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IDENTIFYING OLD TREES TO INFORM ECOLOGICAL RESTORATION IN MONTANE FORESTS OF THE CENTRAL ROCKY MOUNTAINS, USA

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ABSTRACT

Old trees (defined here as ≥150 years old) can be rare in many forests because of past timber harvest, uncharacteristically severe wildfires, and – increasingly – climate change. Old trees provide unique structural, ecological, scientific, and aesthetic values missing in forests containing only younger trees. Here we compile crossdated ages from over 10,000 living and dead trees sampled in montane forests of the central Rocky Mountains in Colorado and southern Wyoming, USA, to examine changes in age structure of the oldest trees since Euro-American settlement and to provide guidelines to aid in identification of old trees for retention during ecological restoration treatments. Eroded stumps (containing only heartwood) were found in over 93% of 179 randomly sampled plots. Number of stumps found in each plot was proportional to reconstructed historical (1860 C.E.) stand basal area. The regional median date of maximum plot tree recruitment was over 150 years older when including stumps versus only living trees, suggesting that if all those harvested trees had survived to the present, the ages of oldest trees would be substantially greater than it is today. However, the regional median age of oldest trees in 1860 before harvesting was not different from the median age of oldest living trees in the current forest (246 *vs*. 248 years), which alternatively suggests that the regional population of oldest trees has recovered to near historical levels in the time since early Euro-American harvests. Each living tree at the time of sampling was assigned to one of three potential age classes based on a subjective assessment of tree morphology: old (likely ≥150 years old), young (likely <150 years old), or transitional (containing a mixture of young and old tree characteristics). Trees assigned to the old and young morphology categories were classified correctly 88% to 96% of the time depending on species as confirmed by their crossdated ages. Regression tree analysis revealed that tree diameter at breast height was not as reliable a predictor of tree age as were morphological characteristics. A measure of site productivity was a significant variable to use to separate transitional morphology trees into old and young age classes, but classification accuracy was not high because of large variability in ages of these trees. Our results suggest that residual live old trees in the current forest, although perhaps not rare compared to historical age distributions, should be retained during restoration treatments, and that using simple morphological and environmental criteria to identify old trees is more reliable than tree size alone.

Keywords: dendrochronology, age structure, ponderosa pine, Douglas-fir, restoration, forest management, basal area.

INTRODUCTION

A principal goal of ecological restoration in frequent-fire forests of western North America is the retention and promotion of old trees (*e.g.* Brown *et al.* 2004; Kolb *et al.* 2007; Hessburg *et al.* 2015). The definition of "old" varies depending on species, location, and disturbance history, but here and in many previous studies old trees are defined as ≥*ca*. 150 years old. Old trees tend to be rare in many forests around the world primarily because of past timber harvest (Blicharska and Mikusinski 2014; Lindemayer *et al.* 2014; Lindenmayer and Laurance 2016). In western North America, intensive harvest began with Euro-American settlement in the middle to late 1800s and continued through much

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of the Twentieth Century. More recently, losses of old trees in frequent-fire forests are caused by uncharacteristically severe disturbances, such as extensive areas of stand-replacing wildfires (*e.g.* Fornwalt *et al.* 2016), as well as competition with surrounding smaller and younger trees that established in the post-settlement fire exclusion era (*e.g.* Biondi 1996; Brown *et al.* 2008). Anthropogenic climate change has also contributed to recent losses of old trees and old forests both in frequent-fire forests and worldwide through increasing drought stress and associated severe insect outbreaks (Allen *et al.* 2010; Ganey and Vojta 2011; Anderegg *et al.* 2013; Lindenmayer and Laurance 2016).

Historically, old trees often made up a majority of the basal area of frequent-fire forests even though they may not have constituted a majority of tree density (Moore *et al.* 1999; Brown *et al.* 2008; Sánchez Meador *et al.* 2010; Franklin *et al.* 2013; Reynolds *et al.* 2013; Hessburg *et al.* 2015; Brown *et al.* 2015). Old trees are essential elements contributing to multi-aged, multi-sized, and variable-density stand structures characteristic of frequent-fire forests (Brown 2006; Brown *et al.* 2008; Franklin *et al.* 2013; Reynolds *et al.* 2013; Brown *et al.* 2015; Battaglia *et al.* 2018). Multi-age structure is common in frequent-fire forests because of past disturbances that resulted in tree-scale to small patch-scale patterns in tree mortality and regeneration (White 1985; Boyden *et al.* 2005; Brown and Wu 2005; Brown *et al.* 2008). Old trees contribute to unique structural, genetic, ecological, aesthetic, and scientific characteristics that are missing in forests containing only young trees (Owen *et al.* 2009; Franklin *et al.* 2013; Blicharska and Mikusinski 2014; Lindemayer *et al.* 2014; Lindenmayer and Laurance 2016). For example, old trees provide unique wildlife habitats (Mazurek and Zielinski 2004; Chambers and Mast 2005), are long-term carbon sinks (Harmon *et al.* 1990), and contain long tree-ring records of past climate and disturbance variability (Schulman 1956; Swetnam and Brown 1992; Stahle 1996; Pederson 2010). Furthermore, preserving old trees and old-growth forests in western North America has been at the center of intense legal and political battles (Yaffee 1994; Langston 1995).

