Twentieth-century decline of large-diameter trees in Yosemite National Park, California, USA

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ABSTRACT

Studies of forest change in western North America often focus on increased densities of small-diameter trees rather than on changes in the large tree component. Large trees generally have lower rates of mortality than small trees and are more resilient to climate change, but these assumptions have rarely been examined in long-term studies. We combined data from 655 historical (1932–1936) and 210 modern (1988–1999) vegetation plots to examine changes in density of large-diameter trees in Yosemite National Park (3027 km^2). We tested the assumption of stability for large-diameter trees, as both individual species and communities of large-diameter trees. Between the 1930s and 1990s, large-diameter tree density in Yosemite declined 24%. Although the decrease was apparent in all forest types, declines were greatest in subalpine and upper montane forests (57.0% of park area), and least in lower montane forests (15.3% of park area). Large-diameter tree densities of 11 species declined while only 3 species increased. Four general patterns emerged: (1) *Pinus albicaulis*, *Quercus chrysolepis*, and *Quercus kelloggii* had increases in density of large-diameter trees occur throughout their ranges; (2) *Pinus jeffreyi*, *Pinus lambertiana*, and *Pinus ponderosa*, had disproportionately larger decreases in large-diameter tree densities in lower-elevation portions of their ranges; (3) *Abies concolor* and *Pinus contorta*, had approximately uniform decreases in large-diameter trees throughout their elevational ranges; and (4) *Abies magnifica*, *Calocedrus decurrens*, *Juniperus occidentalis*, *Pinus monticola*, *Pseudotsuga menziesii*, and *Tsuga mertensiana* displayed little or no change in large-diameter tree densities. In *Pinus ponderosa–Calocedrus decurrens* forests, modern large-diameter tree densities were equivalent whether or not plots had burned since 1936. However, in unburned plots, the large-diameter trees were predominantly *A. concolor*, *C. decurrens*, and *Q. chrysolepis*, whereas *P. ponderosa* dominated the large-diameter component of burned plots. Densities of large-diameter *P. ponderosa* were 8.1 trees ha^{-1} in plots that had experienced fire, but only 0.5 trees ha^{-1} in plots that remained unburned.

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1. Introduction

Large-diameter trees are important forest constituents. Although young trees on productive sites can grow quickly, large diameters are usually associated with greater ages and structural features distinctly different from younger trees (Van Pelt and Sillett, 2008, Fig. 1). Their complex morphology creates habitat for a wide range of organisms including epiphytes (Sillett and Van Pelt, 2007) and understory plants as well as vertebrates (Thomas, 1979; Nadkarni and Matelson, 1989; Meyer et al., 2005). The structure of forest vegetation, particularly its size and complexity, contributes to trophic relationships that in turn further influence the composition of vegetation and animal communities (Pringle et al., 2007; Palmer et al., 2008). Large-diameter trees moderate the local environment (Rambo and North, 2009); serve as a seed source for the surrounding landscape (Keeton and Franklin, 2005); and withstand fires, climate variation, and insect outbreaks that kill or weaken smaller-diameter trees (Hurteau and North, 2009). Large-diameter trees also constitute the source of large snags and logs used by many animal species (Harmon and Hua, 1991; Franklin et al., 2002). Even though large-diameter trees constitute a small proportion of the trees in the forest, they disproportionately influence forest communities for centuries.

The complete developmental sequence of forests containing large-diameter trees is long—generally 200 or more years of growth, punctuated by fire, insect outbreaks, and pathogens before they reach an old-forest condition (Van Pelt, 2007, 2008). Once trees attain great size, changes in morphology occur slowly. Trees

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Fig. 1. An *Abies magnifica* grove of large-diameter trees, snags, logs, and regeneration (2007 composite photo stitched from five originals, J.A. Lutz).

attaining large diameters do so because of interactions among genetics, site productivity, site water availability, existing community structure, weather, and fire regime (Barbour et al., 2002; Stephenson and van Mantgem, 2005; Beaty and Taylor, 2007; Larson et al., 2008). Accordingly, changing fire regimes can, over time, alter older forests (Tomback et al., 2001; Beaty and Taylor, 2007; Fellows and Goulden, 2008).

The densities of large-diameter trees reflect the climate when those trees became established, the present climate, and the nature of climate variation over the lifespan of those trees (Swetnam, 1993; Stine, 1996; Gavin and Brubaker, 1999), as well as the effects of the various agents of mortality. Water availability to plants at a site – an important limiting factor due to the prolonged summer dry season – represents a combination of water supply, water storage capacity, and water demand. Increasing forest densities and warming climate both increase water stress and this can increase tree mortality (van Mantgem and Stephenson, 2007; Ritchie et al., 2008).

Structural change in Sierra Nevada forests can be inferred from several lines of evidence. More open forest conditions and abundant large-diameter trees are evident in repeat photographs (Vale and Vale, 1994; Gruell, 2001) and historical descriptions (Muir, 1911). Compared to the pre-settlement era, Scholl (2007) found that densities of small-diameter trees in unburned forests of Yosemite have increased several-fold, and Vankat and Major (1978) found changes in species cover and density in Sequoia National Park. Using large numbers of historical and modern plots on national forests, Bouldin (1999) found decreases in large-diameter trees, although logging could have contributed to this decline (Barbour et al., 2002).

The decline in numbers of large-diameter trees as a result of timber harvesting is well known (Thomas et al., 2006). However, despite the importance of large trees to ecosystem function and amenity values, their long-term, landscape-scale changes in distribution and abundance of large-diameter trees have received little study, perhaps because the slow changes in older forests lead to an assumption that large trees are resilient to changes in environmental conditions. We compared data from the first comprehensive survey of Yosemite forests made in the 1930s with modern data to test the assumption of stability of large-diameter tree populations by characterizing changes in large-diameter tree density among forest types and for the principal constituent tree species. We sought to identify which portions of species ranges exhibited greater changes in the large-diameter tree component, and whether fire history was an important determinate of large-diameter community stability.

2. Methods

2.1. Study area: physical environment

Yosemite National Park is a contiguous management unit of 3027 km^2 located in the central Sierra Nevada (latitude 37.7°N, longitude 119.7°W); it has been in protected status since 1890 (Russell, 1992). Yosemite's large area, reserved status, and relatively low levels of anthropogenic disturbance make it an ideal location for studying long-term changes in temperate forests. Elevation ranges from 657 m to 3997 m and, although mean elevation rises gradually from the west to the crest of the Sierra Nevada in the east, local relief can be extreme. Soils are primarily granitic in origin, and soil water-holding capacity across the study area averages 9.1 cm (minimum 3.2 cm in shallow or rocky soils; maximum 34.2 cm in soils 200 cm deep) (NRCS, 2007; Lutz, 2008).

Yosemite's climate is Mediterranean, with substantial elevational gradients in temperature and precipitation due to the 3340 m of vertical relief. January mean minimum and maximum temperatures are −14 °C to −2 °C at higher elevations (>3900 m) and 1 °C to 14 °C at lower elevations (<700 m). July mean minimum and maximum temperatures are 2–13 °C at higher elevations and 16–35 °C at lower elevations. Annual precipitation ranges from 804 mm in lower elevations and in rain shadows to 1722 mm (average 1214 mm) at higher elevations, with most precipitation throughout the park falling in the winter as snow. Less than 3% of annual precipitation falls between June and August; consequently most moisture eventually made available to plants comes from the spring snowpack as mediated by the variation in soil water storage (PRISM, 2007; Daly et al., 2008; Lutz, 2008).

