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Historical conditions in mixed-conifer forests on the eastern slopes of the northern Oregon Cascade Range, USA

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ABSTRACT

Historical forest conditions in frequent-fire forests may be increasingly useful in guiding contemporary forest management given (1) projections for increased drought stress associated with climate change and (2) increases in vertical and horizontal fuel connectivity related to changes in land use over the past 150 years. Records from a 1922–25 timber inventory reveal historical variability at the landscape-level on mixed-conifer habitats on the eastern slopes of the Cascade Range in northern Oregon. Live conifers >15 cm dbh (diameter at breast height) were tallied by species and diameter class in a 20% sample of over 50,000 hectares (ha). Forests were predominantly low density (66 tph, standard deviation = 32, range = 0–289) relative to current conditions (312 ± 245, 0–1643 tph). Historical basal area averaged 14 ± 7 (0–70) $m^2\ ha^{-1}$. Total stand density, large tree (>53 cm dbh) density, and ponderosa pine density were relatively stable across a wide moisture gradient (42–187 cm annual precipitation). Large trees dominated total basal area (73 ± 16%) and comprised 42 ± 17% of total trees per hectare (tph). Ponderosa pine contributed 62 ± 27% of basal area. Together, ponderosa pine and Douglas-fir constituted 91 ± 15% of basal area. Large ponderosa pine and Douglas-fir were nearly ubiquitous across the landscape in this historical data set, occurring on 94% and 83% of transects respectively. Large grand fir occurred on 20% of transects but contributed only 2 ± 6% to large tree basal area. Higher-density values (>120 tph), although rare, were distributed throughout the mixed-conifer habitat while large (>1.6 ha) treeless (no conifers >15 cm dbh) areas were almost entirely restricted to higher elevation, colder, wetter habitat types. Currently ponderosa pine no longer dominates large tree basal area, large trees no longer dominate total basal area, and Douglas-fir is now the dominant species across the landscape. Current mean tree densities are more than four times greater than values recorded in the historical cruise, and current basal area is approximately two times greater. Currently, large trees dominate basal area on only 29% of area inventoried compared to 91% in 1922–25. This systematic sample of a large landscape provides information about variability in species composition, densities, and structures at multiple spatial scales, which are highly relevant to management activities to restore and conserve desired ecosystem functions. Forest conditions comparable to those in this historical record have demonstrated resilience and resistance to fire and drought-related stressors in other frequent-fire forests.

1. Introduction

Proposals for restoring mixed-conifer habitats in dry, frequent-fire forest landscapes in the interior Pacific Northwest (PNW) seek outcomes that balance multiple objectives, including reduction of risk of stand-replacement disturbances and increases in future management options for these ecosystems (Gaines et al., 2010; Franklin and Johnson, 2012; North, 2012; USFS, 2012; Franklin et al., 2013). Contemporary mixed-conifer forests in dry forest landscapes are highly vulnerable to drought-induced competitive stresses, severe wildfires, and insect outbreaks as a consequence of both past management and changes in climate (see reviews in Perry et al., 2011; Spies et al., 2011; US FWS, 2011; Stine et al., In press). Today, federal managers and stakeholders seek to restore characteristic processes, functions, and structures – especially older trees of fire- and drought-tolerant species – so as to increase the capacity of these ecosystems to adapt to expected increases in temperature and drought stress while maintaining desired ecosystem functions (Stephens et al., 2010; USFS, 2010; Franklin et al., 2013).

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Ecological restoration incorporates relevant information from diverse sources, including historical records. Historical conditions may be useful guides to management designed to conserve or restore desired functions and processes in frequent-fire ecosystems given projections of warmer climate. Increases in insect activity correlate positively with warmer, drier climate over the past several centuries (Pohl et al., 2006; Bentz et al., 2010; Flower et al., 2014). Increases in fire frequency, area burned, and biomass consumed correspond with warmer, drier climate in historical and contemporary records (Heyerdahl et al., 2008; Lutz et al., 2011; Miller et al., 2012; Abatzoglou and Kolden, 2013; Cansler and McKenzie, 2013; Riley et al., 2013; Zhang et al., 2014). Forest conditions comparable to those in other historical records have demonstrated resilience and resistance to fire and other drought-related stressors (Stephens and Fulé, 2005; Stephens and Gill, 2005; Collins and Stephens, 2010). Consistent with these expectations, methods that merge historical conditions with other sources of information are being developed and implemented at both tree and patch scales (Larson and Churchill, 2012; Larson et al., 2012; Churchill et al., 2013) as well as landscape levels (North et al., 2009; USFS, 2010; Hessburg et al., 2013; Moritz et al., 2013).

Structure and composition of mixed-conifer forests vary substantially across the interior PNW as well as along the Cascade Range (which forms the western boundary of the region) for multiple reasons including variation in climate, topography, species distributions, and disturbance history (Perry et al., 2011; Stine et al., In press). On the east slopes of the Cascade Range in northern Oregon, mixed-conifer forests are characterized by *Pseudotsuga menziesii* (Douglas-fir) and *Abies grandis* (grand fir) (Franklin and Dyrness, 1988). Dry and moist mixed-conifer habitat types may be differentiated by the abundance of species indicative of mesic site conditions, such as grand fir and associated shrubs and herbs (Marsh et al., 1987; Simpson, 2007; Stine et al., In press); however, presence and abundance of these species may vary with disturbance. These mixed-conifer forests are bounded at lower elevations by drier habitat characterized by *Pinus ponderosa* (ponderosa pine) and at upper elevations by wetter and colder habitat types characterized by species such as *Tsuga mertensiana* (mountain hemlock), *Tsuga heterophylla* (western hemlock), *Abies amabilis* (Pacific silver fir), *Abies procera* (noble fir), and *Pinus contorta* (lodgepole pine).

A recently rediscovered 90-year-old timber inventory provides historical landscape-level characterizations of forest structure and composition on mixed-conifer habitats on the eastern slope of the Cascade Range in northern Oregon, USA. In this timber inventory of the Warm Springs Indian Reservation conducted roughly 90 years ago by the Bureau of Indian Affairs (BIA) more than 20% of the area in more than 50,000 ha of mixed-conifer forests was sampled using a systematic strip cruise anchored on documented survey points. Cruisers recorded live conifers at least 15 cm dbh by species and diameter class in 1.6 ha sample units. As a spatially extensive, systematic inventory this data set provides a unique record of historical forest conditions at the landscape level and complements existing historical records and reconstructions for similar forest types. All methods and studies have limitations. The use of multiple sources of information and diverse methods to examine the same or similar systems strengthens our confidence in the inferences drawn from any single study or method.

In this paper we summarize these historical data and interpret them in relation to the following questions: (1) what was the structure and composition of forests (conifers >15 cm dbh) on these mixed-conifer sites in the early 20th century; (2) did forest conditions on dry mixed-conifer sites differ from those on moist mixed-conifer sites; and, (3) how do current conditions on these sites differ from this historical record? Our interest in current conditions on tribal lands is motivated by what this comparison with unique historical data might suggest about conditions and change over time in similar forest types on federal lands. Our purpose is to provide previously scarce data on historical stand- and landscape-level conditions that can be used in developing management goals for ecological restoration of comparable mixed-conifer forests on public lands.

2. Methods

2.1. Study area and site history

Mixed-conifer habitat on the Warm Springs Indian Reservation (hereafter "Reservation") extends for roughly 62 km of latitude north along the eastern slopes of the Cascade Range from Mt Jefferson to the southern slopes of Mt Hood (Fig. 1). Located in the rain shadow of the Cascade Range, the Reservation experiences a continental climate. Summers are typically hot and dry with cold nights while winters are cold and snowy. Within the study area, annual precipitation increases with elevation and ranges from 42 cm at the lowest elevations in the study area to 187 cm at the highest (Fig. 2). Minimum January temperatures range from −7.0 to −3.4 °C, and maximum July temperatures range from 19 to 29 °C across the study area. Precipitation and temperature were derived from spatially gridded estimates modeled from point measurements taken at national and local weather stations and averaged over a 30-year period from 1981 to 2010 (PRISM, 2012). Much of the precipitation on these sites falls as snow during the late fall

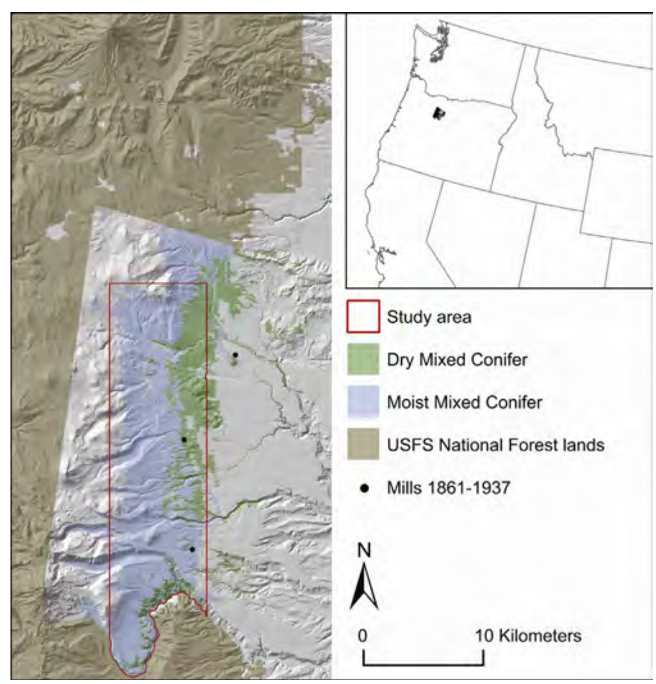

Fig. 1. The Warm Springs Indian Reservation lies south of Mt Hood and encompasses the east slopes of Mt Jefferson east of the crest of the Cascade Range and shares boundaries with National Forest lands. Our study area (red outline) on the Warm Springs Indian Reservation encompasses forests on mixed-conifer habitat types. Habitat classification is represented by the ILAP potential vegetation type map. (See Appendix B for a comparison study results using different vegetation classification models.) Three mills operated intermittently in or near the study area from 1861 to 1937 to provide timber for use on the Reservation. Cruisers noted evidence of logging on tally sheets for transects within a 1.5 km radius of the two mills in the study area. These transects were excluded from the study. Commercial harvests began on the Reservation in the 1940s. An inset map shows the location of the Reservation in the state of Oregon. For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.

