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Historical (1860) forest structure in ponderosa pine forests of the northern Front Range, Colorado

Peter M. Brown, Michael A. Battaglia, Paula J. Fornwalt, Benjamin Gannon, Laurie S. Huckaby, Chad Julian, and Antony S. Cheng

Abstract: Management of many dry conifer forests in western North America is focused on promoting resilience to future wildfires, climate change, and land use impacts through restoration of historical patterns of forest structure and disturbance processes. Historical structural data provide models for past resilient conditions that inform the design of silvicultural treatments and help to assess the success of treatments at achieving desired conditions. We used dendrochronological data to reconstruct nonspatial and spatial forest structure at 1860 in fourteen 0.5 ha plots in lower elevation (~1900–2100 m) ponderosa pine (*Pinus ponderosa* Douglas ex P. Lawson & C. Lawson) forests across two study areas in northern Colorado. Fires recorded by trees in two or more plots from 1667 to 1859 occurred, on average, every 8–15 years depending on scale of analysis. The last fire recorded in two or more plots occurred in 1859. Reconstructed 1860 stand structures were very diverse, with tree densities ranging from 0 to 320 trees·ha⁻¹, basal areas ranging from 0.0 to 17.1 m²·ha⁻¹, and quadratic mean diameters ranging from 0.0 to 57.5 cm. All trees in 1860 were ponderosa pine. Trees were significantly aggregated in 62% of plots in which spatial patterns could be estimated, with 10% to 90% of trees mainly occurring in groups of two to eight (maximum, 26). Current stands based on living trees with a diameter at breast height of ≥4 cm are more dense (range, 175–1010 trees·ha⁻¹) with generally increased basal areas (4.4 to 23.1 m²·ha⁻¹) and smaller trees (quadratic mean diameters ranging from 15.7 to 28.2 cm) and contain greater proportions of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and Rocky Mountain juniper (*Juniperus scopulorum* Sarg.). This is the first study to provide detailed quantitative metrics to guide restoration prescription development, implementation, and evaluation in these and similar ponderosa pine forests in northern Colorado.

Key words: ecological restoration, ponderosa pine, dendrochronology, stand structure, spatial pattern.

Résumé : L'aménagement de plusieurs forêts sèches de conifères dans l'ouest de l'Amérique du Nord vise surtout à favoriser la résilience face aux feux de forêt, au changement climatique et aux impacts de l'utilisation des terres dans l'avenir par la restauration de la structure et des processus de perturbation passés de la forêt. Les données historiques sur la structure fournissent des modèles des conditions passées de résilience qui contribuent à l'élaboration des traitements sylvicoles et aident à évaluer si les traitements réussissent à créer les conditions souhaitées. Nous avons utilisé des données dendrochronologiques pour reconstituer la structure spatiale et non spatiale de la forêt en 1860 dans 14 placettes échantillons de 0,5 ha dans les forêts de pin ponderosa (*Pinus ponderosa* Douglas ex Lawson & C. Lawson) situées à basse altitude (~1900–2100 m) dans deux aires d'étude du nord du Colorado. Les feux détectés chez les arbres dans deux placettes échantillons ou plus de 1667 à 1859 sont survenus en moyenne à tous les 8 ans à 15 ans selon l'échelle utilisée pour l'analyse. Le dernier feu détecté dans deux placettes échantillons ou plus est survenu en 1859. La structure reconstituée des peuplements de 1860 était très diversifiée : la densité des arbres variait de 0 à 320 tiges·ha⁻¹, la surface terrière de 0,0 à 17,1 m²·ha⁻¹ et le diamètre quadratique moyen (D_g) de 0,0 à 57,5 cm. Tous les arbres de 1860 étaient des pins ponderosa. Les arbres étaient significativement regroupés dans 73 % des placettes échantillons dans lesquelles les configurations spatiales pouvaient être estimées : 40 % à 93 % des arbres étaient en groupes d'au moins 2 à 25 arbres. Sur la base des arbres avec un diamètre à hauteur de poitrine ≥ 4 cm, les peuplements actuels sont plus denses (175 à 1010 tiges·ha⁻¹), ont une surface terrière plus élevée (4,4 à 23,1 m²·ha⁻¹) et de plus petites tiges (D_g = 15,7 à 28,2 cm); ils contiennent une plus grande proportion de douglas de Menzies (*Pseudotsuga menziesii* (Mirb.) Franco) et de génévrier saxicole (*Juniperus scopulorum* Sarg.). C'est la première étude qui fournit des mesures détaillées pour appuyer l'élaboration, la mise en œuvre et l'évaluation des prescriptions pour la restauration de ces forêts de pin ponderosa et d'autres forêts semblables dans le nord du Colorado. [Traduit par la Rédaction]

Mots-clés : restauration écologique, pin ponderosa, dendrochronologie, structure des peuplements, configuration spatiale.

1. Introduction

Forest management in many dry pine and mixed-conifer forests of western North America is increasingly focused on promoting ecological resilience through restoration of forest structural complexity and natural disturbance regimes, especially wildfire (Allen et al. 2002; Front Range Fuels Treatment Partnership (FRFTP) 2006; Noss et al. 2006; Reynolds et al. 2013). Ecological resilience is defined as the ability of an ecosystem to maintain characteristic structure and function over time, especially after disturbances (Walker et al. 2004). Resilience in these forests has been compro-

mised by over a century of fire exclusion in what were historically frequent-fire landscapes (Allen et al. 2002; FRFTP 2006; Noss et al. 2006). Cessation of largely low to moderate intensity fires and other land use impacts since Euro–American settlement beginning in the 1800s have promoted denser stands of younger and smaller trees, contributed to the homogenization of canopy structure across landscapes, and resulted in the loss of meadows, openings, and structural diversity (Allen et al. 2002; Larson and Churchill 2012; Reynolds et al. 2013; Dickinson 2014). Such conditions promote uncharacteristically extensive areas of severe crown fires by allowing fire to more readily transition from surface to aerial fuels and to burn more extensively across landscapes when weather conditions are conducive to extreme fire behavior.

Recognition of stand to landscape changes in forest structure has led to landscape-scale ecological restoration efforts in many areas (e.g., FRFTP 2006; Reynolds et al. 2013; Underhill et al. 2014). Restoration strategies often start with silvicultural treatments to restore historical ranges of variation (HRV) in forest structure, followed by restoration of more characteristic fire regimes (Keane et al. 2009). The concept behind this strategy is that historical structure was formed and maintained through time by natural disturbance processes — especially low to moderate severity fires — and demographic processes affected by climate variation and succession dynamics and through space by abiotic factors such as soils and physiographic variation (Larson and Churchill 2012). Site-appropriate quantitative data on the nonspatial (tree species composition, densities, and basal areas and individual-tree sizes and ages) and spatial (numbers and characteristics of tree groups) structure of historical forests provide insight into general ecological processes that affected these patterns, as well as site-specific models to develop operational objectives for silvicultural treatments (Fulé et al. 1997; Fulé 2008; Keane et al. 2009; Churchill et al 2013; Reynolds et al. 2013). Such data also help to evaluate the success of treatments intended to restore resilient forest conditions (Churchill et al. 2013; Reynolds et al. 2013). The use of HRV data to set specific targets for restoration can be debated in the light of current and future climate change and other human impacts (e.g., Fulé 2008). However, managers and ecologists have agreed that historical patterns are one means to develop a scientific basis to define more resilience conditions in many current forests with recent histories of fire exclusion and land use (Fulé 2008; Keane et al. 2009; Larson and Churchill 2012; Churchill et al. 2013; Reynolds et al. 2013; Underhill et al. 2014).

Forests dominated by ponderosa pine (*Pinus ponderosa* Douglas ex P. Lawson & C. Lawson) in the Front Range of Colorado have experienced a series of wildfires over the past two decades that were greater in terms of area of complete tree mortality than what probably occurred in historical fires (Graham 2003; FRFTP 2006; Graham et al. 2012). Although there is debate as to how much forest structure has changed in middle and upper elevation ponderosa pine and mixed-conifer forests of the Front Range (>~2100 m elevation; e.g., Sherriff et al. 2014), there is substantial agreement that lower elevation Front Range ponderosa pine forests (<~2100 m) are outside their HRV in terms of tree densities and landscape coverage of denser stands (Kaufmann et al. 2000; Brown et al. 2001; Veblen and Donnegan 2006; Sherriff and Veblen 2006, 2007; Sherriff et al. 2014). As in other areas of western North America, this recognition has led to landscape-scale restoration efforts (Brown et al. 2001; FRFTP 2006; Clement and Brown 2011; Dickinson 2014; Underhill et al. 2014). The principle goals of restoration are to mitigate wildfire hazard in the rapidly expanding wildland–urban interface of the Front Range and to increase the ecological resilience of these forests in the face of future wildfires and other natural disturbances, climate change, and land use impacts (FRFTP 2006).