2.2. Study area: vegetation

The forest vegetation of Yosemite National Park comprises a mosaic of forest types, species, and structural stages (Franklin and Fites-Kaufman, 1996; Fites-Kaufman et al., 2007). Vegetation types include: subalpine coniferous forest, upper montane coniferous forest, lower montane coniferous forests, broadleaved upland forests, broadleaved woodlands, scrub and chaparral, and grassland, meadow and herb communities. Vegetation covers ∼84% of the park, with the remainder classified as barren areas, which are predominantly sparsely vegetated (<20% cover) with isolated trees or tree islands. Forest zones generally follow gradients of elevation and water availability (Parker, 1982; Vankat, 1982; Stephenson, 1998). The forests of Yosemite National Park are broadly representative of the Sierra Nevada and include forest types dominated by: *Pinus ponderosa*, *Pinus ponderosa–Calocedrus decurrens*, *Abies concolor–Pinus lambertiana*, *Pinus monticola–Pinus jeffreyi*, *Abies magnifica*, *Pinus contorta*, and *Pinus albicaulis–Tsuga mertensiana* (Parker, 1982, 1984a,b, 1986, 1988; Royce and Barbour, 2001; Fites-Kaufman et al., 2007).

Fire has a strong influence on the distribution, age structure, and abundance of Yosemite tree species. Yosemite forests burn with a mixture of severities and with median fire return intervals of 4–187 years (Agee, 1998; van Wagtendonk et al., 2002; Sugihara et al., 2006). A policy of total fire suppression began in 1892 and continued until the early 1970s (van Wagtendonk, 2007). Although park managers have allowed lightning fires to burn under prescribed conditions since 1972, much of the park has remained unburned for many multiples of the median pre-settlement fire return interval (Kilgore and Taylor, 1979; Swetnam, 1993; van

Wagtendonk et al., 2002). Over a hundred years of fire exclusion have allowed some forest communities to develop a "fire debt," an uncharacteristic species composition, structure, patchiness, and fuel loading (Vale and Vale, 1994; van Wagtendonk and Lutz, 2007). Modern vegetation thus reflects a combination of the characteristic vegetation and the effects of fire suppression.

The park has experienced little recent anthropogenic disturbance, but Native American influences (Parker, 2002) were followed by considerable ecosystem modification in the late-19th and early 20th centuries. Logging occurred in lower-elevation western portions of the park between 1913 and 1926. Sheep grazing (Muir, 1911) and the attendant fires set by sheepherders decreased small-diameter tree densities below their pre-settlement conditions (Stephens and Elliott-Fisk, 1998). However, the period of fire exclusion in the 20th century has allowed tree densities and fuel accumulation to rise above pre-settlement levels (Stephens and Collins, 2004; Scholl, 2007).

2.3. Plot data

The earliest comprehensive vegetation data for Yosemite National Park were collected in surveys organized by Albert E. Wieslander between 1932 and 1936 (Wieslander et al., 1933; Coffman, 1934; Wieslander, 1935; Keeler-Wolf, 2007). Wieslander crews mapped continuous areas of forest cover throughout California and included vegetation plots in representative areas of all types of forest cover. Field crew instructions (Wieslander et al., 1933) emphasized the need to select representative plots:

Sample plots should be selected so they are within the exterior boundaries of a well-defined natural association and not with the preconceived idea that certain species should be included in the sample area.

National Park Service field crews collected the data within Yosemite National Park and received additional instructions (Coffman, 1934):

Where the question of arbitrary selection rests with the men in the field care should be exercised that the personal equation shall not enter as a biasing factor, remembering that the human tendency is to favour the better areas in sampling (whether consciously or unconsciously).

The Wieslander survey used 0.2 ac (809.4 m²) rectangular plots, two chains (40.2 m; a chain is a surveying unit of 66 ft) by 1 chain (20.1 m), running along the ground surface. Crews tallied live and dead trees in four diameter classes: 10–30 cm, 31–60 cm, 61–91 cm, and ≥92 cm (converted from data sheet values: 4–11 in., 12–23 in., 24–35 in., ≥36 in.). Wieslander plots were not placed in areas with <20% vegetative cover, so species occupying those sites (e.g., *P. jeffreyi* and *Juniperus occidentalis*) were likely undersampled. We used the 655 Wieslander plots within the park boundaries that had at least one tree ≥10 cm dbh.

The Wieslander protocol also included surveying and mapping forest cover for the Yosemite landscape. The protocol defined vegetation types as patches of continuous vegetation characterized by combinations of dominant overstory species. Forest types were differentiated wherever the cover of individual tree species was ≥20%. The location of the Wieslander plots is not known with sufficient precision to revisit them for the purposes of tree demography, so we used a different set of plots to represent modern conditions.

Between 1988 and 1992, Yosemite Vegetation Inventory (YVI) plots were randomly established within elevation and vegetation strata inside the park boundaries. The plots were circular with 17.84 m radius (1000 m²), established along the ground surface, and with locations recorded by a Global Positioning System. Of the 362 YVI plots, we selected the 137 plots with at least one tree ≥10 cm dbh. In addition, in 1998 and 1999, a group led by the US Geological Survey and The Nature Conservancy (TNC) established randomly located rectangular and circular plots, generally 1000 m² (range: 960–1125 m²) in representative vegetation types throughout the greater Yosemite ecosystem (NatureServe, 2003; NVCS, 2008). Of the TNC plots, we used the 73 plots with at least one tree ≥10 cm dbh within the park boundaries for species summaries. We represented modern conditions with the 210 combined YVI and TNC plots measured from 1988 to 1999.

Because we used two different sets of plots in this analysis, some differences in structure and composition could potentially reflect sampling biases from the Wieslander survey. In portions of California, Wieslander field crews may have been biased towards selecting plots with larger trees or otherwise unrepresentative composition (Sheil, 1995). In the historical context, any selection bias would have been for trees of larger and economically valuable taxa (e.g., *P. ponderosa* and *P. lambertiana*). National Park Service crews sampling in Yosemite received instructions to minimize this effect (Coffman, 1934), and although we tested for some potential sources of bias (below), we cannot entirely rule out a sampling artefact. However, the Wieslander data enabled us to establish a temporal baseline (1932–1999) that would be impossible to duplicate with randomly established plots.

2.4. Data reduction and analysis

We converted tree diameter data from the modern surveys to the four diameter classes used in the Wieslander survey. Based on analysis of the complete diameter distributions, we defined large-diameter trees as those in the ≥92 cm dbh diameter class provided that ≥5% of trees in the Wieslander survey were ≥92 cm dbh. For species with <5% of trees ≥92 cm dbh, we iteratively included smaller diameter classes to reach a threshold of ≥5%. Reducing some large-diameter thresholds allowed forest comparisons considering the actual diameter distributions of each species in the park, while providing a relatively equivalent proportion of each species in the large-diameter class. We reduced the large-diameter threshold to ≥61 cm dbh for *Tsuga mertensiana* and *Pinus contorta* and to ≥31 cm dbh for *Pinus albicaulis*, *Quercus chrysolepis*, *Quercus kelloggii*, *Alnus rhombifolia*, *Alnus tenuifolia*, *Cornus nuttallii*, *Pinus monophylla*, *Pinus sabiniana*, *Populus tremuloides*, *Salix* spp., and *Umbellularia californica*. We adjusted tree densities for slope.

