Mixed-conifer forests of central Oregon: effects of logging and fire exclusion vary with environment

Citation	Merschel, A. G., Spies, T. A., & Heyerdahl, E. K. (2014). Mixed-conifer forests of central Oregon: Effects of logging and fire exclusion vary with environment. Ecological Applications, 24(7), 1670-1688. doi:10.1890/13-1585.1
DOI	10.1890/13-1585.1
Publisher	Ecological Society of America
Version	Version of Record
Terms of Use	http://cdss.library.oregonstate.edu/sa-termsofuse

Ecological Applications, 24(7), 2014, pp. 1670–1688

Mixed-conifer forests of central Oregon: effects of logging and fire exclusion vary with environment

Andrew G. Merschel,[1,4] Thomas A. Spies,[2] and Emily K. Heyerdahl[3]

[1]*College of Forestry, Oregon State University, Corvallis, Oregon 97331 USA*
[2]*USDA Forest Service, Pacific Northwest Research Station, Corvallis, Oregon 97331 USA*
[3]*USDA Forest Service, Rocky Mountain Research Station, Missoula, Montana 59808 USA*

Abstract. Twentieth-century land management has altered the structure and composition of mixed-conifer forests and decreased their resilience to fire, drought, and insects in many parts of the Interior West. These forests occur across a wide range of environmental settings and historical disturbance regimes, so their response to land management is likely to vary across landscapes and among ecoregions. However, this variation has not been well characterized and hampers the development of appropriate management and restoration plans. We identified mixed-conifer types in central Oregon based on historical structure and composition, and successional trajectories following recent changes in land use, and evaluated how these types were distributed across environmental gradients. We used field data from 171 sites sampled across a range of environmental settings in two subregions: the eastern Cascades and the Ochoco Mountains.

We identified four forest types in the eastern Cascades and four analogous types with lower densities in the Ochoco Mountains. All types historically contained ponderosa pine, but differed in the historical and modern proportions of shade-tolerant vs. shade-intolerant tree species. The Persistent Ponderosa Pine and Recent Douglas-fir types occupied relatively hot–dry environments compared to Recent Grand Fir and Persistent Shade Tolerant sites, which occupied warm–moist and cold–wet environments, respectively. Twentieth-century selective harvesting halved the density of large trees, with some variation among forest types. In contrast, the density of small trees doubled or tripled early in the 20th century, probably due to land-use change and a relatively cool, wet climate. Contrary to the common perception that dry ponderosa pine forests are the most highly departed from historical conditions, we found a greater departure in the modern composition of small trees in warm–moist environments than in either hot–dry or cold–wet environments. Furthermore, shade-tolerant trees began infilling earlier in cold–wet than in hot–dry environments and also in topographically shaded sites in the Ochoco Mountains. Our new classification could be used to prioritize management that seeks to restore structure and composition or create resilience in mixed-conifer forests of the region.

*Key words: central Oregon, USA; Douglas-fir (*Pseudotsuga menziesii*); eastern Cascade Range, Oregon, USA; fire exclusion; gradient analysis; grand fir (*Abies grandis*); historical density of ponderosa pine; mixed-conifer forest; mixed-severity fire regime; Ochoco Mountains, Oregon, USA; ponderosa pine (*Pinus ponderosa*); white fir (*Abies concolor*).*

Introduction

In mixed-conifer forests across the North American Interior West, recent land-use change has increased both the density of trees and the dominance of shade-tolerant trees while reducing the density of large, old pine trees (Covington and Moore 1994, Arno et al. 1997, Everett et al. 1997, Sloan 1998, Camp 1999, Smith and Arno 1999, Grissino-Mayer et al. 2004, Perry et al. 2004, Fulé et al. 2009, Scholl and Taylor 2010). In the interior Pacific Northwest, where ponderosa pine (*Pinus ponderosa*) can be successional to Douglas-fir (*Pseudotsuga menziesii*) and grand fir (*Abies grandis*), frequent surface fires historically maintained the dominance of ponderosa pine (Agee 1993). Land-use changes, including fire exclusion, began in the late 19th century (Weaver 1943, Speer 1997, Heyerdahl et al. 2001, Youngblood et al. 2004) and have increased canopy continuity, canopy layering, and the density of grand fir and Douglas-fir (shade-tolerant species; Weaver 1959, Sloan 1998, Powell 2011). These changes were intensified by selective harvesting of large-diameter ponderosa pine and Douglas-fir in the early 20th century followed by management of advanced regeneration (Seidel 1981, Hessburg and Agee 2003), which created canopy gaps that favor development of shade-tolerant trees (Hessburg and Agee 2003, Fitzgerald 2005, Naficy et al. 2010).

Manuscript received 15 August 2013; revised 26 February 2014; accepted 27 February 2014; final version received 19 March 2014. Corresponding Editor: Y. Pan.
[4] E-mail: andrew.merschel@oregonstate.edu

Succession in mixed-conifer forests in the absence of fire has ecological consequences for a variety of plant and animal species. Although late-successional, mixed-conifer forest was a component of many landscapes prior to fire exclusion (Camp et al. 1997), many other relatively open, fire-resilient forests dominated by ponderosa pine have been converted to forests with dense, shade-tolerant understories, which has reduced habitat for at-risk plant and animal species due to increased mortality from high-severity wildfire, insect outbreaks, and drought (Hessburg et al. 1994, Sloan 1998, Camp 1999, Hemstrom 2001, Agee 2003, Fitzgerald 2005, Hessburg et al. 2005, Powell 2011). While fire exclusion can increase habitat for species associated with dense, late-successional forest (e.g., the threatened Spotted Owl *Strix occidentalis*), it simultaneously decreases habitat critical to species associated with open or patchy forests (e.g., the White-headed Woodpecker *Picoides albolarvatus*, a species of concern in Oregon). Managers are currently faced with the dilemma of maintaining habitat for species with a variety of habitat needs while simultaneously restoring the long-term resiliency of mixed-conifer forest to fire and other disturbances (Buchanan 2010).

Mixed-conifer forests are found in a broad range of climatic settings in mountainous topography in central Oregon, USA (Franklin and Dyrness 1988). Given that the physical and climatic environment is associated with variation in structure, composition, and historical disturbance regime (Ohmann and Spies 1998, and Hemstrom 2001), it is likely that the response to fire exclusion and selective harvesting is variable in mixed-conifer forest (Camp 1999, Naficy et al. 2010). Elsewhere in the Interior West, tree ring reconstruction of fire regimes has shown that mixed-conifer forest at lower elevations historically had a frequent low-severity fire regime similar to ponderosa pine forest but that fire frequency decreased and severity increased with elevation (Brown et al. 1999, Veblen et al. 2000, Stephens 2001, Fulé et al. 2003, Sherriff and Veblen 2006, Brown et al. 2008, Fulé et al. 2009, Heyerdahl et al. 2012). However, among these regions the historical predominance of low-, mixed-, and high-severity fire was variable, and appropriate management and restoration actions likely vary within and among regions (Agee 1993). While historical fire regimes have been reconstructed in other regions, they are inadequately described but likely complex in central Oregon. In this region, current debates about the need to restore mixed-conifer forests (Baker 2012) reflect a need to better understand environmental variation in the drivers of 20th-century change as well as variation in the magnitude of change in the density and dominance of shade-tolerant species (Hessburg and Agee 2003, Perry et al. 2004, 2011, Baker 2012).

Spies et al. (2006) suggested that updated definitions of structure and composition were needed to describe the current state of mixed-conifer forest, and they organized it into types based on historical disturbance regime and response to recent land-use changes. Mixed-conifer forest in central Oregon has previously been classified into categories of potential (Johnson and Clausnitzer 1992, Simpson 2007) and current vegetation (Rollins 2009). While potential vegetation classifications effectively stratify mixed-conifer forest into different environmental settings, actual structure and composition within a potential vegetation type varies and depends on the historical disturbance regime, recent land use and management, and the landscape context of an individual site. Classifications of potential vegetation based on current composition are used to infer historical disturbance regimes and vegetation structure, but they are inadequate because they were developed nearly a century after land-use changes and do not account for how historical fire regimes altered potential vegetation. Similarly, classifications of current vegetation do not describe historical vegetation and successional trajectories. A classification that incorporates biophysical setting, historical disturbance regime, and response to recent land-use changes would be more appropriate to guide management and restoration of mixed-conifer forest.

Historical and current structure and composition coupled with land-use history has proven to be a robust approach for describing past forest stand history and past and present forest dynamics (Abrams and Copenheaver 1999, Youngblood et al. 2004, Scholl and Taylor 2010, Taylor 2010). Previous dendroecological studies in mixed-conifer forest of central Oregon were limited in extent (Perry et al. 2004). While Camp (1999) and Hagmann et al. (2013) examined response to land-use changes in other regions, our study is unique in its geographic focus and scope and for characterizing variation in forest structure and dynamics across environments, ranging from hot and dry pine and mixed-conifer forest types to cold and wet mixed-conifer forest across ecoregions.

Our first objective was to identify mixed-conifer forest types based on both historical conditions and response to recent changes in land use. We did this by reconstructing harvested large, old-growth trees from stumps and by sampling live trees and snags at 81 sites and combining these data with existing data sampled similarly at 90 plots for another study (Heyerdahl et al. 2014). Our second objective was to determine how vegetation response to land-use change varied with environmental setting. The resulting characterization of variability in mixed-conifer forest associated with environmental gradients provides a basis for understanding drivers of successional and disturbance dynamics of these forests and a template for ecological management at the subregional scale.

Methods

Study area

We sampled mixed-conifer forests in two subregions: the eastern slope of the Oregon Cascade Range on the

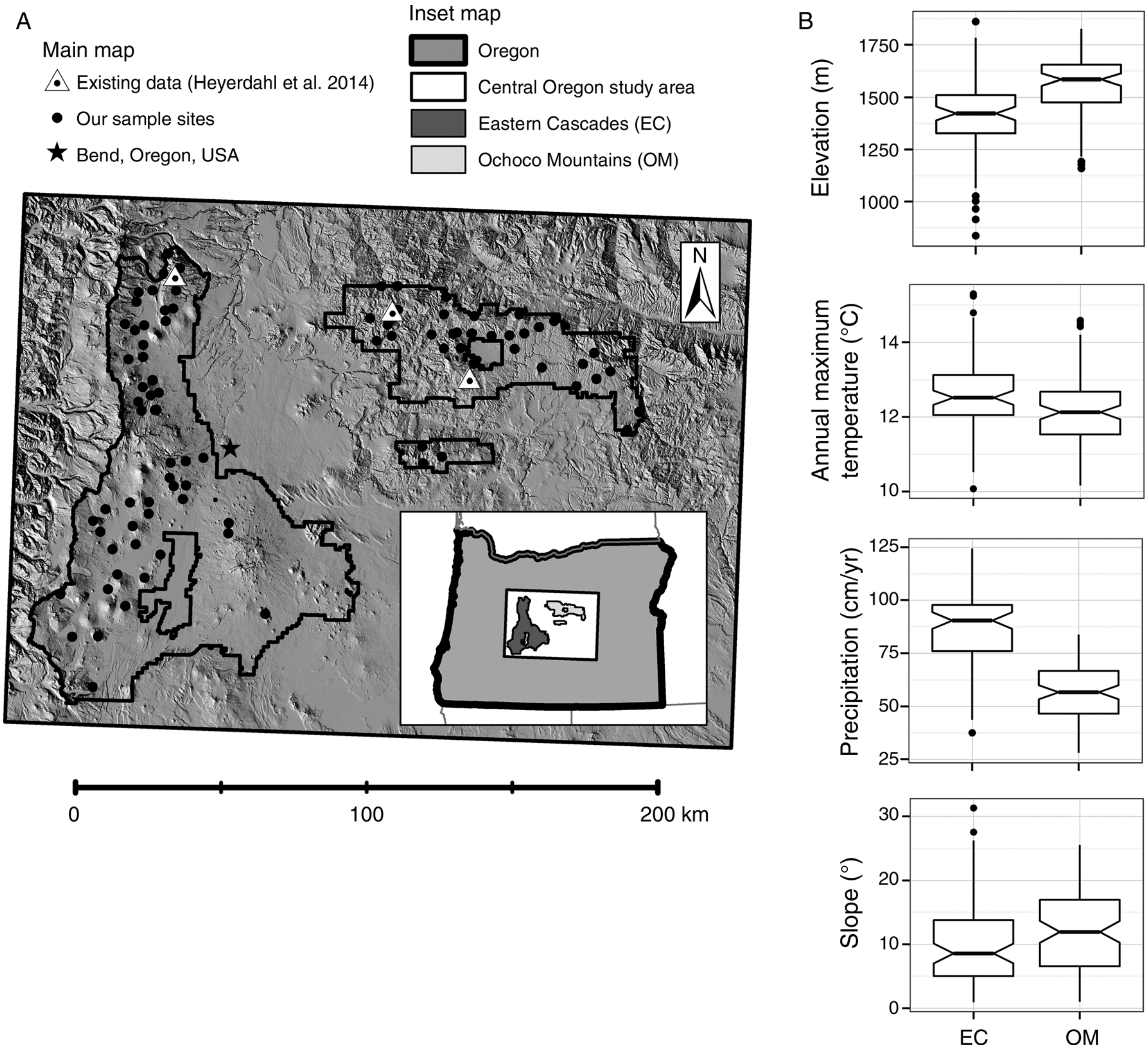

FIG. 1. (A) Locations of mixed-conifer forest sites analyzed for this study, including both those we sampled during this study and existing sites sampled for another study (Heyerdahl et al. 2014) in the eastern Cascade (EC) Range and the Ochoco Mountains (OM) subregions in Oregon, USA. (B) Variation in the environmental settings of the two subregions based on environment at sample sites. The line at the notch of each box represents the median value. Box endpoints represent the first and third quartiles (25% to 75% range of the data). Whiskers extend from the 10th to the 90th percentile. Points represent outliers or data that were outside the 10th to the 90th percentile range represented by the whiskers. Where boxplot notches do not overlap, there is strong evidence that median values are significantly different.