Ecological restoration prescriptions for frequent-fire forests often specify tree retention criteria related to tree size (usually measured by diameter at breast height [DBH]) as a proxy for tree age (*e.g.* DellaSala *et al.* 2003; Schultz *et al.* 2012). However, there are generally poor - albeit often statistically significant - relationships between DBH and age (*e.g.* Swetnam and Brown 2011). The assumption that size equates to age can lead to limitations in restoration treatment goals. For example, a diameter limit on tree removal may be defined in an effort to retain presumably older trees. However, strict adherence to diameter limits may compromise other restoration objectives, such as restoration of meadow areas or reduction of stand basal areas if too many large trees are retained (Abella *et al.* 2006; Sanchez-Meador *et al.* 2015). Conversely, a strict focus on diameter alone may result in old tree removal at especially low productivity sites, where old trees may be smaller than a diameter limit. Dendrochronologists have long been aware of and make use of the concept of "longevity under adversity" (Schulman 1956) to find and sample old trees that contain long records of past climate and ecological variability. Adverse growing conditions in microsite locations (*e.g.* locally rocky or shallow soils) can result in smaller diameter trees that may be much older than surrounding larger trees growing in better microsites. Thus, relying solely on tree diameter to bound harvesting guidelines may result in unintended and often undesirable ecological consequences, especially when old-tree retention is an objective of restoration efforts.

In this study, we compile ages of living and dead trees in frequent-fire montane forests dominated by ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson var. *scopulorum* Engelm.) in the Front Range of the central Rocky Mountains in Colorado and southeast Wyoming, USA. Our main goals are to document post-settlement changes in regional old tree distribution and to provide improved guidelines for retention of old trees during ongoing and future ecological restoration treatments. We compiled crossdated ages from over 10,000 trees in 179 randomly selected plots located across ranges of variability in site conditions in Front Range montane forests. We provide guidelines that will assist forest managers in identifying old trees for retention during landscape-scale assessments and silvicultural treatments using a combination of visually assessed morphological characteristics and

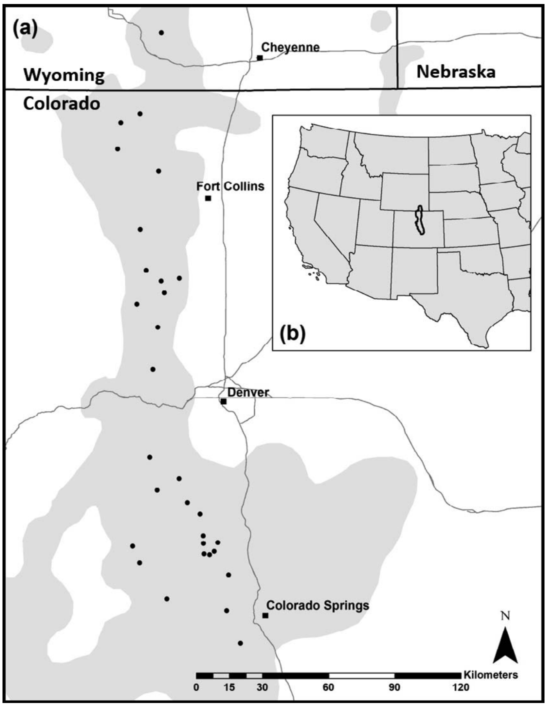

Figure 1. (a) Location of study landscapes (black circles) in the central Rocky Mountains in Colorado and southern Wyoming. Gray shading is range of ponderosa pine, light lines are major highways. (b) Location of the Front Range in the western United States.

local site environmental conditions. Data we present here also provide support for ecological restoration efforts intended to retain and promote old trees across the Front Range montane zone and similar forests throughout the Rocky Mountains (Dickinson 2014; Underhill *et al.* 2014; Addington *et al.* 2018).

METHODS

Study Area

The Front Range of the central Rocky Mountains extends from southwest of Colorado Springs, Colorado, to north of the Colorado–Wyoming border west of Cheyenne, Wyoming (Figure 1). Euro-American settlement of this region began in earnest after discovery of gold in 1858 west of the present-day cities of Golden, Boulder, and Denver. Migration to the region was estimated at over 100,000 people by the mid-1860s (Buchholz 1983). Accompanying this influx was the beginning of intensive land use, including timber harvest, livestock grazing, mining, and construction of transportation and water infrastructure (Veblen and Donnegan 2006). Changes in fire regimes - most notably a reduction in the frequency of spatially extensive fires - also occurred with settlement (*e.g.* Veblen and Donnegan 2006; Brown *et al.* 2015). Timber harvest declined considerably after the mid-20th Century, and recent forest management has primarily focused on wildfire risk reduction or ecological restoration (Addington *et al.* 2018).

Data for analyses presented here come from a study to reconstruct historical (*ca.* 1860 C.E.) forest structure across the range of montane forests of the Front Range (Brown *et al.* 2015; Battaglia *et al.* 2018). Montane forests dominated by ponderosa pine extend from the margins of the Great Plains shortgrass steppe in the east to higher elevations in the west where the montane grades to subalpine forests dominated by lodgepole pine (*Pinus contorta*), Engelmann spruce (*Picea engelmannii*), and subalpine fir (*Abies lasiocarpa*). In the lower montane zone, ponderosa pine occurs in mostly pure stands at lower elevations and on south-facing slopes at higher elevations. Principal co-dominant tree species in higher elevation upper montane forests include Douglas-fir (*Pseudotsuga menziesii*), aspen (*Populus tremuloides*), and limber pine (*Pinus flexilis*). Rocky Mountain juniper (*Juniperus scopulorum*) is a minor component at xeric sites.

