Fire disturbance and forest structure in old-growth mixed conifer forests in the northern Sierra Nevada, California

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Abstract

Question: This study evaluates how fire regimes influence stand structure and dynamics in old-growth mixed conifer forests across a range of environmental settings.

Location: A 2000-ha area of mixed conifer forest on the west shore of Lake Tahoe in the northern Sierra Nevada, California.

Methods: We quantified the age, size, and spatial structure of trees in 12 mixed conifer stands distributed across major topographic gradients. Fire history was reconstructed in each stand using fire scar dendrochronology. The influence of fire on stand structure was assessed by comparing the fire history with the age, size, and spatial structure of trees in a stand.

Results: There was significant variation in species composition among stands, but not in the size, age and spatial patterning of trees. Stands had multiple size and age classes with clusters of similar aged trees occurring at scales of 113 - 254 m\textsuperscript{2}. The frequency and severity of fires was also similar, and stands burned with low to moderate severity in the dormant season on average every 9 - 17 years. Most fires were not synchronized among stands except in very dry years. No fires have burned since ca. 1880.

Conclusions: Fire and forest structure interact to perpetuate similar stand characteristics across a range of environmental settings. Fire occurrence is controlled primarily by spatial variation in fuel mosaics (e.g. patterns of abundance, fuel moisture, forest structure), but regional drought synchronizes fire in some years. Fire exclusion over the last 120 years has caused compositional and structural shifts in these mixed conifer forests.

Keywords: Drought; Fire, Fire return interval; Forest structure; Lake Tahoe; Spatial autocorrelation; Stand dynamics.


Abbreviations: FRI = Fire return interval; GCW = General Creek Watershed; TRMI = Topographic Relative Moisture Index.

Introduction

The structure and dynamics of western conifer forests in North America are linked to recurring fire (Whitlock et al. 2003; Skinner & Chang 1996), and variation in fire regime characteristics are thought to promote forest structural and compositional diversity at local, landscape, and even regional scales (Romme & Knight 1981; Agee 1993; Bekker & Taylor 2001). The importance of fire as a control on the structure and dynamics of western forests, however, has changed since widespread EuroAmerican settlement in the mid-19th Century, especially in the most fire-prone forests. For example, in the mixed conifer forests of California, suppression of wildfires in combination with logging and livestock grazing have dramatically altered forest composition and structure (Vankat & Major 1978; Weatherspoon et al. 1992; Taylor 2000, 2004). These ubiquitous forest changes have limited our understanding of how spatial and temporal variability in fire regimes shaped mixed conifer forest structure and influence their dynamics (Skinner & Chang 1996; Beaty & Taylor 2001; Stephens & Collins 2004).

Prior to widespread EuroAmerican settlement, fire was the most common and widespread disturbance agent influencing the structural development of mixed conifer forests in the Sierra Nevada (Kilgore 1973; Skinner & Chang 1996). Frequent low intensity surface fires – e.g. median fire return interval (MFI) = 3 - 20 a – are thought to create a fine-grained mosaic of multi-aged stands (Kilgore & Taylor 1979; Swetnam 1993; Skinner & Chang 1996). This structure is thought to have developed as a result of self-organizing processes where burn patterns and forest structure interact to maintain the fine-grained mosaic over time (e.g. Bonnicksen & Stone 1981, 1982). Thus, fire regimes and forest structure are thought to be controlled by local, spatial processes, particularly the time it takes for fuel to accumulate so a burned patch can burn again. Yet, recent work in mixed conifer forests suggests that interactions between fire and forest structure may be more complex because fire regimes and fire effects are influenced by landscape and...
regional controls such as topography (e.g. Taylor & Skinner 1998, 2003; Taylor 2000; Beaty & Taylor 2001) or climate variability (e.g. Swetnam 1993; Miller & Urban 1999a, 2000a, 2000b). Thus, variability in the structure of mixed conifer forests may reflect the influence of landscape and regional factors rather than smaller scale self-organizing processes.

