Figs. 2 and 3). There are a few white fir >200 years old. Jeffrey pine occupies a wider range of size and age classes than white fir with trees >300 years old (Fig. 3). Jeffrey pine-white fir group is most common on moderate to steep, south-facing slopes (Fig. 1).

The lodgepole pine-white fir group ($n = 7$) is co-dominated by lodgepole pine and white fir. Lodgepole pine and white fir have similar basal area but the density of white fir is much higher than lodgepole pine. Trees in lodgepole pine-white fir plots are mainly small in diameter (<40 cm dbh and <ca. 120 years old (Figs. 2 and 3), but there are trees in some plots >200 years old. Lodgepole pine-white fir plots occupy valley bottom sites (Fig. 1).

The white fir-red fir group ($n = 14$) is dominated by white fir in terms of basal area and density (Table 1). Trees in this group are multi-size and multi-aged and trees >200 years old are present (Figs. 2 and 3). White fir-red fir stands occur on north-facing slopes at lower slope positions (Fig. 1).

The red fir-western white pine group ($n = 13$) replace white fir-red fir stands on upper slope positions on north aspects (Fig. 1). In this group red fir is the dominant and western white pine, white fir, and Jeffrey pine are important associates. Red fir-western white pine stands are multi-aged and multi-sized stands and include trees >200 years old (Figs. 2 and 3).

The quaking aspen group ($n = 4$) is strongly dominated by quaking aspen, but lodgepole pine and white fir are also present (Table 1). Tree ages in quaking aspen plots ranged from 5 to 140 years old and the age distribution was flat compared to the size class distribution which had peaks in the smallest size classes (Fig. 3). Quaking aspen stands are confined to valley bottom sites with wet soils (Fig. 1).

3.2. Fire regimes

A total of 71 fires were recorded between 1616 and 1893 in the 50 fire scar samples from the 20 sample sites. The length of the fire record and the time of the last fire varied by site (Fig. 4). The average length of a site fire record was 170 years (range, 33–277 years) and all sites last burned in the mid to late 19th century (Fig. 4). Since most sites have a continuous record of fire after 1700, the period 1700–2000 was used for the fire regime analysis.

The mean and median composite FRIs varied among sites and ranged from 8 to 17 years and 8.3 to 17.7 years, respectively. The maximum FRI recorded at a site during the pre-suppression period was 47 years and the minimum was two years. Eighty percent of the sites had skewed distributions with more short than long FRIs. The median and mean composite FRI for the study area as a whole was 3.0 and 4.0 years (range 1–20), respectively (Table 2).

Fire scars occurred mainly (75%) at ring boundaries (dormant season) but scars were also present in the early wood (10.6%) and latewood (14%). There were also some

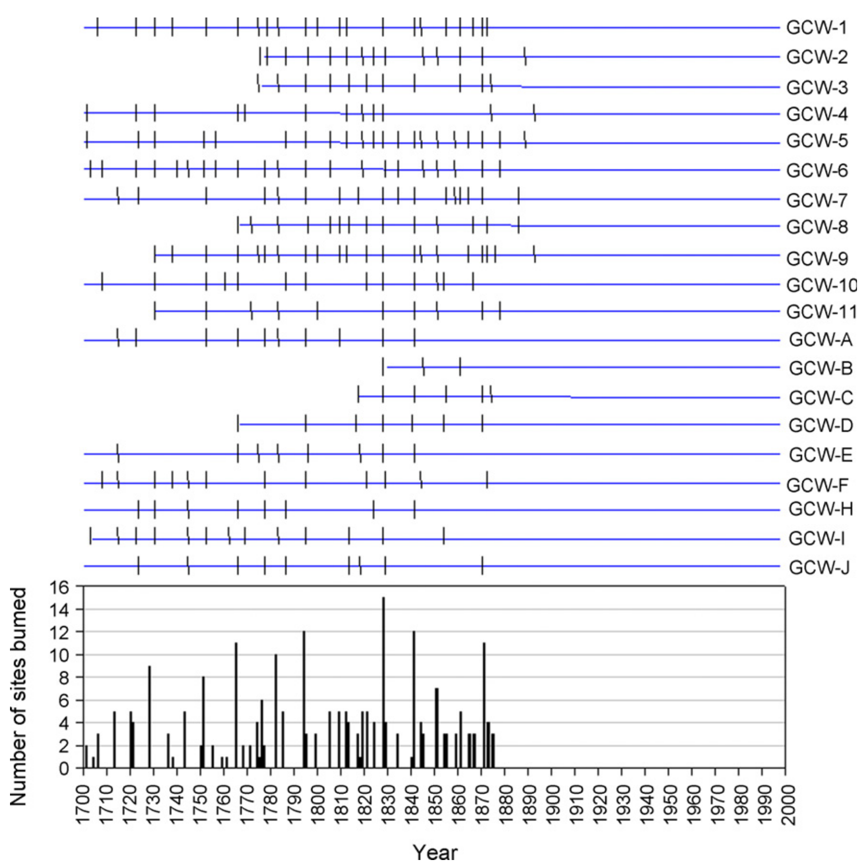

Fig. 4. Fire frequency and extent between 1700 and 1900 for 20 sites in the General Creek Watershed, Lake Tahoe Basin, California. Site codes are given on the right hand side of each site fire chronology.

