Ecological Applications, 20(2), 2010, pp. 362–380

Fire regimes, forest change, and self-organization in an old-growth mixed-conifer forest, Yosemite National Park, USA

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Abstract. Fire is recognized as a keystone process in dry mixed-conifer forests that have been altered by decades of fire suppression. Restoration of fire disturbance to these forests is a guiding principle of resource management in the U.S. National Park Service. Policy implementation is often hindered by a poor understanding of forest conditions before fire exclusion, the characteristics of forest changes since excluding fire, and the influence of topographic or self-organizing controls on forest structure. In this study the spatial and temporal characteristics of fire regimes and forest structure are reconstructed in a 2125-ha mixed-conifer forest. Forests were multi-aged, burned frequently at low severity and fire-return interval, and forest structure did not vary with slope aspect, elevation, or slope position. Fire exclusion has caused an increase in forest density and basal area and a compositional shift to shade-tolerant and fire-intolerant species. The median point fire-return interval and extent of a fire was 10 yr and 115 ha, respectively. The pre-Euro-American settlement fire rotation of 13 yr increased to 378 yr after 1905. The position of fire scars within tree rings indicates that 79% of fires burned in the midsummer to fall period. The spatial pattern of burns exhibited self-organizing behavior. Area burned was 10-fold greater when an area had not been burned by the previous fire. Fires were frequent and widespread, but patches of similar aged trees were <0.2 ha, suggesting small fire-caused canopy openings. Managers need to apply multiple burns at short intervals for a sustained period to reduce surface fuels and create small canopy openings characteristic of the reference forest. By coupling explicit reference conditions with consideration of current conditions and projected climate change, management activities can balance restoration and risk management.

Key words: climate change; dendroecology; ecological restoration; fire regimes; forest age structure; prefire suppression reference conditions; spatial patterns.

Introduction

Fire is recognized as a keystone process that has influenced the composition, structure, and heterogeneity of forested landscapes in western North America for millennia (Swetnam 1993, Whitlock et al. 2003). Fire's role in shaping forest structure and composition changed in the mid-to-late 19th century with Euro-American settlement and then implementation of a federal policy of suppressing fire in 1905 (Agee 1993). The effects of reduced fire frequency have been greatest in forests with surface fires that had burned frequently. Excluding fires has increased forest density and surface and aerial fuels, increasing the risk of high-intensity fire, including crown fire (Scott and Reinhardt 2001). Restoring fire as a process to fire-prone ecosystems is a guiding principle of U.S. National Park Service (NPS) policy (NPS 2006). Comparing contemporary fire regimes and forest conditions to those before fire suppression (hereafter "reference period") can be used to inform management and restoration plans where ecosystems have been highly altered by fire suppression. Forest characteristics and fire regimes at a particular point in time (i.e., onset of fire suppression), however, are the result of interactions in forest development processes (i.e., regeneration, mortality, disturbance) under a varying climate (Millar and Woolfenden 1999). For example, in the western United States, trees in the 19th century established under cooler Little Ice Age conditions while younger trees have established under warmer 20th century climate (Jones and Mann 2004). Climate-related shifts in fire frequency and extent have also occurred (e.g., Grissino-Mayer and Swetnam 2000). Consequently, identification of reference forest conditions and fire regimes should be viewed as a key step in the restoration planning process, rather than a rigid target for restoration design (Allen et al. 2002), which will be complimented with additional ecological and environmental information including the potential of future climate change.

Assessments of prescribed and wildland fire use (WFU) fires (Collins and Stephens 2007) and fire

Manuscript received 17 December 2008; revised 20 May 2009; accepted 22 May 2009. Corresponding Editor: J. Franklin.

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simulation studies (Miller 2007) suggest that their effects can be similar to those in the reference period. Yet, implementation of restoration plans is often hindered by a poor understanding of reference forest conditions, the characteristics and magnitude of forest changes since excluding fire, and the interactions between fire regimes, forest structure, and terrain that regulated forest structure (Stephenson 1999, Taylor and Skinner 2003). Resource managers need better information on spatial and temporal variation in forest structure and fire regimes during the reference period to determine if WFU or prescribed fire regimes are creating novel conditions or those similar to the reference period (Taylor 2000, Agee 2003).

In fire-prone mixed-conifer forests, spatial variation in the fire–forest structure mosaic is controlled by both local spatial processes (i.e., time since last fire) and topography. For example, fire frequency is often higher on south-facing rather than north-facing slopes, and strong differences in vegetation and site conditions among slope aspects can lead to fixed spatial patterns of variation in fire frequency in a landscape (Taylor 2000, Beaty and Taylor 2001, 2008). Similarly, mid and upper slope positions often experience higher severity fire than lower slopes because of higher wind speeds, lower canopy cover, and preheating of fuels (Rothermel 1983), and younger more even-aged stands are often concentrated at these locations (Taylor and Skinner 1998, Beaty and Taylor 2001, 2008). On the other hand, the fire–forest structure mosaic can be controlled by burns that reduce fuels in a burn patch. A burn patch constrains the pattern and effects of future fires until enough fuels accumulate in the burn patch to burn again (Miller and Urban 2000, Collins and Stephens 2007). High fire frequency and the self-organizing time-dependent nature of burn patterns is thought to create shifting patterns of burns and fire effects that promote development of a small scale (<0.2 ha) forest-patch structure (Bonnicksen and Stone 1981, Beaty and Taylor 2007). Matching the spatial patterns of fire occurrence and fire severity in a prescribed burn program with reference patterns would help managers more effectively restore historic fire effects to highly altered forests.

Distinguishing controls on fire regimes and forest structure in mixed-conifer forests before fire suppression is a challenge. Most forests have been logged or burned, and this eliminates evidence of the original forest and fire disturbance preserved in live and dead wood (Fúle et al. 1997). Even in protected areas such as Yosemite National Park (YNP), much evidence of early forest conditions has been consumed by wildfires, prescribed fire, and WFU fires (YNP 2004). Thus, most information on reference fire regimes and forest conditions in mixed-conifer forests come from studies of small stands (Beaty and Taylor 2007, North et al. 2007). However, evidence of topographic or self-organizing controls on fire regimes and forest structure are only likely to emerge at landscape scales (Taylor 2000, Taylor and Skinner 2003).

Our goal was to identify how topographic or self-organizing controls contributed to spatial and temporal variability in fire regimes and forest structure in a California mixed-conifer forest landscape before fire suppression. We address the following specific questions: (1) Do fire-regime parameters vary with topographic settings (slope aspect, slope position) or species composition? (2) Did fire regimes change with initial Euro-American settlement or when fire suppression was implemented? (3) Are spatial and temporal patterns of burns consistent with time-dependent self-organizing behavior? (4) What was the structure of the reference period forest (i.e., density, basal area, size, spatial pattern)? Is it different than an early 20th century timber survey on the same sites, and is it different than the contemporary forest? (5) Are forests at the plot scale multi-aged or even-aged reflecting tree establishment after mainly low- or high-severity fire, respectively? (6) Do patterns of age structure at the landscape scale vary with topography? To answer these questions we developed a spatially explicit network of tree-ring based reconstructions of fire occurrence and forest structure and then discuss our results in the context of prescribed fire use in YNP.

Study Area

Old-growth mixed-conifer forest was studied in a 2125-ha area in the South Fork of the Tuolumne River drainage in Yosemite National Park (YNP), USA (Fig. 1; see Plate 1). Elevations range from 1300 to 2000 m, and the terrain is moderately dissected and contains several small streams. The climate is mediterranean, characterized by warm, dry summers, and cool, wet winters. Annual mean precipitation (1941–2002) in YNP (1560 m above sea level) is 109.1 cm, with most (86%) falling between November and April as snow. Mean monthly temperatures range from 2°C in January to 18°C in July. Soils are developed in Mesozoic aged granite and they are shallow (<1 m), excessively drained, and of medium acidity (Hill 1975, Huber 1987).

Forests in the study area are a mix of ponderosa pine (*Pinus ponderosa*) (nomenclature follows Hickman 1993), incense cedar (*Calocedrus decurrens*), sugar pine (*Pinus lambertiana*), white fir (*Abies concolor*), Douglas-fir (*Pseudotsuga menziesii*), and Jeffrey pine (*Pinus jeffreyi*) which share dominance depending on site conditions and stand history. California black oak (*Quercus kelloggii*) is an associate on drier, south-facing slopes.