National Park Service staff transferred the approximate Wieslander plot locations and forest vegetation polygons to a geographic information system, and Walker (2000) georectified the data (6512 distinct vegetation polygons). We consolidated plots from the Wieslander and modern surveys according to the Wieslander vegetation type polygons. We defined six forest types—two each of subalpine coniferous forests (*Pinus albicaulis–Tsuga mertensiana* forests [n_{Wies} = 64, n_{Mod} = 18] and *Pinus contorta* forests [n_{Wies} = 172, n_{Mod} = 50]), upper montane coniferous forest (*Abies magnifica–Pinus monticola* forests [n_{Wies} = 101, n_{Mod} = 28] and *Pinus jeffreyi–Abies* forests [n_{Wies} = 97, n_{Mod} = 21]), and lower montane coniferous forests (*Abies concolor–Pinus lambertiana* forests [n_{Wies} = 66, n_{Mod} = 21] and *Pinus ponderosa–Calocedrus decurrens* forests [n_{Wies} = 73, n_{Mod} = 38]). We compared the consolidated groups of plots from the Wieslander and modern surveys to analyze changes among vegetation types because the Wieslander plots could not be relocated (Bouldin, 1999; Keeley, 2004). Keeley (2004) found that consolidating Wieslander plots into groups was necessary to sample the range of variation present at hectare or larger landscape scales. Accordingly, we did not

analyze vegetation types with few large-diameter trees (broad-leaved forests, broadleaved woodlands, scrub and chaparral communities, and herbaceous communities) because the number of plots would not have been sufficient to fully characterize the vegetation type.

We conducted a preliminary analysis to verify that the groups of plots in each forest type had equivalent physical attributes (aspect, slope, and elevation) in the modern data set and the Wieslander data set (all comparisons tested with Mann–Whitney tests at α = 0.05). Plot aspects (cosine transformation) were similar and did not differ between the surveys. Plot slopes did not differ between surveys, except for *Abies concolor–Pinus lambertiana* forests, where slopes averaged 12° in the Wieslander survey and 19° in the modern survey. We judged this difference in slope to be immaterial to the analyses. Plot elevations did not differ for the subalpine or upper montane coniferous forest types. In the lower montane coniferous forest types, the mean elevation of the modern plots was lower than that of the Wieslander plots (1736 m vs. 2002 m in the *Abies concolor–Pinus lambertiana* forests type and 1484 m vs. 1706 m the *Pinus ponderosa–Calocedrus decurrens* forests type).

The Wieslander mapping protocol had as a primary objective the delineation of consistent areas of forest cover, so we would therefore expect consistency within the defined vegetation types we used to construct our plot groupings. However, we checked for variation within the lower-elevation vegetation types that might have resulted from differences in mean elevation. To do this, we constructed two scenarios. The first scenario used the complete set of plots from the modern surveys. The second scenario used the modern plots, but pruned those plots that were at lower elevations than the Wieslander plots. The two scenarios showed no differences in the abundance of conifers. *Q. chrysolepis* was more abundant in the full modern data set (lower mean elevation) and *Q. kelloggii* was more abundant in the pruned modern data set (higher mean elevation).

We limited species-level analysis to species with large-diameter trees in ≥8 plots in the Wieslander survey and in ≥3 plots in the modern survey (generally >5% of plots, but 2.4% for *Pseudotsuga menziesii*). For species-level analyses, we calculated large-diameter tree density for each species based on the plots containing at least one tree (dbh ≥10 cm) of that species. For forest type analyses, we calculated the density of large-diameter trees of all species for all plots within each forest type. All comparisons of large-diameter tree density were tested with t-tests at α = 0.05. We tested for homogeneity of variance with Levine's test (α = 0.05) and adjusted P-values accordingly. Because some density distributions did not follow a normal distribution, we also performed non-parametric Mann–Whitney tests. Changes in species ranges could affect large-diameter tree density because of the long time required for trees colonizing previously unoccupied territory to achieve large diameters. Therefore, to differentiate between changes in density within species ranges and changes in species ranges, we calculated large-diameter tree frequency (proportion of plots containing large-diameter trees) for each species in each forest type. We computed richness (species of large-diameter trees per plot) and evenness (Simpson's E) for each forest type.

2.5. Fire exclusion and fire reintroduction

Since the completion of the Wieslander survey in 1936, some parts of the forests have burned; either by lightning-ignited or management-ignited fires, with most fires and area burned being in the lower-elevation forest types. We used park records of fire perimeters to divide modern plots into those that were within an area burned since the initial survey and those that were within an area that had not been burned. At the time of the Wieslander survey (1932–1936), all these plots were within forest areas classified as *Pinus ponderosa–Calocedrus decurrens* forests, with at least 20% *P. ponderosa* canopy cover.

Table 1

Yosemite tree species. Trees observed in Yosemite National Park with their frequencies of occurrence (proportion of plots) and total numbers of trees during the Wieslander (1932–1936) and modern (1988–1999) surveys; limited to trees with dbh ≥10 cm. Nomenclature follows Flora of North America (1993–2007).

| Species	Family	Proportion of plots (%)		Number of trees	
		1932–1936 (n = 655)[a]	1988–1999 (n = 210)[a]	1932–1936 (n = 16,460)[b]	1988–1999 (n = 6891)[b]
Gymnosperms					
Abies concolor	Pinaceae	24.3	26.1	1712	1330
Abies magnifica	Pinaceae	29.9	19.5	2916	563
Calocedrus decurrens	Cupressaceae	14.4	24.8	478	458
Juniperus occidentalis	Cupressaceae	7.2	7.6	223	33
Pinus albicaulis	Pinaceae	9.2	11.0	680	492
Pinus contorta	Pinaceae	41.2	38.5	4912	2122
Pinus jeffreyi	Pinaceae	25.0	12.9	918	123
Pinus lambertiana	Pinaceae	15.0	16.6	437	135
Pinus monophylla	Pinaceae	0.2	1.0	8	12
Pinus monticola	Pinaceae	19.8	11.0	788	71
Pinus ponderosa	Pinaceae	11.0	15.7	658	243
Pinus sabiniana	Pinaceae	0.8	2.4	18	14
Pseudotsuga menziesii	Pinaceae	2.4	5.7	140	40
Sequoiadendron giganteum	Cupressaceae	0.6	0.5	14	1
Tsuga mertensiana	Pinaceae	15.7	8.6	1608	396
Angiosperms					
Acer macrophyllum	Aceraceae	0.3	0.5	13	2
Alnus rhombifolia	Betulaceae	–	4.3	–	96
Alnus incana tenuifolia	Betulaceae	0.3	–	19	–
Cornus nuttallii	Cornaceae	0.2	1.9	4	48
Populus tremuloides	Salicaceae	1.4	0.5	140	41
Populus trichocarpa	Salicaceae	–	1.0	–	8
Quercus chrysolepis	Fagaceae	4.4	11.4	453	472
Quercus kelloggii	Fagaceae	8.5	11.9	290	165
Salix spp.	Salicaceae	–	1.0	–	17
Umbellularia californica	Lauraceae	0.3	1.0	31	9

[a] Total number of plots with live trees ≥10 cm dbh.
[b] Total number of trees ≥10 cm dbh.

