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Historical structure and composition of ponderosa pine and mixed-conifer forests in south-central Oregon



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ABSTRACT

We summarized structure and composition of dry forests from a 90-year-old timber inventory collected by the Bureau of Indian Affairs on the former Klamath Indian Reservation (now part of the Fremont-Winema National Forest). This analysis includes data from 424,626 conifers ≥15 cm dbh on 3068 transects covering 6646 ha. The data represent a 10-20% sample of 38,651 ha of forest growing on sites that are classified as ponderosa pine (Pinus ponderosa) and mixed-conifer habitat types distributed within the 117,672 ha of the study area. Large, drought- and fire-tolerant ponderosa pine dominated these forests. Large tree (>53 cm dbh) basal area ($13 \pm 7 \text{ m}^2/\text{ha}$) contributed $83 \pm 16\%$ of total basal area; $81 \pm 20\%$ of the large-tree basal area was ponderosa pine. Composition and structure of forests on mixed-conifer sites were very similar to those on ponderosa pine sites. Variability in composition and structure was recorded on all habitat types and was highest on moist mixed-conifer sites. Stand densities (trees per hectare, tph) have more than tripled over the past 90 years from 68 ± 28 tph to a current density of 234 ± 122 tph recorded in Current Vegetation Survey data collected by the United States Forest Service. Mean basal area, however, increased by less than 20%. Basal area of large trees (>53 cm dbh) has declined by >50%, and the abundance of large trees as a proportion of the total number of trees per hectare has decreased by more than a factor of five. This landscape-level record of historical forest conditions allows inferences about structure and composition across tens of thousands of hectares. A historical landscape emerges which supports current working hypotheses that frequent, low- to moderate-severity wildfires maintained a predominantly low-density forest dominated by large, fire- and drought-tolerant ponderosa pines across a significant moisture and productivity gradient from the driest ponderosa pine to the mixed-conifer habitat types.

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1. Introduction

Knowledge of historical forest conditions – reference conditions – for landscapes characterized by frequent fire and recurring drought is critical to developing management strategies to address current and projected stressors. Reference conditions incorporate interactions between patterns and processes that shaped dry forests for millennia (Agee, 1993; Stephens et al., 2008). Dry forest ecosystems are currently at risk of major disturbances related to prolonged drought (Spies et al., 2006; Kolb et al., 2007; Breshears et al., 2009; Littell et al., 2009) and large and contiguous wildfires and insect outbreaks (Hessburg et al., 2005; Fettig et al., 2007; Kolb et al., 2007). Reference conditions provide one important basis for setting goals to reduce risk of accelerated losses to fire, drought,

and insects and to increase the potential for conserving ecosystem functions (Swetnam et al., 1999; Franklin et al., 2008; Fulé, 2008).

Human activities over the past 150 years have radically altered the structure, composition, and disturbance regimes of dry forests of the Pacific Northwest (Hessburg et al., 1999; 2000; 2005). Contemporary conditions in dry forests in the western United States include increased tree density, a shift in basal area to dominance by smaller trees, and a shift in species composition to dominance by shade-tolerant species relative to historical conditions (Covington and Moore, 1994; Taylor and Skinner, 1998; Perry et al., 2004; Hessburg et al., 2005; Stephens and Fulé, 2005; Noss et al., 2006). Changes also include substantial reductions in the abundance of large and old trees, loss of habitat due to land-use conversion, and fragmentation of forested ecosystems by the built environment (Bolsinger and Waddell, 1993; Henjum et al., 1994; Wisdom et al., 2000). The capacity of existing dry forests to withstand current and projected stressors without undergoing significant change has been compromised (Noss et al., 2006; Franklin

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et al., 2008; North et al., 2009; Stephens et al., 2010; USFS, 2010; US FWS, 2011). Essentially irreplaceable old trees, which are already dramatically reduced in number and distribution, are at risk along with associated organisms and processes (Spies et al., 2006; Kolb et al., 2007). Management interventions – broadly described as restoration – are needed to conserve remaining old trees and the habitat they provide (Lehmkuhl et al., 2003; US FWS, 2011).

Efforts to conserve existing dry forests and restore their capacity to resist characteristic stressors rely on multiple sources of information, including historical, current, and projected conditions. Emphasis is increasingly placed on restoring the processes that shape systems rather than the structure and composition of any one historical state or condition (Millar et al., 2007; Joyce et al., 2009; Hobbs et al., 2010; Spies et al., 2010a; Stephens et al., 2010). In dry forests, the interaction between spatial patterns in structure and composition on the one hand and fire and droughtrelated processes on the other is so strong that restoring these patterns increases resistance to fire (Fulé et al., 2012; Prichard and Kennedy, 2012) and drought (Kolb et al., 2007; Ritchie et al., 2008; Stephens et al., 2010).

Societal values strongly influence restoration objectives for dry forests and may include retaining or creating conditions that are not consistent with historical conditions but that better meet the current mix of values. Conscious departures from historical conditions include management decisions such as maintaining bitterbrush (*Purshia tridentata*) cover at what may be higher than historical levels to sustain ungulate populations (Johnson et al., 2008) and continuing to suppress fire due to opposition to the re-introduction of fire as a system-structuring process (North et al., 2012).

Climate change is another important consideration in application of historical conditions in restoration treatments. This inventory was conducted from 1914 to 1922 shortly after the end of the Little Ice Age and at the leading edge of the severe droughts of the 1920-1930s (Keen, 1937). Current and projected climates are generally drier and warmer than the climate of the centuries preceding this inventory and during which the inventoried trees would have established and survived. Longer, drier summers are projected for the Pacific Northwest (Salathé et al., 2010) along with increases in fire frequency (McKenzie et al., 2004). Correlation of sediment records with reconstructed climate show increased biomass burning with increases in temperature and drought (Marlon et al., 2012). Increases in length of fire season and the size (Westerling et al., 2006) and severity (Miller et al., 2009) of wildfires have already been observed. Fortunately, treatments suggested to increase mean diameter, shift species composition to favor drought- and fire-tolerant species, and restore spatial heterogeneity in dry forests under current climates are largely consistent with treatments appropriate to at least partially prepare dry forests to deal with expected changes in climate and disturbance regimes (Franklin et al., 1991; Spies et al., 2010a; Stephens et al., 2010; Chmura et al., 2011; Peterson et al., 2011).

Historical conditions in the dry forests of south-central Oregon are uniquely documented in an extensive timber inventory ("cruise") conducted between 1914 and 1922 by the Bureau of Indian Affairs (BIA) on the former Klamath Indian Reservation (now a part of the Fremont-Winema National Forest). The forested area of the reservation was sampled at 10–20% intensity using a systematic grid consisting of one or two 1.6 ha transects per quarter-quarter section (16.2 ha). Transect location was tied to documented survey points of the Bureau of Land Management Public Land Survey System (BLM PLSS). Live conifers at least 15 cm dbh were tallied by species and diameter class. This archived inventory represents a large and systematic sample of historical forest composition and structure over hundreds of thousands of hectares, which complements existing historical records and reconstructions for this area (Table 6). Similar inventory records from other forested areas have been used to understand historical conditions and to validate reconstructions of reference conditions in the central Sierra Nevada in California (Scholl and Taylor, 2010; Collins et al., 2011) and in Australia (Whipp et al., 2010).

Our focus in this paper is on the historical range of variability in structure and composition of dry forests growing on ponderosa pine and mixed-conifer habitat types (potential vegetation types) in three large segments (117,672 ha total) of the former Klamath Indian Reservation as recorded in the 1914–1922 timber inventory. In addition to documenting the historical structure and composition at the stand (1.6 ha) and landscape (>30,000 ha) levels, we compare historical forest conditions on sites identified as ponderosa pine and mixed-conifer habitat types. Our objective is to provide managers and stakeholders with an improved set of reference conditions, in particular reference conditions for mixed-conifer habitat types for which little information has been available.

