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Restoring historical forest conditions in a diverse inland Pacific Northwest landscape

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Citation: Johnston, J. D., C. J. Dunn, M. J. Vernon, J. D. Bailey, B. A. Morrissette, and K. E. Morici. 2018. Restoring historical forest conditions in a diverse inland Pacific Northwest landscape. Ecosphere 9(8):e02400. 10.1002/ecs2.2400

Abstract. A major goal of managers in fire-prone forests is restoring historical structure and composition to promote resilience to future drought and disturbance. To accomplish this goal, managers require information about reference conditions in different forest types, as well as tools to determine which individual trees to retain or remove to approximate those reference conditions. We used dendroecological reconstructions and General Land Office records to quantify historical forest structure and composition within a 13,600 ha study area in eastern Oregon where the USDA Forest Service is planning restoration treatments. Our analysis demonstrates that all forest types present in the study area, ranging from dry ponderosa pine-dominated forests to moist mixed conifer forests, are considerably denser (273–316% increase) and have much higher basal area (60–176% increase) today than at the end of the 19th century. Historically, both dry pine and mixed conifer forest types were dominated by shade-intolerant species. Today, shade-tolerant tree cover has increased in dry pine stands, while mixed conifer stands are now dominated by shade-tolerant species. Federal managers in eastern Oregon are currently required to retain all live trees >53 cm diameter at breast height in the course of forest management activities because this size class is assumed to be under-represented on the landscape relative to historical conditions. However, we found the same or greater number of live trees >53 cm today than in the late 19th century. Restoring historical conditions usually involves removing shade-tolerant trees that established since Euro-American management significantly altered natural disturbance regimes. We evaluated a wide range of tree morphological and environmental variables that could potentially predict the age of grand fir and Douglas-fir, the most abundant shade-tolerant species found within the study area. We describe several morphological characteristics that are diagnostic of tree age and developed decision trees that predict the approximate age of trees using morphological characteristics that are easy to measure in the field such as height to live foliage or height to dead branches. Information about structural and compositional change over time combined with tree-age prediction tools provides a flexible framework for restoring historical conditions and meeting other resource management objectives.

Key words: Blue Mountains Forest Partners; Collaborative Forest Landscape Restoration Program (CFLRP); conditional inference trees; dendroecology; eastern Oregon; General Land Office (GLO); historical conditions; Malheur National Forest; tree morphology; USDA Forest Service.

Received 9 July 2018; accepted 16 July 2018. Corresponding Editor: Debra P. C. Peters.

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Introduction

Restoring ecological resiliency to fire-prone forests is a major goal of federal land managers in the American West (Franklin and Johnson 2012, USDA 2012, Stephens et al. 2016). To address this need, the U.S. Congress has passed legislation that streamlines planning processes and increases coordination among agencies (USDA and USDI 2002, HFRA 2003). Congress also established the Collaborative Forest Landscape Restoration Program (CFLRP, Pub. L. 111-11, Sec 4001), which competitively allocates funding for restoration within priority landscapes managed by the USDA Forest Service (Schultz et al. 2012, Butler et al. 2015, Walpole et al. 2017).

Despite these legislative initiatives, there is increasing recognition that the pace and scale of restoration treatments on western federal lands remains insufficient to prevent undesirable impacts from uncharacteristic fire, insect activity, and drought (North et al. 2012, 2015, Franklin et al. 2014, Seidl et al. 2016). Frequently cited barriers to landscape-scale restoration include misplaced budget priorities (Stephens and Ruth 2005, Hartsough et al. 2008) and disagreement among stakeholders about how to weigh trade-offs between restoration treatments and other multiple use objectives (Olsen and Shindler 2010, McCaffrey et al. 2012, Tempel et al. 2015, Stevens et al. 2016, Davis et al. 2017). A lack of social agreement around restoration treatments often results in legal challenges by interest groups that can significantly curtail the geographic scope of treatments and increase planning costs (Keele et al. 2006, Keiter 2006, Koontz and Bodine 2008).

In the inland Pacific Northwest, as in other fire-prone landscapes across the American West, restoration efforts have focused on restoring historical forest structure and composition, which is assumed to have been well adapted to a broad range of climate and disturbance regimes (Keane et al. 2009, Hessburg et al. 2015, Cannon et al. 2018). Efforts to restore historical forest conditions often enjoy support from diverse stakeholders (Shindler and Mallon 2009, Thompson et al. 2009, Urgenson et al. 2017). Mechanical thinning that removes understory trees in dry, ponderosa pine (*Pinus ponderosa*)-dominated stands is a widely accepted practice (Brown et al. 2004, Stephens et al. 2015). Less information is available about historical conditions in moister mixed conifer stands, and many stakeholders oppose removing trees that have grown large in the absence of fire on productive sites (Tiedemann et al. 2000, Stine et al. 2014).

Many managers and scientists believe that tree age is a more appropriate ecological filter than size and suggest removing some larger trees to protect old shade-intolerant trees from competition and contagious disturbance processes such as fire and insect outbreaks that propagate easily across dense forests (Abella et al. 2006, Franklin and Johnson 2012, Stine et al. 2014, Johnston 2017). However, U.S. Forest Service Land and Resource Management Plans (Forest Plans) that govern management of inland Pacific Northwest federal forests generally prohibit harvesting of live trees >53 cm diameter at breast height (dbh) because this size class of trees is assumed to be under-represented on the landscape (Everett et al. 1994, USDA Forest Service 1995). The Forest Service is permitted to amend Forest Plans to allow removal of larger trees, but court decisions have barred the Forest Service from amending plans without an explanation of how logging of larger trees meets restoration objectives given the characteristics of a specific restoration project planning area (*League of Wilderness Defenders v. Connaughton* 2014).

In this paper, we report the results of a research project that informs restoration strategies for a 13,600-ha planning area managed by the U.S. Forest Service in the Blue Mountains of eastern Oregon, USA. A major goal of the Forest Service's planning effort is to restore historical forest structure and composition to make stands more resilient to future climate and disturbance regimes. Grand fir (*Abies grandis* (Dougl.) Lindl.) and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) are the major late-seral conifer species found within the planning area. Many scientists and managers believe that the density of these shade-tolerant species has increased to undesirable levels, increasing drought stress and risk of uncharacteristic crown fire and insect mortality (Hessburg and Agee 2003, Spies et al. 2006). However, there is also recognition that these species have always been a component of more mesic, productive stands and contribute to wildlife habitat and stand and landscape-scale biodiversity (Beier and Drennan 1997, Daw and

DeStefano 2001, Bull et al. 2007). Therefore, determining how many and which shade-tolerant trees to remove from these more productive sites is critical to meeting the goals of restoration projects.

We used both dendroecological methods and analysis of 19th century General Land Office (GLO) records to reconstruct historical forest structure and composition across a range of forest types within the planning area. This information can be used to set structural and compositional targets for restoration treatments. We also developed tools to distinguish between old and young shade-tolerant trees so that older individuals can be retained and younger individuals can be removed in order to approximate historical forest conditions. Research questions and methods were co-developed with Forest Service managers and a local stakeholder group that convenes representatives from local communities, the wood products industry, and conservation groups. We intend for this type of use-inspired research and joint fact-finding (Keeler et al. 2017) to inform development of future collaborative land management on federal forests of the Inland Pacific Northwest.

Methods

Study area and management context

This research is designed to inform efforts to restore historical forest conditions within the Ragged Ruby planning area (RRPA) on the Malheur National Forest in eastern Oregon. The RRPA is one of 28 planning areas within the 355,025-ha Southern Blues Restoration Coalition CFLRP area, one of 23 high priority landscapes nationwide identified by the U.S. Congress and the Forest Service for augmented funding. The Forest Service has completed National Environmental Policy Act planning for approximately half of the Southern Blues CFLRP area. Most restoration planning to date has targeted restoration treatments in dry ponderosa pine forests. Current and future planning efforts, including planning within the RRPA, target both dry ponderosa pine forests and moist mixed conifer forests.

The RRPA is bisected by the Middle Fork of the John Day River. The RRPA is characterized by a seasonally dry climate with annual precipitation of approximately 510 mm, most of which falls from October to May. The coldest months are December and January with average monthly minimum temperatures of −7.2° and −7.0°C, respectively. The hottest months are July and August with average monthly maximum temperatures of 27.6° and 27.7°C, respectively (PRISM Climate Group database 2014, http://www.prism.oregonstate.edu). Elevations in the planning area range from 1060 to 2475 m (Fig. 1). The RRPA is characterized by relatively diverse vegetation communities. Lower elevation forest stands from the Middle Fork John Day up to approximately 1350 m are dominated by ponderosa pine (*Pinus ponderosa* Dougl. ex Laws) with scattered western juniper (*Juniperus occidentalis* Hook.) and Douglas-fir. Middle and upper elevations are dominated by mixed conifer forests of grand fir, Douglas-fir, ponderosa pine, western larch (*Larix occidentalis* Nutt), and scattered lodgepole pine (*Pinus contorta* Dougl. ex Loud), Engelmann spruce (*Picea engelmannii* Parry ex Engelm), western white pine (*Pinus monticola* Douglas ex D. Don), and Pacific yew (*Taxus brevifolia* Nutt). The RRPA, like most federal forests in eastern Oregon, has experienced extensive cattle grazing since the late 1800s and timber harvest beginning in the 1920s (Mosgrove 1980).

