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Fire disturbance, forest structure, and stand dynamics in montane forests of the southern Cascades, Thousand Lakes Wilderness, California, USA[1]

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Abstract: We examined tree diameter, age structure, and successional trends in 100 montane forest plots to identify the effects of variation in the return interval, severity, and extent of fires on forest structure and dynamics in the southern Cascade Range, California. We classified 100 forest plots into 8 groups based on stand structural characteristics. Median point fire return intervals were shortest in lower montane mixed conifer and Jeffrey pine–white fir stands (13-25 y) and upper montane red fir–white fir stands (14.5-19.5 y), intermediate in lodgepole pine stands (50-76.5 y), and longest in high-elevation red fir–mountain hemlock stands (100 y). Fire severity was mainly moderate to high in all forest structural groups except red fir–mountain hemlock. In the late 19th century, large, mostly high-severity fires burned through all forests. Fire extent varied among structural groups, burning from 13% to 85% of plots in a group on average. Stands differed in composition, but size and age structures were similar across structural groups, with few trees > 100 y old and peaks of establishment between 1895 and 1955 for all groups except red fir–mountain hemlock. Distinct pulses of tree recruitment followed the most recent (1883, 1885, 1889, 1918) large and mainly high-severity fires. Suppression of fire since 1905 has increased understory density of shade-tolerant, fire-intolerant species and caused forest compositional shifts, particularly in lower-elevation Jeffrey pine–white fir and mixed conifer stands, and lodgepole pine stands on well-drained sites. Structural or compositional change is less pronounced in upper montane red fir–white fir and red fir–mountain hemlock forests. The combination of gently sloping terrain with few fire breaks, extensive, moderate- to high-severity fires in all forest types and gradient positions and fire suppression has promoted homogenization of forest structure that may lead to large and severe fires in the future.

Keywords: California, dendrochronology, fire regimes, fire severity, forest structure, vegetation dynamics.

Résumé : Nous avons étudié le diamètre des arbres, la structure d'âge et les tendances successionnelles dans 100 parcelles de forêt de montagne afin d'identifier les effets de variations dans la durée de l'intervalle de retour du feu, dans la sévérité et l'étendue des feux sur la structure et la dynamique forestière dans le sud de la chaîne des Cascades en Californie. Nous avons classé les 100 parcelles forestières en 8 groupes basés sur les caractéristiques structurelles des peuplements. Les intervalles médians de retour du feu en un point étaient les plus courts dans les peuplements de montagne de faible altitude composés de conifères mélangés ou de pins de Jeffrey et sapins argentés (13-25 ans) ainsi que dans les peuplements de montagne d'altitude élevée composés de sapins rouges et argentés (14,5-19,5 ans), ils étaient intermédiaires dans les peuplements de pins tordus de Murray (50-76,5 ans) et les plus longs dans les peuplements d'altitude élevée composés de sapins rouges et de pruches subalpines (100 ans). La sévérité du feu allait principalement de modérée à élevée dans tous les groupes structurels forestiers sauf dans le groupe sapin rouge-pruche subalpine. À la fin du 19e siècle, de grands feux, pour la plupart de sévérité élevée, ont brûlé l'ensemble des forêts. L'étendue du feu variait selon les groupes structurels, brûlant de 13 à 85 % des parcelles d'un groupe en moyenne. La composition des peuplements était variable entre les groupes structurels, mais la taille et les structures d'âge étaient similaires, avec peu d'arbres > 100 ans et des pics d'établissement entre 1895 et 1955 pour tous les groupes sauf pour le groupe sapin rouge-pruche subalpine. Des pics distincts de recrutement ont suivi les grands feux les plus récents (1883, 1885, 1889, 1918), qui pour la plupart étaient des feux de sévérité élevée. La suppression des feux depuis 1905 a augmenté la densité en sous-étage d'espèces tolérantes à l'ombre, mais intolérantes au feu et a causé des changements dans la composition forestière, en particulier dans les peuplements de faible altitude composés de pins de Jeffrey et de sapins argentés et dans ceux de conifères mélangés ainsi que dans les peuplements de pins tordus de Murray sur les sites bien drainés. Les changements dans la structure ou la composition étaient moins importants dans les forêts de montagne d'altitude élevée composées de sapins rouges et argentés et dans celles composées de sapins rouges et de pruches subalpines. La combinaison de terrains en pente douce comprenant peu de barrières contre le feu, du passage de grands feux de sévérité modérée à élevée dans tous les types de forêts et de positions dans le gradient altitudinal, ainsi que la suppression des feux a favorisé une homogénéisation de la structure forestière qui pourrait mener dans le futur à de grands feux sévères.

Mots-clés : Californie, dendrochronologie, dynamique végétale, régimes de feu, sévérité du feu, structure forestière.

Nomenclature: Hickman, 1993.

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Introduction

The structure and dynamics of western coniferous forest landscapes are strongly influenced by natural disturbances such as fire, windstorms, and insect outbreaks (Pickett & White, 1985; Sprugel, 1991; Veblen *et al.*, 2003). In the Pacific Northwest, fire was the most frequent and widespread disturbance affecting forests prior to Euro-American settlement, but fire regimes have changed dramatically since a United States federal policy of fire suppression on public lands was implemented in 1905 (Agee, 1993; Taylor, 2000; Hessburg & Agee, 2003; Stephens & Ruth, 2005). Variation in fire regime characteristics promotes structural diversity at stand and landscape scales as burns kill all trees in some stands and few in others (Romme, 1982; Taylor & Skinner, 1998; Hessburg, Agee & Franklin, 2005; Beaty & Taylor, 2008). On the other hand, fire suppression has been reported to increase forest homogeneity at stand (Taylor, 2000; Taylor & Skinner, 2003; Beaty & Taylor, 2007; North, Innes & Zald, 2007) and landscape scales (Skinner, 1995; Hessburg, Agee & Franklin, 2005).

In the southern Cascades, tree species distribution is controlled primarily by temperature (elevation) and secondarily by soil moisture (Franklin & Dyrness, 1973; Barbour, 1988; Rundel, Parsons & Gordon, 1988; Parker, 1991; 1995). Low-elevation (< 1700 m), well-drained uplands are dominated by Jeffrey pine (*Pinus jeffreyi*) and/or ponderosa pine (*P. ponderosa*). White fir (*Abies concolor*) is locally abundant on mesic sites at low elevation and increases in abundance with higher elevation, forming mixed stands with ponderosa pine, Jeffrey pine, sugar pine (*P. lambertiana*), and incense-cedar (*Calocedrus decurrens*) between 1700 and 2000 m. Between 2000 and 2400 m, the zonal dominant is red fir (*A. magnifica*) and important associates are white fir at low elevations and western white pine (*P. monticola*) at high elevations. Subalpine forests above 2400 m are dominated by mountain hemlock (*Tsuga mertensiana*). Mesic flats that have a high water table, receive cold air drainage, have poor soils, or have experienced high-severity fire are usually occupied by lodgepole pine (*P. contorta* var. *murrayana*) (Franklin & Dyrness, 1973; Zeigler, 1978; Parker, 1991; 1993).