Table 2
Fire return interval (FRI, years) statistics for fires of different extent for the period 1700–1875 in the General Creek Watershed, Lake Tahoe Basin, California

Fire return interval								
Percentage of sites	Fire frequency	Mean	Median	Min	Max	S.D.	Skew.	Kurt.
≥5	71	4.0	3.0	1	20	3.2	2.32	7.75
≥10	63	4.5	4.0	1	20	3.4	1.98	5.79
≥20	38	7.0	7.0	1	20	4.6	0.93	0.57
≥25	28	9.1	9.0	1	20	4.6	0.42	−0.27
≥35	19	13.4	13.0	1	34	7.5	0.85	0.85
≥45	12	21.3	19.5	12	34	8.2	0.42	−1.37
≥75	4	53.0	45.5	21	100	33.8	0.59	−1.48

differences in fire season by slope aspect. Dormant season fires were more common on north-facing slopes (81%) than on south-facing slopes (67%). The position of fire scars in annual growth rings was determined for only 48% of the 279 scars dated in the 50 samples. However, there was no significant difference between the number of known and unknown seasons for north and south facing slopes (χ^2, $P > 0.05$). The total number of scars was not correlated ($P > 0.05$) but the number of unknowns was ($P < 0.05$) indicating that north and south slopes were likely to have scars with undeterminable seasons in the same years.

Fire return intervals varied by time period. The mean composite FRI was similar ($P > 0.05$, *t*-test) in the pre-settlement (3.4 years) and settlement period (3.0 years). However, the mean FRI was longer in the fire-suppression period; no fires were recorded in GCW in the 20th century.

Fire extent varied among years and fire extent was inversely related to fire interval (Table 2, Fig. 4). Twelve fires burned ≥45% of the sites, and the interval between these widespread fires ranged from 12 to 34 years (median = 19.5 years). Intermediate size fires that burned ≥25% of sites occurred 28 times with a median return interval of 9 years (range 1–20 years). Localized fires that burned ≥5% of sites were frequent (median FRI = 3 years) and during the period of record 71 fires burned at least one site. The occurrence of intermediate and widespread fires was similar across the entire study period (Fig. 4).

Fire return intervals varied spatially within the GCW with slope aspect ($P < 0.01$) and topographic position ($P < 0.01$) (Table 3). Median FRIs were shorter on south (9 years) and west aspects (10 years) than on north (13 years) and east aspects (12 years) (Kruskal-Wallis H-test, $P < 0.05$). Median FRIs were also significantly shorter on lower (9 years) and middle (10 years) slope positions than in valley bottoms (14 years) and upper slopes (14 years) (Kruskal–Wallis *H*-test, $P < 0.05$).

The cumulative area burned by low, moderate, and high severity fire varied by topographic position and slope aspect (Table 4). Overall, fire severity was mainly moderate regardless of slope position (58–73%), but upper slopes experienced more high severity fire (36%) than middle (11%) and lower slopes (7%). Lower slopes experienced more low severity fire (36%) than middle (16%) or upper slope positions (5%). South-facing

Table 3
Composite fire return interval (years) statistics for sites by slope aspect, topographic position, and slope pitch in the General Creek Watershed, Lake Tahoe Basin, California

Slope aspect*	*n*	Mean	Median	S.D.	Min.	Max.
North**	87	14.2	12	8.2	3	47
East	43	13.1	12	7.3	2	30
South**	105	10.1	9	5.8	3	31
West	17	12.3	11	6.1	4	27
Topographic position*						
Upper slope	33	14.0	14	6.4	4	29
Middle slope**	87	10.7	10	6.1	2	30
Lower slope**	56	10.8	9	6.6	2	31
Valley bottom**	76	14.1	11	8.5	3	47

* Significant difference among topographic units (Kruskal–Wallis *H*-test, $P < 0.05$).
** Significant difference between pairs of variables (Mann–Whitney *U*-test, $P < 0.05$).

slopes experienced more high severity fire than north-facing on all slope positions (Table 4).

3.3. Fire–climate interactions

Variation in regional climate between 1700 and 1875 influenced fire extent. Local, intermediate and widespread fire occurred during dry years ($P < 0.05$), and widespread fires were also preceded by wet conditions 3 years prior ($P < 0.05$) (Fig. 5a). In contrast, climate conditions were moist ($P < 0.05$) during non-fire years.

Fire extent was also related to variation in ENSO (Fig. 5b). Local, intermediate and widespread fires were associated with a transition from La Niña to El Niño conditions ($P < 0.05$). This pattern was strongest for the most widespread fires. Non-fire years were associated with a transition from neutral to El Niño conditions ($P < 0.05$).

There was also a significant relationship between the PDO and fire extent (Fig. 5c). Positive PDO values preceded fire years and negative PDO values followed fire years ($P < 0.05$). The year of fire occurrence corresponds with transitions between positive (warm) to negative (cold) PDO values. This

Table 4
Percentage of area burned at low, moderate, and high severity by topographic position and slope aspect in the General Creek Watershed, Lake Tahoe Basin, California

	North (%)	South (%)	Total (%)
Lower slopes			
Low	41	30	36
Moderate	57	59	58
High	2	12	7
Middle slopes			
Low	17	15	16
Moderate	75	72	73
High	8	13	11
Upper slopes			
Low	9	3	5
Moderate	87	47	59
High	3	50	36