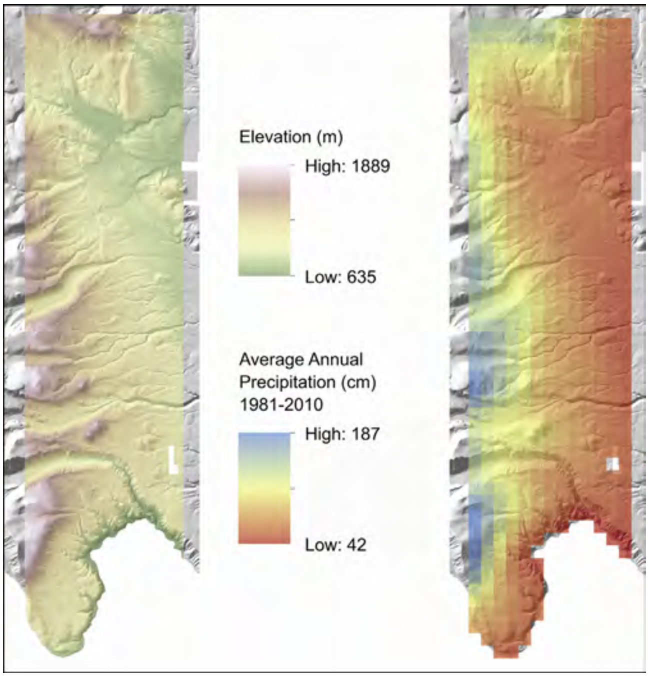

Fig. 2. Elevation values were derived from a 10 m DEM from the National Elevation Dataset (http://ned.usgs.gov/index.html). Annual precipitation derived from spatially gridded estimates modeled from point measurements taken at national and local weather stations and averaged over a 30-year period from 1981 to 2010 (PRISM, 2012). For a color version of this graphic, the reader is referred to the web version of this article.

and winter. Mean elevation in the study area is 1103 m (standard deviation ± 189, range 635–1889) (Fig. 2) and mean slope is 9 ± 8° (0–65) as derived from a 10 m digital elevation map in the National Elevation Dataset.

The Reservation was created by treaty in 1855 from a "little-used part of their traditional homeland" (Logan, 1980). Sawmills operated intermittently on the Reservation from 1861 until 1937 exclusively to provide lumber for use on the Reservation (Fig. 1), except for a brief period between 1909 and 1910 when sales were made to railroad contractors. The first large-scale commercial harvesting began on the Reservation in the 1940s.

Examination of fire scars show decreasing fire frequency with increasing elevation from ponderosa pine to mixed-conifer habitats. Weaver (1959) observed average intervals between fires of 11, 16, 17, and 47 years from fire scars on stumps of four trees 294–510 years old from widely separated locations. In a more comprehensive study, fire scars were recorded at a frequency of 14–55 years on 107 stumps selected to "reveal the most complete fire record" across 20 sections (roughly 5000 ha) in two study areas (Boulder Creek and Lionshead harvest units) (Soeriaatmadja, 1966); these harvest units lie within the current study area on mixed-conifer habitat. Soeriaatmadja (1966) (1) noted a decrease in fire frequency in the Boulder Creek and Lionshead harvest units and (2) inferred a higher probability of crown fire for these sites relative to more xeric areas at lower elevations in his study. He also noted a sharp reduction in the frequency of fire since 1900 relative to the fire scar record of the past 400 years.

2.2. Timber inventory methods 1922–25

Inventory data were collected using systematically located strip surveys which were referenced to documented locations in the Bureau of Land Management Public Land Survey System (BLM PLSS) of land division (Fig. 3). Inventory methods are consistent with those used on the former Klamath Reservation from 1920 to 1922 (Hagmann et al., 2013). Cruisers had the option to adjust area sampled by species to accommodate exceptionally high or low tree densities. Most (92%) transects in this study represent at least a 20% sample of an 8 ha area. At higher elevations in and adjacent to hemlock, noble fir, and lodgepole pine habitat types, cruisers ran a single transect through the center of each quarter–quarter section resulting in a 10% sample of a 16 ha area. Conifers ⩾ 15 cm diameter at breast height (dbh) were tallied by species (Appendix A: Fig. 1). Species recorded by common name included: ponderosa pine, Douglas-fir, white fir (*Abies concolor*) hereafter grand fir, western larch (*Larix occidentalis*), sugar pine (*Pinus lambertiana*), incense cedar (*Calocedrus decurrens*), western white pine (*Pinus monticola*), lodgepole pine (*P. contorta*), western red cedar (*Thuja plicata*), Engelmann spruce (*Picea engelmannii*), western or mountain hemlock recorded primarily as "hemlock", Pacific silver fir, noble fir, white bark pine (*Pinus albicaulis*), and "other". Grand fir intergrades with white fir in eastern Oregon, and many inventories and classifications do not differentiate between them (Simpson, 2007). The inventory tally sheets used on the Warm Springs Reservation were created for use on the former Klamath Indian Reservation where white fir is considered more abundant than grand fir.

2.3. Transfer of historical records to digital data

Records for the 1922–25 timber inventory of the Warm Springs Indian Reservation are archived at The U.S. National Archives and Records Administration facility in Seattle, Washington (NARA, 1922–25). Methods for transfer of archived inventory records to digital data and generation of summary statistics are consistent with those used on the former Klamath Reservation from 1920 to 1922 (Hagmann et al. 2013). We excluded 636 records (9%) from this study because they fell into one or more of the following categories: incomplete or indecipherable (580), cruiser noted evidence of previous or current harvesting (16), or duplicate (check) cruises (40). Transects on which harvesting was noted were within 1.5 km of mill sites (Fig. 1).

We used spatial data available from the BLM (http://www.geocommunicator.gov/GeoComm/lsis_home/home/) to reconstruct timber inventory transects from PLSS quarter–quarter section boundaries with ESRI's ArcMap software (release 10). We linked the resultant polygons to inventory records based on transect location (township, section, quarter–quarter section), number (two transects per quarter–quarter section) and orientation (north–south or east–west). BLM PLSS spatial data do not exist for quarter–quarter section boundaries in three townships in this study area. Transects in these townships are included in analyses independent of transect location and are excluded from analyses dependent on location.

We computed tree density, basal area, diameter distribution, and percent composition for each transect. To calculate basal area, we used mean dbh reported in the inventory record for trees in the 15–41 cm dbh size class. For trees >41 cm dbh, we used the median dbh for each size class to calculate basal area, e.g., 53 cm dbh was used to calculate basal area for trees in the 50–55 cm dbh class. We also computed the density of trees larger than 53 cm (21 in.) because the presence and abundance of trees this large and larger is used to identify old-growth stands in interim old-growth guides (USFS, 1993). In this inventory, trees 50–55 cm dbh were recorded in one size class. For this analysis, we assume half of those trees are smaller than 53 cm dbh.

2.4. Variability in historical structure and composition

We generated summary statistics for the 1922–25 timber inventory data collected as a >20% sample of 54,982 forested hectares distributed within our 64,083 ha study area. The data

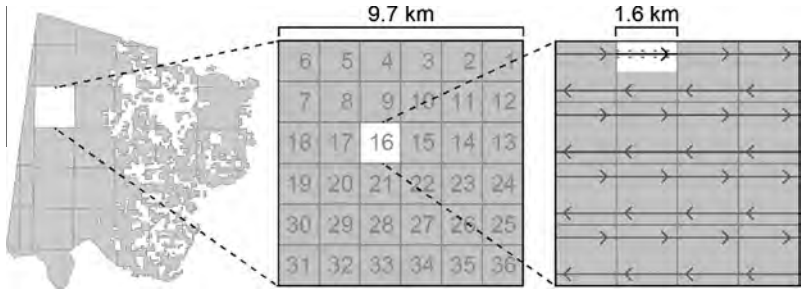

Fig. 3. The Bureau of Land Management Public Land Survey System (BLM PLSS, www.geocommunicator.gov) divides each township into 36 sections and each section into quarter–quarters (16.2 ha). Most transects (83%) ran the length or width (20 chains, 402 m) of a quarter–quarter section (16.2 ha); covered an area of 1.6 ha; and represent a 20% sample of an 8 ha area. Length and area of the remaining transects were adjusted to accommodate variations in the division of land in the BLM PLSS and/or tree density.

set includes 689,173 conifers ⩾15 cm dbh located on 6060 transects which covered a sampled area >11,000 ha. On 89 transects, no trees >15 cm dbh occurred.