3. Results

The combined data sets included 25 species; 21 of those species occurred in both sets while one occurred only in the Weislander survey and three were unique to the modern survey (Table 1). Fourteen of the 21 species were abundant enough to analyze for changes between the two surveys. The Wieslander survey of 655 forest plots tallied 16,460 trees of 22 species $\geq$10 cm dbh, and the modern surveys of 210 forest plots tallied 6891 trees of 24 species $\geq$10 cm dbh (Fig. 2). In the Wieslander survey, slope-adjusted tree density in plots ranged from 12 trees ha^{-1} (one tree per plot) to 1602 trees ha^{-1} (mean 322.3 trees ha^{-1}). In the modern survey, slope-adjusted tree density ranged from 11 trees ha^{-1} (one tree per plot) to 2110 trees ha^{-1} (mean 339.9 trees ha^{-1}). The six

consolidated forest types represent 86% of the vegetated area of the park.

For the 21 tree species occurring in both surveys, the park-wide density of large-diameter trees fell from 45.0 trees ha^{-1} (SE = 1.73) to 34.1 trees ha^{-1} (SE = 2.43) – a decrease of 24% (t-test, Mann–Whitney, both $P < 0.001$) (Table 2). For the 14 most abundant species, the park-wide density of large-diameter trees was 43.9 trees ha^{-1} (SE = 1.73) in the Wieslander survey and 30.7 trees ha^{-1} (SE = 2.28) in the modern survey – a 30% decrease (t-test, Mann–Whitney, both $P < 0.001$). The density of large-diameter trees increased for three of the 14 most abundant species (*P. albicaulis*, *Q. chrysolepis* and *Q. kelloggii*), but the increases were not significant (Table 2). The proportion of plots with large-diameter trees changed little; declines were due to decreasing density within plots.
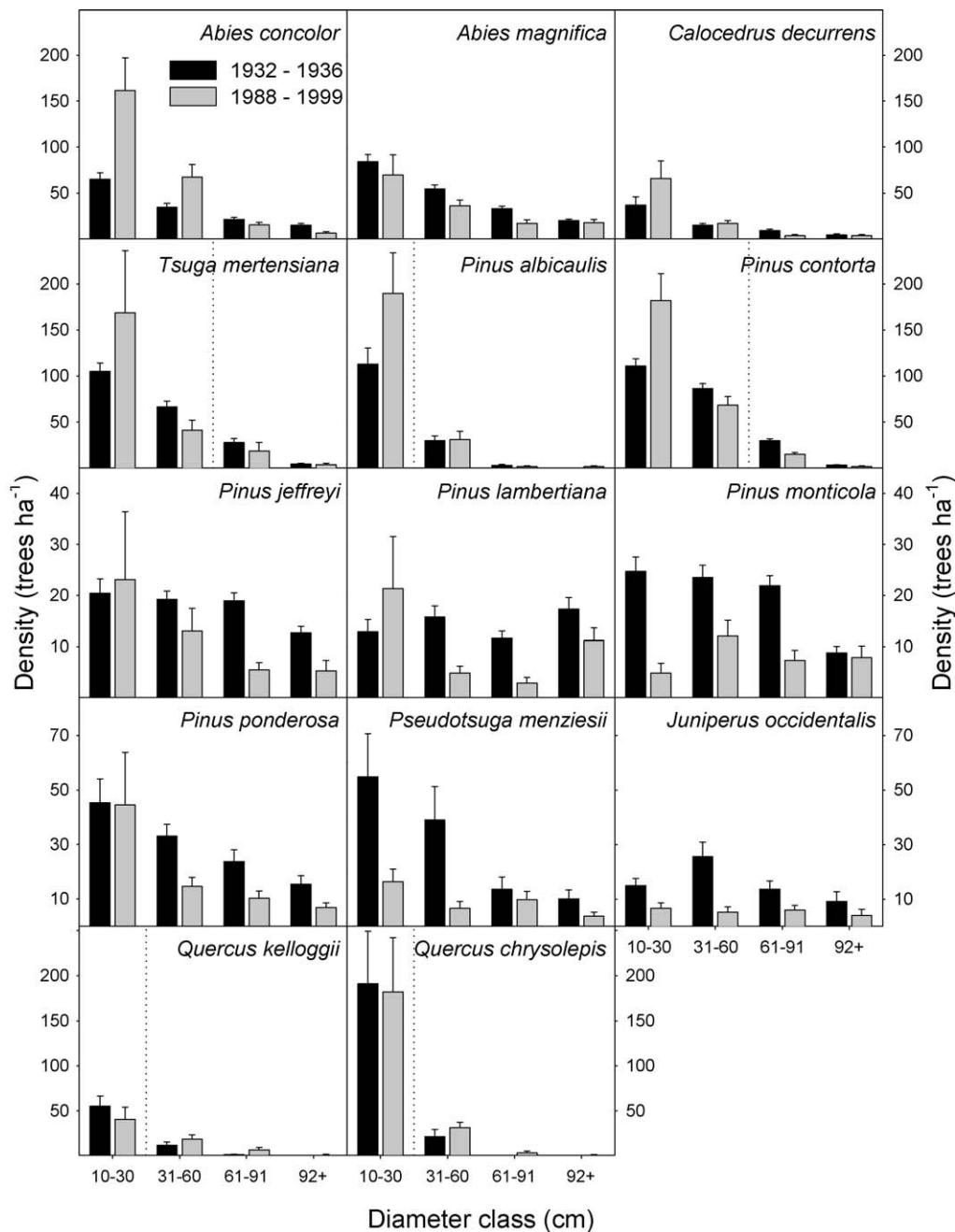
Fig. 2. Diameter class distributions: 1932–1936 and 1988–1999. Change in density of trees (means ± 1 SE) in all plots where each species was present for the Wieslander (1932–1936) and modern (1988–1999) surveys. Dotted vertical lines demarcate trees considered "large diameter." Otherwise, large-diameter trees are those in the $\geq$92 cm diameter class. *Note differing vertical scales.*

Table 2
Park-wide changes in large-diameter tree density between the Wieslander (1932–1936) and modern (1988–1999) surveys.