Yet, the relative importance of local vs. landscape or regional scale influences has not been evaluated in mixed conifer forests, and most retrospective studies have not been designed to address this question. Most work on mixed conifer forest structure composite data collected over wide areas, but composite data on forest structure do not provide an understanding of how fire and the temporal and spatial arrangement of age-classes develop in a particular stand. Moreover, few studies have coupled an analysis of forest age structure, including spatial pattern, with fire disturbance history in the same stand. In mixed conifer forests, our understanding of the relationship between fire and forest structure is based primarily on data (1) from giant sequoia – mixed conifer forests, an unusual variant of limited extent that occurs mainly in the southern Sierra Nevada, (2) from a narrow range of environmental settings, and (3) without records of fire disturbance and forest structure from the same sites (e.g. Bonnicksen & Stone 1981, 1982). Thus, it is unclear, if more typical mixed conifer forests have similar fire-generated structures and dynamics.

This paper examines how fire regimes influence stand structure and dynamics in an old-growth mixed conifer forest in the northern Sierra Nevada on the west shore of Lake Tahoe. The following questions are addressed:

1. How variable are fire regime parameters and stand structural characteristics in mixed conifer forests across a range of environmental settings?
2. How did past fires influence the spatial and temporal patterns of tree regeneration?

To help answer these questions, we quantified the fire history and the age, size, and spatial pattern of trees in twelve old-growth mixed conifer stands located across a range of environmental settings.

Methods

Study area

Fire regimes and forest structure were studied in a 2000 ha area of old-growth mixed conifer forest in the General Creek Watershed (GCW) on the west shore of Lake Tahoe, California (Fig. 1). General Creek drains a formerly glaciated valley and has diverse topography. Elevations range from 1850 to 3000 m and the topographic settings range from flat valley bottoms to moderately steep (ca. 20°) side slopes. 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. Mixed conifer stands in the GCW may be co-dominated by any of six species including Calocedrus decurrens, Pinus lambertiana, Pinus jeffreyi, Abies magnifica, Pinus monticola or Abies concolor (Barbour & Minnich 2000). Montane chaparral, dominated by Arctostaphylos patula, Ceanothus spp. and Quercus spp. (dwarf oaks), may occupy sites that have experienced severe fire or are too poor to support trees (Wilken 1967; Bolsinger 1989; Nagel & Taylor 2005).

Forests in the Lake Tahoe basin have been influenced by people for a long time. The Washoe, who migrated annually from the Great Basin each summer, used the lake and surrounding forests for hunting, and they used fire locally (e.g. meadows and forests near Lake Tahoe) to promote certain plants for food and fiber (Lindström 2000). EuroAmericans first settled in the Lake Tahoe basin in large numbers in the 1860s when silver was discovered in nearby Virginia City, Nevada. Beginning in the 1870s, nearly 70% of the Lake Tahoe watershed was logged to provide fuel wood for silver mining (Elliot-Fisk et al. 1996). Most forest in the basin is second growth and is about 120 years old (Lindström 2000; Taylor 2004). The GCW became part of the California State Park System in 1965, and there has been an active prescribed burning program in the park since the 1980s. None of the stands chosen for this study were logged or
burned with prescribed fire.

Field sampling and sample processing

Old-growth mixed conifer stands were selected for sampling based on several factors, including: (1) presence of large diameter (>1.0 m diameter at breast height [DBH]) stems ≥ 250 a old; (2) homogeneity of stand conditions; (3) sampled stands included the range of variation in old-growth mixed conifer forest structure and composition in the watershed; (4) a range of topographic settings; and (5) the presence of fire scarred trees in or near each stand. Stands meeting these criteria (n = 12) were selected for sampling (Fig. 1; Table 1).

Forests were sampled in 0.5 ha (50 m × 100 m) plots, except for two plots which were larger (0.7 ha, 70 m × 100 m) because of low stand density. The location (UTM coordinates with a GPS), elevation, slope aspect, slope pitch, slope configuration, and topographic position of each plot were recorded. The last four variables were used to calculate each plot’s Topographic Relative Moisture Index (TRMI; Parker 1982) a measure of site moisture conditions that varies from 0 (xeric) to 60 (mesic).