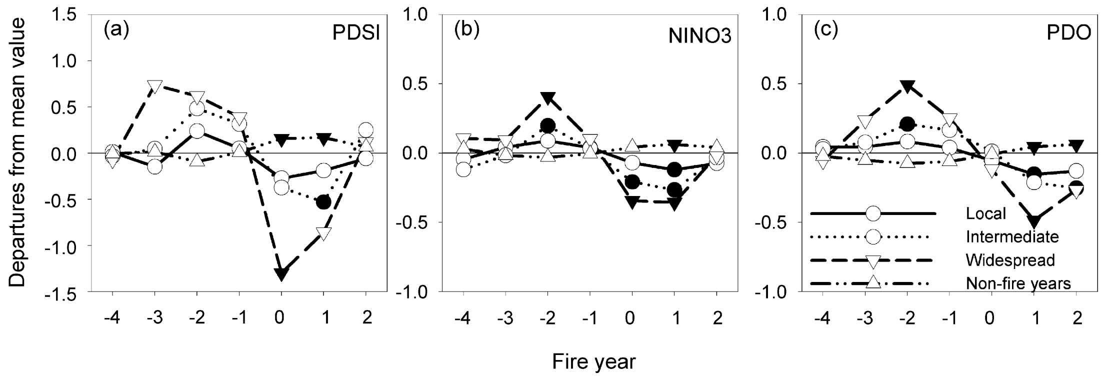

Fig. 5. Superposed epoch analysis of non fire years and fire years of different extent and tree-ring reconstructed PDSI (Cook et al., 1999), NINO3 (Cook, 2000), and PDO (Biondi et al., 2001) for the period 1700–1875 in the General Creek Watershed, Lake Tahoe Basin, California. Local fires burned one or more sites, intermediate fires burned five or more sites, and widespread fires burned eight or more sites. Values along the x-axis indicate years preceding and following a fire (fire year = 0). Filled symbols indicate statistically significant responses ($P < 0.05$) based on bootstrapped confidence interval estimates (95%) of 1000 Monte Carlo simulations of randomly selected epochs (Mooney and Duval, 1993).

pattern was evident for local fires, but was more pronounced for intermediate and widespread fires. In contrast, non-fire years were associated with transitions from cold to warm phase PDO ($P < 0.05$).

3.4. Forest compositional change

The type and magnitude of compositional change in GCW varied by forest compositional group. Successional trends in the absence of fire are indicated in Fig. 6 by vectors that connect the understory, intermediate, and canopy layers in each forest compositional group. The compositional changes are greatest in the Jeffry pine-white fir, lodgepole pine-white fir, and white fir-red fir groups where white fir is increasing. In contrast, the White fir, Red fir-Western white pine, and Aspen groups are experiencing less change.

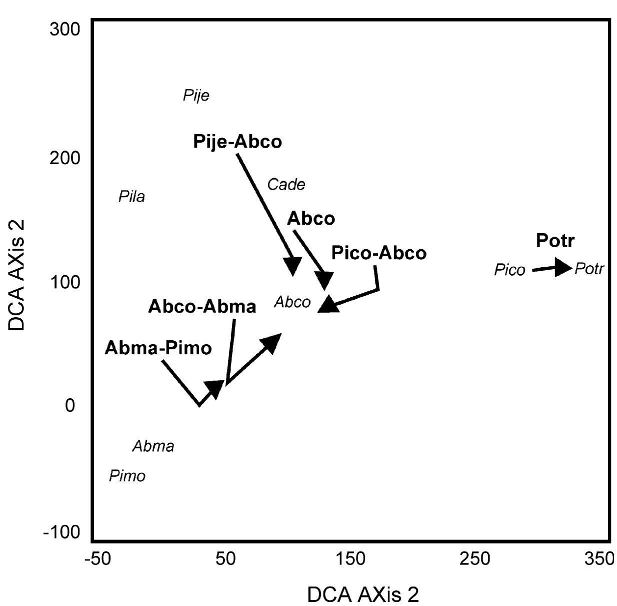

Fig. 6. Compositional differences in the density (stems/ha) of understory, intermediate, and overstory trees in mixed conifer forest types in the General Creek Watershed, Lake Tahoe Basin, California. Vectors show the direction and magnitude of compositional differences between layers. The positions of species abbreviations represent regions of relative dominance. Abco: white fir; Abma: red fir; Cade: incense cedar; Pico: lodgepole pine; Pije: Jeffrey pine; Pila: sugar pine; Pimo: western white pine; Tsme: mountain hemlock; Potr: quaking aspen.

4. Discussion

Mixed conifer forests in the GCW varied considerably in species composition, and species distribution and abundance patterns were controlled by slope aspect, topographically influenced patterns of soil moisture, and elevation. Elevation, slope aspect, and soil moisture are all recognized as important controls on landscape scale patterns of species abundance in the montane forests of the Sierra Nevada (e.g., Parker, 1989; Barbour and Minnich, 2000) and southern Cascades (e.g., Parker, 1991; Taylor, 2000; Bekker and Taylor, 2001). These same variables strongly influenced species distribution and abundance patterns in GCW at landscape scales.

Spatial variation in fire regime parameters in the mixed conifer forest landscape in GCW was related to variation in topographic setting and forest composition. Median FRI were longer on cooler more mesic north-facing slopes dominated by stands of red fir-white fir and red fir-western white pine forest than on warmer and dryer south-facing slopes dominated by Jeffrey pine-white fir forest. Variation in FRI with slope aspect, slope position, elevation, and species dominance has also been identified in mixed conifer forests in the southern (e.g., Kilgore and Taylor, 1979; Caprio and Swetnam, 1995) and eastern (Stephens, 2001) Sierra Nevada, and the spatial patterns in the length of FRI in GCW are consistent with these studies.