Unlike other regions of extensive ponderosa pine forests such as the southwestern United States (e.g., Fulé et al. 1997; Abella and Denton 2009; Sánchez Meador et al. 2010; Reynolds et al. 2013),

quantitative data on historical forest structure are rare or nonexistent for the majority of Front Range forests (Clement and Brown 2011; Dickinson 2014). In this study, we reconstructed the forest structure across two study landscapes in lower elevation ponderosa pine forests in the northern Front Range. Our study was initiated in response to concerns from managers and stakeholders on the Front Range that broadscale, science-based restoration prescriptions based on HRV data were lacking for this region (Clement and Brown 2011). Specific objectives were to reconstruct historical nonspatial stand structures, including tree species composition, densities, basal areas, and size and age distributions, and spatial stand structures at the scale of the 0.5 ha plots, including the number and characteristics of tree groups and their spatial arrangement. We chose 1860 as the date to reconstruct historical forest conditions, as it both marks the beginning of intensive Euro–American settlement in the Front Range with attendant land use changes in Boulder County (e.g., Buchholtz 1983; Veblen and Lorenz 1991) and is the approximate earliest germination date (ca. 150 years ago) that we have confidence in finding evidence of the historical structure. Although caveats are necessary due to an attenuated record over time, reconstructions of stand and forest conditions across the two study landscapes are robust and can serve as useful models for the restoration of stand structures in these and comparable ponderosa pine ecosystems in northern Colorado and western North America.
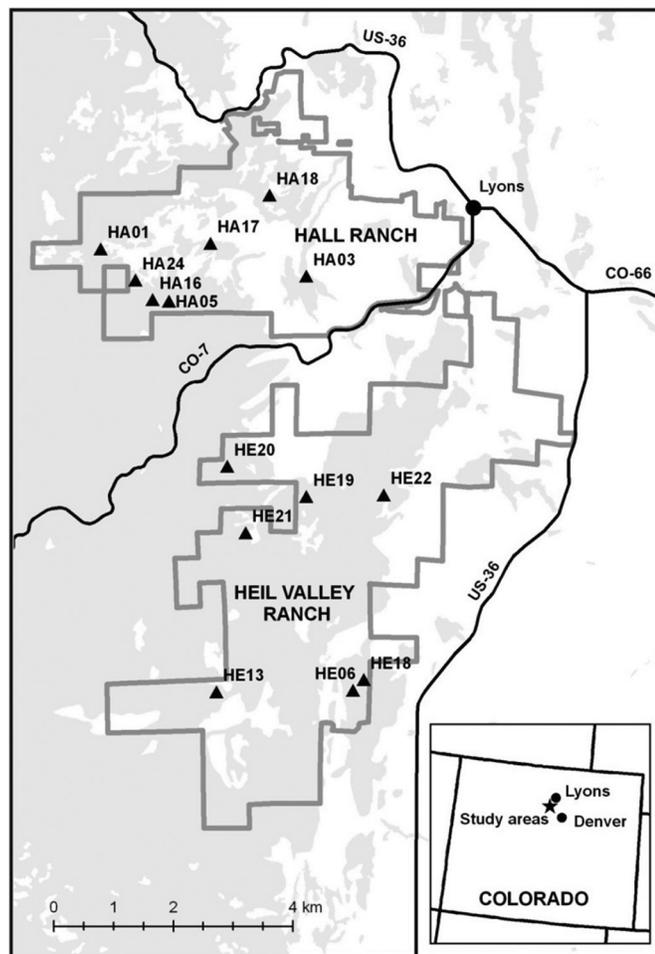
2. Methods

2.1. Study areas

The study was conducted at Hall Ranch (1298 ha in area) and Heil Valley Ranch (1993 ha in area) Open Spaces (Fig. 1), which have been owned and managed by the Boulder County Parks and Open Space (BCPOS) department since the early 1990s. Elevations range from ~1675 m to ~2300 m, increasing from east to west. The study areas comprise a series of sedimentary hogbacks and cuestas forming steep ridges and valleys along with broad undulating benches on the uplands. Soils are mainly coarse textured and shallow. Both areas contain forests and woodlands dominated by ponderosa pine, along with large areas of grasslands and shrublands (Fig. 1). Forest cover decreases to the east as elevation decreases into the shortgrass steppe of the eastern Colorado plains. Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) increases with elevation and in more moist, productive locations, especially north-facing slopes. Rocky Mountain juniper (*Juniperus scopulorum* Sarg.) is a minor component. Annual rainfall for the city of Boulder (elevation, 1660 m) located ~20 km south of the southern edge of the Heil Valley Ranch study area averaged 480 mm from 1893 to 2012. Mean annual maximum and minimum temperatures for the city of Boulder were 17.9 °C and 3.4 °C, respectively, for this same period.

Prior to Euro–American settlement, the northern Front Range was occupied by Ute tribes who dominated much of the central Rocky Mountains since at least the late 1600s. The region was intensively settled by Euro–Americans following a gold rush beginning in 1859 (Buchholtz 1983). Much of that movement centered on the cities of Boulder, Golden, and Denver just south of the study areas. Timber harvest, livestock grazing, and mining were ubiquitous and widespread starting in the early settlement period and continued through much of the twentieth century (Veblen and Lorenz 1991; Veblen and Donnegan 2006). Hall and Heil Valley Ranches were no exception, with histories of livestock grazing, logging, and stone quarrying dating from early Euro–American settlement until just prior to their acquisition by Boulder County. Today, the two areas are used primarily for recreation and secondarily for scientific research.

Fig. 1. Locations of plots in the Hall Ranch (HA) and Heil Valley Ranch (HE) Open Space study areas. Grey shading represents distribution of current forest. Black lines inside the map are highways.

2.2. Field methods

Field work was conducted in 2012 and 2013 in fourteen 0.5 ha (70.7 m × 70.7 m) plots (Fig. 1; Table 1). Plot locations were determined by first randomly locating potential plot locations in areas currently occupied by forest cover and that had not experienced a recent wildfire that would have resulted in destruction of evidence of presettlement trees. Forested areas were determined from available GIS layers for the area. Plots were sampled if the potential plot location met the following criteria: (*i*) the plot center was located or could be moved no more than ~50 m to encompass an area of 0.5 ha that was of relatively uniform slope and aspect, and (*ii*) the plot contained a mean slope steepness that was ≤40%. The latter criterion was necessary to characterize forest structure in areas amenable to mechanical restoration treatments. All final selected plots are located below 2100 m and fall into the Front Range lower montane forest zone (Veblen and Donnegan 2006). Plots are representative of the elevation ranges, forest types, and past management of this area in northern Colorado.

Our goal in each 0.5 ha plot was to characterize nonspatial and spatial stand structures in 1860 prior to intensive land use impacts. As we could not know a priori which trees were alive in 1860, we collected data from all trees in a plot that met one of the following three criteria: (*i*) a living tree with a diameter at breast height (DBH; 1.3 m) of ≥25 cm; (*ii*) a living tree with a DBH of <25 cm if it exhibited old-age morphological characteristics; or

Table 1. Plots sampled at Hall Ranch (HA) and Heil Valley Ranch (HE) Open Space study areas, arranged in order of descending elevation in each study area.

Plot	Elevation (m)	Aspect (°)	Slope (%)	TRMI	SI (m)
Hall Ranch					
HA24	2090	92	20	24	11.8
HA16	2008	60	21	43	12.5
HA05	1995	142	15	30	12.1
HA01	1986	270	18	29	11.6
HA17	1953	0	40	35	12.2
HA03	1907	180	40	22	8.0
HA18	1901	40	18	30	11.2
Heil Valley Ranch					
HE21	2092	72	18	36	15.7
HE19	2070	65	9	39	14.3
HE20	2036	340	36	31	12.5
HE13	1990	85	16	35	12.7
HE22	1960	80	12	32	10.8
HE18	1938	120	31	29	7.7
HE06	1905	260	26	27	11.8

Note: TRMI, topographic relative moisture index (Parker 1982), with higher TRMI values indicating relatively more mesic sites than lower TRMI values. SI, site index base 100 years (Mogren 1956), with higher SI values indicating relatively more productive stands than lower SI values.

(*iii*) a remnant tree (stump, log, or snag). We refer to any tree that met one of these criteria as "presettlement", although we knew that some were not. The 25 cm DBH cutoff for trees alive in 1860 was based on crossdated age and size data for ponderosa pine trees compiled from several previous studies in Front Range forests (Kaufmann et al. 2000; Huckaby et al. 2001; and other unpublished data). These previously collected age–size data documented that ≥95% of all trees >150 years old had a DBH that was ≥25 cm at the time of sampling (although many trees with a DBH ≥25 cm were <150 years old). Morphological characteristics used to identify older 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 and fewer fine branches, a flattened canopy indicating weakening apical dominance as the tree reaches its maximum height for the site, a damaged or dead top, a relatively tall crown base height, and evidence of fire scarring (Huckaby et al. 2003; Abella and Denton 2009). For living presettlement trees (criteria *i* and *ii*), we assigned a category of "young", "transitional", or "old" and recorded species and DBH. For remnant presettlement trees (criterion *iii*), we recorded species, status (stump, log, or snag), diameter at sample height (DSH; ~30 cm above ground level), and whether the tree had bark, sapwood, or heartwood only (eroded). Heartwood is very distinct and persistent in ponderosa pine because of resin deposition, which slows decomposition rates (e.g., Grier and Waring 1974; Fulé et al. 1997). Many of the sampled remnants were eroded stumps for which we were not able to measure the DBH.