People have influenced fire regimes and forest conditions in YNP for millennia (Moratto 1984, Anderson 2005). Prior to Euro-American settlement, the Miwok actively used fire to promote production of acorns, berries, roots, and fiber, and to flush game (Barrett and Gifford 1976). Fire frequency declined in parts of YNP with the introduction of livestock grazing

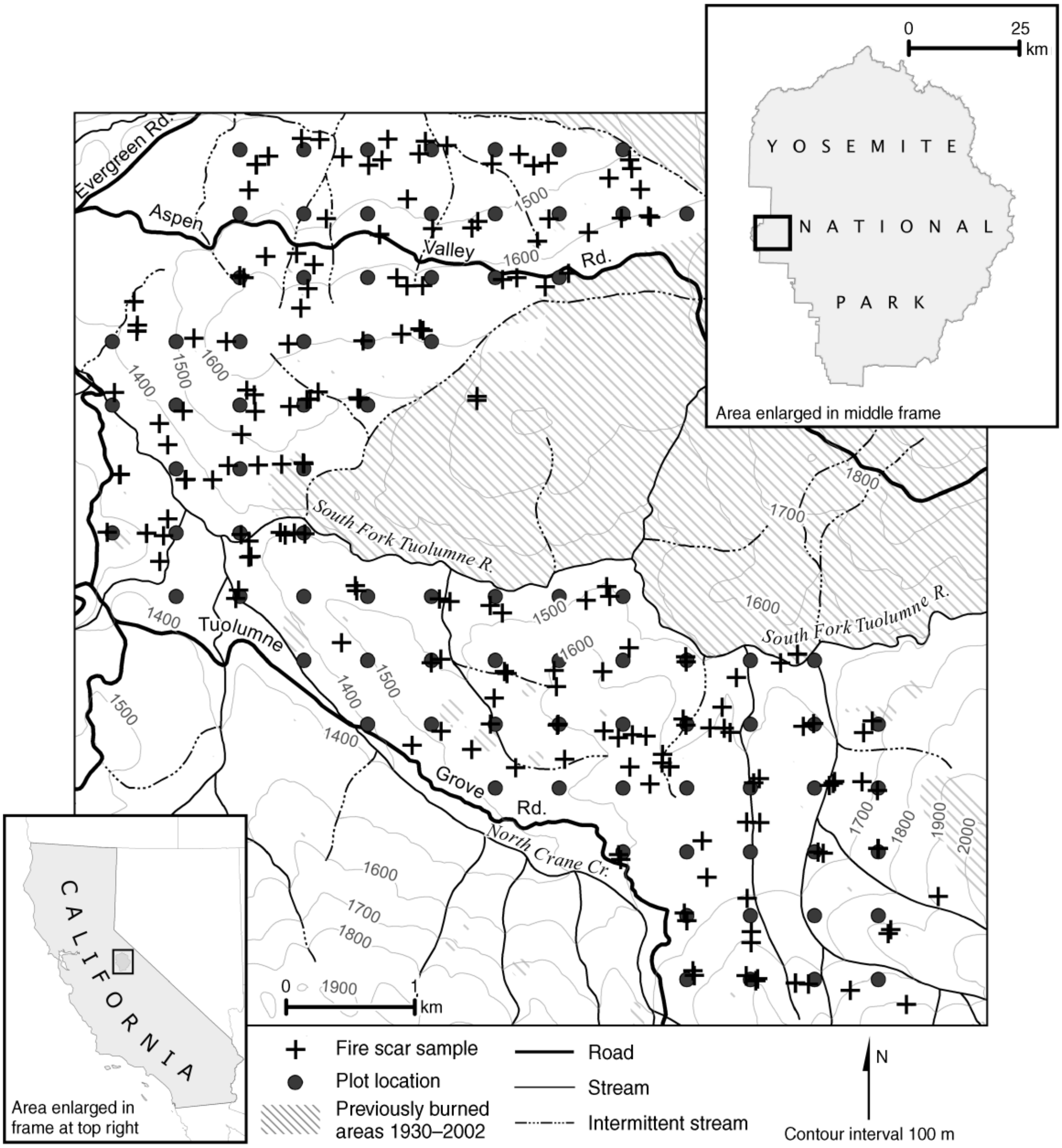

FIG. 1. Location of study area, plots, and fire-scar samples in an old-growth mixed-conifer forest in Yosemite National Park, California, USA.

soon after Euro-American settlement in 1850 (Swetnam et al. 1998). The area was designated a National Park in 1890, and a policy of suppressing fire on federal lands was implemented in 1905 (Pyne 1982). YNP records indicate that the study area was never logged and was last burned by a wildfire in the early 20th century. Areas burned by fires between 1930 and 2002 were not sampled (Fig. 1).

METHODS

Forest structure and composition

Forests were sampled at grid points (n = 85) established at 500-m intervals starting from a randomly chosen point (Fig. 1). Three nested circular plots were used to measure forest characteristics at each point. Large trees (live and standing dead) >35.0 cm diameter (conifer) or >15.0 cm diameter (hardwood) were sampled in a 1000-m^2 plot. Large trees were measured at breast height (dbh) and mapped using distance and azimuth from the plot center. The diameter, location, species, direction of fall, and decay class (Maser et al. 1979) of all logs (>35 cm dbh) rooted in the plot were also recorded. Identical measurements were made for small trees (10–35 cm dbh for conifers, 5–15 cm dbh for hardwoods) in a 250-m^2 plot. Seedlings (0.5–1.4 m tall) and saplings (1.4 m tall, 10.0 cm dbh for conifers, 5.0 cm dbh for hardwoods) were tallied by species in a 100-m^2 plot. The elevation, slope pitch, slope aspect, slope configuration, and topographic position at each point were also recorded. The last four variables were used to estimate a topographic relative moisture index (TRMI) value, an index of relative potential soil moisture based on topography that ranges from 0 (xeric) to 60 (mesic) (Parker 1982).

Variation in species composition among plots was identified by ordinating species importance values using nonmetric multidimensional scaling (NMDS) with Sørenson's distance measure (McCune and Grace 2002). Species importance values (IV) were calculated as the sum of relative density and relative basal area (maximum IV = 200). The contribution of environmental variables to compositional variability was identified by correlating (Pearson product moment) NMDS scores with the environmental variables for each plot (elevation, aspect, TRMI). Aspect values were transformed to a linear scale following Beers et al. (1966) that ranges from 0 (southwest slopes) to 2 (northeast slopes).

Tree ages were determined by coring all measured trees to the pith at a height of 30 cm above the soil surface. Cores were sanded to a high polish and annual growth rings were cross-dated using standard dendroecological techniques (Stokes and Smiley 1968). The date of the innermost ring was used as the estimate for tree age.

Not all trees (19%) could be aged because the pith was rotten or they were too large to extract a complete core. Ages for trees with incomplete cores were estimated in the following way. First, a regression equation between core length and tree diameter was developed for each species. All regressions were significant ($P < 0.001$) with r^2 values ranging from 0.61 to 0.89. Second, the missing length for an incomplete core was estimated by subtracting core length from predicted length. For cores with a predicted length that was shorter than the actual core, the actual core length was used. Finally, the width of the earliest 5 years' growth on complete cores was measured to determine the mean number of rings/centimeter for each species. The number of years represented by the missing length was then added to incomplete cores to estimate tree age.

Age structure

Age structural patterns were characterized in two ways. At the plot scale, we counted the number of stems in 20-yr age classes in each plot. Counts were made for both all age classes (20–600 yr) and for the age classes of stems that established in the reference period (>100 yr old). At the landscape scale, we grouped plots with similar reference period age-class distributions using cluster analysis. Plots were grouped by density of stems of each species in 20-yr age classes using Ward's method and relative Euclidean distance. Topographic influences on variation in age structure were identified by comparing the frequency distribution of species' age classes for plots grouped by elevation (low, 1312–1514 m; medium, 1516–1716 m; high, 1717–1920 m), aspect (north, east, south, west), and topographic position (valley bottom, lower slope, mid slope, upper slope, ridge top) for both all stems and stems > 100 yr old using Kolmogorov-Smirnov two-sample tests.

Forest reconstruction

Forest composition and structure were reconstructed for 1899: the year of the last widespread fire. A reconstruction for an earlier year would be incomplete because fires consume evidence of the earlier forest. We used the method described by Fúle et al. (1997) with modifications for tree species in California mixed-conifer forests. The following steps, summarized from Fúle et al. (2002) were followed: (1) the diameter of live trees in 1899 was determined by subtracting radial growth since 1899 from cored trees; (2) the death date for dead trees was estimated using tree decay class and diameter-dependent tree decomposition rates (Thomas et al. 1979, Rogers et al. 1984); (3) decomposition rates for each species were calculated for average (50th percentile), fast (25th percentile), and slow (75th percentile) decomposition to evaluate the sensitivity of reconstructed forest characteristics to decomposition rates; (4) the sizes of trees in the year they died was estimated using mean radial growth rates from 1899–2002 from the cores of trees alive in 1899.

We identified the influence of the historic fire regime and fire suppression on the spatial and temporal pattern of tree regeneration by analyzing the spatial structure of tree ages using statistical tests of spatial autocorrelation. We calculated Moran's I (Moran 1948, Cliff and Ord 1973) to identify the spatial characteristics of tree ages in each plot for postfire suppression (250-m^2 plot) and reference trees (1000-m^2 plot). Moran's I is a weighted correlation coefficient that detects departures from spatial randomness. Positive values for Moran's I indicate that trees of similar age occur close together, whereas negative values indicate that trees of similar age are separated from each other. Values of Moran's I were calculated for successive 1-m distance classes up to 15 m for postfire suppression trees and up to 30 m for reference period trees to identify the scale of spatial autocorrelation; significance was tested using two-tailed tests (Upton and Fingleton 1985). The frequencies of significant Moran's I values were then summarized for all plots.

Forest timber survey in 1911

To assess the forest reconstruction, we compared our reconstructed values for 1899 with measurements of forest conditions in 1911 in the same area. The purpose of the survey was to assess timber volume on the newly established Stanislaus National Forest in California. From the survey notes that included measured distances from land survey markers, we determined that seventeen timber survey belt transects were sampled in our study area in 1911 (Timber Survey Field Notes 1911). Transects were two chains wide × 20 chains long and included ~21 ha of forest in our study area. In each transect, surveyors recorded the dbh of all live trees >15.2 cm dbh (6 in) by species and grouped them into 15.2 cm (6 in) dbh classes. Forest characteristics in 1899 and 1911 were compared using a Kruskal-Wallis *H* test.