Deschutes National Forest, and across the Ochoco Mountains on the Ochoco National Forest (Fig. 1A). Throughout the Interior West, the structure and composition of this forest type vary with temperature and precipitation, which in turn vary strongly with topography and distance from the Pacific Ocean (Ohmann and Spies 1998, Camp 1999) so that different forest types can occur in similar topographic settings across the region. Because climatic vs. topographic drivers may vary across the more topographically rugged Ochoco Mountains, which are further east than the eastern Cascades, and there are clear differences in the climates of these subregions (Fig. 1B), we analyzed the subregions separately.

Throughout central Oregon, land-use change since the late 19th century is similar to much of the Interior West (Hessburg and Agee 2003). Domestic livestock grazing began in the 1860s and rapidly intensified within a few decades (Coville 1898, Hodgson 1913, Wentworth 1948, Oliphant 1968). Industrial clear-cutting and high-grade logging of ponderosa pine was heaviest from 1925 to 1946 but continued until the late 20th century (Hessburg and Agee 2003). Forest fires were largely excluded by the late 1800s (Speer 1997, Heyerdahl et al. 2001, Youngblood et al. 2004, Heyerdahl et al. 2014), followed by active fire suppression, which was most effective after World War II (Pyne 1997, Hessburg and Agee 2003).

Site selection

Our goal was to sample the range of variation in the structure and composition in late-successional, mixed-conifer forests in the eastern Cascade and Ochoco Mountains. We combined 81 sites that we sampled extensively across the two subregions (46 sites in the eastern Cascades and 35 sites in the Ochoco Mountains) with 90 plots that were intensively sampled on dense grids at three sites for another study (one site with 30 plots in the eastern Cascades and two sites with 60 total plots in the Ochoco Mountains; Heyerdahl et al. 2014; Fig. 1A).

The potential sampling area included mixed-conifer forests identified by potential vegetation (plant association groups), distributed across a wide range of forest structures using current vegetation (Gradient Nearest Neighbor [GNN] Map; Ohmann and Gregory 2002; *available online*).[5] We excluded areas near roads (<55 m) or the edge of patches (<60 m) and areas burned severely in the Bear and Bryant Complex and Davis Lake fires in 2003 (Eckert et al. 2008). We limited the potential sampling area to mixed-conifer plant association groups (including Wet Ponderosa Pine, Douglas-Fir, and Grand–White Fir) using local classifications (Bauer 1988, Ochoco National Forest 2008), including Wet Ponderosa Pine because it is often transitional to the Douglas-Fir and Grand–White Fir plant association groups (Simpson 2007). The map of current vegetation (GNN) was used to limit the potential sampling area to forested areas (>20% canopy) within putative areas of older forest (>5 large trees/ha). We defined large trees as those > 50 cm in diameter at breast height (dbh) of 137 cm, consistent with old-growth definitions of large trees in the region (Hopkins et al. 1992), and eastside screens, which prohibit harvest of trees with dbh > 50 cm (Brown 2012). We stratified our random sample site locations by the current density of large trees by placing half of the sites in areas where GNN mapping predicted >5 large trees/ha, and the other half in areas with predicted densities of >25 large trees/ha. We included sites that currently have low canopy cover and low densities of large trees to include areas that may have been recently thinned or harvested, as well as sites with low densities of large trees resulting from low productivity or disturbance history.

Historical and modern forest composition and structure

To characterize structure and composition, we used a widely employed design validated for measuring large and small (<50 cm dbh) trees at the scale of 1 ha: the Forest Inventory and Analysis Annual Plot Design (Bechtold and Patterson 2005). Each site was sampled with four adjacent circular plots (0.1 ha), and each plot contained one subplot (0.02 ha; Merschel 2012). In each plot, we recorded the species and dbh of all large live trees and snags (>50 cm dbh), and the species, cut height, and diameter at cut height (dch) for all large stumps (>50 cm dch). In each subplot, we recorded the same information but for all trees and snags >10 cm dbh. White fir (*Abies concolor*) and grand fir (*Abies grandis*) hybridize in parts of central Oregon but are difficult to distinguish in the field (Zobel 1973); we did not attempt to separate these species but combined them and refer only to grand fir.

We found widespread evidence of selective harvesting in both subregions, but harvesting intensity varied. At least five large stumps (range 0 to 70 large stumps/ha; mean 18 stumps) occurred in most (60%) of the sites. In the office, we identified large trees from the 966 stumps measured at our sites by projecting the diameter at *breast* height of each stump that was at least 50 cm in diameter at *cut* height. Cut heights ranged from 10 to 120 cm (mean 44 cm), so we derived species-specific empirical taper equations for ponderosa pine, grand fir, and Douglas-fir (Appendix A) by measuring the diameter of 50 live trees of each species at 10 cm, 40 cm, and 137 cm on trees in several of our plots in both subregions. We developed separate equations for the average taper from 10 cm to breast height and from 40 cm to breast height to accommodate the range in cut heights. We included these reconstructed large trees in our identification of forest types and also considered harvesting intensity in our interpretations of differences in recent succession among those types.

Chronologies of tree establishment

We collected increment cores from only 62 of the 81 sites we sampled because nearly all the large trees (>50 cm dbh) had been harvested from the remaining sites. We bored up to 12 trees for each species represented at a site (commonly ponderosa pine, Douglas-fir, or grand fir) by extracting three cores from four dbh classes (10–29 cm, 30–49 cm, 50–69 cm, and >70 cm). However, we sometimes sampled fewer than 12 trees because shade-tolerant species were often absent from the large-diameter classes, and intolerant species were often absent from the small-diameter classes. We did not remove wood samples from stumps but instead bored large trees of the same species that were within 50 m of the plot center in areas of similar stand structure and composition. In total, we sampled 1433 trees with a range of 15 to 42 trees per site (mean 23 trees).

Cores were collected at a height of 40 cm, but at 1.37 m for trees with rot. All increment cores were mounted and sanded until the cell structure was visible with a binocular microscope (Stokes and Smiley 1996). We visually crossdated the oldest and highest quality samples using the list-year method (Yamaguchi 1991), then measured the widths of these rings using a Velmex sliding stage micrometer with a precision of 0.001 mm (TA Unislide, Bloomfield, New York, USA). Cross-

[5] http://lemma.forestry.oregonstate.edu/data

dating accuracy was evaluated statistically using the software program COFECHA, Version 6.06P (Holmes 1983, Grissino-Mayer 2001), and samples with potential errors identified by COFECHA were visually checked, redated, and remeasured as necessary. We assigned calendar years to the annual rings of the remaining samples using a combination of visual crossdating of ring widths and cross-correlation of measured ring-width series (Holmes 1983, Swetnam et al. 1995). For cores that did not intersect the pith, we estimated the number of rings to pith geometrically (average correction 6 yr, range 1–20 yr; Applequist 1958, Duncan 1989). We could not crossdate and/or estimate pith dates for samples from 54 large trees, so we excluded them from analyses of establishment history but included them in analyses of composition and structure.

We incorporated establishment data collected for this study with existing data on the composition, structure, and establishment dates of mixed-conifer forest that were collected in 90 plots for another study in central Oregon (Heyerdahl et al. 2014; Fig. 1). In 30 plots (0.17 ha average) at each of three gridded 800-ha sites, the species and dbh of 30 live or dead trees (stumps, snags, or logs) > 20 cm dbh was recorded, for a total of 2702 trees. Increment cores from live trees and partial sections from dead trees were removed at 15 cm height from trees lacking rot, and establishment dates were obtained through crossdating for most of them (2126 trees). Small trees (10–19.9 cm dbh) were tallied by species and diameter class in a 5.64 m radius subplot. We applied the taper equations (Appendix A) to identify large harvested trees from the 123 stumps that occurred at these sites.

Age structure was similar for sites we sampled vs. those sampled by Heyerdahl et al. (2014), despite differences in our sampling schemes. Most of the dead ponderosa pine that were aged in this way were one to several centuries old, and most dead Douglas-fir and grand fir were <110 years old with the exception of 10 large old Douglas-fir distributed across the three sites. To avoid the hazards of interpreting static age structure of live trees (Johnson et al. 1994), we did not interpret a lack of trees in any age class at the present as evidence that there never were any individuals in that age class. In our interpretations of age structure we allow for an alternative hypothesis that a lack of trees within an age class may arise from past mortality and a lack of available evidence on the landscape.

Classification of forest types based on historical and modern composition and structure

We identified forest types with hierarchical agglomerative clustering, using a Sorensen distance measure with a flexible beta method of $\beta = 0.25$. For this and subsequent multivariate analyses, we used PC ORD, version 6 (McCune and Mefford 2010). We created one species–size matrix for each subregion that included both stand composition and structure in a combined species–size variable. We assigned the three major species (ponderosa pine, Douglas-fir, and grand fir) to four dbh size classes (10–29 cm, 30–49 cm, 50–69 cm, >70 cm), and three minor tree species (western larch, lodgepole pine, and western juniper) to two (<50 cm and >50 cm dbh). However, lodgepole pine did not occur in the >50 cm size class, resulting in 17 unique species–size class variables. For each variable, we calculated the combined density of live trees, snags, and reconstructed stumps. We replaced all zeros with ones (McCune and Grace 2002), then log-transformed the matrices because density varied more than an order of magnitude within some classes. Using Euclidean distance, we identified four potential outliers, i.e., densities > 2 SD from the mean of that species–size variable. All of these outliers had high densities of understory trees but were retained in subsequent analyses because there was no ecologically meaningful reason to exclude them.

The resulting dendrograms were scaled by Wishard's objective function (the sum of the error sum of squares from each group centroid to the group members), which was scaled to the percent of information remaining (McCune and Grace 2002). Dendrograms were pruned by examining stem length and branching distribution to identify nodes that maximized both within-group homogeneity and between-group differences, while minimizing the number of groups (McCune and Grace 2002).

Environmental setting of forest types

We identified the climatic and topographic settings of the forest types with clustering using nonmetric multidimensional scaling (NMS; Mather 1976). As input to NMS, we constructed an environmental matrix for each subregion that included 13 quantitative variables describing the location, climate, and physiographic setting of each site (Table 1). NMS was conducted using the slow and thorough autopilot method with random starting configurations. Two hundred and fifty runs were conducted, with a maximum of 500 iterations per run with a stability criterion of 0.00001. Significance of the ordination axes was evaluated with a Monte Carlo test with 250 iterations. We related the structure and composition of our forest types to the environmental matrix with a biplot overlay where the length of vectors was proportional to the strength of correlation between environmental variables and ordinations axes.

