



Changes in forest structure since 1860 in ponderosa pine dominated forests in the Colorado and Wyoming Front Range, USA



Mike A. Battaglia^{a,*}, Benjamin Gannon^b, Peter M. Brown^c, Paula J. Fornwalt^a, Antony S. Cheng^b, Laurie S. Huckaby^a

^a USDA Forest Service, Rocky Mountain Research Station, 240 West Prospect Road, Fort Collins, CO 80526, United States

^b Colorado Forest Restoration Institute, Colorado State University, Fort Collins, CO 80523, United States

^c Rocky Mountain Tree-Ring Research, 2901 Moore Lane, Fort Collins, CO 80526, United States

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ABSTRACT

Management practices since the late 19th century, including fire exclusion and harvesting, have altered the structure of ponderosa pine (*Pinus ponderosa* Douglas ex P. Lawson & C. Lawson) dominated forests across the western United States. These structural changes have the potential to contribute to uncharacteristic wildfire behavior and effects. Locally-relevant information on historical forest structure can improve efforts to restore more fire adapted conditions. We used a dendrochronological approach to reconstruct pre-settlement era (ca. 1860) structure for 170, 0.5-ha plots in montane ponderosa pine-dominated forests of the Colorado and Wyoming Front Range. Historical reconstructions were quantitatively compared with current conditions to highlight key departures. In lower montane forests, historical basal area averaged $6.3 \text{ m}^2 \text{ ha}^{-1}$, density averaged 97 trees ha^{-1} , and quadratic mean diameter (QMD) averaged 26.5 cm, while current basal area averaged $17.6 \text{ m}^2 \text{ ha}^{-1}$, density averaged $438 \text{ trees ha}^{-1}$, and QMD averaged 24.3 cm. Similar trends were observed in upper montane forests, where historical basal area averaged $9.5 \text{ m}^2 \text{ ha}^{-1}$, historical density averaged $163 \text{ trees ha}^{-1}$, and historical QMD averaged 29.4 cm, while current basal area averaged $17.2 \text{ m}^2 \text{ ha}^{-1}$, current density averaged $389 \text{ trees ha}^{-1}$, and current QMD averaged 25.2 cm. Most differences between historical and current conditions were significant. Across the montane zone, ponderosa pine dominated historical (88% and 83% of basal area in the lower and upper montane, respectively) and current forests (80% and 74% of basal area, respectively), but pine dominance decreased primarily due to infilling of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco). Much of this establishment occurred around the period of settlement (1861–1920) and continued throughout the 20th century. Results from this study help inform ecological restoration efforts that seek to integrate elements of historical forest structure and aim to increase the resilience of Front Range ponderosa pine forests to future wildfires and a warmer climate.

1. Introduction

Historically, relatively frequent, low- to mixed-severity fire shaped the structure of ponderosa pine (*Pinus ponderosa* Douglas ex P. Lawson & C. Lawson) dominated forests across the western United States (U.S.), creating and maintaining heterogeneous but generally open conditions (Hessburg et al., 2000; Larson and Churchill, 2012; Reynolds et al., 2013; Bigelow et al., 2017; Addington et al., 2018). Since the mid- to late-19th century, the structure of these forests has been increasingly affected by human land and fire management practices. Logging, livestock grazing, and mining activities during the Euro-American settlement era, combined with post-settlement fire suppression, have increased stand density and homogeneity across much of the ponderosa

pine range (Covington and Moore, 1994; Belsky and Blumenthal, 1997; Hessburg and Agee, 2003; Hessburg et al., 2005). Fire behavior simulation studies from across the western U.S. have demonstrated that this change in forest structure has led to increased potential for crown fire initiation and spread (Fulé et al., 2002; Brown et al., 2008; Van de Water and North, 2011; Taylor et al., 2014). These dense structural conditions are more susceptible to uncharacteristically large, high-severity wildfires that often produce undesirable ecological and social outcomes (Paveglio et al., 2015). For example, recent wildfires have created large patches of complete tree mortality (Waltz et al., 2014; Steel et al., 2015; Collins et al., 2017), resulting in sparse post-fire tree regeneration (Keyser et al., 2008; Collins and Roller, 2013; Chambers et al., 2016; Rother and Veblen, 2016; Owen et al., 2017), the loss of

* Corresponding author.

E-mail address: mbattaglia@fs.fed.us (M.A. Battaglia).

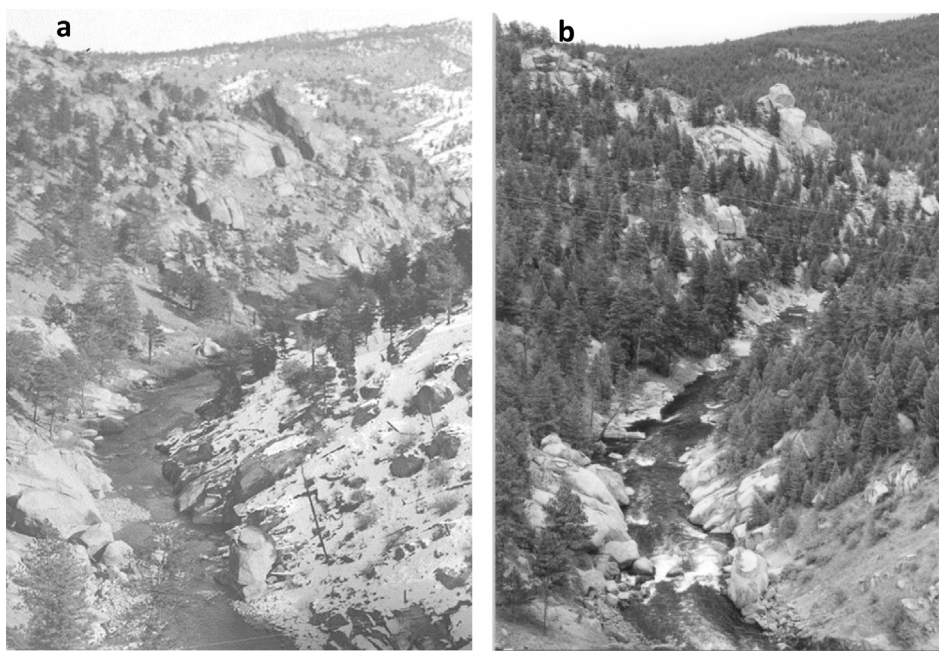


Fig. 1. Paired photographs demonstrating forest conditions along the South Platte River on the Pike National Forest, Colorado in 1903 (a) and 1999 (b). The 1903 photograph is from the Denver Water Department archives. The 1999 photograph is credited to Laurie S. Huckaby, USFS.

already-rare old trees (Spies et al., 2006; Kolb et al., 2007; Fornwalt et al., 2016), alterations to threatened species habitat (Kotliar et al., 2003; Stephens et al., 2016), and increased erosion and sedimentation of water supply systems (Moody and Martin, 2001; Rhoades et al., 2011; Smith et al., 2011). Human development in ponderosa pine dominated forests further exacerbates the situation as policymakers and land managers face pressure to continue suppressing all wildfires – even ecologically appropriate ones – within and surrounding developed areas – to protect life, property, and highly-valued assets (Theobald and Romme, 2007).

In response to recent large and severe wildfires, national-level policies – including the 2000 National Fire Plan, the 2003 Healthy Forests Restoration Act, and the 2009 Forest Landscape Restoration Act that established the Collaborative Forest Landscape Restoration Program (CFLRP) – have directed federal land management agencies to fund programs that restore resiliency and sustainability to ponderosa pine dominated and other frequent-fire forests (Schultz et al., 2012). It is widely held that the scientific rationale and guidance for restoration, through these policies, should be grounded in an understanding of local historical range of variability (HRV) of forest structure and fire regimes (Morgan et al., 1994; Landres et al., 1999; Keane et al., 2009). Much of our knowledge of historical ponderosa pine forest structure in the southern Rocky Mountains comes from the southwestern U.S. where open, low density, uneven-aged forests of medium- to large-sized trees were associated with frequent (1–12 years), low-severity fire regimes (Fulé et al., 1997; Allen et al., 2002; Reynolds et al., 2013). However, studies in other regions suggest fire regimes for some ponderosa pine dominated forests were characterized by a wider range of fire frequency and severity (Brown et al., 1999; Baker et al., 2007; Sherriff and Veblen, 2007), which contributed to a more heterogeneous forest structure than described for the southwest (Perry et al., 2011; Addington et al., 2018). Furthermore, differences in biophysical characteristics such as elevation, topography, geology, and climate, can drive local variation in historical forest structures and fire regimes (Larson and Churchill, 2012; Lydersen et al., 2013; Churchill et al., 2013; Johnston et al., 2016; Johnston, 2017; Rodman et al., 2017). Thus, a thorough understanding of local historical variation is critical to forming ecologically-appropriate restoration goals (Brown et al., 2004; Schoennagel et al., 2004).