Fire severity is an important component of fire regimes that strongly affects forest structure, and a gradient in fire severity in the southern Cascades and Sierra Nevada appears to parallel gradients in temperature and moisture related to elevation. Fires in warmer, low-elevation pine and mixed pine–white fir forests are characterized as being low in severity, with burns killing mainly seedlings and saplings (Kilgore & Taylor, 1979; Kobziar, Moghaddas & Stephens, 2006; Schwilk *et al.*, 2006; van Mantgem, Stephenson & Keeley, 2006; Scholl & Taylor, 2010). Higher-elevation forests dominated by red fir experience mixed-severity fires (Taylor & Halpern, 1991; Chappell & Agee, 1996; Scholl & Taylor, 2006). There are few fire severity data for subalpine mountain hemlock forests, but they are thought to have a mixed-severity fire regime (Agee, 1993). Few studies have identified patterns of fire severity in lodgepole pine forests in this region, but they provide evidence for the occurrence of both stand-replacing, high-severity fire and low-severity surface fire (Bekker & Taylor, 2001; Taylor & Solem, 2001; Caprio, 2008). Unlike the Rocky Mountain variety of lodgepole pine (*P. contorta* var. *latifolia*), lodgepole pine in the Cascades and Sierra Nevada is not serotinous and is thought to be less dependent on stand-replacing fire for regeneration (Parker, 1986b; Rundel, Parsons & Gordon, 1988; Parker, 1993).

Most low-elevation forests in the southern Cascades and Sierra Nevada have experienced a shift in composition from fire-tolerant ponderosa pine, Jeffrey pine, and sugar pine to fire-intolerant incense-cedar and white fir since the onset of fire suppression (Vankat & Major, 1978; Kilgore & Taylor, 1979; McNeil & Zobel, 1980; Taylor, 2000; Youngblood, Max & Coe, 2004; Collins & Stephens, 2007; Scholl & Taylor, 2010). Fire suppression effects on higher-elevation forest types are more difficult to evaluate because pre-fire suppression fire return intervals are longer and in some cases exceed the length of the fire suppression period. Lodgepole pine stands are thought to follow 2 or more successional pathways after a fire. On sites receiving cold air drainage or with poor soils (low nutrients, poorly drained) lodgepole pine is thought to be self-replacing, while on better sites lodgepole pine establishes first following a fire and then red fir or white fir establishes under the pine canopy (Zeigler, 1978; Agee, 1993; Parker, 1993; Taylor & Solem, 2001). However, data are insufficient to evaluate if these are typical post-fire pathways for lodgepole pine forest development. There has also been little research on the effects of fire suppression on higher-elevation red fir, western white pine, and mountain hemlock forests. Some research suggests there has been little effect from fire suppression (Chappell & Agee, 1996; Scholl & Taylor, 2006), while other research has reported increases in red fir density similar to low-elevation mixed conifer forests, suggesting that red fir forests may be outside their historical range of variability with regard to forest structure and fire return intervals (Vankat & Major, 1978; Taylor, 1993; 2000).

The goal of this study was to identify the role of fire disturbance in shaping the compositional and structural variability of montane forest ecosystems in the southern Cascades. In a previous paper (Bekker & Taylor, 2001) we used fire-scar dendrochronology to quantify variation in fire regimes across gradients of forest composition, elevation, and potential soil moisture. Here we use stand structural analysis, re-analysis of fire regime data from fire extent maps, and ordination to test the hypothesis that variation in forest structure and composition is related to fire regime variation (return interval, severity, and size) and that fire suppression in the twentieth century has caused changes in forest density and composition, particularly at lower elevations. Our specific objectives were to 1) identify the relative importance of different fire regime characteristics influencing forest structure and composition and determine whether structural and compositional changes are associated with the onset of fire suppression efforts; and 2) identify forest successional trends and typical post-fire pathways by analyzing compositional dissimilarity between tree size classes within structural groups.

Methods

STUDY AREA

Our study was conducted in the 6618-ha Thousand Lakes Wilderness (TLW), part of the Lassen National Forest, located at the southern tip of the Cascade Range in northern California (Figure 1). Elevations in TLW range from 1700 to 2646 m, and the climate is characterized by cold, wet winters and warm, dry summers (Major, 1977). Mean monthly temperatures at Manzanita Lake (1750 m), 13 km south of TLW, range from –1 °C in January to 17 °C in July, and annual precipitation averages 105 cm, with most (84%) falling as snow between November and April. Depth of April snowpack commonly exceeds 5 m above 2400 m in elevation (Taylor, 1990; 1995). Soils in TLW are derived from Tertiary and Quaternary volcanic rocks that have been extensively modified by Pleistocene glaciation (Kane, 1980; Norris & Webb, 1990). Soil depth is highly variable, but most soils are well-drained, except those in the Thousand Lakes Valley. The southern and western portions of TLW are mountainous and dominated by Crater (2646 m), Magee (2606 m), and Fredonyer (2458 m) peaks, part of the former Thousand Lakes Volcano, while the eastern portion is part of a gently sloping volcanic tableland interrupted by tephra cones.

CLASSIFICATION OF FOREST STRUCTURE

We characterized forest structure in TLW by sampling stands across strata of elevation, slope aspect, and forest cover (Figure 1). Stands that were similar to surrounding forests in structure, composition, and environment were sampled in 400-m^2 plots, and the geographic location of each plot was determined using a handheld GPS unit. The species and diameter at breast height (dbh) of all live trees ≥ 4.0 cm dbh were measured, and seedlings (0.5–1.4 m tall) and saplings (> 1.4 m tall, < 4.0 cm dbh) were counted in each plot. Forest structural groups with similar size-class distributions were identified using Ward's method of cluster analysis, which minimizes the within-cluster sum of squares (Everitt, 1993). The variables used in the cluster analysis were the density (ha^{-1}) of seedlings, saplings, and trees of each species in 10-cm dbh classes from 4 cm to ≥ 144 cm dbh.

To construct tree age structures for each forest-structural group and identify forest characteristics in relation to fire, we cored an average of 19 trees (range 11–27) across the