We assessed distinctiveness of the forest types in environmental ordination space visually and also statistically using the Multi-Response Permutation Procedure (MRPP; Biondini et al. 1988). Prior to MRPP, we equalized variance and standardized variables measured on different scales by subtracting the mean and dividing by the standard deviation of each environmental variable. We then used MRPP to test the hypothesis of no difference among groups in environ-

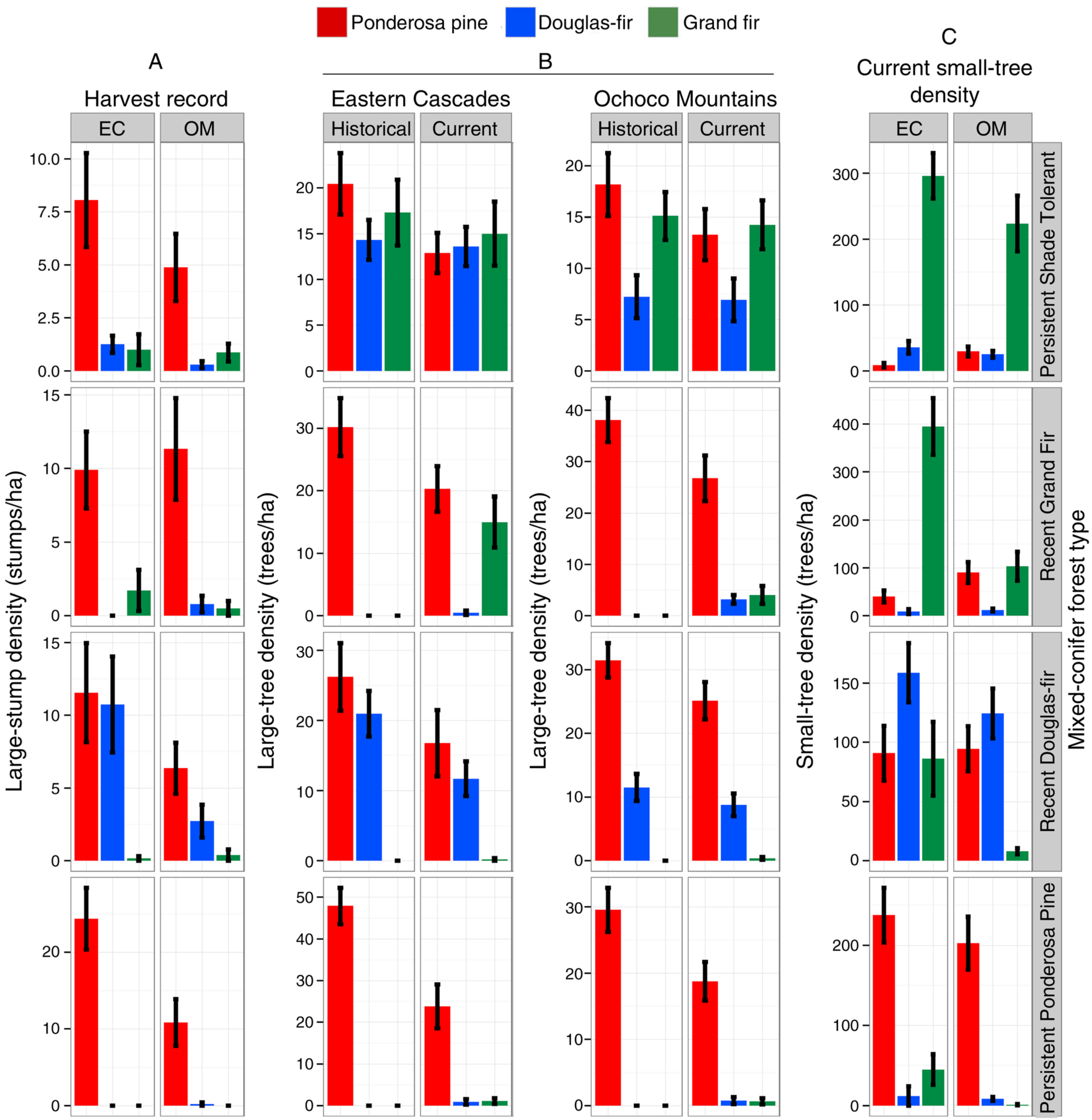

FIG. 2. Reconstructed and current composition and structure of the four mixed-conifer forest types (right-hand axis labels) in the eastern Cascades (EC) and Ochoco Mountains (OM) subregions. (A) Stump density by type and subregion, (B) historical vs. current density of large trees by type and subregion, and (C) current small-tree density. Values are means ± SE. All four types include a small percentage of minor tree species that are not shown (0–17%).

mental ordination space using Euclidean distance because Sorenson's distance measure is incompatible with the negative numbers produced through standardization.

Environment and variation in initiation of shade-tolerant cohorts

We assessed whether the timing of infilling by shade-tolerant trees varied with climate and topography using linear regression with the NMS ordination axes as predictors of the mean age of shade-tolerant trees at each site, i.e., the mean age of the most shade-tolerant species at each site (grand fir at 75% of sites and Douglas-fir at the other sites). We used axis 1 as the sole predictor variable in the eastern Cascades because axis 2 was primarily associated with latitude, and we had a greater percentage of plots in the northern portion of the subregion. These regressions met the assumptions of linearity (assessed with residual plots and standardized residual vs. predicted value plots) and equal variance (assessed with quantile–quantile plots).

TABLE 1. Environmental variables used to assess relationships between environment and species–size variables or forest types in the eastern Cascade Range and the Ochoco Mountains of Oregon, USA.

Variable	Units	Description
Physical location		
Easting	m	*x*-coordinate of sample site in Universal Transverse Mercator North American Datum 83 projection
Northing	m	*y*-coordinate of sample site in Universal Transverse Mercator North American Datum 83 projection
Climate		
Temperature	°C	mean annual maximum temperature (1971–2000; PRISM 2012)
Precipitation	cm	total annual precipitation (1971–2000; PRISM 2012)
Topographic position		
Elevation	m	sample height above sea level
Slope gradient	%	slope steepness
Transformed aspect	unitless	aspect, transformed to a continuous variable ranging from 0 (southwest) to 2 (northeast; Beer 1966). Asp = 1 + cos(45° − aspect)
Direct incident radiation	$\mathrm{MJ \cdot cm^{-1} \cdot yr^{-1}}$	maximum potential annual solar radiation (McCune and Dylan 2002)
Heat load	unitless	index of potential direct incident radiation adjusted for aspect and slope (McCune and Dylan 2002)
Potential relative radiation	unitless	relative annual solar insolation, accounting for shading by surrounding topographic features (Pierce et al. 2005)
Topographic position index (TPI)	m	focal pixel height above the minimum elevation in a neighborhood of radius 150 m (fine), 300 m (medium), and 450 m (coarse); neighborhood diameter is 1/4 the median slope length (Weiss 2001)

RESULTS

Classification of forest types based on historical and modern composition and structure

We identified four structure–composition types, hereafter forest types, in each subregion (Fig. 2; see Plate 1). Dendrograms for both subregions were pruned with ~40% information remaining, and branching was concentrated at short distances, producing five and four homogenous forest types in the eastern Cascade Range and Ochoco Mountains, respectively (Appendix B). The four types we identified in the Ochoco Mountains were analogous in historical and modern forest structure and composition to those we identified in the eastern Cascades but had lower tree densities. We do not describe one of the eastern Cascades types further (High-elevation Grand Fir), because it included only five sites and lies near, but outside, the upper elevational limit of mixed-conifer forests in the subregion. We included these five sites in nonmetric multidimensional scaling (NMS) ordinations to capture the upper limit in elevation of the mixed-conifer forest in the eastern Cascades. The remaining eight forest types included 14–26 sample sites (mean 21). The data upon which we based these classifications are publicly available (Merschel et al. 2014).

Our forest types describe both historical conditions and response to recent changes in land use because they include reconstructed large (>50 cm dbh) overstory trees as well as young trees that established in the last century. Both elements were included in development of forest types to identify associations of historical structure and composition and recent successional trajectories with environmental setting in subsequent ordinations. We named the types to reflect the dominant understory tree species and indicated the historical predominance of that species in the type. In Persistent Ponderosa Pine sites, large and small trees were dominated by ponderosa pine (Fig. 2B, C). Small trees also included minor amounts of Douglas-fir, grand fir, and minor species (lodgepole pine in the eastern Cascades and western juniper in the Ochoco Mountains). In Recent Douglas-fir sites, large trees were codominated by ponderosa pine and Douglas-fir. Small trees were dominated by Douglas-fir and grand fir in the eastern Cascades, but only by Douglas-fir in the Ochoco Mountains. In Recent Grand Fir sites, large trees were dominated by ponderosa pine, but large grand fir was codominant in the eastern Cascades. Small trees were dominated by grand fir in the eastern Cascades, but codominated by grand fir and ponderosa pine in the Ochoco Mountains. In Persistent Shade Tolerant sites, large trees were a mix of ponderosa pine, Douglas-fir, and grand fir, with a minor component of western larch in both subregions. Small trees were dominated by grand fir.

In the 20th century, the density of large trees was roughly halved by harvesting in all forest types (Fig. 2A). Historical and current large-tree densities differed significantly in each subregion (14 trees/ha [df = 135, t = 4.4, P = 0.001] in the eastern Cascades vs. 8 trees/ha [df = 186, t = 3.3, P = 0.001] in the Ochoco Mountains; two-sample t tests). However, the mean reduction varied among forest types from 6 to 26 trees/ha. Ponderosa pine was preferentially harvested in all types with the exception of Recent Douglas-fir in the eastern Cascades, where large Douglas-fir also were harvested (40% reduction in mean density of large Douglas-fir). In the eastern Cascades, large ponderosa pine reduction was highest in the Persistent Ponderosa Pine type (mean 26 trees/ha, median 33 trees/ha). In contrast, in the Ochoco

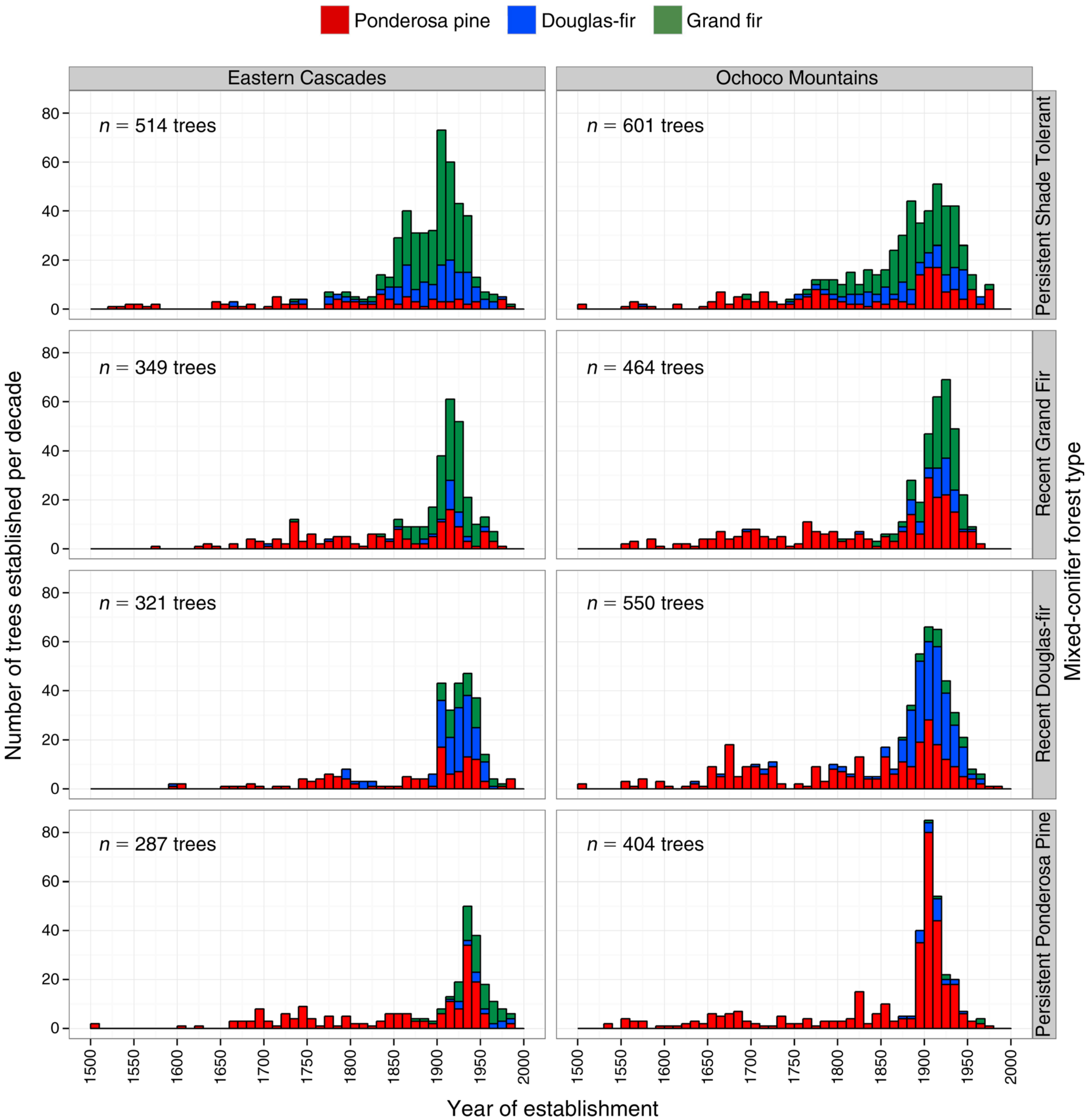

FIG. 3. Dates of tree establishment over a 500-year period, by forest type, including live trees sampled for this study plus live and dead trees sampled for another study (Heyerdahl et al. 2014). The total number of trees sampled is reported for each type by subregion. Minor species (4% of samples) are not shown.