We used cluster analysis to identify groups of transects that are most similar in basal area, diameter class, and species composition. We used the k-medoids method of cluster analysis with the pam (partitioning around medoids) algorithm (Kaufman and Rousseeuw, 2009) as implemented in the fpc package (Hennig, 2013) in R (R Development Core Team, 2013) on Bray–Curtis dissimilarities generated with the vegan package (Oksanen et al., 2011) in R. We used indicator species analysis to guide our selection of ecologically meaningful grouping (Dufrêne and Legendre, 1997). We used non-metric multidimensional scaling (NMS) ordination as implemented in PC-ORD v. 6 and proposed by McCune et al. (2002) to graphically represent variation in species composition and structure in the same data matrix used for cluster analysis. For more information on the methods used, please see Appendix B.

2.5. Comparison of dry and moist mixed-conifer habitat

The use of widely accepted vegetation classifications facilitates communication with managers and stakeholders regarding sites where study results might be relevant. Site classifications based upon vegetative indicators, such as habitat types (sensu Daubenmire, 1966), identify areas that have comparable environmental and potential vegetative conditions (plant associations). Plant association classifications have been developed for use on National Forest lands (e.g., Dyrness et al., 1974; Kovalchik, 1987; Topik et al., 1988; Lillybridge et al., 1995). Efforts to extend and standardize them continue (Simpson, 2007; Henderson et al., In preparation). Habitat types are widely accepted among resource managers as useful indices for recognizing areas of similar environmental conditions and management potential; however, they have also been criticized as being subjective and variable.

As no standardized, peer-reviewed map of habitat types is available at the regional level, we compared maps from two models of habitat type distribution to explore how differences in vegetation classification systems would influence our results. We compared a publicly available map of habitat types developed by the ILAP (Integrated Landscape Assessment Project, http://oregonstate.edu/inr/ilap) team with a proprietary vegetation classification generated from plot data collected on the Reservation specifically to develop plant associations for use as a management tool (Marsh et al., 1987). Summary statistics generated from both maps were comparable for dry and moist mixed-conifer habitat (Appendix C) even though division of the study area between the two habitat types differed greatly. Because the ILAP map is publicly available, we use the ILAP map in this study.

2.6. Comparison of past and current conditions

Current conditions were summarized from Continuous Forest Inventory (CFI) data (USDI BIA, 1983) collected on 535 plots in 2007 by representatives of the Warm Springs Tribes and BIA. CFI plots are located on a grid with approximately 1 km spacing and are uniformly distributed across the study area in both dry and moist mixed-conifer habitat. All trees >12.7 cm dbh on a 16-m radius plot (0.08 ha) are inventoried by species. For this study,

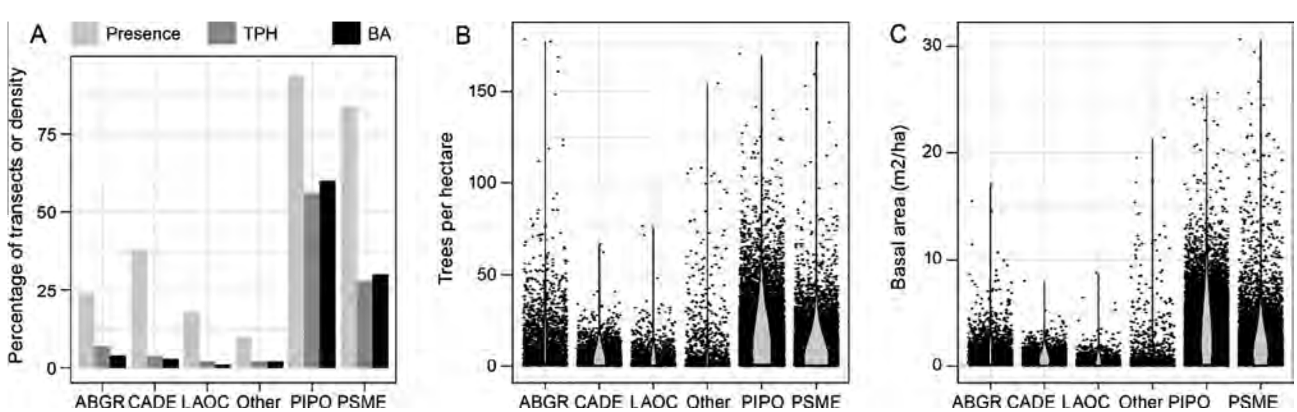

Fig. 4. (A) Percentage of transects in a 1922–25 timber inventory on which the species was present (Presence) and percentage of total density in the study area as measured by trees per hectare (TPH) and basal area (BA). Historical data were collected between 1922 and 1925 using strip survey methods to generate a 20% sample of the timber volume across the landscape. Violin plots of tph (B) and basal area (C) show how frequently particular densities occurred on the landscape for each species. The width of the gray shapes reflects the frequency of the data points (black dots) at a particular density value for each species. Low densities of ponderosa pine and Douglas-fir were most common, but high densities of several species were recorded in some areas. ABGR = *Abies grandis* (grand fir), CADE = *Calocedrus decurrens* (incense cedar), LAOC = *Larix occidentalis* (western larch), Other = species occurring on fewer than 3% of transects, PIPO = *Pinus ponderosa* (ponderosa pine), PSME = *Pseudotsuga menziesii* (Douglas-fir).