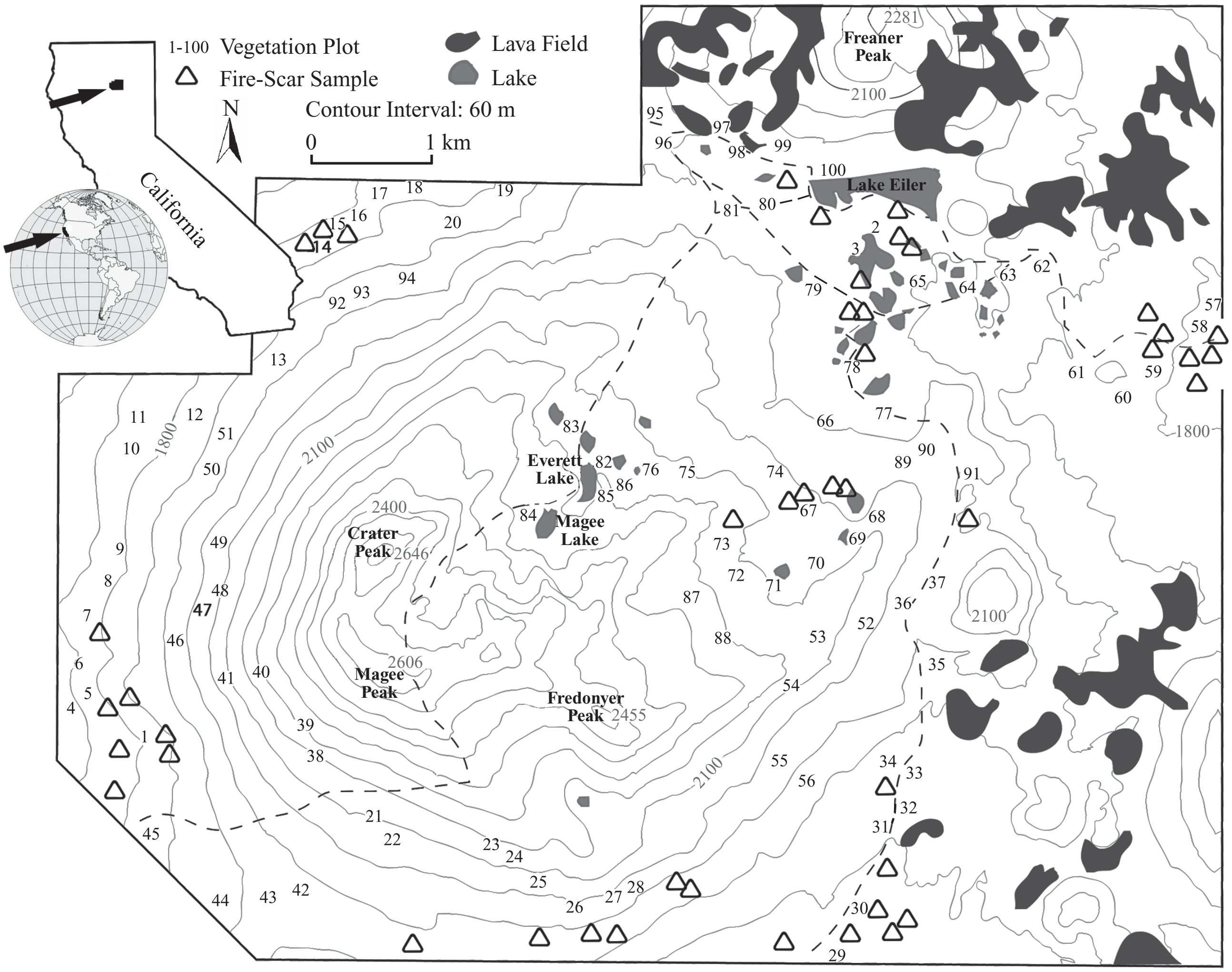


FIGURE 1. Location of study area, vegetation plots, and fire-scar samples in the Thousand Lakes Wilderness, southern Cascades, California.

range of stem diameters present in each plot 30 cm above the ground. Samples were prepared using successively finer sandpaper to 400 grit, and the oldest annual ring was used as an estimate of tree age. We used geometric correction (Applequist, 1958) to add years to cores that did not include the pith. Tree age structure for each size-structural group was developed by combining all stem ages from plots into 20-y age classes to identify major pulses of establishment that could represent a response to fire. Cores were not crossdated, and no attempt was made to correct for time to grow to coring height, but crossdated fire scar samples from the site (Bekker & Taylor, 2001) revealed very few missing rings, and most trees were cored 30 cm from the ground, so the 20-y age classes should be broad enough to encompass any error in the age estimates.

FIRE REGIME PARAMETERS

We used maps of fire extent in TLW from Bekker and Taylor (2001) to quantify fire regime parameters (extent, return interval, severity) associated with variation in the characteristics of the forest-structural groups. Evidence used to create the maps included crossdated fire scars in partial cross-sections and radial growth changes in trees and tree-age cohorts from the plots that were associated with known fire dates from scars (Arno & Sneck, 1977; Barrett & Arno, 1988). Fire boundaries were drawn equidistant between points with and without fire evidence in a given year, except when potential barriers to fire spread (*e.g.*, lava flows, rock outcrops, water bodies, short-needle fuel beds) were encountered, and the area of each fire was then determined with a planimeter (*cf.* Taylor, 2000). Hessl *et al.* (2007) found that this method of reconstructing fire extent produces ecologically meaningful and realistic representations of fire and conservative estimates of area burned compared to other boundary interpolation methods.

To identify the effect of fire return interval on forest structural characteristics we used the fire extent maps to calculate composite and point fire return intervals using plots with fire evidence as points in the landscape. Composite intervals were calculated as the mean and median interval between fires occurring in any plot within a given structural group, whereas point intervals were calculated by plot and then summarized as the grand mean and grand median in each structural group. Using fire extent maps to calculate the intervals excludes small fires that only leave evidence in single plots and thus produces longer intervals than calculations based on all fire scar evidence.

We identified variation in fire severity among structural groups using 2 methods. First, we counted the number of occupied 20-y age classes in each plot for all stems and for stems > 100 y old. Plots that have experienced high-severity fires should have trees in fewer age classes than those that have experienced low- and moderate-severity fires (Agee, 1993). Although frequent low- or moderate-severity fires could kill all small trees over a 20-y period, thus leaving an age class open, it is more likely that some trees would survive these events. Second, we used landscape-scale patterns of fire severity mapped in our previous work (Bekker & Taylor, 2001) for parts of 3 individual fires (1883, 1889, and 1918). Because recent and repeated burns consume evidence of previous fires (Fulé, Covington & Moore, 1997) we could not map severity for earlier fire years. The maps were produced from field reconnaissance, tree age data in plots, and forest patches evident on 1939–1941 and 1993 aerial photographs. Patches of forest that burned at different severity were identified on the aerial photographs using the relative density of short, even-aged stems and taller, emergent trees that survived successive fires. We determined whether plots were located in low (> 20 emergent stems·ha^{-1}), moderate (10–20 emergent stems·ha^{-1}) or high (< 10 emergent stems·ha^{-1}) severity patches.

The effect of fires on stand structure will be clearest if the fires are both high-severity and extensive. Large but low-severity fires kill few trees and thus do not create distinct pulses of establishment (Agee, 1993), while the effects of high-severity but small fires can be masked by the lack of change in plots where the fires did not burn. To determine fire sizes by structural group we calculated the mean proportion of plots burned by each fire in each group. We could not use the fire extent maps in Bekker and Taylor (2001) to determine fire sizes directly because plots in structural groups were not contiguous in the landscape, but sizes based on proportion of plots burned were very similar (0.96 Pearson's *r*) to those based on the extent maps.

We investigated successional trends in TLW by using ordination to identify compositional dissimilarity between size classes. In mixed-age stands, tree diameter is often poorly correlated with age, so there are limitations to using size to infer population dynamics. The overall correlation (Pearson's *r*) between dbh and age for the study area was 0.57 and varied by species (mountain hemlock 0.49; lodgepole pine 0.52; red fir 0.52; white fir 0.60; western white pine 0.66; Jeffrey pine 0.76; sugar pine 0.76; ponderosa pine 0.91). These moderately strong but significant ($P < 0.01$) correlations suggest that dbh is a reasonable indicator of tree age. We first calculated the mean density (ha^{-1}) of stems of each species in understory (< 23.9 cm dbh), intermediate (24–43.9 cm dbh), and overstory (≥ 44 cm dbh) size classes for each forest-structural group. We then used detrended correspondence analysis (Gauch, 1982) to ordinate species density in each size class in each structural group. Compositional differences between size classes were represented using vectors with the length of the vector proportional to the magnitude of the difference. This approach assumes that understory abundance is a reasonable indicator of future stand composition in the absence of a disturbance.