Fire history

The history of fire (i.e. dates, return interval, extent, season) in each of the 12 plots was reconstructed from fire scars preserved in the annual growth rings of live and dead pines (n = 34) collected in or adjacent to (≤ 100 m) each plot. Partial cross-sections were removed with a chainsaw (Arno & Sneck 1977) and sample locations were identified with a GPS and plotted on a 1:24 000 topographic map. Fire dates in the cross-sections were identified by first sanding wood samples to a high polish and then cross-dating (Stokes & Smiley 1968) the tree rings in each sample. The calendar year of each tree-ring with a fire scar lesion in it was then recorded as the fire date.

The season each fire burned was inferred from the position of the fire scar within the annual growth ring (e.g. Baisan & Swetnam 1990). Scar positions were classified as either growing season (i.e., occurring in early- or late-wood) or dormant season (i.e., occurring at the ring boundary). In the northern Sierra Nevada, the growing season is between May and August, and dormant season fires represent fires that burn in late summer or fall after trees stop growing for the year (e.g. Caprio & Swetnam 1995).

Spatial and temporal variation in the frequency and extent of fire based on the fire history data was evaluated using standard statistical (i.e., S-Plus) and specialized fire history software (i.e., FHX2, Grissino-Mayer 2001). Fire return interval (FRI) statistics were computed for both composite and point fire chronologies at each site.

Differences in FRI statistics and the shape of the FRI distributions among stands were assessed with distribution free statistical tests (e.g. Kruskal-Wallis H test, Kolmogorov-Smirnov two-sample tests; Sokal & Rohlf 1995). The number of plots burned in a given year was used as an indirect measure of fire extent. Landscape scale FRI statistics were calculated from CFRIs from each plot for years with: (1) small fires (one or more plots burned), (2) intermediate fires (five or more plots burned), and (3) widespread fires (eight or more plots burned).

Temporal changes in fire regimes in the study area that may be related to land use change were identified by comparing fire frequency during the pre-settlement (1700 - 1850), settlement (1850 -1900), and fire suppression (1900 - 2000) periods using a composite of all the fire scar samples. A composite fire chronology was used for the temporal analysis because they are considered to be more sensitive than individual samples to changes in the temporal pattern of burning related to land use change (Dieterich 1980).

Forest structure and composition

Forest structure and composition were determined by measuring and mapping stems within a 10 m x 10 m grid in each plot. Stem locations in a cell were determined by measuring the distance (x, y) of all live and standing dead trees (≥ 5.0 cm DBH), live saplings (stems ≥1.4 m tall < 5.0 cm DBH), and live seedlings (0.5 - 1.4 m tall) from the origin (0, 0) of each cell with a measuring tape. The species, diameter at breast height (DBH), height class (i.e. suppressed, intermediate, co-dominant, dominant) and condition (live or dead) of each tree was
then recorded. The location (x, y), diameter, height class, and species of logs ≥ 5 cm rooted in each cell were also recorded. Standing dead trees and logs were visually classified as either pre- or post-fire suppression recruits based on diameter, species, bark morphology, and level of decomposition.

Variation in species composition among the twelve plots was identified by ordinating the basal area of species in each plot with principal components analysis (PCA; Gauch 1982). Compositional gradients were then identified by correlating PCA axis scores and species’ basal area values using Pearson’s correlation coefficient (Sokol & Rohlf 1995). Topographic factors underlying the compositional gradients were also identified by correlating basal areas with topographic data collected at each site. Finally, fire regime parameters for each plot were correlated with PCA axis scores to identify whether fire regime parameters varied with species composition.