Fire regimes

Fire-regime parameters (i.e., frequency, fire-return interval, severity, extent, seasonality, rotation) were reconstructed using four types of data: (1) written fire records for Yosemite National Park (YNP), USA; (2) fire dates from fire-scarred trees; (3) radial growth patterns in tree cores; and (4) the age structure of trees in the plots. Fire dates were identified from fire scars in wood samples collected from live and dead trees (n = 209) with a chainsaw (Arno and Sneck 1977). Samples with the largest number of visible fire scars within a 9-ha area centered on each grid point were collected. A mean of two samples (range of one to five) were collected at each grid point. All recorded fires in samples for a grid point were combined to create a grid-point fire history. Fire dates were determined by sanding each wood sample to a high polish and cross-dating the annual rings (Stokes and Smiley 1968). The calendar year of tree rings with fire-scar lesions in it was recorded as the fire date.

Fires may injure but not scar a tree and the injury can cause a sudden change in radial growth (Arno and Sneck 1977). Consequently, we used radial growth suppressions and releases (200% change in radial growth for five years compared to the previous five years' growth) to identify fire dates from cores at a grid point. Dates of growth suppression or release were only recorded as a fire date if there was a fire date from a fire-scar sample from an adjacent grid point.

Fire seasonality.—The relative position of each fire scar within an annual growth ring was used to infer the season in which each fire burned. Scar positions were assigned to one of five categories (Baisan and Swetnam 1990): (1) early, first one-third of earlywood; (2) middle, second one-third; (3) late, last one-third; (4) latewood; or (5) dormant, at ring boundary. In this strongly winter-wet, summer-dry climate, dormant-season fires are interpreted to occur in late summer or in fall after growth has stopped for the year, rather than before growth in early spring (Caprio and Swetnam 1995).

Fire-return intervals.—Composite (CFI) and point (PFI) fire-return intervals were used in our fire-regime analysis. Composite records were derived from all grid-point fire histories or subunits (slope-aspect group) in the study area. CFI are more sensitive than point records to changes in burning conditions that may affect scarring of trees (Dieterich 1980). PFI are calculated from the record of successive fires in a single tree and reflect the time dependence of fire occurrence associated with fuel accumulation at a single point (Dieterich 1980, Kitzberger and Veblen 1997).

1. *Spatial patterns*.—Spatial variation in fire-return intervals was identified by comparing CFI and PFI for grid points in the four slope–aspect groups using a distribution-free Kruskal-Wallis *H* test.

2. *Temporal patterns*.—Temporal variation in CFI that may be related to land-use changes were identified by comparing fire frequency during the presettlement (up to 1850), settlement (1850–1904), and fire-suppression (1905–2002) periods using a composite record of fire from all samples. An all-sample composite fire record was used because they are more sensitive to changes in temporal patterns of burning related to land-use changes than samples from a small area (Dieterich 1980).

3. *Fire extent*.—Area burned in the study area was estimated by applying a ratio method to the number the grid points recording a fire in a given year (Taylor and Skinner 1998). Burn area was estimated as

$$A_i = (\mathrm{AT} \times \mathrm{NS}_i)/(\mathrm{NST} - \mathrm{NRE})$$

where A_i is the area burned in the ith year, AT is the study area size (ha), NS_i is the number of grid points with a record of the fire in the ith year, NST is the total number of grid points, and NRE is the number of grid points without samples of sufficient age to record the fire in the ith year. The accuracy of this method decreases as NRE increases, so we chose a cutoff date of 1575 ($n = 27$ grid points) for fire-area estimates to reduce errors associated with a larger sample size.

4. *Fire rotation*.—Fire rotation (FR) is the number of years needed to burn an area equal in size to the study area (Heinselman 1973) and was calculated using the burn area estimates. Fire rotations were calculated for each century, and for the presettlement, settlement, and fire-suppression periods. For a given period, some parts of the study area may have burned more than once, and others not at all.

5. *Fire severity*.—Fire severity at plot and landscape scales was inferred from the age structure groups and counts of the number of 20-yr age classes occupied by trees. Fires can burn with variable severity across a landscape, killing most or all trees in some stands and few in others. Even-aged stands usually develop after high-severity fires while several-aged stands reflect moderate-severity fires that kill only parts of the stand. Stands that experience low-severity fire, in contrast, are multi-aged but may not have distinct age classes related to fire (Agee 1993). We counted the number of 20-yr age classes occupied by trees in a plot for all age classes, and for reference period age classes (>100 yr). Presumably, plots with trees in many age classes experienced less severe fire than those with stems in few age classes. We also calculated the mean number of fires that burned in each age structural group using the corresponding grid point CFI.

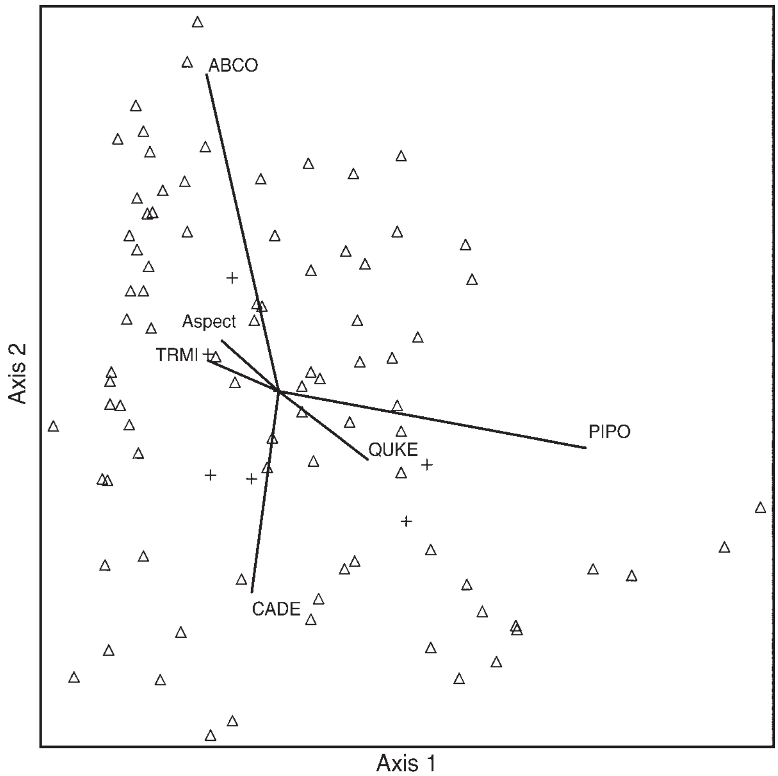

FIG. 2. Ordination of plot scores ($n = 85$) for the first and second axes of a nonmetric multidimensional scaling (NMDS) analysis of species' importance values in an old-growth mixed-conifer forest in Yosemite National Park, California. Lines (radiating from centroid) show Pearson correlation vectors of species and environmental variables with ordination axes. All correlation vectors have $r^2 \geq 0.20$, and vector length represents strength of correlation. Species acronyms are ABCO (*Abies concolor*), CADE (*Calocedrus decurrens*), PILA (*Pinus lambertiana*), PIPO (*Pinus ponderosa*), PSME (*Pseudotsuga menziesii*), and QUKE (*Quercus kelloggii*). TRMI is the topographic relative moisture index.

Fuel limitation and fire occurrence

The influence of previous burns on subsequent fires at the same location was assessed by using the dates of successive fires at a grid point. The dates of pairs of consecutive fires were used to estimate the frequency that the second fire in a consecutive pair burned at the same grid point or a different grid point. Frequencies were also calculated for fire pairs in the presettlement, settlement, and fire-suppression periods to identify changes in frequency related to land-use change. Finally, the number of grid points burned by only the first fire or second fire were multiplied by 25 ha (area represented by a grid point) to compare area burned by the previous and subsequent fires in each category.

RESULTS

Forest conditions

Contemporary forest composition.—The nonmetric multidimensional scaling (NMDS) of species IV separated plots on the basis of species composition (Fig. 2). The first NMDS axis separates plots strongly dominated by ponderosa pine (*Pinus ponderosa*; $r = 0.93$) and California black oak (*Quercus kelloggii*; $r = 0.50$) from stands that were more evenly mixed. White fir (*Abies concolor*; $r = 0.94$) was positively correlated, while incense cedar (*Calocedrus decurrens*; $r = -0.75$), California black oak ($r = -0.44$), and ponderosa pine ($r = -0.40$) were negatively correlated with NMDS axis 2. Variation in species IV was related to environmental conditions. Slope aspect ($r = -0.40$), and TRMI ($r = -0.45$), were correlated ($P < 0.05$) with NMDS axis 1. This indicates that ponderosa pine and black oak are concentrated on drier and warmer slope aspects. In contrast, white fir dominates cooler mesic sites. There was no correlation between mean grid point fire-return interval (FRI) and NMDS axis scores.