The Malheur National Forest works closely with the Blue Mountains Forest Partners (BMFP) to plan and implement forest restoration projects within the Southern Blues CFLRP area (Brown 2012). The BMFP has created a "zones of agreement" document that describes silvicultural activities that the BMFP membership agree are necessary to restore forests (www.bluemountainsforestpartners.org/work/zones-of-agreement/). The zones emphasize restoration treatments where forests have experienced significant departure from historical conditions. Specifically, the zones call for (1) retaining and improving the survivability of older conifers by thinning that removes ladder fuels and reduces overall forest density, (2) shifting composition from shade-tolerant species to shade-intolerant species, and (3) creation of age-based rather than size-based tree retention strategies.

Data collection and laboratory procedures

To develop tools to determine the age of shade-tolerant species, we randomly located

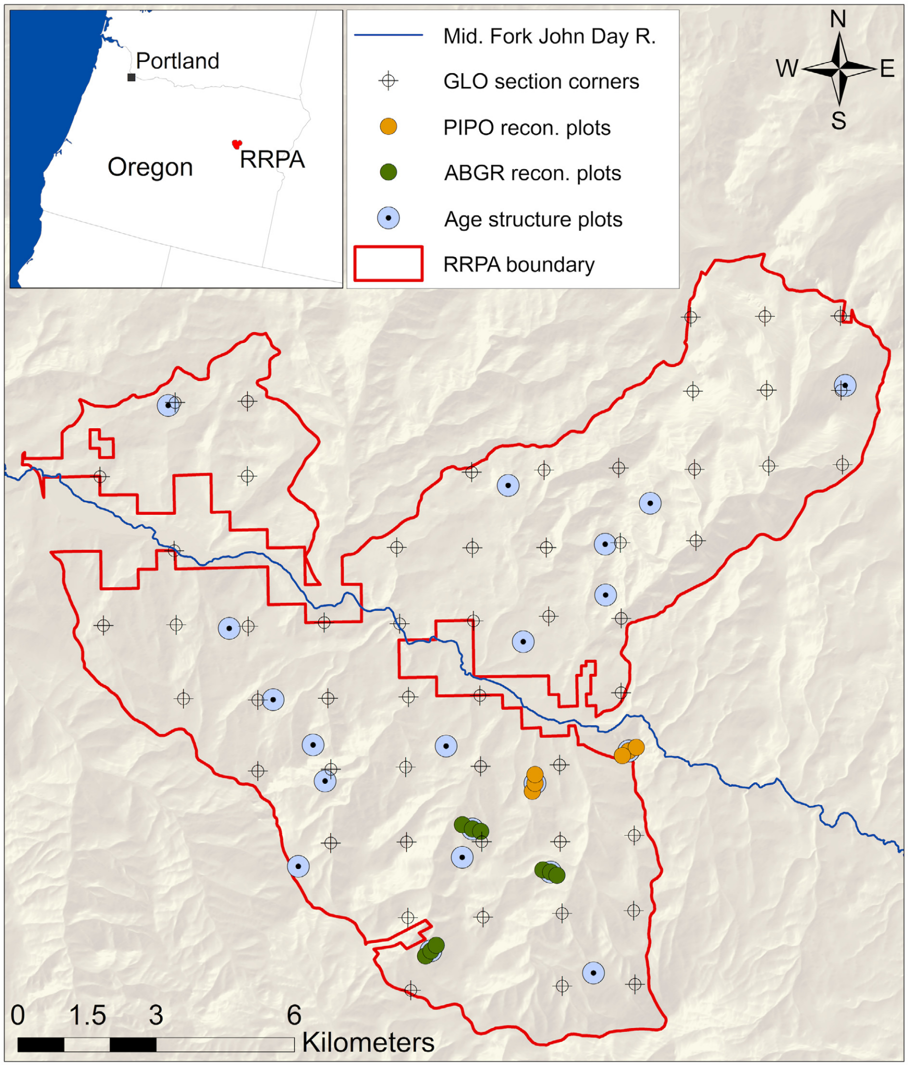

Fig. 1. Map of the Ragged Ruby Planning Area (RRPA) on the Malheur National Forest (MNF) in the Blue Mountains of eastern Oregon. Data used to develop tools to predict tree age were collected in randomly located age structure plots. Historical and contemporary forest structure and composition data were collected in ABGR and PIPO reconstruction plots. Historical reconstructions were corroborated using data about trees recorded by General Land Office (GLO) surveyors at section corners ("GLO section corners").

twenty 0.5-ha plots within the RRPA. Within each of these plots ("age structure plots"), we extracted a tree core from 2 to 3 of the closest grand fir or Douglas-fir trees from plot center within four different diameter bins: 13–38 cm, 38–51 cm, 51–64 cm, and >64 cm. We cored trees as close to the ground as practical, usually within 20–50 cm above mineral soil, and cored trees multiple times in order to intercept the pith or extract a tree ring estimated in the field to be within five years of the pith. For each tree, we recorded 11 different morphological characteristics (Table 1). We also calculated 9 different environmental variables for each tree we cored (Table 2). To model tree growth between the germination horizon and coring height, we destructively sampled 35 young (<70 yr old) trees of different species in approximate proportion to the species sampled and removed a cross section at the mineral soil horizon and another cross

Table 1. Measured morphological characteristics of trees cored in age structure plots.

Morphological characteristic	Description
Species	One of two categorical variables: ABGR or PSME
dbh	Diameter at breast height
Height	Tree height
Crown class	One of five variables: Open-grown, dominant, co-dominant, intermediate, understory
Max crown	Maximum crown radius
Height live foliage	Height from the ground to the nearest live foliage
Height dead branch	Height from the ground to the nearest dead branch
Max live branch	Maximum diameter of largest live branch (estimated)
Max dead branch	Maximum diameter of largest dead branch (estimated)
Fissure depth	Distance between that part of the bark closest to the center of the tree and the outside portion of the bark
Platelet width	Width of the four largest bark platelets at breast height

section at a randomly selected distance between mineral soil and 80 cm.

To reconstruct historical structure and composition, we selected five of the age structure plots located in the southwestern portion of the planning area. This portion of the planning area was selected for sampling because it encompasses the full range of elevations within the planning area. Within these plots, we established a smaller 0.1-ha circular plot around plot center. In order to capture variability in historical structure and composition within each area, we located two additional 0.1-ha plots along the same slope contour 150 m from the central plot, for a total of 15 0.1-ha plots (“reconstruction plots”) within five discrete sites.

Plots were relocated along a randomly selected azimuth when they fell within a treeless area, a clear-cut, or other conditions (e.g., occupied hunting camps) that made data collection unfeasible. Relocation of one set of reconstruction plots placed these plots just outside of the RRPA (Fig. 1), but we collected data in these plots anyway since environmental conditions and vegetation were very similar to the original location.

Within each reconstruction plot, we extracted a tree core at breast height as close to the pith as possible from every live tree estimated to have established prior to the year 1910 (using a key for tree age developed from data collected in age structure plots). We then used a chainsaw to remove a complete or partial cross section from all dead trees >30 cm dbh, cut at breast height and including the pith (if intact) and outermost annual growth ring. We were able to identify 92% of dead trees to species in the field based on

Table 2. Environmental variables calculated using coordinates of cored trees.

Environmental variable	Description	Source
Elevation	Height above sea level	Calculated in GIS
Slope	Steepness of slope (%)	Calculated in GIS
Aspect	Transformed aspect continuous variable ranging from 0 to 2 (aspect = 1 + cos (45°—aspect))	Calculated in GIS
PVT	Potential vegetation type	ILAP Ecoshare, *available online*;* Hemstrom et al. 2012
VPD	Thirty-year average annual average difference between actual vapor pressure and saturation vapor pressure at the same temperature (hPa)	PRISM (2014), *available online*;†
Solar insolation	Total solar radiation derived from hemispherical viewshed algorithms	Johnston et al. (2016)
TPI	Topographic position index calculated as the focal pixel height above the minimum elevation within a 300 m radius of each sampled tree	Johnston et al. (2016)
ASW	Total growing season water holding capacity of soil column estimated from soil depth, soil texture, and parent material	NRCS, *available online*;‡ Carlson (1974)
Density	The number of trees >5 cm dbh within twice the crown radius of the sampled tree	Calculated in the field.