Tree age structure in each plot was determined by coring all trees to the pith at 30 cm above the soil surface in randomly selected 10 m × 10 m cells until ≥ 20% of all trees had been cored. Then, all trees > 40 cm DBH in each plot were cored to ensure that all stems that established prior to the last fire were included in the sample. This cutoff was selected based on diameter – age relationships identified from preliminary sampling of tree ages across a range of size classes and was used to reduce redundant sampling of fast growing Abies concolor that established after fire suppression. The cores were cross-dated (Stokes & Smiley 1968) and the year of the innermost tree ring in each core was used as the estimate of tree age. Some cores did not reach the pith (9.8%) because of heart-rot or their radius exceeded the length of increment borers. The amount of missing growth was estimated using DBH - radius regression equations for each species which were all highly significant (r² = 0.80 – 0.88; P < 0.001). The number of years added to incomplete cores was the product of the average annual radial growth/year of the innermost portion of the intact core and the estimated missing distance to the pith.

In order to identify differences in age structures among stands, we compared the age-class distributions of each plot using Kolmogorov-Smirnov two sample tests (Sokol & Rolf 1995) and calculated the percentage of stands with similar and different tree age distributions. We also calculated the mean number of stems > 100 a old and counted the number of occupied 20-a age classes in a given plot. This analysis also provides evidence of past fire severity as stands experiencing high severity fire would have fewer ages classes than those that experience low and intermediate severity burns (Agee 1993).

To identify the influence of past fires on the spatial and temporal patterns of tree regeneration, we identified the type, scale, and intensity of the spatial pattern of tree ages using statistical tests of spatial autocorrelation. For each plot, we evaluated the spatial characteristics of the ages of large diameter (> 40 cm DBH) trees using Moran’s I (Moran 1948, Cliff & Ord 1973). Moran’s I is a weighted correlation coefficient that detects departures from spatial randomness. Positive values of Moran’s I indicate that trees with similar ages occur close together whereas negative values indicate that trees with similar ages are separate from each other. Values of Moran’s I were calculated for successive 3-m distance classes up to 24 m to identify the scale of spatial autocorrelation; significance was identified using two tailed tests (Upton & Fingleton 1985). The frequency of significant Moran’s I values for each distance class was then summarized for all plots. Finally, the ages of large trees (> 40 cm DBH) were mapped to visually interpret and confirm the spatial autocorrelation analysis.

**Results**

**Forest compositional patterns**

Species dominance in the 12 plots varied with environmental settings. PCA of species basal area separated stands along two compositional gradients (Fig. 2). Abies magnifica and Pinus monticola were positively correlated (P < 0.01) and A. concolor, Calocedrus decurrens, and P. jeffreyi were negatively correlated with PCA axis 1 (P < 0.05; Table 2). Axis 1 was positively correlated (P < 0.01) with slope aspect (expressed in linear form from south (low values) to north (high values)) and negatively correlated (P < 0.01) with slope configuration (expressed in linear form from convex (low values) to concave (high values)). PCA axis 2 separated plots dominated by P. jeffreyi (positive correlation but not significant P > 0.05) from mixed stands with abundant C. decurrens, P. lambertiana and P. contorta (negative correlation P < 0.05; Fig. 2; Table 2). PCA Axis 2 scores were not significantly correlated with any of the environmental variables (Table 2). Composite mean and median FRIs were positively correlated (P < 0.05) with PCA axis 1 indicating a shortening of the period between fires in mixed stands on south slopes (Table 2).
Table 2. Pearson correlation coefficients of species basal area, topography and fire history with PCA axis scores of an ordination of species basal area in 12 plots of old-growth mixed conifer forests in the Lake Tahoe Basin (* p < 0.05, ** p < 0.01) Slope aspect and configuration were transformed into linear values (see Parker 1982).