Results

FOREST STRUCTURE AND COMPOSITION

Eight forest-structural groups were identified in TLW by the cluster analysis of tree size-classes, and they fall into well-known compositional groups. Two mixed conifer (MC) groups were identified that differ in stand structure and composition (Figure 2a). MC-1 stands occupy west-facing slopes from 1750 to 1965 m and are characterized by a very dense understory (stems < 34 cm dbh) of white fir with some sugar pine and a sparse overstory (stems > 54 cm dbh) of mainly sugar pine and ponderosa pine. Understory trees

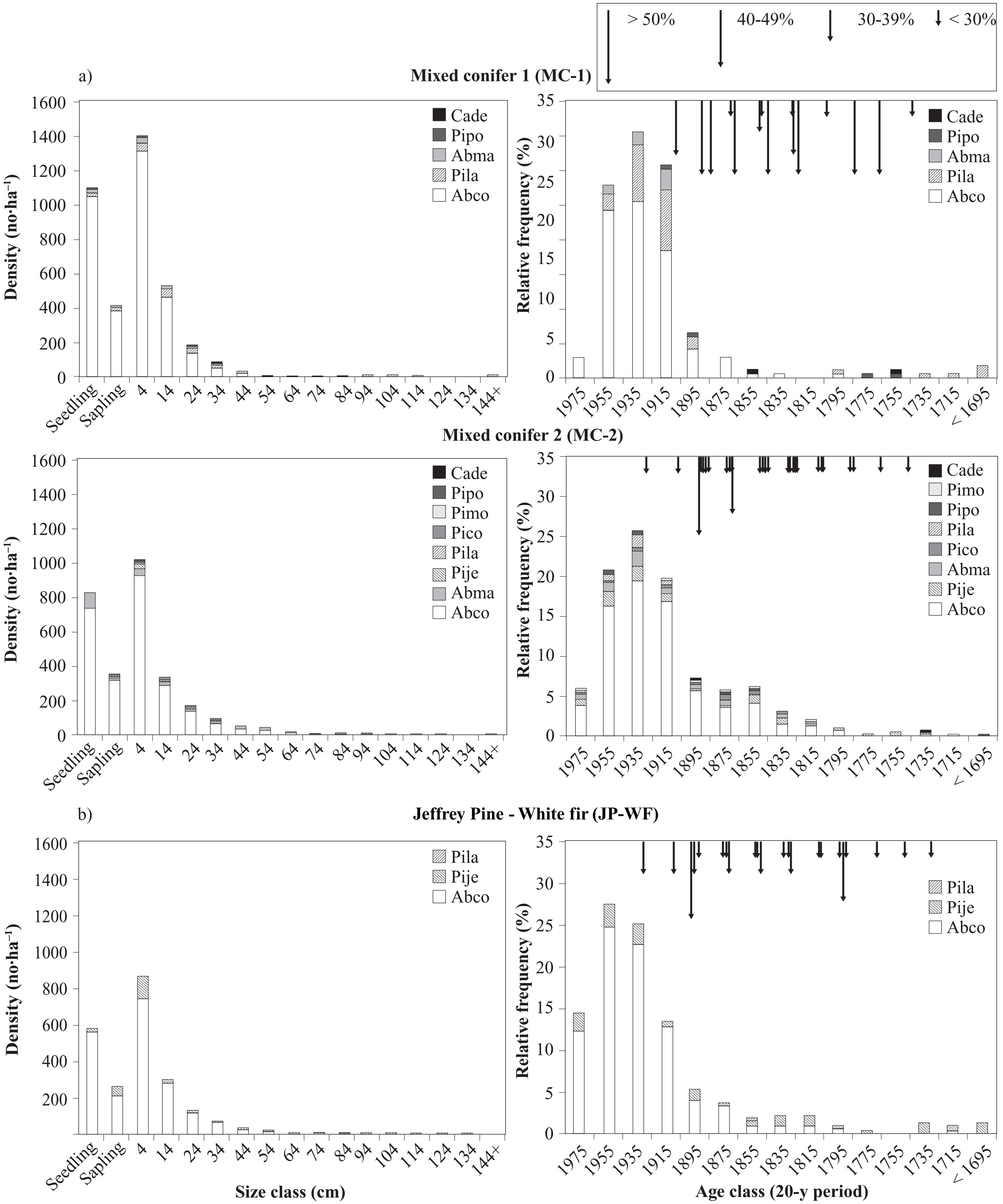
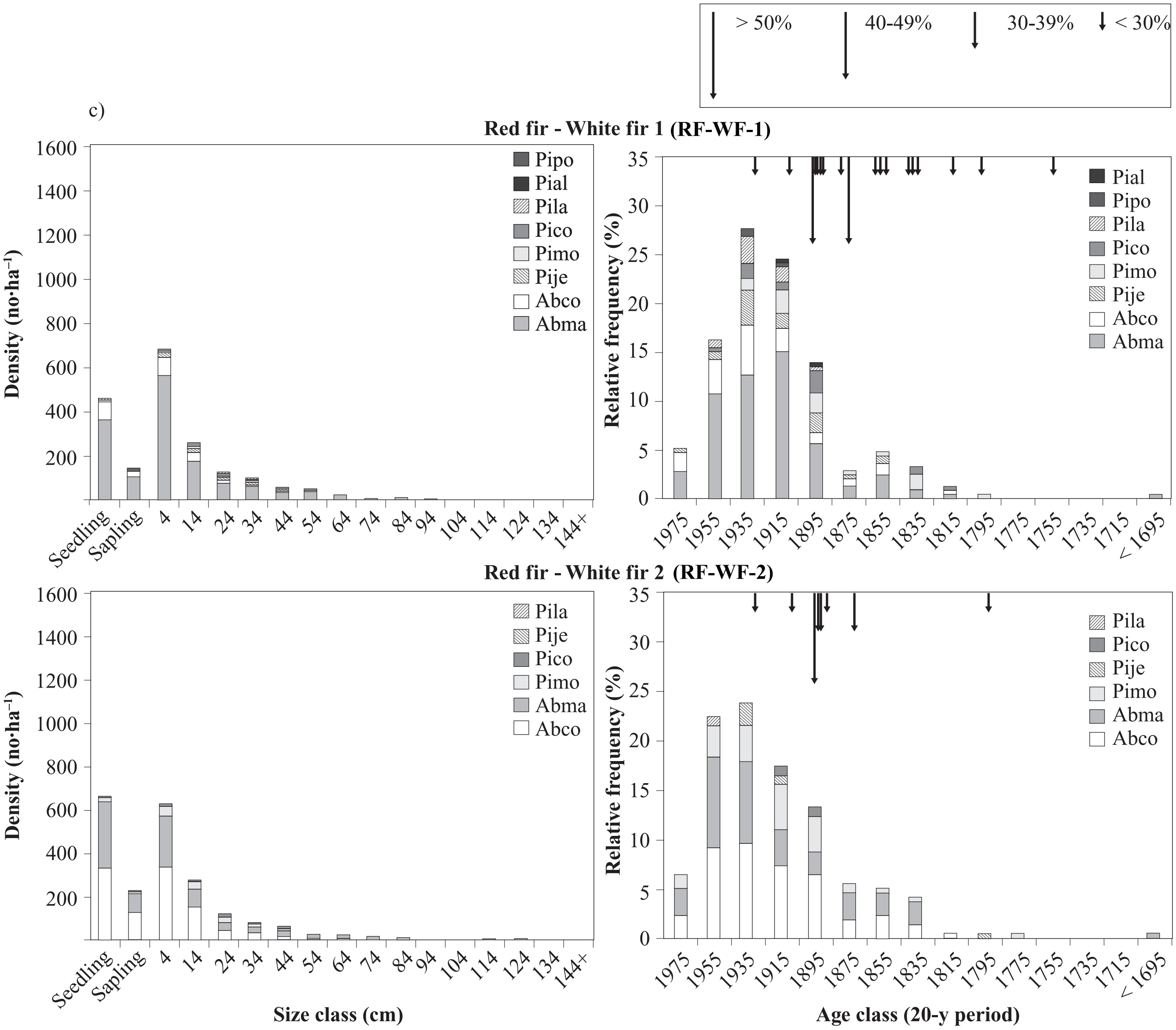


FIGURE 2. Average size and age distributions for a) mixed conifer, b) Jeffrey pine–white fir, c) red fir–white fir, d) lodgepole pine, and e) red fir–mountain hemlock forest structural groups identified by cluster analysis of stand density data. Numbers on x-axes indicate lower bounds of 10-cm size classes and upper-bounds of 20-y age classes. Only a subsample of trees were aged in each plot, and the y-axis is the relative frequency of all aged stems in a structural group. Arrows indicate individual fires, and their length indicates fire size expressed as the percentage of plots burned in a structural group. Species are white fir (Abco), red fir (Abma), Jeffrey pine (Pije), sugar pine (Pila), lodgepole pine (Pico), western white pine (Pimo), ponderosa pine (Pipo), whitebark pine (Pial), mountain hemlock (Tsme), and incense-cedar (Cade).

in MC-1 are mostly 40–100 y old, and the overstory pines are > 200 y old. MC-2 stands occur on all slope aspects from 1750 to 2070 m and also have a dense understory of mainly white fir, but red fir, Jeffrey pine, lodgepole pine, and western white pine are present too. The overstory of MC-2 stands is denser than MC-1 stands and includes Jeffrey pine, more white fir, and less ponderosa and sugar pine. Most understory stems are 20–100 y old, with many overstory stems 100–200 y old and some Jeffrey pine and white fir > 200 y old.