Note: dbh, diameter at breast height; ILAP, Integrated Landscape Assessment Project.
* http://ecoshare.info/ilap/
† http://prism.oregonstate.edu
‡ http://www.nrcs.usda.gov/wps/portal/nrcs/site/soils/home/

morphological clues. The remaining dead trees were identified to species in the laboratory based on cellular structure of wood. We also removed partial cross sections from any dead tree <30 cm that we believed may have established prior to the year 1910. Finally, within each plot we cored between 10% and 90% of younger trees present to gain a better understanding of successional change over time and to verify that our field estimates of age did not overlook any older trees. We also recorded dbh and species of all live trees ≥6.4 cm dbh in each reconstruction plot for comparison to historical structure and composition.

All wood samples were sanded and visually dated. Each annual growth ring was measured to 0.001 mm precision with a computer-controlled Velmex or Acu-Gage linear measuring system (Velmex, Bloomfield, New York, USA; Acu-Gage Systems, Hudson, New Hampshire, USA). Cross-dating accuracy was verified using COFECHA software (Grissino-Mayer 2001). We estimated the number of rings between the oldest ring and the pith (if missing) of each tree core or partial cross section using the geometric method described by Duncan (1989).

We corroborated tree ring reconstructions of historical structure and density by analyzing GLO records. As with all unsettled lands in the American West, the RRPA was divided into 2.6-km^2 sections by the GLO in the 19th century. At the corner of each section, surveyors employed by the GLO erected a monument. To aid in relocation of monuments, surveyors were instructed to blaze the closest tree >6.4 cm dbh in each of the four quadrants created by section lines. For each blazed tree, surveyors recorded the species, dbh, and distance to the section corner monument (White 1983). In January 2017, we accessed digital scans of handwritten GLO field notes from Bureau of Land Management web pages (glorecords.blm.gov). We transcribed species, dbh, and distance to the monument for all trees that surveyors noted at each of the 53 section corners located within the RRPA.

Because managers and stakeholders are particularly interested in determining reference conditions for different forest types, we divided the RRPA into two forest types for the purposes of historical reconstructions. We categorized GLO section corners and reconstruction plots as ponderosa (hereafter "PIPO") sites if those corners/plots are mapped as ponderosa pine or Douglas-fir potential vegetation types (PVTs) by the Integrated Landscape Assessment Project (ILAP; http://ecoshare.info/ilap/; Hemstrom et al. 2012). GLO section corners and reconstruction plots mapped as grand fir PVTs were categorized as grand fir ("ABGR") sites.

Analysis of historical and contemporary forest structure and composition

Basal area, tree density, and species composition are common metrics used to characterize forest stands targeted for restoration treatments. Our goal was to estimate basal area, density, and species composition of live trees in the year 1880 within different forest types and compare these estimates to current conditions. We estimated basal area of each live and dead tree within reconstruction plots in the year 1880 by converting cross-dated tree ring widths to basal area increment, standardizing basal area increment by diameter, and subtracting the basal area between the year trees were sampled (2016) and 1880 from total basal area calculated from dbh recorded in the field (Johnston 2017).

We adjusted reconstructed 1880 basal area increment based on two factors. First, bark thickness generally decreases as a function of the size of trees, and we used the equations in Dolph (1981) to reduce 1880 diameter of trees based on the smaller size of trees during the reconstruction period. Dolph did not model western larch, Engelmann spruce, juniper, or lodgepole, and we used either ponderosa pine or white fir equations for these species. We also noted that tree cores shrunk by an average of 5% (range of <1–9%) during the period between removal from trees and measurement in the laboratory. We did not measure shrinkage of partial cross sections form dead trees, but we increased the inside the bark diameter of all wood samples by 5% to account for water loss in measured samples.

We calculated historical density as trees per hectare by converting 1880 basal area to dbh and multiplying the number of trees ≥6.4 cm dbh in 1880 in each 0.1-ha plot by 10. We selected the year 1880 to reconstruct historical structure and composition because GLO surveys for the RRPA were completed in the year 1881 (potentially before tree growth in 1881 was complete). The late 19th century is also a reasonable period to establish reference conditions because frequent-fire characteristic of the natural fire regime had been excluded from most stands on the Malheur National Forest between 1880 and 1900 (Johnston et al. 2016). We report historical and contemporary basal area and forest density only for trees ≥6.4 cm dbh because GLO surveyors only recorded information for trees ≥6.4 cm dbh.

The outermost annual growth ring of 20 of the 99 dead trees we sampled in reconstruction plots was laid down prior to 1880, suggesting that these trees may have died before 1880. However, we included these trees in estimates of 1880 live forest structure in order to create conservative estimates of historical density (i.e., we erred on the side of higher density estimates).

To calculate historical density from GLO surveyor notes at section corners, we employed the "angle methods" first proposed by Morisita (1957). Morisita's equations can be used to calculate density estimates from distances to the nearest tree within equal-sized sectors such as the quadrants created by the intersection of section lines. This method has been demonstrated to provide an accurate and unbiased estimate of forest density both with simulated data and within dry mixed conifer stands where true density has been established by a total tree census (Hanberry et al. 2011, Levine et al. 2017).

General Land Office surveyors were instructed to record distance to the nearest tree ≥6.4 cm in each of the four quadrants created by the intersection of section lines if there was a tree within 60 m (300 links) of the monument marking the section corner. Surveyors recorded four trees at 38 of 53 section corners within the RRPA. Three trees were recorded at one section corner, two trees at 11 section corners, and one tree at three section corners. It is unclear whether these vacant quadrants resulted from inconsistent or incorrectly applied GLO survey procedures, or whether vacant quadrants represent areas where no trees were available within 60 m in 1880.

To investigate this issue, we visited a total of ten section corners where fewer than four trees were recorded. In five of these corners, we were unable to definitively establish the location of the historical monument. In four of the five corners where we were reasonably certain we had located the 1880 survey monument, there were scablands or other treeless areas in the quadrant(s) where tree data would otherwise have been recorded. In the fifth case, where surveyors had noted only two trees, we found the area to be well stocked with older trees that we believe should have been recorded by surveyors. We ultimately excluded the section corner where only one tree was recorded from analysis. Where surveyors recorded information about two or three trees, we used the method described by Warde and Petranka (1981), who derive correction factors to account for empty quarters.

We calculated confidence intervals (CIs) for GLO density estimates using the equations published by Mitchell (2007). We bootstrapped CIs for estimates of basal area and density derived from reconstruction plots (Davison and Hinkley 1997). We tested for statistically significant differences between historical and contemporary forest density and basal area using non-parametric pivotal bootstrap regression implemented with R's "np" package (Racine 1997, Hayfield and Racine 2008).

Tools for determining tree age

We used data from destructively sampled trees to create a simple linear regression model that estimated the number of annual growth rings between mineral soil and the height at which we cored each tree as a function of coring height, species, and the width of the 10 rings closest to the pith on each wood sample (a surrogate for growth rate). We determined the age of the trees we cored by adding the pith age from cross-dated tree cores to the number of years between coring height and mineral soil predicted by the linear model.

We explored the relationship between tree age and morphological and environmental variables (Tables 1, 2) using random forest implemented with R's "randomForest" package (Liaw and Wiener 2002). The random forest algorithm fits large numbers of simple decision trees to bootstrapped subsets of data. Each decision tree node is split using the most accurate of a subset of randomly selected predictors. The bootstrapped data subsets are used to make predictions with the remaining data. For each tree grown using a bootstrapped sample, the squared error rate for observations left out of the bootstrapped sample is calculated. This "out of bag" error rate is averaged across all trees in the forest and used as a measure of variable importance (Breiman 2001). In essence, tree morphological and environmental variables were considered important in predicting the age of trees if randomly scrambling the values of that variable significantly degraded the predictive power of an ensemble of simple regression models.

We created a variety of simple and multiple linear regression models to predict tree age using manual stepwise selection procedures to identify variables to include in final models. Variable performance was evaluated using Akaike information criterion, coefficient of determination (coefficient of multiple determination in the case of multiple regression), and P values with an alpha of 0.05. When potential predictor variables were strongly correlated with each other (Pearson's $r > 0.60$), we selected the variable with the highest correlation with age. We used mixed models implemented in R's "lme4" package that included a random intercept for each age structure plot to account for dependence among trees within the same plot (Bates et al. 2015).

Because we were strictly interested in predicting tree age based on morphological and environmental variables, we report marginal coefficients of determination (R^2_m), which describe the proportion of variance explained only by fixed factor(s) (Nakagawa and Schielzeth 2013). We examined a variety of diagnostic residual plots to ensure that normality and homoscedasticity model assumptions were met.