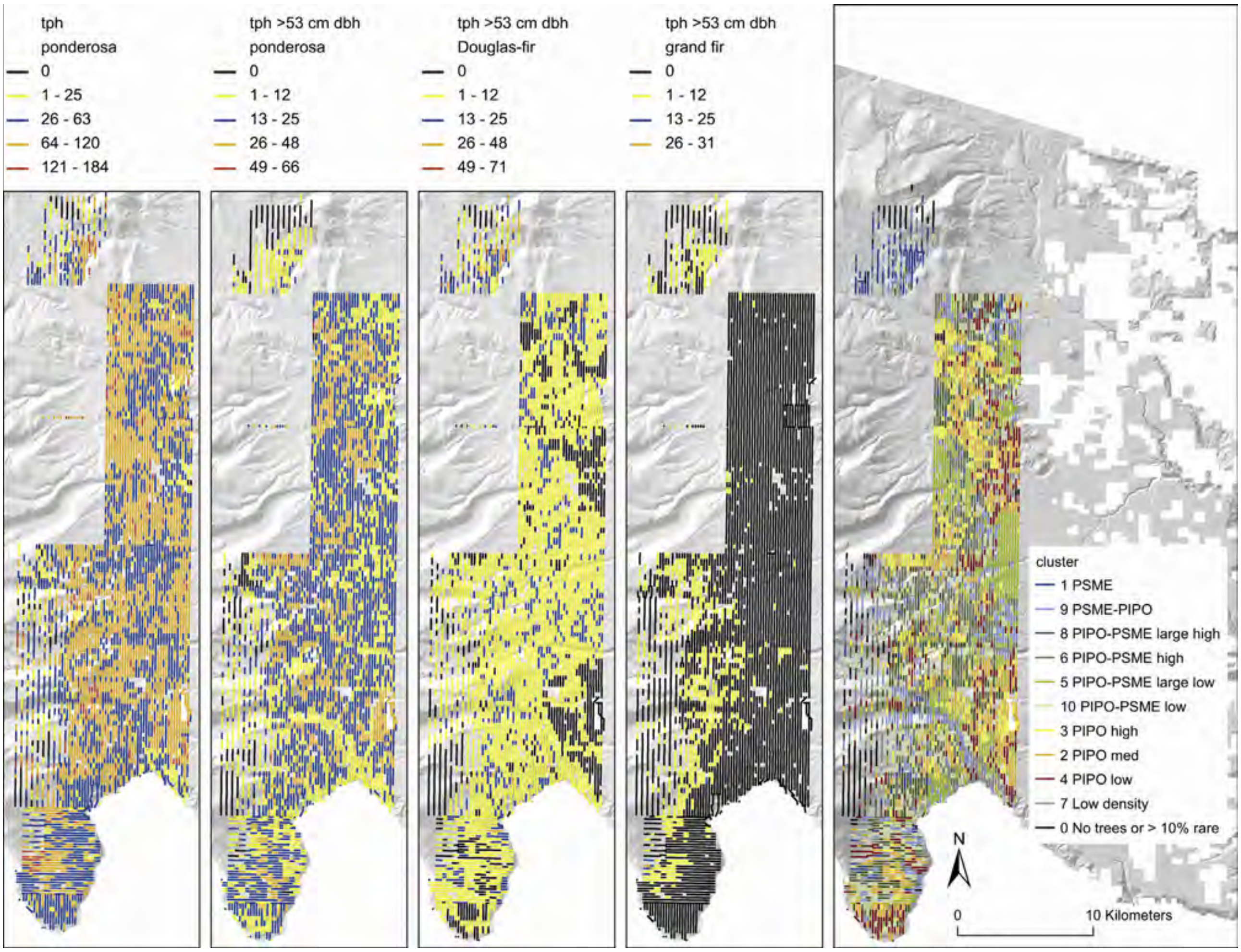

Fig. 5. Spatial distribution of density by species in a 1922–25 timber inventory. Historical data were collected between 1922 and 1925 using strip survey methods to generate a 20% sample of the timber volume across the landscape. Median density for all conifers >15 cm dbh is 63 tph; 95th percentile is 120 tph. Median density for all conifers >53 cm dbh is 25 tph; 95th percentile is 48 tph. 95th percentile values are shown in red and were widely distributed across the study area. Please refer to the web version of this article to view colors referenced in the legends. Spatial distribution of cluster groups identified through k-medoids cluster analysis on basal area by species and diameter class. Data for the three townships that appear empty in this figure are included in summary statistics; however, spatial data does not yet exist for them.

trees <15 cm dbh were excluded. Hardwood trees and Pacific yew (*Taxus brevifolia*) were also excluded from this analysis as these species were not included in the 1922–25 BIA timber inventory. Neither the plot size nor grid match the transect size and grid of the 1922–25 timber inventory data. However, as a systematically distributed sample of a landscape, they are used by representatives of the Warm Springs Tribes and the BIA to represent current conditions. To compare change over time exclusive of the effects of extensive harvesting, we used a subset of 61 CFI plots (hereafter "Intact") that according to CFI records had experienced no fire or harvest until the last inventory before harvesting. Inventory data for Intact plots were collected in 1972 (20 plots), 1979 (11 plots), 1987 (28 plots), and 1997 (2 plots). It is reasonable to assume that except in roadless areas, some selective harvesting of large ponderosa pine trees occurred before the CFI plots were established in 1957 (Rich Botto personal communication).

Table 1
Landscape-level distribution of historical trees per hectare by size class and species. Historical data were collected between 1922 and 1925 using strip survey methods to generate a 20% sample of the timber volume across the landscape. The first data column (All) shows the percentage of all conifers >15 cm dbh in each size class. The next three columns show the percentage of the three most abundant species in each size class.

dbh (cm)	Percent tph in each size class				
	All	Ponderosa	Douglas-fir	Grand fir	
15–53	60	52	27	11	90%
53–81	34	62	29	4	95%
81–101	5	61	36	1	98%
101+	1	53	44	1	98%
	100%				

3. Results

3.1. Historical structure and composition

3.1.1. Variability in density

Mean basal area for all transects was 14 ± 7 (0–64) $m^2\ ha^{-1}$ and mean tree abundance was 66 ± 32 (0–289) tph. The wide range of values recorded across the landscape reflects the inclusion of rare conditions (>95th percentile values). The 95th percentile values for density on all transects were 25 $m^2\ ha^{-1}$ basal area and 120 tph. These higher tree densities, although rare, were widely distributed across the study area (Fig. 5). Large (>1.6 ha) treeless (no conifers >15 cm dbh) areas were also rare and were, in this case, almost entirely restricted to the upper-elevation boundary of the study area in or adjacent to colder, wetter habitat types characterized by Pacific silver fir, hemlocks, and lodgepole pine (Fig. 5).

3.1.2. Variability by size class

Forests in this landscape were dominated by large trees (>53 cm dbh). Large trees contributed more than half of the basal area on 85% of transects. Large diameter trees comprised 42 ± 17% of trees on each transect. Mean quadratic mean diameter (QMD) was 52 ± 8 cm. Large trees were nearly ubiquitous across the landscape occurring on 99% of transects (Fig. 5). More than 25 large tph were recorded on 52% of transects. Mean abundance of large trees for all transects was 26 ± 14 tph. Most of the trees larger than 53 cm dbh were smaller than 81 cm dbh (Table 1). The largest trees in the record (203 cm dbh) were Douglas-fir, but ponderosa and sugar pine larger than 180 cm dbh were recorded.

3.1.3. Variability in species composition

Ponderosa pine was the most constant tree species (recorded on 94% of transects) and the most abundant species (58 ± 30% of tph) at the landscape level (Fig. 4). Ponderosa pine dominated total basal area (62 ± 27%) and basal area of large trees (64 ± 27%). Douglas-fir was the second most abundant species at the landscape-level and was recorded on 84% of transects. Douglas-fir contributed 28 ± 24% of all trees, 29 ± 24% of total basal area, and 29 ± 24% of the basal area of large trees. Together ponderosa pine and Douglas-fir composed 91 ± 15% of the basal area across the study area. Incense cedar was recorded on 38% and grand fir on 24% of transects. Both species contributed minimally to landscape level densities but grand fir did dominate density on some transects. Neither western larch (recorded on 8% of transects) nor sugar pine (recorded on 2% of transects) were common at the landscape level. Most sugar pines (63%) were >81 cm dbh. On the Reservation sugar pine is at the northern extremity of its range and western larch is near the southern boundary of its range. Other species were present but contributed little to total density.

3.1.4. Variability between groups identified through cluster analysis

Douglas-fir dominated transects were separated from ponderosa pine dominated transects on axis 1; low-density transects from high density transects on axis 2; and greater to lesser abundance of large trees on axis 3 (Appendix B). The ordination represented 87% of the variation in the distance matrix with 47% on axis 1, 29% on axis 2, and 11% on axis 3. Clustering in 10 groups ($p = 0.0006$) was selected to maximize the amount of variation explained by clustering balanced by a practical interest in keeping the number of groups low to make differentiating between them manageable and relevant to resource managers.

Clustering by basal area by diameter class and species isolated some of the lowest and highest basal area values, e.g., groups 1, 3, 4, and 7. The majority of the densities are relatively tightly clustered around the middle 50 percent of the values as indicated by the 95th percentile values (Fig. 7). Extreme values substantially higher than the 95th percentile values are represented in almost all groups (Fig. 7). These high density transects were widely distributed across the structure and composition types represented by the cluster groups and were also widely distributed spatially throughout the study area (Fig. 5).

Of the 10 groups, three were strongly dominated by ponderosa pine (mean proportion of total basal area 84–91%). Four groups