<table>
<thead>
<tr>
<th>Species composition</th>
<th>Axis 1</th>
<th>Axis 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Abies concolor</td>
<td>-0.62 *</td>
<td>-0.17</td>
</tr>
<tr>
<td>Abies magnifica</td>
<td>0.78 **</td>
<td>-0.25</td>
</tr>
<tr>
<td>Calocedrus decurrens</td>
<td>-0.52 *</td>
<td>-0.43</td>
</tr>
<tr>
<td>Pinus contorta</td>
<td>-0.16</td>
<td>-0.52 *</td>
</tr>
<tr>
<td>Pinus jeffreyi</td>
<td>-0.72 **</td>
<td>0.44</td>
</tr>
<tr>
<td>Pinus lambertiana</td>
<td>-0.35</td>
<td>-0.76 **</td>
</tr>
<tr>
<td>Pinus monticola</td>
<td>0.68 **</td>
<td>-0.26</td>
</tr>
</tbody>
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<table>
<thead>
<tr>
<th>Topography</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Elevation</td>
<td>-0.41</td>
<td>0.09</td>
</tr>
<tr>
<td>Slope aspect</td>
<td>0.72 **</td>
<td>-0.33</td>
</tr>
<tr>
<td>Slope steepness</td>
<td>0.18</td>
<td>0.12</td>
</tr>
<tr>
<td>Slope position</td>
<td>0.04</td>
<td>-0.11</td>
</tr>
<tr>
<td>Slope configuration</td>
<td>-0.73 **</td>
<td>-0.22</td>
</tr>
<tr>
<td>TRMI</td>
<td>0.33</td>
<td>-0.24</td>
</tr>
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</table>

<table>
<thead>
<tr>
<th>Fire history</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of fires</td>
<td>-0.38</td>
<td>-0.20</td>
</tr>
<tr>
<td>Mean point fire return interval</td>
<td>0.33</td>
<td>-0.01</td>
</tr>
<tr>
<td>Median point fire return interval</td>
<td>0.28</td>
<td>-0.05</td>
</tr>
<tr>
<td>Mean composite fire return interval</td>
<td>0.48 *</td>
<td>-0.10</td>
</tr>
<tr>
<td>Median composite fire return interval</td>
<td>0.55 *</td>
<td>-0.10</td>
</tr>
</tbody>
</table>

Table 3. Basal area (m²·ha⁻¹) and density (stems/ha) of live trees > 5.0 cm DBH in 12 plots of old-growth mixed conifer forest in the Lake Tahoe Basin, California.