In consultation with the Forest Service and the BMFP, we identified the morphological characteristics that timber operators could consistently, reliably, and easily measure in the field. We used these variables as well as environmental variables to develop simple decision trees based on conditional inference frameworks (CIFs) implemented in R's "party" package (Hothorn et al. 2006). Conditional inference frameworks use the random forest algorithm to predict a response, in this case age of trees, based on recursively partitioning selected explanatory variables. In addition to ease of interpretation, CIFs minimize bias in estimates of variable importance through the use of permutation tests and are robust to multicollinearity among variables and uneven scales of measurement (Strobl et al. 2007, 2008). We developed these tools exclusively for shade-tolerant species (grand fir and Douglas-fir) because western larch is rarely targeted for removal and managers already have a high degree of confidence that they can readily identify older ponderosa pine because this species undergoes obvious changes to its bark color and structure as it ages.

Results

Historical and contemporary forest structure and composition

We reconstructed historical structure and composition by sampling 129 live and 99 dead trees in 15 0.1-ha plots within five separate sites. All trees were successfully cross-dated. All plots in two lower elevation sites fell within ILAP ponderosa pine or Douglas-fir PVTs and were classified as PIPO sites. Almost all live trees in those plots were ponderosa pine no grand fir was reconstructed in these plots in the year 1880. All plots in three sites fell within ILAP grand fir PVTs and were classified as ABGR sites. All three ABGR sites today consist of a mix of grand fir, Douglas-fir, western larch, and ponderosa pine. Between 5% and 45% of reconstructed 1880 basal area was grand fir (Fig. 2).

The first PIPO site (PIPO 1) consisted of low biomass stands (mean plot basal area = 6.2 m^2/ha) that our reconstructions estimated were dominated by a few medium- to large-sized ponderosa pine in 1880. By 2016, a number of large pines had died or been removed by logging, but mean plot basal area had almost doubled (to 11.2 m^2/ha) after 136 yr. More than half of contemporary basal area consisted of younger Douglas-fir and western juniper trees. Our reconstruction methods indicated that the second PIPO site (PIPO 2) consisted of relatively high biomass stands (mean = 20.2 m^2/ha) dominated by medium- and large-sized ponderosa pine and a few western larch in 1880. By 2016, all the larch had died and approximately one-third of the larger pine had died or been removed by logging. Overall stand basal area increased by a third (mean = 31.1 m^2/ha) primarily due to an increase in younger pine and Douglas-fir (Fig. 2).

Our reconstructions indicated that the first ABGR site (ABGR 1) consisted of relatively high biomass stands (mean plot basal area = 18.8 m^2/ha) dominated by medium- and large-sized ponderosa pine in 1880. Approximately 12% of plot

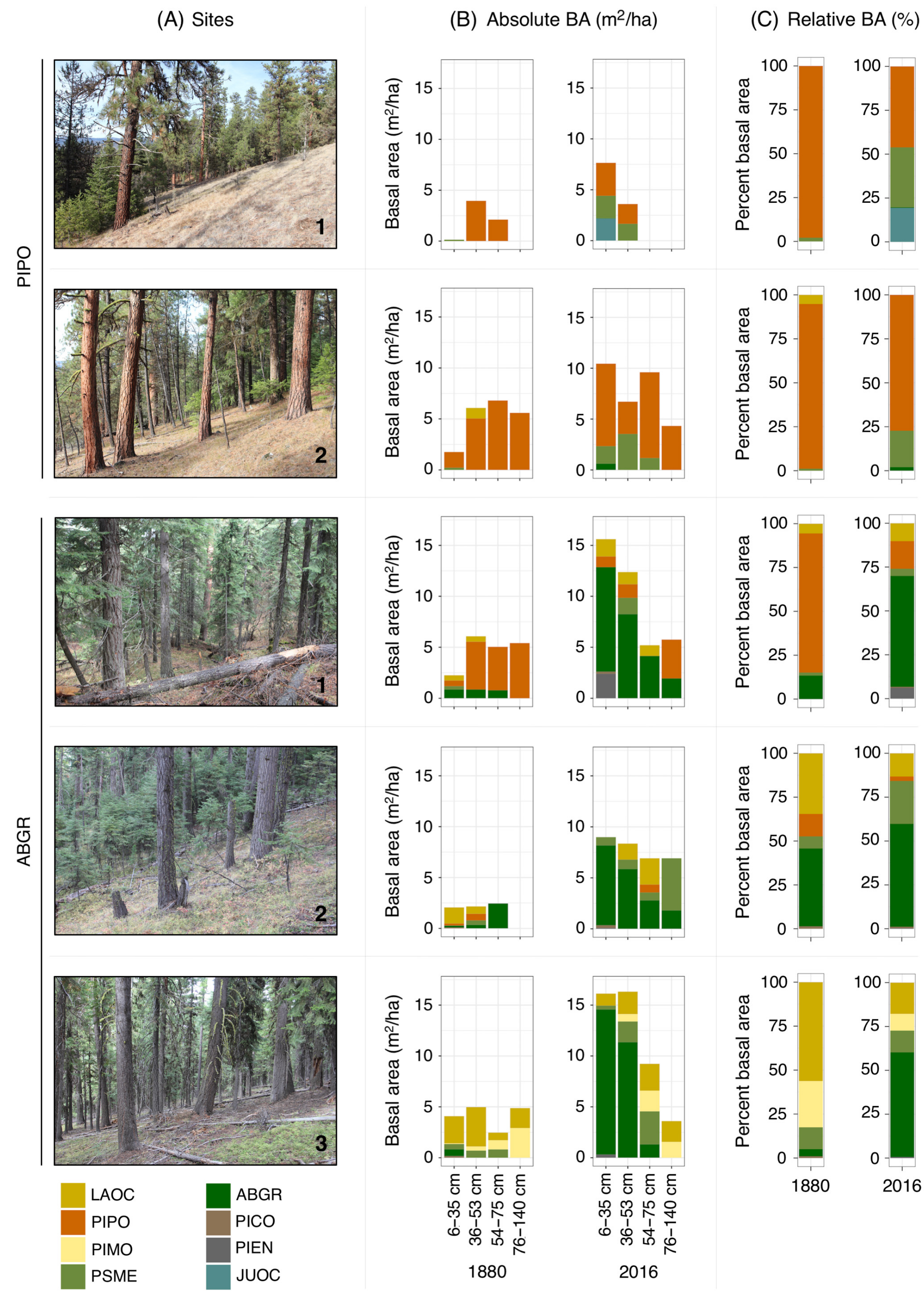

Fig. 2. Basal area of reconstruction plots in 1880 and 2016. (A) Photographs of the two PIPO and three ABGR

(Fig. 2. *Continued*)
sites (each site consisted of three plots). (B) Basal area in 1880 (left) and 2016 (right) in four diameter bins. (C) Species basal area as a percentage of total basal area in 1880 (left) and 2016 (right). Example photographs are somewhat unrealistic in that we chose photographs that allow a view into stands—many stands, especially ABGR stands, were much more dense than represented here.

basal area estimated for the year 1880 consisted of grand fir. By 2016, a number of large pine had been removed by logging or died, but mean plot basal area had more than doubled to 39.0 m^2/ha due to an increase in all size classes of grand fir. Our reconstructions indicated that the second ABGR site (ABGR 2) was a low biomass stand (mean = 6.7 m^2/ha) dominated by small to medium sized larch and grand fir in 1880. By 2016, mean plot basal area had more than quadrupled to 31.2 m^2/ha due to an increase in grand fir and Douglas-fir in all size classes. The third ABGR site (ABGR 3) consisted of relatively high biomass stands (mean = 16.4 m^2/ha) dominated by larch and western white pine in 1880. By 2016, mean plot basal area had almost tripled to 45.3 m^2/ha due to an increase in small- to medium-sized grand fir (Fig. 2). Our reconstructions indicated that basal area in all ABGR plots increased by 176% between 1880 and 2016.

There was no statistically significant difference between estimated mean plot basal area in PIPO and ABGR stands in 1880 (P = 0.88). Mean PIPO reconstructed plot basal area was 13.2 m^2/ha (CI = 3.9–22.6 m^2/ha), and mean ABGR reconstructed plot basal area was 14.0 m^2/ha (CI = 9.8–18.1 m^2/ha) in 1880. There was a significant difference between PIPO and ABGR basal area in 2016 ($P < 0.01$). Basal area in PIPO and ABGR plots in 2016 averaged 21.2 m^2/ha (CI = 11.5–30.8 m^2/ha) and 38.5 m^2/ha (CI = 32.4–44.6 m^2/ha), respectively (Fig. 3A).

There was a statistically significant difference in forest density between PIPO and ABGR plots in the year 1880 and between PIPO and ABGR plots in the year 2016 ($P \leq 0.01$). There was also a statistically significant increase in forest density in both PIPO and ABGR plots between reconstructed 1880 forest density and density in 2016 ($P \leq 0.01$). We estimated that PIPO plots had an average of 73.3 trees/ha (CI = 36.7–110.0 trees/ha) in 1880, while ABGR plots had an average of 137.8 trees/ha (CI = 105.3–170.2 trees/ha). In 2016, PIPO plots had an average of 305.0 trees/ha (CI = 164.4–445.6 trees/ha), while ABGR plots had an average of 514.4 trees/ha (CI = 396.5–632.4 trees/ha; Fig. 3B). Overall density between 1880 and 2016 increased by 316% in PIPO plots and by 273% in ABGR plots between 1880 and 2016.