Mountains, large ponderosa pine reduction was highest in Recent Grand Fir type (mean 11 trees/ha, median 25 trees/ha).

Large trees are not necessarily old trees. Although large shade-tolerant trees now dominate many sites in the Recent Douglas-fir and Recent Grand Fir types, the majority of these trees (87%) established after 1890. Therefore, the historical density of large trees that we report includes only the species that were common in that type before 1890 (Fig. 2B). Ponderosa pine was included in all types, Douglas-fir in the Persistent Shade Tolerant and Recent Douglas-fir types, and grand fir in the Persistent Shade Tolerant type. Douglas-fir was included in the Recent Douglas-fir type because the harvest record demonstrated that Douglas-fir were historically present in both subregions.

Age structure and forest response to recent land-use change

After 1890, density increased dramatically in all types (Fig. 3), but the timing of that increase varied, beginning earlier in Persistent Shade Tolerant sites than in sites of the other forest types (mid-1800s vs. late 1800s to early 1900s). In all forest types, the number of trees

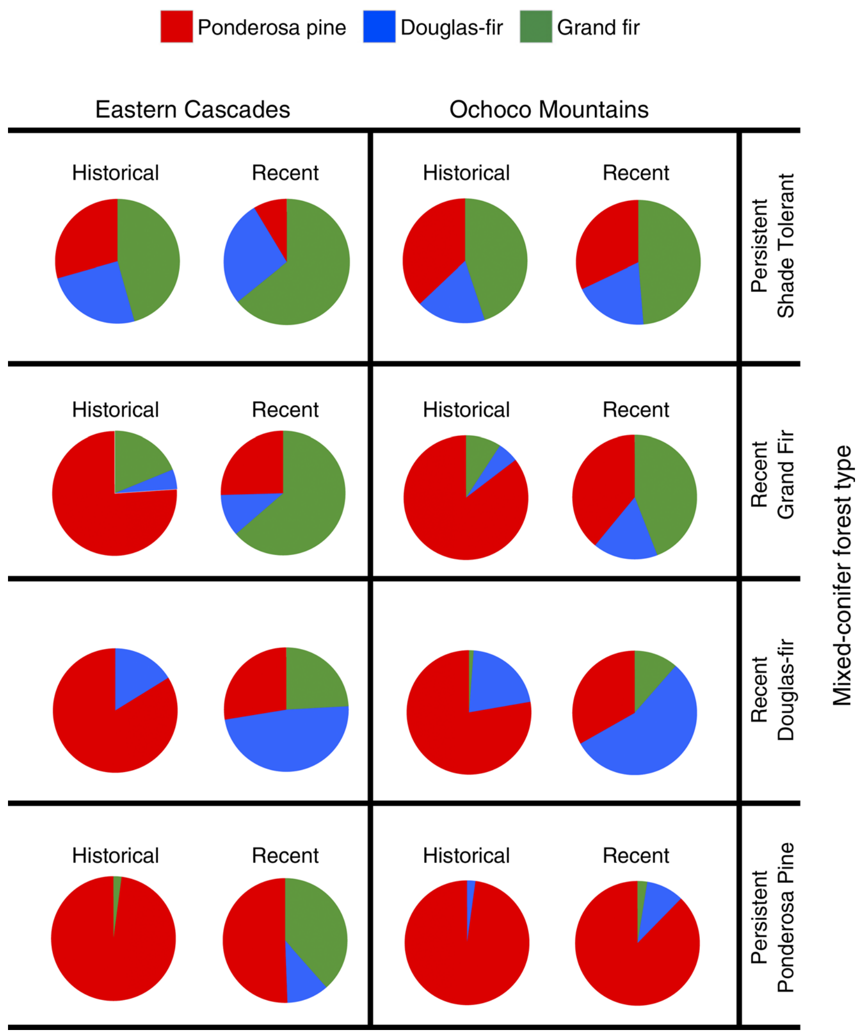

FIG. 4. Composition of trees established in the historical vs. the recent period (i.e., before vs. after 1890) by type and subregion.

establishing has decreased in each decade since ~1940. Historically, ponderosa pine dominated the overstory of all but the Persistent Shade Tolerant forest type, where shade-tolerant species codominated, but this dominance has decreased since 1890. Some large ponderosa pines established during each decade from 1600 to 1890 and indeed composed the majority (78–98%) of all trees established in those decades except in the Persistent Shade Tolerant type (Fig. 4). However, since 1890, establishment has been dominated by shade-tolerant species in all forest types (66–90% eastern Cascades; 61–66% Ochoco Mountains), except in the Persistent Ponderosa type (46% eastern Cascades; 12% Ochoco Mountains; Fig. 4).

Environmental setting of forest types

The eight forest types occurred in different environmental settings. A two-dimensional solution was chosen for the NMS ordination of sample sites in environmental space for the eastern Cascades, and it explained nearly all the variability in the data set (Fig. 5A, C; axis 1 $r^2 = 0.593$, axis 2 $r^2 = 0.300$, total $r^2 = 0.893$). Final stress was 13.99 after 72 iterations, with a final instability of 0.0001 ($P = 0.0040$ that a similar value could have been obtained by chance from a Monte Carlo simulation with 250 runs). Similarly, a two-dimensional solution was chosen for the NMS ordination of sample sites in environmental space for the Ochoco Mountains (Fig. 5B, D; axis 1 $r^2 = 0.619$, axis 2 $r^2 = 0.246$, total $r^2 = 0.845$). Final stress was 16.94 after 45 iterations, with a final instability of 0.0001 ($P = 0.0040$). The degree of stability, Monte Carlo simulation results, and cumulative variability explained by the two-axis solutions for both the eastern Cascades and Ochoco Mountains ordinations indicate highly significant NMS results (McCune and Grace 2002).

Our forest types display significant ($P < 0.0001$) within-group structure in environmental space in both the eastern Cascades and Ochoco Mountains (chance corrected A of 0.063 and 0.057, respectively), but

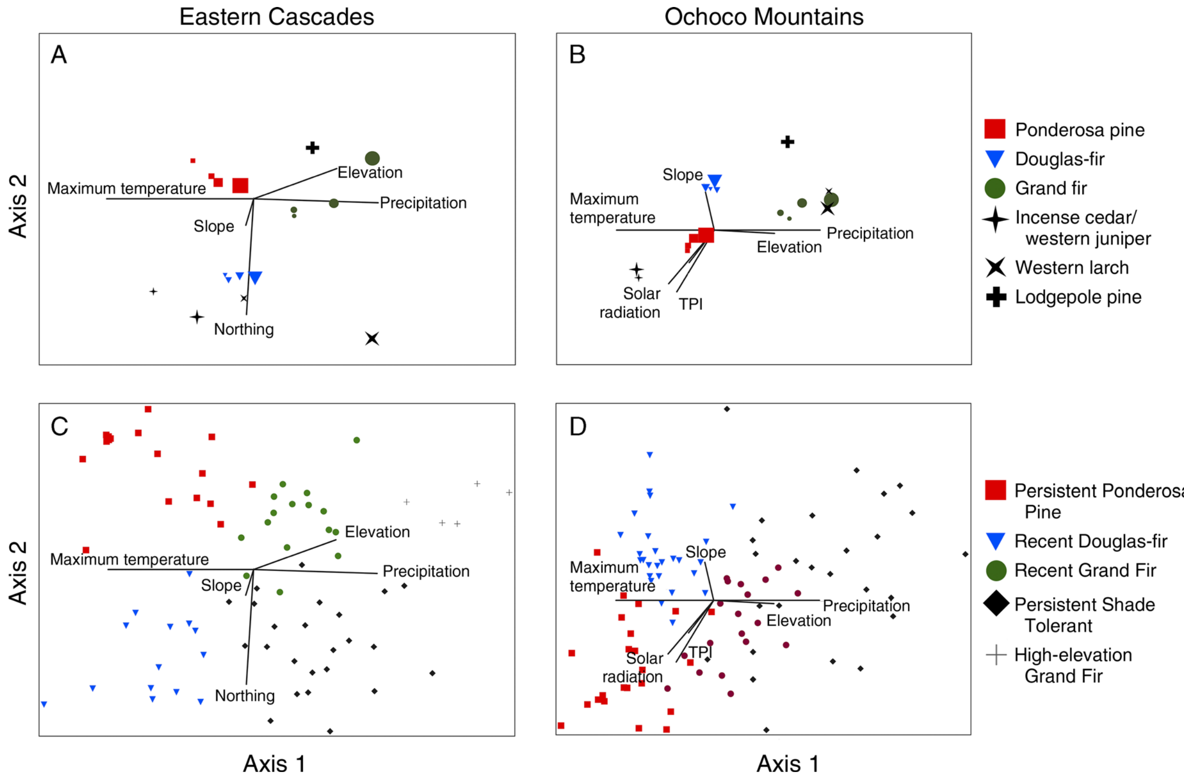

FIG. 5. Nonmetric multidimensional scaling (NMS) ordination results for (A and C) the eastern Cascades and (B and D) the Ochoco Mountains. Panels (A and B) show distribution of species–size classes in environmental space, and species icons are scaled by diameter at breast height class (i.e., small 10–29 cm, medium 30–49 cm, large 50–69 cm, and very large >70 cm dbh). Panels (C and D) show distribution of sample sites coded by forest type in environmental space. Biplot overlays express relationships between ordination axes and environmental variables. Only environmental variables with $r > |0.125|$ (Pearson's correlation coefficient; Fig. 6) are displayed, with vector length proportional to the r value. See Table 1 for descriptions of variables.

analogous types occurred in different environmental spaces in the two subregions. The Multi-Response Permutation Procedure (MRPP) A-statistic describes within-group homogeneity (McCune and Grace 2002). An A-statistic of 1.0 indicates that all samples within groups are identical, while an A-statistic of 0.0 indicates that homogeneity equals expectation by chance. In community ecology, A-statistic values are commonly <0.1. In addition, the species–size classes (Fig. 5A, B) and forest types (Fig. 5C, D) are grouped in ordination space, indicating that they occur in distinct environmental space. Biplot overlays indicate the strength of correlations between the ordination axes and environmental variables, and they indicate how structure–composition variables, sites, and the forest types they comprise are related to environmental gradients in each subregion.

In the eastern Cascades, ordination axis 1 represents variation in climate variables that change with elevation (Fig. 6A; negatively correlated with maximum temperature and positively correlated with average annual precipitation). Small ponderosa pine were strongly and negatively correlated with axis 1, while grand fir was strongly and positively correlated with this axis (Fig. 6E). Therefore these species rarely occurred together as small ponderosa pine occurred in hot–dry environments and small grand fir occurred in warm–moist and cool–wet environments (Fig. 5A). Ordination Axis 2 represents variation in latitude (Fig. 6B; negatively correlated with northing), and has a weak relationship with topographic variation (Fig. 6B; positively correlated with elevation and heat load and negatively correlated with slope). Douglas-fir in all size classes were strongly correlated with axis 2 (Fig. 6F), indicating that this species was primarily associated with sites to the north and weakly associated with steep sites on northern aspects.