We established 179 0.5-ha (70.7m × 70.7m) plots randomly-located within 30 study landscapes that cover ranges of elevation, climate, and physiography where ponderosa pine occurs in the Front Range (Figure 1). This study includes tree age data from nine plots and two landscapes not analyzed by Battaglia *et al.* (2018) because of site conditions that challenged full reconstruction of historical stand conditions for that study, but in which we sampled living tree ages. Study landscapes were selected in contiguous areas of montane forest managed by federal, state, or county agencies, with boundaries based either on township/range boundaries to include four to six sections each (1036 to 1554 ha) or management boundaries such as state parks or county open spaces. Within each landscape, we generated random coordinates for potential plot locations in areas currently occupied by ponderosa pine and which did not have documented post-settlement fires (since the late 1800s). This latter criterion was necessary to constrain sampling to areas where evidence of historical forest structure was reasonably intact. Plots were sampled if the plot center was located or could be moved no more than *ca.* 100 m to encompass an area of 0.5 ha of relatively uniform slope and aspect and was less than or equal to a mean slope of 40%. Slope angle was used to select stands where mechanical restoration treatments are most likely to occur. The elevation range of sampled plots was from 1662 to 2844 m a.s.l.

Field Sampling

Detailed field methods for the stand reconstruction study are reported in Brown *et al.* (2015) and Battaglia *et al.* (2018). For this analysis, we compiled crossdated tree ages from increment cores collected from living trees and cross-sections collected from dead trees (stumps, logs, and snags) in each plot. All cores and cross-sections were sampled at *ca.* 30-cm height on tree boles. Most trees used in this analysis were sampled in four circular 500-m^2 subplots centered in four quadrants (defined by cardinal directions) of the main 0.5 ha plot. We also include additional trees with age data from the main plot, which were collected for fire history or age confirmation. In subplots we took sections from sound remnants (from which it was feasible to obtain a cross-section) and cored all living trees ≥ 25 cm DBH or additional living trees < 25 cm DBH that met our old-age criteria (see below). We also collected increment cores from the five closest living trees to each of the subplot centers from trees < 25cm DBH that did not exhibit old-age characteristics. These trees were sampled to characterize current structure of smaller living trees. A repeated coring method was used to minimize pith offset for assigning pith dates during crossdating (Appendix A).

DBH of living trees and species for both living and dead trees were recorded. We also recorded one of three subjectively assigned morphological categories for living trees: young (likely to be <150 years old), old (likely ≥150 years old), or transitional (with a mix of old and young morphological characteristics). These age categories were assigned at the time of increment core sampling and are based on subjective assessments of tree characteristics indicative of age status (Huckaby *et al.* 2003a, 2003b; Van Pelt 2008). Morphological characteristics used to identify an old tree included: orange-yellow to occasionally grey bark with large, smooth plates; relatively open crown; large-diameter branches relative to the main stem; flattened crown (indicating weak apical dominance); tall crown base height as lower branches are shed by self-pruning or lost by scorch from past surface fires; or evidence of longer disturbance history such as fire-created catfaces, lightning-strike scars, or a damaged or dead (spike) top. Morphological characteristics of young trees included: dark bark with small, heavily dissected and rough plates with generally wide fissures; cone-shaped crown with low crown base height; small diameter branches relative to the main stem; and no evidence of disturbance history. Transitional trees had intermediate characteristics of young and old trees; for example, orange-to-grey colored rough bark plus a higher crown base height but no crown flattening or large branches. We provide examples of characteristics of old and young trees in Figure 2; however, for additional photographic and descriptive details of various morphological evidence that can be used to distinguish old-age *vs.* young-age trees, please consult Keen (1948), Huckaby *et al.* (2003a, 2003b), Abella and Denton (2009), and Van Pelt (2008)[1]. For dead trees, we also recorded status (stump, log, or snag), diameter at sample height (DSH; *ca.* 30 cm above ground level), and whether the tree had bark, sapwood, or heartwood only (eroded outside surface).

Crossdating

Cores were mounted on wooden mounts and cross-sections were glued as needed for stability.

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[1] It is beyond the scope of this paper to include comprehensive photographic examples of morphological characteristics used to assess age, and we direct interested readers to Huckaby *et al.* 2003b (A Field Guide to Old Ponderosa Pine Trees in the Colorado Front Range; https://www.fs.fed.us/rm/pubs/rmrs_gtr109) and Van Pelt 2008 (Identifying Old Trees and Forests in Eastern Washington; https://www.dnr.wa.gov/publications/lm_hcp_east_old_growth_hires_part01.pdf).

Figure 2. Examples of young-tree (left) and old-tree (right) morphological characteristics in ponderosa pine. For additional photographic examples and descriptions, we refer readers to Huckaby *et al*. 2003b and Van Pelt (2008).

Core and cross-section surfaces were prepared using a combination of planing, belt sanding, and hand sanding up to 400 grit sandpaper. All samples were crossdated using local skeleton plot chronologies developed for each study landscape and cross-checked against chronologies downloaded from the International Tree-Ring Data Bank (https://www.ncdc.noaa.gov/data-access/paleoclimatology-data/datasets/tree-ring). Overlaid concentric circles of varying circumference were used to estimate distance and number of rings to pith for cores and cross-sections that did not intersect pith but contained visible inside ring curvature (Applequist 1958; Appendix A). Any cores or cross-sections that either could not be crossdated or for which we were not able to estimate a pith date were excluded from this analysis. We did not make any correction for age from the 30-cm height crossdated ages to point of germination (see Appendix A for further discussion).