There was no significant difference between density of trees >53 cm dbh estimated in 1880 and present in 2016 in PIPO plots (P = 0.89), but a significant difference between density of trees

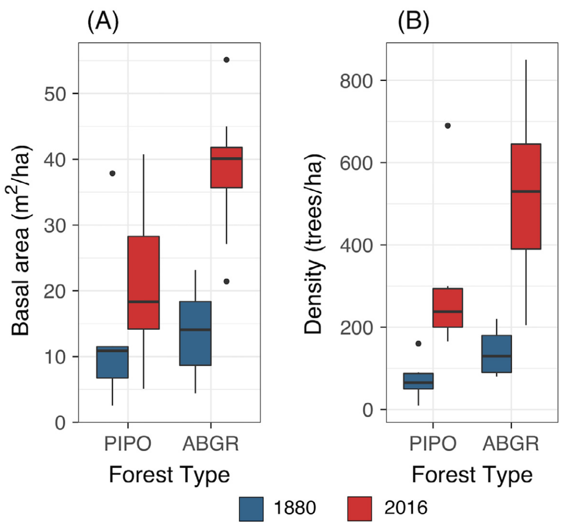

Fig. 3. Boxplots showing (A) basal area and (B) forest density in reconstruction plots in 1880 and 2016. The lower and upper hinges of boxplots correspond to the first and third quartiles of basal area and forest density observations within plots within each forest type. The black line dividing the box represents the median observation. There was a statistically significant difference between historical forest density in PIPO and ABGR stands. There was no significant difference in historical basal area between forest types. There is a statistically significant difference between contemporary PIPO and ABGR plot basal area and density. Note that there is a greater difference between contemporary ABGR and PIPO stands than there was historically.

>53 cm dbh over time in ABGR plots (P = 0.02). There was an estimated average of 20.0 trees/ha >53 cm (CI = 0.9–39.1) in PIPO plots in 1880 and an average of 18.3 trees/ha >53 cm (CI = 2.9–33.8 trees/ha) in 2016. Density of trees ≥53 cm doubled in ABGR plots from an average of 16.7 trees/ha (CI = 8.7–24.6) in 1880 to 32.2 trees/ha (CI = 22.1–42.4) in 2016.

Historical forest density of trees >6.4 cm dbh calculated using Warde and Petranka equations from all GLO section corners (except the one corner where only one tree was recorded) was 62.5 trees/ha. Density calculated when excluding corners where less than four trees were recorded using Morisita equations was 75.5 trees/ha. Because we were not completely sure about the reason for vacant quarters and because we did not want to underestimate historical density, subsequent analysis was undertaken using only those section corners where surveyors recorded a tree in every quarter. Density estimates from these fully stocked section corners were ~15% lower than estimates derived from dendroecological reconstructions. Density in PIPO forests calculated from 1881 GLO records was 55.1 trees/ha (CI = 43.4–70.0). Density in ABGR forests in 1881 was 105.8 trees/ha (CI = 85.4–131.2; Fig. 4). Mean dbh of trees recorded at section corners in 1881 was 45.5 cm for PIPO forests and 37.9 cm for ABGR forests. Mean dbh of trees within PIPO and ABGR reconstruction plots was 41.0 and 27.7 cm, respectively.

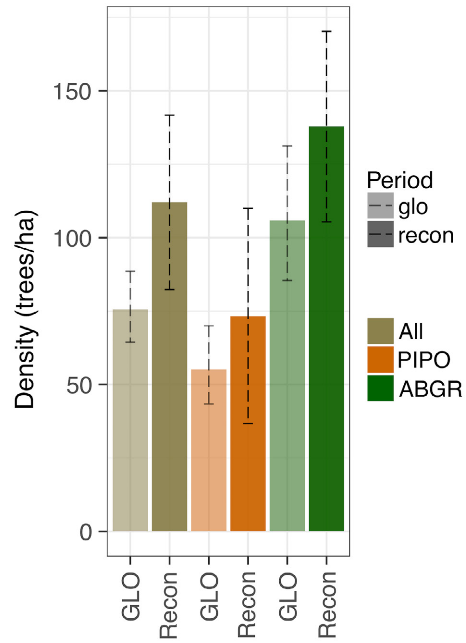

Fig. 4. Historical forest density estimates and confidence intervals for estimates (whiskers) for (from left to right) all General Land Office (GLO) section corners and all reconstruction plots, PIPO section corners and reconstruction plots, and ABGR section corners and reconstruction plots. GLO reconstructions are the lighter shade of each color. Note that analysis of GLO data using Morisita equations results in somewhat lower forest density estimates than reconstruction plot estimates, although differences are consistent across forest types.

Tools for determining tree age

To develop tools to distinguish between young and old shade-tolerant trees, we sampled a total of 139 grand fir and 77 Douglas-fir in 20 age structure plots. All trees were successfully cross-dated. There was considerable error associated with estimates of the age between coring height and mineral soil. Although we were generally able to core trees quite close to the ground (mean coring height was 37.2 cm), many grand fir appear to have experienced significant growth suppression as seedlings. The number of growth years between mineral soil and a 40 cm coring height as determined by cross-dating cross sections from destructively sampled trees ranged from 3 to 36 yr. Although adding width of rings around the pith (a surrogate of growth rate) as a predictor variable improved the precision of estimates, CIs for estimates of growth years between coring height and mineral soil still often encompassed as many as 20 yr.

Available soil water (ASW), bark fissure depth, and topographic position index (TPI) were the most influential predictors of grand fir age identified by random forest analysis (Fig. 5A). The most influential predictors of Douglas-fir age were height to the first dead branch, PVT, tree height, and elevation (Fig. 5B). Integrating environmental variables and additional tree morphological characteristics into models significantly improved the ability to predict tree age over models that used dbh alone to predict age (Tables 3, 4).

The most parsimonious multivariate linear mixed model for grand fir included fissure

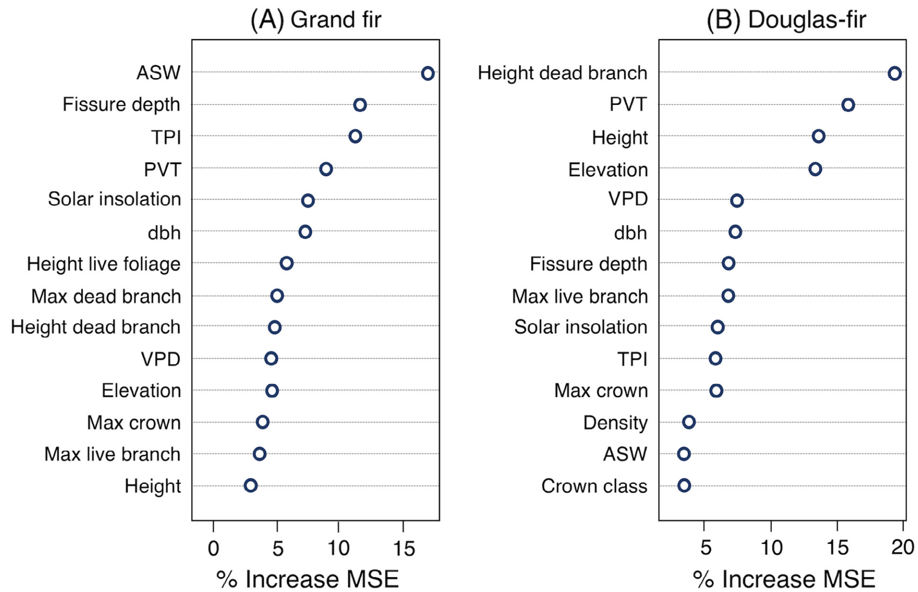

Fig. 5. Random forest results for grand fir and Douglas-fir age prediction. Percent increase MSE refers to the increase in mean standard error of predictions when the value of each predictor variable is randomized. Variables with the highest increase in MSE have greater predictive power of tree age. See Tables 1, 2 for an explanation of variables. Only the top 14 variables of 20 total variables tested are shown here.

Table 3. Comparison of final model and dbh only model to predict age of grand fir.

Model predictors	df	AIC	ΔAIC	AIC wt
Fissure Depth, Max Diam Dead Branch, ASW × TPI	8	760.2	–	0.998
dbh	4	772.7	12.5	0.002

Notes: AIC, Akaike information criterion; ASW, available soil water; dbh, diameter at breast height; TPI, topographic position index. See Table 1 for explanations of variable abbreviations.

Table 4. Comparison of final model and dbh only model to predict age of Douglas-fir.