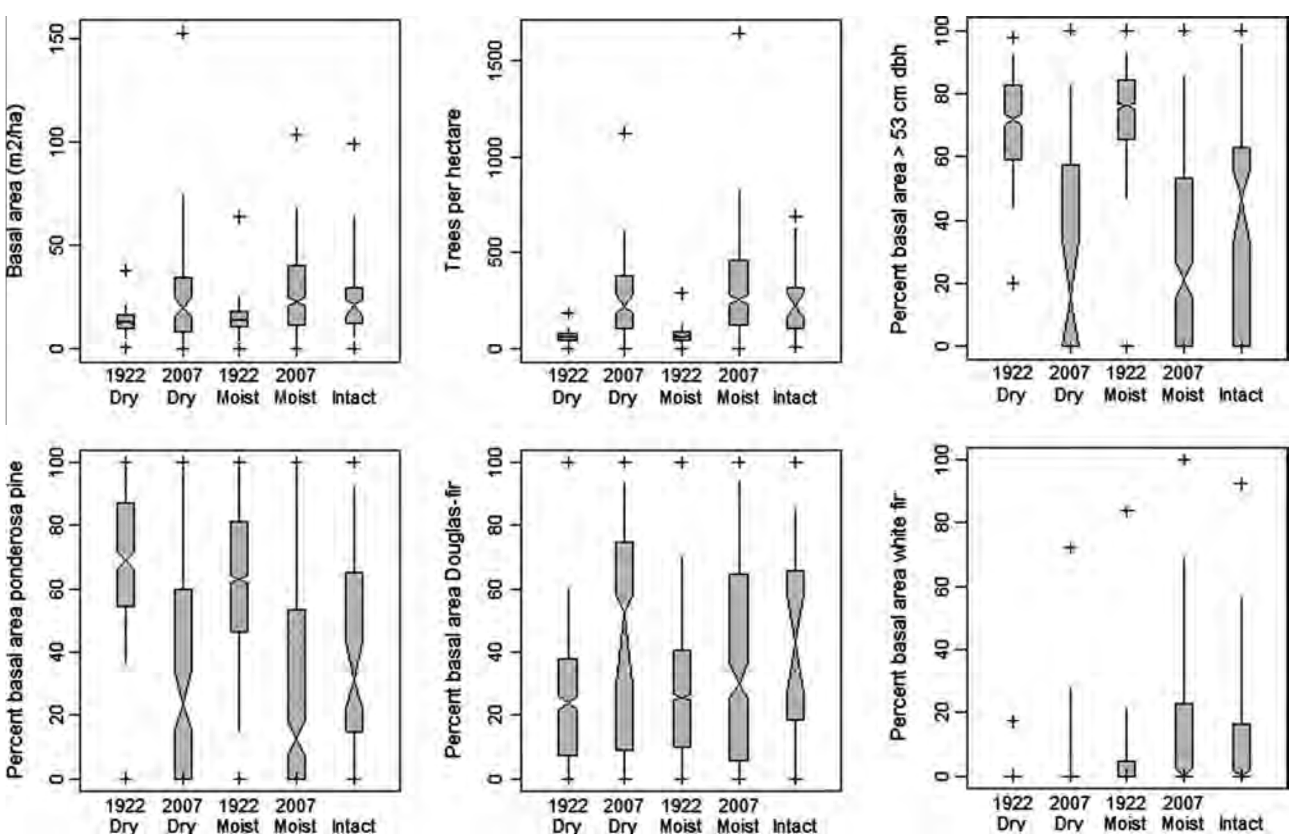

Fig. 6. Comparison of structure and composition by habitat type (dry and moist mixed conifer) between historical (1922) and current (2007) forest conditions. Historical data were collected between 1922 and 1925 using strip survey methods to generate a 20% sample of the timber volume across the landscape. Continuous Forest Inventory (CFI) plots re-measured in 2007 reflect contemporary forest conditions. Data for CFI plots with low harvest and fire history (Intact) provide an indication of structure and composition on forested sites without intensive harvest but with fire suppression 50–70 years after the BIA timber inventory in the 1920s. Box plots of tree density measured by number of trees (top left), basal area (top middle), proportion of the basal area in trees >53 cm dbh (top right), and proportion of basal area that is ponderosa pine (bottom left), Douglas-fir (bottom middle), and grand fir (bottom right). Boxes represent the middle 50% of the data, the center notch represents median values, whiskers extend to the 5th and 95th percentile values, and pluses represent the most extreme values.

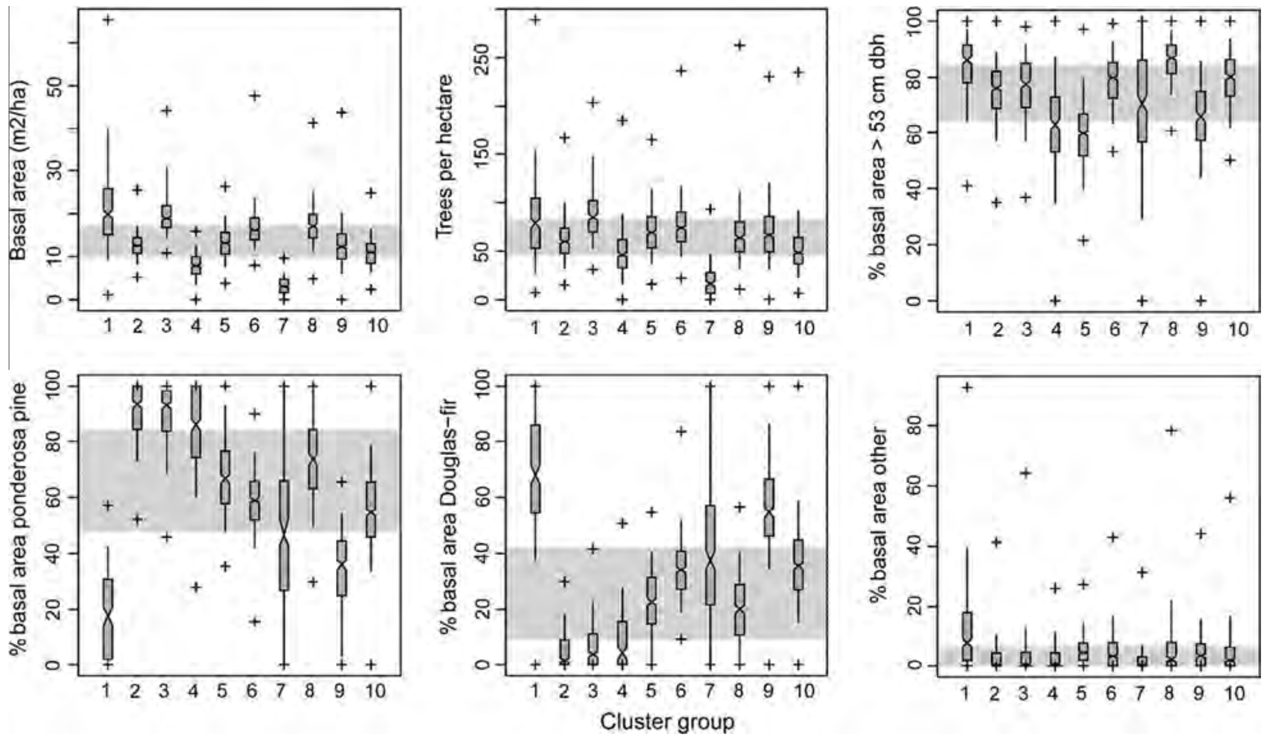

Fig. 7. Distribution of historical density, tree size, and species composition for groups identified through cluster analysis on basal area by species and diameter class. Historical data were collected between 1922 and 1925 using strip survey methods to generate a 20% sample of the timber volume across the landscape. Box represents the middle 50% of the data, the center notch represents median value, whiskers extend to the 5th and 95th percentile values, and pluses represent the most extreme values. Gray bar behind box plots indicates the range of values spanned by 50% of the entire data set of all ten cluster groups. Cluster groups were named for dominant species. "Low" indicates relatively lower basal area and "Large" indicates more basal area in trees >53 cm dbh than other groups with similar species composition. 1 PSME, 2 PIPO-med, 3 PIPO-high, 4 PIPO-low, 5 PIPO-PSME-large-low, 6 PIPO-PSME-high, 7 Low, 8 PIPO-PSME-large-high, 9 PSME-PIPO, 10 PIPO-PSME-low.

were dominated by ponderosa pine (mean proportion of total basal area 55–73%) with Douglas-fir contributing means of 20–36% to total basal area. The PIPO groups occupied 30% ($n = 1743$) of the study area and the PIPO-PSME groups occupied an additional 48% ($n = 2807$). Transects in group 1 PSME were predominantly (67%) located in the two northern and western most townships of the Reservation (Fig. 5) where moist mixed-conifer habitat abuts western hemlock habitat. Two groups were more common on dry mixed-conifer habitat and one on moist mixed-conifer habitat. Other groups were more evenly represented across the study area (Table 3).

3.2. Comparison of historical forest conditions on dry and moist mixed-conifer sites

Structure and composition of forests on dry and moist mixed-conifer sites were similar in the distribution of values describing density and abundance of ponderosa pine, Douglas-fir, and large trees (Table 2 and Fig. 6). For example, median and 95th percentile values for total basal area were 13 and 22 $m^2\ ha^{-1}$ for dry and 14 and 24 $m^2\ ha^{-1}$ for moist mixed-conifer sites respectively; median and 95th percentile values for abundance of trees were 63 and 108 tph on dry and 67 and 128 tph on moist mixed-conifer sites respectively. However, density, proportion of Douglas-fir and grand fir, and abundance of large trees were marginally higher on moist mixed-conifer habitat, and more variance in density, structure, and species composition were recorded on moist mixed-conifer sites (Table 2 and Fig. 6). As alluded to in Section 3.1.4, cluster groups were fairly evenly represented across both dry and moist mixed-conifer habitat (Table 3) with for three exceptions. Two lower density groups (4 PIPO-low, 5 PIPO-PSME-large-low) were more common on dry mixed-conifer sites and a higher density group (8 PIPO-PSME-large-high) was more common on moist mixed-conifer sites. This was not a consistent trend however as other relatively low, medium, and high density cluster groups were represented almost equally on both dry and moist mixed-conifer sites.

3.3. Comparison of past and current conditions

Current forest conditions are both denser and more variable than conditions in the early 1920s (Table 2 and Fig. 6). Currently, mean tree abundance is more than four times greater and mean basal area is roughly twice what it was historically across the landscape on these mixed-conifer sites. Mean basal area of large ponderosa pines has been reduced by two-thirds on dry mixed-conifer sites and by more than half on moist mixed-conifer sites. Douglas-fir and grand fir have both increased in number and basal area for both small and large trees. The proportion of the study area on which at least 50% of the trees are Douglas-fir or grand fir has more than tripled. While the total basal area in ponderosa pine has not decreased as dramatically as large ponderosa pine basal area, ponderosa pine as a proportion of mean basal area, tree count, and large trees has decreased by more than half.