A Jeffrey pine–white fir (JP–WF) group occupies mainly north- and east-facing slopes between 1765 and 2030 m. The understory is dominated by white fir and is dense, but less so and less diverse (only Jeffrey pine, white fir, and sugar pine) than the MC groups (Figure 2b). The overstory is moderately dense and contains roughly equal amounts of Jeffrey pine and white fir, but the largest stems (> 64 cm dbh) are mostly (60%) Jeffrey pine. Overstory stems are 140–300 y, while most understory stems are 80–100 y.

Two red fir–white fir (RF–WF) groups differ in stand structure and in the relative abundance of the 2 species (Figure 2c). RF–WF-1 stands are concentrated on dry, southwest-facing slopes between 1900 and 2170 m and have moderately dense overstories and sparse understories. Both the understory and overstory are dominated by red fir, mixed with white fir, Jeffrey pine, and western white pine. RF–WF-2 stands occupy more mesic slope aspects from 1920 to 2150 m and have less dense overstories than RF–WF-1 stands. The overstory is strongly dominated by



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red fir, while white fir is relatively more abundant in the understory, and western white pine is an important associate. Most overstory stems in both groups range from 120 to 200 y old, and understory stems began to establish 100–120 y ago.

Two lodgepole pine (LP) groups were identified, and they vary in stand structure and composition (Figure 2d). LP-1 stands occur around lake margins in the Thousand Lakes Valley from 1950 to 2055 m. The understory of these stands is very dense and is dominated by lodgepole pine, but white fir is also abundant. Overstory stems are sparse and are a mixture of lodgepole pine, Jeffrey pine, red fir, and white fir. Most lodgepole pine stems are 40–160 y old, but stems > 180 y old are also present, and most white fir began to establish about 100 y ago. LP-2 stands are located on the lower slopes surrounding the Thousand Lakes Valley from 1955 to 2110 m and have fewer species and a less dense understory and denser overstory than LP-1 stands. The understory of LP-2 stands is mainly red fir and lodgepole pine, and the overstory contains approximately equal amounts of red fir and western white pine. Lodgepole pine, western white pine, and red fir stems in these stands range from 40 to 180 y, but most red fir began to establish about 100 y ago.

One red fir–mountain hemlock (RF–MH) group was identified, and these stands occupy the highest elevations in TLW (2120–2210 m). They have the lowest-density understory of any groups, and they are composed of approximately equal amounts of red fir and mountain hemlock, with some western white pine (Figure 2e). The overstory is also sparse and is about half western white pine and half mountain hemlock and red fir. Most trees are 80–200 y old, but younger and older stems are present too.

FIRE REGIME PARAMETERS

Fire return intervals and fire sizes varied by forest-structural group (Table I). Median point fire return intervals were short (13–25 y) in MC-1, RF–WF-2, RF–WF-1, MC-2, and JP–WF stands, intermediate (50–76.5 y) in LP-1 and LP-2 stands, and longest (100 y) in RF–MH stands, and median composite fire return intervals followed similar patterns. The last fire with evidence in more than 1 plot occurred in 1918.

Fire sizes also varied by structural group, but fire severity was primarily high across structural groups, and recent fires were both large and primarily high-severity. Fire sizes, expressed as the mean percentage of plots burned, were smallest (17–24%) in MC-2, RF–WF-1, and JP–WF stands, intermediate (36–54%) in RF–WF-2, LP-2, MC-1, and RF–MH stands, and largest (85%) in LP-1 stands (Table I). The mean number of occupied 20-y age classes was similar and low (5.3–6.0 for all stems; 2.1–3.0 for stems > 100 y old), indicating primarily high-severity fires across all structural groups except RF–MH (7.6 for all stems; 6.3 for stems > 100 y old). All 3 of the individual fires (1883, 1889, 1918) for which severity was determined were also primarily high-severity events across all structural groups, and they were among the most extensive (Table II). The 1889 fire was the largest recorded in the study area, the 1883 fire was 4th largest, and the 1918 fire was the 7th largest. Three other extensive fires also occurred in the 19th century, in 1864, 1885, and 1829. A fire in 1783 was the third largest overall and was the only fire to burn plots in all structural groups.

FOREST STRUCTURE AND FIRE REGIMES

Pulses and peaks of tree establishment in most structural groups reflect variation in fire characteristics, particularly recent large and severe fires (Figure 2), which likely consumed evidence of previous fires and thus weakened the relationship between fire and stand characteristics further back in time. Increased establishment in the first age class following the most recent large and severe fire is evident in all structural groups except RF–MH. Peak establishment occurs later, likely reflecting a combination of time required to grow to coring height, especially for seedlings that started under shrubs (Nagel & Taylor, 2005), and time required for reseeding from a forest edge (Greene & Johnson, 2000) following severe fire.

The effect of recent large and severe fires is particularly clear for the lowest-elevation MC and JP–WF groups. Fires in MC-1 stands were less frequent but primarily larger than those in MC-2 stands, and accordingly there were relatively fewer trees in MC-1 stands, particularly trees > 100 y old (Figure 2a). Both MC groups experienced peaks of establishment between 1915 and 1935, after the last large and high-severity fire (1889) in each group. Fires in JP–WF stands were slightly less frequent and more severe than those in MC stands, and fire sizes were intermediate (Figure 2b). Tree establishment and survival before 1900 was also intermediate. The last large fire in JP–WF stands, which was also high-severity, occurred later (1918) than in MC stands, and peak establishment also occurred later, between 1935 and 1955.

The return interval and size of fires and number of occupied 20-y age classes in RF–WF stands were within the range of those occurring in the lower elevation MC and JP–WF forests, and age structures were generally similar (Figure 2c). Both RF–WF groups showed peak establishment between 1915 and 1935, after the last large and high-severity fire (1889) in each group, which also burned at least 50% of plots in MC-1, MC-2, and JP–WF stands. Few trees survived the large fires that burned both RF-WF groups in 1864, 1883, and 1889.

The dominant effect of large and high-severity fires is also evident in the age structures of LP stands (Figure 2d). Major fires occurred in both LP groups in 1783 and 1883, and peak establishment occurred between 1895 and 1915, following the last large and high-severity fire (1883). A small pulse of establishment is evident in LP-2 stands following the 1783 fire, but no regeneration is evident following that fire in LP-1 stands. A fire in 1829 also burned both groups, but it was much larger in LP-1 (9 of 9 plots) than LP-2 stands (1 of 5 plots), and establishment and survival of trees in LP-1 stands is accordingly low between 1795 and 1835.