In ponderosa pine-dominated forests of the Colorado and Wyoming Front Range, elevation has been identified as a dominant control on the historical fire regime (Sherriff and Veblen, 2007; Sherriff et al., 2014). Historical mean fire return intervals ranged from ~10–60 years (Veblen et al., 2000; Brown and Shepperd, 2001; Hunter et al., 2007; Sherriff and Veblen, 2007; Brown et al., 2015) with lower elevations experiencing more frequent fires. In lower montane forests, where ponderosa pine was the major component and often the only overstory tree species, fires were relatively frequent (10–20 years) historically and dominated by low-severity fire effects (Sherriff and Veblen, 2007; Sherriff et al., 2014; Brown et al., 2015). In the upper montane zone, where greater proportions of Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Mirb. Franco)), aspen (*Populus tremuloides* Michx.), and lodgepole pine (*Pinus contorta* Douglas ex Loudon) intermixed with ponderosa pine, historical fire return intervals were longer (20–50+ years) and more heterogeneous with patches (10–100 ha) of stand-replacing and moderate-severity fire (where fire reduces the basal area or canopy cover 20–70%) (Brown et al., 1999; Schoennagel et al., 2011; Sherriff et al., 2014). Differences in historical fire regimes across the elevational gradient of the Front Range suggest that historical forest structure, and thus restoration goals, might also vary across lower and upper montane zones (Sherriff et al., 2014; Addington et al., 2018).

A collaborative group of stakeholders identified over 300,000 ha of Front Range ponderosa pine-dominated forests in need of restoration (Underhill et al., 2014), but the lack of broad-scale scientific information on historical forest structure has been a barrier to progress (Cheng et al., 2015). Information that currently guides restoration of forest structure on the Front Range includes historical descriptions, repeat historical photographs, and dendrochronological reconstructions. Historical descriptions (Jack, 1900) and photographs (Veblen and Lorenz, 1991; Kaufmann et al., 2001; Fig. 1) can be important components of the historical forest narrative, but they lack quantitative data for informing silvicultural prescriptions. Previous dendrochronological reconstructions in the Colorado Front Range focused primarily on fire regimes using fire history and tree establishment data (Brown et al., 1999; Sherriff and Veblen, 2006; Schoennagel et al., 2011) without a direct comparison of current and historical forest structure metrics. Several studies have reported a substantial increase in forest density for lower montane ponderosa pine forests (Sherriff and Veblen, 2006;

Schoennagel et al., 2011; Sherriff et al., 2014; Brown et al., 2015), but quantification of other important forest structure metrics are limited to one study with a small geographic extent (Brown et al., 2015). Moreover, dendrochronological reconstructions for upper montane forests are lacking, and generalizations about the lack of departure across the montane zones ignore other important drivers such as past timber harvests and fire suppression or fire exclusion (Naficy et al., 2010, 2016; Merschel et al., 2014).

We implemented a spatially extensive dendrochronological study of ponderosa pine dominated forests of the Colorado and Wyoming Front Range to examine how forest structure has deviated from historical (ca. 1860) conditions. Much of the sampled area showed signs of early Euro-American timber harvesting, and all sites have experienced fire suppression over the past century. Specifically, our objectives were to reconstruct historical stand conditions, including tree densities, basal areas, tree size class distribution, and species composition, and to compare reconstructed and contemporary values of trees ≥ 4 cm diameter at breast height (DBH) for both lower and upper montane zones. We hypothesized that, relative to historical conditions, tree density and basal area in both the lower and upper montane forests have increased, that size distributions have shifted toward smaller trees, and that Douglas-fir has become more abundant.

2. Methods

2.1. Study area

Our study area spans the montane zone (between 1600 and 2900 m elevation) of the Front Range, which is the eastern terminus of the Rocky Mountains that runs from just west of Cheyenne, Wyoming, U.S. in the north, to just west of Colorado Springs, Colorado, U.S. in the south, and is bounded by the Great Plains to the east (Fig. 2). Moving west from the Great Plains, the Front Range increases in elevation and transitions from a series of north-south oriented, parallel hogback ridges into a complex topography of steeply dissected slopes, valleys, and interfluvial areas (Chronic and Williams, 2002). Soils are dominated by coarse-textured Ustolls and fine-textured Cryoboralfs derived from gneiss, granite, and schist parent materials (Chronic and Williams, 2002). The climate of the Front Range is continental. Within our study area, mean annual precipitation ranges from 384 to 682 mm, and mean annual temperature ranges from 3.3° to 9.8°C (Prism 2014), with the wettest and coolest conditions occurring at higher elevations. During the summer months, the North American monsoon often develops and produces locally heavy precipitation in the form of brief but intense thunderstorms. Snow dominates precipitation from October to May, but a snowpack does not persist (Veblen and Donnegan, 2006).

High topographic variability influences the distribution of forest types in the montane zone (Peet, 1981). We use the classification of lower and upper montane forests from Kaufmann et al. (2006), which accounts for the effect of latitude on local elevation ranges. Ponderosa pine dominates lower montane forests, which occur between 1600 and 2600 m of elevation (Kaufmann et al., 2006). Rocky Mountain juniper (*Juniperus scopulorum* Sarg.) sometimes co-occurs with ponderosa pine, as does Douglas-fir, primarily on northerly aspects and wetter sites. Gambel oak (*Quercus gambelii* Nutt.) is often found in the southern Front Range growing as a shrub lifeform at lower elevations. In the upper montane zone (ranging from ~2300 to 2900 m elevation; Kaufmann et al., 2006), ponderosa pine dominates southerly aspects, and a ponderosa pine-Douglas-fir mix co-dominates northerly aspects. Aspen, lodgepole pine, and limber pine (*Pinus flexilis* James) also intermix with ponderosa pine and Douglas-fir in the upper montane zone, forming a complex landscape mosaic of stand age and composition.

2.2. Field methods

For this study, field methods followed those outlined in Brown et al.

(2015). We sampled a total of 170 plots that were 0.5 ha in size and that were randomly located within 28 sample areas distributed across the Front Range (Fig. 2; Table 1). Sample area selection was not entirely random due to land ownership and access constraints, but our sampling captured a representative area of the montane forest zone. Sample areas were generally 1036–1554 ha in size on National Forest System lands, or they matched the boundaries of County, State, and National Parks. A geographic information system (GIS) was used to randomly generate potential plot locations within each sample area, constrained to the extent of montane forest types (dominated or co-dominated by ponderosa pine and/or Douglas-fir) and locations with consistent slope ($\leq 40\%$), aspect, and landform. Final plot selection was made after a site visit to verify that plot location requirements were met and the plot lacked evidence of post-settlement disturbances that could potentially degrade the dendrochronological record (e.g., recent fires, heavy equipment harvesting, roads, or campsites). If a plot location did not meet the required conditions, but it could be moved no more than ~100 m into an area that met the conditions, the plot was sampled. We characterized the plot environment by slope, slope position, slope shape, and aspect.

The 0.5-ha (70.7 m \times 70.7 m) plots were oriented with plot boundaries aligned to cardinal directions. We divided the plots into quadrants and located circular 0.05-ha (12.7-m radius) subplots at the quadrant centers (total of 0.2 ha sampled per plot) to collect the historical and current forest structure data for trees ≥ 4 cm DBH described here. The full plot was used to inventory and map pre-settlement (ca.1860) live trees and remnants (stumps, logs, and snags) based on old-age morphology (Huckaby et al., 2003) for a separate analysis of historical spatial patterns. Fixed-area sampling within the subplots was used to inventory potential live and remnant pre-settlement trees for the historical reconstruction. Within the subplots, we targeted potential live pre-settlement trees by focusing our inventory and dendrochronology sampling on trees ≥ 25 cm DBH or with old-age morphology. The 25 cm DBH threshold corresponds to the lower 5th percentile of DBH for pre-settlement trees in a large Front Range tree age and size dataset compiled by the authors (unpublished data). Morphological characteristics used to identify old trees included bark that was relatively smooth, unfissured, and predominately orange or gray rather than black, a relatively open crown with primarily large-diameter branches, a flattened crown indicating weakening apical dominance, a damaged or dead top, an elevated crown base height, and evidence of fire scarring (Huckaby et al., 2003; Brown et al., 2015). Data collected for each live tree included species, DBH, diameter at sample height (30 cm; DSH), and apparent age class based on morphology in classes of *young* (< 100 years), *transitional* (100–150 years), and *old* (> 150 years). Trees > 150 years old and < 25 cm DBH were also included in the *old* tree dataset based on the old tree morphological characteristics criteria. Increment cores were collected at ~30 cm height from all potential live pre-settlement trees unless prevented by rot. Two dominant or co-dominant trees per subplot were measured for height to compute site index (Mogren, 1956). We also inventoried all potential remnant pre-settlement trees within the subplots and recorded species, form (stump, log, or snag), condition (whether the remnant had bark, sapwood, or was eroded to the heartwood), DBH (when possible), DSH, and apparent age class based on morphology. Cross-sections were collected at ~30 cm height from sound remnants using a chainsaw. To supplement the current structure captured by the fixed-area sampling, we used *n*-tree distance sampling (Lessard et al., 2002) to inventory the 5 closest apparent live post-settlement trees (4.0–24.9 cm DBH, and lacking old-age morphology) to each subplot center, up to a maximum search distance of 12.7 m (the subplot radius). For each tree we recorded species, DBH, and DSH, and collected a core at 30 cm height. We also recorded the distance to the furthest tree for determining the sampled area. Note that the morphology-based age classes used for live trees were replaced with actual ages determined from the crossdated increment cores for analysis (more below).