In the Ochoco Mountains, a similar relationship between ponderosa pine, grand fir, and variation in climate is expressed on ordination axis 1 (Fig. 6G). Ponderosa pine (<70 cm dbh) and grand fir are strongly associated with axis 1 and are found at opposite ends of the climatic gradient (Fig. 5B). Variation in composition is additionally related to solar intensity and topography (Fig. 6C, D; potential direct incident radiation, heat load, and relative radiation are negatively correlated with axis 1 and axis 2, and slope is positively correlated with axis 2). The strong negative correlation between Douglas-fir and axis 2 demonstrates that Douglas-fir was common at steep sites with low solar radiation. In contrast, small ponderosa pine was common at sites

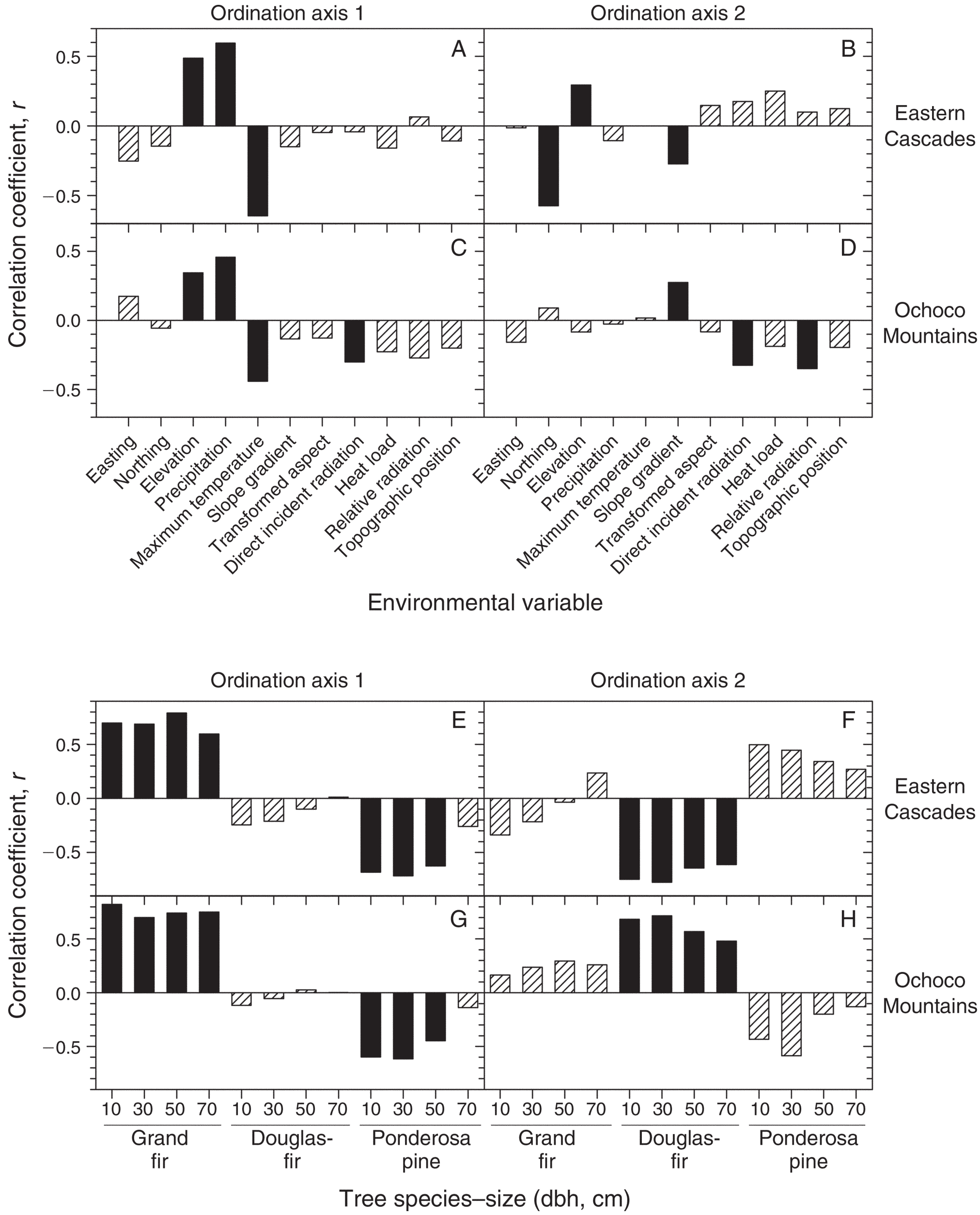

FIG. 6. (A–D) Correlation (Pearson's r) between ordination axes and environmental variables, and (E–H) ordination axes and structure and composition, by subregion. Solid bars highlight $r > |0.250|$; shaded bars highlight $r < |0.250|$. See Table 1 for descriptions of variables.

with shallow slopes and high solar intensity (Fig. 5B). Large ponderosa pine were poorly correlated with either axis in either subregion, consistent with its common presence in all forest types, regardless of environment.

Forest types are composed of distinct combinations of species–size classes (Fig. 2), that generally occurred in different environments (Fig. 5C, D). The Persistent Ponderosa Pine and Recent Douglas-fir types occupied relatively hot–dry environments consistent with the environmental distribution of small-diameter ponderosa pine and Douglas-fir, respectively. The distinctiveness of these types in environmental space is related to the strong association of the Recent Douglas-fir type with latitude in the eastern Cascades and topography in the Ochoco Mountains. The Recent Grand Fir Type was associated with warm–moist environments at intermediate elevations where large overstory ponderosa pine were associated with developing understory canopies of grand fir. Lastly, the Persistent Shade Tolerant type was found in cold–wet, high-elevation environments where shade-tolerant species were common among large overstory trees.

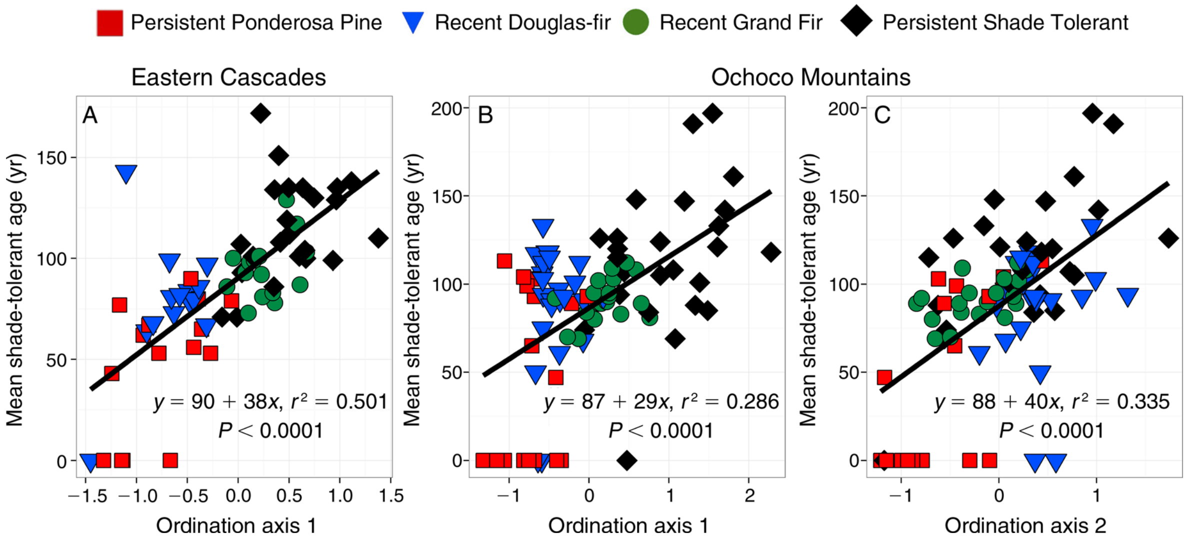

FIG. 7. (A) Variation in the mean age of shade-tolerant trees by forest type and axis 1 score (a synthetic climatic gradient of increasing precipitation and decreasing temperature) in the eastern Cascades. Variation in the mean age of shade-tolerant trees by forest type and (B) axis 1 score, and (C) axis 2 score (a synthetic gradient of increasing topographic shading) in the Ochoco Mountains. At the majority of sites where shade-tolerant age is equal to zero, shade- tolerant trees were locally absent. At four sites, shade tolerant trees < 20 cm dbh were present but not cored.

Environment and variation in initiation of shade-tolerant cohorts

In the eastern Cascades, shade-tolerant trees infilled earlier in progressively cooler and wetter environments (increasing values along axis 1; Fig. 7A). Axis 1 explained half of the variance in mean shade-tolerant age in the eastern Cascades ($r^2 = 0.50$). The timing of infill similarly varied with climate in the Ochoco Mountains ($r^2 = 0.28$), but topography was also important ($r^2 = 0.34$), indicating that shaded sites have older shade-tolerant trees than would be expected based on their climatic environment alone (Fig. 7B).

DISCUSSION

Land-use changes of fire exclusion and logging have been a barrier to our understanding of historical structure, composition, and function in mixed-conifer forests in the Interior West in general (Hemstrom 2001, Agee 2003) and in central Oregon in particular. We demonstrate that environmental gradients at landscape and regional scales are strongly related to the historical and current structure and composition of this widely distributed general forest type. Additionally, our findings demonstrate that ignoring legacies of land-use change (sensu Foster et al. 2003) can lead to erroneous conclusions about historical ecosystem structure and function, which in turn may result in poor management and restoration strategies. Our study builds on previous dendroecological studies of mixed-conifer forests in other areas of the western United States (Arno et al. 1997, Sloan 1998, Camp 1999, Scholl and Taylor 2010). With the exception of Perry et al. (2004) and Heyerdahl et al. (2014), little dendroecological work has been done in mixed-conifer forest in central Oregon. Most of these studies have focused on relatively small landscapes and typically did not span wide environmental gradients where contrasting fire histories and successional patterns would be expected.

Our classification of mixed-conifer forest types is a heuristic device for understanding variation in a multivariate continuum of forest conditions and simplifying complexity for management purposes. The clustering algorithm identified forest types that differed more in composition than in size distributions and density. Understory species composition transitions from dominance of ponderosa pine and Douglas-fir to grand fir as sites became progressively wetter and cooler in both the eastern Cascades and in the Ochoco Mountains. However, ordinations suggest the distribution of Douglas-fir is additionally associated with variation in latitude and topography. Douglas-fir was prominent at hot and dry environments associated with northern latitudes in the Recent Douglas-fir forest type of the eastern Cascades, which Simpson (2007) suggested is related to decreasing depth and particle size of Mazama ash deposits. In the Ochoco Mountains, the distribution of Douglas-fir and therefore the Recent Douglas-fir type was associated with topography, as Douglas-fir was often found on steep sites with high terrain shading. This is consistent with the environmental distribution of several Douglas-fir plant associations described in the Blue and Ochoco Mountains (Johnson and Clausnitzer 1992). Additional associations between topographic setting and species composition may have been obscured by the wide range in elevation, precipitation, and temperature associated with the broad geographic distribution of sample sites. For example, structure and composition at two sites on north slopes may have differed because the sites were at contrasting elevations. This agrees with the finding of Ohmann and Spies (1998) that variation in composition related to topographic setting in central Oregon occurs at fine geographic scales.