Statistical Analysis

We used regression tree analysis to model tree age (years) against 42 tree and plot predictor variables (Appendix B). We hypothesized that age would be most strongly related to tree morphology and/or DBH, but modified by stand and site conditions, *i.e.* either denser stands and/or stands in less productive sites would tend to have older trees for a given DBH. We ran regression tree models both with and without morphology as a tree-level variable to specifically isolate its influence on model performance. We fit the regression tree model using binary recursive partitioning (Breiman *et al.* 1984) in the rpart package (Therneau *et al.* 2015) of

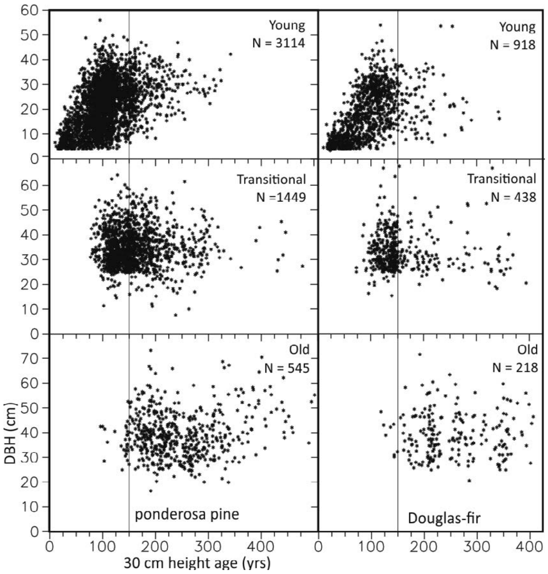

Figure 3. Crossdated ages of 30-cm height increment cores from live ponderosa pine (left panels) and Douglas-fir (right panels) trees against tree DBH by field-assigned morphology classes. Light line in each panel is at 150 years.

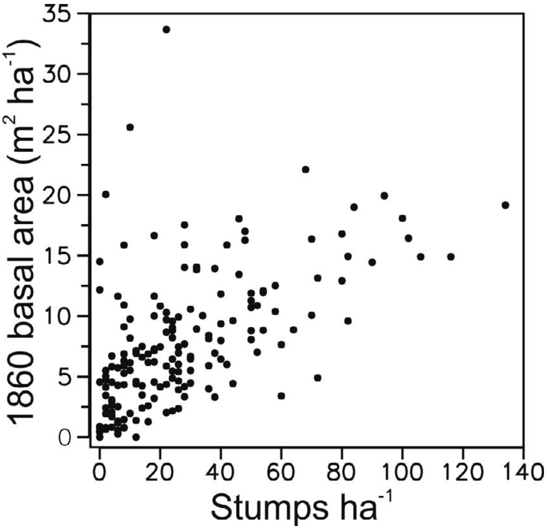

Figure 4. The number of stumps ha^{-1} sampled in 170 plots relative to the reconstructed historical (1860) stand basal area ($r = 0.56$, $p < 0.01$, $N = 170$) from Battaglia *et al.* (2018).

R version 3.1.2 (R Core Team 2016). The regression tree was simplified using an approach that balanced the cross-validated accuracy and the model complexity parameter (cp). We selected the tree that corresponds to the largest cp that is within one standard error of the cross-validation error of the overall smallest cp.

RESULTS

A total of 8079 live trees and 1969 dead trees were crossdated from the 179 plots (Table 1). Crossdated tree ages confirm that most live trees subjectively classified in the field as young or old based on tree morphology were assigned to the correct age category (Figure 3; Table 2). Of the 1446 ponderosa pine and 437 Douglas-fir trees that were classified as transitional, 84.0% and 81.1%, respectively, were between 100 and 200 years in age at 30-cm bole height (Figure 3). Pith offsets were generally low: 27.8% of all samples contained pith, 73.2% were estimated to be ≤5 rings from pith, and 95.3% were estimated to be ≤10 rings from pith (Appendix A).

Eroded stumps were found in most (93.9%) of the 0.5-ha plots. The number of stumps sampled in each plot was proportional to the reconstructed 1860 basal areas in 170 of the plots analyzed by Battaglia *et al.* (2018; Figure 4). Most plots (85.5%) also contained crossdated eroded stumps (usually collected from a subplot) where the stump pith date predated 1860, in all cases by several decades. Across the entire region, the median 30-cm-height pith dates of the oldest individual tree in each plot using either ages of stumps or living trees was over 150 years older than that of median age considering only the oldest living trees present in the current forest (Figure 5). However, the regional median age of oldest trees in 1860 before harvesting was not different from the median age of oldest living trees in the current forest (246 years with an interquartile range [IQR] of 152–334 years in the historical forest *vs*. 248 years with an IQR of 191–331 years in the current forest; Figure 6).

Results from regression tree analysis confirm that tree morphology was the most significant predictor of the 30-cm-height ages of living trees (Figure 7). The regression tree model including morphology had a cross-validated R^2 of 0.53, whereas a model excluding it had a cross-validated R^2 of 0.38. DBH in the model including morphology was a significant variable only to divide young morphology trees into younger and older groups (although note

Table 1. Numbers of crossdated living and dead (stumps, logs, and snags) trees and trees that contained pith or on which a pith date could be estimated by species.

	Live trees		Dead trees	
Species	No. crossdated	No. (%) with pith	No. crossdated	No. (%) with pith
Abies concolor	6	6 (100)	0	–
Juniperus scopulorum	137	127 (93)	17	6 (35)
Pinus concolor	140	121 (86)	38	22 (58)
Picea engelmannii	8	8 (100)	0	–
Pinus flexilis	272	239 (88)	89	48 (54)
Pinus ponderosa	5477	5231 (96)	1718	1407 (82)
Picea pungens	14	14 (100)	0	–
Populus tremuloides	141	112 (79)	0	–
Pseudotsuga menziesii	1884	1768 (94)	107	93 (87)
Totals	8079	7626 (94)	1969	1576 (80)

Table 2. Confusion matrix of trees from the three most common species sampled classified as old or young in the field based on morphology compared to crossdated ages. Note that this table does not include trees classified in the field as transitional, which we recognized at the time of sampling would be difficult to adequately separate into either of the old or young age categories. Numbers in parentheses are percentages of total trees in each column for each species. Crossdated ages are based on 30-cm height increment cores.