We next established four 500 m² circular subplots in the center of each quadrant (defined by cardinal directions) of the main 0.5 ha plot. We had five goals in each subplot: (*i*) for the subplot to serve as a reference point to measure distance and azimuth to each presettlement tree and remnant; (*ii*) to collect increment cores and cross sections from all subplot presettlement trees to characterize tree ages and to refine age, size, and morphology relationships of living presettlement trees over the entire plot; (*iii*) to measure DSH in addition to DBH on living presettlement trees to develop plot-level DSH to DBH regressions with which to estimate DBH for remnant trees; (*iv*) to characterize species, age, and density of "postsettlement" living trees that were ≥4 cm to <25 cm DBH and without old-age morphological characteristics (i.e., trees that did not meet either criteria *i* or *ii* above for a presettlement tree); and (*v*) to determine the height of two domi-

nant living presettlement trees in each subplot (if present) for esti-
mation of site indices (SI; Mogren 1956). For goal *i*, increment cores
were collected from all living presettlement trees and cross sec-
tions were cut with a chainsaw from all remnant trees at a height
of ~30 cm above ground level. The 30 cm height was chosen as it
was both convenient for turning an increment borer and for col-
lecting the tops of stumps. Increment cores had to be no more
than an estimated five rings from the pith to minimize pith offset
for later determination of pith dates (e.g., Brown et al. 2008). For
goal *iii*, we collected increment cores at ~30 cm above ground
level from the five postsettlement trees nearest to subplot center
and measured distance to subplot center for the farthest individ-
ual for calculation of densities, ages, and composition of post-
settlement trees in each quadrant. Species, DBH, and DSH of each
of these trees were also recorded. We also collected cross sections
from any fire-scarred trees found in or within ~100 m of the main
plot to reconstruct fire timing and frequency.

2.3. Laboratory methods and analyses

2.3.1. Plot environmental characterization

We characterized environmental variation between plots by
their elevations, topographic relative moisture indices (TRMI),
and SI (Table 1). TRMI is the sum of four topographic parameters
that affect soil moisture holding capacity: aspect, slope, topo-
graphic position, and slope shape (Parker 1982). Higher values
indicate moister conditions. These parameters were recorded in
the field for each plot. The SI is an estimate of site productivity
and was estimated from the mean of site index trees measured in
subplots (Mogren 1956).

2.3.2. Fire and stand age histories

All increment cores and cross sections were prepared, surfaced,
and crossdated using standard dendrochronological methods
(Speer 2010). We used locally developed master chronologies for
visual and skeleton plot crossdating of samples. On increment
cores and cross sections that did not include pith but that had
visible inside ring curvature, pith dates were estimated using
overlaid concentric circles of varying circumferences that took
into account both mean inside ring widths and estimated distance
to pith (Applequist 1958; Brown et al. 2008). Only after crossdating
of ring series was complete did we assign dates for fire scars. Any
tree-ring samples that could not be crossdated were not used in
subsequent analyses.

Fire-scar dates were compiled into composite chronologies for
each plot using the program FHX2 (Grissino-Mayer 2001). Fire-scar
dates used in the composites were those recorded on at least two
trees in either study area. This minimum filtering was intended to
eliminate false positives (i.e., scars formed by factors other than
fire; Brown et al. 2008). We defined a period of analysis within
which to estimate fire frequency based on a minimum of two plots
in each study area recording fires. Fire frequencies for each study
area and for both areas combined were estimated for the period of
analysis based on plot composite chronologies.

Pith dates for trees sampled in the subplots were compiled into
5-year age classes for comparison of age structure within and
between plots and with the fire chronologies. We did not correct
for the age to coring height but use the 30 cm height pith dates
from increment cores or cross sections for age structure analysis.
Our goal with the age structure is to look at general patterns in
seedling ages and sizes that were present in the plots in 1860 and
to compare overall timing of tree ages with the last fire dates
within plots and across the two study areas. We did not attempt to
compare plot-level fire timing with potential patterns of tree re-
cruitment that may have been indicative of fire severity within
plots (sensu Brown et al. 2008) because of the low numbers of
fire-scarred trees collected in some plots.

Fig. 2. Empirical correction factor applied to stumps to estimate tree
diameters (cm) in 1860 from heartwood diameters (cm) measured in
the field. N = 586; standard error of the model = 8.2 cm (dashed lines).
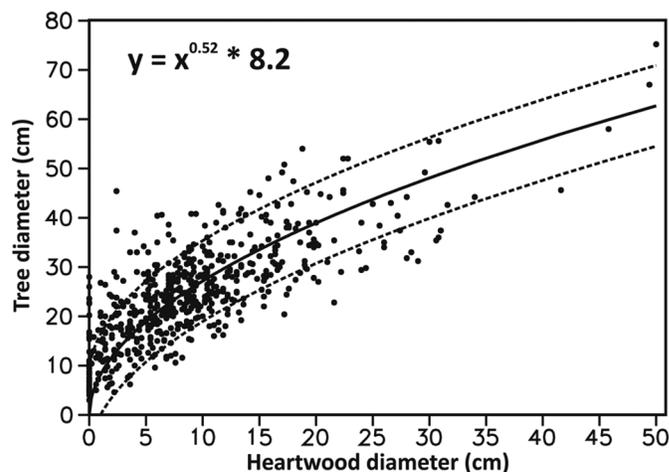
2.3.3. Nonspatial stand structure

Tree densities (TPH; trees·ha⁻¹), species composition, basal areas
(BA; m²·ha⁻¹), and quadratic mean diameters (QMD; cm) for each
plot in 1860 were estimated based on ages, sizes, and species of
presettlement trees alive in 1860 in the four subplots. Estimates of
the 1860 stand structure are robust, as all potential presettlement
trees in subplots were crossdated. We, therefore, know which of
the subplot trees were alive in 1860 and, using the increment core
or cross section collected from the tree, can estimate tree size at a
height of 30 cm at that date. Note, however, that we may be
missing some trees that were alive in 1860 but evidence of their
presence has decayed (see further comments in the Discussion).
Tree density and species composition were determined from the
number and species of trees alive in the four 500 m² subplots in
1860. The DSH in 1860 of each of these trees was then estimated to
determine tree DBH and tree and stand BA. For living trees or
recently dead trees with bark or sapwood that were alive in 1860,
we determined the ratio of core or section radius at 1860 to total
radius multiplied by field-measured DSH to estimate DSH in 1860
(Bakker 2005; Brown and Cook 2006). For stumps or other rem-
nant trees missing sapwood but with pith dates before 1860, we
either were able to measure DSH in 1860, or if the outside date was
earlier than 1860, we assumed that the tree was alive in 1860. The
majority of remnants sampled in all plots were eroded stumps
with outside dates sometime before 1860. We assumed that these
were cut sometime after 1860 but were present in the 1860 forest.
For these trees, we used a regression equation relating ratio of
heartwood radius to total tree radius measured on living trees in
the subplots to estimate DSH in 1860 (sensu Brown and Cook 2006;
Brown et al. 2008). We assumed that only heartwood was present
on eroded stumps. The regression equation was derived from liv-
ing trees sampled over both study areas (Fig. 2). Tree DBH was then
estimated from the reconstructed DSH measurements using plot-
specific linear regression equations derived from DBH and DSH
measurements from living sample trees in the subplots: DBH =
DSH(Y), where Y varied by plot but ranged from 0.83 to 0.88 (R^2 for
all models ranged from 0.82 to 0.91; P < 0.001 for all). Tree BA was
then calculated from the estimated DBH and summed across the
plot.

We next calculated TPH, species composition, BA, and QMD of
the current (2012) forest based on living trees in the subplots. The
TPH of the current forest was calculated as the sum of the living
presettlement trees in subplots scaled to unit basis plus the mean
of postsettlement tree density from the four subplots. Note that
this measurement of density does not include trees with a DBH