2. Methods

2.1. Study area and site history

The former Klamath Indian Reservation (hereafter Reservation) extends from the eastern slopes of the Cascade Range into the Basin and Range Province in south-central Oregon (latitude 42.2–43.4°N, longitude 122-121.6°W). At the time of the timber inventory, Reservation forests were managed by the US Indian Service (subsequently renamed the BIA). In 1954 the federal government ended its trust relationship with the Klamath Tribes. The majority of the forestlands of the Reservation were acquired by the federal government leading to the creation of the Winema National Forest (NF) with smaller portions of the Reservation incorporated into the Fremont NF. The Klamath Tribes work with federal and state resource agencies, as well as other entities with shared conservation and resource management goals, on lands within and outside of the former Reservation that are important to the Tribes' interests.

The inventory data from three large segments of the Reservation, each >30,000 ha, were selected for study: (1) Wildhorse Ridge-Yamsi Mountain (hereafter Wildhorse), (2) South Chiloquin (hereafter Chiloquin) and (3) Black Hills (Fig. 1). They were selected because portions of these three areas have experienced little timber harvest and offer excellent opportunity for eventual resampling of inventory transects to assess changes in vegetation primarily due to fire suppression. In addition, all three areas encompass current or proposed restoration projects.

Wildhorse, Chiloquin, and Black Hills areas collectively span the moisture and productivity gradients that fully represent the spectrum of dry forest types (ponderosa pine and dry and moist mixed-conifer habitat types) that are the focus of this study (Table 1). Moisture and productivity gradients are inferred in this study from habitat type classifications, which were created using indicator plants as described in Section 2.3. These forests span an elevation range of 1270–2300 m. The Reservation experiences a continental climate. Summers are typically hot and dry with cold nights while winters are cold and snowy. Most precipitation falls as snow during fall and winter.

Forests of the study area are strongly influenced by tephra deposits from Mount Mazama; parent materials and topography strongly influence forest composition and productivity through their influence on available moisture and temperature extremes (Dyrness and Youngberg, 1966; Carlson, 1979; Franklin and Dyrness, 1988). The immature soils of the central Oregon pumice zone exhibit low heat storage, poor heat transfer, and rapid response to temperature change at the surface, which can exacerbate



Fig. 1. Former Klamath Indian Reservation (black outline). Ponderosa pine and mixed-conifer habitat types are inferred from a map of modeled potential vegetation types (Henderson et al., In prep.). Fort Klamath marks the site of the first sawmill (steam-powered, 1864) in Klamath County. The railroad reached Kirk in 1911 from Klamath Falls (~40 miles south) where it arrived in 1909. Before the treaty of 1864 which established Reservation boundaries, villages and resource use of the Klamath Tribes centered on the marshes, the Williamson and Sprague Rivers, and seasonal camps at higher elevations in the Cascade Range. The extent of Klamath Marsh and Upper Klamath Lake are depicted here after extensive drainage through the 1990s, not as they would have appeared in the late nineteenth century (National Research Council, 2004). Ponderosa pine – habitat types are mapped as three distinct potential vegetation types: Ponderosa pine – Lodgepole pine (PIPO-PICO), Ponderosa pine – Dry (PIPO Dry), and Ponderosa pine – Xeric (PIPO Xeric). The study includes two classifications of mixed-conifer forest: Mixed Conifer – Dry (Mixed Dry) and Mixed Conifer – Moist (Mixed Moist).

Table 1

Annual precipitation and minimum January and maximum July temperatures derived from spatially gridded estimates modeled from point measurements taken at national and local weather stations and averaged over a 30-year period from 1971–2000 (PRISM, 2006).

	Precipit	ation (cm)	Tempe	Temperature (°C)						
			January	/ min	July max					
	Low	High	Low	High	Low	High				
PIPO Xeric PIPO Dry	37.5 37.4	63.9 78.8	-8.3 -8.3	-6.2 -6.2	24.8 25.3	29.2 29.1				
PIPO-PICO Mixed Dry Mixed Moist	47.3 42.0 46.2	99.4 100.1 109.7	-8.9 -8.5 -8.6	-6.4 -5.9 -5.7	25.1 23.6 22.2	28.3 28.6 28.1				

the potential for frost throughout the year and lethal surface temperatures during hot weather (Carlson, 1979). Also, these coarse pumice soils loosely hold abundant water which creates conditions conducive to frost heaving and rapid drying during summer (Carlson, 1979). Douglas-fir is scarce on soils of this type within the study area. At the southern edge of the pumice zone (Chiloquin), weathered basalt, andesite, breccia, pyroclastic, and sedimentary rocks have a greater influence on soils (Carlson, 1979) and Douglas-fir becomes a significant element in the forests.

Lightning ignitions associated with dry thunderstorms commonly occur in the intermountain west (Rorig and Ferguson, 1999). No fire history reconstructions were found for the study area. Volland (1963) estimated a 30- to 50-year fire return interval (FRI) for the previous 300 years from observations of fire scars on stumps and live trees on ponderosa pine sites in the Upper Williamson River basin, which includes the Wildhorse study area. This is comparable to the high end of fire histories reconstructed for ponderosa pine and mixed-conifer forests elsewhere in eastern Oregon (Weaver, 1959; Soeriaatmadja, 1966; McNeil and Zobel, 1980; Bork, 1984) (Table 2).

 Table 2

 Reconstructed historical fire return intervals (FRI) in forests east of the Cascade Range in Oregon.

Ponderosa pine or mixed conifer	FRI (years)	Location	Source
Ponderosa pine	11-16	Warm Springs Indian Reservation	Weaver (1959)
Mixed conifer	47	Warm Springs Indian Reservation	Weaver (1959)
Both	3-36	Warm Springs Indian Reservation	Soeriaatmadja (1966)
Mixed conifer	<3->50	Crater Lake National Park	McNeil and Zobel (1980)
Ponderosa pine	7-38	Deschutes National Forest	Bork (1984)

We found little record of human activity substantially altering the abundance and species composition of these forests prior to the inventory, except around heavily used or inhabited areas, which centered on marshes and rivers (Spier, 1930). Klamath Indians made use of multiple conifer species for diverse purposes, and old scars, which may have resulted from bark stripping, were observed on ponderosa pine near settled areas (Colville, 1898). Specific information on Native American fire use on Reservation forests was not found. However, historical use of fire for cultivation of desired species is supported by tribal memory, contemporary practice, and declines in extent of cover and/or vigor of these species; wokas (yellow pond lily, Nuphar polysepalum) in marsh-edge environments; thinleaf huckleberry (Vaccinium membranaceum) in subalpine environments east of the Reservation on the Cascade crest; and, perhaps, other species in sagebrush (Artemisia spp.) communities (Deur. 2009).

Only minor timber harvesting, if any, is believed to have occurred within the study areas before the inventory and no evidence to the contrary has been found. Detailed records of timber harvest volume and area on the Reservation date back to 1912. Prior to 1912, any activity would likely have been along the Sprague, Link, and Williamson Rivers. After the Southern Pacific railroad reached Klamath Falls in 1909 and Kirk in 1910 (Fig. 1), extensive railroad logging activity began on the Reservation (Bowden, 2003) but did not include our study areas. The few transects on which any mention of harvesting or clearing was recorded were excluded from this analysis. Timber harvests in the Wildhorse area date to 1939, in Black Hills to 1932, and in Chiloquin to 1919 (NARA, 1955?).

Heavy grazing by sheep, cattle, and horses is correlated with altered fire regimes in many dry forests (Rummell, 1951; Savage and Swetnam, 1990; Belsky and Blumenthal, 1997). However, low numbers of domestic grazing animals (primarily cattle) are recorded on the Reservation prior to the timber inventory and their activity centered along marshes and rivers (GPO, 1890; GPO, 1891; Colville, 1898). In 1919, members of the Klamath Tribes owned ~7000 cattle, 2500 horses, and no sheep; no grazing leases were offered to non-Tribal members (GPO, 1918).