Current and historical forests

The mixed-conifer forest types we identified varied in their responses to some changes in land use. For example, changes in composition were clear in the Recent Douglas-fir and Recent Grand Fir types and were likely the result of fire exclusion. The ubiquitous presence of large, multiaged ponderosa pine at all sites in these types, regardless of environmental setting, suggests historical fires were frequent and predominantly low severity with respect to mature trees. Current dominance of young Douglas-fir and grand fir suggests that the historical fire regime was necessary to maintain dominance of ponderosa pine in the respective environments of the Recent Douglas-fir and Recent Grand Fir types. Fire history data support this inference as fire regimes at half the sites were mixed in severity, but frequent surface fires dominated with only relatively small patches of infrequent high-severity fire (Heyerdahl et al. 2014). We considered that the occurrence of past cool and wet climates from 1602 to 1620 and from 1820 to 1845 (Fye et al. 2003, Cook et al. 2011) may have resulted in periods of less frequent fire and increased moisture that allowed densification and dominance of shade-tolerant species that are now common in all but the Persistent Ponderosa Pine type today. Douglas-fir and grand fir are unable to survive low-severity fire until they attain adequate size and bark thickness at ~40 years of age, but mature individuals show moderate to high resistance to fire (Howard and Aleksoff 2000, Steinberg 2002). Douglas-fir and grand fir commonly established prior to fire exclusion in the Persistent Shade Tolerant type in both subregions and were found with old-growth ponderosa pine. This establishment pattern suggests that fire-free intervals were somewhat longer at sites in the Persistent Shade Tolerant forest type, and that fires ranging from low to high severity were likely part of the historical disturbance regime. Although evidence of old shade-tolerant cohorts may have been lost to fire and decay in other types, it is unlikely that a fire could remove all evidence of these species that are fire resistant at maturity while leaving a legacy of 30 to 40 ponderosa pine/ha. Therefore, the lack of old shade-tolerant trees in the Recent Douglas-fir and Recent Grand Fir types suggests that current high densities of mature shade-tolerant trees may be a novel condition in comparison to historical forest structure and composition between 1600 and 1900.

The forest types also varied in the timing of infilling by shade-tolerant trees, with infilling occurring earlier in relatively moist Recent Grand Fir sites than in drier Recent Douglas-fir and Persistent Ponderosa Pine sites. Furthermore, in the Ochoco Mountains, infilling also occurred earlier at sites with lower solar radiation, which was associated with the Recent Douglas-fir type. However, the timing of infilling may also be related to the timing of local land-use changes. The sites sampled by Heyerdahl et al. (2014) covered a relatively small portion of our study area (2400 ha) but included more than half the sites we analyzed. The last widespread fire at one of those sites, McKay Creek, occurred in 1870, two years after George Millican introduced cattle grazing to the area (Heyerdahl et al. 2014). Our analysis included 30 sites from this area, all of which showed an increase in tree recruitment following the date of this last widespread fire. The rapid decline in tree establishment after 1930, and lack of tree establishment in the past seven decades in all types, suggests full stocking in stands 50 to 60 years after fire exclusion that continues to limit establishment and growth throughout the mixed-conifer forest type, consistent with earlier findings elsewhere in the Interior West (McNeil and Zobel 1980, Everett et al. 2007).

Industrial harvesting reduced the median density of large (>50 cm dbh) early seral trees by 50%, similar to assessments of large-tree reduction in mixed-conifer forests elsewhere in the region (Harrod et al. 1999, Hagmann et al. 2013). However, harvest intensity and reconstructed large-tree density varied among our forest types and subregions. Ponderosa pine was the primary species harvested in all types except the Recent Douglas-fir type of the eastern Cascades, where Douglas-fir was also harvested. Larger reductions of large ponderosa pine in Persistent Ponderosa Pine and large ponderosa pine and Douglas-fir in Recent Douglas-fir types in the eastern Cascades are potentially related to relative accessibility of low-elevation stands and the prevalence of large Douglas-fir and ponderosa pine at these sites. In the drier Ochoco Mountains, the reconstructed density of large ponderosa pine was highest at Recent Grand Fir sites, which intuitively had the largest reduction in density of large ponderosa pine. Concentrated harvest at Recent Grand Fir sites may also be related to their relative accessibility in comparison to steeply sloped Recent Douglas-fir sites, and Persistent Shade Tolerant sites, which were restricted to upper elevations and historically had a lower density of large ponderosa pine.

We likely overestimated the historical density of large trees because our historical estimates included trees that may have recruited in response to harvest of large overstory trees. Overestimates are most likely to occur for shade-tolerant species in the Persistent Shade Tolerant type as grand fir releases following harvest of an existing ponderosa pine canopy (Seidel 1981). However, we included shade-tolerant species in our historical estimates of large-tree density in the Persistent Shade Tolerant type because stand structure and age structure indicated they were present prior to land-use changes. Similarly, Douglas-fir was included in the Recent Douglas-fir type. Although large grand fir are now relatively common in the Recent Grand Fir type

PLATE 1. Structure and composition of four structure-composition types in old-growth mixed-conifer forest: (top left) Persistent Ponderosa Pine, (top right) Recent Douglas-fir, (bottom left) Recent Grand Fir, and (bottom right) Persistent Shade Tolerant. Photo credits: A. G. Merschel.

(median density 16 trees/ha in the eastern Cascades), we did not include this species in historical large tree density because there was no evidence that grand fir was common in the type prior to land-use changes. The slow growth of mature ponderosa pine and lack of evidence of old shade-tolerant species suggest that the reconstructed density of ponderosa pine alone best represents historical densities of large trees in the Recent Grand Fir and Persistent Ponderosa Pine types. Historical estimates of large trees elsewhere in the region are similar to and support our reconstructed values (35 trees/ha >53 cm dbh in dry and moist mixed-conifer forest of the eastern Cascades [Hagmann et al. 2013]; 27–32 trees/ha >50 cm dbh in mixed-conifer forest in the Blue Mountains [USFS Inventories 1916–1932, *unpublished data*]; and 38 trees/ha >50 cm dbh in moist mixed-conifer forest in the Blue Mountains [J. D. Johnston, *personal communication*]).

We demonstrated that mixed-conifer forests in central Oregon are much denser now than they were historically, even in comparison to higher estimates of historical density calculated from General Land Office records (Baker 2012). We found mean modern tree densities of 346 to 536 trees/ha compared to historical estimates of 152 trees/ha (trees > 10 cm dbh; Munger 1917) and 64 to 78 trees/ha (trees > 15 cm dbh; Hagmann et al. 2013). Additionally, modern forests were composed primarily of small trees (only 7% of all trees were >50 cm dbh), while Hagmann et al. (2013) reported that 45–55% of all trees were >53 cm dbh in the early 20th century. Relatively high densities (>275 trees/ha) were common among our sample sites despite thinning of small-diameter trees in 21 of them. Although Baker's (2012) historical density estimates are much higher than other estimates for the region (Munger 1917, Hagmann et al. 2013), they are still lower than the least dense areas we found in contemporary forests. Baker (2012) estimated that the 25th to 75th percentile for density was 170–352 trees/ha, whereas the 25th to 75th percentile in current forests was 298–586 trees/ha. In this comparison, we excluded stands in the Persistent Shade Tolerant type because Baker avoided areas where shade-tolerant species dominated.

We lack written records or reconstructions of past conditions in the Ochoco Mountains, but recent land-use change was similar across the region, and we expect that similar increases in density and changes in structure and composition occurred in this subregion (Hessburg and Agee 2003, Powell 2011). Age structure was remarkably similar in both subregions, suggesting densification and shifts in composition to shade-tolerant species was widespread following land-use change in mixed-conifer forest of central Oregon.

Alternative hypotheses about drivers of change in mixed-conifer forest

Although forest structure and composition can potentially arise in various ways, consideration of other lines of evidence can narrow the possibilities. The wave of tree establishment that began in ~1900 that we documented in mixed-conifer forests was likely caused by a variety of factors, including changes in fire regimes, selective tree harvesting, and domestic livestock grazing. Here we consider alternative hypotheses related to the relative importance of these factors. First, infilling was caused either by (1) an increase in fire severity and area burned or (2) a lack of fire. We believe the evidence more strongly supports the second alternative, a lack of fire. It has been suggested that the current high densities of shade-tolerant trees resulted from a historical regime of moderate- to high-severity fire, based on reconstructions of historical forests from archival records (air photos and General Land Office records; Baker 2012). However, the widespread wave of establishment we observed across central Oregon is not consistent with this suggestion because it would require moderate- to high-severity fires occurring over an immense area in the eastern Cascades and Ochoco Mountains in a short period of time just before 1900. Such fires are not recorded in written archives or tree-ring records from the region. Rather, fire history studies in the Pacific Northwest document a dramatic decrease in low-severity fire frequency and extent beginning in the late 19th century (Bork 1984, Speer 1997, Heyerdahl et al. 2001, Heyerdahl et al. 2014). It is more likely that our second alternative, the exclusion of fire, provided an opportunity for all major tree species, particularly shade tolerants, to invade understories across the landscape at rates that were related to site moisture conditions and the timing of fire exclusion.

Lack of fire, however, is likely not the sole mechanism of the wave of establishment following Euro–American settlement. The coolest and wettest climatic period of the past three centuries (1885–1917; Garfin and Hughes 1996, Fye et al. 2003) coincided with widespread heavy grazing in central Oregon (Robbins 1997) and was followed by widespread industrial tree harvesting (Hessburg and Agee 2003). Cool, wet conditions and grazing both facilitate seedling establishment and simultaneously limit fire spread, which in turn is necessary for seedling survival. Youngblood et al. (2004) suggested that abundant tree recruitment in central Oregon was associated with increased moisture availability that accompanied the cool and wet climate of the late 19th and early 20th centuries, while Heyerdahl et al. (2002, 2008) found that cool and wet climatic periods are associated with decreased fire size and occurrence. Grazing also decreases area burned by interrupting the continuity of the fine fuels necessary for fire spread, and favors conifer establishment by reducing competition with bunchgrasses and forbs and exposing mineral seedbeds (Weaver 1950, Rummell 1951, Zimmerman and Neuenschwander 1984, Kolb and Robberrecht 1996). Widespread heavy grazing in the late 19th and early 20th centuries is well documented in both subregions. In the eastern Cascades, 80 000 sheep grazed annually on the Three Sisters District of the Deschutes National Forest in the late 19th century (Coville 1898), and grazing allotments were given to 152 500 sheep and 17 900 cattle in the Ochoco Mountains in the early 20th century (Hodgson 1913). Grazing was followed by selective logging, which also stimulates conifer regeneration by exposing mineral seedbeds, reducing overstory competition, and creating small canopy gaps that favor shade-tolerant species (Seidel 1981, Grissino-Mayer et al. 2004, Naficy et al. 2010). The relative importance of a favorable climate, grazing, and logging in determining contemporary age and stand structure in mixed-conifer forest is unknown. However, it is likely that a synergy of these mechanisms and the disruption of Native American burning (Robbins 1997) facilitated fire exclusion and resulted in abundant tree recruitment in the 20th century, and ultimately, uncharacteristically dense mixed-conifer forest with a high proportion of shade-tolerant trees.

Management implications

Differentiating mixed-conifer forest into dry, moist, and wet potential vegetation types solely by current composition (presence of grand fir or Douglas-fir) confounds our understanding of historical structure and composition and resilient conditions in mixed-conifer forest. Our results suggest that historically, grand fir was largely absent or transient in the Persistent Ponderosa Pine, Recent Douglas-fir, and Recent Grand Fir types because frequent fires prevented its establishment and development in all but the Persistent Shade Tolerant Type. Similarly, Douglas-fir was likely a minor component of the Recent Douglas-fir type, although it dominates this type today. Many of our sites would likely be classified differently in the 1800s than they are today, demonstrating that current predominance of shade-tolerant species in mixed-conifer forest does not necessarily indicate that the historical disturbance regime had long fire-return intervals and/or large patches of high-severity fire. For example, our Recent Grand Fir sites based on historical composition would be classified as dry with a low-severity fire regime in the early 20th century, but are typically classified as "moist–dry" or "moist" with a mixed-severity fire regime based on current composition (Stine et al. 2014).