Forest reconstruction.—The forest reconstruction method was not sensitive to variation in decomposition rates (Fig. 3). There were no differences ($P > 0.05$, Kruskal-Wallis H test) in the reconstruction estimates of average density, basal area, or diameter for the three decomposition rates. Many of the dead trees under all three decomposition models (fast decomposition rate [25th percentile] = 392, average [50th] = 467, slow [75th] = 501) were assigned death dates late enough in the 20th century that their estimated germination dates were after 1899 so they were not included in the forest reconstruction. Given the low sensitivity of the reconstruction to

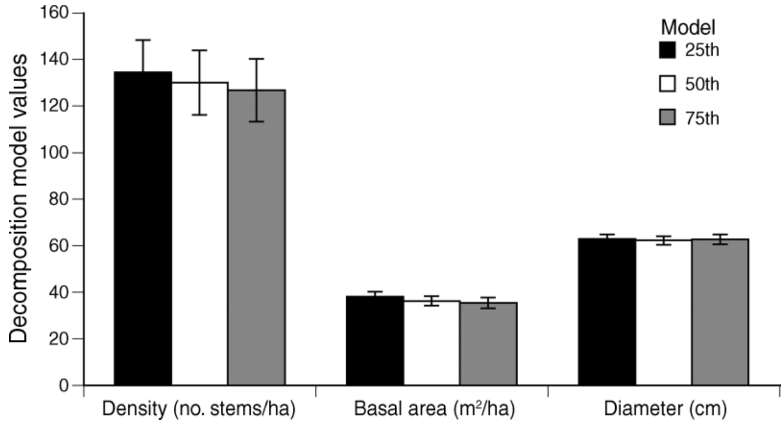

FIG. 3. Density, basal area, and quadratic mean diameter (all values mean ± SE) for the reference forest estimated using three decomposition condition models (25th, 50th, 75th) for death date of trees that were dead in 2002. Values are for trees >10 cm dbh.

variable decomposition rates, we only report the reconstructed values for the 50th percentile model.

Contemporary and reconstructed forest characteristics.—The composition and structure of the contemporary and reference forest were different (Table 1). On average, the contemporary forest had threefold more trees, twice the basal area, and trees that were 20% smaller (dbh) than in the reference forest ($P < 0.01$, Kruskal-Wallis test). The forest change since 1899 was not uniform among species or across variables. White fir ($P < 0.001$), incense cedar ($P < 0.01$), and Douglas-fir (*Pseudotsuga menziesii*; $P < 0.05$) density and basal area increased between 1899 and 2002; density increases were smaller but not significant for other species. On the other hand, the basal area for all species except ponderosa pine, was higher ($P < 0.05$) in the contemporary than reference forest. The diameters of contemporary white fir, ponderosa pine, and black oak were also larger ($P < 0.001$) than in the reference forest. Overall, white fir and incense cedar are proportionally more abundant in the contemporary than reference forest. The shape of the diameter distribution for most

TABLE 1. Structural characteristics of the contemporary (2002) and reference (1899) mixed-conifer forest in Yosemite National Park, California, USA.

Tree species and year	Density (no. trees/ha)				Basal area (m^2/ha)			
	Mean	Median	SD	Range	Mean	Median	SD	Range
Abies concolor								
2002	248.9	240	196.7	0–750	17.5	16.3	13.8	0–53.9
1899	25.3***	10	37.2	0–200	1.8***	0	3.7	0–19
Calocedrus decurrens								
2002	128.1	70	152.2	0–800	18	15.9	14.8	0–69
1899	57.5**	40	64.6	0–370	9***	6.3	9.8	0–57.2
Pinus lambertiana								
2002	48.7	10	89.3	0–400	11.4	3.7	15.5	0–70.5
1899	17.9	10	25	0–130	6.8*	0.2	11.8	0–52
Pinus ponderosa								
2002	44.2	20	75.1	0–470	16.8	15.8	18.4	0–84.9
1899	37.4	20	54.3	0–340	10.4	7.6	11.8	0–55.4
Pseudotsuga menziesii								
2002	12.6	0	33.4	0–200	2.7	0	9.7	0–60.2
1899	3.4*	0	15.2	0–110	1.2*	0	6.3	0–46.1
Quercus kelloggii								
2002	33.5	0	67.2	0–360	2.9	0	6.4	0–43.5
1899	18	0	40.5	0–270	0.7*	0	1.9	0–11.5
All trees								
2002	516.1	490	242.4	90–1220	69.4	66.7	25.9	20.7–150.8
1899	159.5***	120	117.3	40–650	29.9***	24.3	19.6	0.3–88.9

Notes: All trees >10 cm dbh are included. For each characteristic and tree species, mean values marked with asterisks were significantly different (Krusakal-Wallis H test).

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

species was also similar in 1899 and 2002 ($P > 0.05$, Kolmogorov-Smirnov two-sample test; Fig. 4). Only incense cedar and sugar pine (*Pinus lambertiana*) had different diameter distributions in 1899 and 2002 ($P < 0.05$).

The spatial autocorrelation analysis revealed a patchiness in the spatial structure of tree ages that was more pronounced in the reference than contemporary forest (Table 2). In the reference forest, there was a high frequency (71%) of positive spatial autocorrelation in the plots with a concentration between trees of similar age at distances of 1–10 m and 22–30 m. Negative spatial autocorrelation was also frequent (61%), with a concentration at distances of 12–21 m, which represent distances between groups of different age. Positive (41%) and negative (55%) spatial autocorrelation was less frequent in the contemporary forest and the frequencies of either pattern were similar at distances of 1–15 m.

Comparison with 1911 forest survey

The characteristics of the 1911 forest were also different than the contemporary forest (Table 3). Overall, the contemporary forest had more trees ($P < 0.001$) and a higher basal area ($P < 0.001$) than the survey forest. The density and basal area increases were greater ($P < 0.05$) for white fir and incense cedar than for other species ($P > 0.05$). The mean diameter for white fir and incense cedar were also smaller in 2002 than in 1911 ($P < 0.01$).

The characteristics of the reference forest were similar to values for the 1911 survey (Table 3). There was no difference ($P > 0.05$) in either the total, or species', density or basal area between the 1911 and reference forest. The mean diameter of a reconstructed tree in 1899, however, was larger ($P < 0.05$) than in the survey forest, but the opposite was true for white fir ($P < 0.001$).

Fire regimes

Fire record.—A total of 286 fire years were recorded in the 209 samples. Fires were recorded between 1575 and 2002.

1. *Fire season*.—The position of fires within annual growth rings indicate that fires burned mainly late in the growing season (latewood = 38.7%) or after growth ended for the year (dormant = 39.8%). Growing-season fires were less frequent, with 14% in the last third of earlywood, 6.4% in the middle third of earlywood, and 1.1% in the first third of earlywood.

2. *Fire-return intervals (FRI)*.—The statistical analysis of FRI includes the mean fire interval, median fire interval, and the Weibull median probability interval (WMPI) as measures of central tendency (Grissino-Mayer 2001). The fire-interval distribution had similar measures of central tendency, was positively skewed, and had more short fire-return intervals than long intervals (Table 4). The composite mean FRI for all fires was 1.5 yr, and it was longer for more widespread fires that scarred 10% or more (2.6 yr), or 25% or more (10 yr) of the grid points. The mean and median point FRI were 12.4 yr and 10 yr, respectively, similar to CFI for widespread fires.

3. *Spatial pattern*.—Slope aspect, potential soil moisture, and forest composition in the study area covary (Fig. 2). However, there was no spatial variation ($P > 0.05$; Kruskal-Wallis H test) in the composite FRI and point FRI by slope aspect group (Table 4). Mean and median composite fire-return interval (CFI) and point fire-return interval (PFI) values were similar on the different slope aspects.

4. *Temporal patterns*.—Fire occurrence over the entire study area varied by time period (Table 5). The mean interval between fires ($P > 0.05$, t test) was similar in the presettlement (1.2 yr) and settlement periods (1.2 yr), but longer (6.2 yr) during the fire-suppression period ($P < 0.01$). No widespread burns occurred during the fire-suppression period.

5. *Fire extent*.—Eighty-one percent of the fires intersected the boundary of the study area. This suggests that the actual extent of individual fires is larger than the reconstructed values. Nevertheless, fire extent varied among years and by time period (Fig. 5). The mean and median burn area for the period 1575–2002 was 205 ha and 115 ha (range 25–1946 ha), respectively (Table 6).

TABLE 1. Extended.

Quadratic mean diameter (cm)			
Mean	Median	SD	Range
32.1	29.7	11.8	15.3–70.2
24***	16.3	21.9	1–93.8
56.8	50.7	31.7	12.2–118.7
47.5	46.3	25.3	5.3–113.4
80.8	69.7	59	10.2–215
73.2	66.3	51.6	1–190.1
86.2	90.1	33.1	22–159.5
66.6***	66.5	28.3	16.8–131.1
45.9	41.3	25.3	14.5–111.3
61.4	64.8	35.8	16.4–104.7
31.9	31.6	12.8	13.4–72.9
18.9***	16	12	2.6–56.7
43.9	43.3	11.4	19.2–80.6
52.7*	50.7	22	8.2–110.8