2.2. Methods: historical inventory

The inventory was completed in two phases: 1914–1919 and 1920–1922. Methods have been reconstructed from the inventory record (NARA, 1914–1922) (Appendix A: sample inventory records) and from an inventory report (NARA, 1914). The two periods differed in transect density, sample area represented by a single record, and in data recorded (Table 3). Ponderosa pine (*Pinus ponderosa*), sugar pine (*Pinus lambertiana*), Douglas-fir (*Pseudotsuga menziesii*), and white fir (*Abies grandis-Abies concolor*) were inventoried from 1914 to 1919; all conifer species were inventoried from 1920 to 1922. Summaries of data collected after 1919 within each study area show that the species not included in the earlier cruise period represented minor components of conifer density ≥ 15 cm dbh in each study area. The inventory represents a 10%

(1914–1919) or 20% (1920–1922) sample of the forest in each study area. Conifers \geq 15 cm diameter at breast height (dbh) were tallied by species. Trees 15–46 cm (1914–1919) or 15–41 cm (1920–1922) dbh were recorded as one size class. Larger trees were binned in 5 cm interval diameter classes. An average diameter was recorded for trees in the 15–41 cm class from 1920 to 1922.

Transect locations were tied to surveyed points in the BLM PLSS (Fig. 2, www.geocommunicator.gov). Transects were oriented north-south or east-west to facilitate travel across the terrain. Transects were two chains (40 m) wide and ran the length or width (typically 20 chains, 402 m) of a guarter-guarter section (\sim 16 ha). From 1914 to 1919, transects ran through the center of a quarterquarter section, and each inventory sheet reflects the combined count of trees on all four transects per guarter section $(\sim 64.7 \text{ ha})$. A total transect area of 6.5 ha per guarter section $(4 \times 1.6 \text{ ha})$ was inventoried vielding a 10% sample. From 1920 to 1922, cruisers ran two transects per quarter-quarter section and located each transect five chains (100 m) from the guarter-guarter section boundary. Tallies from each transect were recorded separately yielding a 20% sample per half quarter-quarter section (8 ha). From 1920 to 1922, cruisers adjusted area sampled to accommodate exceptionally high or low tree density. For example, in low-density ponderosa pine, cruisers might inventory 100% of the trees on a half or full quarter-quarter section while reducing cruise intensity to 10% for small-diameter lodgepole.

Cruisers worked in teams of three men. The lead man paced distances and navigated with a compass while a second man measured trees standing within one chain (20 m) of the transect center line; the third man recorded tree counts. Diameters were taken with Biltmore sticks or by ocular estimation depending on cruiser's experience. Trees \geq 91 cm dbh were typically measured with the Biltmore stick.

2.3. Methods: analysis

Inventory data were transferred from archived BIA records (NARA, 1914–1922) to database files. Transects were digitally reconstructed from a BLM PLSS spatial data layer (USGS, 2010) using ESRI's ArcMap software (release 10). The resultant polygons were linked to inventory records based on the recorded transect location and orientation.

Tree density, basal area, diameter distribution, and percent composition were computed for each transect. Mean dbh of 28 cm was assumed for trees 15–46 cm dbh inventoried from 1914 to 1919. This value was derived from the mean dbh weighted by tree count for the 201,555 trees of between 15–46 cm dbh of the same species recorded after 1919. After 1919, cruisers estimated mean dbh for trees 15–41 cm dbh and recorded trees 41–46 cm dbh in a separate size class. Mean dbh for each size class was used in basal area calculations, e.g., 53 cm dbh was used to calculate basal area for trees in the 50–55 cm dbh class. Mean values and standard deviation were weighted by transect area to accommodate the difference in area represented by an individual

Table 3

Methods used during the two phases of the 1914–1922 timber inventory of the former Klamath Indian Reservation. Differences between the two periods include changes in transect density and location, grain of the data set (the amount of area represented by a single record), and the number of species inventoried.

	Transect			Tally sheet				
	Width (m)	Length (m)	Area (ha)	# Of transects	Area (ha)	% Cruise	Smallest diameter class (cm)	Species
1914–1919 1920–1922	40 40	402 402	1.6 1.6	4 1	64.7 8.1	10 20	15.2–45.7 15.2–40.6	Ponderosa pine, sugar pine, white fir, Douglas-fir All conifer

Historical forest conditions derived from timber inventory data collected 1914–1922. Transect means are followed by standard deviation and range. Summary includes all transects that fall at least 90% within mapped habitat types (Fig. 1) in the three study areas. Tree density for the portion of each study area inventoried after 1919 is reported separately. With the exception of lodgepole pine in Wildhorse (which was inventoried after 1919), species excluded from the inventory from 1914 to 1919 comprise a minor portion of the density in areas inventoried after 1919 ("All species 1920" and "Plot area (ha) 1920").