Ponderosa pine	Field-classified old morphology	Field-classified young morphology
Crossdated ≥ 150 yrs old	515 **(94.5)**	374
Crossdated < 150 yrs old	30	2740 **(88.0)**
Douglas-fir	Field-classified old morphology	Field-classified young morphology
Crossdated ≥ 150 yrs old	210 **(96.3)**	84
Crossdated < 150 yrs old	8	834 **(90.8)**
Limber pine	Field-classified old morphology	Field-classified young morphology
Crossdated ≥ 150 yrs old	17 **(94.4)**	16
Crossdated < 150 yrs old	1	126 **(88.7)**

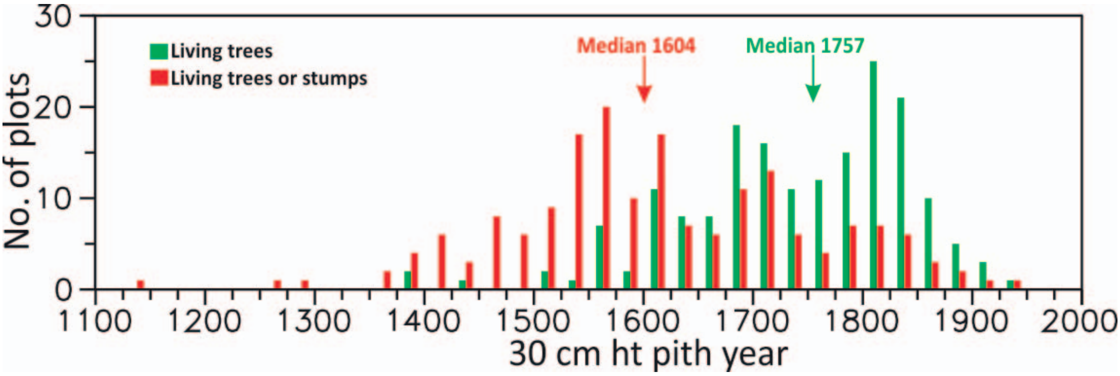

Figure 5. Current (green bars) and historical (red bars) regional oldest trees by 25-yr age classes across the Front Range ponderosa pine zone. Data are 30-cm height pith dates of oldest trees in plots ($n = 179$) recorded by only living trees (green bars) or by either living trees or eroded stumps (red bars). Median dates are for the two distributions. The distributions are different in a Kolmogorov-Smirnov comparison of the two data sets ($D = 0.4525$, $P < 0.001$).

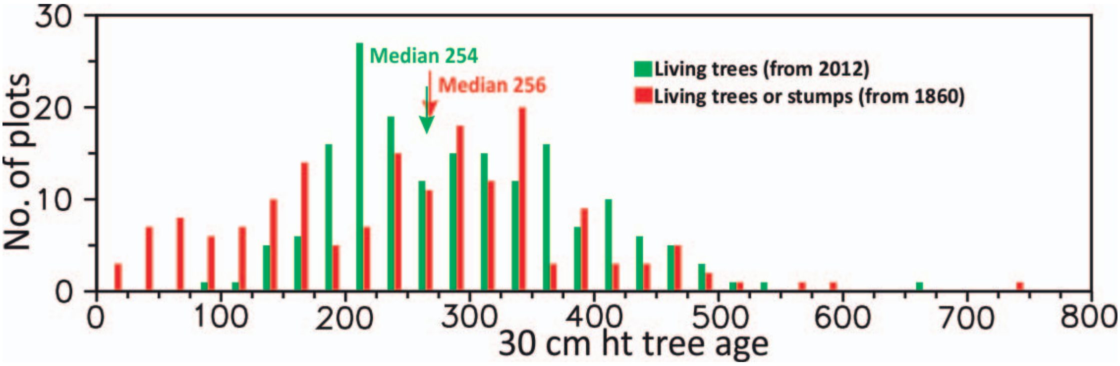

Figure 6. Current (green bars) and historical (red bars) distributions of ages of oldest tree in each plot. Ages are from 2012 in the current stand (living trees only) and from 1860 in the historical stand (living trees or stumps). The distributions are similar in a Kolmogorov-Smirnov comparison of the two data sets (D = 0.1106, P = 0.247).

that both groups are still classified as young trees <150 years old; see also Figure 3, top panels). DBH was not a significant predictor of tree age in transitional or old morphology trees (also see the relationships between these two variables in Figure 3, middle and bottom panels). Transitional morphology trees were able to be divided by site index (a measure of stand productivity) into younger and