Only 2 fires were recorded in RF–MH stands, in 1783 and 1883, and there is no clear relationship between these fires and age structure (Figure 2e). The structure is unimodal, with establishment between 1795 and 1915, peaking between 1815 and 1895. Although more trees > 200 y old

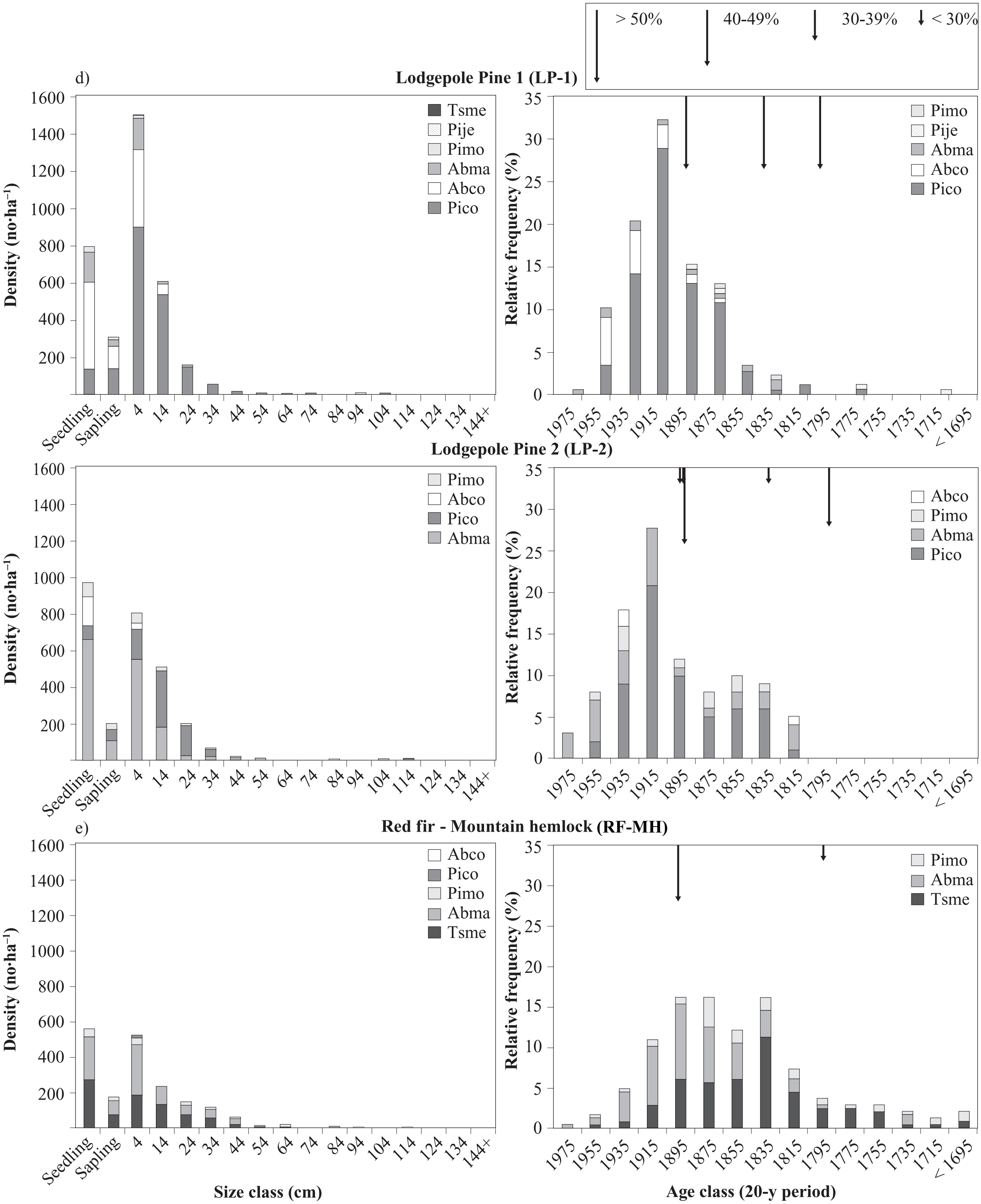

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TABLE I. Fire return interval, severity expressed as the number of 20-y age classes occupied, and fire extent in forest structural groups (see text) identified by the cluster analysis of 100 plots in the Thousand Lakes Wilderness.

Structural group	Point FRI (y)		Composite FRI (y)		Severity (Number of 20-y age classes occupied)						Extent (Mean % of plots burned)
					All stems			Stems > 100 y			
	Mean	Median	Mean	Median	Mean	Min	Max	Mean	Min	Max	
MC-1	22.4	13.0	11.1	10.5	5.6	3	9	2.6	1	5	45
MC-2	29.5	20.5	7.0	4.5	6.0	3	9	2.8	0	6	13
JP–WF	33.8	25.0	8.6	7.0	5.3	3	8	2.3	0	5	24
LP-1	55.6	50.0	50.0	50.0	5.9	3	8	3.0	1	5	85
LP-2	75.8	76.5	35.3	46.0	5.4	4	7	3.0	1	5	40
RF–WF-1	27.8	19.5	10.6	8.0	5.3	3	8	2.1	0	4	17
RF–WF-2	25.7	14.5	9.0	7.5	5.8	4	9	2.5	0	5	36
RF–MH	100.0	100.0	100.0	100.0	7.6	4	11	6.3	3	10	54

TABLE II. Fire extent, percentage of plots burned in the study area, and ID number (see Figure 1) of plots burned for the largest fires in the Thousand Lakes Wilderness, California.

Year	Size (ha)	% Plots burned	Plots burned (ID)
1889	1684	57	1; 4–56; 92–94
1864	1119	41	1; 4–12; 21–34; 38–39; 40–52; 55–56
1783	823	38	1–9; 14–18; 37; 57–70; 74–75; 77–80; 89–91
1883	776	32	2–3; 23–28; 36–37; 63–67; 72–76; 78–82; 85–86; 89–91; 100
1885	663	19	23–36, 52–56
1829	453	23	1–7; 29–31; 57–59; 62–66; 77–80; 100
1918	428	13	29–36; 52–56

are present in these stands than in any other structural group, relatively few apparently survived the 1783 fire. Many trees survived the only large fire recorded, in 1883, and establishment declined thereafter.

SUCCESSIONAL CHANGE

The differences in composition and density between canopy layers varied among structural groups (Figure 3). The length of vectors connecting canopy layers indicates the magnitude of compositional differences between layers in species density space. Vectors in MC-1, MC-2, and JP–WF stands all demonstrate a change from pine dominance to white fir, although the vectors are shorter for MC-2 stands. Vector lengths are longest in lodgepole pine stands, with both groups showing a strong shift from other species (*e.g.*, red fir, western white pine, and Jeffrey pine) in the canopy to lodgepole pine in the intermediate layer. Between the intermediate and understory layers LP-2 stands then shift back to red fir, while LP-1 stands shift to white fir. The RF–WF and RF–MH groups show little compositional change.

Discussion

The forest structural groups in TLW identified by the cluster analysis reflect the response of species to variation in topographically controlled temperature and moisture gradients, and the compositional pattern in TLW is similar to other locations in the southern Cascades (Taylor, 1990; Parker, 1991; 1992; Taylor, 2000; Beaty & Taylor, 2001; Taylor & Solem, 2001). Jeffrey, ponderosa, and sugar pines are concentrated at the lowest elevations and driest slope aspects, while mountain hemlock dominates the highest elevations and most mesic aspects. White fir and red fir dominate mid-elevations on all slope aspects, and lodgepole pine is concentrated in mesic flats.