Species	Large-diameter threshold (cm)	Density 1932–1936 (trees ha^{-1})	Density 1988–1999 (trees ha^{-1})	Change (%)	P-value	
					t-Test	Mann–Whitney
Abies concolor	≥92	15.1	6.5	−57	<0.001	0.012
Abies magnifica	≥92	20.0	17.8	−11	ns	ns
Calocedrus decurrens	≥92	4.6	3.9	−15	ns	ns
Juniperus occidentalis	≥92	9.2	4.1	−56	ns	ns
Pinus albicaulis	≥31	32.4	33.6	4	ns	ns
Pinus contorta	≥61	32.6	16.6	−49	<0.001	<0.001
Pinus jeffreyi	≥92	12.6	5.3	−58	0.003	0.008
Pinus lambertiana	≥92	17.3	11.1	−36	0.073	0.123
Pinus monticola	≥92	8.8	7.9	−10	ns	ns
Pinus ponderosa	≥92	15.4	6.9	−55	0.017	0.247
Pseudotsuga menziesii	≥92	10.1	3.6	−64	0.085	0.100
Quercus chrysolepis	≥31	22.9	35.8	57	ns	0.086
Quercus kelloggii	≥31	13.5	26.7	98	ns	ns
Tsuga mertensiana	≥61	31.9	21.8	−32	ns	ns
All 14 common species	Above	43.9	30.7	−30	<0.001	<0.001
All 21 species	Above[a]	45.0	34.1	−24	<0.001	<0.001

ns: results were neither significant nor potentially significant, $P \geq 0.250$.

  [a] The threshold for large-diameter of less common species was 31 cm dbh (see Section 2).

Large-diameter density did not decline uniformly throughout species ranges (Fig. 3). Four general patterns of change emerged among eight of the 14 abundant species: (1) for *P. albicaulis*, *Q. chrysolepis*, and *Q. kelloggii*, increases in density of large-diameter trees occurred throughout species ranges; (2) for *P. jeffreyi*, *P. lambertiana*, and *P. ponderosa*, proportional decreases in large-diameter tree density were greatest in the lower-elevation portions of their ranges (Fig. 3); (3) for *A. concolor* and *P. contorta*, proportional decreases were approximately uniform throughout their ranges (Fig. 3); and (4) densities of large-diameter *A. magnifica*, *C. decurrens*, and *P. monticola* were relatively unchanged. Changes in densities of *Juniperus occidentalis*, *Pseudotsuga menziesii*, and *Tsuga mertensiana* showed no pattern with respect to the consolidated forest types.

Considering the 14 most common species as a group (Table 2), overall large-diameter density declines were significant for two of the six forest types—the *Pinus jeffreyi–Abies* forests (t-test, P = 0.02) and the *Pinus contorta* forests (t-test, P = 0.002; Mann–Whitney, P < 0.001) (Fig. 4). Decreases in other forest types were not significant (t-test and Mann–Whitney, P > 0.05).

Frequency of large-diameter trees (proportion of plots with large-diameter trees) decreased for *P. jeffreyi* and *T. mertensiana* (Fig. 5). Frequency of large-diameter trees increased for *C. decurrens*, *J. occidentalis*, *P. albicaulis*, *Pseudotsuga menziesii*, *Q. chrysolepis* and *Q. kelloggii* (Fig. 5). Frequency of large-diameter *A. concolor*, *A. magnifica*, *P. lambertiana*, *P. monticola*, and *P. ponderosa* was unchanged.

Large-diameter tree richness (number of species represented by large-diameter trees per plot) decreased in all forest types except in *Abies magnifica–Pinus monticola* forests. Large-diameter tree evenness (Simpson's E) was similar between the mid-1930s and the 1990s, except for the *Pinus jeffreyi–Abies* forests type where evenness decreased.

3.1. Effects of fire on density of large-diameter trees

Large-diameter tree response to fire varied by forest type. In *Pinus ponderosa–Calocedrus decurrens* forests, large-diameter tree density was similar in burned and unburned plots, although the species composition of the large-diameter population was different. In *Pinus jeffreyi–Abies* forests, large-diameter tree density declined in burned plots but species composition was similar between burned and unburned plots. Statistically significant changes (t-test, P > 0.05) in large-diameter tree densities were

not observed in other forest types due to the small number of plots established in areas that burned since the 1930s.

In *Pinus ponderosa–Calocedrus decurrens* forests, 19 modern plots burned at least once between the two survey dates while 23 plots remained unburned. Burned and unburned plots had similar spatial distributions throughout Yosemite. Physical attributes of burned and unburned plots were similar: mean elevations were 1472 m and 1500 m, mean slope was 13.3° and 14.2°, and aspect distributions were similar for burned and unburned plots, respectively. Overall densities for trees ≥10 cm dbh were higher in unburned plots (464 trees ha^{-1} vs. 205 trees ha^{-1}; t-test, P = 0.007), with the difference due entirely to smaller-diameter trees (Fig. 6). Large-diameter tree density in burned and unburned plots was similar (34 trees ha^{-1} and 35 trees ha^{-1}, respectively, Fig. 2). However, species representation in the large-diameter trees differed between burned and unburned plots (Fig. 6). In burned plots, large-diameter *P. ponderosa* density was higher—8.1 trees ha^{-1} vs. 0.5 trees ha^{-1} in unburned plots (t-test, P = 0.006). Unburned plots had higher densities of large-diameter *A. concolor* (3.3 trees ha^{-1} vs. 1.2 trees ha^{-1}), *C. decurrens* (3.8 trees ha^{-1} vs. 2.3 trees ha^{-1}), and *Q. chrysolepis* (9.8 trees ha^{-1} 1 vs. 6.1 trees ha^{-1}). Unburned plots also had some large-diameter *Cornus nuttallii* and *Umbellularia californica*, which were both absent from burned plots. Large-diameter *Q. kelloggii* density was similar at 15.2 trees ha^{-1} whether burned or unburned. Except for *P. ponderosa*, the differences were not statistically significant for individual species (t-test, P > 0.10).