	Wildhorse			Chiloquin				Black Hills		
	PIPO-PICO ^a	Mixed Dry	Mixed Moist	PIPO Xeric	PIPO Dry	Mixed Dry	Mixed Moist	PIPO Xeric	PIPO Dry	Mixed Dry
# Of transects Plot area (ha) Plot area (ha) 1920 Study area (ha)	1098 2321 2321 9190	408 667 667 3302	291 471 471 2356	233 407 385 2159	13 70 2 785	17 79 5 939	675 1711 896 13,110	38 99 99 445	153 353 256 2,382	137 440 149 3,715
# Of trees	140,440	46,300	36,857	14,777	2837	6118	132,029	3347	17,788	23,003
Basal area (m²/ha) All species % Ponderosa pine % Sugar pine	$14 \pm 5 (1-28) \\95 \pm 22 (0-100) \\0 \pm 0 (0-4)$	16 ± 4 (4–28) 98 ± 11 (68–100) 0 ± 7 (0–18)	18 ± 4 (5–36) 82 ± 31 (0–100) 2 ± 6 (0–41)	8 ± 4 (0-29) 96 ± 6 (47-100) 0 ± 1 (0-10)	12 ± 13 (3–63) 97 ± 4 (88–100) 0 ± 1 (0–2)	19 ± 7 (9–34) 85 ± 12 (45–100) 0 ± 7 (0–2)	19 ± 9 (0-83) 54 ± 25 (0-100) 2 ± 5 (0-39)	8 ± 3 (0-15) 99 ± 5 (77-100) 0 ± 1 (0-5)	12 ± 5 (3–28) 97 ± 8 (49–100) 1 ± 4 (0–32)	19 ± 11 (2–55) 72 ± 22 (36–100) 19 ± 17 (0–51)
Basal area of trees ≥53 cm	DBH									
All species % Total BA % Ponderosa pine % Sugar pine % White fir	$11 \pm 5 (0-26) \\ 80 \pm 20 (0-98) \\ 100 \pm 17 (0-100) \\ 0 \pm 0 (0-5) \\ 0 \pm 0 (0-2) \\ \end{array}$	$\begin{array}{c} 13 \pm 4 \ (3-26) \\ 84 \pm 10 \ (47-97) \\ 100 \pm 11 \ (79-100) \\ 0 \pm 7 \ (0-21) \\ 0 \pm 3 \ (0-20) \end{array}$	$15 \pm 4 (1-34) \\ 84 \pm 10 (16-98) \\ 86 \pm 29 (0-100) \\ 2 \pm 6 (0-41) \\ 11 \pm 20 (0-72) \\ \end{array}$	$\begin{array}{l} 6 \pm 3 \; (0{-}24) \\ 79 \pm 11 \; (33{-}100) \\ 96 \pm 7 \; (49{-}100) \\ 0 \pm 1 \; (0{-}13) \\ 0 \pm 1 \; (0{-}14) \end{array}$	$10 \pm 11 (2-54) \\ 85 \pm 11 (60-96) \\ 98 \pm 4 (88-100) \\ 0 \pm 1 (0-2) \\ 1 \pm 2 (0-6)$	$16 \pm 6 (5-28) \\ 83 \pm 7 (54-88) \\ 85 \pm 12 (47-100) \\ 0 \pm 7 (0-3) \\ 7 \pm 7 (0-21)$	$\begin{array}{c} 16 \pm 8 \; (0 - 78) \\ 83 \pm 18 \; (0 - 98) \\ 59 \pm 25 \; (0 - 100) \\ 2 \pm 6 \; (0 - 52) \\ 31 \pm 27 \; (0 - 100) \end{array}$	$6 \pm 3 (0-13) 74 \pm 18 (0-95) 98 \pm 17 (0-100) 0 \pm 1 (0-8) 0 \pm 1 (0-7) $	$10 \pm 6 (2-28) \\ 85 \pm 12 (33-99) \\ 97 \pm 9 (42-100) \\ 1 \pm 4 (0-37) \\ 1 \pm 3 (0-35) \\ \end{array}$	$18 \pm 12 (1-54) 94 \pm 12 (36-100) 72 \pm 23 (31-100) 19 \pm 18 (0-57) 8 \pm 9 (0-31) $
Tree density (tph)	72 + 26 (5, 225)	70 + 10 (22 - 152)	70 : 20 (21 - 21 ()	20 + 10 (1 - 120)	52 : 52 (20, 200)	00 + 41 (52, 100)	70 + 20 (0, 200)	40 + 20 (2, 02)	51 + 22 (15 - 140)	52 + 26 (14, 114)
All species All species 1920	$72 \pm 26 (5-225)$ $72 \pm 26 (5-225)$ $77 \pm 21 (0, 100)$	$70 \pm 18 (32 - 152)$ $70 \pm 18 (32 - 152)$ $90 \pm 18 (14, 100)$	$78 \pm 29 (21 - 216)$ $78 \pm 29 (21 - 216)$ $66 \pm 26 (0, 100)$	$38 \pm 16 (1-120)$ $38 \pm 15 (1-101)$ $97 \pm 6 (50, 100)$	$52 \pm 53 (20 - 260)$ 29 ± NA (NA)	$88 \pm 41 (52 - 166)$ 70 ± 14 (53 - 83) 86 ± 12 (45 ± 100)	$78 \pm 39 (0-296)$ $70 \pm 43 (0-296)$ $40 \pm 26 (0, 100)$	$40 \pm 20 (2-82)$ $40 \pm 20 (2-82)$ $98 \pm 7 (56, 100)$	$51 \pm 22 (15 - 146)$ $56 \pm 25 (15 - 146)$ $05 \pm 0 (48, 100)$	$52 \pm 26 (14 - 114)$ $51 \pm 23 (14 - 99)$ $74 \pm 10 (20, 100)$
% Sugar pine % White fir	$0 \pm 0 (0-1)$ $0 \pm 0 (0-2)$	$0 \pm 6 (0-10)$ $0 \pm 4 (0-17)$	1 ± 4 (0–33) 17 ± 29 (0–59)	$0 \pm 0 (0-6)$ $0 \pm 1 (0-12)$	$0 \pm 0 (0-1)$ $1 \pm 2 (0-7)$	$0 \pm 6 (0-1)$ $8 \pm 7 (0-20)$	$1 \pm 3 (0-29)$ $52 \pm 30 (0-100)$	$0 \pm 0 (0-1)$ $0 \pm 1 (0-4)$	1 ± 2 (0–18) 1 ± 3 (0–22)	16 ± 15 (0-45) 10 ± 10 (0-35)
% Douglas-fir % Lodgepole pine ^{b,c}	0±0(0-0) 23±31(0-100)	0 ± 0 (0–0) 10 ± 17 (0–86)	0 ± 5 (0–10) 13 ± 17 (0–83)	1 ± 4 (0–47) 0 ± 0 (0–0)	2 ± 3 (0–6) 0 ± 1 (0–0)	5 ± 10 (0–51) 0 ± 5 (0–0)	6 ± 11 (0–64) 2 ± 12 (0–100)	0 ± 1 (0–0) 2 ± 7 (0–44)	0 ± 0 (0–3) 3 ± 8 (0–49)	0 ± 0 (0-0) 0 ± 5 (0-0)
% White pine ^b % Incense cedar ^b	0 ± 0 (0-0) 0 ± 0 (0-0)	$0 \pm 0 (0-0)$ $0 \pm 0 (0-0)$	3 ± 6 (0–38) 0 ± 0 (0–1)	0 ± 0 (0–0) 1 ± 3 (0–16)	0 ± 0 (0–0) 2 ± 1 (2–2)	0 ± 0 (0–0) 3 ± 4 (0–6)	0 ± 1 (0–0) 1 ± 3 (0–35)	0 ± 0 (0–0) 0 ± 1 (0–2)	0 ± 0 (0–0) 1 ± 4 (0–36)	0 ± 0 (0–0) 3 ± 5 (0–23)
tph < 53 cm tph ≥ 53 cm	46 ± 29 (2–211) 27 ± 11 (0–56)	37 ± 20 (5–117) 33 ± 10 (7–63)	41 ± 30 (2–177) 37 ± 10 (5–78)	22 ± 12 (0–86) 17 ± 7 (1–50)	25 ± 26 (2–122) 26 ± 29 (4–139)	45 ± 27 (21–99) 42 ± 16 (16–75)	43 ± 30 (0-227) 35 ± 18 (0-147)	26 ± 18 (1–63) 15 ± 7 (0–32)	26 ± 22 (3–111) 25 ± 11 (3–54)	14 ± 22 (0–78) 38 ± 23 (3–105)
% tph ≥ 53 cm % Area ≥ 25 tph ≥ 53 cm	37 ± 5 (0–91) 49	47 ± 4 (8–91) 80	47 ± 6 (3–96) 89	43 ± 3 (11–100) 12	51 ± 11 (20–93) 39	48 ± 6 (22–62) 92	44 ± 5 (0–96) 67	37 ± 3 (0–76) 8	48 ± 4 (9–93) 43	73 ± 6 (11–100) 71

^a PIPO: *Pinus ponderosa* (Ponderosa pine), PICO: *Pinus contorta* (lodgepole pine).
 ^b Estimates for abundance of these species is restricted to areas cruised after 1919.

^c Above 1450 m elevation, lodgepole pine was less abundant ($5 \pm 15\%$) in the PIPO-PICO PAG.



Fig. 2. Transect layout during the two inventory periods. The Bureau of Land Management Public Land Survey System divides each township into 36 sections and each section into quarters (64.7 ha) and quarter-quarters (16.2 ha). Inventory data from 1914 to 1919 represent a 10% sample compiled per quarter section from four transects run through the center of each quarter-quarter section. During1920–1922 data for each transect were recorded separately representing a 20% sample of 8.1 ha.

inventory record in the two sample periods, 1914–1919 (6.5 ha) and 1920–1922 (1.6 ha).

Density of trees larger than 53 cm (21 in.) dbh is used here to characterize dry forests. The presence and abundance of trees >21 in. dbh is used to identify old-growth stands in interim old-growth guides (USFS, 1993). In addition, a 21-in. dbh limit for tree harvesting was adopted as an interim measure in 1994 to slow harvest of old trees until more appropriate metrics could be identified (USFS, 1994). New metrics for identifying old trees and stands have been developed (Van Pelt, 2008) and are being adopted, but the 21-in. screen is still operational on timber sales in federal dry forests outside of the area of the Northwest Forest Plan. In this inventory, trees 50–55 cm dbh were recorded in one size class. For this analysis, half of those trees are assumed to be smaller than 53 cm dbh.