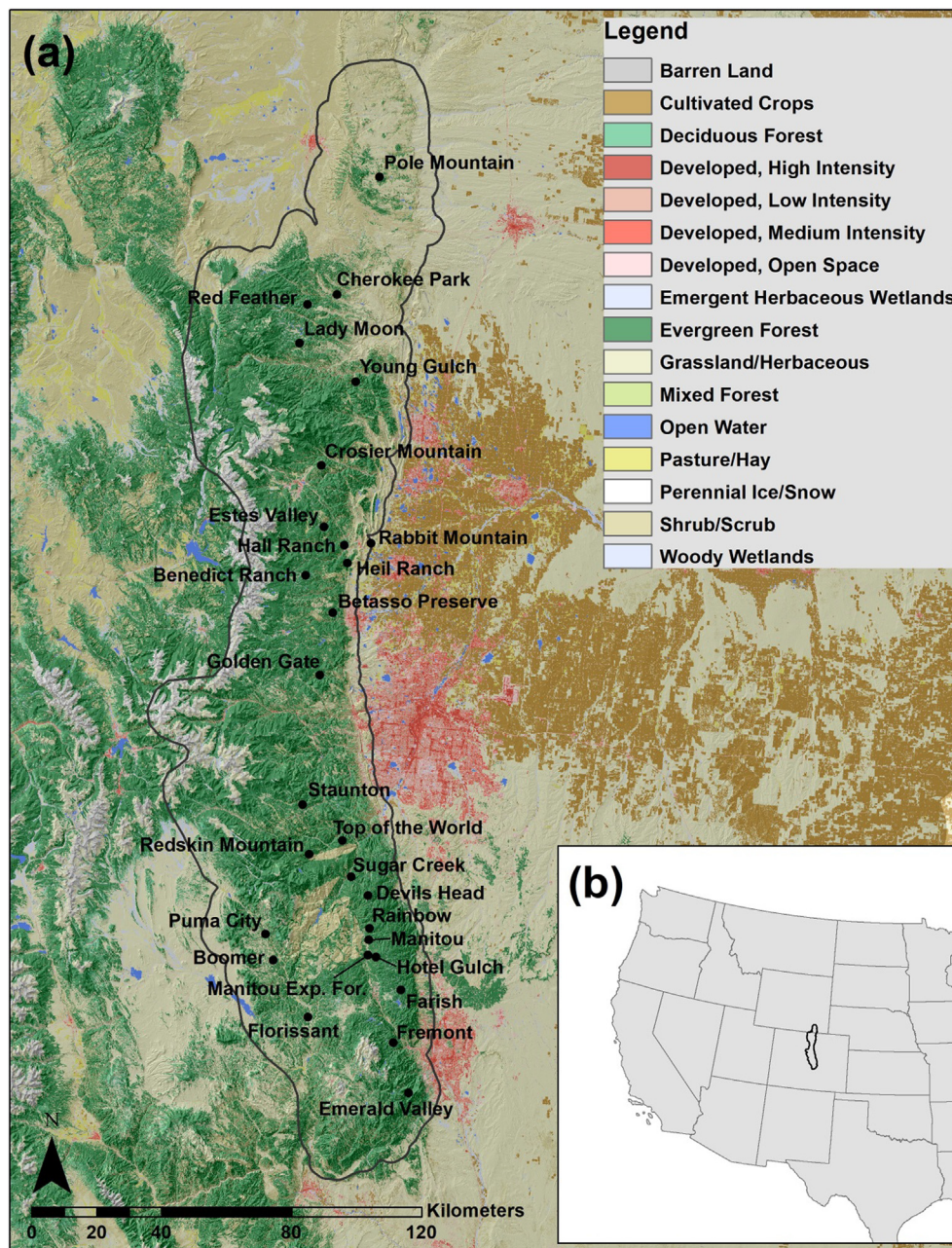


Fig. 2. Locations of the study area and the 28 sample areas distributed across the Colorado and Wyoming Front Range (a) within the western United States (b). Map source: National Land Cover Dataset 2011.

Table 1

Summary characteristics for the lower (n = 85) and upper montane (n = 85) plots measured along the Front Range. Site index is for ponderosa pine base age 100 (Mogren, 1956). TRMI is the topographic relative moisture index (Parker, 1982) with higher TRMI values indicating relatively more mesic sites than lower TRMI values.

Life zone	Elevation (m)		Aspect				Slope (%)		Site index (m)		TRMI	
	Mean	Range	%N	%E	%S	%W	Mean	Range	Mean	Range	Mean	Range
Lower montane	2208	1662–2601	19	33	19	29	20.3	2–50	12.9	5.5–17.0	29.1	10–52
Upper montane	2584	2302–2838	28	28	34	10	17.7	2–43	12.8	8.0–17.1	29.7	10–50.5

2.3. Dendrochronological methods

Cores and cross-sections were prepared using standard dendrochronological methods; samples were planed and sanded until cell structure was visible (Speer, 2010). Cores and cross-sections were

visually crossdated using both chronologies developed for each sample area, and existing chronologies from the International Tree-Ring Data Bank (<https://www.ncdc.noaa.gov/data-access/paleoclimatology-data/datasets/tree-ring>). We recorded the innermost ring date, pith date (estimated using concentric ring diagrams if pith was not present

on the sample but innermost ring curvature was present [Speer, 2010]), outside date, and outside date type (presence of bark/death date, outside without bark, or scar). For pre-settlement trees (pith date \leq 1860) we measured the radius from pith to 1860, and if the sample was complete (contained the bark or death date), we also measured the radius from the pith to the end of the heartwood, and from the pith to the outside of the sapwood (excluding bark).

2.4. Data calculations

We first determined which trees were alive in 1860 to calculate historical density using one of several methods depending on tree status and the availability of dendrochronology data. First, any live tree with a pith data pre-dating 1860 was assigned to the 1860 forest. Second, any live tree with a missing, damaged, or undateable core was assigned to the 1860 forest based on field assigned morphology; if classified as *young*, the tree was not included in the 1860 forest, and if *old*, it was included. Third, any live tree with a missing, damaged, or undateable core and with an apparent age class of *transitional* was assigned to the 1860 forest using a multiple logistic regression model based on species, DBH, and morphology, with a random plot effect, using the *glmer* function (Bates et al. 2014) in R (R Core Team, 2014). The model was built from 6444 trees and had a 3-fold cross validated overall accuracy of 75.5%, a pre-settlement producer's accuracy of 69.2% (*sensu* Aronoff, 2005), and a pre-settlement user's accuracy of 73.9% (*sensu* Aronoff, 2005), when used as a binary classifier at $p = 0.5$ for transitional trees. Fourth, any pre-settlement remnant tree with a crossdated section or a core was assigned to the 1860 forest based on pith or inside dates ($n = 1408$; 34.5% of remnants). Some of these remnants were assumed to be trees that died well before 1860 ($n = 162$; 4.0% of remnants), and they were excluded from historical estimates because their outside dates were centuries older than 1860, and their outside surfaces were heavily weathered. Fifth, for a remnant tree that did not yield a sample, or for which the samples could not be dated ($n = 2679$; 65.5% of remnants), we conservatively assigned it a pre-settlement status if it was an eroded remnant ($n = 1010$; 25.8% of remnants), and we used our multiple logistic regression model to assign a pre-settlement status if it was a bark or sapwood remnant ($n = 1372$; 33.6% of remnants).

Historical tree DBH values were then estimated to determine historical plot BA and QMD. We first reconstructed DSH to match the height at which cores and cross sections were collected because most of the pre-settlement remnants were stumps. For live pre-settlement era trees with complete crossdated cores, historical DSH was determined first by multiplying the field measured DSH by the ratio of the core's measured radius to 1860 to the total core radius. In the case of an incomplete core, the radius to 1860 was doubled to estimate DSH. If no core measurements were available ($n = 297$, 13.5% of live pre-settlement era trees), the field measured DSH was multiplied by the plot mean of radius to 1860 over total radius; this approximated an average size reduction factor for pre-settlement trees in the plot. If too few trees were available to inform this reduction factor at the plot-level, then the sample area mean was used. This method should be most accurate for trees close in age to those used to calculate the reduction factor, but it can introduce error when applied to trees that are much younger or older than the mean age. For remnants trees with crossdated sections containing the 1860 ring, the radius to 1860 was doubled to estimate the historical DSH. The majority of sampled remnants were eroded to the heartwood and had outside dates pre-dating 1860. We used the measured heartwood and total radius measurements from the pre-settlement cores to model the relationship between heartwood and total tree diameter using linear regression analysis (similar to Brown and Cook, 2006; Brown et al., 2015). We developed separate models (Eqs. (1)–(3)) for ponderosa pine, Douglas-fir, and limber pine. The ponderosa pine model was also applied to any of the rare species ($n = 48$, 2.5% of eroded remnants), which lacked sufficient sample sizes to construct species-specific models.

$$\begin{aligned} \text{Ponderosa pine tree diameter (cm)} &= 0.96 \times \text{heartwood diameter} \\ &+ 18.22 \quad (n = 1570; r^2 = 0.48); \end{aligned} \quad (1)$$

$$\begin{aligned} \text{Douglas-fir tree diameter (cm)} &= 1.11 \times \text{heartwood diameter} + 3.79 \quad (n \\ &= 419; r^2 = 0.90); \end{aligned} \quad (2)$$

$$\begin{aligned} \text{Limber pine tree diameter (cm)} &= 1.03 \times \text{heartwood diameter} + 6.53 \quad (n \\ &= 48; r^2 = 0.87); \end{aligned} \quad (3)$$

These equations were applied to field-measured DSHs to estimate an 1860 DSH for each eroded remnant tree. The historical diameters of bark or sapwood remnants without crossdated sections were estimated by multiplying field-measured DSH by the plot mean of radius to 1860 to total radius from the live tree cores. A 10% bark correction factor was added for any of the diameter reconstruction methods that measured or predicted the 1860 diameter of only wood (e.g., measuring to the 1860 ring on a remnant cross-section does not include bark). We used the DBH and DSH measurements from live trees to quantify empirical DSH to DBH correction factors. DSH to DBH correction factors of 0.83, 0.79, and 0.82 were used for ponderosa pine (based on $n = 5614$ samples), Douglas-fir ($n = 1846$), and all other species combined ($n = 754$), respectively. Species other than ponderosa pine and Douglas-fir were pooled due to low sample sizes.