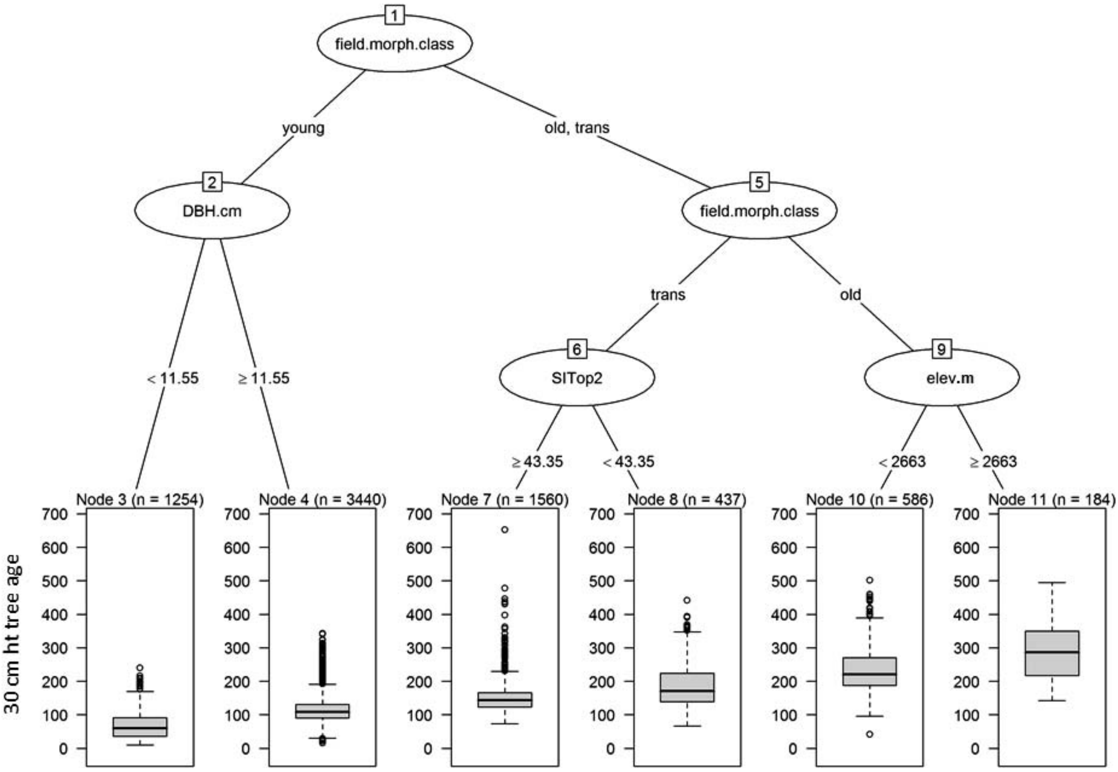

Figure 7. Regression tree results predicting 30-cm height tree age of living trees from tree and plot variables (Appendix B). Significant predictors included field morphology class (young, transitional, old), DBH (cm), site index (tree height in feet, base 100) calculated from the two best site trees, and elevation (m).

older age groups, although note that there was still a large overlap in these two classes (Figure 7). Finally, among the old morphology trees there was a significant difference in ages between upper-elevation and lower-elevation plots, with a dividing point at 2663m (Figure 7).

DISCUSSION

Impacts of Logging on Forest Age Structure

Logging appears to have had a major impact on the maximum ages of trees across the Front Range ponderosa pine zone (Figure 5). The amount of harvest in any one stand was related to the historical stand basal area (Figure 4), which suggests that harvest was proportional to the amount of timber present. Ponderosa pine is an excellent timber tree, tall and straight-growing, and ponderosa pine forests were easily accessed by loggers for building needs in the rapidly growing cities along the Front Range throughout the late 1800s and early to mid-1900s (Veblen and Donnegan 2005). Early logging practices tended to preferentially harvest larger trees. The presence of often much older stumps than living trees in a majority of the stands we sampled suggests a net loss of old tree abundance at stand-scale to landscape-scale. However, if we consider the distribution of oldest-aged trees in the reconstructed 1860 C.E. forests across the Front Range (Battaglia *et al.* 2018), there is very little difference between this and the distribution of oldest-aged living trees in the current forest (Figure 6). It is also likely that the pre-settlement disturbance regime of relatively frequent, low- to moderate-severity fires and other disturbances tended to reduce the presence of old trees, constraining maximum age structure similar to that of selective harvesting. This hypothesis is supported by the presence of the oldest living trees in higher elevation stands, where fire frequency was less during the historical period (*e.g.* Sherriff *et al.* 2014). Old trees also often have defects that make them less merchantable and these trees that escaped harvest are now 150 years older than they were in 1860. It is only if many of the trees harvested since 1860 were still alive today that the distribution of oldest trees would be different in the current forest (Figure 5).

The presence of eroded stumps harvested in the late 1800s or early 1900s in over 93% of our randomly located plots highlights the importance of sampling dead trees as evidence of historical forest structure and disturbance regimes. Age structure sampled from only living trees present after harvest may give a false impression that the historical forest was more even-aged than it was at settlement, which can in turn lead to misinterpretation of the resulting disturbance regimes as containing more severe fire behavior than what was historically present (Brown *et al.* 2008; Stevens *et al.* 2016). Furthermore, in areas such as the Front Range where timber harvest was widespread, sampling strategies intended to reconstruct fire or forest histories must consider that the majority of the area saw some level of harvest when designing a site selection protocol. Certainly there are caveats to sampling in harvested areas, namely the possibility of decayed historical evidence and complicated interpretation of historical dynamics (*e.g.* Brown *et al.* 2008, 2015; Naficy *et al.* 2010). Sampling only unharvested stands may minimize the chance of missing smaller-diameter cohorts in age structures or other evidence caused by decay since harvest. Also, unharvested stands may serve as examples of different forest development patterns or disturbance regimes at landscape or regional scales. Nevertheless, our results suggest that a site selection strategy that avoids harvested areas may not capture ecological variability representative of the broader range of environmental conditions and disturbance dynamics across a region. Our site selection was biased in terms of landscape management histories in that we did not sample in Rocky Mountain National Park, which saw very little pre-settlement harvest, and we did not sample stands in areas over 40% slope. However, we believe that our age structure results are representative of montane forest across the Front Range and central Rocky Mountain region (see also Battaglia *et al.* 2018).