Fig. 3. Fire and 30 cm height pith dates from crossdated trees sampled in Hall Ranch (HA) and Heil Valley Ranch (HE) plots. Plots are arranged by elevation in landscapes (as in Table 1). Tree pith dates for remnant trees (stumps, logs, or snags; red bars) and living trees (green bars) are shown by 5-year periods for each plot, with dates of fires represented by inverted triangles. Fire dates recorded by trees in at least two plots are indicated by vertical lines and labeled at the bottom of the graph. Histograms to the far left of the graph are pith dates of any trees that predate 1600 in a plot.
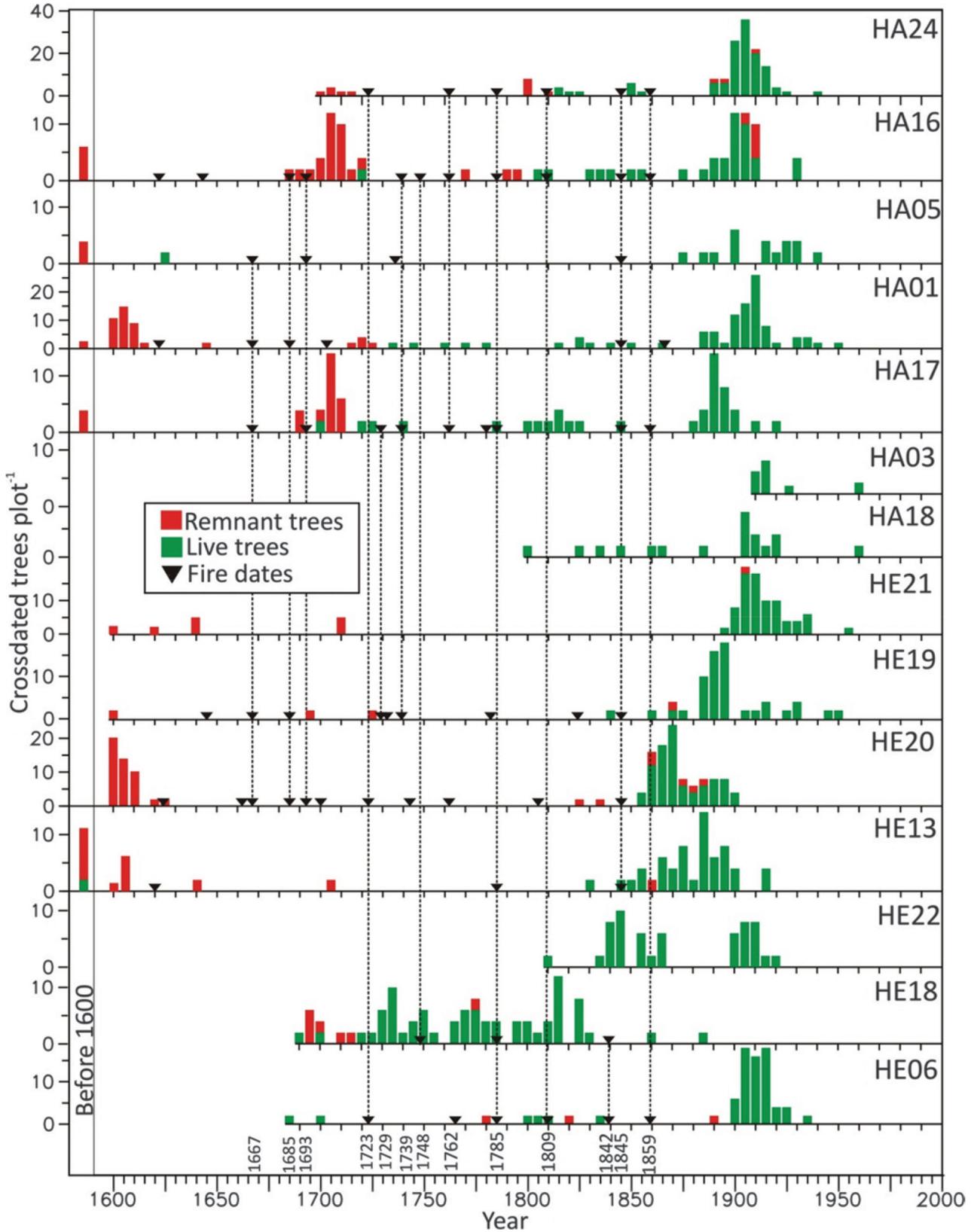
of <4 cm, as these were not measured in subplots. Thus, these data are not the same set of data as the estimated historical forest structure, which includes all trees present in subplots in 1860 regardless of size. Furthermore, because of the difference in evidence used to develop the two data sets (measurements of living trees vs. reconstructed data), the two data sets are not subjected to the same level of precision and should not be considered to be directly comparable. Rather, our goal with describing the current forest is to compare general trends in structure from the historical forest. The TPH of the postsettlement trees was estimated as the number of trees within a circular plot of the radius of the farthest tree sampled in each subplot scaled to a per hectare basis (Brown et al. 2008). The BA of the current forest was then calculated from DBH measurements of both pre- and post-settlement trees in the subplots, and the QMD was estimated from the plot BA and density.

2.3.4. Spatial stand structure

A major goal of this study was to estimate spatial patterns of trees present in 1860, especially the presence and characteristics of tree groups. Groups are defined as at least two trees with interlocking crowns, which we further define as being ≤6 m between center points of tree stems (e.g., based on a review of previous studies cited in Larson and Churchill (2012)). We first had to estimate which trees were present in 1860 across the entire plot. This was done using tree status (remnant or living), morphology of living trees (young, transitional, or old), condition of remnants (whether bark, sapwood, or only heartwood was present), and DBH measured in the field, coupled with crossdated ages of subplot trees. For living and remnant trees sampled in subplots, we knew which were present in 1860 based on crossdated tree ages. For living trees sampled over the rest of the plot, we used both morphology classifications (young, transitional, and old) and DBH–age regressions derived from crossdated living trees in the subplots. We assigned all "old" living trees to the 1860 forest based on their morphology. Trees classified in the field as "young" were not included in the 1860 forest. We then used a DBH–age regression equation derived from living trees sampled over both study areas to assign "transitional" living trees to either pre- or post-1860 status based on their measured DBH and the SI of the plot (DBH = 0.085age + 1.275SI; $n = 679$; $R^2 = 0.63$, $P < 0.001$). The size cutoff for assigning a tree to the 1860 forest (age = 152 years in 2012) ranged from 22.7 to 32.9 cm, depending on plot SI (Table 1). Eroded remnant trees (i.e., with only heartwood remaining) were assigned to the 1860 forest based on an assumption that all of them were older than 1860. Most of these were stumps, harvested presumably sometime in the late 1800s or in the early to middle 1900s. Other remnant trees (with bark or sapwood present) were assigned to the 1860 forest based on the DBH–age regression equation.

Once we had assigned trees to the 1860 forest for each plot, we then estimated both global and local tree spatial patterns (per recommendations in Larson and Churchill (2012)). Tree locations (x, y) over the entire plot were determined from trigonometric conversions of distances and azimuths measured for each tree from quadrant subplot centers. We evaluated the cumulative local tree spatial pattern for each plot using Ripley's K, a second-order statistic based on counts of tree occurrences within a circular neighborhood around each tree (Ripley 1977). The spatstat package (Baddeley and Turner 2005) for R v. 3.1.2 (R Core Team 2014) was used to calculate the square root transformation (Besag 1977) of Ripley's K, $L(d) - d$, at 1 m lag distances over the range of 0 to 17 m (25% of the plot maximum distance) with 999 Monte Carlo simulations of complete spatial randomness (CSR) used to construct approximate two-sided 95% acceptance envelopes for each plot. To complement visual interpretation of the $L(d) - d$ graphs, departure from CSR was formally evaluated using a global goodness-of-fit test (Loosmore and Ford 2006) for the 0 to 17 m range.

Table 2. Fire frequency (years) from 1667 to 1859 for Heil Valley Ranch and Hall Ranch Open Space study areas.

Site	MFI (SD)	MeFI	WMPI	WMode	Range
Hall Ranch	14 (9)	12	12	9	3–36
Heil Valley Ranch	9 (6)	7	8	6	3–23
Combined either	8 (6)	4	7	4	2–20
Combined both	15 (10)	12	12	10	3–36

Note: Fire frequencies are for fire years recorded only in HA or HE study areas, for fire years recorded at either study area, and for fire years recorded in both study areas for the period of analysis. MFI, mean fire interval plus standard deviation (SD); MeFI, mean fire interval; WMPI, Weibull distribution median probability interval (Grissino-Mayer 2001); WMode, Weibull distribution modal interval (Grissino-Mayer 2001).

We then determined local spatial patterns using numbers and characteristics of tree groups. A group was defined as trees occurring at a distance of ≤6 m from each other, which was meant to approximate the scale of interaction among mature tree crowns. We calculated percentage of trees in groups, modal and maximum group sizes, and the number of groups per hectare for each plot. Note that we are limited in estimating the upper end of the group size, as individuals or groups along the plot edges may be members of groups that extend outside of the plots. We also calculated the percent of plot area in open space, individual canopy cover, and group canopy cover, based on a crown diameter of 6 m for each tree.

3. Results

3.1. Fire and stand age history

A total of 925 trees were crossdated from the 14 plots, with 893 trees with pith or from cores from which pith could be estimated (97% of crossdated trees; Fig. 3). An additional 19 trees were sampled (2% of all cores or cross sections collected) but could not be crossdated, as they were mostly from remnant stumps that contained too few rings to be able to find the dating. A total of 298 of the 925 crossdated trees (32%) were present in plots in 1860. Of these, 135 trees were still living in 2012 (19% of a total of 717 living trees sampled) and 163 trees were remnants (78% of a total of 208 remnants sampled). The majority (142 trees; 87% of the 163 total) of the remnant trees alive in 1860 were eroded stumps, with only heartwood remaining. The majority (100 trees; 74% of the 135 total) of the living trees present in 1860 were from a single plot, HE18 (Fig. 3). Eroded stumps were found in all plots except HE18, HE22, and HA03 (the latter of which had no trees present in 1860 at all).

A total of 83 fire scars were analyzed from all plots (Fig. 3). Fire scars were found almost exclusively on stumps or other remnant trees. Dates of fires recorded by trees in at least two plots are at the bottom of Fig. 3, with the last of these fires recorded in 1859. Three trees in plot HA01 recorded fire scars in 1867, which was the last certain fire date recorded in any of the plots.

A period of analysis to determine fire frequency was defined from 1667 to 1859 (Fig. 3). Fire dates recorded in two or more plots during the period of analysis (dates at bottom of Fig. 3) were used to determine fire frequencies within each study area, across either landscape, or between fires recorded in both landscapes (Table 2).

3.2. Nonspatial stand structure

We mapped and collected data from a total of 1955 living and remnant trees in the 14 plots. The majority of trees were ponderosa pine, with only 72 trees (4%) being either Douglas-fir or Rocky Mountain juniper. Of all crossdated trees, only two Douglas-fir trees were alive in 1860; both were fire-scarred stumps from plot HE20 and established in the early 1600s. However, both of these Douglas-fir trees were sampled outside of the subplots and, therefore, are not included in the 1860 structure. No Rocky Mountain junipers predated 1860.