Transects were assigned to previously defined habitat types to facilitate comparison of forest conditions along an inferred moisture gradient (from the driest sites where ponderosa pine is the climax species to dry and moist mixed-conifer sites). The use of widely accepted vegetation classifications facilitates communication with managers and stakeholders regarding sites where the results might be relevant. Habitat types identify areas that have comparable environmental and potential vegetative conditions (plant associations). This systematic use of plant indicators for classifying habitats and identifying sites with similar management potential was first developed by Daubenmire (1966). Habitat type classifications have been developed for all federal lands in the Pacific Northwest, and plant associations are the basis for identifying specific habitat types with some of the earliest in the central Oregon pumice region being those of Dyrness and Youngberg (1966) and Volland (1963). Correlations between productivity, plant associations, and environmental variables have been documented (Zobel et al., 1976; Gholz, 1982; Churchill et al., 2013). Use of plant associations allows for ready communication with a diverse array of potential users and extrapolation of results of studies, such as ours.

We used a publicly available map based on documented plant associations to assign inventory plot locations to habitat types (Fig. 1). The map depicts a projected distribution of potential vegetation types (PVTs) generated from existing plant association group (PAG) maps and Random Forest Nearest Neighbor imputation modeling using vegetation plot data (including Forest Inventory and Analysis, USFS Current Vegetation Survey, and USFS Ecoplots) and geophysical variables describing climate, typography, soil, and spectral reflectance as inputs (Henderson et al., In prep.). These PVTs represent a level of vegetation classification developed by the ILAP (Integrated Landscape Assessment Project) team that uses expert opinion to assign plant associations (Federal Geographic Data Committee (FGDC), 2008) to PVTs based on similarity in growth rate, disturbance regime, and response to management.

We focus on three major groups of dry forest sites based upon habitat types: ponderosa pine, dry mixed conifer, and moist mixed conifer. Detailed information on the plant associations included in each of these groups is found in Hopkins (1979a,b), Volland (1985), and Simpson (2007). Ponderosa pine sites are represented by three distinct PVTs: Ponderosa pine - Xeric (hereafter PIPO Xeric sites), Ponderosa pine - Dry (hereafter PIPO Dry sites), and Ponderosa pine - Lodgepole pine (hereafter PIPO-PICO sites). PIPO Xeric sites are found at the lower forest line and largely identified by plant associations dominated by an understory of big sagebrush (Artemisia tridentata) and a significant presence of western juniper (Juniperus occidentalis) in the tree layer (M. Simpson, USDA FS, personal communication). PIPO Dry sites are commonly characterized by understories dominated by bitterbrush (Purshia tridentata). PIPO-PICO sites are similar to the PIPO Dry sites but exhibit higher levels of soil moisture availability as indicated by higher cover of herbs. such as needlegrass (Stipa occidentalis), in the understory.

Both dry and moist mixed-conifer sites are distinguished by increased abundance of white fir, which is absent or rare on ponderosa pine sites. The dry and moist mixed-conifer sites are distinguished from each other by the associated shrubs and herbs. The dry mixed-conifer sites (hereafter Dry Mixed) are commonly characterized by White fir/snowbrush plant associations. Moist mixed-conifer sites (hereafter Moist Mixed sites) are characterized by several plant associations – such as White fir/snowbrush/strawberry, White fir/serviceberry, and White fir/sedge (Johnson et al. 2008) – that are indicative of cooler and moister conditions than on the Dry Mixed sites.

Transects were assigned to PVTs and, by extension, to habitat or site types using ESRI's ArcMap software (release 10). For areas sampled after 1919, transects (1.6 ha) falling at least 90% within a ponderosa pine or mixed-conifer habitat type were selected for this analysis. The majority of the Chiloquin and Black Hills study areas were inventoried before 1919 (Fig. 1), while all of Wildhorse was inventoried in the early 1920s. Protocol during the earlier inventory period was to combine data for all transects in each quarter section on a single record. We assigned quarter sections to a habitat type if at least 90% of the area of the quarter section fell within the mapped area of a single habitat type.

Contemporary forest conditions were approximated with Current Vegetation Survey (CVS, www.fs.fed.us) data collected between 1998 and 2006 and restricted to live trees ≥ 15 cm dbh. CVS plots (n = 95) classified in the field by survey crews as ponderosa pine or dry or moist mixed-conifer plant associations and

located within the townships in each of the three study areas were included in this comparison. The CVS inventory system used a series of nested, fixed-radius subplots with each 1-ha sample unit located on a 2.74 km square grid (Max et al., 1996).

3. Results

Our results are based on a population of 424,626 conifers ≥ 15 cm dbh located on 3068 transects covering a sampled area of 6646 ha. This represents a 10–20% sample of 38,651 ha of ponderosa pine and dry and moist mixed-conifer sites within the 117,672 ha of the combined study areas.

3.1. Summary for all dry forest transects

Stands with moderate basal areas, low tree densities, and dominance of large-diameter ponderosa pines characterized the inventoried forests across all of the habitat types from PIPO Xeric to Moist Mixed sites. Stand basal areas averaged 16 m²/ha over all plots with a standard deviation (SD) of \pm 7 m²/ha (Table 5). Basal area values ranged from 0 to 83 m²/ha, but the 95th percentile value was 24 m²/ha basal area (Fig. 3). Large diameter trees (>53 cm dbh) made up 83 ± 16% of total basal area (Table 5). Ponderosa pine overwhelmingly dominated both total (78% ± 21%) and large tree basal area (81 ± 20%, Table 5). Tree densities averaged 68 ± 29 tph (range = 0–296 tph, Table 5) with a 95th percentile value of 121 tph (Fig. 3). Mean large tree density (>53.3 cm)



Fig. 3. Box plots of basal area and density for all 1914–1922 inventory transects falling at least 90% within mapped habitat types for all three study areas in the former Klamath Indian Reservation. Boxes represent the middle 50% of the data, the center horizontal bars represent median values, whiskers extend to the 95th and 5th percentile values, and pluses represent the most extreme values. PIPO: *Pinus ponderosa* (Ponderosa pine), PICO: *Pinus contorta* (lodgepole pine).

was surprisingly similar to mean small tree density $(15-53 \text{ cm dbh}) -38 \pm 27 \text{ vs. } 30 \pm 14 \text{ tph respectively}$ (Table 5). Small diameter trees (15–53 cm dbh) contributed just over 50% to mean

Table 5

Comparison of current and historical forest conditions. USFS Current Vegetation Survey (CVS) data collected 1997–2006 was used to estimate current structure and composition. CVS data was restricted to plots located within the townships encompassed by the three study areas and to live trees \geq 15 cm dbh. Ponderosa pine summary here includes areas classified as PIPO-PICO^a, PIPO Dry, and PIPO Xeric.