<table>
<thead>
<tr>
<th>Plot</th>
<th>Abies concolor</th>
<th>Abies magnifica</th>
<th>Calocedrus decurrens</th>
<th>Pinus contorta</th>
<th>Pinus jeffreyi</th>
<th>Pinus lambertiana</th>
<th>Pinus monticola</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>GCW-1</td>
<td>32.7</td>
<td>0.7</td>
<td>29.2</td>
<td>24.5</td>
<td>9.8</td>
<td>7.0</td>
<td>30.9</td>
<td>57.8</td>
</tr>
<tr>
<td>GCW-2</td>
<td>24.2</td>
<td>3.6</td>
<td>10.2</td>
<td>21.3</td>
<td>9.8</td>
<td>7.0</td>
<td>30.9</td>
<td>74.8</td>
</tr>
<tr>
<td>GCW-3</td>
<td>10.5</td>
<td>0.0</td>
<td>0.1</td>
<td>26.5</td>
<td>9.8</td>
<td>7.0</td>
<td>30.9</td>
<td>34.0</td>
</tr>
<tr>
<td>GCW-4</td>
<td>7.5</td>
<td>54.9</td>
<td>21.2</td>
<td>20.8</td>
<td>9.8</td>
<td>7.0</td>
<td>30.9</td>
<td>114.3</td>
</tr>
<tr>
<td>GCW-5</td>
<td>4.5</td>
<td>28.4</td>
<td>0.2</td>
<td>14.1</td>
<td>9.8</td>
<td>7.0</td>
<td>30.9</td>
<td>50.2</td>
</tr>
<tr>
<td>GCW-6</td>
<td>41.2</td>
<td>0.1</td>
<td>10.2</td>
<td>46.1</td>
<td>9.8</td>
<td>7.0</td>
<td>30.9</td>
<td>107.9</td>
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<tr>
<td>GCW-7</td>
<td>60.7</td>
<td>12.0</td>
<td>6.8</td>
<td>22.1</td>
<td>9.8</td>
<td>7.0</td>
<td>30.9</td>
<td>68.5</td>
</tr>
<tr>
<td>GCW-8</td>
<td>46.4</td>
<td>24.2</td>
<td>1.2</td>
<td>4.5</td>
<td>9.8</td>
<td>7.0</td>
<td>30.9</td>
<td>68.4</td>
</tr>
<tr>
<td>GCW-9</td>
<td>13.1</td>
<td>0.7</td>
<td>2.1</td>
<td>9.3</td>
<td>9.8</td>
<td>7.0</td>
<td>30.9</td>
<td>25.2</td>
</tr>
<tr>
<td>GCW-10</td>
<td>26.4</td>
<td>12.0</td>
<td>6.8</td>
<td>6.8</td>
<td>9.8</td>
<td>7.0</td>
<td>30.9</td>
<td>54.7</td>
</tr>
<tr>
<td>GCW-11</td>
<td>29.5</td>
<td>8.7</td>
<td>20.2</td>
<td>17.9</td>
<td>9.8</td>
<td>7.0</td>
<td>30.9</td>
<td>62.3</td>
</tr>
<tr>
<td>Mean</td>
<td>29.5</td>
<td>8.7</td>
<td>20.2</td>
<td>17.9</td>
<td>9.8</td>
<td>7.0</td>
<td>30.9</td>
<td>62.3</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Density (stems/ha)</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>GCW-1</td>
<td>966</td>
<td>20</td>
</tr>
<tr>
<td>GCW-2</td>
<td>454</td>
<td>29</td>
</tr>
<tr>
<td>GCW-3</td>
<td>96</td>
<td>29</td>
</tr>
<tr>
<td>GCW-4</td>
<td>132</td>
<td>2</td>
</tr>
<tr>
<td>GCW-5</td>
<td>1072</td>
<td>64</td>
</tr>
<tr>
<td>GCW-6</td>
<td>120</td>
<td>184</td>
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<tr>
<td>GCW-7</td>
<td>740</td>
<td>2</td>
</tr>
<tr>
<td>GCW-8</td>
<td>366</td>
<td>2</td>
</tr>
<tr>
<td>GCW-9</td>
<td>824</td>
<td>78</td>
</tr>
<tr>
<td>GCW-10</td>
<td>506</td>
<td>430</td>
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<tr>
<td>GCW-11</td>
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<td>14</td>
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<tr>
<td>GCW-12</td>
<td>226</td>
<td>90</td>
</tr>
<tr>
<td>Mean</td>
<td>468</td>
<td>96</td>
</tr>
</tbody>
</table>
Forest structure

Live tree density and basal area in the plots averaged 616 stems/ha and 62.3 m²·ha⁻¹, respectively. However, both of these stand characteristics varied among species and plots (Table 3), except for Abies concolor. A. concolor density was at least five-fold greater than any other species. Comparisons of the age and size distributions of each plot to every other plot (n = 66) indicated that, overall, trees had similar size and age structures (74% of comparisons, Kolmogorov-Smirnov two sample tests, P > 0.05). However, the form of the age and size distributions varied by species (Fig. 3). A. concolor and A. magnifica had reverse-

of old trees (> 200 a old). In all plots, there was a large pulse of A. concolor establishment that began about 120 a ago (Fig. 3). Calocedrus decurrens and Pinus jeffreyi were present in a wide range of size and age classes, including stems >155 cm DBH and > 400 a old. Most P. jeffreyi and C. decurrens were > 100 a old, suggesting continuous but low recruitment at least until recently. Pinus lambertiana and P. monticola were present at low densities across a range of size and age classes. Dead trees were abundant and on average, comprised 20% of standing trees. Of the dead stems, far more were A. concolor (60%) than P. jeffreyi (18%), C. decurrens (2%), or A. magnifica (2%).

Table 4. Spatial autocorrelation of tree ages of stems > 40 cm DBH calculated using Moran’s I for old-growth mixed conifer forests in the Lake Tahoe Basin, California. Data are the number of plots (n = 12) exhibiting significant (P < 0.05) spatial autocorrelation at a given scale.