Identifying Old Trees for Retention during Ecological Restoration Treatments

This study provided a unique opportunity to compare subjective estimates of tree age based on tree morphology with a large number of crossdated tree ages. We found that easily assessed morphological characteristics can usefully predict obviously old trees (≥*ca.* 150 years old) and obviously young trees ($<$*ca.* 150 years old) with 88% to 96% accuracy in ponderosa pine, Douglas-fir, and other common tree species in Colorado Front Range forests (Table 2). Ponderosa pine and Douglas-fir trees tend to have consistent morphological characteristics throughout their ranges, which can be used to distinguish old *vs.* young trees (Keen 1943; Huckaby *et al.* 2003a,b; Van Pelt 2008). Restoration treatments with a goal to retain old trees in similar ponderosa pine-dominated forests could do so with some confidence using morphological characteristics, and these characteristics will be better to use than DBH alone (Figure 7). However, we were not able to capture all variability in ages using morphology alone (Table 2; Figure 3), and managers and other interested stakeholders must recognize that some old trees may still be removed during treatments. The only sure means to determine age is, of course, to take increment cores and use crossdating methods.

Morphology is a less effective indicator of age for both ponderosa pine and Douglas-fir when trees have young and old age characteristics, those we termed "transitional" (Figure 3). Regression tree results suggest that site index (SI) can be useful to separate some older from younger trees with transitional morphologies, but there is still a great deal of overlap in tree ages between stands of varying SI (Figure 7). SI is a measure of site productivity often used by foresters and easily calculated from heights and ages of dominant trees sampled during timber inventories (Avery and Burkhart 2015). Young trees classified as transitional were found more often in more productive sites ($SI \geq 43.35$ feet base 100), whereas older transitional trees were found more often in poorer sites ($SI < 43.35$ feet base 100). This suggests that managers selecting for old trees should consider retaining more of the transitional morphology trees found in poorer sites, while removing more from relatively more productive sites. These results furthermore support arguments against using a "one-size-fits-all" diameter limit on tree removal across a project area as a strategy to conserve old trees (Abella *et al.* 2006; Sanchez-Meador *et al.* 2015). We found poor relationships between DBH and age, especially in the transitional morphology trees (Figure 3, center panels), and DBH was not a significant determinant of tree age for transitional and old trees in the regression tree analysis that included morphology as a variable (Figure 7). Rather, our results suggest that site conditions are the more important variable to consider in assessing whether a tree with transitional morphology should be retained or removed. This should encourage land managers and restoration ecologists to consider landscape-scale patterns of stand structural and compositional diversity in relation to environmental variability rather than focus on tree distributions only by individual stands (*e.g.* Addington *et al.* 2018). For example, more transitional trees of all size classes should be retained in less productive sites to promote old tree retention at a project or landscape scale, whereas fewer should be retained in more productive sites. This combination could then still maintain project-wide goals for reductions in tree basal areas or density distributions, but better conserve as many old trees as possible, assuming that this is a goal of restoration treatments. DBH may still determine which transitional trees to keep or remove in poor versus productive sites, but with the added knowledge that more of the larger trees in productive sites will likely be young and therefore amenable to removal. Again, however, land managers, ecologists, and other interested stakeholders must recognize that without coring and aging of ring series, old trees will still undoubtedly be removed during restoration treatments.

Another consideration is that young trees with crossdated ages $<$ 150 years old that we classified as transitional or old in the field based on their morphology (Figure 3) were likely classified based on structural characteristics that may have important ecological functions. These include a broken or snag top, flat crown, large limbs, or other features that may have more ecological or structural significance to wildlife habitat or other considerations than similar-aged trees consisting of only young-tree structural characteristics. Tree age is, of course, only one component in design and implementation of restoration strategies across landscapes, and other individual tree characteristics should also be considered in assessing which trees to keep or remove during treatments.

To plan ecological restoration at spatial scales encompassing several tens of thousands of hectares, managers and practitioners must make rapid, efficient decisions as to what trees to keep or remove during restoration implementation. Photo field guides such as Huckaby *et al.* (2003b) and Van Pelt (2008) aid in visual identification of old tree characteristics, and efforts such as these should be expanded to other species and regions around the world. Furthermore, our field assignments of trees into old, transitional, or young categories did not utilize any sort of quantitative ruleset of characteristics to define the morphology classes. However, other research has attempted to use more objective measures to characterize old age morphology with some success. For example, Weisberg and Ko (2012) used detailed field measurements on singleleaf piñon pine (*Pinus monophylla*) to find that tree size, a measure describing crown diminishment, and a combination of variables describing tree "stubbiness" (short stature and wide girth) were able to adequately capture variation in tree ages. They concluded that these characteristics could still be summarized into the overall "look" of a tree without having to collect specific measurements, but because these are based on measured variables they could be rapidly quantified and assessed through perhaps LIDAR profiles or other objective means. Van Pelt (2008) and Pederson (2010) also list several variables (*e.g.* crown dimensions, bark platiness) that could be amenable to quantification in regard to tree age, and could provide additional morphological characteristics useful for distinguishing old from young trees. Future work with our plot data should involve measurement of specific morphological or allometric variables on trees of known age that will help to refine our ability to visually assess tree ages in Front Range forests, and provide improved methods for retaining and promoting old trees across the central Rocky Mountain region.

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APPENDIX A. MINIMIZING PITH OFFSET.

We attempted to minimize pith offset when collecting increment cores from living trees using a repeated coring method. Our field protocol called for cores saved for age estimations to be within an estimated 5 rings from pith. After insertion of the increment borer to a depth estimated to be beyond pith, the core was backed off 360° to tell if pith was to the right or left of the tangent. If the first core was not close enough to pith, a second core was removed parallel to the first core but moved to the left or right the estimated distance to pith missed by the first tangent. The first core was put back partially into its hole, with enough sticking out of the tree to be able to core parallel to it. If the second core was not close enough, we would then collect a third core. Usually we would stop after three cores, at that point taking the closest core of the three for age determination.