4. Discussion

4.1. Decline of large-diameter trees

Large-diameter tree densities declined most in the more extensive higher elevation forest types (Fig. 4). Along with the decline in large-diameter densities, the diversity of the large-diameter tree component also declined. The density of large-diameter *A. concolor* – a species often thought to proliferate when fire is excluded – showed significant declines (Fig. 3 and Table 2), as did large-diameter *P. contorta*, *P. jeffreyi*, and *P. ponderosa*. However, the density of large-diameter *P. albicaulis* – reported to be declining in the Rocky Mountains and Pacific Northwest because of *Cronartium ribicola* (Tomback et al., 2001) – did not decline (Fig. 3 and Table 2). The 4% increase in density of large-diameter *P. albicaulis* is modest but consistent with increases in smaller-diameter individuals of this
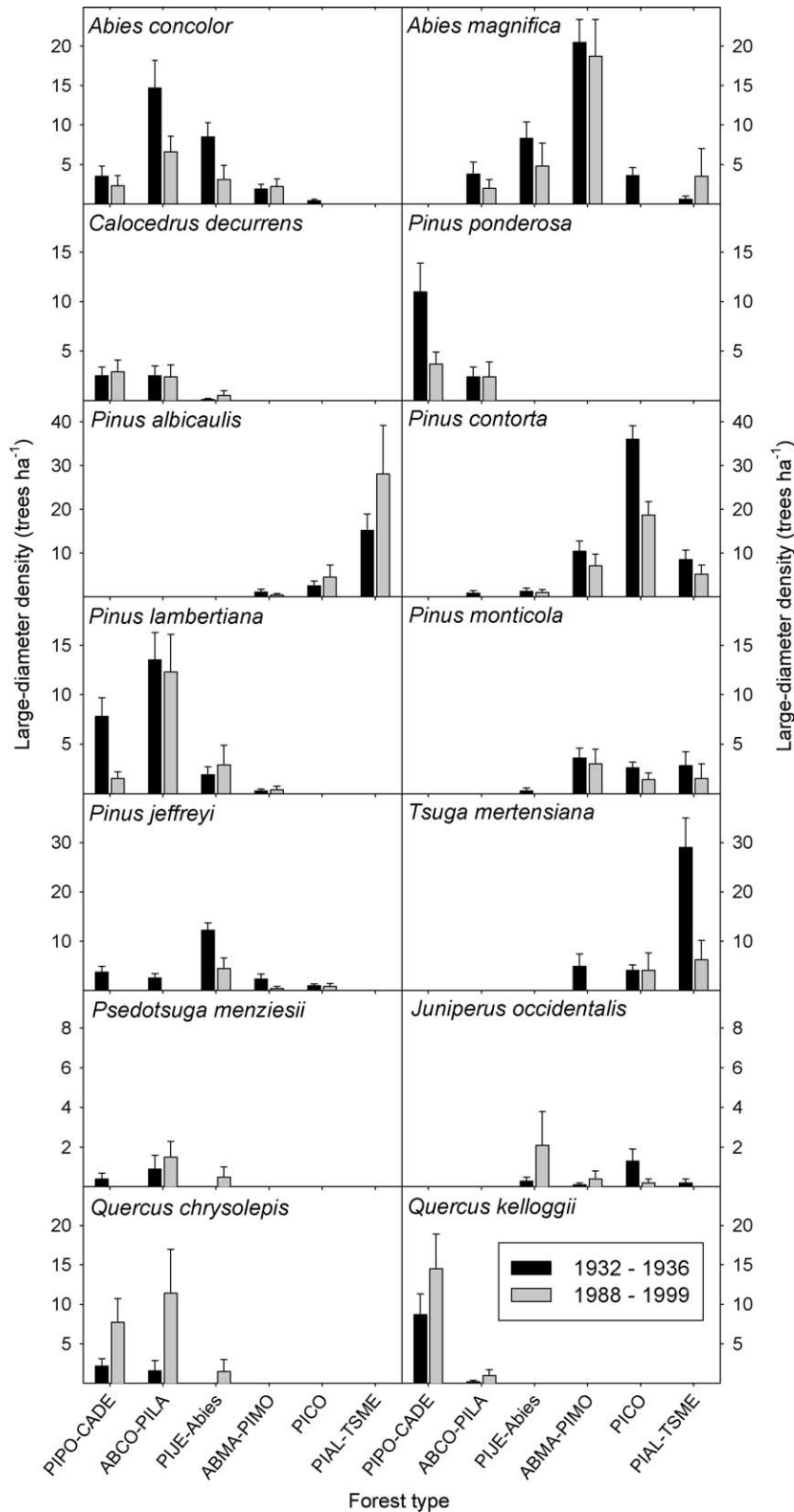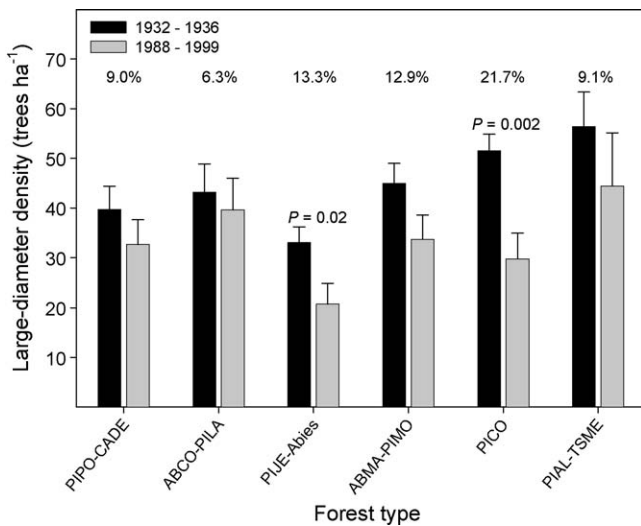
Fig. 3. Densities of large-diameter trees of 14 abundant species in six forest types between the Wieslander (1932–1936) and modern (1988–1999) surveys (vegetation type mean ± SE). Elevation (mean ±SD): *Pinus ponderosa–Calocedrus decurrens*, 1625 ± 289 m; *Abies concolor–Pinus lambertiana*, 1938 ± 281 m; *Pinus jeffreyi–Abies*, 2235 ± 225 m; *Abies magnifica–Pinus monticola*, 2517 ± 215 m; *Pinus contorta*, 2704 ±261 m; and *Pinus albicaulis–Tsuga mertensiana*, 2939 ± 230 m. Note differing vertical scales.

and other treeline species (Peterson et al., 1990; Nemani et al., 2003; Millar et al., 2004). Declining large-diameter tree density must eventually reduce the number of large standing snags and coarse woody debris that serve as vertebrate and invertebrate habitat (Graber, 1996; Schowalter and Zhang, 2005). A continuing decrease

in the number of large-diameter trees could lead to a "snag famine" until such time as climate and fire regimes facilitate recruitment of trees into large-diameter classes.

Densities of all trees increased or stayed the same while large-diameter tree densities declined (see also Bouldin, 1999; Smith

Fig. 4. Combined densities of large-diameter trees of all species in six forest types between the Wieslander (1932–1936) and modern (1988–1999) surveys (vegetation type mean ± SE). Percentages above histograms indicate the proportion of park area covered by the forest type. Elevation (mean ± SD): *Pinus ponderosa–Calocedrus decurrens*, 1625 ± 289 m; *Abies concolor–Pinus lambertiana*, 1938 ± 281 m; *Pinus jeffreyi–Abies*, 2235 ± 225 m; *Abies magnifica–Pinus monticola*, 2517 ± 215 m; *Pinus contorta*, 2704 ± 261 m; and *Pinus albicaulis–Tsuga mertensiana*, 2939 ± 230 m.

et al., 2005; Fellows and Goulden, 2008; Lutz, 2008; North et al., 2009). This was unexpected as we hypothesized that the largest tree diameter classes would exhibit lower mortality rates than the smaller diameter trees, which typically experience annual mortality rates of 3–8% from a variety of causes (Lutz and Halpern, 2006); this is because larger trees purportedly have greater resistance to the effects of wildfire and changes in climate.

Many alternative explanations for the decline in densities of large trees exist and one cannot differentiate among potential causes or among years when the declines were greatest with a chronosequence study. Large-diameter trees in the Sierra Nevada have experienced decadal periods with low mortality rates (van Mantgem et al., 2004) and high demographic stability, with mean turnover rates between 0.77% and 1.03% (Stephenson and van Mantgem, 2005; van Mantgem and Stephenson, 2005). However, the observational periods in these studies were small fractions of overall tree lifespans.

Elsewhere in the west, annual mortality rates in mature and old stands have been similarly low; ∼0.5% to 0.9% for *Pseudotsuga/Tsuga* (Debell and Franklin, 1987; Bible, 2001); ≤1.8% for *Picea/Tsuga* (Harcombe, 1986), and 0.3% for *Sequoia sempervirens* (Busing and Fujimori, 2002). However, recent studies have found increases from the long-term average mortality rate of ∼1% to 2% (Smith et al., 2005; van Mantgem and Stephenson, 2007; Ritchie et al., 2008), including a recent doubling in mortality rates in old-growth forests throughout western North America (van Mantgem et al., 2009).