<table>
<thead>
<tr>
<th>Distance class (radius, m)</th>
<th>3</th>
<th>6</th>
<th>9</th>
<th>12</th>
<th>15</th>
<th>18</th>
<th>21</th>
<th>24</th>
</tr>
</thead>
<tbody>
<tr>
<td>Positive autocorrelation</td>
<td>2</td>
<td>5</td>
<td>8</td>
<td>5</td>
<td>3</td>
<td>3</td>
<td>3</td>
<td>2</td>
</tr>
<tr>
<td>Negative autocorrelation</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>3</td>
</tr>
</tbody>
</table>
Forest spatial patterns

The spatial pattern of large tree (> 40 cm DBH) ages were similar in the 12 plots (Table 4). In most stands (83%), there was a pattern of positive spatial autocorrelation ($P < 0.05$) at distance classes of 6-12 m; three plots (GCW-2, 4, 10) also exhibited negative spatial autocorrelation ($P < 0.05$) at a distance class of 24 m. This indicates that large trees occur in small groups of similarly aged trees with some overlap in tree ages among groups of trees. This pattern is confirmed on three representative stem maps from the plots (Fig. 4).

Fire history

Fire record

A total of 34 fire scarred wood samples were collected in the 12 plots. The average fire record length for a given plot was 189 a (range, 101 - 277 a), and all stands last burned in the mid to late 19th century (Table 5).

Fire return intervals

The median composite FRI for all plots was 3 a (range 1 - 20 a), and median composite FRIs for individual plots ranged from 7.5 to 17 a (Table 5). Mean point FRIs were longer and ranged from 10 to 43 a (Table 5). The 12 plots had similar mean and median composite FRI (Kruskal-Wallis $H$-test, $P > 0.05$) except for GCW-11, which had a longer mean FRI (Kruskal-Wallis $H$-test, $P < 0.05$). The plots also had similar fire interval distributions (Kolmogorov-Smirnoff test, $P > 0.05$) except for GCW-11.

Table 5. Fire return interval (FRI, yr) statistics and forest structural characteristics in 12 stands of old-growth mixed conifer forests, Lake Tahoe Basin, California. There were no differences in mean composite FRI among stands ($p > 0.05$, Kruskal-Wallis $H$-Test).
Fire season

The position of fire scars within annual growth rings was determined for 50% of the 279 scars. Scars were mainly (75.2%) at ring boundaries (dormant season) but scars were present in early-wood (10.6%) and late-wood (14.2%) indicating that some fires burned during the growing season.

Fire extent

Fire frequency and extent were inversely related over the period of record (Fig. 5). The median FRI for widespread fires was 32 a (range 13-36 a) which was longer than the median for intermediate (median = 13.5 a, range 7-23 a) or local fires (median = 3 a, range 1-9 a).

Temporal changes

Mean composite FRIs did not vary between the pre-EuroAmerican (1700-1849; \( n = 39 \); MFI = 3.7 a) and EuroAmerican settlement (1850-1900; \( n = 14 \); MFI = 3.0 a) periods (\( t \)-test, \( P > 0.05 \)). However, no fires burned in the sampled stands during the fire suppression period (1900-2000).

Forest age structure and fire regimes

The age structure and temporal patterns of regeneration in the plots was similar. All possible comparisons of tree age-class distributions indicate that most species and plots had a similar age structure (mean = 74%; range 9–100%; Kolmogorov-Smirnov test, \( P > 0.05 \)). Moreover, trees occupied a large numbers of 20-a age classes and on average there was 14 (range 6-23) occupied age-classes for all stems, and 11 (range 3-15) occupied age-classes for stems > 100 a old (Table 5). There were no large age-class peaks in any of the plots, or across plots, that were coincident with fire dates.

Discussion

Variation in stand structure and fire regimes

Our first research question was how variable were fire regimes and stand structure across a range of environmental settings? There was considerable variation in species composition across sites related to local topographic conditions. Species composition varied from mainly pine-dominated stands on south facing slopes to \( A. \ magnifica \) dominated stands on north aspects. \( P. \ jeffreyi \), and especially \( P. \ contorta \), occupied harsh valley bottom sites that experience cold air drainage (e.g. Parker 1986). The species-environment associations in GCW are consistent with those of other mixed conifer forests in the Sierra Nevada (e.g. Vankat 1982; Beaty & Taylor 2001).