Spatial variation in the length of FRI in the GCW is related to topographic factors that influence species composition and in turn the production, moisture, structure and flammability of fuels (Biswell, 1989; Agee, 1993). First, long-needled Jeffrey pine is most abundant on south aspects whereas short-needled white and red fir is dominant on north slopes and the highest elevation sites. Surface fuel beds of long-needled pines are less dense than those of short-needled fir (e.g., Albini, 1976; van Wagtendonk, 1998), and fire spread and fire intensity are greater in lower than higher density fuel beds (Albini, 1976; Rothermel, 1983). Second, fuel moisture is lower for a longer period each year on south than north slopes, so the period surface fuels can carry fire each year is longer on south facing slopes. Finally, rates of fine fuel production are higher in pine than in fir dominated mixed conifer forests so a fire can burn again sooner on a south- than a north-facing slope (e.g., Agee, 1993; Stohlgren, 1988).

The season of burn has a strong influence on a species' response to fire (e.g., Kauffman and Martin, 1989; Kauffman, 1990). Burns in the GCW occurred mainly (75%) during the dormant season). Burns in other mixed conifer or pine-dominated forests in the northern Sierra Nevada (Taylor, 2004), and further north in the Klamath Mountains (e.g., Taylor and Skinner, 2003) and southern Cascade Range (e.g., Beaty and Taylor, 2001; Norman and Taylor, 2003) are also concentrated in the dormant season (75–90%) after trees have stopped growth for the year. In contrast, burns in mixed conifer forests in northern Mexico and the southern Sierra Nevada are concentrated in the growing season. In Jeffrey pine mixed conifer forests in the Sierra de San Pedro Martir, 99% of burns occurred during the growing season (Stephens et al., 2003). Farther north, in mixed conifer forests in Sequoia-Kings Canyon National Park 50% of the fires occurred late in the growing season and only 30% occurred in the dormant season (Caprio and Swetnam, 1995). This north–south gradient in season of burn may be related to differences in the onset of summer drought along the Sierra Nevada-Cascade axis (e.g., Major, 1977; Parker, 1994). An earlier onset of drought in the south would increase the length of time fuels are dry enough to burn each year. This geographic variation in season of burn may lead to regionally distinct fire effects in mixed conifer forests despite high similarity in species composition.Variation in fire severity has been identified as an important cause of structural diversity in forested landscapes because burns may kill all trees in some stands and few in others (e.g., Romme, 1982; Taylor and Skinner, 1998; Bekker and Taylor, 2001). In GCW, spatial variation in stand structure that reflects burn severity was related to topography, particularly slope aspect and slope position. Overall, high severity fire effects were greatest on upper slopes, lowest on lower slopes, and intermediate on middle slopes. Higher fire-induced tree mortality at middle- and upper-slope positions is probably related to higher fire line intensities at these locations. Middle and upper slope positions often experience higher fire line because of higher effective wind speeds, lower canopy cover, and preheating of fuels as fires move up a slope (e.g. Rothermel, 1983).

The topographically influenced pattern of fire severity promotes development of forests with different characteristics at different locations within the landscape. On lower slopes and valley bottoms, frequent low severity surface fires kill mainly seedlings, saplings, and small diameter trees while leaving most thick-barked large diameter trees intact. This pattern of low severity fires promotes uneven aged stands that are open with trees in a wide range of size- and age-classes. Tree regeneration is intermittent and occurs in small (113–254 m^2) overlapping patches creating a fine-grained mosaic of even-aged groups of trees (Beaty and Taylor, 2007). On upper slopes high severity fires generated coarse grained stands of montane chaparral or even-aged patches of trees and this type of forest structure contrasts sharply with the fine-grained patterns observed at intermediate and lower slope positions. Similar landscape patterns of stand structure in mixed conifer forests have been observed in areas with much steeper terrain in the Klamath Mountains (Taylor and Skinner, 1998) and the southern Cascades (Beaty and Taylor, 2001). This suggests that interactions between topography and fire severity promoted structural heterogeneity in mixed conifer forest landscapes, at least during the pre-fire suppression period.

Fire regimes varied by historical time period and FRI increased dramatically with the onset of Comstock logging in the late 19th century and then implementation of fire suppression management. Similar declines in fire occurrence have been observed in California mixed conifer forests in the southern Cascades (Taylor, 2000; Beaty and Taylor, 2001; Norman and Taylor, 2003), Klamath Mountains (Taylor and Skinner, 2003; Fry and Stephens, 2006), northern Sierra Nevada (Stephens and Collins, 2004; Moody et al., 2006) and southern Sierra Nevada (Kilgore and Taylor, 1979; Caprio and Swetnam, 1995). The current fire free period (ca. 115 years) is unprecedented within at least the last 400 years and exclusion of fire has caused changes in vegetation in GCW at both stand and landscape scales. The abundance of fire intolerant white fir has increased dramatically, shifting species composition away from more fire tolerant species such as Jeffrey pine, sugar pine (*Pinus lambertiana* Dougl.), and incense-cedar (*Calocedrus decurrens* Torr.). Moreover, areas that were montane chaparral at the time of the last fire have been invaded by trees, mainly white fir, and the establishment dates of these even-aged stands coincide with the last fire date. Of course, there is spatial variation in the magnitude of change in the watershed. The greatest compositional changes have occurred in pine-dominated stands in valley bottoms and on south aspects. Red fir dominated stands on north-facing slopes, in contrast, have experienced less compositional change but they have increased in density. Continued absence of fire is likely to lead to further compositional and structural shifts in the mixed conifer forests in GCW.