	Current Vegetati	on Survey (CVS) 199	07–2006		Timber inventory 1914–1922					
	Ponderosa pine	Mixed dry	Mixed moist	All	Ponderosa pine	Mixed Dry	Mixed Moist	All		
Number of plots Plot area (ha)	55 55	24 24	12 12	95 95	1539 3276	562 1186	966 2182	3068 6646		
Basal area (m²/ha) All species % Ponderosa	17 ± 8 (0–34) 85 ± 18 (21– 100)	24 ± 7 (8–37) 39 ± 24 (4–82)	24 ± 12 (11–55) 20 ± 19 (0–65)	19 ± 9 (0–55) 63 ± 33 (0–100)	13 ± 5 (0–28) 96 ± 19 (0– 100)	17 ± 8 (2–55) 87 ± 16 (36– 100)	19 ± 8 (0-83) 60 ± 26 (0- 100)	16 ± 7 (0-83) 78 ± 21 (0- 100)		
Basal area of trees ≥ 5 .	3 cm dbh									
All species % Total BA	5 ± 4 (0–16) 27 ± 19 (0–80)	8 ± 5 (0-21) 33 ± 19 (0-83)	10 ± 11 (2–41) 39 ± 19 (7–74)	6 ± 6 (0-41) 30 ± 19 (0-83)	10 ± 5 (0-28) 80 ± 18 (0- 100)	15 ± 8 (1–54) 88 ± 11 (36– 100)	16 ± 8 (0-78) 83 ± 16 (0- 98)	13 ± 7 (0-78) 83 ± 16 (0- 100)		
% Ponderosa	91 ± 20 (0-100)	41 ± 35 (0-100)	36 ± 27 (0-76)	67 ± 37 (0-100)	99 ± 15 (0– 100)	87 ± 17 (31– 100)	65 ± 26 (0– 100)	81 ± 20 (0– 100)		
% White fir	2±9(0-55)	24 ± 25 (0-100)	54 ± 33 (0-100)	15 ± 26 (0-100)	0 ± 1 (0–35)	4±6(0-31)	27 ± 26 (0– 100)	13 ± 16 (0– 100)		
Tree density (tph) and	species composition									
All species	217 ± 121 (0- 543)	286 ± 130 (109– 572)	233 ± 90 (104– 378)	234 ± 122 (0– 572)	63 ± 24 (1– 225)	64 ± 22 (14– 156)	78 ± 37 (0– 296)	68 ± 29 (0- 296)		
% Ponderosa	81 ± 24 (5–100)	34 ± 25 (4-83)	15 ± 23 (0-85)	59 ± 36 (0-100)	81 ± 26 (0- 100)	85 ± 18 (14– 100)	45 ± 29 (0- 100)	67 ± 26 (0– 100)		
% White fir	1 ± 3 (0–10)	40±26 (2-81)	80 ± 24 (13– 100)	21 ± 32 (0-100)	0±0(0-22)	4±7 (0-35)	45 ± 30 (0- 100)	19±0 (0– 100)		
% Lodgepole	14±24 (0-95)	1 ± 3 (0-14)	1 ± 3 (0-9)	9±20 (0-95)	19 ± 27 (0- 100)	8 ± 16 (0-86)	6 ± 14 (0- 100)	13 ± 22 (0- 100)		
Tree density 15–53 cm	dbh and \geq 53 cm D	ВН								
tph < 53 cm	205 ± 119 (0- 531)	265 ± 131 (96– 560)	207 ± 94 (92– 357)	217 ± 121 (0- 560)	38 ± 26 (0- 211)	29±20(0- 117)	43 ± 30 (0– 227)	38 ± 27 (0- 227)		
$tph \ge 53 \text{ cm}$	12 ± 9 (0-42)	21 ± 12 (0-45)	26 ± 30 (4-114)	16 ± 15 (0-114)	24 ± 11 (0- 56)	35±16(3– 105)	35 ± 17 (0– 147)	30±14 (0- 147)		
$%$ tph \ge 53 cm	7 ± 6 (0-28)	9±7 (0-32)	12 ± 14 (1–52)	8±8(0-52)	39 ± 2 (0- 100)	55±9 (8-100)	45±4 (0-96)	44 ± 10 (0- 100)		
% area ≥ 25 tph ≥ 53 cm	5	38	25	17	42	76	71	58		

^a PIPO: Ponderosa pine (Pinus ponderosa), PICO lodgepole pine (Pinus contorta).

tree density in historical forests. The range extends from zero small trees to zero large trees although those conditions were recorded on a minority of the area inventoried, <4% and <6% respectively.

3.2. Species composition

Ponderosa pine dominated (>72%) average basal area in forests on all of the habitat types and study areas, except the Moist Mixed sites in the Chiloquin area where 54% of the basal area was ponderosa pine (Table 4). Ponderosa pine also constituted the majority of the basal area of small trees (15–53 cm dbh) on the ponderosa pine and Dry Mixed sites (Fig. 4). More than 74% of all trees recorded on each transect were ponderosa pine except on Moist Mixed sites (Table 4).

Associated tree species varied with forest type. White fir was infrequently present on ponderosa pine sites and uncommon on Dry Mixed sites. White fir was co-dominant with ponderosa pine on Moist Mixed sites. White fir constituted 45 ± 29% of the total basal area and $27 \pm 26\%$ of the large tree basal area while ponderosa pine constituted 45 ± 30% of total basal area but, by contrast, $65 \pm 26\%$ of the large tree basal area (Table 44). On Dry Mixed sites, abundance of large-diameter white fir (>53 cm dbh) varied from 0 to 20 tph with a mean of 4 ± 4 tph; abundance on Moist Mixed sites ranged from 0 to 116 with a mean of 11 ± 13 tph. Large sugar pines were prominent in forests on Dry Mixed sites in the Black Hills area (Table 4). Representation of other tree species was very low on all ponderosa pine sites, except for lodgepole pine in Wildhorse (Table 4). On ponderosa pine sites on pumice soils (PIPO-PICO sites), lodgepole pine was most abundant in areas adjacent to lower elevation, poorly drained flats and prairies. Above 1450 m elevation, lodgepole pine was less abundant (5 ± 15%) on the PIPO-PICO sites.

3.3. Variability by forest type

Stand basal areas increased gradually along the moisture and productivity gradient represented by the sequence from PIPO Xeric to Moist Mixed sites (Fig. 3). However, the trend toward increasing tree density is very weak, particularly when the PIPO Xeric sites are excluded. Forests on PIPO Xeric and PIPO Dry sites, which are located at the southern boundary of the central Oregon pumice zone, contrast with the PIPO-PICO sites located near the center of the pumice zone. The higher densities and basal area of the forests on PIPO-PICO sites are more similar to the mixed-conifer habitat types than the drier ponderosa pine habitat types. The wider range recorded for basal area on mixed-conifer sites (0–83 m²/ha) reflects greater variability in those stands than in stands on ponderosa pine sites (0–30 m²/ha, Fig. 3, Table 5).

3.4. Variability at the landscape level

Substantial variability existed in the historical landscape at the scale of the sample transects as evidenced by the ranges reported for each habitat type (Table 5, Fig. 3) and differences within the same habitat type in different areas (Table 4). Variability around the mean condition described in Section 3.1 is evident in the full range of values recorded, which was 0-83 m²/ha for basal area. 0-296 tph for density, and 0-100% for percent large trees and percent ponderosa pine (Table 5). Species composition varied substantially within habitat types between study areas for some metrics: white fir was much more abundant in Moist Mixed sites in Chiloquin than Wildhorse, sugar pine was abundant only in the Dry Mixed in the Black Hills, and lodgepole pine was more abundant in the Wildhorse area. Stand structure on the Dry Mixed sites in the Black Hills was most strongly dominated by large trees $(73 \pm 6\% \text{ of tph} > 53 \text{ cm dbh})$. The wide range of values recorded across the landscape reflects the inclusion of more rare and extreme conditions than the narrower range indicated by the standard deviations and 95th percentile values that reflect the preponderance of low-density forests dominated by large ponderosa pine trees as described in Section 3.

3.5. Comparison of past and current conditions

Mean forest density has increased by more than 300% during the last 90 years, as measured by number of trees per hectare,



Fig. 4. Basal area of trees 15–53 cm dbh and >53 cm dbh by species in the 1914–1922 timber inventory for the three areas analyzed within the former Klamath Indian Reservation.

Table 6	
Reference conditions from records and reconstructions of dry forests in central and south central Orego	n

Density (tph)		BA $(m^2 ha^{-1})$			% trees >53 cm dbh	% BA ≥53 cm dbh	Area sampled	Trees sampled	Location	Source			
Mean	Min	Max	SE	%Pine	Mean	SE	%Pine			()			
Current canopy dominants and co-dominants													
	51	54		39– 96						32	Min = 50 cm dbh	Deschutes NF	Merschel (2012)
54	34	94	5	100	17	1.0	100			12	Mean = $60 \text{ cm dbh}(\text{SE} = 3)$	Metiolius RNA	Youngblood et al. (2004)
57	35	79	8	100	18	1.9	100			5	Mean = $61 \text{ cm dbh}(\text{SE} = 2)$	Pringle Falls RNA	Youngblood et al. (2004)
25				100						6	Min = 53 cm dbh	South central	Shuffield (2011)
Histor	ical rec	ords &	у rec	construct	ions								
131				87	29		86	37	71	12	Min = 15 cm dbh	Lake County	Munger (1912) ^a
31				100	14		100	81	95	16	Min = 15 cm dbh	Crook County	Munger (1912) ^a
126				63	31		74	42	80	64	Min = 15 cm dbh	Klamath County	Munger (1912) ^a
	40	80								3	Trees >150 years old	Deschutes NF	Perry et al. (2004)
	133	152								2	Trees established by 1900	Pringle Falls RNA	Morrow (1985) ^b
53										6	Trees >150 years old	South central	Shuffield (2011)

^a Munger selected, in his own words, "well stocked" or "fully stocked" sample areas.