One possible explanation advanced for declines in large-diameter trees is that those trees represent a declining cohort from forests that established after stand-initiating events that affected large portions of the park. In that case, large-diameter tree decline would have been a function of longevity and time since the stand-initiating event. Early successional species (e.g., *P. ponderosa* and *P. lambertiana*) would be expected to have declined, but species that readily establish in the understory would not be expected to have declined. However, large-diameter trees of shade-tolerant species (e.g., *A. concolor*) declined significantly. Furthermore, the pre-settlement fire regime has been one of low- and moderate-severity fires (at least in sequoia groves) for centuries (Swetnam, 1993). In *Pinus contorta* forests where fire

is less frequent and potentially more severe, evidence suggests continuous recruitment without stand-replacing fires (Parker, 1986, 1988). It is therefore unlikely that park-wide wildfires led to the establishment of a cohort that is now in decline.

Increased water stress – whether arising from extrinsic climatic change or intrinsic changes in stand density – we view as the leading candidate for the underlying cause of the recent doubling in mortality rates in old-growth forests throughout western North America (van Mantgem et al., 2009), although the proximate causes of mortality may vary (Ferrell, 1996; Guarín and Taylor, 2005; Das et al., 2007, 2008). Fire exclusion has lead to increases in tree density that predispose larger conifers to bark beetle (*Dendroctonus* spp. and *Scolytus* spp.) attack and increase susceptibility to infections by the native pathogen *Heterobasidion annosum*, both of which contribute to mortality (Sherman and Warren, 1988; Rizzo and Slaughter, 2001).

The decline in large-diameter trees could accelerate as the climate in California becomes warmer by mid-century (Hayhoe et al., 2004). A temperature increase – even without a decrease in precipitation – will increase evaporative demand, decrease snowpack, increase the length of the snow-free period, increase the length of the growing season, and thereby increase annual climatic water deficit. In addition, fires are expected to increase in number, start earlier, last longer, burn larger areas, and become more severe (Westerling et al., 2006; van Wagtendonk and Lutz, 2007; Lutz et al., in press).

When climate changes rapidly compared to the centuries-long lifespan of trees, there is a shorter period of the optimum conditions in which to attain those large diameters. Increased water stress on sites where large-diameter trees are now present could lead to elevated mortality (Stephenson et al., 2006; van Mantgem and Stephenson, 2007; van Mantgem et al., 2009), but time is required for trees establishing on newly favourable sites to grow to large diameters. Therefore, when climate is changing rapidly, we should expect densities of large-diameter trees to be lower than in stable climatic conditions, whether they are warm or cold. The decrease in densities of large-diameter trees could, therefore, be an indicator of climate change that is beyond the recent natural range of variation in these forests.

4.2. Limitations to the data and calculations

The four bins of the Wieslander survey provide relatively coarse differentiation among diameter classes, especially for *P. albicaulis* and *Quercus* spp., the only species that showed increases (Table 2 and Fig. 2). Warming temperatures may explain increases in large-diameter *P. albicaulis* and prolonged fire exclusion may have provided the time necessary for the fire-adapted *Quercus* spp. to grow into our definition of "large diameter." However, the three species that showed increasing densities are among the least massive tree species in Yosemite and their increased large-diameter density represents a small change in overall forest structure.

With respect to potential biases in plot establishment (Sheil, 1995), we found lesser declines in economically valuable species (Table 2), and significant declines in *A. concolor* and *P. contorta*—the reverse of what might be expected if the Wieslander crews favoured charismatic individuals or species. We also found that excluding plots with only one large-diameter tree (12% of Wieslander plots and 21% of modern plots) made the difference in density between the two data sets even larger. Large-diameter trees are patchily distributed, and we could not exclude the possibility of sampling artefacts in plots with more than one large-diameter tree (68% of Wieslander plots and 60% of modern plots).

Our confidence in our inferences about the declining large-diameter tree densities based on the Wieslander plots is
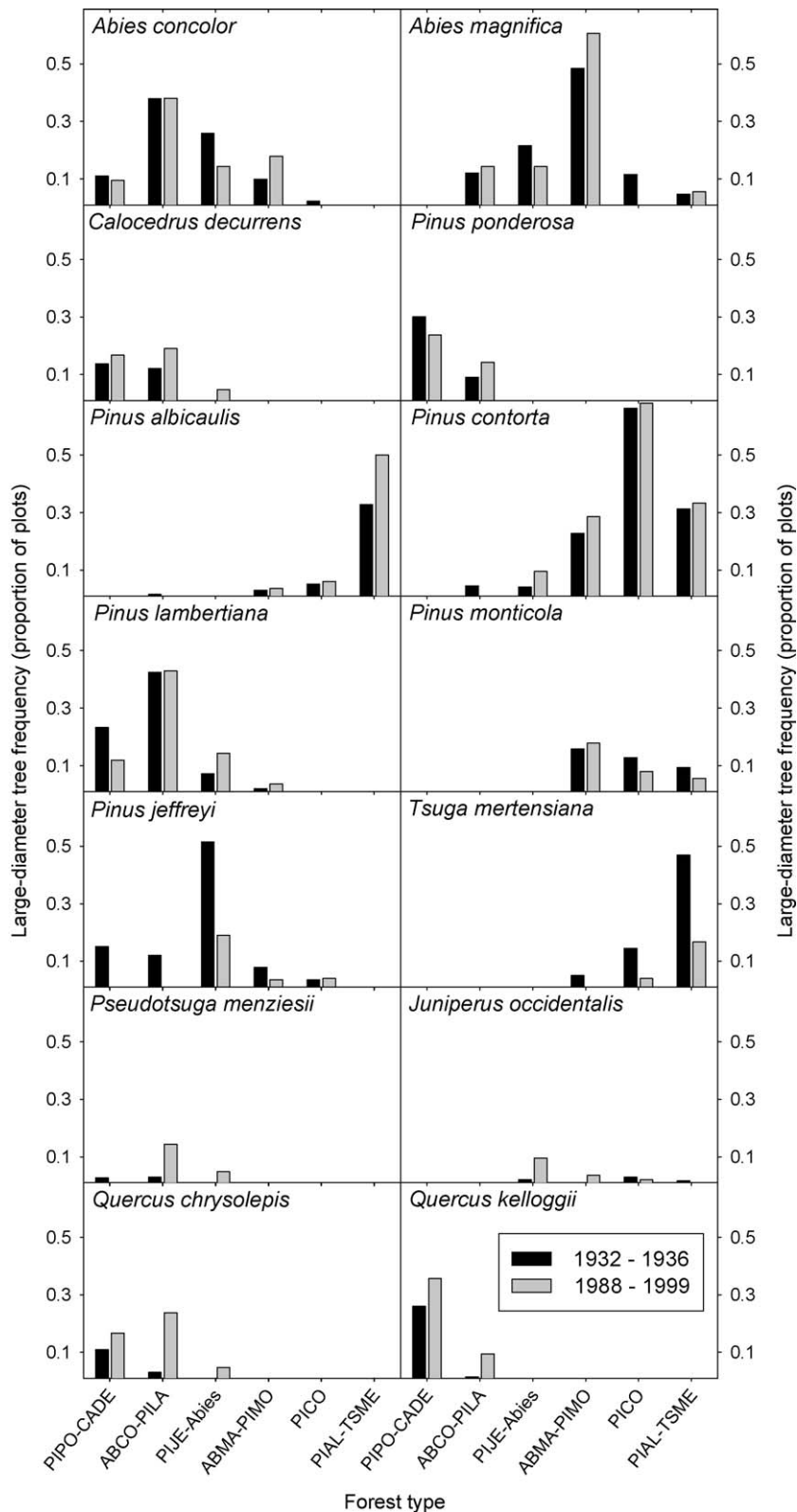
Fig. 5. Frequencies of large-diameter trees of 14 abundant species in six forest types between the Wieslander (1932–1936) and modern (1988–1999) surveys. Elevation (mean ± SD): *Pinus ponderosa–Calocedrus decurrens*, 1625 ± 289 m; *Abies concolor–Pinus lambertiana*, 1938 ±281 m; *Pinus jeffreyi–Abies*, 2235 ± 225 m; *Abies magnifica–Pinus monticola*, 2517 ± 215 m; *Pinus contorta*, 2704 ± 261 m; and *Pinus albicaulis–Tsuga mertensiana*, 2939 ± 230 m.