Fire regimes in mixed conifer forests were also strongly influenced by the regional control of climate variation. Both small and widespread fires in GCW occurred in years when conditions were dry and non-fire years were associated with wet conditions. The wet-dry climate pattern associated with widespread fires may be related to ENSO teleconnections and regional rainfall patterns. ENSO is recognized as a primary driver of interannual climate variability, and during El Niño events, conditions are generally wetter than average in California due to a stronger sub-tropical jet-stream bringing warm, moist air off of the Pacific Ocean (Schoner and Nicholson, 1989; Mo and Higgins, 1998). During La Niña events the situation is reversed and conditions are dryer than average in much of California. In GCW, intermediate and widespread fires occurred in years when NINO3 values were negative (i.e., La Niña conditions). Moreover, years with intermediate and widespread burning were preceded by moist El Niño conditions 2–3 years before the fire year.

Variation in ENSO has been identified as an important control on variation in fire regimes in other pine dominated forests in the American southwest (Swetnam and Betancourt, 1998), Colorado (Kitzberger et al., 1997), northeast Oregon (Heyerdahl et al., 2002), and Mexico (Heyerdahl and Alvarado, 2003). Synchronized widespread fires in these regions tended to occur during dry years associated with La Niña events that were preceded by wet years that were associated with El Niño events (Swetnam and Baison, 2003). In the Pacific Northwest, the association between ENSO and fire was opposite that observed in California and the Southwest (Morgan et al., 2001; Heyerdahl et al., 2002). In the Pacific Northwest El Niño events promote dryer than average conditions (Redmond and Koch, 1991; Cayan et al., 1999; Hoerling et al., 1997) and increased fire activity occurs during these periods (Heyerdahl et al., 2002). The fire-ENSO relationship observed in GCW exhibits a pattern similar to pine forests in the American Southwest. However, variation in pre fire suppression fire regimes in pine dominated forests in northern California are not consistently associated with ENSO variation (e.g., Norman and Taylor, 2003; Taylor and Beaty, 2005; Fry and Stephens, 2006; Moody et al., 2006). The inconsistent relationship between variation in ENSO and fire regimes is probably related to interannual variation in the north-south position of zonal precipitation that is associated with ENSO and the geographic position of northern California near the ENSO pivot zone (Dettinger et al., 1998).

Variation in the PDO also had a strong influence on fire occurrence and extent. More widespread burning occurred in years preceded by positive PDO values (warm phase PDO) and followed by significantly negative values (cold phase PDO). The fire-PDO pattern corresponds with wetter than average conditions in the years before and dry condition during and following widespread fires. This pattern is similar to ENSO but it occurs on a longer (decadal) timescale. Warm sea surface temperatures in the northeastern Pacific and cold sea surface temperatures in the western and central north Pacific during positive (warm) phases of the PDO promote enhanced westerly flow similar to El Niño winters (Gershunov et al., 1999). This may result in wetter than normal conditions in the northern Sierras. The opposite pattern exists during negative (cold) phases of the PDO and may result in drier than normal conditions in the northern Sierra Nevada similar to La Niña winters (Gershunov et al., 1999). There is an emerging body of evidence that variation in the PDO is an important driver of variation in fire occurrence and extent in western forests during both the pre and post fire suppression periods (Norman and Taylor, 2003; Westerling and Swetnam, 2003; Taylor and Beaty, 2005; Schoennagel et al., 2005; Trouet et al., 2006).

5. Conclusions

Spatial variation in topography and interannual variability in climate are potentially important controls that effect variation in mixed conifer forest fire regimes and forest structure (Taylor and Skinner, 1998, 2003; Beaty and Taylor, 2001; Taylor and Beaty, 2005). In GCW, fire regime parameters (e.g., FRI, fire severity, fire extent) during the pre-fire suppression period varied with slope aspect, slope position, and climate. Mixed conifer stands that were multi-aged and multi-sized and developed under a regime of frequent low or moderate severity fire occurred on valley bottoms and lower slope positions whereas upper slopes were more complex with both multi- and even-aged forests or brush fields that developed after high severity fire. The spatially variable fire regime created structural heterogeneity at landscape scales. Moreover, the fire disturbances that generated these variable fire effects were temporally synchronized by climate, particularly drought which was driven by variation in ENSO and PDO. Thus, mixed conifer forest fire regimes and fire effects are not simply controlled by the spatial patterns and dynamics of burning and post fire fuel production. Instead, exogenous factors related to topography and climate mediated mixed conifer forest development and promoted structural diversity at landscape scales.

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References

Agee, J.K., 1993. Fire ecology of Pacific Northwest forests. Island Press, Washington, DC.

Albini, R., 1976. Estimating wildfire behavior and effects. USDA Forest Service General Technical Report INT-GTR-156.

Alley, W., 1984. The palmer drought severity index: limitations and assumptions. J. Climatol. Appl. Meteorol. 23, 1100–1109.

Arno, S.F., K.M. Sneck, 1977. A method for determining fire history in coniferous forests of the mountain west. USDA Forest Service General Technical Report INT-GTR-42.

Baison, C.H., Swetnam, T.W., 1990. Fire history on a desert mountain range: Rincon Mountain Wilderness, Arizona, USA. Can. J. Forest Res. 20, 1559–1569.