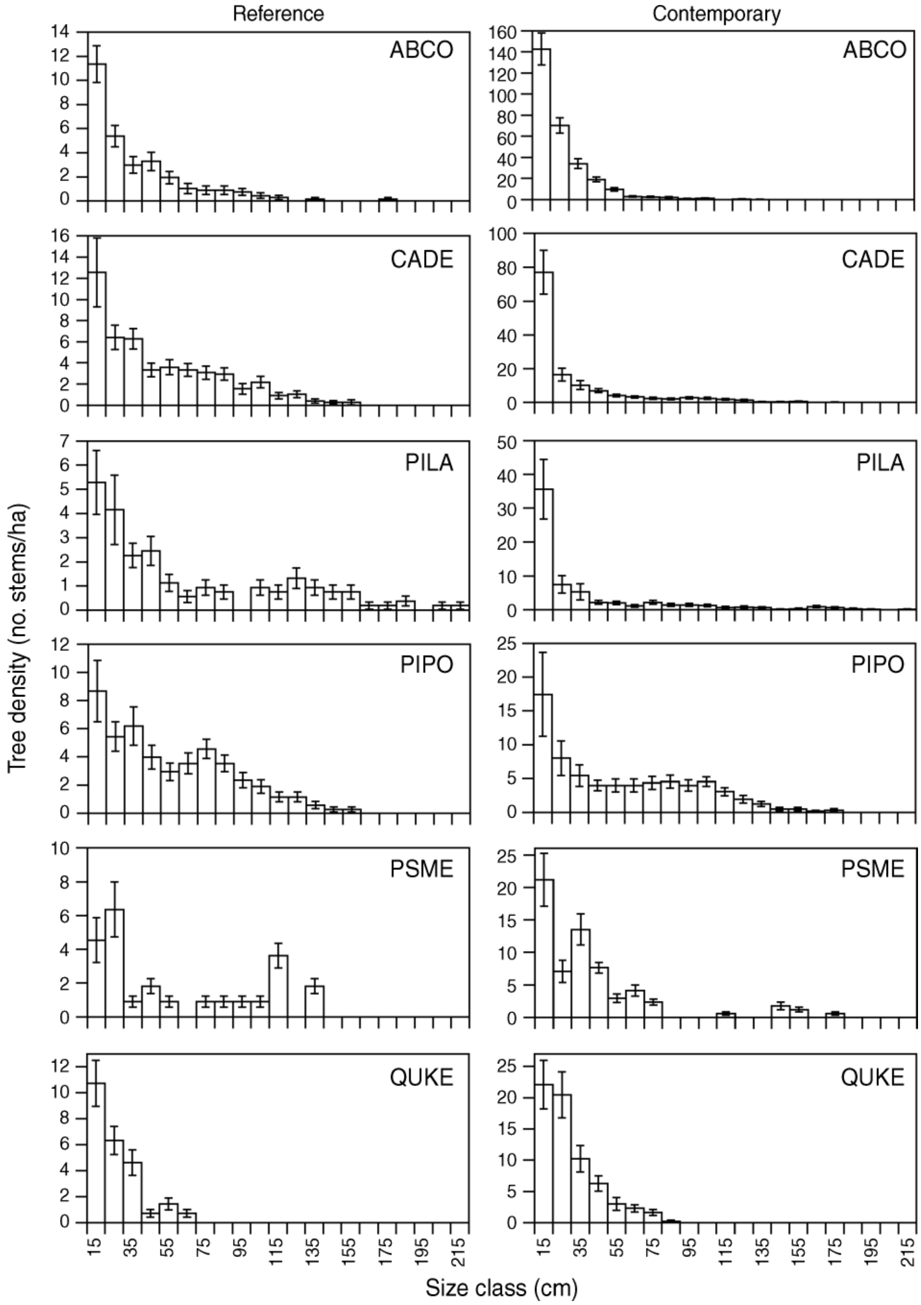

FIG. 4. Density of trees >10 cm dbh (mean ± SE) by size class (dbh) in the contemporary and reference old-growth mixed-conifer forest in Yosemite National Park. Note that the *y*-axis scale is different on each graph. See Fig. 2 for species acronyms.

The mean extent of a fire was similar ($P > 0.05$) in the presettlement and settlement periods but smaller ($P < 0.001$) in the fire-suppression period. Mean burn area in the 19th century was similar ($P > 0.05$) to the 18th century but larger than the 17th and 20th century ($P < 0.001$). The burn area distribution was positively skewed, and only 19 fires burned >500 ha since 1575. Most (79%) of these larger burns occurred in the 19th century.

6. *Fire rotation.*—Fire rotation also varied by time period (Table 6). Fire rotation for the presettlement period was 13 yr and 10 yr for the settlement period. In contrast, the fire rotation for the fire-suppression period was 378 yr. The shortest fire rotation was in the 19th century (8 yr) because of the high frequency of large fires during this period.

Fuel limitation and fire occurrence.—The spatial pattern of consecutive pairs of fires indicates that fires

PLATE 1. Old-growth mixed conifer forest in Yosemite National Park that has not burned since 1899. The large-diameter trees are ponderosa pine, while the dense layer of smaller-diameter trees are mainly white fir, which established during the fire-suppression period. Considerable amounts of surface fuel have also accumulated since 1899. Photo credit: A. E. Scholl.

burned different sites more than previously burned sites. Few consecutive fires (9%) burned the same site; most (91%) burned different sites. The area re-burned (4375 ha) by consecutive fires was small compared to the area burned on sites that had not been burned by the previous fire (47 150 ha). The re-burn relationship was consistent (mean 9%, range 7.2–10.7%) across time periods (century, presettlement, settlement), except during the fire-suppression period when no fires re-burned the same site.

Contemporary forest age structure and fire severity.— Six age–class structural groups were identified from the cluster analysis of stems >100 yr old (Fig. 6, Table 7). All species were present in each structural group, and ponderosa pine, incense cedar, and sugar pine were all well distributed among age classes with old individuals (>300 yr) in each group.

Group 1 included low-density plots with stems of ponderosa pine, incense cedar, and sugar pine in a wide range of age classes. White fir, Douglas-fir, and black oak stems were <300 yr old and white fir, incense cedar, and sugar pine <100 yr old were abundant. On average, plots burned 27 times and had stems in 5.5 age classes

TABLE 2. Spatial autocorrelation of tree ages calculated using Moran's *I* in a mixed-conifer forest in Yosemite National Park.

Forest analysis, spatial autocorrelation	Distance (m)																													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
2002																														
+	4	4	1	4	3	4	2	1		2																				
−		4	1		2	4	6	2	2	6																				
1899																														
+	3	6	2	8	3	9	6	3	5	3		1			2	1	2	1	1	3	2	4	5	4	6	5	4	4	5	5
−				3	3	3	3	3	3	2	1	4	6	3	5	5	8	7	7	3	5	3	1		3	1	2	1		2

Note: Data are the number of plots ($n = 85$) exhibiting significant ($P < 0.05$) positive (+) or negative (−) spatial autocorrelation at a given scale. Analysis for the contemporary (2002) forest was restricted to stems in the 250-m^2 plot (distances ≤15 m between trees), while the analysis for the 1899 forest used stems in the l000-m^2 plot (distance ≤30 m between trees).

TABLE 3. Structural characteristics of the contemporary (2002), reference (1899), and the 1911 timber survey mixed-conifer forest in Yosemite National Park.

	Density (no. trees/ha)				Basal area (m^2/ha)			
Species and year	Mean	Median	SD	Range	Mean	Median	SD	Range
Abies concolor								
2002	181.2[a]***	160	140.8	0–500	17.7[a]***	16.1	14.2	0–57.4
1911	13.2[b]	2	21.5	0–63.8	3.7[b]	1	7	0–27.8
1899	10[b]	0	17.9	0–90	1.8[b]	0	3.9	0–20.6
Calocedrus decurrens								
2002	74.5[a]	40	90.7	0–480	17.9[a]***	15.1	15	0–69.4
1911	33.7[b]*	13	43.3	0.5–158.6	4.4[b]	3.9	3.5	0–12.9
1899	31.3[b]**	30	28.3	0–140	8.9[b]	6.3	9.8	0–55
Pinus lambertiana								
2002	31.6	10	52.7	0–210	11.4	2.2	15.7	0–67.4
1911	7.5	8	6.9	0–19.2	2.9	0.7	3.4	0–10.2
1899	12.9	10	19.1	0–80	6.9	0.4	11.8	0–50.5
Pinus ponderosa								
2002	38.1	20	56.6	0–330	16.8	15.2	18.5	0–86.1
1911	42.8	30	42.8	0–145.2	8.3	5.5	7.9	0–25.8
1899	29.5	20	34.6	0–150	10.4	7.8	11.8	0–54.8
Pseudotsuga menziesii								
2002	9.8	0	25.8	0–150	2.8	0	9.9	0–60.7
1911	2.2	0	7.2	0–31	1.3	0	4.4	0–19.3
1899	2.5	0	10.8	0–70	1.1	0	6	0–43
All trees								
2002	335.2[a]***	340	146.6	30–750	66.6[a]***	63.1	27.8	18.1–142.1
1911	99.4[b]	80	66.2	8.3–216.3	20.6[b]	24	10.6	0.7–34.4
1899†	86.2[b]	80	50.4	0–280	29.1[b]	23.7	20.2	0–85.9

Notes: Only data for conifer trees ≥15.2 cm dbh are included. Values followed by the same lowercase letter were not significantly different (Kruskall-Wallis *H* test).
* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.
† No oaks are included in these data.

>100 yr old, which suggests a pattern of intermittent recruitment after mainly low-severity fire.

Group 2 plots were dense, and there were a large number of trees between 80 and 200 yr old. There were a few stems of ponderosa pine, incense cedar, and sugar pine >300 yr old. Plots on average had stems in 5.6 age classes and they burned 25.9 times, suggesting a pattern of intermittent regeneration under a regime of frequent low-severity fire.

Plots in Groups 3 and 4 were moderately dense and were distinguished by an abundance of 100–300 yr old sugar pine and incense cedar, with a low density of >140-yr-old ponderosa pine. Plots burned on average 20.9–28.6 times, and had on average 4.7–5.9 age classes. The high frequency of fire and pattern of intermittent recruitment, again, suggests a regime of mainly low-severity fire.