Fig. 4. Pith dates on crossdated living trees classified in the field as "old", "transitional", or "young" based on tree morphology. Circles represent trees with predicted presence in 1860 using field morphology and DBH–age regression to split "transitional" trees, and triangles represent predicted absence. Note that for the 1860 stem maps, the trees in this figure were assigned membership based on their crossdated pith dates. Vertical dashed line is at year 1860.
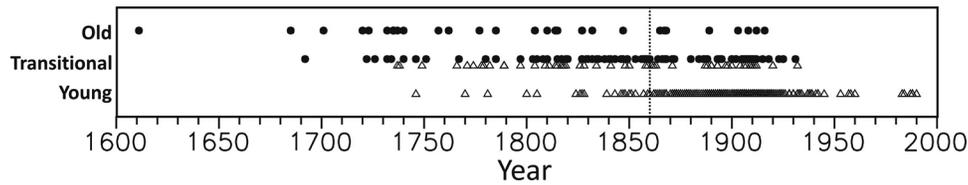
Fig. 5. Pith dates and diameter at breast height (DBH; 1.3 m) of living trees sampled from subplots as "presettlement" trees (i.e., ≥25 cm DBH or with old-age characteristics if <25 cm DBH; blue circles) and living trees sampled from subplots as "postsettlement" trees (i.e., trees <25 cm DBH and without old-age characteristics; black triangles). Note that many of the trees sampled as "presettlement" based mainly on their ≥25 cm dbh were not classified correctly after crossdating, whereas only four of the "postsettlement" trees were not classified correctly after crossdating (these were included in estimates of the 1860 structure for their respective plots). Vertical dashed line is at year 1860. Horizontal dashed lines are at 25 cm and 4 cm DBH, between which we sampled postsettlement trees.
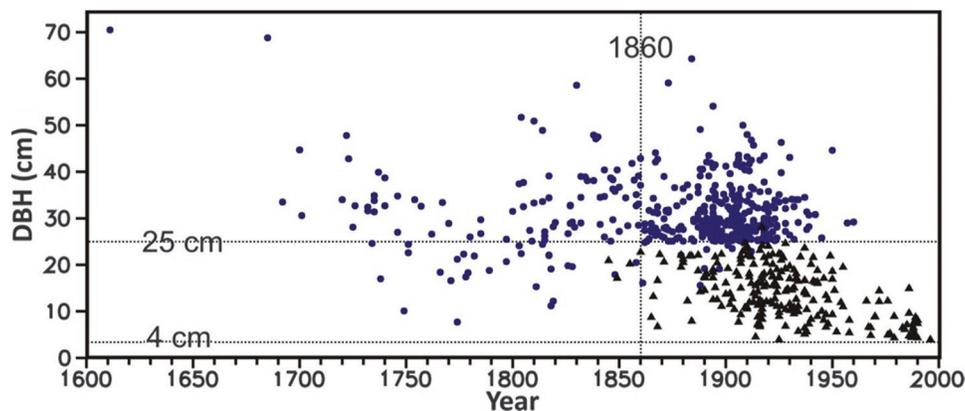
Crossdated living trees from subplots subplots confirm that tree morphology was a useful but imperfect substitute for tree age, even after applying the DBH-age regression equation to reclassify the "transitional" trees (Fig. 4). Since morphology was used to determine if live trees outside the subplots are part of the 1860 forest for the spatial analysis it is important to recognize that the live component of the pattern has some uncertainty. However, using the ≥25 cm DBH cutoff coupled with tree morphology for trees with a DBH of <25 cm did successfully captured nearly all of the trees alive in 1860 across all plots (Fig. 5). Only four of the 414 postsettlement living trees were collected from subplots established before 1860 (Fig. 5). Figure 5 also shows the generally poor relationship between age and DBH for the living trees and that use of morphological characteristics was necessary to more fully capture the 1860 trees in the subplots.

Reconstructed stand structure in 1860 varied considerably between plots (Table 3). Tree diameter distributions also varied between plots (Fig. 6), with several exhibiting multiple size classes that correspond roughly to age distributions (Fig. 3). All plots are forested today, generally containing more trees, with a greater BA, and containing more smaller diameter trees than the reconstructed 1860 forests (Table 4).

### 3.3. Spatial stand structure

Similar to nonspatial structural metrics, reconstructed spatial patterns in 1860 varied considerably between plots (Table 5; Fig. 7). For the global spatial patterns, 8 of the 13 plots with adequate tree cover present in 1860 exhibited aggregation at some spatial scale according to the $L(d) - d$ statistic (Table 5), with most aggregating at some or all scales above 3–12 m (for examples, see Fig. 7). Five plots had tree spatial patterns that did not show signs of aggregation and did not significantly differ from CSR, and an additional plot was too sparse to analyze patterns for. For the local patterns, 10% to 90% (mean, 74%) of

Table 3. Plot structural metrics for trees estimated to have been present in 1860 in plots at Hall Ranch (HA) and Heil Valley Ranch (HE) Open Space study areas.

Plot	TPH	BA	QMD
Hall Ranch			
HA24	90	4.2	24.3
HA16	165	14.7	33.6
HA05	20	5.2	57.5
HA01	170	17.1	35.8
HA17	145	10.8	30.8
HA03	0	0.0	—
HA18	25	0.3	11.7
Heil Valley Ranch			
HE21	50	2.9	27.0
HE19	25	0.8	20.1
HE20	110	12.5	38.1
HE13	100	3.7	21.8
HE22	90	0.5	8.1
HE18	320	7.0	16.7
HE06	35	2.3	29.1
Minimum	0	0.0	0.0
25% quartile	28	1.2	17.5
Mean	96	5.8	25.3
75% quartile	136	9.8	32.9
Maximum	320	17.1	57.5

Note: Structural metrics: trees per hectare (TPH; trees·ha⁻¹), tree basal area (BA; m²·ha⁻¹), and stand quadratic mean diameter (QMD; cm).

Fig. 6. Historical (1860) diameter distributions by plot for Hall Ranch (HA) and Heil Valley Ranch (HE) study areas. Note that HA03 is not shown, as it had no trees in 1860. TPH, trees per hectare (tree density); BA, basal area.
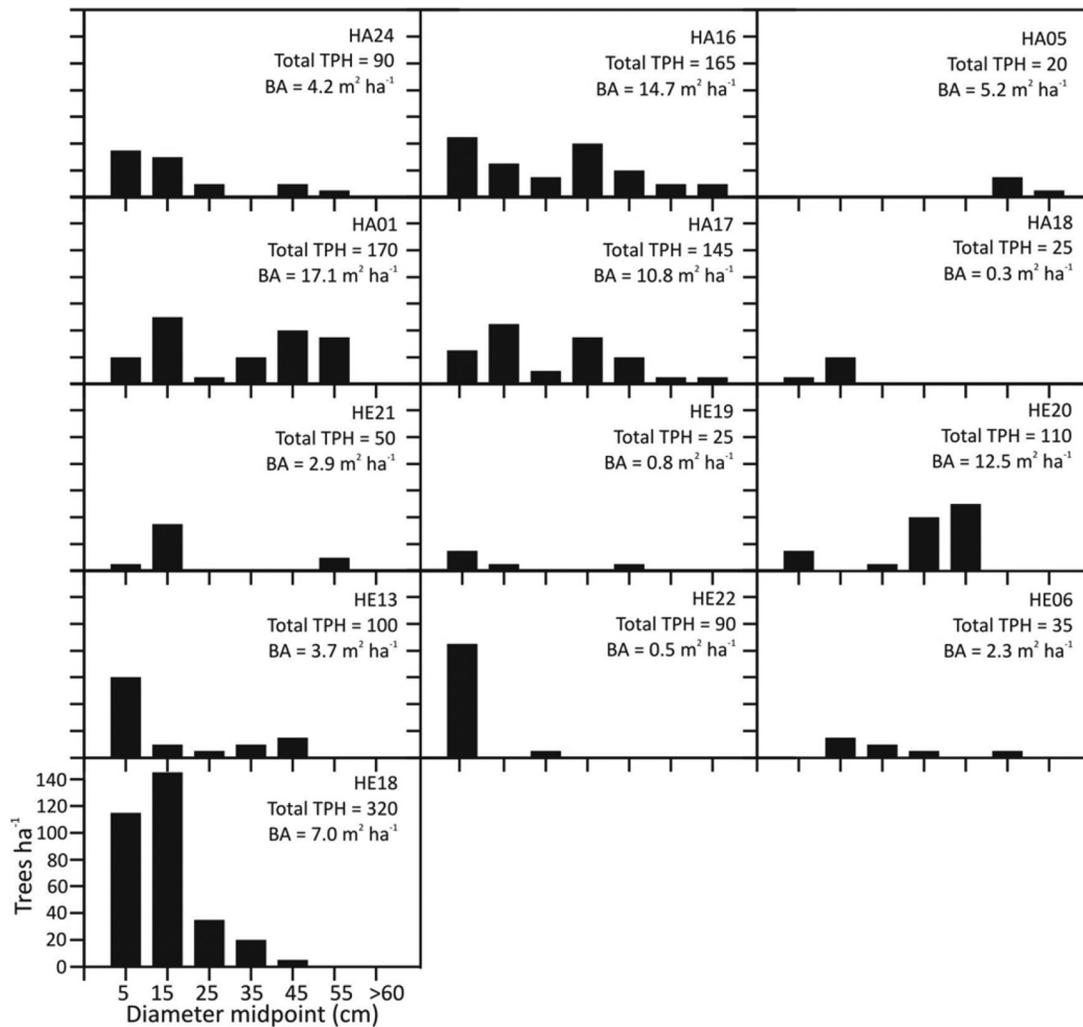
trees were found in groups of mostly two to eight trees (mode, two trees), with a density of 0–36 groups·ha⁻¹. The one plot that was too sparse to analyze global spatial patterns for had no trees in groups. On average, plots were very open in 1860, with 79% open space, 7% canopy cover from individual trees, and 14% canopy cover from groups (Table 5). Even the densest plot, HE18, had 48% open space despite having a random spatial distribution with 90% of plot trees in groups, including the top two largest groups recorded across all plots (16 and 26 trees).