Barbour, M.G., Minnich, R.A., 2000. California upland forests and woodlands. In: Barbour, M.G., Billings, W.D. (Eds.), North American Terrestrial Vegetation. Cambridge University Press, Cambridge, pp. 159–200.

Barrett, S.W., Arno, S.F., 1988. Increment-borer methods for determining fire history in coniferous forests. USDA Forest Service General Technical Report INT-GTR-244.

Beaty, R.M., Taylor, A.H., 2001. Spatial and temporal variation of fire regimes in a mixed conifer forest landscape, Southern Cascades, California, USA. J. Biogeogr. 28, 955–966.

Beaty, R.M., Taylor, A.H., 2007. Fire disturbance and forest structure in old-growth mixed conifer forests in the northern Sierra Nevada, Lake Tahoe Basin, California, USA. J. Veg. Sci. 18, 879–890.

Bekker, M.F., Taylor, A.H., 2001. Gradient analysis of fire regimes in montane forests of the southern Cascade range, Thousand Lakes Wilderness, California, USA. Plant Ecol. 155, 15–28.

Biondi, F., Gershunov, A., Cayan, D.R., 2001. North Pacific decadal climate variability since 1661. J. Climate 14, 5–10.

Biswell, H.H., 1989. Prescribed burning in California wildland vegetation management. University of California Press, Berkeley, CA, US.

Bolsinger, C., 1989. Shrubs of California's chaparral, timberland, and woodland: area ownership and stand characteristics. USDA Forest Service Resource Bulletin PNW-RB-160.

Bonnicksen, T.M., Stone, E.C., 1981. The Giant Sequoia-Mixed Conifer forest community characterized through pattern analysis as a mosaic of aggregations. Forest Ecol. Manage. 3, 307–328.

Bonnicksen, T.M., Stone, E.C., 1982. Reconstruction of a presettlement Giant Sequoia-Mixed Conifer forest community using the aggregation approach. Ecology 63, 1134–1148.

Brown, P.M., Swetnam, T.W., 1994. A cross-dated history from coast redwood near Redwood National Park, California. Can. J. Forest Res. 24, 21–31.

Caprio, A.C., Swetnam, T.W., 1995. Historic fire regimes along an elevational gradient on the west slope of the Sierra Nevada, California. In: Brown, J.K., Mutch, R.W., Spoon, C.W., Wakimoto, R.H. (Eds.), Symposium on fire in wilderness and park management, USDA Forest Service Intermountain Research Station, Missoula, MT, pp. 173–179.

Cayan, D.R., Redmond, K.T., Riddle, L.G., 1999. ENSO and hydrologic extremes in the western United States. J. Climate 12, 2881–2893.

Cocke, A.E., Fulé, P.Z., Crouse, J.E., 2005. Comparison of burn severity assessments using differenced Normalized Burn Ratio and ground data. Int. J. Wildland Fire 14, 189–198.

Cook, E.R., 2000. Niño 3 Index Reconstruction. International Tree-Ring Data Bank. IGBP PAGES/World Data Center-A for Paleoclimatology. Data Contribution Series #2000-052. (NOAA/NGDC Paleoclimatology Program: Boulder, CO).

Cook, E.R., Meko, D.M., Stahle, D.W., Cleaveland, M.K., 1999. Drought reconstructions for the continental United States. J. Climate 12, 1145–1162.

Dettinger, M.D., Cayan, D.R., Diaz, H.F., Meko, D.M., 1998. North–south precipitation patterns in western North America on interannual-to-decadal time scales. J. Climate 11, 3095–3111.

Diaz, H.F., Markgraf, V., 2000. El Nino and the Southern Oscillation: multiscale variability and global and regional impacts. Cambridge University Press, Cambridge.

Dietrich, J., 1980. The composite fire interval—a tool for more accurate interpretation of fire history. USDA Forest Service General Technical Report GTR-RM-81.

Eliott-Fisk, D.L., Cahill, T.C., Davis, O.K., Duan, L., Goldman, C.R., Gruell, G.E., Harris, R., Kattlemann, R., Lacey, R., Leisz, D., Lindstrom, S., Machida, D., Rowntree, R.A., Rucks, P., Sharkey, D.A., Stephens, S.L., Ziegler, D.S., 1996. Lake Tahoe Case Study. Sierra Nevada Ecosystem Project: Final Report to Congress. Addendum I. University of California Centers for Water and Wildland Resources, Davis, Ca. pp. 217–276.

Fry, D.L., Stephens, S.L., 2006. Influence of humans and climate on the fire history of a Ponderosa pine-mixed conifer forest in the southeastern Klamath Mountains, California. Forest Ecol. Manage. 223, 428–438.

Gauch, H.G., 1982. Multivariate Analysis in Community Ecology. Cambridge University Press, New York.

Gershunov, A., Barnett, T.P., Cayan, D.R., 1999. North Pacific interdecadal oscillation seen as factor in ENSO-related North American climate anomalies. EOS T. Am. Geophys. Un. 80, 25–36.

Haurwitz, M.W., Brier, G.W., 1981. A critique of the superposed epoch analysis method: its application to solar weather relations. Mon. Weather Rev. 109, 2074–2079.

Heyerdahl, E.K., Alvarado, E., 2003. Influence of climate and land use on historical surface fires in pine-oak forests, Sierra Madre Occidental, Mexico. In: Veblen, T.T., Baker, W.L., Montenegro, G., Swetnam, T.W. (Eds.), Fire and Climatic Change in Temperate Ecosystems of the Western Americas. Springer-Verlag, New York, pp. 196–217.