Group 5 plots were low density with stems of 140–300 yr old incense cedar, ponderosa pine, and black oak scattered among age classes. These plots burned on average 26.7 times and contained 4.4 age classes. The intermittent pattern of establishment with a high number of fires per age class (6.1) suggests a regime of frequent low-severity fire.

Group 6 plots were moderately dense and are distinguished by 140–340 yr old incense cedar and abundant 160–200 yr old ponderosa pine. Plots in this group, on average, contained six age classes and burned 11.3 times. Frequent fire, intermittent recruitment, and the large number of occupied age classes suggest a regime of low-severity fires.

The spatial pattern of plots in the age–class groups in the study area was heterogeneous and not associated with topography. The frequency distribution of age-class groups did not vary with slope aspect, elevation, or topographic position ($P > 0.05$). Furthermore, there was no association between topographic variables and density of stems ≤100 yr old in the age-class groups. There were, however, more stems ≤100 yr old than >100 yr old in each group ($P < 0.05$, Kruskall-Wallis *H* test), suggesting that fire suppression caused an increase in density of stems in all age–class groups.

DISCUSSION

Tree species distribution and abundance in our study area was controlled by temperature and moisture that was related to topographic setting. For example, warmer, drier sites were preferred by ponderosa pine and black oak, while white fir was most abundant on cool, mesic north-facing slopes. The species–topography associations in our forest are similar to mixed-conifer forests elsewhere in California (Barbour 1988).

TABLE 3. Extended.

Quadratic mean diameter (cm)			
Mean	Median	SD	Range
36.9^{a***}	34.7	11.2	22.9–70.5
74.2^{b***}	70.4	23.8	44.3–122.1
42.9^{c***}	37.3	22.7	22.9–99.1
67.1^{a*}	64.7	27.8	22.9–118.9
50.4^{b}	51.3	18.6	22.5–95.1
58.9^{b}	53.3	22.8	22.9–114.3
87.8	75.6	57.6	22.9–221
71.4	69.6	29.9	19–130.1
82.5	83.8	48.2	22.9–190.5
87.9^{a***}	90.7	31.8	22.9–160
57.6^{b}	48.9	23.4	21.3–105.9
69.3^{b}	69.9	26.5	22.9–129.5
54.8	42.7	35.8	22.9–160.5
79	74.5	8.7	73.5–89
69.6	72.6	37	22.9–119.6
53.2^{a**}	52.1	14	25.5–100.8
53.8^{a*}	49.4	15.2	32.6–87.4
67.5^{b}	62.8	25.3	22.9–129.5

Topographic setting can also influence spatial patterns of fire frequency by influencing species composition, the production and structure of fuels, fuel moisture, and barriers to fire spread (Taylor and Skinner 2003). For example, fire frequency decreases with elevation in southwestern (Cocke et al. 2005), northwestern (Taylor 2000), and Rocky Mountain (Schoenagel et al. 2004) U.S. forests. Cooler temperatures, deeper snow packs, and later snowmelt in spring shorten the period fuels are dry enough to burn at high elevation compared to warmer, drier sites at low elevation. In the Sierra Nevada mountains, fine fuel production is also greater in lower than upper montane forests (Keifer et al. 2006), so fire can re-burn a patch sooner at low elevation. High elevation forests are also dominated by short-needled species of fir, pine, and hemlock (Parker 1989). Fuel beds of short-needled species have a high bulk density and fire spread and intensity are lower compared to the fuel beds of long-needled pines (Agee 1993).

Despite a strong association between warmer, drier sites and long-needled pines (i.e., ponderosa pine [*Pinus ponderosa*]), and cooler, moister sites and short-needled fir, there was no spatial variation in fire frequency related to topography in our study area. Fire frequency was similar at all elevations and slope aspects. In some mixed-conifer forest landscapes, spatial patterns of fire frequency are strongly related to topographic setting. Fire frequency

TABLE 4. Point and composite fire-return interval (FRI) statistics for a mixed-conifer forest in Yosemite National Park.

Slope aspect, type of sample	No. intervals	Mean FRI (yr)	Median FRI (yr)	WMPI (yr)	SD (yr)	Min. (yr)	Max. (yr)	Skewness	Kurtosis
Study area									
Point (PFI)	500	12.4	10	10.7	10.1	2	84	3.1	14.5
Composite	286	1.5	1	1.2	1.6	1	16	5.5	34.5
>10% scarred	129	2.6	2	2.3	1.8	1	11	2	5.7
>25% scarred	33	10	9	9.2	6.1	2	28	1	0.7
North									
Point (PFI)	500	11.8	9	9.7	12	1	179	6.9	79.5
Composite	200	1.9	1	1.5	3.4	1	43	9.6	109.3
>10% scarred	119	2.5	2	2.3	1.8	1	12	2.2	7
>25% scarred	36	8.4	6.5	7.1	6.6	1	34	1.7	4.2
East									
Point (PFI)	437	12.3	10	10.8	9	2	69	2	6.2
Composite	158	2.5	2	1.7	5.8	1	69	10	110
>10% scarred	158	2.5	2	1.7	5.8	1	69	10	110
>25% scarred	50	6.6	4	5	6.9	1	34	2.5	6.9
South									
Point (PFI)	346	10.6	9	9.3	7.8	1	53	2.5	8.3
Composite	140	2.6	2	2	3.9	1	31	5.9	39.3
>10% scarred	113	3.3	2	2.2	7.9	1	84	9.7	96.8
>25% scarred	72	4	4	3.6	2.4	1	10	0.7	−0.3
West									
Point (PFI)	500	12.4	10	10.7	10.1	2	84	3.1	14.5
Composite	220	1.9	1	1.4	3.4	1	41	8.4	83.9
>10% scarred	118	2.8	2	2.4	2.5	1	19	3.2	14.5
>25% scarred	36	9.2	7	6.9	10.2	1	52	2.8	8.1

Notes: WMPI is the Weibull median probability fire interval. Composite fire-return intervals are more sensitive than point records to changes in burning conditions that may affect scarring of trees (Dieterich 1980). PFIs are calculated from the record of successive fires in a single tree and reflect the time dependence of fire occurrence associated with fuel accumulation at a single point (Dieterich 1980, Kitzberger and Veblen 1997).

TABLE 5. Composite fire-return interval (FRI; years) statistics for the presettlement (1700–1849), settlement (1850–1904), and fire-suppression (1905–2002) periods in a mixed-conifer forest in Yosemite National Park.

Fire frequency and time period	Years	FRI (yr)		
		Mean	Median	Range
All fires				
All years	1575–2000	1.4	1	1–16
Presettlement	1575–1849	1.2	1	1–10
Settlement	1850–1904	1.2	1	1–3
Fire suppression	1905–2002	6.2**	5	2–16
10% scarred				
All years	1575–2000	2.5	2	1–10
Presettlement	1575–1849	2.4	2	1–10
Settlement	1850–1904	2.8	2	1–9
Fire suppression	1905–2002	–	–	–
25% scarred				
All years	1575–2000	10	9	2–28
Presettlement	1575–1849	10.7	9	3–28
Settlement	1850–1904	7.3	7.5	2–16
Fire suppression	1905–2002	–	–	–

Notes: Values followed by asterisks were statistically different (t test). Dashes in cells indicate that no fires in the suppression period were large enough to be recorded by 10% or 25% of the recording trees.

** $P < 0.01$.

is higher on warmer, drier pine-dominated south-facing slopes and lower on fir-dominated cool, mesic north-facing slopes (Beaty and Taylor 2001, 2008, Heyerdahl et al. 2001), a pattern consistent with differences in the period fuels are dry enough to burn each year. However, the terrain in those other sites is more incised and complex with greater contrasts in fuel structure, fuel moisture, and species composition among slopes. Topographic control on the spatial patterns of fire frequency may only emerge when terrain complexity exceeds a certain threshold (Taylor and Skinner 2003, Kellogg et al. 2008).

Spatial variation in fire frequency can also be influenced by the time-dependent process of fuel accumulation. A patch burned by a fire can only burn again when there is enough fuel to carry a fire. This time-dependent, self-organizing behavior would constrain fire spread and influence the spatial structure of the fire–forest patch mosaic (Taylor and Skinner 2003). In our study area, few successive fires burned the same site again, a pattern also evident for recent wildland fire use (WFU) fires in mixed-conifer forests elsewhere in Yosemite National Park (YNP), USA (Collins et al. 2009). More importantly, area burned by successive fires was 10-fold greater in places that had not been burned by the previous fire. Thus, the spatial structure of successive fires exhibits self-organizing behavior, and fire occurrence and extent are influenced by the location of previous burns. This effect is less prominent in dry years, however, when fires burned across the fuel patch mosaic. Between 1650 and 1900, fivefold more area burned in the 10 driest years than in the 10 wettest (Cook and Krusic 2004: grid point 047). Greater desiccation of fuels during drought reduces the fuel limitation effect (Miller and Urban 2000). Larger burns were also more frequent after 1775, a climate-related fire regime shift that may be related to the strength and interaction of the El Niño-Southern Oscillation and Pacific Decadal Oscillation that affect the fire climate of this region (Taylor and Beaty 2005).