^b Selection criteria for sample areas included a minimum of 75 tph > 45 cm dbh.

and shifted toward a dominance of shade-tolerant species on mixed-conifer sites (Table 5). The increases in densities are due to increased populations of small diameter (15–53 cm) trees as there has been a substantial decrease in the densities of large diameter (>53.3 cm) trees (Table 5). The mean relative abundance of large trees as a proportion of total density has decreased by more than a factor of five and the percentage of the forest that supports at least 25 large-diameter tph (>53 cm dbh) has declined similarly (Table 5). Reductions in the abundance and proportion of large trees are universal on all habitat types. Changes in species composition as a proportion of density are more apparent on mixed-conifer sites.

There has been only a modest increase in forest density (<20%) as measured by mean stand basal area during the last 90 years, but it has been accompanied by a large reduction in basal area in large trees (>50%, Table 5). These statistics emphasize the dramatic change in overall stand structure from forests dominated by a few large trees to a much denser forest dominated by many small trees.

4. Discussion

4.1. Key findings

The prevalence of low-density forests composed primarily of large-diameter ponderosa pines leads us to conclude that a disturbance regime of frequent low- to moderate-severity fires was the dominant influence on the structure and composition of forests in this landscape for several centuries prior to the 1914–1922 inventory. The preponderance of low-density stands and pine dominance, even on the moister mixed-conifer sites, supports this inference. The structure and composition recorded 90 years ago is consistent with those of contemporary forests subject to frequent low- and moderate-severity disturbance (Stephens and Fulé, 2005; Stephens and Gill, 2005; Collins et al., 2011).

Site classifications based upon vegetative indicators, such as habitat types (*sensu* Daubenmire, 1966), are widely accepted as useful indices for recognizing areas of similar environmental conditions and management potential, although they have also been criticized as being subjective and variable. Indeed, several maps of habitat types have been developed for our study area. However, in this study the accuracy with which transects are assigned to ponderosa pine and dry and moist mixed-conifer sites is not a critical issue because the most fundamental findings of the study are not subtle. Low-density, pine-dominated forests occupied essentially all of the forested landscape that we studied and major changes have occurred in these forests during the subsequent century. On Moist Mixed sites in Chiloquin stands were predominantly low-density, but ponderosa pine comprised less than 50% of mean tph and just over 50% of mean basal area. The differences between the historical forest on ponderosa pine and mixed-conifer habitat types were minimal except on Moist Mixed sites in Chiloquin where white fir were more abundant in both small and large diameter tree classes. Both the strong constancy and the exceptions to the predominantly low-density, pine-dominated conditions in historical forest conditions present important considerations as managers and stakeholders consider and plan appropriate restoration activities.

Large and old ponderosa pines are the structural backbone of the dry forest ecosystems of the Pacific Northwest (Franklin and Johnson, 2012). The significant reduction in populations of large ponderosa pine evident over the last 90 years makes conservation of existing trees in the landscapes a high priority in restoration efforts. Although old tree populations are reduced and at risk on both ponderosa pine and mixed-conifer sites, we suggest that restoration activities intended to insure continued survival of ponderosa pine probably have highest priority on mixed-conifer sites where increases in biomass in contemporary forests on these sites are greater than on ponderosa pine sites due to the greater productivity of mixed-conifer sites. Increased density as well as the growth form and persistent live lower limbs on shade-tolerant white firs have led to larger accumulations of ground, ladder, and crown fuels and increased inter-tree competition for moisture and nutrient resources on mixed-conifer sites. Hence, remaining old ponderosa pine trees may be at greater risk from both severe wildfire and competitively-induced mortality on mixed-conifer sites.

Loss rates for large trees can be determined by comparing the historical inventory with more recent surveys and with CVS data (Table 5). The Audubon Society and US Forest Service inventoried area supporting forests with at least 25 tph > 53 cm dbh of any species in the 1990s (Johnson et al., 2008). At that time, 19% of the ponderosa pine sites, 26% of the dry mixed-conifer sites, and 28% of the moist mixed-conifer sites supported at least 25 tph > 53 cm dbh. These estimates include large trees of all species. Henjum et al. (1994) estimated that only 5–8% and 2–8% of old-growth ponderosa pine remained on the Winema and Fremont NF, respectively. While we do not have access to age data in the historical timber inventory, analyses of tree size and age correlations show that ponderosa pine >53 cm dbh in this area are

probably, but by no means always, at least 150 years old (Morrow, 1985; Youngblood et al., 2004; Van Pelt, 2008; Shuffield, 2011). Using CVS data to estimate current forest conditions, abundance of large trees decreased by almost 50% while basal area in large trees decreased by 64% since the time of the timber inventory (1914–1922, Table 5). The percentage of the area inventoried that supports at least 25 large-diameter tph (>53 cm dbh) decreased by 70%, and the mean proportion of ponderosa pine in large-tree basal area decreased by 53% on Dry Mixed sites and 44% on Moist Mixed sites (Table 5). The contemporary estimates of large tree abundance contrast markedly with both the population levels of large trees and the collective area supporting at least 25 tph > 53 cm dbh that we found in the historical forests (Table 4 and 5).

One important artifact of the scale at which the data were recorded (1.6 ha transect for 1920–1922 or four 1.6 ha transects from 1914 to 1919) is the ubiquitous mix of tree sizes which might lead one to infer that large areas of single-story older forest were absent. Unfortunately, at the coarse scale of this inventory, any fine-scale patterning would not be apparent. The majority of the variability in structure in frequent-fire forests has been observed at spatial scales smaller than 0.4 ha (Larson and Churchill, 2012). The scale at which the inventory data were recorded homogenizes this patchiness, which has been shown to include widely spaced individuals, clusters of large trees, dense patches of regeneration, and small openings (Franklin and Van Pelt, 2004; Larson and Churchill, 2012). This fine-scale patchiness is still evident today in ponderosa pine sites on the Reservation that have not been either intensively logged or burned (Johnson et al., 2008).

4.2. Comparisons with other historical records or reconstructions

The capacity for records and reconstructions of historical forests to represent conditions on a larger landscape has been questioned due to potential subjectivity in site selection and limited spatial extent (Bell et al., 2009). This timber inventory, consisting of transects systematically located to provide a 10-20% sample of the Reservation forests from lower to upper timberline, overcomes both of those limitations and is a record - not a reconstruction of tree density by diameter and species for trees ≥ 15 cm dbh. A landscape overwhelmingly occupied by low-density forests and dominated by large trees and fire- and drought-tolerant species is evident from these records. This historical landscape is consistent with most of the other reconstructions and records of historical forest conditions in central Oregon (Munger, 1917; Perry et al., 2004; Youngblood et al., 2004; Merschel, 2012; Shuffield, 2011) (Table 6) although none of these other studies approaches the spatial extent of the historical timber inventory data reported here.

Systematic sampling of a large forested area, as done here, avoids the problem of subjectivity in selection of sample sites. For example, Munger's (1912) principal objective was to provide information on potential future yields so he selected "well-stocked areas"; he acknowledges that his selected stands may be "high" in stocking and not representative of the average conditions due to the exclusion of areas of lower density and of the gaps and openings typical of dry forests (Munger 1912).