Several studies have demonstrated the importance of variation in fire severity in promoting structural diversity in montane and upper montane forests in California at landscape scales (Taylor & Skinner, 1998; Beaty & Taylor, 2001; 2008). Moderate- to high-severity fires can strongly affect forest structure by killing many trees and promoting development of post-fire even-aged stands. On the other hand, low- to moderate-severity burns kill mainly smaller stems and thin-barked species, which promotes development of multi-aged forest stands. Our knowledge of the relative importance of high-severity fire in shaping montane and upper montane forest structure in California landscapes before widespread fire suppression and disturbance by Euro-Americans is limited, however. Evidence from the TLW indicates that high-severity fire was important in shaping stand structure in all but the highest-elevation forest. Forests in TLW differed in composition and density, but they had very similar size structures, and all except RF–MH had unimodal age structures with peaks of establishment between 1895 and 1955. All structural groups except RF–MH experienced primarily moderate- to high-severity fire based on the low number of occupied 20-y age classes. Moreover, shrub-fields (*Arctostaphylos patula*), which often establish following severe fires (Nagel & Taylor, 2005), were frequently found adjacent to plots, and dead shrubs were common beneath the canopy in JP–WF, MC, and RF–WF forests.

The 3 individual fires we could identify severity for (1883, 1889, and 1918) were mainly high-severity, and they were also widespread. Although widespread fires are not always more severe than small ones (Beaty & Taylor, 2007), the correspondence between fire extent and severity in TLW suggests that other large fires (*e.g.*, 1783, 1829, 1864) may also have been moderate- to high-severity events. In the

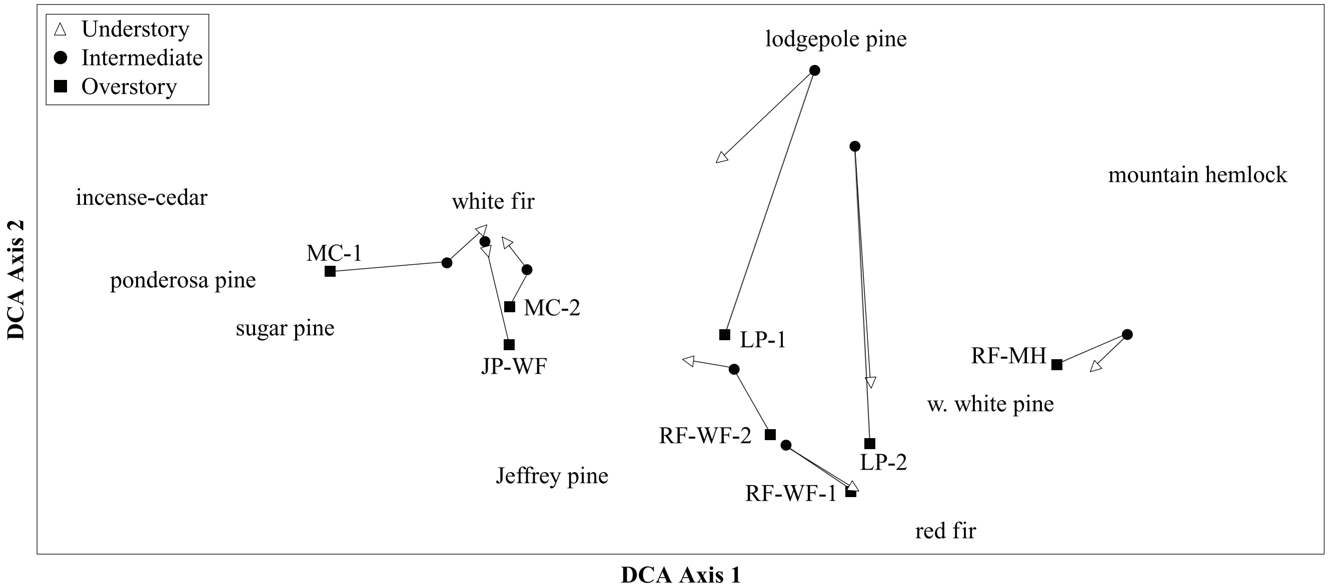

FIGURE 3. Patterns of species replacement in forest-structural groups. Vectors show the direction and magnitude of compositional differences between successively lower canopy layers. Acronyms are for forest-structural groups (see text). Species names represent regions of relative dominance in DCA species space.

nearby Cub Creek Research Natural Area, widespread and high-severity fires also burned in 1829, 1864, and 1889 (Beaty & Taylor, 2001), and extensive fires occurred in these years in other locations in the Cascades as well (Taylor, Trouet & Skinner, 2008). These fires all occurred in dry or very dry years in northern California according to tree-ring reconstructions of the Palmer Drought Severity Index (PDSI) (Cook & Krusic, 2004), and Taylor, Trouet, and Skinner (2008) demonstrated that regional fire activity is high in warm and dry years in all forest types in the southern Cascades. Climate has been increasingly identified as a key driver of moderate- and high-severity fire in western coniferous forests (Schoennagel, Veblen & Romme, 2004; Westerling *et al.*, 2006). The occurrence of high-severity fire in dry years in TLW is consistent with this view.

Fire severity in some montane forest landscapes in California (Taylor & Skinner, 1998; Beaty & Taylor, 2001; Beaty & Taylor, 2008) varies with slope position. Low- to moderate-severity fires are most common on valley bottoms and lower slopes, while moderate- to high-severity fires occur mainly on upper slopes. In TLW, there was little variation in fire severity by slope position. For example, RF–WF forests located on middle and upper slopes generally did not experience higher-severity fire than MC and JP–WF forests on lower slopes. Patterns of fire severity on the relatively gentle terrain in the TLW may be related more to periods of rapid spread and high fire intensity driven by wind and the presence of flammable shrub fields. Topographic control on spatial patterns of fire severity may emerge only when terrain complexity exceeds a certain threshold (Miller & Urban, 1999; 2000; Taylor & Skinner, 2003; Kellogg *et al.*, 2008).

Fire suppression in TLW is evident by the absence of fire since 1918 and massive 20th century tree establishment in most structural groups. Although differences among structural groups in the timing of the initial pulse of 20th century establishment correspond to differences in the date of the last large and severe fires, the large number and continually increasing proportion of shade-tolerant and fire-intolerant white fir and red fir suggests the effects of fire suppression. Understory density has also increased since 1918 in all structural groups, and the pattern is strongest in the lower-elevation MC and JP–WF forests and weakest in higher-elevation RF–MH. Montane pine-dominated forests that once experienced frequent fire in the southern Cascades (Taylor, 2000), Sierra Nevada (Vankat & Major, 1978; van Wagtendonk & Fites-Kaufman, 2006; Collins & Stephens, 2007; North, Innes & Zald, 2007), and in the interior west (Brown & Wu, 2005; Cocke, Fulé & Crouse, 2005; Sakulich & Taylor, 2007) have experienced increases in density due to fire suppression. The interpretation of increased density from stand structural analysis is supported by detailed reconstructions of early forest conditions (Fulé, Covington & Moore, 1997; Taylor, 2004; North, Innes & Zald, 2007), early forest survey data (McKelvey & Johnston, 1992; Scholl & Taylor, 2010) and forests with similar composition in northern Mexico with an intact fire regime (Minnich *et al.*, 2000; Stephens & Fry, 2005; Stephens & Gill, 2005). Increases in 20th century tree establishment may also be due to improved climatic conditions, but the asynchrony between peaks of establishment among stands (*e.g.*, peak establishment in LP stands occurred earlier than in those dominated by white fir and red fir, and the last large and severe fire also occurred earlier in LP stands) suggests that any climatic contribution is less important than changes in the fire regime.