Variation in fire severity has an important influence on forest heterogeneity because fires may kill all trees in some stands and few in others. Stand development after high-severity fire leads to even-aged or several-aged stands, while forests that experience low- or moderate-severity fires have trees in many age classes because few trees are killed in a stand (Agee 1993). Our forests were multi-aged and all stands had trees >300 yr old. When trees >100 yr old were assigned to 20-year age classes, a mean plot had stems in 5.3 different age classes, and half of the plots had stems in 6–10 age classes. While the majority of older trees were fire-resistant pines, old fire-sensitive white fir (*Abies concolor*) and incense cedar (*Calocedrus decurrens*) were present. Similar multi-aged stands of old-growth mixed-conifer forest have been described in other areas in California (Taylor and Skinner 2003, North et al. 2005, Beaty and Taylor 2007). These data are a clear indicator that burns were mainly low in severity and patchy enough for young white fir and incense cedar to grow to a fire-resistant size.

The spatial structure of the reference forest also supports the view of a predominance of low-severity fire effects on stand development. Intense surface fires following the death of a canopy tree would create a mineral soil seedbed favorable to pine and fir regeneration (Burns and Honakala 1990). With adequate seed and moisture, seedlings would establish in the burn patch leading to a forest mosaic comprised of small groups of similar aged trees. Trees of similar age that established in YNP before 1899 were frequently clustered at small to intermediate spatial scales (i.e., 2–10 and 20–25 m distances). Small clusters (6–12 m distance) of similar aged prefire-suppression trees that existed alone or overlapped are also characteristic of old-growth stands in the northern Sierra Nevada, USA (Beaty and Taylor 2007). Thus, the multi-aged structure of these forests can be viewed as an aggregation of small overlapping groups of even-aged trees driven by low-severity fire (Bonnicksen and Stone 1981, Beaty and Taylor 2007).

There was a strong effect of land-use change on fire regimes, but it was not evident until after 1905 when a policy of fire suppression was implemented on U.S. National Forest lands. Fire frequency and fire rotation were similar in the pre-Euro-American settlement and settlement periods suggesting that a presettlement fire regime prevailed until fire suppression was implemented. The >37-fold increase in fire rotation from 10 to 378 yr after 1905 is a strong indicator of the change in fire regimes caused by fire suppression. Similar reductions in

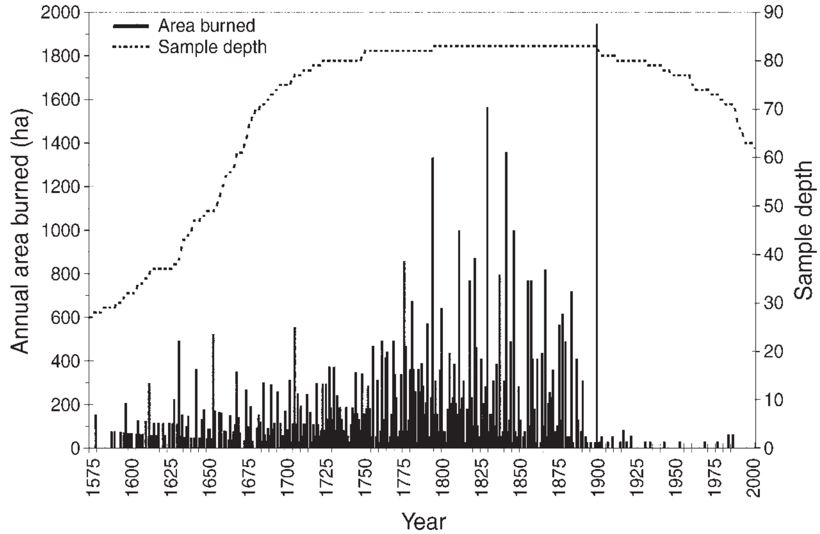

FIG. 5. Annual area burned (ha) and sample depth for the period 1575–2000 in an old-growth mixed-conifer forest in Yosemite National Park. Sample depth is the number of gridpoints in the study area that were recording fires at that time.

fire frequency and extent caused by fire suppression have been identified in other California mixed-conifer forests (e.g., Caprio and Swetnam 1995, Taylor 2000, Taylor and Skinner 2003, Beaty and Taylor 2008).

Fire suppression has caused an increase in forest density and a shift in composition from shade-intolerant fire-resistant pines and oaks to fire-intolerant and shade-tolerant white fir and incense cedar throughout California (Minnich et al. 1995, Taylor 2000, Taylor and Skinner 2003, Beaty and Taylor 2007). Yet, the magnitude of change since the onset of the fire-suppression period is difficult to assess because early forest survey data are scant (McKelvey and Johnson 1992), and few studies have employed dendroecological reconstruction techniques that account for the death of trees since the onset of fire suppression (e.g., Fúle et al. 1997). Our reconstruction supports written descriptions of mixed-conifer stands as being low in density, and having a large proportion of large-diameter shade-intolerant and fire-tolerant pines and oak (Sudworth 1900, Leiberg 1902). At the time of fire-regime disruption, YNP mixed-conifer forests had on average 160 trees/ha with a mean size >52 cm dbh, and a mean basal area of 29.2 m^2/ha. About half of the trees were also pine or oak. In 2003, after more than 100 yr of fire suppression, there were threefold more trees, twofold more basal area, and the mean size of a tree was 20% smaller. There was also a strong shift in forest composition; only a quarter of the trees in 2003 were pine or oak and there was a nearly 10-fold increase in the density of white fir.

Our estimate of forest conditions in 1899 should be viewed cautiously. Forest reconstructions using dendroecology are based on field evidence, and complete decay can eliminate the physical legacy of the original forest. Our oldest estimated year of tree death was 1930 for a 40 cm dbh sugar pine (*Pinus lambertiana*). The absence of earlier death dates suggests that small diameter trees alive in 1899 that died in the first few decades of the 20th century may have decomposed completely by 2002. The complete decay problem probably varies by species. Studies of snag fall and log decay (Kimmey 1955, Harmon et al. 1987, Morrison and Raphael 1993) indicate that small white fir decay faster than the pines or incense cedar. Consequently, our reconstruction method is more reliable for larger diameter trees and for species with slower decomposition rates and underestimates small tree density. The bias in reconstruction is less likely to influence our 1899 estimates of basal area, and the density and size of larger diameter trees. There was also a record of spot fires in the study area after 1899, and spot fires could have consumed large-diameter snags and logs leading to an underestimate of basal area and mean tree diameter.

Despite uncertainties in the reconstruction method, comparison of forest conditions in 1899 with data from

TABLE 6. Average fire size and fire rotation by time period in a mixed-conifer forest in Yosemite National Park.

Time period	Fire size (ha) Mean	Median	Range	Fire rotation (yr)
1575–2000	205	115	25–1946	16
Presettlement, 1575–1849	203	130	26–1562	13
Settlement, 1850–1904	266	102	26–1946	10
Fire suppression, 1905–2002	39	28	26–80	378
1600–1699	120	89	30–520	24
1700–1799	217	159	26–1331	10
1800–1899	300	179	26–1946	8
1900–2000	39	28	26–80	334