Model predictors	df	AIC	ΔAIC	AIC wt
dbh, Elevation, TPI	6	731.4	–	0.99
dbh	4	744.7	13.3	0.01

Notes: AIC, Akaike information criterion; dbh, diameter at breast height; TPI, topographic position index. See Table 1 for explanations of variable abbreviations.

depth, maximum diameter of dead branches, and an interaction of ASW and TPI ($R_m^2 = 0.53$, $P < 0.01$; Table 5). The most parsimonious multivariate linear mixed model for Douglas-fir included dbh, elevation, and TPI ($R_m^2 = 0.57$, $P < 0.01$; Table 6).

Table 5. Parameter estimates and variation for the top linear mixed-effect model of grand fir age.

Term	Estimate	SE	CI
Fissure depth	1.39	0.3	0.80–2.00
Max dead branch	0.6	0.19	0.23–0.96
ASW	−14.47	6.66	−28.16 to −0.79
TPI	−6.52	2.12	−10.54 to −2.40
ASW × TPI	1.65	0.52	0.63–2.63

Notes: Model parameters include fissure depth, max diameter dead branch, and the interaction of ASW and TPI. Parameter 95% confidence intervals (CI) were estimated from 1000 bootstrapped samples. See Table 1 for explanations of variable abbreviations. ASW, available soil water; SE, standard error; TPI, topographic position index.

Although individual tree morphological characteristics (e.g., dbh or tree height) were relatively poor predictors of tree age, several individual morphological characteristics can potentially serve as thresholds to identify trees that have reached a certain age. Although grand fir between 51 and 89 cm dbh could be anywhere from 76 to 284 yr old, no grand fir we sampled that was >89 cm dbh was less than 150 yr old. Douglas-fir between 51 and 76 cm dbh were between 75 and 288 yr old, but

Table 6. Parameter estimates and variation for the top linear mixed-effect model of Douglas-fir age.

Term	Estimate	SE	CI
dbh	1.27	0.12	1.03–1.52
Elevation	0.18	0.04	0.10–0.25
TPI	−0.77	0.32	−1.43 to −0.11

Notes: Model parameters include dbh, Elevation, and TPI. Parameter 95% confidence intervals (CI) were estimated from 1000 bootstrapped samples. See Table 1 for explanations of variable abbreviations. dbh, diameter at breast height; SE, standard error; TPI, topographic position index.

no Douglas-fir >76 cm was less than 150 yr old (Fig. 6).

No grand fir we sampled with live foliage within 1.2 m of the ground was older than 150 yr old. Similarly, all grand fir in which the first dead branch present on the bole was more than 3 m from the ground were older than 150 yr old. All Douglas-fir sampled that had live foliage within at least 3 m from the ground were less than 150 yr old. All but one Douglas-fir sampled in which the first dead branch was more than 3 m off the ground was older than 150 yr old (Fig. 6).

Statistical models that integrate a range of tree morphological characteristics and environmental variables can provide reasonably accurate estimates of tree age. But carrying out complex measurements in the field is cost prohibitive in the course of landscape-scale restoration activities, so we developed a number of conditional inference trees to simplify implementation of procedures to retain older trees in the course of treatments. Splits in these trees identify the probability of a tree falling into one of three age classes: "Young" trees are less than 125 yr old, "mature" trees are between 125 and 175 yr old, and "old" trees are more than 175 yr old. Examples of two of these conditional inference trees are interpreted in Figs. 7, 8.

Discussion

Uncertainty about historical reconstruction methods

Both dendroecological reconstructions and GLO records have been widely used to describe historical conditions (Hanberry et al. 2012, Williams and Baker 2012, Abella et al. 2015, Brown et al. 2015, Rodman et al. 2017, Battaglia et al. 2018). Both lines of evidence involve inherent uncertainties, and there is considerable discussion of the merits and pitfalls of these methods in the scientific literature (Fulé et al. 1997, Hanberry et al. 2011, Barth et al. 2015, Levine et al. 2017). Several important sources of uncertainty should be addressed here. Our dendroecological reconstructions may underestimate historical basal area and density to the extent that we did not sample trees that were alive in 1880 but were removed by fire or decomposition before 2016. However, previous work demonstrates that our reconstruction methods are sensitive to change over time and not simply the availability of wood evidence (Johnston 2017).

Despite the sensitivity of our methods, it is inevitable that an unknown number of trees alive in 1880 have disappeared and do not contribute to our historical basal area or density estimates. However, 20% of the dead wood we sampled had outer rings dating before 1880 (one sample had no bark but a completely intact outer surface and an outer ring dating to the year 1637). The outer ring of many of these samples included sapwood, indicating that the early date was not just a function of decay of outer rings. These samples suggest that dead trees decay quite slowly in the Blue Mountains and we believe that there is a strong possibility that our reconstruction methods may slightly overestimate historical basal area and density because we assumed that all dead trees with cross-dated tree rings before 1880 were alive in 1880 when some of those trees may actually have died before that date.

Small trees decay more quickly than large trees, and small trees are thus less likely to be detected by our reconstruction methods (Harmon et al. 1986). Even in contemporary stands with significant numbers of small trees, the majority of stand basal area is found in large trees, so our basal area estimates are less likely to be biased than our density estimates. Grand fir decays somewhat more quickly than ponderosa pine, and so it is possible that we underestimate the historical abundance of grand fir relative to ponderosa pine (Harmon et al. 1986, Dunn and Bailey 2012). However, grand fir often persists longer as a snag, which slows decomposition, and we found numerous dead grand fir with outer rings laid down prior to 1880 (Dunn and Bailey 2012). On balance, we do not believe that our methods significantly underestimate the historical abundance of grand fir, although we almost certainly do not capture the density of smaller grand fir.

Reconstructions based on GLO data may underestimate historical basal area and density if surveyors ignored trees closer to the monument in favor of larger or more vigorous trees. However, previous studies suggest little or no bias in surveyor's selection of trees—several studies note that surveyors were paid by the mile and were thus incentivized to measure smaller trees closer to section corners rather than larger trees farther from the monument (Bourdo 1956, Habeck 1994, Delcourt and Delcourt 1996, Manies et al. 2001).

Our use of multiple lines of evidence to reconstruct historical conditions should give managers and stakeholders a high degree of confidence that forests in the RRPA ranging from dry pine sites to moister mixed conifer sites are significantly departed from historical conditions. Estimates of historical forest density derived from GLO records are somewhat lower than estimates derived from dendroecological reconstructions, although CIs for both estimates overlap (Fig. 4). Notably, both methods demonstrated higher density estimates in ABGR than in PIPO forest stands and significantly lower historical densities compared to current conditions.

There is also good agreement between our estimates of historical conditions, other dendroecological investigations, and analysis of historical

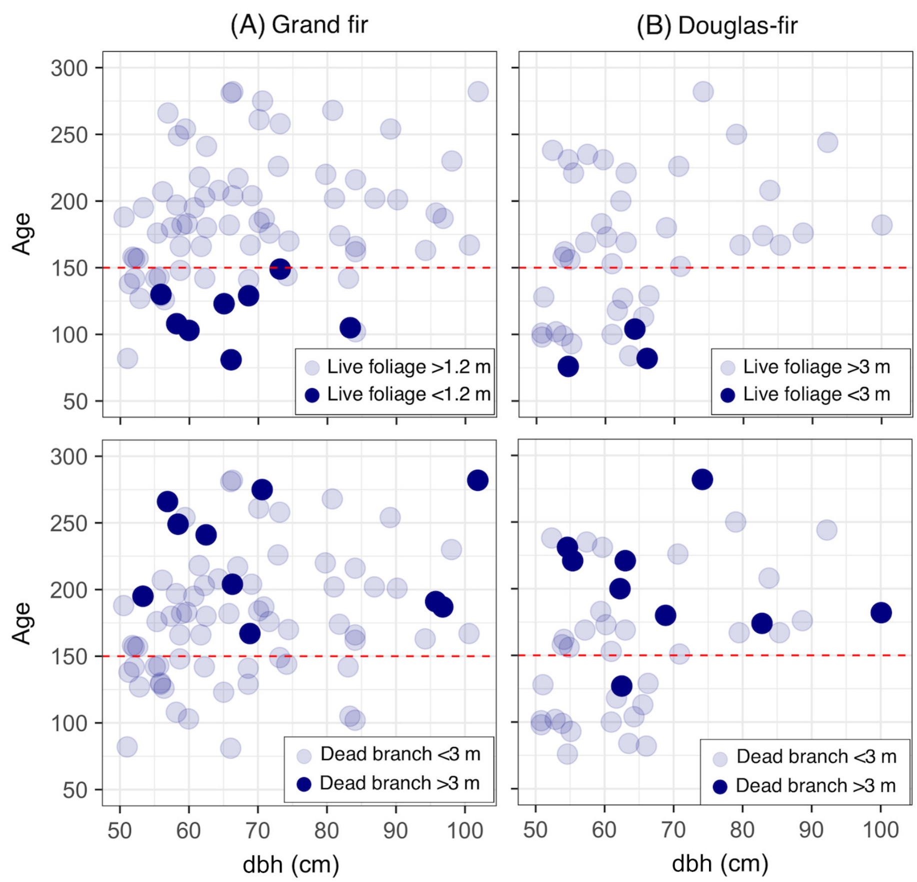

Fig. 6. Relationship between tree age and diameter at breast height (dbh) for grand fir (left) and Douglas-fir (right) between 50 and 105 cm dbh. Solid points indicate all trees that meet the condition identified in the inset box. The presence of live foliage within 1.2 m from the ground on grand fir and within 3 m from the ground on Douglas-fir is diagnostic of a tree less than 150 yr old. Trees with no dead branches (including any branch with no live needles or a small wooden nub flush with the tree bole) within 3 m of the ground are diagnostic of trees that are older than 150 yr of age.