4. Discussion

4.1. Fire and stand age history

As in ponderosa pine forests throughout its range, widespread episodic fires ceased largely coeval with Euro–American settlement. The last fire recorded in more than one plot occurred in 1859 (Fig. 3), the beginning of the gold rush that brought intensive Euro–American settlement along with accompanying changes in land use. Widespread livestock grazing was probably the initial cause of fire cessation. A pattern of fire exclusion after introduction of grazing is common in dry conifer ecosystems throughout western North America (e.g., Savage and Swetnam 1990; Touchan et al. 1995; Swetnam and Baisan 1996; Stephens et al. 2003; Brown and Wu 2005). Historical fires in lower elevation ponderosa pine forests spread across landscapes primarily through grass and herbaceous fuels, and intensive grazing disrupted stand to landscape

patterns of surface fuel continuity. Active fire suppression by land management agencies would have further contributed to fire exclusion beginning in the early twentieth century. Although we did not reconstruct variations in fire severities in this study, we suspect that a majority of historical fire behavior was surface fire, with small patches (<1 to <100 ha) of crown mortality also possible during some of the past fire events (e.g., Brown et al. 1999; Sherriff and Veblen 2007; Sherriff et al. 2014).

Fire frequencies at both plot and landscape scales (Table 2) are comparable with those found in previous fire history studies in lower elevation Front Range ponderosa pine forests (Brown et al. 1999; Veblen et al. 2000; Veblen and Donnegan 2006; Sherriff and Veblen 2006). Fires occurred, on average, every 8–15 years depending on the spatial scale analyzed, either within plots or between the two study areas combined (Table 2). This average is also within the range of fire frequencies found by many other fire-scar based studies in ponderosa pine forests throughout its range (e.g., Swetnam and Baisan 1996; Fulé et al. 1997; Brown et al. 2008). However, a lack of spreading fires after 1859 is in contrast to some localities found in other studies in the northern Front Range (e.g., Veblen et al. 2000). These other studies found both an increase in fires during the early settlement period and in fires extending into the early twentieth century in some sites. It may be that we are missing some local fire dates in the late nineteenth or early twentieth centuries. For example, fire scars were recorded on

Table 4. Plot structural metrics for living trees with a diameter at breast height (DBH; 1.3 m) of ≥4 cm at Hall Ranch (HA) and Heil Valley Ranch (HE) Open Space study areas.

Plot	TPH	BA	QMD
Hall Ranch			
HA24	790	23.1	19.3
HA16	510	16.8	20.5
HA05	175	10.3	27.4
HA01	725	14.9	16.2
HA17	530	14.7	18.8
HA03	220	4.4	16.0
HA18	525	10.1	15.7
Heil Valley Ranch			
HE21	1010	22.1	16.7
HE19	350	21.8	28.2
HE20	825	22.0	18.4
HE13	680	18.6	18.7
HE22	635	15.3	17.5
HE18	515	19.7	22.1
HE06	615	20.4	20.6
Minimum	175	4.4	15.7
25% quartile	511	14.8	16.9
Mean	579	16.7	19.7
75% quartile	714	21.5	20.5
Maximum	1010	23.1	28.2

Note: Structural metrics: trees per hectare (TPH; trees·ha^{-1}), tree basal area (BA; m^2·ha^{-1}), and stand quadratic mean diameter (QMD; cm).

three trees in plot HA01 in 1867 but not in surrounding plots. However, we are confident that we collected enough fire-scarred samples that we did not miss any landscape-scale fires that occurred between plots.

The cessation of fires in the mid-1800s was followed by an increase in tree establishment in all but one plot (HE18; Fig. 3). A pattern of fire cessation followed by increases in tree density and landscape coverage has been found in all previous studies of ponderosa pine forests throughout its range (e.g., Fulé et al. 1997; Sherriff and Veblen 2006; Brown and Wu 2005; Brown and Cook 2006). In most plots, dramatic pulses of recruitment are evident shortly after the last fire dates (Fig. 3). These pulses of recruitment were likely not the result of widespread tree mortality during the fires, because we found no evidence of logs or snags resulting from such an event in any plot. Rather, abundant tree establishment and survivorship are related to the lack of fire after the mid-1800s. Episodic fires prior to the mid-1800s would have acted as a density-independent control on tree recruitment by killing a majority of seedlings and smaller saplings in most locations before they had a chance to reach maturity (Brown and Wu 2005). Once mature, a ponderosa pine tree is relatively immune to mortality from surface fires because of its high crown and thick bark. However, younger seedlings and saplings are susceptible to mortality from fire (Battaglia et al. 2009).

4.2. Nonspatial stand structure

Stand structures in 1860 were very diverse across the two study areas (Table 3; Fig. 6). Several of the plots were very open, with very few trees estimated to have been present in 1860. HA03 today is forested but was unforested in 1860. HA03 is adjacent to open grasslands, and it is likely that this entire area was grassland historically and has seen tree encroachment since settlement. The densest stand was HE18 (Table 3), located on a southeast-facing, xeric, and very rocky ridge near the margins of the Great Plains. Current herbaceous understory cover here is low compared with

other plots or even compared with surrounding areas on the ridge. We found fire-scarred trees in the vicinity of the plot but not in the plot itself. It is likely that trees were located in this area because they were relatively protected from past fires owing to the lower surface fuels and higher proportion of rocks. HE18 also was one of only three plots that did not show any sign of previous harvest in the form of stumps, likely because of the short stature of the trees and generally poor growing conditions.

Historical tree densities and basal areas reconstructed by this study (Table 3) generally fall within ranges of similar metrics found by other studies in ponderosa pine forests from throughout the western US, although mean tree diameters tend to be smaller. Sánchez Meador et al. (2010) summarized structural characteristics from several studies in northern Arizona ponderosa pine forests that used both historical forest inventories and reconstruction methods. Historical tree densities found by these studies ranged from 12 to 255 TPH and BA ranged from 4.6 to 18.8 m^2·ha^{-1}. Mean historical diameters ranged from 33.2 to 53.0 cm. Similar historical data from Brown and Cook (2006) found mean densities of 127 trees·ha^{-1}, BA of 15.8 m^2·ha^{-1}, and QMDs of 50.5 cm in ponderosa pine forests of the Black Hills. Ponderosa pine forests in both the Southwest and Black Hills tend to be more productive, hence the larger trees in these landscapes relative to the northern Front Range.

For nonspatial stand structure estimates (Table 3), we made a number of assumptions in estimating both the number of trees present in each plot in 1860 and the sizes of the trees, especially from stumps missing sapwood and bark. We have good confidence in estimating tree densities from extant evidence as all trees from the subplots were crossdated, and we, therefore, know which were present in 1860. Less certain are tree sizes and hence BA and QMD estimates. Almost half of the crossdated trees that make up the 1860 forest structure estimates were eroded stumps. Heartwood of ponderosa pine stumps can persist for several decades after bark and sapwood have decayed (e.g., Fulé et al. 1997; Brown et al. 2008) but only depending on the amount of heartwood present in the tree at the time of harvest. Smaller stumps with correspondingly less heartwood harvested early in the settlement period may have completely disappeared by the time of our sampling (Brown and Cook 2006). We also depended on the amount of heartwood in these trees to estimate DSH in 1860. In some cases, we were able to measure the DSH from the sample when the outside date postdated 1860, but in most cases, we used the heartwood to total tree radius regression equation (Fig. 2). It is possible that tree sizes were larger because of heartwood erosion in addition to sapwood erosion since the tree was cut and that BA and QMD estimates shown in Table 3 were greater than what we reconstructed. We also were able to estimate sizes of a number of smaller trees based mainly on living trees in plots (i.e., reconstructed 1860 tree diameters as shown in Fig. 6). However, we may be missing other small trees cut early in the plot history that have since disappeared from the plots either through natural or human mortality and subsequent decay because of less heartwood content. Fires after harvest also may have burned up stump evidence, although we attempted to control for this by deliberately avoiding areas where recent fires (within the past few decades) are known to have occurred. However, we assume for the purposes of 1860 stand reconstructions that the loss of evidence from any source has been minimal and that the overall trends in the reconstructed stand structures are robust.

We also are somewhat confident in our ability to define living trees that established by 1860 over the entire plot using both size and morphological criteria (Fig. 5), but our ability to use morphological criteria alone for determining tree age is less certain (Fig. 4). We were able to define the older trees relatively well, but the "transitional" trees (with both old and young morphological characteristics) were problematic. Field morphology was not highly effective at identifying pre-settlement trees that established soon before or after 1860 because they do not yet show

Table 5. Spatial metrics over 0.5 ha plots for trees present in 1860 in Hall Ranch (HA) and Heil Valley Ranch (HE) Open Space study areas.