Continued dominance of ponderosa pine in Persistent Ponderosa Pine sites suggests composition is more resilient to the exclusion of frequent fire in dry environments with high solar intensity. However, these forests are still much denser than they were historically. In comparison, Recent Douglas-fir and Recent Grand Fir types have changed in both density and composition and so have departed further from historical conditions than the Persistent Ponderosa Pine type. Relatively high available moisture in Recent Grand Fir sites results in higher productivity, predisposing these sites to large increases in the density and dominance of shade tolerants. Furthermore, they are often close to Persistent Shade Tolerant sites, which provide shade-tolerant seed sources. In many Recent Grand Fir and Recent Douglas-fir sites, small-diameter ponderosa pine are unable to replace the large ponderosa pine lost to harvesting because they are excluded by developing canopies of shade-tolerant trees. Although common today, developing canopies of shade-tolerant trees do not necessarily mean that a well-developed, late-successional grand fir stand will occur even in the absence of fire. Drought, insects, and disease are likely to reduce the potential for a productive, dense, old-growth grand fir stand to develop on many Recent Grand Fir sites. For example, Cochran (1998) found that grand fir in relatively moist sites in the eastern Cascades succumbed to high mortality from a variety of diseases during dry periods even if grand fir had previously grown vigorously on these sites for several decades. Hence developing canopies of shade tolerants may be transient or unstable and not likely to develop long-lived overstories of large-diameter, shade-tolerant trees characteristic of the Persistent Shade Tolerant type. All types are more susceptible to insect and drought mortality and high-severity wildfire as higher density and predominance of shade tolerants decreases resiliency to these disturbances (Hemstrom 2001, Hessburg et al. 2005, Powell 2011).

Managers seeking to restore the structure of mixed-conifer forest or create more fire- and drought-resilient vegetation must prioritize the use of limited resources. We have demonstrated that changes in mixed-conifer forest from fire exclusion and logging in these subregions vary, at least in part, with environmental factors. This variability can be used as a basis for prioritizing silvicultural treatments across these landscapes. Precise boundaries of areas that should be treated or not treated to increase resiliency of mixed-conifer forest do not currently exist; however, on an individual site basis, we have demonstrated that stand and age structure, composition, and environment can be effectively used to rank sites in terms of degree of change or departure from presettlement conditions. Persistent Shade Tolerant sites, where large-diameter shade-tolerant trees established before 1900, likely had longer fire-return intervals historically and have experienced relatively less change related to fire exclusion. If these stands are left untreated, they can provide habitat for plant and animal species that require dense stand conditions. In Persistent Ponderosa Pine, Recent Douglas-fir, and Recent Grand Fir sites, thinning of understory trees and large-diameter grand fir that established after 1900 would create compositions and structures that are more similar to pre-Euro–American conditions and more resistant to high-severity fire. Reduction of overall stand density and dominance of shade-tolerant species is also compatible with restoring logged large-diameter ponderosa pine and Douglas-fir as this simultaneously accelerates their recruitment (Cochran and Barrett 1999, Fitzgerald 2005) and increases the vigor and resilience of extant old-growth trees to drought and insects (Latham and Tappeiner 2002, Kolb et al. 2007). The historical spatial pattern of large-diameter trees can be approximated in thinning operations to restore horizontal complexity where stands have been simplified (Harrod et al. 1999, Youngblood et al. 2004, Churchill et al. 2013).

Conclusions

We identified four mixed-conifer forest types in the eastern Cascades and Ochoco Mountains of central Oregon. Historically, ponderosa pine was common and persistent in all types, and shade tolerants were rare or absent in all but the Persistent Shade Tolerant Type, which was found in cold–wet sites. In both subregions we found selective logging halved the density of large fire-resistant trees, and large shade-tolerant trees have replaced them in all but the driest environments. Following land-use changes, densification occurred in all types, but successional trajectories differed among types, and they are clearly distinct in composition today. Variation in contemporary composition was most strongly associated with variation in temperature and precipitation, but topography was also associated with the distribution of shade-tolerant species, particularly in the Ochoco Mountains. The historical establishment record we found in these forests is consistent with a low-severity fire regime with infrequent, small patches of mixed- or high-severity fire. The common presence of old shade tolerants in the Persistent Shade Tolerant type suggests a longer fire-return interval and mixed-severity fire regime prior to fire exclusion, and that structure and composition in these areas may be within their historical range of variation. Stands that are dominated by shade-tolerant trees today, but lacked this component prior to fire exclusion, are most departed from historical conditions based on shifts in composition in addition to increases in density.

Acknowledgments

We thank Steven Fitzgerald, John Bailey, Jennifer McKay, Matthew Reilly, Paul Hessburg, Dave Powell, Mike Simpson, Keala Hagmann, and two anonymous reviewers for comments on earlier drafts. This work was facilitated through collaboration with the Deschutes and Ochoco National Forests, and we thank Robin Vora for his assistance in coordinating and implementing the project. We thank Claire Rogan for assistance in the field; and Harold Zald, Patrick Fekety, and James Johnston for assistance with dendrochronological work.

Literature Cited

Abrams, M. D., and C. A. Copenheaver. 1999. Temporal variation in species recruitment and dendroecology of an old-growth white oak forest in the Virginia Piedmont, USA. Forest Ecology and Management 124:275–284.

Agee, J. K. 1993. Fire ecology of Pacific Northwest forests. Island Press, Washington, D.C., USA.

Agee, J. K. 2003. Historical range of variability in eastern Cascade forests, Washington, USA. Landscape Ecology 18:725–740.

Applequist, M. B. 1958. A simple pith locator for use with off-center increment cores. Journal of Forestry 56:141.

Arno, S. F., H. Y. Smith, and M. A. Krebs. 1997. Old growth ponderosa pine and western larch stand structures: influences of pre-1900 fire and fire exclusion. GTR-INT-495. USDA Forest Service, Intermountain Research Station, Ogden, Utah, USA.

Baker, W. L. 2012. Implications of spatially extensive historical data from surveys for restoring dry forests of Oregon's eastern Cascades. Ecosphere 23:1–39.

Bauer, P. 1988. Plant associations of the Deschutes National Forest based on "Plant Associations of the Central Oregon Pumice Zone." Deschutes National Forest Data Library. http://www.fs.fed.us/r6/data-library/gis/deschutes/metadata/pag.htm

Bechtold, W. A., and P. L. Patterson. 2005. The enhanced forest inventory and analysis program—national sampling design and estimation procedures. GTR-SRS-80. USDA Forest Service, Southern Research Station, Asheville, North Carolina, USA.

Beers, T. 1966. Notes and observations: aspect transformation in site productivity research. Journal of Forestry 64:691–692.

Biondini, M. E., P. W. Mielke, Jr., and K. J. Berry. 1988. Data-dependent permutation techniques for the analysis of ecological data. Vegetation 75:161–168.

Bork, J. L. 1984. Fire history in three vegetation types on the eastern side of the Oregon Cascades. Ph.D. thesis, Oregon State University, Corvallis, Oregon, USA.

Brown, P. M., M. R. Kaufmann, and W. D. Shepperd. 1999. Long-term, landscape patterns of past fire events in a montane ponderosa pine forest of central Colorado. Landscape Ecology 14:513–532.

Brown, P. M., C. L. Wienk, and A. J. Symstad. 2008. Fire and forest history at Mount Rushmore. Ecological Applications 18:1984–1999.

Brown, S. J. 2012. The Soda Bear project and the Blue Mountain Forest Partners: US Forest Service collaboration. Journal of Forestry 110:446–447.

Buchanan, J. B. 2010. Balancing competing habitat management needs for northern Spotted Owls and other bird species in dry forest landscapes. Pages 109–117 *in* T. D. Rich, C. Arizmendi, D. W. Demarest, and C. Thompson, editors. Proceedings of the Fourth International Partners in Flight Conference: Tundra to tropics. McAllen, Texas, USA.

Camp, A. E. 1999. Age structure and species composition changes resulting from altered disturbance regimes on the eastern slopes of the Cascades Range, Washington. Journal of Sustainable Forestry 9:39–67.

Camp, A. E., C. Oliver, P. F. Hessburg, and R. Everett. 1997. Predicting late-successional fire refugia pre-dating European settlement in the Wenatchee Mountains. Forest Ecology and Management 95:63–77.

Churchill, D. J., A. J. Larson, M. C. Dahlgreen, J. F. Franklin, P. F. Hessburg, and J. A. Lutz. 2013. Restoring forest resilience: from reference spatial patterns to silvicultural prescriptions and monitoring. Forest Ecology and Management 291:442–457.

Cochran, P. H. 1998. Examples of mortality and reduced annual increments of white fir induced by drought, insects, and disease at different stand densities. GTR-PNW-525. USDA Forest Service, Pacific Northwest Station, Portland, Oregon, USA.

Cochran, P. H., and J. W. Barrett. 1999. Growth of ponderosa pine thinned to different stocking levels in central Oregon: 30-year results. GTR-PNW-508. USDA Forest Service, Pacific Northwest Station, Portland, Oregon, USA.

Cook, B. I., R. Seager, and R. L. Miller. 2011. On the causes and dynamics of the early twentieth-century North American pluvial. Journal of Climate 24:5043–5059.

Coville, F. V. 1898. Forest growth and sheep grazing in the Cascade Mountains of Oregon. Bulletin Number 15. USDA, Division of Forestry, Washington D.C., USA.

Covington, W. W., and M. M. Moore. 1994. Southwestern ponderosa forest structure: change since Euro–American settlement. Journal of Forestry 42:39–47.

Duncan, R. P. 1989. An evaluation of errors in tree age estimates based on increment cores in Kahikatea (*Dacrycarpus cacrydioides*). New Zealand National Science 16:31–37.

Eckert, B. E., J. D. Walstad, and J. C. Tappeiner II. 2008. An illustrated guide to fire in central Oregon forests. Contributions in Education and Outreach, No. 1. Forest Research Laboratory, Oregon State University, Corvallis, Oregon, USA.

Everett, R., D. Baumgartner, P. Ohlson, R. Schellhass, and R. Harrod. 2007. Development of current stand structure in dry fir–pine forests of eastern Washington. Journal of the Torrey Botanical Society 134:199–214.

Everett, R., D. Schellhaas, D. Spurbeck, P. Ohlson, D. Keenum, and T. Anderson. 1997. Structure of northern Spotted Owl nest stands and their historical conditions on the eastern slope of the Pacific Northwest Cascades, USA. Forest Ecology and Management 94:1–14.

Fitzgerald, S. A. 2005. Fire ecology of ponderosa pine and the rebuilding of fire-resilient ponderosa pine ecosystems. GTR-PSW-198. USDA Forest Service, Pacific Southwest Research Station, Albany, California, USA.

Foster, D., F. Swanson, J. Aber, I. Burke, N. Brokaw, D. Tilman, and A. Knapp. 2003. The importance of land-use legacies to ecology and conservation. BioScience 53:77–88.

Franklin, J. F., and C. T. Dyrness. 1988. Natural vegetation of Oregon and Washington. Oregon State University Press, Corvallis, Oregon, USA.

Fulé, P. Z., J. E. Crouse, T. A. Heinlein, M. M. Moore, W. W. Covington, and G. Verkamp. 2003. Mixed-severity fire regime in a high-elevation forest of Grand Canyon, Arizona, USA. Landscape Ecology 18:465–486.

Fulé, P. Z., J. E. Korb, and R. Wu. 2009. Changes in forest structure of a mixed conifer forest, southwestern Colorado, USA. Forest Ecology and Management 258:1200–1210.

Fye, F., D. Stahle, and E. Cook. 2003. Paleoclimatic analogs to twentieth century moisture regimes across the United States. Bulletin of the American Meteorological Society 84:901–909.

Garfin, G. M., and M. K. Hughes. 1996. Eastern Oregon divisional precipitation and Palmer drought severity index from tree-rings. Laboratory of Tree-Ring Research, University of Arizona, Tucson, Arizona, USA.

Grissino-Mayer, H. D. 2001. Evaluating crossdating accuracy: a manual and tutorial for the computer program COFECHA. Tree-Ring Research 57:205–221.

Grissino-Mayer, H. D., W. H. Romme, L. M. Floyd, and D. D. Hanna. 2004. Climatic and human influences on fire regimes of the southern San Juan Mountains, Colorado, USA. Ecology 85:1708–1724.

Hagmann, K., J. F. Franklin, and K. N. Johnson. 2013. Historical structure and composition of ponderosa pine and mixed-conifer forests in south-central Oregon. Forest Ecology and Management 304:492–504.

Harrod, J. R., B. H. McRae, and E. W. Hartl. 1999. Historical stand reconstruction in ponderosa pine forests to guide silvicultural prescriptions. Forest Ecology and Management 114:433–446.

Hemstrom, M. A. 2001. Vegetative patterns, disturbances, and forest health in Eastern Oregon and Washington. Northwest Science 75:91–109.

Hessburg, P. F., and J. K. Agee. 2003. An environmental narrative of inland Northwest United States forests, 1800–2000. Forest Ecology and Management 178:23–59.