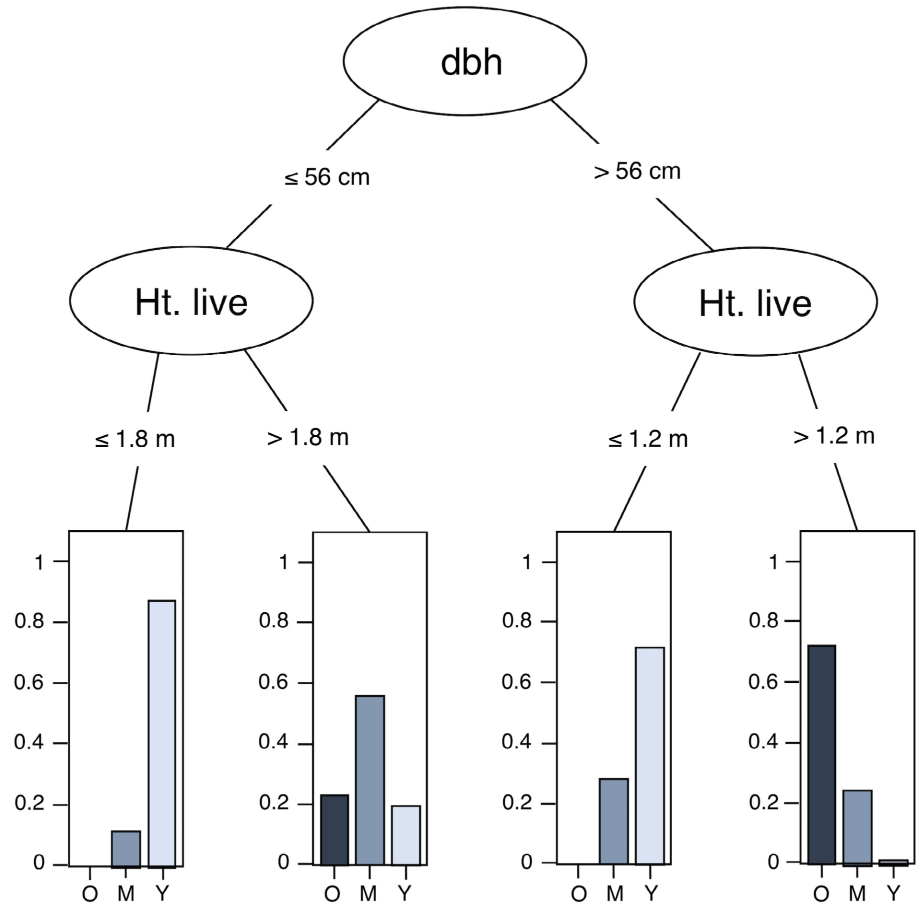

Fig. 7. Example conditional inference tree for determining the approximate age of grand fir in the Ragged Ruby planning area. "Ht. live" refers to the height in meters to the lowest live foliage present on the tree. The bars at the bottom of the graph refer to the probability that a tree within that decision tree split is an old tree greater than 175 yr of age ("O"), a mature tree between 125 and 175 yr of age ("M"), or a young tree less than 125 yr old ("Y"). This tree is interpreted as follows: Grand fir less than 56 cm diameter at breast height (dbh) and with any live foliage within 1.8 m of the ground are most likely to be young trees. Grand fir less than 56 cm dbh with no live foliage within 1.8 m of the ground are most likely to be mature, although they have approximately a 20% chance of being young or old. Grand fir greater than 56 cm dbh and with live foliage within 1.2 m of the ground are most likely to be young or mature, while grand fir greater than 56 cm dbh with the first live foliage more than 1.2 m off the ground are most likely to be old or mature.

timber inventories (Hagmann et al. 2013, 2014, 2017, Merschel et al. 2014, Johnston 2017). Unlike analysis of historical timber inventories (Hagmann et al. 2013, 2014), our dendroecological reconstructions do not provide landscape-scale estimates of historical forest density because we deliberately excluded areas with few or no trees. General Land Office records may provide landscape estimates of density because section corners are systematically located. The difference between our dendroecological reconstructions and GLO estimates may simply reflect the difference between density in forested stands versus density across an entire landscape.

Comparison with other studies

Williams and Baker (2012) analyzed GLO records from the Blue Mountains using a "Voronoi-based plotless density estimator" and reported mean historical forest density of

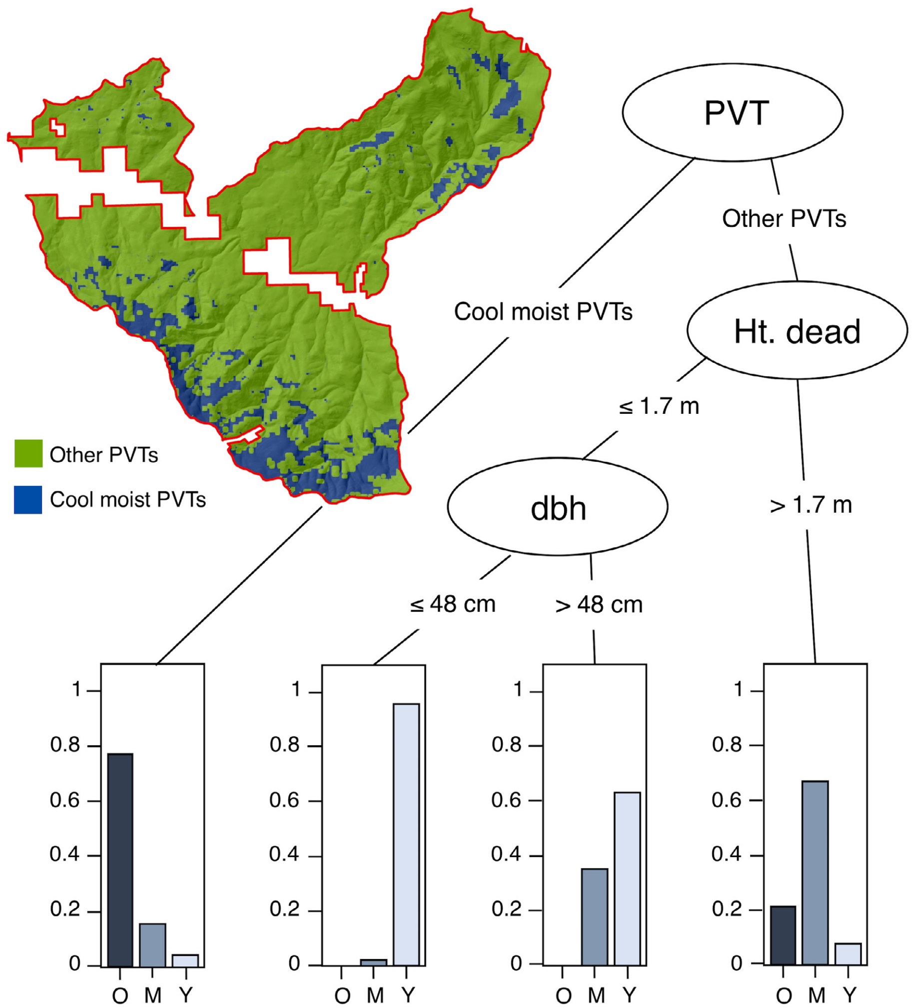

Fig. 8. Example conditional inference tree for determining the approximate age of Douglas-fir in the Ragged Ruby planning area. PVT refers to Integrated Landscape Assessment Project potential vegetation type (refer to Table 2). Cool moist PVTs and other PVTs are illustrated in the inset map (refer to Fig. 1). "Ht. dead" refers to the height to the first dead branch on the tree bole (includes any branch without live foliage or a small wooden nub flush with the bole). This tree is interpreted as follows: Douglas-fir in cool moist PVTs are most likely to be old or mature. Douglas-fir in all other PVTs with any dead branches within 1.7 m of the ground and less than 48 cm diameter at breast height (dbh) are overwhelmingly likely to be young, while trees with branches within 1.7 m of the ground and greater than 48 cm dbh are likely to be young or mature. Trees in PVTs other than cool moist PVTs with dead branches more than 1.7 m from the ground are likely to be mature or old.