Because we only inventoried live trees ≥ 4 cm DBH in the current forest, we focus our comparison of reconstructed 1860 versus current densities, basal areas, and quadratic mean diameters only on reconstructed trees ≥ 4 cm DBH. Subplot and variable radius plot data were combined by first normalizing by sampled area and then summing (density, basal area, and size class distributions). Our variable radius subplot sampling was meant to target only post-settlement era trees using size and morphology criteria, but we also captured a small number of pre-settlement era trees (as confirmed by crossdated cores). To consider historical and current tree records from the variable radius plots equivalently, we pooled the tree lists and variable radius areas sampled by plot for all density calculations.

Stand structural stage was calculated for 1860 and current forest structures. Structural stages are used to depict the stage of stand development and are based on stand level tree diameter and total canopy cover (Vandendriesche 2013). For the Front Range there are four structural stages: 1 (nonstocked); 2 (trees < 2.54 cm DBH); 3 (2.54–22.9 cm DBH); 4 (> 22.9 cm DBH). Canopy cover is estimated by calculating relative stand density index (RD; total Stand SDI/maximum SDI) which is then assigned to one of 3 canopy density categories (open = $RD < 30$; moderately open = $RD > 30 \leq 47$; closed = $RD > 47$). SDI is a measurement of relative density that integrates QMD and tree density (see Eq. (4)).

$$SDI = \sum_i^N \left(\frac{DBH_i}{25} \right)^{1.6} \quad (4)$$

2.5. Data analysis

We used repeated-measures generalized linear mixed models in SAS 9.4 (PROC GLIMMIX; SAS Institute Inc., Cary, North Carolina, USA) to compare historical and current forest structure variables for each of the lower and upper montane zones. Species composition values were converted to a proportion, rescaled using the methods of Smithson and Verkuilen (2006) to accommodate 0 and 1 values, and modeled with a beta distribution. Sample area was included as a random effect. Time period was included as a random effect, with plot designated as the repeated-measures subject and with the two time periods for each plot correlated by a compound symmetry covariance structure. We compared time periods using least squares means with a Tukey adjustment. Significance was determined with an $\alpha = 0.050$.

Table 2

Least square means and 95% confidence intervals of stand characteristics for lower and upper montane historical and current ponderosa pine dominated forests along the Front Range.

<i>Lower montane (n = 85)</i>			
	Basal area (m ² ha ⁻¹)	Density (trees ha ⁻¹)	QMD (cm)
Historical	6.3 (5.1, 7.8)	97 (62, 153)	26.5 (24.4, 28.7)
Current	17.6 (15.2, 20.3)	438 (330, 582)	24.3 (22.3, 26.4)
<i>Upper montane (n = 85)</i>			
	Basal area (m ² ha ⁻¹)	Density (trees ha ⁻¹)	QMD (cm)
Historical	9.5 (8.0, 11.3)	163 (124, 214)	29.4 (27.5, 31.4)
Current	17.2 (14.8, 19.9)	389 (310, 488)	25.2 (23.5, 27.1)

3. Results

A total of 22,761 trees were measured in the 170 plots. These included 13,741 live trees, 2579 logs, 1863 snags, and 4578 stumps (9020 total remnants). A total of 7551 live trees and 1652 remnant trees were crossdated. Most plots (95.3%) contained at least one eroded stump, and 75.9% of the plots contained at least one crossdated eroded stump where the stump pith date is known to have predated 1860, in all cases by several decades to centuries.

3.1. Lower montane forests

Basal area, density, and QMD in current lower montane forests have changed markedly since 1860. Average forest basal area increased 3-fold ($p < 0.0001$), density increased by more than 4-fold ($p < 0.0001$), and QMD decreased by 8% ($p = 0.0400$) compared to 1860 reconstructions (Table 2). Historically, average basal area was 6.3 m² ha⁻¹ with an average QMD of 26.5 cm compared to the contemporary basal area of 17.6 m² ha⁻¹ with a QMD of 24.3 cm. Average density was historically 97 trees ha⁻¹ and it was 438 trees ha⁻¹ currently.

High variability in basal area, density, and QMD was evident across the lower montane, both historically and currently (Fig. 3a–d). As a general pattern, historical basal area and density distributions were skewed toward lower values, while current distributions were skewed toward middle and upper values (Fig. 3a and b). There is some overlap between historical and current basal area (in the range of 5–20 m² ha⁻¹) and density (100–600 trees ha⁻¹) distributions; however, 80% of plots had historical basal areas less than 10 m² ha⁻¹ compared to 10–15% currently, and 80% of plots had historical densities below 180 trees ha⁻¹ compared to 15% currently. Historical and current QMDs overlapped across much of their distributions, but historically 15% of plots had QMDs that exceeded 35 cm, while none did currently (Fig. 3c). Moreover, lower montane forest plots were historically dominated by open-canopied forest structures (structural stages 3A and 4A) (Fig. 3d). Over time, canopy cover has increased, shifting open-canopied structures toward closed-canopied structures (structural stages 3B and 4B).

Lower montane forests also experienced a shift in species composition and tree size class distributions. The contribution of Douglas-fir to both basal area ($p < 0.0001$) and density ($p < 0.0001$) has increased significantly since 1860 with a concurrent decrease in the proportion of ponderosa pine tree density ($p < 0.0010$) (Table 3).

Historically, ponderosa pine was found in each diameter class up to 70 cm, although the majority of trees were less than 50 cm (Fig. 4a), while Douglas-fir was limited to diameter classes less than 40 cm with the majority of trees less than 20 cm (Fig. 4a) when present. Current diameter distributions still contain trees within each of the diameter classes up to 60 cm, but with a substantial increase in density for both ponderosa pine and Douglas-fir, especially in the < 30 cm diameter classes (Fig. 4b). In addition, Rocky Mountain juniper contributed to

increased density in the 20 cm and smaller sized classes (Fig. 4b).

Patterns of increased density were also evident in the tree establishment record for current live trees (Fig. 4c). Tree establishment accelerated in the 1860s and peaked around the 1900–1920s. Establishment slowed after the 1920s, but was similar in magnitude to establishment rates in the early 1800s. Furthermore, Douglas-fir was establishing at higher rates than ponderosa pine during the mid to late 20th century.

3.2. Upper montane forests

Similar to lower montane forests, upper montane forests saw a significant increase in basal area and density coupled with a decrease in QMD, although changes were greatest in the lower montane zone. Current forest density is ~2.4 times greater than historical ($p < 0.0001$), basal area has nearly doubled ($p < 0.0001$) and QMD is 17% smaller ($p < 0.0001$) when compared to the 1860 forest condition (Table 2). Historically, average basal area was 9.5 m² ha⁻¹ with an average QMD of 29.4 cm compared to the current basal area of 17.2 m² ha⁻¹ with a QMD of 25.2 cm. Average forest density increased from 163 trees ha⁻¹ to 389 trees ha⁻¹ (Table 2).

Similar to the lower montane forest zone, both historical and contemporary upper montane forest conditions were highly variable (Fig. 5a–d). Generally, both historical basal area and density distributions were left-skewed, while current distributions were concentrated towards the middle and to the right (Fig. 5a and b). While there was overlap of historical and current basal area and density, 80% of plots had historical basal areas less than 14 m² ha⁻¹ compared to 35% of current plots, and 80% of plots had historical densities below 256 trees ha⁻¹ compared to 30 to 35% of current plots. Historical and current QMD values overlapped over much of their distribution (Fig. 5c), but over 10% of plots had historical QMDs that exceeded 40 cm while current forests had < 5%. Moreover, 50 percent of historical QMD were above 30 cm, whereas only 20% are currently above 30 cm. Like the lower montane, there has been a shift in the dominant structural stages (Fig. 5d). Historical upper montane forests were dominated by open-canopied forest structures (structural stages 3A and 4A), while current forests contain a greater abundance of closed-canopied structures (Fig. 5d).

As in the lower montane forest zone, forest composition and tree size distributions have also shifted in the upper montane zone. Although current forest structure was still dominated by ponderosa pine, the contribution of Douglas-fir to basal area and density increased significantly ($p < 0.0001$) since 1860 (Table 3). Historically, ponderosa pine was found in each diameter class up to 80 cm, although the majority of trees were ≤ 50 cm (Fig. 6a). Historically, Douglas-fir was concentrated in diameter classes ≤ 50 cm with the majority ≤ 20 cm (Fig. 6a). The current forest has a substantial increase in density for ponderosa pine and Douglas-fir, especially in diameter classes ≤ 30 cm (Fig. 6b). In addition, limber pine, lodgepole pine, and quaking aspen also contributed to increased density in size classes ≤ 30 cm (Fig. 6b). In contrast to the lower montane zone, the upper montane zone had a muted peak in establishment between 1880 and 1920, and more gradual 20th century recruitment (Fig. 6c). Over the 20th century there was a gradual increase in establishment of species other than ponderosa pine.