Mean abundance of large trees is comparable in historical (26 ± 14) and current (24 ± 32) forest stands, but the distribution differs substantially. Historically, the median was 25 tph; in 2007, it was 12 tph. The composition of large trees shifted from historical dominance by ponderosa pine to current dominance of Douglas-fir. Mean abundance of large ponderosa pine has been reduced by more than two thirds in the dry mixed-conifer and by more than half in the moist mixed-conifer habitat. Historically, large ponderosa pine were recorded on more than 97% of transects in the study area; in 2007, however, ponderosa pine >53 cm dbh

Table 2
Historical forest conditions derived from timber inventory data collected 1922–1925 compared with current conditions (2007) and with conditions on sites with no recorded harvest or fire activity (Intact). Transect means are followed by standard deviation and range. Summary of historical timber inventory (1922–25) includes all transects that fall at least 90% within mapped habitat types (Appendix B). Historical data were collected using strip survey methods to generate a 20% sample of the forested area of the Reservation. Plot area varied by species. Continuous Forest Inventory (CFI) plots ($n = 535$) remeasured in 2007 reflect contemporary forest conditions. Data for 61 CFI plots with low harvest and fire history (see Section 2.6) provide an indication of structure and composition on forested sites without intensive harvest but with fire suppression 50–70 years after the 1922–25 BIA timber inventory.

	1922–25		2007		Intact
	Dry MC	Moist MC	Dry MC	Moist MC	
# of transects	741	2907	98	437	25
Plot area (ha)	1283–1950	5660–9341	8	35	5
Basal area					
All (m^2 ha^{-1})	13 ± 5 (1–38)	15 ± 7 (0–64)	26 ± 25 (0–153)	27 ± 20 (0–104)	24 ± 18 (0–99)
Ponderosa (m^2 ha^{-1})	9 ± 4 (0–28)	9 ± 5 (0–43)	6 ± 7 (0–24)	6 ± 8 (0–47)	8 ± 6 (0–27)
% Ponderosa	70 ± 21 (0–100)	62 ± 25 (0–100)	34 ± 36 (0–100)	29 ± 35 (0–100)	39 ± 30 (0–100)
% Douglas-fir	25 ± 19 (0–100)	28 ± 22 (0–100)	45 ± 34 (0–100)	37 ± 32 (0–100)	43 ± 29 (0–100)
% Grand fir	0 ± 1 (0–17)	4 ± 8 (0–84)	4 ± 12 (0–72)	15 ± 23 (0–100)	12 ± 21 (0–92)
Basal area ⩾ 53 cm DBH					
All (m^2 ha^{-1})	9 ± 4 (0–27)	11 ± 6 (0–63)	11 ± 20 (0–140)	10 ± 13 (0–77)	11 ± 13 (0–76)
Ponderosa (m^2 ha^{-1})	6 ± 4 (0–23)	7 ± 4 (0–40)	2 ± 5 (0–24)	3 ± 6 (0–32)	6 ± 6 (0–23)
% of total BA	70 ± 15 (20–98)	73 ± 16 (0–100)	28 ± 31 (0–100)	29 ± 30 (0–100)	42 ± 32 (0–100)
% Ponderosa	69 ± 21 (0–100)	66 ± 23 (0–100)	36 ± 42 (0–100)	34 ± 43 (0–100)	61 ± 39 (0–100)
% Douglas-fir	27 ± 20 (0–100)	28 ± 22 (0–100)	48 ± 42 (0–100)	42 ± 42 (0–100)	27 ± 34 (0–100)
% Grand fir	0 ± 1 (0–11)	2 ± 6 (0–100)	4 ± 15 (0–100)	8 ± 24 (0–100)	6 ± 17 (0–70)
Trees per hectare (tph)					
All	65 ± 25 (6–188)	70 ± 32 (0–289)	271 ± 211 (0–1124)	322 ± 251 (0–1643)	248 ± 172 (12–692)
QMD (cm)	52 ± 7 (30–73)	52 ± 9 (0–86)	34 ± 13 (0–78)	34 ± 13 (0–113)	38 ± 12 (18–75)
Tph ⩾ 53 cm					
All	25 ± 10 (1–69)	28 ± 14 (0–142)	23 ± 34 (0–198)	24 ± 32 (0–173)	28 ± 28 (0–111)
% tph ⩾ 53 cm	41 ± 15 (5–94)	42 ± 16 (0–100)	12 ± 19 (0–100)	12 ± 20 (0–100)	19 ± 23 (0–100)
Ponderosa	18 ± 9 (0–61)	18 ± 11 (0–91)	5 ± 10 (0–49)	7 ± 14 (0–86)	14 ± 15 (0–49)
Douglas-fir	6 ± 6 (0–37)	8 ± 9 (0–111)	13 ± 27 (0–173)	12 ± 23 (0–136)	9 ± 16 (0–74)
Grand fir	0 ± 0 (0–4)	1 ± 2 (0–31)	1 ± 6 (0–49)	2 ± 8 (0–86)	3 ± 12 (0–86)
Area occupied (%)					
⩾25 tph ⩾ 53 cm	49	53	40	43	61
0 tph 15–53 cm	0	4	1	0	2
0 tph > 53 cm	0	1	44	38	30
0 Ponderosa tph > 53 cm	0	5	72	72	39
<25 tph	8	14	4	2	2
>50% BA Ponderosa	87	67	27	26	30
>50% BA Douglas-fir	8	16	53	36	46
>50% BA Grand fir	0	0	2	9	7

Table 3
Percentage of each structure and composition cluster group (All) and percentage associated with either dry or moist mixed conifer habitat (*Appendix* B: Fig. 1). Gray bars highlight the cluster groups most strongly associated with one or the other of the two habitat types. Only transects falling at least 90% within a single habitat type were included in the summary of cluster groups by habitat type.

	Cluster group	All	Dry	Moist
1	PSME	7	25	75
2	PIPO-med	12	53	47
3	PIPO-high	9	47	53
4	PIPO-low	9	67	33
5	PIPO-PSME-large-low	12	65	35
6	PIPO-PSME-high	15	45	55
7	Low	6	43	57
8	PIPO-PSME-large-high	9	32	68
9	PSME-PIPO	10	53	47
10	PIPO-PSME-low	12	47	53
		100		

were recorded on 28% of the CFI plots. The spatial distribution differs substantially as well. Historically, large trees were recorded on all transects except the 89 transects (1%) on which no trees >15 cm dbh were recorded; in 2007, they were recorded on only 57% of the CFI plots.

In the "Intact" CFI plots, mean basal area values for both small and large ponderosa pine trees are comparable to those recorded in the historical timber inventory. However, total mean densities are higher, the QMD is smaller, and abundance of shade-tolerant species is higher. Mean proportion of ponderosa pine basal area and of large tree basal area are both roughly 40% lower than the mean proportions in the historical timber inventory; however, these values are both higher than the current forest conditions in the larger study area.

4. Discussion

Our objectives in this study were to address the following questions for this data set and study area: (1) what was the structure and composition of forests (conifers >15 cm dbh) on these mixed-conifer sites in the early 20th century; (2) did forest conditions on dry mixed-conifer sites differ from those on moist mixed-conifer sites; and, (3) how do current conditions on these sites differ from this historical record?

4.1. Key findings

Historically these dry and mixed conifer forests were predominantly low density relative to current conditions and dominated by large (>53 cm dbh) ponderosa pine and Douglas-fir trees across a wide moisture gradient (42–187 cm average annual precipitation). Similarly, the relatively rare higher tree densities were distributed across the full moisture gradient on both dry and moist mixed-conifer sites. Large (>1.6 ha) treeless (no conifers >15 cm dbh) areas were also rare and were, in this case, almost entirely restricted to the upper-elevation boundary of the study area in or adjacent to colder, wetter habitat types characterized by Pacific silver fir, hemlocks, and lodgepole pine.

Historical forest conditions varied little between dry and moist mixed conifer sites in terms of both overall densities and proportion of basal area that was provided by large trees. While there was substantial overlap in the distribution of descriptive statistics on both habitat types, moist mixed conifer sites did support higher densities, greater species diversity, and more variability than dry mixed-conifer sites. These differences, while potentially ecologically important, were subtle compared to the similarity between historical conditions on dry and moist mixed-conifer sites and to the contrast between historical and current conditions. Currently ponderosa pine no longer dominates large tree basal area, large trees no longer dominate total basal area, and Douglas-fir is now the dominant species across the landscape. Current mean tree densities are more than four times greater and current basal area is approximately two times greater than values recorded in the historical cruise. Currently, large trees dominate basal area on only 29% of area inventoried compared to 91% in 1922–25.

Again, our interest in current conditions on these tribal lands is motivated by the availability of a unique historical data set and our interest in changes on comparable federal lands for which landscape-level historical records have not yet been located.

4.2. Comparison with other historical records or reconstructions

Quantitative historical information on mixed-conifer forests of eastern Oregon and Washington is not abundant, especially compared to information available for ponderosa pine forests. However, enough exists to allow preliminary comparisons of historical forest conditions and inferences about fire regimes on mixed-conifer habitat in this study with those found in other areas.