167.3 trees/ha. Their estimate is more than twice as high as our estimates of mean density using Warde and Petranka (62.5 trees/ha) or Morisita (75.5 trees/ha) equations. Levine et al. (2017) tested a variety of plotless density estimators on simulated data and in dry forest stands where true density had been established by a complete census and found that Williams and Baker's Voronoi estimator overestimated density by a factor of 1.2–3.8. Our use of multiple lines of evidence to determine historical density provides further evidence that methods used by Williams and Baker (2011, 2012) are unreliable.

Williams and Baker (2011, 2012) claim that their estimates of historical density in the Blue Mountains are cross-validated by tree ring reconstructions. However, the only tree ring study they cite as corroborating their estimates is Morrow (1986). Morrow's study was undertaken more than 250 km west of Williams and Baker's Blue Mountains study site. Morrow subjectively selected high-density stands (more than 75 pine >250 yr old/ha) in order to investigate spatial patterns of old-growth trees on such productive sites. We can find no formal estimates of historical density in the Blue Mountains reported in Morrow's study, let alone one that corroborates Williams and Baker's findings.

Implications of historical reconstructions for restoration treatments

Local stakeholders have collaboratively developed guidance for managers (the "zones of agreement document" described in the introduction) that recommends restoration treatments when forest stands are significantly departed from historical conditions. We reconstructed historical conditions across a range of forest types spanning a broad productivity gradient. Although historical forest composition differed dramatically, all stands were historically dominated by shade-intolerant species—ponderosa pine at less productive, lower elevation sites and western larch and western white pine at more productive, higher elevation sites. All stands experienced significant increases in basal area and density over the past 140 yr (Fig. 2). But grand fir-dominated stands have experienced a greater degree of change than ponderosa pine-dominated stands. Reconstructions indicate a 60.2% increase in density in ponderosa pine-dominated stands and a 176% increase in density in grand fir stands over the past 140 yr. These findings suggest that if restoration of historical conditions is a goal of managers, then treatments in moister mixed conifer stands should be a priority.

Compositional shifts from shade-intolerant to shade-tolerant species combined with significant increases in forest density at all sites suggest that frequent-fire disturbance exerted a strong historical control on stand structure and composition throughout the RRPA. The results of this study indicate that restoring historical conditions will require removal of a significant portion of contemporary stand basal area, especially in moister and more productive stands (Johnston 2017).

Retaining all trees >53 cm dbh may handicap restoration of historical forest conditions for two reasons: First, many stands, particularly moister and more productive stands, currently have more trees >53 cm dbh than were historically present. Second, many trees >53 cm in contemporary stands are a different species than was present historically and retaining these trees will exacerbate compositional shifts from shade-intolerant to shade-tolerant species (Spies et al. 2006, Stine et al. 2014). At a landscape scale, the number of trees >53 cm dbh may remain below historical levels due to past clearcutting, but tree mortality associated with competition operates at stand scales, and so it is appropriate to focus on stand scales when restoring historical conditions.

Achieving compositional targets (i.e., restoring stands to the historical proportion of different species) is likely to be more important to achieving resiliency objectives than structural targets (i.e., restoring stands to historical basal area or density). Shade-tolerant species like grand fir and Douglas-fir have greater photosynthetic area per unit of basal area than shade-intolerant species like ponderosa pine and western larch (Grier and Running 1977, Waring 1983, Bond et al. 1999, Sherich et al. 2007). Reducing forest density to historical levels while maintaining a higher proportion of shade-tolerant species than was historically present will likely result in higher stand water use, greater drought stress, and increased risk of mortality from fire and insect disturbance than desired (Waring and Pitman 1985, McDowell et al. 2008, McDowell and Allen 2015).

Historical conditions are a useful guide for managers, but restoration efforts should also be informed by current economic and social considerations as well as expected future ecological change (Duncan et al. 2010). Several factors make restoring historical conditions in the RRPA an appropriate and feasible goal. Managers have reliable information about historical structure and composition. And, to the best of our knowledge, few if any forests in the RRPA have crossed ecological thresholds (Groffman et al. 2006) that would prevent restoration of historical conditions. Reducing basal area below historical levels may be advisable in order to adapt to future climate regimes, which are almost certain to be warmer and drier in coming decades than during the late 19th century (Mote and Salathe 2010, Wimberly and Liu 2014). Experimental restoration treatments implemented within an adaptive management framework may yield critical insights about managing in the face of future change.

Use of tools for determining tree age

Scientists and stakeholder groups have suggested the use of age thresholds to determine which trees will be retained in the course of restoration treatments. The BMFP zones of agreement document, for instance, recommend retaining trees that were established prior to the 1860s, when widespread mining and grazing operations disrupted natural disturbance regimes. Franklin and Johnson (2012) describe a comprehensive strategy for restoration of dry forests in eastern Oregon that usually involves retaining trees older than 150 yr, although they suggest that in some cases a 200-yr-old threshold may be appropriate.

We recommend a flexible tree retention age threshold with the goal of conserving “Old” trees (>175 yr old) in the course of restoration treatments. “Young” (<125-yr-old) and “mature” (125- to 175-yr-old) trees may either be cut or retained depending on the degree to which individual treatment unit structure and composition is departed from historical conditions (Figs. 7, 8). In addition to accounting for the error associated with early tree growth and the inherent imprecision of age estimates based on morphological characteristics, this strategy acknowledges the dynamic nature of tree mortality and recruitment over time. Some trees that are older than a specific threshold, for example, 150 yr, would likely have been removed by fire disturbance if fire had not been excluded from the landscape at the end of the 19th century. Similarly, it is possible that many younger trees that would need to be removed to meet basal area or density targets when using a strict age threshold would have survived a natural disturbance regime (Dunn and Bailey 2016).

Different retention strategies for different forest types in the RRPA will likely be necessary. For instance, restoring historical forest conditions will require removing most young Douglas-fir from dry ponderosa pine stands. But in some moist mixed conifer stands, there is relatively little Douglas-fir regeneration and retaining younger Douglas-fir will be necessary to approximate historical conditions. Historical reconstructions indicate that basal area in PIPO stands was similar to ABGR stands, but that ABGR stands were somewhat denser. This suggests that basal area was historically distributed across a wider range of age classes in ABGR stands. Restoring historical conditions will likely involve removing most trees below a certain age threshold in ponderosa pine stands to concentrate basal area in older trees. Restoring historical conditions in ABGR stands will involve cutting a mix of both older and younger trees to spread post-treatment basal area through a range of age classes.

Tools to determine tree ages are designed to be adapted to different circumstances and used in different combinations to suit different objectives. A single morphological characteristic may serve as a retention guideline, for instance, all grand fir with the first dead branch more than 3 m from the ground could be retained (Fig. 6). Or, existing Forest Plan diameter limits may be appropriate in a portion of the RRPA landscape where large trees are scarce. Alternatively, existing diameter limits could be implemented on a subset of morphological or environmental conditions, for instance, all Douglas-fir trees within cool moist PVTs greater than 53 cm and with the first dead branches more than 1.7 m from the ground could be retained (Fig. 8).

A variety of management objectives besides restoring historical forest conditions are likely to inform tree retention strategies in the RRPA and elsewhere. For instance, retaining large young shade-tolerant trees in certain areas may be appropriate to provide habitat for wildlife associated with large cavities (Bull et al. 1997, Pilliod et al. 2006). Successful restoration of large landscapes requires managers to be flexible and adaptable based on site-specific conditions and restoration objectives.

Conclusions

Good agreement between the results of dendroecological reconstructions and analysis of GLO records should give managers a high degree of confidence that significant reductions in basal area and density across a wide range of forest types are necessary to restore historical conditions. Cutting some trees >53 cm dbh is likely necessary to approximate historical conditions, particularly in mixed conifer stands. We describe a variety of morphological and environmental characteristics that are predictive of tree age and provide a reasonable basis for distinguishing between young and old shade-tolerant trees. Conditional inference decision trees provide a flexible framework to tailor retention guidelines for individual species based on existing and desired post-treatment conditions.

Acknowledgments

Keala Hagmann and two anonymous reviewers provided helpful comments on a draft manuscript. Alex Held, Hana Maaiah, Lexa McAllister, Claire Ochoa-Moreland, and Jordan Woodcock provided field and laboratory assistance. Kevin Mitchell provided helpful advice about use of Morisita equations. Consultation with members of the Blue Mountains Forest Partners including Susan Jane Brown and Mark Webb and staff at the Malheur National Forest including Tony Bertel, Steve Beverlin, Sasha Fertig, and Amanda Lindsay was critical to developing methodology and interpreting results. We thank Boyd Britton for his support of collaborative, science-based management of the Malheur National Forest. Funding was provided by the Northeast Oregon Forest Resource Advisory Committee through Title II of the Secure Rural Schools and Community Self-Determination Act of 2000 (Pub. L. 110-343). The authors declare no conflict of interest.

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