Heyerdahl, E.K., Brubaker, L.B., Agee, J.K., 2002. Annual and decadal climate forcing of historical fire regimes in the interior Pacific Northwest, USA. Holocene 12, 597–604.

Hoerling, M.P., Kumar, A., Zhong, M., 1997. El Niño, La Niña, and the nonlinearity of their teleconnections. J. Climate 10, 1769–1786.

Holmes, R.L., Adams, R.K., Fritts, H.C., 1986. Tree-Ring Chronologies of Western North America: California, Eastern Oregon, and Northern Great Basin. Laboratory of Tree-Ring Research, University of Arizona, Tucson.

Kauffman, J.B., 1990. Ecological relationships of vegetation and fire in Pacific Northwest Forests. In: Walstad, J.D., Radosevich, S.R., Sandberg, D.V. (Eds.), Natural and Prescribed Fire in Pacific Northwest Forests. Oregon State University Press, Corvallis, OR.

Kauffman, J.B., Martin, R.E., 1989. Fire behavior, fuel consumption, and forest-floor changes following prescribed understory fires in Sierra Nevada mixed conifer forests. Can. J. Forest Res. 19, 455–462.

Kilgore, B.M., 1973. The ecological role of fire in Sierran conifer forests. Quaternary Res. 3, 496–513.

Kilgore, B.M., Taylor, D., 1979. Fire history of a Sequoia-mixed conifer forest. Ecology 60, 129–142.

Kitzberger, T., Veblen, T.T., Villalba, R., 1997. Climatic influences on fire regimes along a rain forest-to-xeric woodland gradient in northern Patagonia, Argentina. J. Biogeogr. 24, 35–47.

Lindström, S., 2000. A contextual overview of human land use and environmental conditions. In: Murphy, D.D., Knopp, C.M. (Eds.), Lake Tahoe watershed assessment. Pages 23–122. USDA Forest Service General Technical Report PSW-GTR-175.

Major, J., 1977. California climate in relation to vegetation. In: Barbour, M.G., Major, J. (Eds.), Terrestrial Vegetation of California. John Wiley & Sons, New York.

McKelvey, K.S., Johnston, J.D., 1992. Historical perspectives on forests of the Sierra Nevada and the Transverse Ranges of southern California: forest conditions at the turn of the century. USDA Forest Service General Technical Report PSW-GTR-133.

Means, J.E., 1989. Estimating the date of a single bole scar by counting tree rings in increment cores. Can. J. Forest Res. 19, 1491–1496.

Mo, K.C., Higgins, R.W., 1998. Tropical influences on California precipitation. J. Climate 11, 412–430.

Moody, T.J., Fites-Kaufman, J., Stephens, S.L., 2006. Fire history and climate influences from forests on the northern Sierra Nevada, USA. Fire Ecol. 2, 115–141.

Mooney, C.Z., Duval, R.D., 1993. Bootstrapping: A Nonparametric Approach to Statistical Inference. Sage Publications, Newbury Park, CA.

Morgan, P., Hardy, C., Swetnam, T.T., Rollins, M.G., Long, D.G., 2001. Mapping fire regimes across space and time: understanding coarse and fine-scale patterns. Int. J. Wildland Fire 10, 329–342.

Nagel, T., Taylor, A.H., 2005. Fire and persistence of montane chaparral in mixed conifer forest landscapes in the northern Sierra Nevada Lake Tahoe Basin, California, USA. J. Torrey Bot. Soc. 132, 442–457.

Norman, S.P., Taylor, A.H., 2003. Tropical and north Pacific teleconnections influence fire regimes in pine-dominated forests of north-eastern California. J. Biogeogr. 30, 1081–1092.

North, M., Hurteau, M., Fiegener, R., Barbour, M., 2005. Influence of fire and El Niño on tree recruitment varies by species in Sierran mixed conifer. For. Sci. 51, 187–197.

Palmer, W.C., 1965. Meteorological drought. Weather Bureau Research Paper 45. US Department of Commerce, Washington, DC.

Parker, A.J., 1982. The topographic relative moisture index: an approach to soil-moisture assessment in mountain terrain. Phys. Geogr. 3, 160–168.

Parker, A.J., 1989. Forest/environment relationships in Yosemite National Park, California, U.S.A. Vegetation 82, 41–54.

Parker, A.J., 1991. Forest/environment relationships in Lassen Volcanic National Park, California, U.S.A. J. Biogeogr. 18, 543–552.

Parker, A.J., 1994. Latitudinal gradients of coniferous tree species, vegetation, and climate in the Sierran-Cascade axis of northern California. Vegetation 115, 145–155.

Parsons, D.J., DeBenedetti, S.H., 1979. Impact of fire suppression on a mixed-conifer forest. Forest Ecol. Manage. 2, 21–33.

Redmond, K.T., Koch, R.W., 1991. Surface climate and streamflow variability in the western United States and their relationship to large scale circulation indices. Water Resour. J. 27, 2381–2399.

Romme, W.H., 1982. Fire and landscape diversity in subalpine forests of Yellowstone National Park. Ecol. Monogr. 52, 199–221.

Rothermel, R.C., 1983. How to predict the spread and intensity of forest and range fires. USDA Forest Service INT-GTR-143.

Russel, W.H., McBride, J.R., Rowntree, R., 1998. Revegetation after four stand replacing fires in the Lake Tahoe Basin. Madroño 45, 40–46.