Although our mixed conifer stands were compositionally variable they had similar structural characteristics (i.e., size, age, spatial pattern). While we found significant variation in stand density and basal area, values among stands overlapped and there are broadly similar reported values in other California mixed conifer forests (e.g. Bonnicksen & Stone 1981, 1982; Taylor 2000; Beaty & Taylor 2001; Taylor & Skinner 2003; North et al. 2004). Despite this variation, the stand age and size structure were similar among stands. All stands had populations of trees that occupied a wide range of size and age classes and they had abundant populations of young \( A. \ concolor \) that established after the last fire in the 19th century. A mixed species overstory of large diameter older trees and abundant young \( A. \ concolor \) in the understory and mid-canopy is characteristic of mixed conifer forests that have experienced a century or more of fire exclusion (e.g. Bonnicksen & Stone 1981, 1982; Taylor 2000; Beaty & Taylor 2001; Taylor & Skinner 2003; North et al. 2004).

The spatial patterning of trees was similar among stands despite variation in composition and environmen-
Fire influences on spatial and temporal patterns of tree regeneration

The patterns described above inform the second question addressed in this study: how do patterns of fire effects influence the spatial and temporal patterns of tree regeneration? Prior to EuroAmerican settlement, frequent surface fires influenced old-growth stand structure by killing mainly seedlings, saplings, and small diameter trees while leaving most thick-barked, large diameter trees intact. This pattern of burning promoted open stand conditions in a wide range of size- and age-classes. This suggests that tree regeneration was temporally intermittent with spatial overlap among regeneration patches, a pattern that has been alluded to in other mixed conifer forests (e.g. Taylor & Skinner 2003; Norman 2002; North et al. 2005).

The spatial autocorrelation of tree ages suggests that successful recruitment into the canopy often occurs in small patches (113-254 m²). These patch sizes are similar to sapling patch sizes in mixed conifer forests in northern Mexico that have not experienced fire suppression (Stephens & Fry 2005). Thus, the multi-age structure of these forests is an aggregation of small overlapping even-aged patches.

The temporal and spatial pattern of tree establishment may be related to variation in both local patterns of fire severity and the length of fire free periods. The spatial autocorrelation of tree ages suggests that openings, such as those caused by death of a canopy tree by torching, are locations where trees establish. Subsequent survival of established trees in a burn patch may then be dependent on the length of time before the patch burns again (Brown & Wu 2006). Once the trees mature their relatively thick bark make them more resistant to fire than thin-barked seedlings or saplings (Agee 1993). Infilling would be inhibited by fire soon after seedlings established. Given the patchy nature of fires and the longevity (e.g. > 350 a) of trees, periods with less fire and higher tree establishment may result in structural attributes that persist for decades or even centuries (Savage et al. 1996). Finally, there was little evidence that widespread fires were more severe than smaller burns. For example, there were no strong peaks in the age-class distribution of stands associated with widespread fire years.
Conclusions

Fire and forest structure interact in mixed conifer forests to create and perpetuate similar stand characteristics across a range of environmental settings.

This suggests that, at the stand scale, fire occurrence is controlled primarily by spatial variation in fuel mosaics (e.g. patterns of abundance, fuel moisture, forest structure). Regional climate variation (i.e. drought) appears to synchronize fires among stands in some years and this may also influence stand structure. Yet, there were no strong peaks in the age-class distribution of stands that corresponded with years of more widespread burning. Moreover, tree establishment in mixed conifer forests may be more synchronized by variation in precipitation and other climatic conditions associated with El Niño than with surface fires (North et al. 2005). Thus, the composition, structure and dynamics of mixed conifer forests are influenced by both local processes that shape the nature of patch development and large scale climate variation. However, the dominant influence on forest composition and structure over the last 120 years has been fire exclusion, and this may have reduced the resilience of these forests to future fire by increasing live and dead fuels, their susceptibility to drought and insect induced mortality (Garin & Taylor 2005) and the risk of high severity fire.

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