Hessburg, P. F., J. K. Agee, and J. F. Franklin. 2005. Dry forest and wildland fires of the inland Northwest USA: contrasting the landscape ecology of the pre-settlement and modern era. Forest Ecology and Management 211:117–139.

Hessburg, P. F., R. G. Mitchell, and G. M. Filip. 1994. Historical and current roles of insects and pathogens in eastern Oregon and Washington forest landscapes. GTR-PNW-327. USDA Forest Service, Pacific Northwest Station, Portland, Oregon, USA.

Hessburg, P. F., R. B. Salter, and K. M. James. 2007. Re-examining fire severity relations in premanagement era mixed conifer forests: inferences from landscape patterns of forest structure. Landscape Ecology 22:5–24.

Heyerdahl, E. K., L. B. Brubaker, and J. K. Agee. 2001. Spatial controls of historical fire regimes: a multiscale example form the interior west, USA. Ecology 82:660–678.

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

Heyerdahl, E. K., D. A. Falk, and R. A. Loehman. 2014. Data archived with the International Multiproxy Paleofire Database, IGBP PAGES/World Data Center for Paleoclimatology. NOAA/NCDC Paleoclimatology Program, Boulder, Colorado, USA. www.ncdc.noaa.gov/paleo/impd/paleofire.html

Heyerdahl, E. K., K. Lertzman, and C. M. Wong. 2012. Mixed-severity fire regimes in dry forests of southern interior British Columbia, Canada. Canadian Journal of Forest Research 42:88–98.

Heyerdahl, E. K., D. McKenzie, L. D. Daniels, A. E. Hessl, J. S. Litell, and N. J. Mantua. 2008. Climate drivers of regionally synchronous fires in the inland Northwest (1651–1900). International Journal of Wildland Fire 17:40–49.

Hodgson, A. H. 1913. A history of the Ochoco National Forest. United States Forest Service. http://hdl.handle.net/1957/10019

Holmes, R. L. 1983. Program COFECHA user's manual. Laboratory of Tree-Ring Research, University of Arizona, Tucson, Arizona, USA.

Hopkins. B., S. Simon, M. Schafer, and T. Lillybridge. 1992. Region 6 interim old growth definition for grand fir/white fir series. USDA, Forest Service, Region 6.

Howard, J. L., and K. C. Aleksoff. 2000. *Abies grandis*. Fire effects information system. USDA Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory. http://www.fs.fed.us/database/feis/

Johnson, C. G., and R. R. Clausnitzer. 1992. Plant associations of the Blue and Ochoco Mountains. R6 ERW TP 036-92. USDA Forest Service, Pacific Northwest Station, Portland Oregon, USA.

Johnson, E. A., K. Miyanishi, and H. Kleb. 1994. The hazards of interpretation of static age structures as shown by stand reconstructions in a *Pinus contorta–Picea engelmannii* forest. Journal of Ecology 82:923–931.

Kolb, P. F., and R. Robberrecht. 1996. *Pinus ponderosa* seedling establishment and the influence of competition with the bunchgrass *Agropyron spicatum*. International Journal of Plant Science 157:509–515.

Kolb, T. E., J. K. Agee, P. Z. Fule, N. G. McDowell, K. Pearson, A. Sala, and R. H. Waring. 2007. Perpetuating old ponderosa pine. Forest Ecology and Management 249:141–157.

Latham, P., and J. Tappeiner. 2002. Response of old-growth conifers to reduction in stand density in western Oregon forests. Tree Physiology 22:137–146.

Mather, P. M. 1976. Computational methods of multivariate analysis in physical geography. J. Wiley and Sons, London, UK.

McCune, B., and K. Dylan. 2002. Equations for potential annual direct incident radiation and heat load. Journal of Vegetation Science 12:603–606.

McCune, B., and J. B. Grace. 2002. Analysis of ecological communities. MjM Software Design, Gleneden Beach, Oregon, USA.

McCune, B., and M. J. Mefford. 2010. PC-ORD. Multivariate analysis of ecological data. Version 6.243 beta. MjM Software, Gleneden Beach, Oregon, USA.

McNeil, R. C., and D. B. Zobel. 1980. Vegetation and fire history of a ponderosa pine and white fir forest in Crater Lake National Park. Northwest Science 54:30–46.

Merschel, A. G. 2012. Mixed-conifer forests of central Oregon: structure, composition, history of establishment and growth. Thesis. Oregon State University, Corvallis, Oregon, USA.

Merschel, A. G., T. A. Spies, and E. K. Heyerdahl. 2014. Structure and composition data for mixed-conifer forests in central Oregon. Forest Service Research Data Archive, Fort Collins, Colorado, USA. http://dx.doi.org/10.2737/RDS-2014-0018

Munger, T. T. 1917. Western yellow pine in Oregon. USDA Bulletin No. 418. U.S. Government Printing Office, Washington, D.C., USA.

Naficy, C., A. Sala, E. Keeling, J. Graham, and T. H. Deluca. 2010. Interactive effects of historical logging and fire exclusion on ponderosa pine forest structure in the northern Rockies. Ecological Applications 20:1851–1864.

Ochoco National Forest. 2008. Plant association groups. Ochoco National Forest Data Library. http://www.fs.fed.us/r6/data-library/gis/ochoco/index.shtml

Ohmann, J. L., and M. J. Gregory. 2002. Predictive mapping of forest composition and structure with direct gradient analysis and nearest neighbor imputation in coastal Oregon, U.S.A. Canadian Journal of Forest Research 32:725–741.

Ohmann, J. L., and T. A. Spies. 1998. Regional gradient analysis and spatial pattern of woody plant communities of Oregon forests. Ecological Monographs 68:151–182.

Oliphant, J. O. 1968. On the cattle ranges of the Oregon country. University of Washington Press, Seattle, Washington, USA.

Perry, D. A., P. F. Hessburg, C. N. Skinner, T. A. Spies, S. L. Stephens, T. H. Taylor, J. F. Franklin, B. McComb, and G. Riegel. 2011. The ecology of mixed severity fire regimes in Washington, Oregon, and Northern California. Forest Ecology and Management 262:703–717.

Perry, D. A., H. Jing, A. Youngblood, and D. R. Oetter. 2004. Forest structure and fire susceptibility in volcanic landscapes of the Eastern High Cascades, Oregon. Conservation Biology 18:913–926.

Pierce, P. B., T. Lookingbill, and D. Urban. 2005. A simple method for estimating potential relative radiation (PRR) for landscape-scale vegetation analysis. Landscape Ecology 20:137–147.

Powell, D. C. 2011. Active management of dry forests in the Blue Mountains: silvicultural considerations. White Paper F14-SO-WP-Silv-4USDA. Forest Service, Pacific Northwest Region, Pendleton, Oregon, USA.

PRISM Climate Group, Oregon State University. 2012. http://prism.oregonstate.edu

Pyne, S. J. 1997. Fire in America: a cultural history of wildland and rural fire. University of Washington Press, Seattle, Washington, USA.

Robbins, W. G. 1997. Landscapes of promise: the Oregon story, 1800–1940. University of Washington Press, Seattle, Washington, USA.

Rollins, M. G. 2009. LANDFIRE: a nationally consistent vegetation, wildland fire, and fuel assessment. International Journal of Wildland Fire 18:235–249.

Rummell, R. S. 1951. Some effects of livestock grazing on ponderosa pine forest and range in central Washington. Ecology 32:594–607.

Scholl, A. E., and A. H. Taylor. 2010. Fire regimes, forest change, and self-organization in an old-growth mixed-conifer forest, Yosemite National Park, USA. Ecological Applications 20:362–380.

Seidel, K. W., and P. H. Cochran. 1981. Silviculture of mixed conifer forests in eastern Oregon and Washington. GTR-PNW-121. USDA Forest Service, Portland, Oregon, USA.

Sherriff, R. L., and T. T. Veblen. 2006. Ecological effects of changes in fire regimes in *Pinus ponderosa* ecosystems in the Colorado Front Range. Journal of Vegetation Science 17:705–718.

Simpson, M. 2007. Forested plant associations of the Oregon East Cascades. R6-NR-ECOL-TP-03-2007. USDA Forest Service, Pacific Northwest Region, USA.

Sloan, J. P. 1998. Historical density and stand structure in an old-growth forest in the Boise Basin of central Idaho. Pages 258–266 *in* T. L. Pruden and L. A. Brennan, editors. Proceedings of the Tall Timbers Fire Ecology Conference. Fire in ecosystem management: shifting the paradigm from suppression to prescription. Tall Timbers Research Station, Tallahassee, Florida, USA.

Smith, H. Y., and S. F. Arno. 1999. Eighty-eight years of change in a managed ponderosa pine forest. GTR-INT-23. USDA Forest Service, Intermountain Research Station, Ogden, Utah, USA.

Speer, J. H. 1997. A dendroecological record of pandora moth (*Coloradia pandora*, Blake) outbreaks in central Oregon. Thesis. University of Arizona, Tucson, Arizona, USA.

Spies, T. A., M. A. Hemstrom, A. Youngblood, and S. Hummel. 2006. Conserving old-growth forest diversity in disturbance-prone landscapes. Conservation Biology 20:351–362.

Steinberg, Peter D. 2002. *Pseudotsuga menziesii* var. glauca. Fire Effects Information System. USDA Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory. http://www.fs.fed.us/database/feis/

Stephens, S. L. 2001. Fire history differences in adjacent Jeffrey pine and upper montane forests in the eastern Sierra Nevada. International Journal of Wildland Fire 10:161–167.

Stine, P., et al. 2014. The ecology and management of moist mixed-conifer forests in eastern Oregon and Washington: a synthesis of the relevant biophysical science and implications for future land management. GTR-PNW-XXX. USDA Forest Service, Portland, Oregon, USA, *in press*. http://www.fs.fed.us/pnw/publications/MMC_Synthesis_24Feb14.pdf

Stokes, M. A., and T. L. Smiley. 1996. An introduction to tree-ring dating. University of Arizona Press, Tucson, Arizona, USA.

Swetnam, T. W., B. E. Wickman, H. G. Paul, and C. H. Baisan. 1995. Historical patterns of western spruce budworm and Douglas-fir tussock moth outbreaks in the northern Blue Mountains, Oregon since A.D. 1700. GTR-PNW-484. USDA Forest Service, Portland, Oregon, USA.

Taylor, A. H. 2010. Fire disturbance and forest structure in an old-growth *Pinus ponderosa* forest, southern Cascades USA. Journal of Vegetation Science 21:561–572.

Veblen, T. T., T. Kitzberger, and J. Donnegan. 2000. Climatic and human influences on fire regimes in ponderosa pine forests in the Colorado Front Range. Ecological Applications 10:1178–1195.

Weaver, H. 1943. Fire as an ecological and silvicultural factor in the ponderosa-pine region of the Pacific slope. Journal of Forestry 41:7–15.

Weaver, H. 1950. Shoals and reefs in ponderosa pine silviculture. Journal of Forestry 48:21–22.

Weaver, H. 1959. Ecological changes in the ponderosa pine forest of the Warm Springs Indian Reservation in Oregon. Journal of Forestry 57:15–20.

Weiss, A. 2001. Topographic position and landforms analysis. Poster Presentation. ESRI User Conference, San Diego, California, USA.

Wentworth, E. N. 1948. America's sheep trails: histories, personalities. Iowa State College Press, Ames, Iowa, USA.

Yamaguchi, D. K. 1991. A simple method for cross-dating increment cores from living trees. Canadian Journal of Forest Research 21:414–416.

Youngblood, A., T. Max, and K. Coe. 2004. Stand structure in eastside old-growth ponderosa pine forests of Oregon and northern California. Forest Ecology and Management 199:191–217.

Zimmerman, G. T., and L. F. Neuenschwander. 1984. Livestock grazing influences on community structure, fire intensity, and fire frequency within the Douglas-fir/ninebark habitat type. Journal of Range Management 37:104–110.

Zobel, Donald B. 1973. Local variation in intergrading *Abies grandis*–*Abies concolor* populations in the central Oregon Cascades: needle morphology and periderm color. Botanical Gazette 134:209–220.

Supplemental Material

Appendix A

Taper equations used to reconstruct diameter at breast height of stumps (*Ecological Archives* A024-199-A1).

Appendix B

Dendrogram results of hierarchical cluster analysis (*Ecological Archives* A024-199-A2).