4. Discussion

This spatially extensive dendrochronological study demonstrated that both lower and upper montane ponderosa pine dominated forests of the Front Range experienced substantial changes in forest structure since ca. 1860. Across the lower montane zone, basal area increased 179% and density increased 352%, while QMD decreased 8%. Although the magnitude of the changes in the upper montane zone were less than the lower montane zone, there were still substantial increases of in

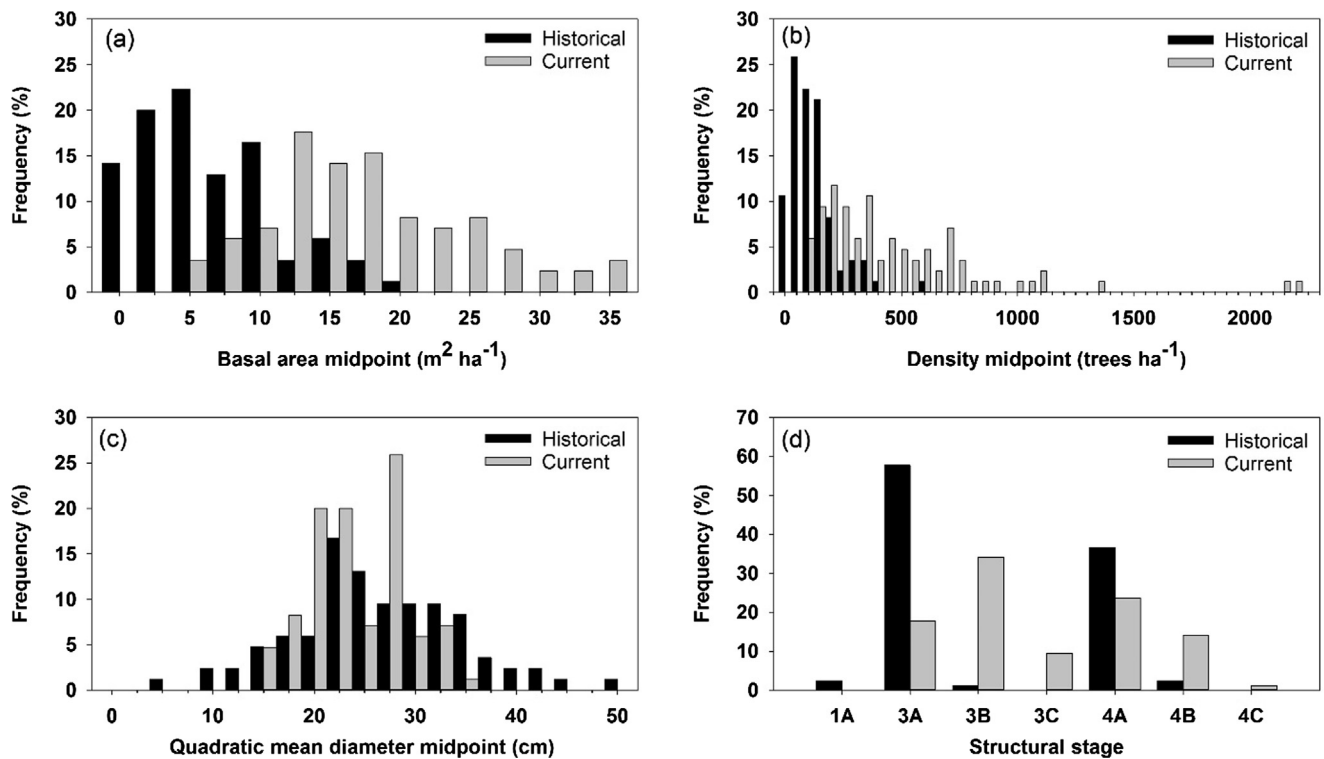


Fig. 3. Frequency distribution of historical 1860 (black bars) and current (gray bars) basal area (a), tree density (b), quadratic mean diameter (c), and structural stage (d) of lower montane forests of the Front Range.

basal area (139%) and in density (81%), and a 14% decrease in QMD. While this trend of increased density, smaller tree diameters, and increased presence of shade tolerant species in fire-adapted forests is prevalent across the Western U.S. (Fulé et al., 1997; Hessburg et al., 2000; Brown and Cook, 2006; Battaglia and Shepperd, 2007; Fulé et al., 2009; Haggmann et al., 2014; Stephens et al., 2016; Rodman et al., 2016; Johnston, 2017), differences in quantitative values of historical stand structure across the wide biophysical settings and geographic range of ponderosa pine exist (Merschel et al., 2014; Rodman et al., 2017). For example, many historical forest reconstructions were done in more productive regions than the Front Range. Historical ponderosa pine diameters from the Cascade Range (Harrod et al., 1999; Haggmann et al., 2013, 2014, 2017; Merschel et al., 2014), the western Blue Mountains (Churchill et al., 2017), the Sierra Nevada (Collins et al., 2011; Lydersen et al., 2013), and the Southwest (Sánchez Meador et al., 2010; Sánchez Meador and Moore, 2011) commonly exceed 50 cm. More productive regions had historically higher basal area ranges and often lower tree densities (Reynolds et al., 2013; Churchill et al., 2017) than

we observed in the Front Range. These inter-regional differences highlight the importance of considering the local ecology and abiotic conditions when developing restoration guidelines and silvicultural prescriptions.

Reconstructions of Front Range historical forest structure are limited. Williams and Baker (2012) used 1880s General Land Office (GLO) survey records to reconstruct a regional data set of trees > 10 cm DBH in the lower and upper montane forest zones of the northern Colorado Front Range. They reported mean densities of 217 trees ha⁻¹, with 40% of plots having densities < 100 trees ha⁻¹, 44.6% having > 200 trees ha⁻¹, and 37.5% having > 250 trees ha⁻¹. In comparison, our study, which reconstructed stands for trees ≥ 4 cm DBH, showed a lower mean density of 97 trees ha⁻¹ in the lower montane zone and 163 trees ha⁻¹ in the upper montane zone. Our study demonstrated ~50% and 45% of stands in the lower and upper montane forest zones had densities < 100 trees ha⁻¹. In contrast, the percentages for the denser stands in Williams and Baker (2012) far exceed our estimations. In our study, only 15 and 10% of lower montane and 30 and 20% of upper

Table 3

Least square means and 95% confidence intervals of species composition by basal area and trees per hectare for lower and upper montane historical and current ponderosa pine dominated forests along the Front Range.

Lower montane (n = 85)						
	% Basal area			% TPH		
	Ponderosa pine	Douglas-fir	Other	Ponderosa pine	Douglas-fir	Other
Historical	88.2 (82.1, 92.5)	6.0 (3.8, 9.4)	1.4 (0.9, 2.3)	86.9 (78.4, 92.3)	7.7 (4.2, 13.5)	1.5 (0.9, 2.7)
Current	80.2 (72.6, 86.1)	14.9 (10.2, 21.4)	1.8 (1.1, 2.8)	74.6 (62.5, 83.8)	16.5 (9.6, 26.9)	6.0 (4.1, 8.6)
Upper montane (n = 85)						
	% Basal area			% TPH		
	Ponderosa pine	Douglas-fir	Other	Ponderosa pine	Douglas-fir	Other
Historical	83.1 (74.6, 89.2)	8.4 (4.7, 14.6)	8.1 (5.5, 11.8)	77.5 (67.0, 85.4)	13.6 (8.8, 20.5)	8.5 (0.3, 75.4)
Current	73.6 (62.8, 82.1)	15.9 (9.6, 25.1)	8.7 (6.0, 12.5)	62.7 (50.5, 73.4)	19.6 (13.2, 28.2)	16.5 (1.4, 73.2)