4.2.1. Historical densities from records

Forest conditions comparable to those reported in this study – predominantly low density (16 ± 7 m^2 ha^{-1} and 68 ± 29 tph) stands dominated by large trees (83 ± 16% of basal area) especially large ponderosa pine trees (81 ± 20% of large tree basal area) – were recorded in the BIA timber inventory 1914–22 of the former Klamath Indian Reservation (hereafter "Klamath") (Fig. 4 in this study and Fig. 3 in Hagmann et al., 2013). Lower mean basal areas on the Warm Springs relative to the Klamath reflect a smaller large tree population on the Warm Springs. Ponderosa pine and sugar pine contributed more to stand densities on dry mixed-conifer sites and white fir on moist mixed-conifer sites on the Klamath than on the Warm Springs. This difference is primarily because Douglas-fir is almost completely absent on the coarse pumice soils that dominate on the Klamath.

Munger's (1917) report on ponderosa pine in eastern Oregon provides valuable information but was a selected sample of "well-stocked areas" rather than a representative or systematic sampling of the pine forests. Munger's survey of an aggregated plot area of 218 ha distributed across counties south and east of the Reservation in areas that would probably currently be classified as mixed-conifer habitat (inferred from species composition) shows average densities of 105–147 tph and 23–29 m^2 ha^{-1} of basal area for conifers >15 cm dbh. These values fall at the high end of the range of average densities recorded for 1.6 ha transects in the 1922–25 BIA timber inventory, which employed a systematic sampling design that would include gaps and openings typical of dry forests and that Munger excluded in his study. Munger's principal objective was to estimate potential future yields. Munger reports average densities derived from a selective sampling of fully stocked areas. In his words, "*The figures for the total stand per acre on these tracts are high and should not be considered as being estimates of the yield over large areas in the locality … sample acres are taken only in well stocked areas where there are no bare ledges, meadows, or other openings such as are scattered through yellow pine forests and reduce the yield for a large tract.*" (Munger, 1917). Munger (1917) concludes that because ponderosa pine is "a rather unsuccessful competitor of the more tolerant species, Douglas fir, white fir, and lodgepole pine, it is largely excluded from soils moist enough for these species to thrive in". As is demonstrated in this study and the Klamath study, however, "more tolerant species" are currently abundant on mixed-conifer sites where ponderosa pine historically dominated (see Fig. 4 this study and Table 5 in Hagmann et al., 2013).

4.2.2. Historical densities from reconstructions or current conditions

Perry et al. (2004) sampled ponderosa pine and mixed-conifer habitat on the Deschutes NF in 16 plots with a total sampled area of 3.2 ha and reported abundance of all trees >150 years old ranged from 0 to 80 tph. Merschel et al. (2014) inferred historical densities from live tree and stump counts in mixed-conifer forests on the Deschutes National Forest (NF) immediately south of the Warm Springs Reservation. They found the density of large trees (>50 cm dbh) reduced to about half of historical densities, based on comparisons between existing live and dead tree counts. Historical abundance of large trees (>50 cm dbh) in mixed-conifer habitat on the Deschutes NF is comparable to levels observed in this study with a mean of 21–30 tph (standard deviation ±17–19 tph, range 0–85 tph) (Merschel et al., In press).

Baker (2012) reconstructed forest density for dry forests on the eastern slopes of the Cascade Range in Oregon from General Land Office (GLO) survey data for 8 marker trees per section (259 ha) and estimated a mean density of 246 tph and median of 211 tph for the northern region, which includes townships both north and south of our study area. By contrast, our findings based on the BIA timber inventory records, which include an average of >3000 trees per section (259 ha), found average densities of 66 ± 32 (0–289) tph and 14 ± 7 (0–70) m^2 ha^{-1}. We have much greater confidence in our density data since it is a systematic sample of conifers >15 cm dbh on 20% of 50,000 ha collected expressly for the purpose of estimating available timber supply. In an earlier study (Hagmann et al., 2013), we compared 1914–22 timber inventory records for the Klamath Indian Reservation with reconstructed densities estimated from GLO survey data (Baker, 2012) for the same area in both studies and again found that estimated densities from GLO survey data were substantially higher. Our conclusion is that Baker's reconstructions from GLO survey data overestimate historical densities.

4.2.3. Historical and current densities of large trees

The large and old trees that historically dominated these mixed-conifer sites have been substantially reduced in number. Large and old fire- and drought-tolerant trees are the structural backbone of dry forest ecosystems and make many unique contributions to ecological function (Kolb et al., 2007; Franklin and Johnson, 2012; Lutz et al., 2012; Franklin et al., 2013). Existing large and old fire- and drought-tolerant trees are essentially irreplaceable given that several centuries are required to grow replacements. In this study, both mean abundance (tph) and spatial distribution of large diameter ponderosa pine have been substantially reduced. Douglas-fir and, to a lesser extent, grand fir have replaced ponderosa pine where it was removed from the landscape. Mean abundance of large trees of all species is comparable to historical mean abundance; however, the distribution has changed substantially. Historically, large trees (predominantly ponderosa pine and secondarily Douglas-fir) were more evenly distributed across this landscape, which may reflect a spatial pattern important to some ecosystem functions and processes, e.g., provision of habitat and facilitation via hydraulic redistribution. In other studies in eastern Oregon and Washington, mean abundance of large trees is currently about half of what it was historically (Harrod et al., 1999; Hagmann et al., 2013; Merschel et al., In press).

4.2.4. Historical fire regimes

High-severity fire effects were documented at the upper elevation boundary of moist mixed-conifer habitat adjacent to colder, wetter habitat types. Cruisers generated contour and cover type maps at the time of the inventory (NARA, 1922–25) on which they identified "burned over" areas. These burn patches were located above 1000 m elevation; adjacent to or in wetter, colder forest types; and extended beyond the upper boundary of the timber cruise. Transect records in these burn patches include species such as Pacific silver fir, noble fir, western and mountain hemlock, and lodgepole pine. These "burned over" areas, located where huckleberry fields are maintained to this day, may reflect, at least in part, management practices to maintain huckleberry productivity. In 1901, USGS surveyor Fred Plummer noted the presence of fire on trails leading to huckleberry fields (Langille et al., 1903). In his 1910 report of an examination of timber on the Reservation, cruiser Charles Webster also reported that nearly all the burned areas at higher elevations were near trails (NARA, 1910). These areas differ from the rest of the study area in the abundance and contiguity of transects on which no trees or fewer than 25 tph were recorded. Except in these areas, large tracts with few trees (<25 tph) were uncommon at the time of the inventory (Fig. 5). The absence of stands composed solely of small-diameter trees provides further support for our inference that large stand-replacing disturbance events were either absent or uncommon on the mixed conifer habitat in this study area; such stands would presumably have existed if large gaps or openings had been created. Proposals for future analysis of this data set include exploration of the potential to infer disturbance regime from tree structure and composition as well as additional inventory data describing fire damage, beetle infested trees, and understory vegetation.

The BIA timber inventory fits well with earlier inventories and descriptive accounts of site condition and fire effects in supporting inferences of a predominantly low- to moderate-severity fire regime throughout the mixed-conifer forest. In Plummer's 1901 USGS survey of townships encompassed by this study, ponderosa pine was the most abundant species by volume; ground fuels were light or very light, and burned area averaged 5% of the timbered area (Langille et al., 1903). Plummer defined burn areas as having been marked by fires "of comparatively recent occurrence" on which the regeneration has not reached merchantable size. On townships in range 10 (the lower elevation portion of this study) which encompass moist mixed-conifer to ponderosa pine habitats, Plummer's estimates of area burned per townships in range 10 vary from ~400 ha to 0 with an average of 2% of the timbered area burned. At higher elevations, townships in range 9 encompass a range of forest conditions from colder, wetter habitat types such as mountain or western hemlock and Pacific silver fir to moist mixed-conifer habitats; Plummer's estimate of burned area for these townships ranged from 0 to 1600 ha with 12% of the timbered area burned. On BIA timber inventory transects in the boundary zone between moist mixed-conifer and wetter forest types, large patches (>1000 ha) with low density and fewer than 2 tph > 53 cm dbh were recorded. Cruisers described site conditions on transects in this area as "old burn". At lower elevations in the interior of the mixed-conifer habitat, patches smaller than 150 ha had fewer than 2 tph > 53 cm dbh. Consistent with these earlier records, both Weaver (1959) and Soeriaatmadja (1966) inferred relatively frequent fire (<55 years between fire scars) from their assessment of fire-scarred trees with increased severity and decreased frequency on moister sites.