strengthened by several factors: (1) the large number of plots in this analysis (865); (2) explicit instructions to the Wieslander survey team in Yosemite to avoid site selection bias; (3) our stratification of plots by forest types; and (4) the statistical analysis of plot physical attributes. Other studies comparing Wieslander

and modern data (Bouldin, 1999; Fellows and Goulden, 2008) have identified similar patterns of forest change over the 20th century. Although there are some serious issues with using historical data, and there is no way to entirely rule out site selection bias, the Wieslander data remain the best available data set for early 20th
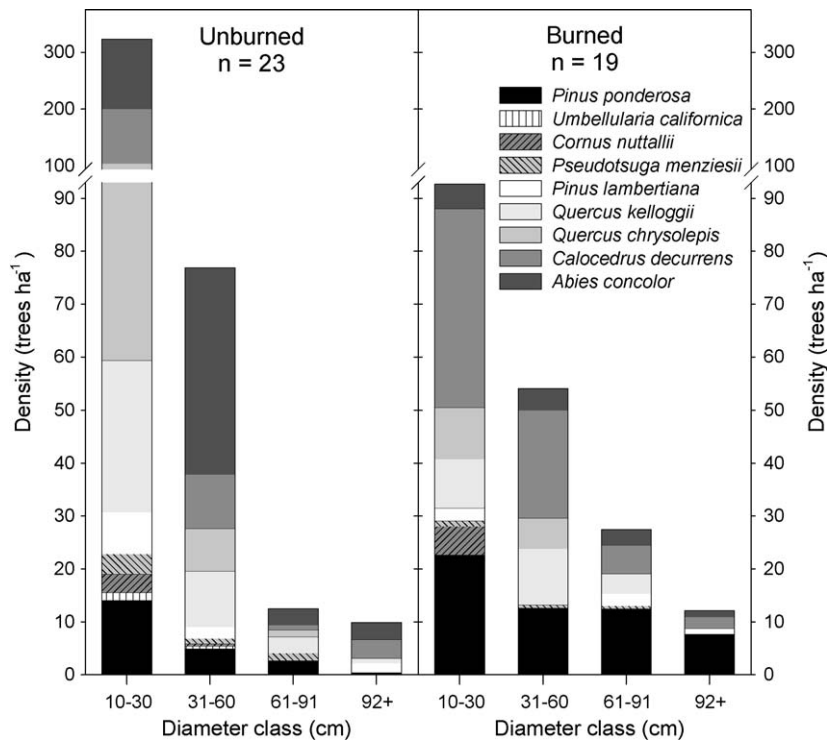
Fig. 6. Diameter distributions by species for *Pinus ponderosa–Calocedrus decurrens* forests that were unburned (left) and burned (right) in the period since 1936. All plots were within areas mapped as *Pinus ponderosa–Calocedrus decurrens* forests with at least 20% *P. ponderosa* canopy during the Wieslander survey (1932–1936). Not shown: one tree each of *Abies magnifica*, *Juniperus occidentalis*, and *Pinus jeffreyi*.

century conditions in the Sierra Nevada. And because we compared effects among forest types (Figs. 1–3) as well as absolute changes in large-diameter tree density, the differences among forest types could still be indicative of relative changes even if changes in any one forest type were influenced by data collection.

4.3. Implications for reintroduction of fire

Because the Wieslander field crews avoided areas of recent burns (Wieslander et al., 1933), areas unburned between 1936 and the modern sampling are likely to have been unburned throughout the entire 20th century. Prolonged periods of fire exclusion contribute to dense stands with increased density-dependent

mortality and decreased recruitment of shade-intolerant species (Parsons and DeBenedetti, 1979; Bouldin, 1999). Conversely, burned areas experience fire-related mortality, reflecting species susceptibilities, fuel loads and fire characteristics. Following a period of fire exclusion, reintroduction of fire may cause more tree mortality than historical fires would have caused (Perrakis and Agee, 2006), but first-entry prescribed burns are often of limited burn severity (van Wagtendonk and Lutz, 2007).

Plots in *Pinus ponderosa–Calocedrus decurrens* forests that had experienced fire in the 20th century retained large-diameter *P. ponderosa*. Plots not experiencing 20th century fire had almost no large-diameter *P. ponderosa* (Fig. 6). Instead, the large-diameter component was characterized by *A. concolor* and *C.*

Fig. 7. Characteristic *Pinus ponderosa–Calocedrus decurrens* forests. Left: a stand that was burned in 1978 by a prescribed fire and again in 1996 by a wildfire (2007 photo, J.W. van Wagtendonk). Right: a stand unburned since 1936 (2008 photo, J.A. Lutz).

decurrens—fire-intolerant species when small, but fire resistant once they become large (Figs. 6 and 7). Although low-severity or moderate-severity fire would reduce densities of smaller *A. concolor* and *C. decurrens*, higher severity would be likely be necessary to kill trees >92 cm dbh. We lack specific data on the pre-fire vegetation in the burned plots (except that *P. ponderosa* canopy was >20%), and differences between burned and unburned plots could be attributable to causes other than fire exclusion. However, these compositional differences in the large-diameter component suggest that lower-elevation forests that remain unburned for a century may retain their changed composition (relative to pre-fire suppression) even after the reintroduction of fire.

5. Conclusions

Our strong inference from this research is that the largest trees of most species in Yosemite are in decline. This decrease in large-diameter tree density throughout much of Yosemite can be interpreted as a long-term change in forest structure during the 20th century. Furthermore, in the lower montane *P. ponderosa–C. decurrens* forests, where there was less decrease in overall large-diameter tree densities; large-diameter tree composition differed between stands where fire had been excluded and those that had experienced fire. This contrast in composition reinforces the management objective of reintroducing fire to these forests. The park-wide changes in large-diameter structure and composition show that, far from being the most unchanging component of Yosemite forests, large-diameter tree populations are undergoing directional change on multi-decadal timescales.

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