Plot	Percent of trees in groups	Maximum group size (no. of trees)	Groups per hectare	Percent open space	Percent individual-tree canopy cover	Percent group canopy cover	$L(d) - d$ trends	DCLF GoF p value
Hall Ranch								
HA24	74	9	18	82	6	12	Aggregated	0.002
HA16	70	16	28	68	12	20	Aggregated	0.007
HA05	10	2	2	89	10	1	Random	0.425
HA01	87	11	22	70	5	26	Aggregated	0.001
HA17	86	12	26	75	4	21	Aggregated	0.085
HA03	N/A	N/A	N/A	100	0	0	N/A	N/A
HA18	38	2	6	92	5	2	Random	0.351
Heil Valley Ranch								
HE21	65	6	18	81	8	11	Aggregated	0.084
HE19	59	5	14	85	7	8	Random	0.305
HE20	84	15	20	73	5	22	Aggregated	0.004
HE13	81	8	32	75	6	19	Aggregated	0.051
HE22	55	9	8	86	7	7	Aggregated	0.003
HE18	90	26	36	48	7	45	Random	0.220
HE06	25	3	6	86	11	3	Random	0.467

Note: Percent area calculations are based on 6 m diameter crowns for all trees. $L(d) - d$ was interpreted as aggregation when trending positive and exceeding the upper bounds of the approximate 95% acceptance envelope over some distances within the 0–17 m range, complemented by the Diggle–Cressie–Loosmore–Ford (DCLF) goodness-of-fit (GoF) test (Loosmore and Ford 2006) over the same distance range. Plot HA03 did not have any trees present in 1860.

consistent, definitive old tree morphological characteristics. We will continue to explore the use of both size and morphological criteria, coupled with site environmental characteristics, to define older vs younger trees. Further sampling for age, size, and morphology across the range of ponderosa pine across the Front Range will help further refine these relationships, which are especially crucial for retaining older trees in restoration treatment implementation. Because of generally poor relationships between tree sizes and ages (e.g., data shown in Fig. 5), incorporation of morphological characteristics will aid in retaining smaller old trees in addition to large ones in future mechanical restoration treatments.

4.3. Spatial stand structure

Similar to nonspatial structure, spatial arrangement of individual trees and groups in the 1860 forests also exhibited a great deal of diversity (Table 5; Fig. 7). Diversity in tree clusters, single trees, and openings have been found throughout the range of ponderosa pine where spatial patterning has been analyzed (Larson and Churchill 2012). Such diversity is important for providing tree regeneration niches, understory diversity, wildlife habitat, and in structuring fuel complexes (Larson and Churchill 2012; Reynolds et al. 2013). In our study, a majority of trees in most plots were found in groups with other trees (Table 5), although we are limited in assessing spatial arrangements beyond the 0.5 ha plot size. In spatially aggregated plots, 1860 era trees were typically found only in portions of a plot rather than scattered throughout the plots (e.g., HA01 and HE22, Fig. 7). Historical spatial patterning of trees was undoubtedly the result of complex pattern-process interactions between soil and microsite characteristics, fire timing, fuelbeds, spatiotemporal variability in overstory mortality, seed caching by corvids and small mammals, and climate variation that created a diversity of tree spatial arrangements within stands and through time (e.g., Brown and Wu 2005; Larson and Churchill 2012; Churchill et al. 2013). For example, although we did not explicitly map microsites within plots, notes and photographs suggest that some of the historical tree locations may be explainable by locally shallower or rockier soils. These areas were locations where surface fuels may have been reduced relative to surrounding deeper soils and thus locations at which the likelihood of seedling survivorship during recurrent surface fires would have been higher. Other possibilities for tree aggregation may relate to differences in seedling survivorship in needle vs.
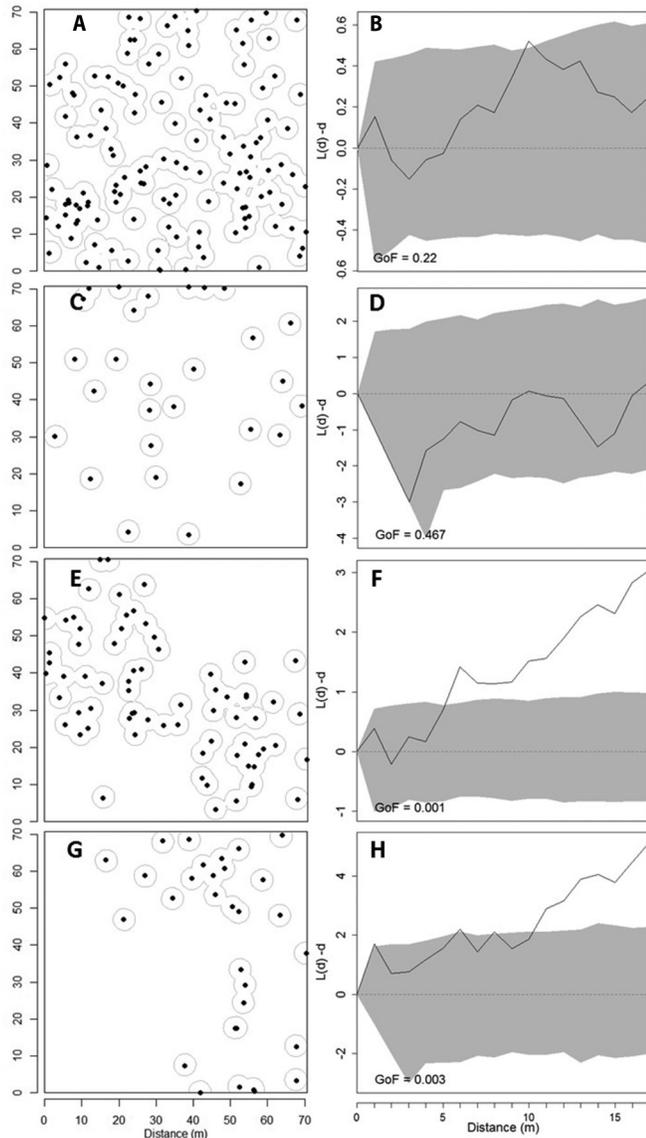
grass fuelbeds. If a seedling established in a needle fuelbed below the canopy of an existing overstory, it may have had a better chance at surviving a fire than a seedling in the middle of a grassy meadow (Lezberg et al. 2008; Battaglia et al. 2009). For example, Abella et al. (2013) found strong variations in soil characteristics under openings vs. tree groups in historical forests of northern Arizona and argued that local patterns within stands were largely self-reinforcing.

4.4. Implications for ecological restoration and treatment prescriptions

Spatiotemporal variability in fire timing and undoubtedly fire severity (e.g., Sherriff et al. 2014) before 1859 coupled with variation in climate regimes, landscape physiography, and other ecological processes resulted in high diversity in tree ages, sizes, and nonspatial and spatial structures (Tables 3 and 5; Figs. 3 and 6). However, fire exclusion coupled with timber harvest resulted in contemporary stands that are denser and made up of smaller trees (Table 4). Such conditions have most likely shifted fire behavior from largely surface fires with patchy overstory mortality to fires with greater proportions of passive and active crown fire, as has happened during recent fires in other locations across the frequent fire zone of ponderosa pine forests both in the Front Range (e.g., Graham 2003; Graham et al. 2012) and across its range in North America.

The spatial and nonspatial structural data that we reconstructed for the 1860 forest provide both justification and guidance for restoration of historical forest structure across our two study areas and in similar low-elevation ponderosa pine ecosystems. Presettlement stand structures (Tables 3 and 5) are increasingly used as models for design of silvicultural treatments (e.g., Fulé et al. 1997; Brown et al. 2008; Larson and Churchill 2012; Churchill et al. 2013; Reynolds et al. 2013; Underhill et al. 2014). Silvicultural prescriptions should focus primarily on recreating stand- to landscape-scale variability with mosaics of individual trees, groups of trees of varying sizes, and openings of diverse sizes and arrangements, rather than focus on any central tendencies within individual metrics (Churchill et al. 2013; Reynolds et al. 2013; Dickinson 2014; Underhill et al. 2014). For example, many of the past fuel treatment prescriptions in this area were designed to reduce canopy continuity and fire hazard alone and tended to focus solely on reducing TPH and BA without consideration of spatial patterning. Past fuels treatments in the Boulder County

Fig. 7. Reconstructed 1860 stem maps (left panels) and associated $L(d) - d$ graphs (right panels) from four of the 14 Hall Ranch (HA) and Heil Valley Ranch (HE) plots: A and B, HE18; C and D, HE06; E and F, HA01; and G and H, HE22. The locations (x, y) of tree stems are shown by solid circles, with 6 m diameter crowns or group canopy boundaries shown in light gray. $L(d) - d$ is plotted (solid black line) against the theoretical mean for complete spatial randomness (CSR; dashed gray line) and the approximate 95% acceptance envelope (shaded gray). The top two rows illustrate random spatial patterns in dense (A and B) and open (C and D) stands, whereas the bottom two rows illustrate aggregated spatial patterns in dense (E and F) and open (G and H) stands. GoF, goodness of fit.

elements of historical stand and landscape diversity, rather than simply to reduce tree density in any one stand (Dickinson 2014; Underhill et al. 2014). The study we have outlined here also has been expanded across the range of ponderosa pine in the Front Range and will provide regional estimates of historical stand structures that will be used for ecological restoration efforts beyond Boulder County properties.