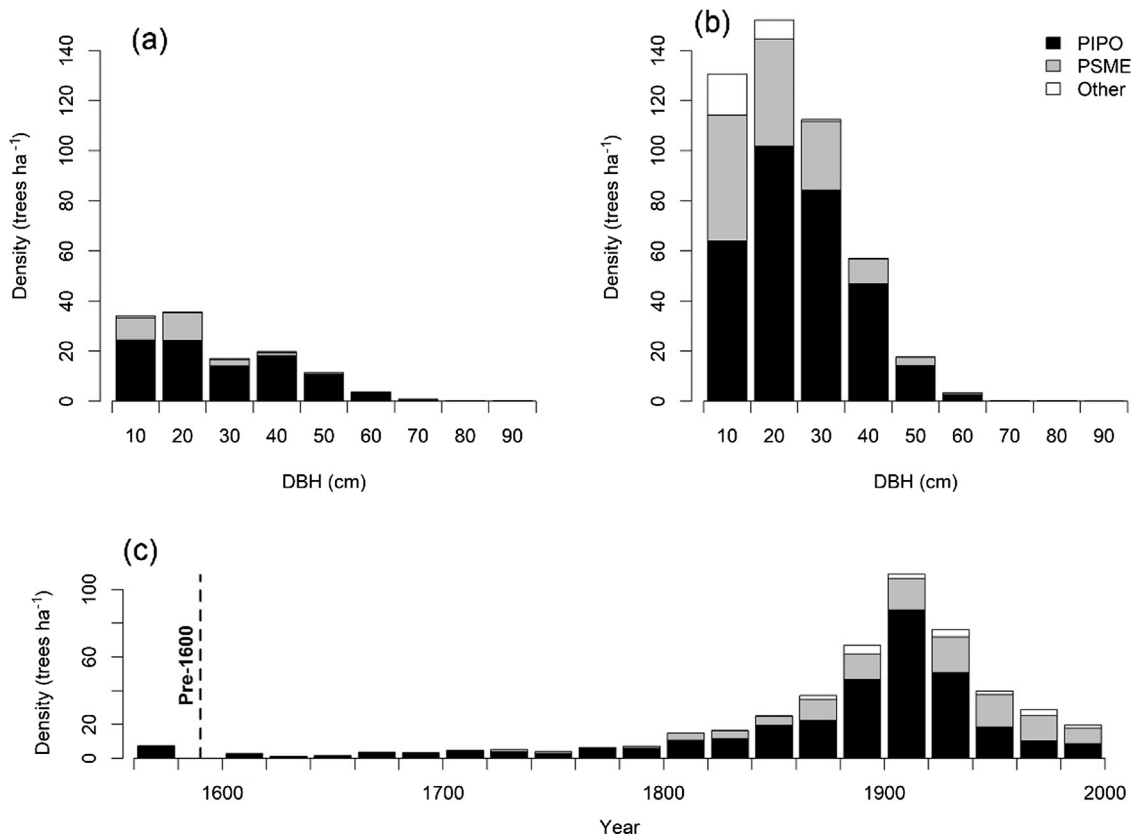


Fig. 4. Average diameter distribution of historical (a) and current (b) lower montane forests along the Front Range for ponderosa pine (PIPO; black bars), Douglas-fir (PSME; gray bars), and other species (Other; white bars; primarily Rocky Mountain juniper). (c) Average tree establishment over the past several centuries. Data are shown for ponderosa pine (PIPO; black bars), Douglas-fir (PSME; gray bars), and other species (Other; white bars; primarily Rocky Mountain juniper). Data in (b) utilizes all the reconstruction data while data in (c) utilizes only the dated reconstruction data.

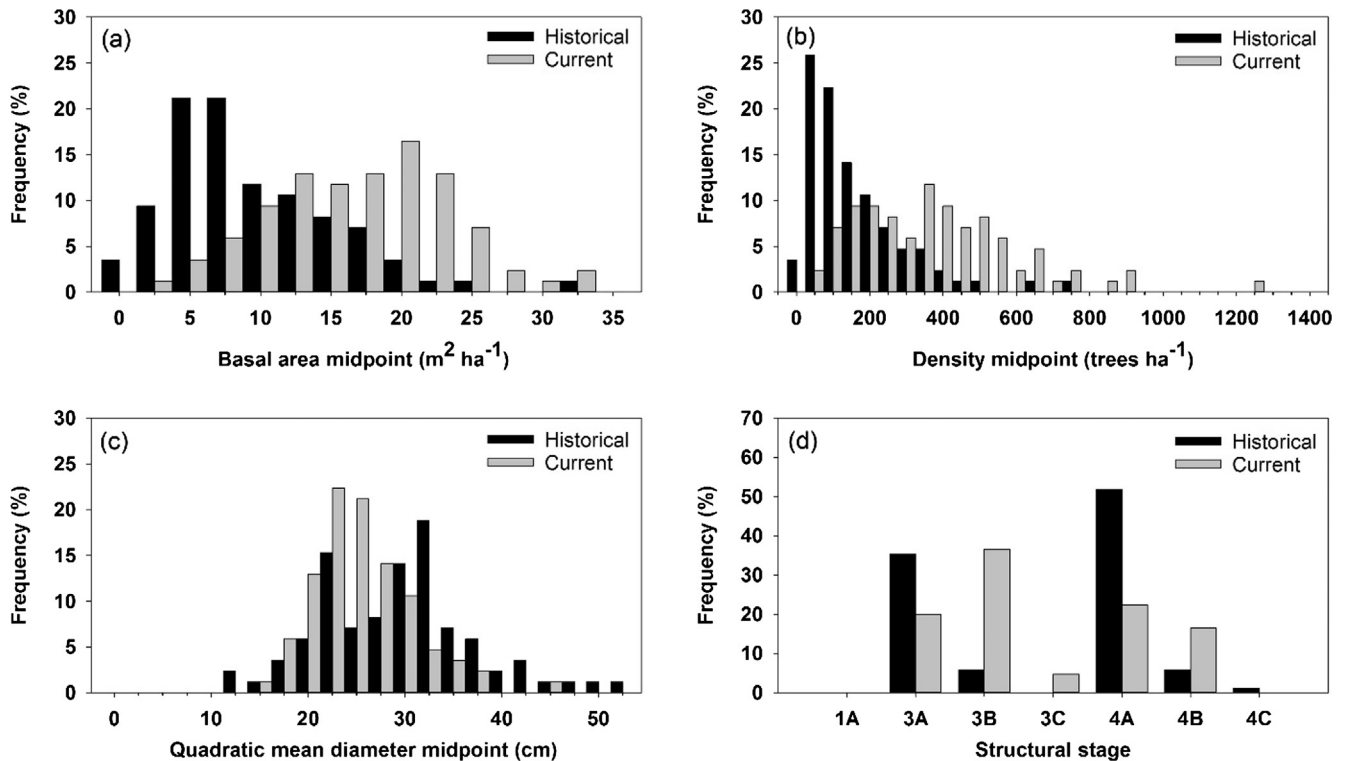


Fig. 5. Frequency distribution of historical 1860 (black bars) and current (gray bars) basal area (a), tree density (b), quadratic mean diameter (c), and structural stage (d) of upper montane forests of the Front Range.

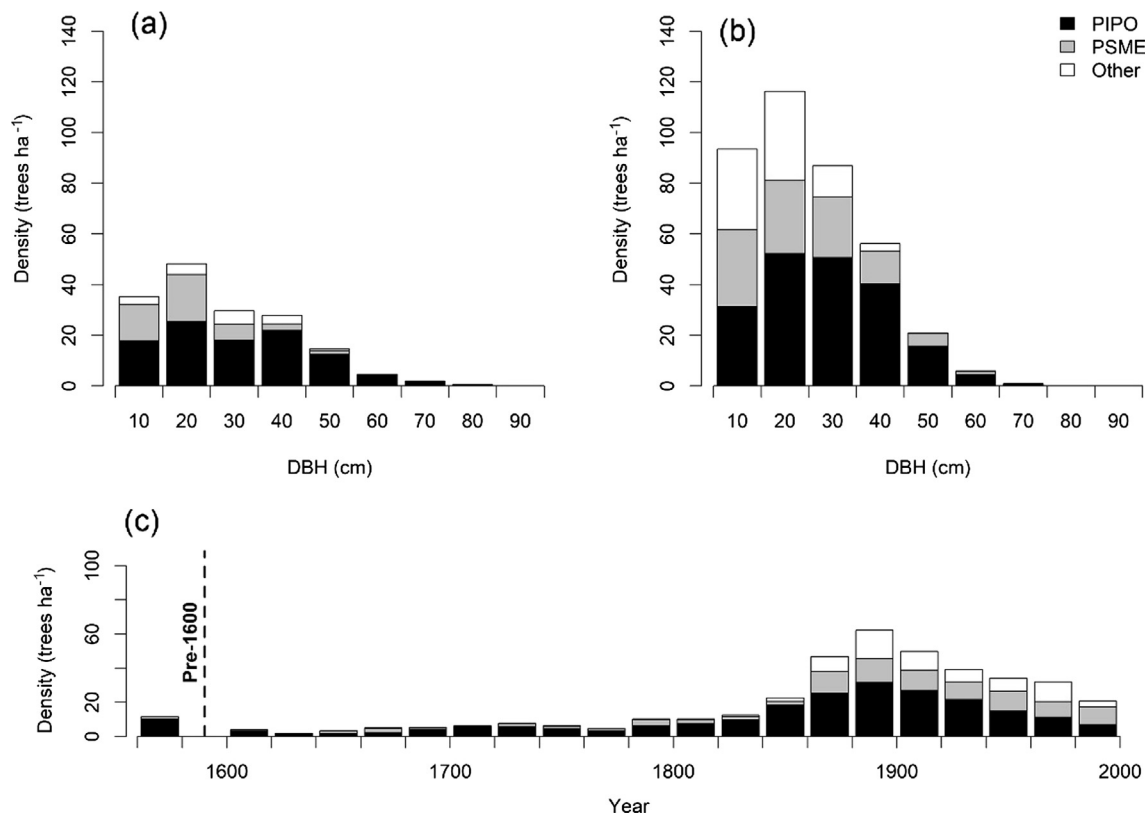


Fig. 6. Diameter distribution of historical (a) and current (b) upper montane forests along the Front Range for ponderosa pine (PIPO; black bars), Douglas-fir (PSME; gray bars), and other species (Other; white bars; primarily lodgepole pine). (c) Average tree establishment over the past several centuries. Data are shown for ponderosa pine (PIPO; black bars), Douglas-fir (PSME; gray bars), and other species (Other; white bars; primarily lodgepole pine). Data in (b) utilizes all the reconstruction data while data in (c) utilizes only the dated reconstruction data.

montane forest stands exceeded > 200 trees ha^{-1} and > 250 trees ha^{-1} , respectively. While our reconstruction dates differ (1860 here, and 1880s in Williams and Baker, 2012), it is unlikely that ~ 20 years of establishment and growth explain the discrepancies. Furthermore, our estimations included trees 4–10 cm DBH whereas Williams and Baker (2012) did not consider trees < 10 cm DBH. Similar overestimations using GLO data (Baker, 2012; Baker, 2014) have also been observed for reconstructed forests across the west (Fulé et al., 2013) such as ponderosa pine and mixed conifer forests of south-central Oregon (Hagmann et al., 2013; Hagmann et al., 2017), mixed conifer forests on the eastern slopes of the Oregon Cascade Range (Hagmann et al., 2014; Merschel et al., 2014), and ponderosa pine and mixed conifer forests of the California Sierra Nevada (Collins et al., 2011; Collins et al., 2015; Stephens et al., 2015; Levine et al., 2017). Furthermore, Levine et al. (2017) found an error in the method of density calculation by Williams and Baker (2012) that likely explains some of the discrepancy between Williams and Baker (2012) and other estimates and tree ring-based reconstructions, with the error reported by Levine et al. (2017) to be on the order of twice the true densities, roughly what we found with our tree-ring based reconstruction method.