Landscape-level conditions in the 1922–25 timber inventory record differ from two studies of historical fire regime in comparable forest types. In the first of these two studies, a reconstruction of historical forest conditions using photo interpretation of aerial images from the 1930–40s, the authors found widespread evidence of partial and stand-replacing fire (Hessburg et al., 2007). Hessburg et al. focused primarily on eastern Washington; the study includes only one sampled area in Oregon, a subwatershed just south of the Warm Springs Reservation in the Deschutes National Forest. Differences in the topography and the variables measured in the two studies confound comparison. Greater homogeneity in fire behavior may be expected in areas with simpler topography (Kennedy and McKenzie, 2010), like this study area, when compared to more topographically complex areas, like some of the subwatersheds in northern Washington studied by Hessburg et al. Hessburg et al. inferred fire severity from the proportion of canopy cover in each size class where total canopy cover includes trees <12.7 cm dbh (Hessburg et al., 1999). Our data set includes tree counts only for trees >15 cm dbh. Developing a crosswalk between these two studies could extend the value of both studies. Consistent with the 1922–25 timber inventory, interpretations from aerial imagery of the 1930–40s recorded dominance of ponderosa pine. Hessburg et al. (2007) found that in eastern Washington, 71% of the area had understories dominated by pole-sized and larger trees (12.7–63.5 cm dbh). In this study, however, landscapes were not dominated by small trees; trees 15–53 cm dbh were more abundant than trees >53 cm dbh on only 28% of transects inventoried. Currently, trees 15–53 cm dbh are more abundant than trees >53 cm dbh on 94% of the study area. It is reasonable to infer that frequent fire contributed to the suppression of small tree density. Another contrast between these two studies is in the finding of medium (10^1–10^2 ha) to large (10^3 ha) patches of stand initiation structure. In this study, the only large (>150 ha) patches of stand initiation structure were at the upper elevation boundary of the moist mixed-conifer habitat where it interleaves with wetter, colder forest types. Transects in this area differ from the rest of the mixed-conifer habitat in abundance and contiguity of area occupied by few (<25 tph) or no trees, less ponderosa pine, and fewer large trees. Baker (2012) also inferred historical fire regime from historical forest conditions; however, Baker's reconstruction of forest densities using General Land Office survey data is based on a data set of 8 marker trees per section (259 ha) and the validity these reconstructed densities has been disputed (Hagmann et al., 2013) as well as inferred fire regime (Fulé et al., 2013).

4.3. Relevance to contemporary management

Ecological restoration focused on increasing the capacity of dry forest ecosystems to withstand characteristic and novel stressors relies on multiple sources of information and incorporates diverse objectives (USFS, 2010; Franklin and Johnson, 2012; North, 2012; Churchill et al., 2013; Hessburg et al., 2013). The goal of such restoration efforts is to increase the resistance and resilience of dry forest landscapes to disturbance processes that influenced the structure and composition of these forests in the past and that are likely to occur in the current landscapes. The goal is not to restore historical conditions for their own sake. However, restoring the historical patterns that characterized these forests for centuries is consistent with treatments to foster adaptation to projected changes in climate and disturbance regimes (Fulé, 2008; Keane et al., 2009; Moritz et al., 2011; Moritz et al., 2013).

Large ponderosa pine were widely distributed and dominated the basal area of historical forests in this 20% sample of >50,000 ha of mixed-conifer forest in the Warm Springs study area and of >38,000 ha of ponderosa pine and mixed-conifer habitat on pumice soils in the Klamath study area (Hagmann et al. 2013). Existing old and large, fire- and drought-tolerant trees may be at increasing risk of accelerated mortality associated with fire, insects, pathogens, and drought stress because of the increased densities and compositional changes in the forests (Guarín and Taylor, 2005; Lutz et al., 2009; Van Mantgem et al., 2009; Ager et al., 2010; Ganey and Vojta, 2011; Stephenson et al., 2011; Fettig, 2012). Current management proposals for frequent-fire forests on federal lands seek to increase options for the future of these socio-ecosystems and maintain the components most difficult to replace, i.e., large old trees which are the structural backbone of the dry forest ecosystems of the Pacific Northwest (Franklin and Johnson, 2012). Recent studies suggest that remaining old tree populations are being lost faster than they can be replaced (Lutz et al., 2009; Stephenson et al., 2011; van Mantgem et al., 2011). Conservation of existing large ponderosa pine is a high priority for ecological restoration efforts given the substantial reduction in their populations as documented in this and other studies.

Heterogeneity at multiple spatial scales is a key component of ecological restoration focused on restoring and conserving processes and functions in dry forest ecosystems, including provision of habitat to promote biodiversity (Hessburg et al., 1999; Lindenmayer and Franklin, 2002; Lydersen and North, 2012; Churchill et al., 2013; Franklin et al., 2013). In this study and an earlier study (Hagmann et al., 2013), we describe forest conditions at spatial scales larger than 1.6 ha. In addition to the predominantly low densities dominated by large ponderosa pine and Douglas-fir, the widespread distribution of higher density stands and of large trees may have supported processes and functions critical to maintaining currently desirable ecosystem services and functions. Similarly, the near absence of large treeless areas (except at higher elevations where huckleberry fields were located) may also prove to be a critical pattern to conserving or restoring resilience and resistance to current and projected conditions. Again, historical conditions may provide insights to inform contemporary management given today's goals and objectives but should not be viewed as targets for restoration.

Our spatially extensive studies, complement studies of historical forest conditions at smaller spatial scales to describe the variability of historical mixed-conifer forests with a dominant pine component. Abundant variability in structure in frequent-fire forests has been observed at small spatial scales, typically <0.4 ha (Larson and Churchill, 2012; Lydersen et al., 2013; Fry et al., 2014). This variability is often described as a patchy mosaic of widely spaced individuals, clusters of large trees, dense patches of regeneration, and small openings (Franklin and Van Pelt, 2004; Larson and Churchill, 2012). Recent work has quantified variability in forest conditions at smaller spatial scales to provide guides for restoration of spatial heterogeneity (Churchill et al., 2013). These studies demonstrate that the historical mixed-conifer forest incorporated substantial variability across the landscape in species, density, and number of large trees. Thus, it is important to combine the small-scale variability described in other studies with the variability at larger spatial scales as described here to fully understand the structure and dynamics of historical mixed-conifer forests as a guide to ecological restoration.

Average conditions, as important as they are, mask significant variability and are an egregious oversimplification of historical conditions (Stephens and Gill, 2005; Collins et al., 2011) For example, 0.31% of the 6149 transects fall at the mean densities for both tph and basal area for dry and moist mixed-conifer habitat, and on none of those transects did large tree basal area match the habitat mean. Focusing on average conditions may enable communication of key concepts. However, restoring heterogeneity at multiple spatial scales will be essential to meet the objectives of ecological restoration (Churchill et al., 2013; Franklin et al., 2013).

This historical inventory (also see Hagmann et al., 2013) provides strong evidence that forests on these mixed-conifer sites were predominantly – not exclusively – low-density, pine-dominated, and have undergone substantial changes in composition and density. Forests and, especially, the remaining population of old trees on mixed-conifer sites may be more vulnerable to projected changes to climate and disturbance regimes than less productive sites (Franklin et al., 2013; Merschel et al., In press; Stine et al., In press). However, controversy about the appropriateness of restoration activities, especially harvest, in dry forest habitat continues (Hanson et al., 2009, 2010; Spies et al., 2010; Williams and Baker, 2012, 2014; Fulé et al., 2013). Questions about historical fire regimes and the extent of high-severity fire effects fuel debate (Stephens et al., 2013). One assumption could be that mixed-conifer sites have not really undergone change due to fire suppression and other activities – i.e., dense forests and abundance of shade-tolerant species were characteristic on these sites. Another assumption could be that since these forests have only missed a few of their historical fire return intervals they have a lower priority for restoration. Our data provide no support for such assumptions.

Some may dismiss this inventory as a snapshot in time and suggest that these forests could have emerged following extensive stand replacing fire. We argue that the abundance of large ponderosa pine in this record suggests these forest conditions persisted at least for several centuries prior to the inventory and these trees are not likely to have resulted from extensive stand-replacing fire given (1) current conditions on these forests where Douglas-fir and grand fir are more abundant than ponderosa pine with active fire suppression, (2) the record of frequent fire recorded on these sites (Weaver, 1959; Soeriaatmadja, 1966), and (3) the correspondence of this study and our conclusions with records and studies conducted over more than a century and reviewed most recently by Stine et al., In press.

Further research on the historical disturbance regime suggested by this spatially extensive and intensive, individual tree record is warranted. Additional data collected at the time of the inventory is available (e.g., Appendix A) that might support inferences about historical disturbance regimes and resulting spatial patterns. Our hypothesis is that frequent fire suppressed the potential productivity of these sites which is expressed currently under active fire suppression. The topography of this study area, a gentle slope to the crest of the Cascade Range dissected by deep, river canyons, contrasts sharply with more rugged topography elsewhere in the frequent-fire forests of the Pacific Northwest. More syntheses of existing historical data sets and reconstructions is warranted to explore consistent and divergent traits of frequent-fire systems despite widely ranging geophysical variables and conifer species distributions.

Data on variability in historical structure and composition of mixed-conifer forests at the landscape level can help inform restoration efforts. These spatially extensive timber inventories of 20% of the forested area provide insight into historical conditions at the stand and landscape level and can help resolve disputes about potential bias or representativeness of sites selected subjectively and of studies conducted at smaller spatial scales. These records also provide quantitative corollaries to descriptive accounts of historical forests. These spatially extensive inventories illustrate that mean conditions rarely existed on the landscape and provide insight into the range of variability that existed historically. The findings in this study may be of interest to stakeholders in frequent-fire forests generally, but perhaps most relevant to stakeholders in similar forest types where Douglas-fir and grand fir would be expected to dominate in the absence of frequent fire and where topography offers minimal impediment to fire spread.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2014.06.044.

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