Schoennagel, T., Veblen, T.T., Romme, W.H., Sibold, J.S., Cook, E.R., 2005. ENSO and PDO variability affect drought induced fore occurrence in Rocky mountain subalpine forests. Ecol. Appl. 15, 2000–2014.

Schoner, T., Nicholson, S.E., 1989. The relationship between California rainfall and ENSO events. J. Climate 2, 1258–1269.

Skinner, C.N., 1995. Changes in spatial characteristics of forest openings in the Klamath Mountains of northwestern California, USA. Landscape Ecol. 10, 219–228.

Skinner, C.N., Chang, C., 1996. Fire Regimes, past and present. Sierra Nevada Ecosystem Project: Final Report to Congress. vol. 2, Assessments and scientific basis for management options. University of California Centers for Water and Wildland Resources, Davis, Ca. pp. 1041–1069.

Sokal, R.R., Rohlf, F.J., 1995. Biometry. Freeman, San Franciso.

Stephens, S.L., 2001. Fire history of adjacent Jeffrey pine and upper montane forests in the eastern Sierra Nevada. Int. J. Wildland Fire 10, 161–176.

Stephens, S.L., Collins, B.M., 2004. Fire regimes of mixed conifer forests in the north-central Sierra Nevada at multiple spatial scales. Northwest Sci. 78, 12–23.

Stephens, S.L., Skinner, C.N., Gill, S.J., 2003. Dendrochronology-based fire history of Jeffrey pine-mixed conifer forests in the Sierra San Pedro Martir, Mexico. Can. J. Forest Res. 33, 1090–1101.

Stephens, S.L., Fry, D.L., 2005. Spatial distribution of regeneration patches in an old-growth Pinus jeffreyi mixed conifer forest in northernwestern Mexico. J. Veg. Sci 16, 693–702.

Stephens, S.L., Gill, S.J., 2005. Forest structure and mortality in an old-growth Jeffrey pine-mixed conifer forest in northwestern Mexico. Forest Ecol. Manage. 205, 15–28.

Stohlgren, T.J., 1988. Litter dynamics in two Sierran mixed conifer forests, I. Litter fall and decomposition rates. Can. J. Forest Res. 18, 1127–1135.

Stokes, M.A., Smiley, T.L., 1968. An Introduction to Tree-Ring Dating. University of Chicago Press, Chicago.

Swetnam, T.T., Betancourt, J.L., 1998. Mesoscale disturbance and ecological response to decadal climatic variability in the American Southwest. J. Climate 11, 3128–3147.

Swetnam, T.W., 1993. Fire history and climate change in giant sequoia groves. Science 262, 885–889.

Swetnam, T.W., Baison, C.H., 2003. Tree-ring reconstructions of fire and climate history in the Sierra Nevada and Southwestern United States. In: Veblen, T.T., Baker, W.L., Montenegro, G., Swetnam, T.W. (Eds.), Fire and Climatic Change in Temperate Ecosystems of the Western Americas. Springer-Verlag, New York, pp. 158–195.

Taylor, A.H., 2000. Fire regimes and forest changes in mid and upper montane forests of the southern Cascades, Lassen Volcanic National Park, California, USA. J. Biogeogr. 27, 87–104.

Taylor, A.H., 2004. Identifying reference conditions on early cut-over lands, Lake Tahoe, Basin, USA. Ecol. Appl. 14, 1903–1914.

Taylor, A.H., Beaty, R.M., 2005. Climatic influences on fire regimes in the northern Sierra Nevada, USA. J. Biogeogr. 32, 425–438.

Taylor, A.H., Skinner, C.N., 1998. Fire history and landscape dynamics in a late-successional reserve, Klamath Mountains, California, USA. Forest Ecol. Manage. 44, 1–17.

Taylor, A.H., Skinner, C.N., 2003. Spatial and temporal patterns of historic fire regimes and forest structure as a reference for restoration of fire in the Klamath Mountains. Ecol. Appl. 13, 704–719.

Trouet, V., Taylor, A.H., Carleton, A.M., Skinner, C.N., 2006. Fire-climate interactions in forests of the American Pacific coast. Geophys. Res. Lett. 33, L18704.

Vankat, J.L., Major, J., 1978. Vegetation changes in Sequoia National Park, California. J. Biogeogr. 5, 377–402.

van Tongeren, O.F.R., 1995. Cluster analysis. In: Jongman, R.H.G., ter Braak, C.J.F., van Tongeren, O.F.R. (Eds.), Data Analysis in Community and Landscape Ecology. Cambridge University Press, Cambridge, pp. 174–212.

van Wagtendonk, J., 1995. Large fires in wilderness areas</CT>. In: Brown, J., Mutch, R., Spoon, C., Wakimoto, R. (Eds.), Symposium on fire in wilderness and park management, proceedings, USDA Forest Service General Technical Report INT-GTR-320, pp. 113–116.

van Wagtendonk, J., 1998. Fuel bed characteristics of Sierra Nevada Conifers. Western J. Appl. Forest. 13, 73–84.

Weatherspoon, C.P., Skinner, C.N., 1995. An assessment of factors associated with damage to tree crowns from the 1987 wildfires in northern California. For. Sci. 41, 430–451.

Westerling, A., Swetnam, T.W., 2003. Interannual to decadal drought and wildfire in the western United States. EOS. T. Am. Geophys. Un. 84, 545–560.

Wilken, G., 1967. History and fire record of a timberland brushfield in the Sierra Nevada of California. Ecology 48, 302–304.