Once the core was mounted, sanded, and crossdated, we would then estimate pith offset using overlaid concentric circles of varying widths printed on transparency film that take into account both innermost ring curvature and widths (Applequist 1958). Two dates were recorded for each tree, that of the innermost ring visible on the tree plus the estimated pith date. If pith was present on the core, these two dates were the same. The differences between the two dates for trees are shown in Figure A1. Almost 75% of our cores met the field criterion of an estimated ≤5 rings from pith.

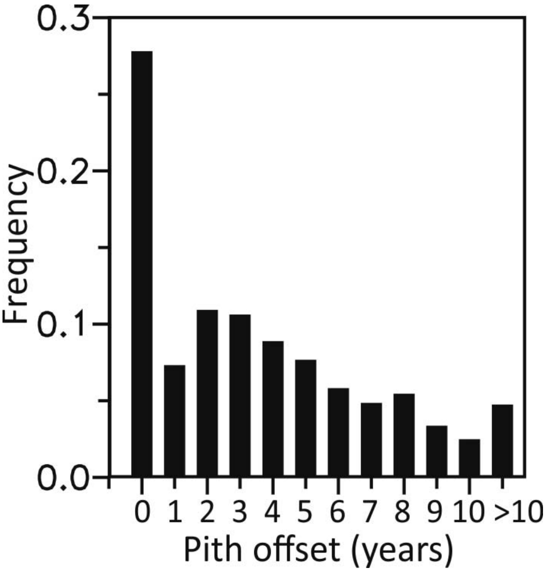

Figure A1. Pith offset on increment cores collected for the study ($n = 7626$). Pith offset is the number of estimated rings to a pith date from the innermost ring date on a core.

Appendix B. Potential predictors of tree age used to fit regression tree analysis.

Predictor	Type of measurement	Scale of measurement	Description
spp	Categorical	Tree	Tree species
field.morph.class	Categorical	Tree	Field morphology (young, transitional, old)
DBH.cm	Continuous	Tree	DBH (cm)
tree.ht.m	Continuous	Tree	Tree height (m; only available for site index trees; 4–8 trees per plot)
UTME	Continuous	Plot	UTM easting
UTMN	Continuous	Plot	UTM northing
elev.m	Continuous	Plot	Elevation (m)
aspect.class	Continuous	Plot	Aspect (degrees)
slope	Continuous	Plot	Slope (%)
slope.position	Categorical	Plot	Slope position (bottom, lower, middle, upper, ridge)
slope.shape	Categorical	Plot	Slope shape (concave, straight, convex)
TRMI	Continuous	Plot	Topographic relative moisture index (Parker 1982)
SIMean	Continuous	Plot	Site index (ft) calculated from all site trees (Mogren 1956)
SITop2	Continuous	Plot	Site index (ft) calculated from two best site trees (Mogren 1956)
per.sand	Continuous	Plot	Soil sample, percent sand
per.silt	Continuous	Plot	Soil sample, percent silt
per.clay	Continuous	Plot	Soil sample, percent clay
per.coarse	Continuous	Plot	Soil sample, percent coarse material
sol.rad	Continuous	Plot	Solar radiation (MJ m^{-2} yr^{-1}) calculated from GIS

Appendix B. Continued.

Predictor	Type of measurement	Scale of measurement	Description
annual.twi	Continuous	Plot	Annual topographic wetness index, calculated from GIS
summer.twi	Continuous	Plot	Summer topographic wetness index, calculated from GIS
winter.twi	Continuous	Plot	Winter topographic wetness index, calculated from GIS
mean.temp	Continuous	Plot	Mean temperature (degrees C), from PRISM*
mean.precip	Continuous	Plot	Mean precipitation (cm), from PRISM*
may.precip	Continuous	Plot	Mean May precipitation (cm), from PRISM*
june.precip	Continuous	Plot	Mean June precipitation (cm), from PRISM*
july.precip	Continuous	Plot	Mean July precipitation (cm), from PRISM*
may.to.july.precip	Continuous	Plot	Mean May to July precipitation (cm), from PRISM*
DI	Continuous	Plot	Drainage index, calculated from GIS
PI	Continuous	Plot	Productivity index, calculated from GIS
Kaufmann	Categorical	Plot	Forest type (Kaufmann *et al.* 2006)
Sherriff	Categorical	Plot	Forest type (Sherriff *et al.* 2014)
density	Continuous	Plot	Current tree density (trees per ha; ≥4cm DBH)
BA	Continuous	Plot	Current basal area (m^2 ha^{-1}; ≥4cm DBH)
SDI	Continuous	Plot	Current stand density index (≥4cm DBH)
QMD	Continuous	Plot	Current quadratic mean diameter (cm; ≥4cm DBH)
PIPO.density	Continuous	Plot	Current PIPO** tree density (trees per ha; ≥4cm DBH)
PIPO.BA	Continuous	Plot	Current PIPO** basal area (m^2 ha^{-1}; ≥4cm DBH)
PSME.density	Continuous	Plot	Current PSME** tree density (trees per ha; ≥4cm DBH)
PSME.BA	Continuous	Plot	Current PSME** basal area (m^2 ha^{-1}; ≥4cm DBH)
other.density	Continuous	Plot	Current other tree species density (trees per ha; ≥4cm DBH)
other.BA	Continuous	Plot	Current other tree species basal area (m^2 ha^{-1}; ≥4cm DBH)

*http://prism.oregonstate.edu/

**PIPO = *Pinus ponderosa*; PSME = *Pseudotsuga menziesii*