The size and age structures of upper montane RF–WF forests show similar patterns of increasing understory density compared to lower montane forests, although dense understory stems began to establish earlier. Density increases in upper montane forests have also been attributed to the effects of fire suppression (Reynolds, 1959; Vankat & Major, 1978). Red fir is slightly less shade-tolerant and more fire-tolerant than white fir (Parker, 1986a), and fires do kill red fir stems in the understory (Kilgore & Briggs, 1972; Taylor, 1993; Chappell & Agee, 1996). Both white and red fir can regenerate continuously (Gordon, 1970; Parker, 1986a; Taylor, 1993; Chappell & Agee, 1996; Scholl & Taylor, 2006), so an increase in fire return interval could cause an increase in forest density. Median point return intervals of 14.5–19.5 y suggest that these forests may be outside the historical range of variability with respect to fire frequency. These point fire return intervals are shorter than those reported for forests with a similar composition in other parts of the southern Cascades (Taylor, 2000) and Sierra Nevada (Pitcher, 1987; Scholl & Taylor, 2006), and maximum point return intervals of 100 y were observed in TLW. Relatively continuous shrub fuels in our study area may have promoted spread to upper-elevation forest types compared to other fir-dominated forests in the southern Cascades.

The effects of fire suppression are not as evident in LP age and size structures. Median point intervals of 50–76.5 y in TLW and maximum point intervals of 100 y are not much shorter than the length of the fire suppression period. Long fire return intervals have also been reported for other lodgepole pine forests in the southern Cascades (mean composite FRI 59–67 y; Taylor & Solem, 2001) and the southern Sierra Nevada (mean composite FRI 31–98 y; Caprio, 2008). The longer fire return intervals in higher elevation LP and MH–RF forests are consistent with FRI patterns along elevation gradients in other parts of the western US (Schoennagel, Veblen & Romme, 2004; Cocke, Fulé & Crouse, 2005). 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.

LP stands had the highest understory densities of any structural group except MC-1, but they are not as dominated by shade-tolerant fir species as the lower montane groups, and lodgepole pine is still the dominant understory species in LP-1 stands. Three fires (1783, 1829, and 1883) were recorded in LP-1 stands, and each one burned a minimum of 78% of plots in this structural group. The size and severity of the 1883 fire explains the low density of large overstory trees and high understory density of LP-1 stands. High densities of lodgepole pine are typical of young stands developing after high-severity fire in many lodgepole pine forests (Sibold *et al*., 2007). Fires were more frequent and smaller in LP-2 stands on the slopes surrounding the Thousand Lakes Valley. Most of these fires were probably surface burns, producing a multi-aged structure with relatively less dense understories and denser overstories than LP-1 stands.

Understory densities in RF–MH stands are also increasing, but they were the lowest of any structural group, suggesting that fire suppression has had little impact on these forests. The single fire (1883) recorded in these stands did not have any clear effect on age structure or stand density. Fire return intervals suggest that the period of fire suppression is not much shorter than the fire return interval, so these stands are probably not outside of their historical range of variability. The low number of trees in age classes prior to 1775–1795, and the increase in establishment thereafter, suggests that the extensive 1783 fire may have been moderate- to high-severity and burned many plots in this group, but most evidence of the fire was subsequently erased.

The ordination of canopy layers illustrates compositional shifts from shade-intolerant and fire-tolerant species to shade-tolerant and fire-intolerant species over the past 100 y, probably due to > 100 y of fire suppression. This pattern is also characteristic of conifer forests that once experienced frequent fire elsewhere in the western US (Schoennagel, Veblen & Romme, 2004; Cocke, Fulé & Crouse, 2005; Sakulich & Taylor, 2007). Although compositional changes are evident in all structural groups in TLW except for RF–MH stands, there is variation among groups. Compositional changes in MC-2 stands are not as strong as those in MC-1 and JP–WF stands. There is some pine regeneration in these stands, and although white fir is increasing dramatically in density, it is also relatively abundant in the overstory and intermediate layers. MC-2 stands are on average higher in elevation than MC-1 and JP–WF groups, which favours white fir over pines in the Lassen region (Barbour, 1988; Parker, 1991).

Lodgepole pine in the southern Cascades and northern Sierra Nevada occurs as self-replacing stands on topographic lowlands with poorly drained soils and cold air drainage and as a seral species undergoing replacement by red fir or white fir on better sites (Parker, 1986b; 1992; 1993; Taylor, 2000; Taylor & Solem, 2001). In the interior western US, lodgepole pine establishes after high-severity fire and is a seral species (Schoennagel, Veblen & Romme, 2004) except on harsh sites with few competitors (Despain, 1983). In TLW, the 2 LP groups are differentiated by these same characteristics. The overstories are dominated by species (*e.g*., red fir, western white pine, and Jeffrey pine) that are more fire-resistant and longer-lived than lodgepole pine, while the intermediate layers are dominated by lodgepole pine that established after the large and moderate- to high-severity 1883 fire. Thus, the stands exhibit a strong compositional shift from other species in the overstory towards lodgepole pine in the intermediate layers, and the magnitude of the change between overstory and intermediate layers is amplified by the few Jeffrey pine, western white pine, and red fir overstory stems that survived previous fires. LP-1 and LP-2 stands then diverge between the intermediate and understory layers, with LP-2 stands shifting strongly towards red fir and LP-1 stands shifting more weakly towards white fir. Lodgepole pine is regenerating well in LP-1 stands despite the high density of the understory, and the poorly drained soils and cold air drainage of the Thousand Lakes Valley probably help to maintain lodgepole pine in these stands. LP-2 stands occur on lower slopes surrounding the valley on better-drained volcanic soils where red fir is more successful. Overall, LP-1 stands are more compositionally stable than LP-2 stands, but the presence of fir species in the understories of both groups suggests that fire is important in maintaining lodgepole pine in TLW, as has been found for sites in the southern Sierra Nevada (Caprio, 2008).

The relatively short vector lengths in RF–WF and RF–MH stands indicate that they are mostly compositionally stable. The compositional stability and coexistence of red fir, mountain hemlock, and western white pine in RF–MH stands on high-elevation, north-facing slopes with occasional moderate- to high-severity fire is consistent with other studies in the Cascades (Taylor, 1990; Chappell & Agee, 1996).

Conclusion

Structural variation in TLW forests reflects the influence of extensive and moderate- to high-severity fires, particularly in the late 1800s, as well as fire suppression efforts beginning in the early 1900s. All forest-structural groups except the highest elevation RF–MH have few stems > 100 y old and exhibit distinct pulses of recruitment that occurred soon after the last large fire to burn a group. Most groups have also undergone increases in density and are experiencing compositional shifts from shade-intolerant and fire-tolerant pines to shade-tolerant and fire-intolerant fir in response to fire suppression. These changes are most pronounced in lower montane mixed conifer and JP–WF forests and those dominated by lodgepole pine, but increases in the understory density of shade-tolerant species are also evident in upper montane RF–WF forests where fires were less frequent prior to suppression efforts. Lodgepole pine forests, particularly stands located on lower slopes surrounding the Thousand Lakes Valley, are the most unstable compositionally and will be increasingly dominated by red fir and white fir in the absence of fire in the future.

Fire regimes in low-elevation mixed conifer forests have been characterized as frequent and low- to moderate-severity (Kilgore, 1973; Kilgore & Taylor, 1979; Bonnicksen & Stone, 1982; Agee, 1993). However, high-severity fires had a dominant influence on mixed conifer stands in TLW, as well as all other forest-structural groups except RF–MH. Moreover, extensive and high-severity fires burned across all slope positions and aspects (Bekker & Taylor, 2001), probably due to the relatively undifferentiated topography of TLW. These extensive and severe fires have produced similar size structures across forest types. Continued fire suppression will homogenize forest structure and composition at stand and landscape scales, and these characteristics combined with the smooth terrain of TLW may perpetuate a regime of large and severe fires.

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