Reference data for small trees are rare; among the cited studies only Munger (1912, 1917) provides this information (Table 6). Few records exist and reconstructions are limited by availability of evidence (live and dead trees), since small trees are much more ephemeral than large trees – e.g., increasingly vulnerable to loss over time due to fire, insects, disease, and decomposition (Fulé et al., 1997; Harrod et al., 1999; Mast et al., 1999). However, Moore et al. (2004) have demonstrated the potential for reasonable accuracy in reconstructing historical forest conditions. For central and south-central Oregon, Munger's (1912; 1917) record of stand structure and composition for 93 ha of ponderosa pine-dominated stands in Klamath, Lake, and Crook counties was the only one that we could find for trees smaller than 50 cm dbh. Density of small trees (15-53 cm dbh) was 8, 80, and 81 tph in Munger's three samples; these records are well within the range (0-227, mean = 38, SD = 26 tph) recorded in our more spatially extensive and systematic sample.

The singular exception to the congruence between our conclusions from the historical inventory and other existing historical records and reconstructions is a recent study (Baker, 2012) suggesting that approximately half the Chiloquin study area supported forests with a density of >143 tph. Baker (2012) reconstructed historical forest conditions in eastern Oregon using General Land Office (GLO) survey data, which consist of eight trees per section (64 ha). Four townships (T35-36S R8-9E) in his study area overlap our Chiloquin study area. GLO survey data collected 1866–1895 would include a record of ~1152 trees marking section and guarter section corners in this four township area while the BIA timber inventory includes 1,63,558 trees on 1355 transects. Density recorded in the BIA timber inventory across all habitat types ranged from 0 to 296 tph with a mean density of 60 ± 37 tph and a 95th percentile value of 132 tph for the same four township area.

Reconstructed tree density based on GLO data (Baker, 2012) is nearly 2.5 times the mean tree density recorded in the timber inventory for the same area leading us to conclude that the Baker (2012) reconstruction significantly overestimates historical tree densities on the Reservation. We found that densities of 143 tph or greater occurred in fewer than 106 ha (3%) of the 3789 ha inventoried between 1914 and 1922 in the four township area. It is also notable that all the denser inventory transects are on moist mixedconifer sites.

The large differences in densities between the inventory and the reconstruction based on GLO data cannot be reconciled by differences in diameter limits and timing of the two datasets. The reconstruction based on GLO data includes trees $\geq 10 \text{ cm dbh}$; the BIA timber inventory includes trees $\geq 15 \text{ cm dbh}$. Trees 10-20 cm dbh contributed approximately 20% to total tree density across the entire study area of the reconstruction based on GLO data (Baker, 2012). In Munger's surveys (1912; 1917) trees 10-15 cm dbh were 17% of all trees $\geq 10 \text{ cm dbh}$. Given these two data points, one can surmise that trees between 10 and 15 cm dbh constitute less than 20% of historical density. Hence, the difference of 5 cm in the diameter limit between these two studies does not account for the differences in estimated densities.

Disturbances to the four township area between the time of the GLO survey and the time of the BIA inventory is also unlikely to explain the large discrepancy between the reconstruction based on GLO data (Baker, 2012) and the BIA inventory of 1914–1922. The original land survey of these four townships was conducted from 1866 to 1895 (blm.gov/or/landrecords/survey). The BIA inventory of this area occurred from 1915 to 1920, roughly 20-50 years after the GLO survey. A large decrease in density would not be expected unless the area was disturbed by logging, fire, or insect activity, but we found no evidence or record of such disturbances. In the late 1890s, a United States Geological Survey report recorded no logging in the four townships and classified 5% (1821 ha) of the area as "badly burned" (areas where at least 75% of the forest was burned within "white man's occupancy of the region") (Leiburg, 1900). Commercial logging began in this area in 1919 (NARA. 1955?) in an area inventoried in 1915. Stand-replacing fire effects ("no timber, old burn") were noted on only five BIA timber inventory transects (8 ha) in this area and these were in and adjacent to sites classified as dry and moist Shasta red fir (Abies magnifica) habitat types, not ponderosa pine or mixed-conifer sites. Abundant mortality attributed to fire was recorded on another four BIA timber inventory transects (6.5 ha) in moist mixed-conifer. The BIA inventory record is consistent with Leiburg's description of the area in 1890. Thus, it seems unlikely that disturbance between the time of the GLO survey and that of the timber inventory would explain the large discrepancy in reconstructed tree density based on GLO data versus recorded tree density in the timber inventory. Given the mean density of 60 ± 37 tph and the 95th percentile value of 132 tph recorded in the BIA timber inventory, we conclude that the Baker (2012) reconstruction significantly overestimates historical tree densities for this area.

Lodgepole pine was and still is more abundant in the northern portion of the Reservation, which lies closer to the center of the central Oregon pumice zone, than it is in the southern portion of the Reservation near the southern boundary of the pumice zone. Shuffield (2011) found that lodgepole pine density has increased exponentially since 1880 and that increased density results in both ponderosa and lodgepole pines taking longer to reach breast height in south-central Oregon. In the historical inventory record, plots with a relatively high percentage of lodgepole pine on PIPO-PICO sites were predominantly found along the edges of lower-elevation drainage areas. Above 1450 m elevation, lodgepole pine was less abundant ($5 \pm 15\%$) on the PIPO-PICO sites. Proposals to manage ponderosa pine – lodgepole pine sites so as to favor an increased percentage of ponderosa pine are consistent with this historical record.

4.3. Relevance to restoration management on ponderosa pine and mixed-conifer sites

For this area, the inventory data are unique in the level of detail recorded at an extensive spatial scale, and they provide the first significant record of historical conditions on mixed-conifer sites of eastern Oregon. Controversy about the appropriateness of restoration activities in mixed-conifer forests and on mixed-conifer habitats remains (e.g., Hanson et al., 2009; Hanson et al., 2010; Spies et al., 2010b; Baker, 2012). Stakeholders have argued that restoration may be justified based on historical conditions on ponderosa pine sites but not on mixed-conifer sites. One assumption is 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. Others have argued that since these forests have only missed a few of their historical fire return intervals they have a lower priority for restoration. There has been a lack of data to either refute or support these arguments about mixed-conifer sites.

The historical inventory of Reservation lands provides strong evidence that forests on mixed-conifer sites were predominantly low-density, pine-dominated, and have undergone massive changes in composition and density. The forests on these mixedconifer habitats are arguably at much greater potential risk of catastrophic damage from wildfire, drought, and insects than they were historically, even though they have typically missed fewer fire return intervals than the ponderosa pine sites. Important factors contributing to this are the greater productivity of mixedconifer sites and the occurrence of more shade-tolerant species, such as white fir. The productivity of the mixed-conifer sites may result in faster accumulation of fuels. Furthermore, the fuels on these sites include highly flammable ladder fuels composed primarily of white fir, which aggressively colonize the mixed-conifer habitats under fire suppression. Abundant white fir trees not only provide fuel ladders, but as they grow larger and denser, they also provide competition for light, moisture, and nutrients, thereby reducing the vigor of old pines and making them more vulnerable to bark beetle attack.

Heterogeneity at multiple spatial scales is a key component in restoration of the capacity of dry forests to withstand current and projected stressors while maintaining desired ecosystem services (Franklin and Johnson, 2012). The preponderance of lowdensity stands dominated by large ponderosa pine provides an important reference for restoration activities as does the variability both within and around the dominant condition.

As expressed in the introduction, efforts to conserve existing dry forests and restore their capacity to withstand characteristic stressors rely on multiple sources of information and incorporate diverse objectives (USFS, 2010; Franklin and Johnson, 2012; North, 2012; Churchill et al., 2013; Hessburg et al., 2013). Restoring patterns and processes that characterized these forests for centuries is consistent with this goal. Historical reference data can inform our understanding of how and where systems have changed. Additionally, they can provide a model for structures and compositions that are well suited to the drought-related stressors and fire regimes characteristic of dry forests. Our interest in resurrecting this historical record is to provide information relevant to the management of contemporary dry forests given current and projected conditions. Ideally, these data will help build the social license necessary to restore patterns and processes that maintain structures and compositions resilient to characteristic dry forest stressors such as, drought, fire, insects, and pathogens.

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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.2013.04. 005.

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