Most dendrochronological work on the Front Range has explored tree establishment in relation to climate, fire history, or other disturbances, and has focused on areas with limited harvesting activity in the northern portion of the Front Range. There is agreement with our findings that lower montane forests (< 2200 m) have substantially increased in density since the late 19th century (Veblen and Lorenz, 1986; Mast et al., 1998; Sherriff and Veblen, 2006; Sherriff et al., 2014; Brown et al., 2015). Historically, these forests were dominated by frequent (8–20 years average intervals), low-severity surface fires with small patches of overstory mortality (Sherriff and Veblen, 2006; Sherriff et al., 2014; Brown et al., 2015) that acted as a density-independent

control on tree recruitment by killing many of the fire-susceptible seedlings and saplings (Brown and Wu, 2005; Battaglia et al., 2009), maintaining mostly low density, highly age diverse, multi-cohort forests. After Euro-American settlement along the Colorado Front Range (c. 1859; Buchholtz, 1983), a general decrease in episodic fires was observed (Veblen et al., 2000; Sherriff and Veblen, 2006; Brown et al., 2015). This cessation of fire, along with favorable climatic conditions for regeneration and establishment in the late 1800s (Mast et al., 1998; Brown and Wu, 2005; Veblen and Donnegan, 2006) and widespread livestock grazing (Jack, 1900; Ingwall, 1923; Veblen and Donnegan, 2006), allowed for substantial tree establishment (Sherriff and Veblen, 2006; Brown et al., 2015).

In contrast to more localized studies along the northern Front Range that suggest the upper montane zone is less departed, or that currently high densities are accommodated within a functioning mixed-severity fire regime (Sherriff and Veblen, 2006; Schoennagel et al., 2011; Sherriff et al., 2014), we found that forest density in upper montane forests significantly increased since 1860 across the entire Front Range. Some have attributed the current high densities in the upper montane zone to establishment pulses following high-severity fire (Sherriff and Veblen, 2006; Sherriff et al., 2014; Schoennagel et al., 2011), yet early harvesting, grazing, and later fire suppression were also factors that shaped these forests, for which scientific control is difficult. Our 1860 reconstruction date occurs after the widespread fires that burned around 1851 in the southern Front Range (Brown et al., 1999) and 1859–1860 in the northern Front Range (Sherriff and Veblen 2006; Schoennagel et al., 2011; Sherriff et al., 2014), some of which created fairly large patches (10–100 ha) of tree mortality (Brown et al., 1999). Brown et al. (1999) found direct evidence of patchy stand-replacing fire effects, with logs killed by the 1851 fire in treeless openings. In contrast, we did not observe any complete stand-replacing effects of these

fires in our data. While it is difficult to fully reconstruct forest structure further back in time to test the representativeness of the reconstruction date, our study spanned over 200 miles north to south and clearly captured regional scale patterns that are larger than any single disturbance event. Most upper montane forests of the Front Range have missed multiple fire cycles, based on a mean fire return interval of ~20–60 years (Brown et al., 1999; Veblen et al., 2000; Donnegan et al., 2001; Veblen and Donnegan, 2006). Thus, it is highly likely that much of the modern increase in density is due to fire exclusion and fire suppression as has been seen throughout much of the range of ponderosa pine in western North America (e.g., Covington and Moore, 1994; Belsky and Blumenthal, 1997; Hessburg and Agee, 2003; Hessburg et al., 2005; Reynolds et al., 2013; Addington et al., 2018). Upper montane forests experienced a smaller recruitment pulse around the turn of the 20th century compared to lower montane forests and more sustained tree recruitment through recent decades (Figs. 4c and 6c), suggesting that current densities are not just legacies of earlier fires.

This study also demonstrated a shift in the relative dominance of ponderosa pine and Douglas-fir since 1860, which is further evidence of fire exclusion via regeneration and release of a more shade-tolerant conifer. Current montane forests included proportionally more Douglas-fir at the expense of ponderosa pine. Examination of tree establishment data for the entire montane zone showed pulsed recruitment around the turn of the 20th century, dominated by ponderosa pine in the lower montane, but with a more even mix between ponderosa pine, Douglas-fir, and other species in the upper montane. The turn of the century pulse had a strong influence on current forest composition, but establishment during more recent decades included proportionally more Douglas-fir and species other than ponderosa pine, suggesting that denser forests are favoring the more shade tolerant Douglas-fir over the shade intolerant ponderosa pine. An increase in ponderosa pine establishment was also reported in a study of lower montane forests in northern Colorado (Sherriff and Veblen, 2006), however, that study did not find a difference in the amount of Douglas-fir establishment since 1860. Sherriff and Veblen (2006) reported that tree establishment data in their plots did not support the hypothesis that Douglas-fir had invaded previously pure stands of ponderosa pine in either the lower or upper montane forests. Our data did not follow that same pattern. Across our study area, 19% of lower and 32% of upper montane forest plots showed that Douglas-fir established where there had been no Douglas-fir in 1860.

Much of the data for the lower and upper montane forests indicated a substantial pulse in tree establishment around the period of settlement (~1860–1920), before active fire suppression began in the 1920s (Mast et al., 1998; Kaufmann et al., 2000; Ehle and Baker, 2003; Sherriff and Veblen, 2006; Schoennagel et al., 2011). Our establishment data also captured a major pulse of tree recruitment, but in contrast to some studies (Mast et al., 1998; Ehle and Baker, 2003; Sherriff and Veblen, 2006; Schoennagel et al., 2011), we saw continued tree establishment during the fire suppression era after 1920, similar to Kaufmann et al. (2000). Continuous recruitment throughout the 20th century means these forests were still uneven-aged, just with higher densities. During that same period, we observed considerable Douglas-fir establishment. This was not the case for another study in the northern Front Range (Sherriff and Veblen, 2006); however, Kaufmann et al. (2000) did observe Douglas-fir ingrowth in their southern Front Range study.

In line with the establishment data, we observed a substantial increase in density for both ponderosa pine and Douglas-fir in the smaller size classes. This recruitment of smaller diameter trees reduced quadratic mean diameters. While the decrease in quadratic mean diameter was small, further examination of individual plot diameter distributions revealed substantial variation in trends through time, including stands that had relatively small trees in 1860, but have now grown into larger diameter classes. These trees were likely too small to harvest at the

beginning of the 20th century. Nevertheless, while few trees on the historical landscape were larger than 50–60 cm, most of those were lost to logging.

The differences between our observed tree recruitment and density increases and those observed in more localized studies may be due to location of sampling relative to past harvesting activities. In contrast to Sherriff and Veblen (2006) and Schoennagel et al. (2011), we did not avoid previously harvested areas. Over 97% of our randomly selected plots contained evidence of past harvest. Late 19th and early 20th century harvests removed many of the larger diameter trees, providing stumps that could be used to reconstruct the pre-harvest forest. Harvesting can create soil conditions (i.e., bare mineral soil) that promote the establishment of ponderosa pine and Douglas-fir, especially with mid to late 20th century forest harvesting practices. Although harvesting would also create an increase in light available for the understory plant community to develop and compete with the tree regeneration, livestock grazing often reduced understory competition for moisture and nutrients. In contrast, tree recruitment historically occurred within brief temporal windows following fires or other disturbances, many of which removed little of the overstory. Without fire to thin the regeneration throughout the 20th century, both unharvested and harvested areas increased in density and abundance of ponderosa pine, and especially the more fire-sensitive Douglas-fir. Continued harvesting activities throughout the Front Range during the 20th century allowed further opportunities for regeneration to establish. Similar results have been reported in the southern Front Range (Kaufmann et al., 2000), the northern Rockies (Naficy et al., 2010), and central Oregon (Merschel et al., 2014). Since much of the Front Range was impacted by human activities through the late 1800s and early 1900s (e.g., Veblen and Lorenz, 1991) stands that were harvested likely represent the broader patterns in landscape conditions.