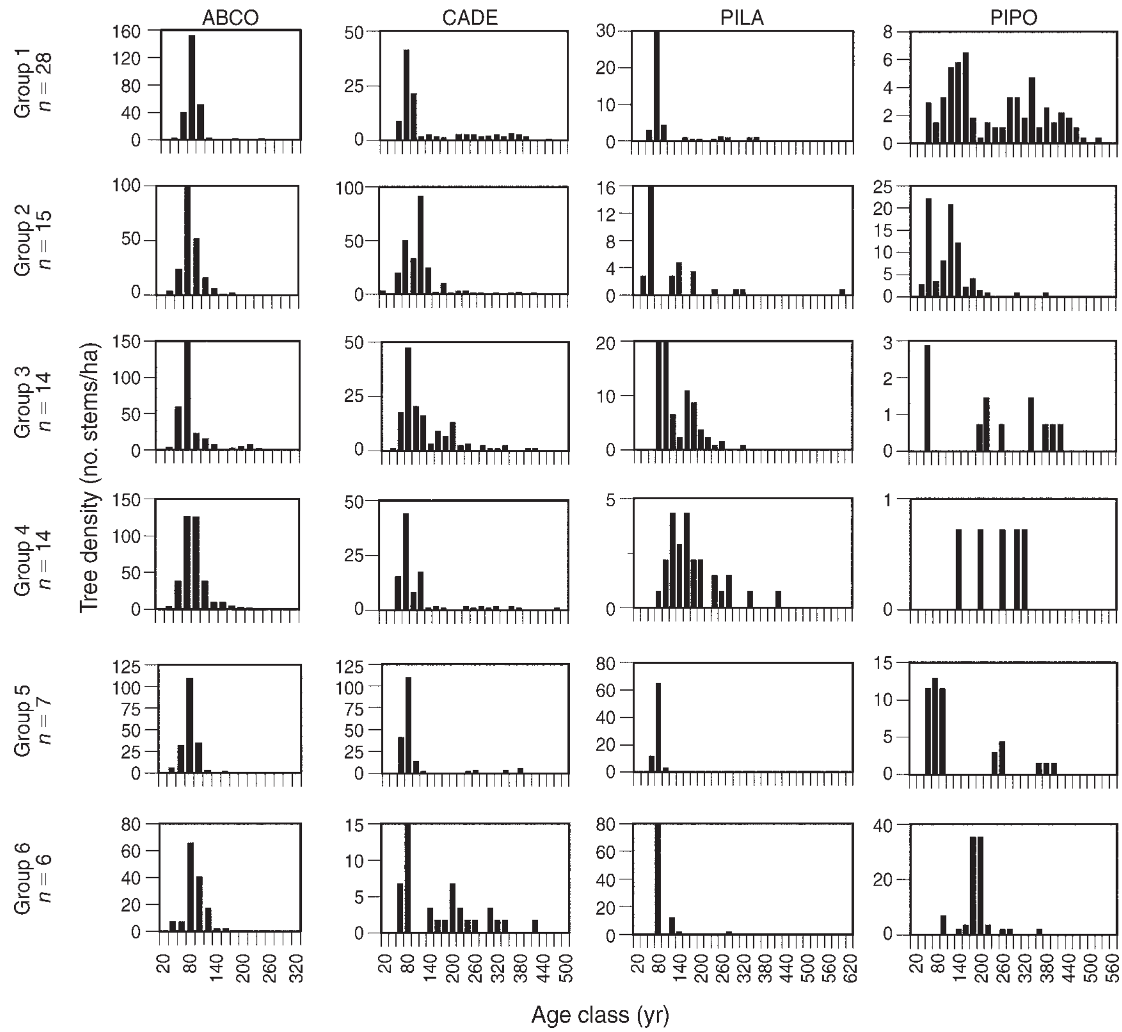

FIG. 6. Mean age class distribution for six age class groups identified by cluster analysis of stems/ha in 20-yr age classes in an old-growth mixed-conifer forest in Yosemite National Park, California; n = number of plots. Groups are plots with similar reference period age-class distributions. Stands were grouped statistically using only trees >100 years old to identify different types of forest structure prior to 1900. However, many trees established during the last 100 years because of fire suppression. Trees <100 years old trees are shown, but the groups were identified using only the older trees. See Fig. 2 for species acronyms.

TABLE 7. Mean density and number of occupied age classes for trees >100 yr old and trees of all ages in age class groups identified by cluster analysis of trees >100 yr old in a mixed-conifer forest in Yosemite National Park.

		Stem density, trees >100 yr (no. stems/ha)			All stems (no. stems/ha)			No. 20-yr age classes >100 yr		No. 20-yr age classes, all stems			
Group	N	Mean	Range	SD	Mean	Range	SD	Mean	Range	Mean	Range	Mean no. fires	No. fires per age class
1	28	92.5	20–300	57	459	90–960	236	5.5	2–10	7.9	4–12	27	4.9
2	15	257	30–680	187	622	110–1180	315	5.6	3–9	8.2	5–11	25.9	4.6
3	14	151	50–340	100	519	300–820	189	5.9	2–10	8.5	6–11	28.6	4.8
4	14	127	60–340	81	499	270–780	163	4.7	3–7	7.2	5–11	20.9	4.4
5	7	99	30–140	36	664	180–1040	353	4.4	3–6	7.4	6–10	26.7	6.1
6	6	153	90–200	46	405	220–600	161	6	4–7	7.8	5–10	11.3	1.9

Notes: Mean number of fires and number of fires per age class are given for each group. Groups are plots with similar reference period age-class distributions. For descriptions of each group see *Results: Fire regimes: Contemporary forest age structure and fire severity*.

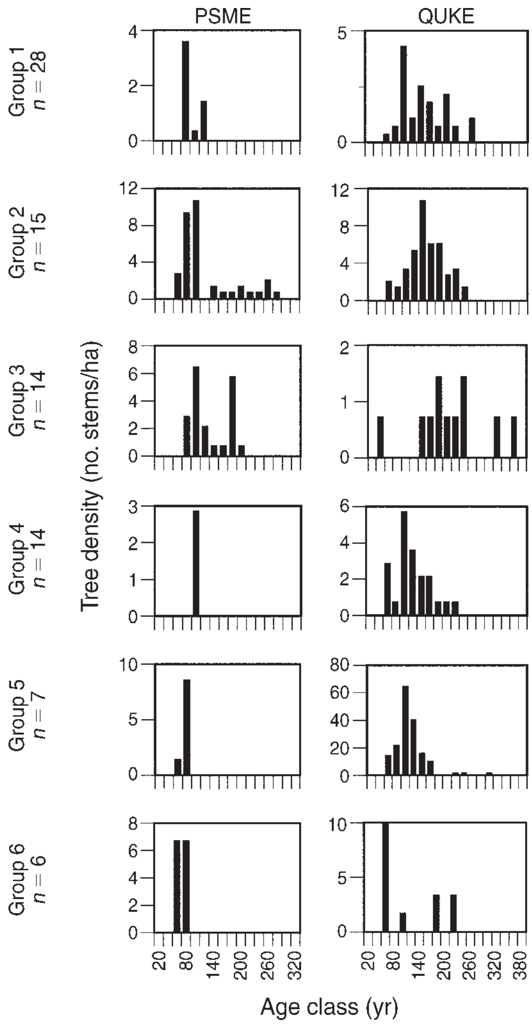

FIG. 6. Continued.

a timber survey in 1911 in the same location suggests that the reconstruction estimates are reliable. The reconstructed mean density of 86 trees/ha vs. 99 trees/ha for the survey was statistically similar suggesting a minor influence of the use of broad decay classes on estimating tree death dates and forest density. The reconstructed values for mean basal area (29.1 m^2/ha vs. 20.6 m^2/ha) and tree size (67.5 cm vs. 53.8 cm) were also statistically similar to survey values but higher. The higher values for diameter and basal area for the reconstruction may be related to greater post-1899 variability in radial growth from the massive infilling of trees in various sized gaps after the onset of fire suppression (e.g., Biondi 1999, North et al. 2007). We used a mean growth rate that included growth since 1899 from all trees that were alive in 1899 for our diameter estimates of trees that died between 1899 and 2002.

More than a century of fire suppression has altered the effects of frequent low- and moderate-severity fire on forest structure and composition and led to a large increase in forest fuels in YNP mixed-conifer forests (Keifer et al. 2006). U.S. National Park Service policy emphasizes use of prescribed fire or WFU fires to reintroduce fire as a regulating disturbance process and reduce the risk of severe fire in highly altered forests (NPS 2006). Prescribed fire is the primary tool available for managers to restore fire in the western boundary forests of YNP; WFU poses a high risk of fire spread to adjacent non-park lands (YNP 2004). Prescribed burning successfully reduces surface fuels and kills small diameter trees from crown scorch (Mutch and Parsons 1998). Surface fuels, however, recover quickly as small fire-killed trees fall to the ground, and it takes only 10 years for fuels to return to 85% of prefire levels (Keifer et al. 2006).

Prescribed fires in YNP are less intense than wildfires or WFU and kill fewer trees, leaving a more uniformly dense canopy that can carry a high intensity crown fire (van Wagtendonk and Lutz 2007). Breaking up the dense canopy of $<$100-yr-old trees with prescribed fire is a challenge. Many postfire-suppression trees have grown to a size that makes them resistant to low-severity fire (Stephenson 1999, van Wagtendonk and Lutz 2007), and injury from prescribed fire may kill more old-growth pines than burns did during the reference period (Swezy and Agee 1991). Multiple re-burns at relatively short intervals (5–10 yr) will need to be applied for a sustained period to reduce surface fuels and thin the canopy (Keeley and Stephenson 2000, Miller and Urban 2000). Canopy gaps, created by severe prescribed fire in YNP are small in size (mean = 2 ha), and most burns are low and moderate severity and create smaller gaps (van Wagtendonk and Lutz 2007). Patch sizes of similar aged trees in the reference forest (100–2000 m^2) are consistent with low-severity fire, tree regeneration in gaps created by torching of single trees or groups of several trees, and the self-limiting nature of the historical fire regime. Although more severe fire effects can restore density and basal area to reference conditions more quickly (Miller and Urban 2000, Fúle et al. 2004), there was no clear evidence of high-severity fire effects in our forest. Thus, application of high-severity prescribed fire would create novel conditions compared to fire effects over the last four hundred years.

High-severity fire in California mixed-conifer forests has increased in extent in recent decades because of the effects of climate change, particularly temperature, on burning conditions in these fuel-rich forests (Miller et al. 2009). Climate projections with increased atmospheric carbon dioxide and general circulation models predict continued warming in California into the 21st century (Hayhoe et al. 2004). Climate change heightens the risk of stand-replacing fire in these highly altered forests. Restoration of the self-limiting fuel–fire–forest structure mosaic that characterized these forests before fire suppression with prescribed fire would reduce the risk of unusual high-severity fire. By coupling explicit reference conditions with consideration of current conditions and projected future changes, management activities can be chosen that balance restoration goals and risk management. Moreover, use of prescribed fire as the restoration agent in boundary forests will connect them to interior forests where the fire regime is a mixture of WFU and wildfires. Increasing connectivity among ecosystems with a process that has influenced forest adaptation for millennia should promote the capacity for species persistence and migration under a changing climate (Millar et al. 2007).

Acknowledgments

This research was completed with assistance of many individuals. We thank K. Paintner, M. Beasley, and B. Mattos in Yosemite National Park for logistical support. An able group assisted in the field: Mike Connelly, Morgan Windram, Jamie McCrory, Mike Mirobelli, Andrew Geenwald, Amanda McCarron, Irene McKenna, Charles Bache, Laura Rogers, Kathleen Kelliher, Casey Deck, and Alejandro Guarin. We thank Rick Carr, Andrea Grove, Dave Schmidt, Valerie Trouet, and John Sakulich for assistance in the lab. C. Skinner and M. Beaty provided helpful comments on an earlier draft of this paper. This project was funded by a Joint Fire Sciences Program Grant (01-3-3-12) to A. H. Taylor and K. Paintner.

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