Our study demonstrated that increased tree establishment after 1860 led to increased canopy cover (i.e., relative density) in the lower montane forests. Based on our reconstructions, in 1860, the majority of forests were either habitat structural stage 3A or 4A, where canopy cover was < 40% (Vandendriesche 2013). Ingrowth of trees increased forest density and canopy cover to higher than 40% and in some cases 60%. Repeat photography in northern Colorado shows that tree cover has increased in many lower montane forests (Veblen and Lorenz, 1991; Platt and Schoennagel, 2009). In a study examining changes in canopy cover with aerial photographs taken in 1938 and 1999, Platt and Schoennagel (2009) found a 13% increase in canopy cover for elevations ranging from 1737 to 2084 m and a 5% increase from 2085 to 2431 m in the northern Colorado Front Range. Based on our and others data on timing of tree recruitment, by 1938 forests were probably already denser than those pre-settlement. Kaufmann et al. (2001) estimated that historically over 90% of the Cheesman landscape in the southern Front Range had < 30% canopy cover, compared to 47 to 55% of the landscape in 1996. Unfortunately, current canopy cover of the Cheesman landscape is non-existent because it is in the center of a > 20,000 ha treeless patch created by the 2002 Hayman Fire (Fornwalt et al., 2016). Since we avoided sampling in known post-settlement wildfire areas, we do not record such major shifts in canopy cover.

In contrast to the lower montane, Platt and Schoennagel (2009) did not find an increase in tree cover between 1938 and 1999 at elevations exceeding 2432 m. However, our data suggest that by 1938 substantial numbers of trees had already established in the upper montane zone after fire exclusion had begun, and that these forests were likely not reflective of pre-settlement patterns in forest structure. Furthermore, a recent study (Dickinson, 2014) mapped current forest cover and evidence of 1860 forest cover along 20 1-km long transects across the upper montane zone of the Front Range. That study reported an increase in mean forest canopy cover from 57% in 1860 to 83% currently. In addition, Dickinson (2014) reported that any location on the landscape is 3.7 times more likely to be forested currently in comparison

with 1860. The majority of the increased cover occurred through the loss of small (< 50 m in length) rather than large openings, indicating ingrowth of trees by seeding over short dispersal distances (Dickinson, 2014). Sherriff and Veblen (2006) also suggested that most of the area had already infilled by 1938 as indicated by their establishment data, further suggesting that the results of Platt and Schoennagel (2009) do not reflect changes between pre-settlement era historical and current upper montane zone forests.

Determination of departure from HRV involves some evaluation of how changes in forest structure translate to changes in ecosystem function. Although we observed high variability in historical and current forest structure, the mean trajectory toward higher basal area, density, and Douglas-fir composition can alter fire behavior. For example, increases in forest density have undoubtedly resulted in increased canopy bulk density and continuity, decreased canopy base height, and changes in fuelbed composition, similar to results found in other studies (e.g. Fulé et al., 2012). Numerous studies have demonstrated that these changes in the arrangement and composition of fuels can alter patterns of fire behavior both spatially and temporally (Fulé et al., 2002; Van de Water and North, 2011; Hoffman et al., 2015; Parsons et al., 2017; Ziegler et al., 2017). The observed increases in density and basal area, and decrease in quadratic mean diameter, suggest modern forests are more likely to promote crown fire initiation and spread (Hessburg et al., 2005; Roccaforte et al., 2008; Fornwalt et al., 2016; Ziegler et al., 2017). It is clear that historically lower montane forests experienced low-severity fire (Sherriff and Veblen, 2007; Sherriff et al., 2014; Brown et al., 2015) and upper montane forests experienced mixed-severity fire, with patches (on the order of 10–100 ha; e.g., Brown et al., 1999) of high to complete tree mortality. This historical fire regime would have likely created a mosaic of stands with varying structure that would continue to promote both active and passive tree torching on a small scale (< 10 ha; Sherriff et al., 2014). This is in strong contrast to the extremely large (1000–10,000 ha) areas of complete stand-replacing patches created by recent fires (e.g., Graham, 2003; Fulé et al., 2013; Fornwalt et al., 2016). Furthermore, recent wildfires in the Front Range demonstrate that current forest conditions are neither resistant nor resilient to wildfire, with sparse to non-existent regeneration in large high severity patches (Chambers et al., 2016; Rother and Veblen, 2016).

4.1. Limitations

As with any historical reconstruction method, we are limited by the preserved evidence of past historical structures (Brown et al., 2015). We sought to minimize this uncertainty by avoiding places with documented post-settlement fires. Similar reconstruction techniques in Arizona were very effective at detecting historical trees from live and remnant tree evidence (Huffman et al., 2001). Still, we must acknowledge the potential for loss of evidence due to rot and decay; our methods are most prone to missing small trees of species with decay-prone wood that died early in the post-settlement period. Given the low historical forest densities observed in this study, the likelihood that mortality from insect and disease was high among small size classes of any conifer species is quite low. We note that quaking aspen was almost entirely absent from our historical reconstructions; only four quaking aspen were identified as part of the 1860 forest and they were all live trees that established in the prior decade. The absence of aspen from our historical reconstructions may be due to its decay-prone wood and our consistent slope and landform sampling criteria, which precluded sampling in the narrow riparian zones where aspen is most common. Considering the high value of aspen for wildlife habitat and as a natural fuel break, restoration should enhance these poorly represented features on the landscape. Although conifer species are more decay resistant than aspen, it is possible that inter-species differences in decay could bias our results towards decay-resistant species (i.e., ponderosa pine). Our methods for reconstructing historical tree diameters varied

from precise measurements of crossdated cores and cross-sections to approximations using models to shrink or grow the measured trees or remnant materials to the 1860 reconstruction date. Due to the approximations necessary to make use of an imperfect record, there is more uncertainty in metrics that depend on reconstructed tree diameters. In particular, our method to “grow” remnants that had eroded to growth rings dated before the 1860 reconstruction date comes with a moderate degree of uncertainty. Many remnants were inventoried in the field that were too rotten to extract a sound sample, or that were sampled, but could not be crossdated in the lab. Our methods to shrink any undated remnants with sapwood or bark present, and to grow any eroded remnants, were based on our best assessment of the transition rates between these conditions and the timing of past harvests. Thus, data we present here should be considered as general trends in historical forest structures, and not as absolute values.

4.2. Management implications

This study demonstrates that a substantial shift in montane forest structure and composition has occurred along the Front Range since the period of Euro-American settlement. These widespread changes have the potential to promote undesirable fire behavior and effects (Ziegler et al., 2017). Restoration activities that utilize elements and patterns of the historical forest structure are important for increasing the resilience of these forests. When developing restoration prescriptions, it is important to recognize the variability in forest structure and species composition that existed under an intact fire regime. This variability was a function of both biophysical drivers and past disturbance history. It is obvious that restoration activities will reduce density, however, applying uniform densities across all stands within a project unit is not justified nor possible to implement. Rather, restoration should focus on and incorporate variability in density and species composition in relation to moisture gradients and other abiotic factors to provide the diversity identified in the desired conditions outlined in local restoration guidelines (Dickinson et al., 2014; Addington et al., 2018). Furthermore, consideration of scale (i.e., stand to project unit to landscape) and implementation of different prescriptions can help avoid the same prescription over large areas (i.e., homogeneity of heterogeneity).

Recent Front Range forest restoration projects include objectives to both reduce fire hazard and move forest structure towards historical conditions (Underhill et al., 2014; Briggs et al., 2017; Ziegler et al., 2017; Cannon et al., in press). While restoring forest structure is important, future entries with prescribed fire and/or mechanical treatments is helpful to maintaining more fire resilient forest structures (Battaglia et al., 2008; Fulé et al., 2012; Stevens et al., 2014) that can better accommodate future wildfire and minimize the effects of other disturbances such as insect outbreaks. Strategic placement of restoration treatments can foster a landscape that is better adapted to wildfire without uncharacteristically-large patches of tree mortality. This is also critical to improving human safety and protecting property and infrastructure (e.g., reservoirs) in the wildland-urban interface (Safford et al., 2009; Kennedy and Johnson, 2014; Jones et al., 2017).

As we move forward under an uncertain climate, it is critical to incorporate knowledge from research and monitoring into management plans to improve the resilience of forested ecosystems, especially with changing disturbance and climatic regimes (Nagel et al., 2017; Schoennagel et al., 2017). Over the past several decades, the western U.S. has observed increased temperature (McGuire et al., 2012; Lukas et al., 2014), increased wildfire activity (Dennison et al., 2014; Westerling, 2016), and expansion of the wildland urban interface (Theobald and Romme, 2007; Martinuzzi et al., 2015). Future projections (Theobald and Romme, 2007; Lukas et al., 2014; Abatzoglou and Williams, 2016) indicate that these increases will continue and result in longer fire seasons, increased fire frequency, negative impacts to infrastructure, and decreased forest resiliency (Liu et al., 2013; Rocca et al., 2014). Assessing departure in forest structure from HRV is an

important first step in identifying areas that have become ecologically vulnerable and it provides insight into adaptive strategies for enhancing resilience to changing disturbance regimes (Keane et al., 2009; Johnston et al. 2016; Schoennagel et al., 2017). Incorporating adaptation strategies that consider tree phenotypical functional traits (Strahan et al., 2016; Laughlin et al., 2017), such as bark thickness, can improve survival to more frequent fires. Likewise, managing stands at lower densities can bolster resistance and resilience to drought conditions (Bottero et al., 2017; Gleason et al., 2017). Consideration of changes in climatic factors that foster the ability for a specific tree species to survive and reproduce can provide insight into which species to favor or remove (Nagel et al., 2017). With forward-thinking restoration strategies, managers can promote forest structures that are adapted to local climate and fire regimes, improve wildfire response options (Thompson et al., 2016), and conserve native species' habitats (Hessburg et al., 2016; Schoennagel et al., 2017).

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2018.04.010>.

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