A major question for the future is what will be the role of fire across these and other ponderosa pine landscapes. Ecological restoration is not a single event but a process. Stand and landscape structures will need to be maintained once they have been restored, and a focus on natural disturbances and other ecological processes will need to be implemented (Falk 2006). In the past, a great deal of the structural diversity was maintained by relatively frequent surface fires that killed a majority of tree regeneration before it had a chance to reach canopy status (Brown and Wu 2005). In locations such as the BCPOS landscapes and other forests near wildland–urban interfaces, reintroduction of fire will prove difficult owing both to their proximity to private land and other developments and to considerations for smoke management above the major urban areas of the Colorado Front Range. However, it is not a question of if fire will ever again occur in these landscapes but when it will occur and what kind of fire behavior will dominate. Wildfires may even be expected to increase in the future under projected warmer and drier conditions (e.g., Seager and Vecchi 2010; Rangwala et al. 2012). Restoration of forest structure should provide managers with a measure of "comfort" for reintroducing prescribed fires to these landscapes sometime in the future. However, over the long term, managers — and more importantly, policymakers and the general public — must consider permitting managed wildfire use where naturally ignited fires are allowed to burn over selected areas under less extreme weather conditions. Smoke will still be a concern under these types of fire scenarios, but the alternative is wildfire that occurs under more extreme weather conditions and will be much more destructive to forest resources, wildlife habitats, watersheds, and homes and other human infrastructure. Landscape-scale ecological restoration efforts will be critical to mitigate damaging effects from future wildfires across the range of ponderosa pine forests and to maintaining these ecosystems into the future.

Acknowledgements

References

Abella, S.R., and Denton, C.W. 2009. Spatial variation in reference conditions: historical tree density and pattern on *Pinus ponderosa* landscape. Can. J. For. Res. **39**(12): 2391–2403. doi:10.1139/X09-146.

Abella, S.R., Denton, C.W., Steinke, R.W., and Brewer, D.G. 2013. Soil development in vegetation patches of *Pinus ponderosa* forests: interface with restoration thinning and carbon storage. For. Ecol. Manage. **310**: 632–642. doi:10.1016/j.foreco.2013.09.022.

Allen, C.D., Savage, M., Falk, D.A., Suckling, K.F., Swetnam, T.W., Schulke, T., Stacey, P.B., Morgan, P., Hoffman, M., and Klingel, J.T. 2002. Ecological restoration of southwestern ponderosa pine ecosystems: a broad perspective. Ecol. Appl. **12**: 1418–1433. doi:10.1890/1051-0761(2002)012[1418:EROSPP]2.0.CO;2.

Applequist, M.B. 1958. A simple pith locator for use with off-center increment cores. J. For. **56**: 141.

study areas were largely "spacing-based" mechanical treatments, with relatively uniform residual tree densities and sizes and a lack of larger openings (e.g., >0.1 ha; Ziegler 2014; Dickinson 2014). However, fine-scale spatial patterning and diverse landscape structures are important factors for increasing the resilience of ponderosa pine ecosystems (Churchill et al. 2013; Reynolds et al. 2013). Mosaics of tree groups, individuals, and openings affect patterns of burning (e.g., Ziegler 2014), susceptibility to bark beetles, and spatiotemporal patterns of tree recruitment and mortality (Churchill et al. 2013). Major goals of restoration treatments in the Boulder County and similar landscapes should be to restore

Baddeley, A., and Turner, R. 2005. spatstat: an R package for analyzing spatial point patterns. J. Stat. Softw. **12**: 1–42.

Bakker, J.D. 2005. A new, proportional method for reconstructing historical tree diameters. Can. J. For. Res. **35**(10): 2515–2520. doi:10.1139/x05-136.

Battaglia, M.A., Smith, F.W., and Shepperd, W.D. 2009. Predicting mortality of ponderosa pine regeneration after prescribed fire in the Black Hills, South Dakota, U.S.A. Int. J. Wildl. Fire, **18**: 176–190. doi:10.1071/WF07163.

Besag, L. 1977. Contributions to the discussion of Dr. Ripley's paper. J. R. Stat. Soc. Series B Stat. Methodol. **39**: 193–195.

Brown, P.M., and Cook, B. 2006. Early settlement forest structure in Black Hills ponderosa pine forests. For. Ecol. Manage. **223**: 284–290. doi:10.1016/j.foreco.2005.11.008.

Brown, P.M., and Wu, R. 2005. Climate and disturbance forcing of episodic tree recruitment in a southwestern ponderosa pine forest. Ecology, **86**: 3030–3038. doi:10.1890/05-0034.

Brown, P.M., Kaufmann, M.R., and Shepperd, W.D. 1999. Long-term, landscape patterns of past fire events in a montane ponderosa pine forest of central Colorado. Landsc. Ecol. **14**: 513–532. doi:10.1023/A:1008137005355.

Brown, P.M., D'Amico, D.R., Carpenter, A.T., and Andrews, D.M. 2001. Restoration of montane ponderosa pine forests in the Colorado Front Range: a forest ecosystem management plan for the City of Boulder. Ecol. Restor. **19**: 19–26.

Brown, P.M., Wienk, C.L., and Symstad, A.J. 2008. Fire and forest history at Mount Rushmore. Ecol. Appl. **18**: 1984–1999. doi:10.1890/07-1337.1.

Buchholtz, C.W. 1983. Rocky Mountain National Park: a history. Colorado Associated University Press, Boulder, Colorado.

Churchill, D.J., Larson, A.J., Dahlgreen, M.C., Franklin, J.F., Hessburg, P.F., and Lutz, J.A. 2013. Restoring forest resilience: from reference spatial patterns to silvicultural prescriptions and monitoring. For. Ecol. Manage. **291**: 442–457. doi:10.1016/j.foreco.2012.11.007.

Clement, J., and Brown, P.M. 2011. Front range roundtable, collaborative forest landscape restoration project 2011: ecological, social, and economic monitoring plan. Colorado Forest Restoration Institute, Colorado State University. Available from http://warnercnr.colostate.edu/images/pictures/upload/cfri/Roundtable-CFLRP-Monitoring-Plan-062511.pdf [accessed 14 April 2015].

Dickinson, Y. 2014. Landscape restoration of a forest with a historically mixed-severity fire regime: what was the historical landscape pattern of forest and openings? For. Ecol. Manage. **331**: 264–271. doi:10.1016/j.foreco.2014.08.018.

Falk, D.A. 2006. Process-centered restoration in a fire-adapted ponderosa pine forest. Journal for Nature Conservation, **14**: 140–151. doi:10.1016/j.jnc.2006.04.005.

Front Range Fuels Treatment Partnership (FRFTP). 2006. Living with fire: protecting communities and restoring forests — findings and recommendations of the Front Range Fuels Treatment Partnership Roundtable. Available from http://www.frftp.org/docs/report.pdf [accessed 14 April 2015].

Fulé, P.Z. 2008. Does it make sense to restore wildland fire in changing climate? Restor. Ecol. **16**: 526–531. doi:10.1111/j.1526-100X.2008.00489.x.

Fulé, P.Z., Covington, W.W., and Moore, M.M. 1997. Determining reference conditions for ecosystem management of southwestern ponderosa pine forests. Ecol. Appl. **7**: 895–908. doi:10.1890/1051-0761(1997)007[0895:DRCFEM]2.0.CO;2.

Graham, R.T. (*Technical Editor*). 2003. Hayman fire case study. USDA Forest Service, Rocky Mountain Research Station, Ogden, Utah, General Technical Report RMRS-GTR-114.

Graham, R., Finney, M., McHugh, C., Cohen, J., Calkin, D., Stratton, R., Bradshaw, L., and Nikolov, N. 2012. Fourmile Canyon Fire findings. USDA Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, General Technical Report RMRS-GTR-289.

Grier, C.C., and Waring, R.H. 1974. Conifer foliage mass related to sapwood area. For. Sci. **20**: 205–206.

Grissino-Mayer, H.D. 2001. FHX2—software for analyzing temporal and spatial patterns in fire regimes from tree rings. Tree-Ring Res. **57**: 115–124.

Huckaby, L.S., Kaufmann, M.R., Stoker, J.M., and Fornwalt, P.J. 2001. Landscape patterns of montane forest age structure relative to fire history at Cheesman Lake in the Colorado Front Range. *In* Ponderosa pine ecosystems restoration and conservation: steps toward stewardship. R.K. Vance, W.W. Covington, and C.D. Edminster (*tech. coords.*). U.S.D.A. Forest Service, Proceedings RMRS-P-22. Pages 19–27.

Huckaby, L.S., Kaufmann, M.R., Fornwalt, P.J., Stoker, J.M., and Dennis, C. 2003. Identification and ecology of old ponderosa pine trees in the Colorado Front Range. USDA Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, General Technical Report RMRS-GTR-110. and Field guide to old ponderosa pines in the Colorado Front Range. General Technical Report RMRS-GTR-109.

Kaufmann, M.R., Regan, C.M., and Brown, P.M. 2000. Heterogeneity in ponderosa pine/Douglas-fir forests: age and size structure in unlogged and logged landscapes of central Colorado. Can. J. For. Res. **30**(5): 698–711. doi:10.1139/x99-255.

Keane, R.E., Hessburg, P.F., Landres, P.B., and Swanson, F.J. 2009. The use of historical range and variability (HRV) in landscape management. For. Ecol. Manage. **258**: 1025–1037. doi:10.1016/j.foreco.2009.05.035.

Larson, A.J., and Churchill, D.C. 2012. Tree spatial patterns in fire-frequent forests of western North America, including mechanisms of pattern formation and implications for designing fuel reduction and restoration treatments. For. Ecol. Manage. **267**: 74–92. doi:10.1016/j.foreco.2011.11.038.

Lezberg, A.L., Battaglia, M.A., Shepperd, W.D., and Schoettle, A.W. 2008. Decades-old silvicultural treatments influence surface wildfire severity and post-fire nitrogen availability in a ponderosa pine forest. For. Ecol. Manage. **255**: 49–61. doi:10.1016/j.foreco.2007.08.019.

Loosmore, N.B., and Ford, E.D. 2006. Statistical inference using the *G* or *K* point pattern spatial statistics. Ecology, **87**: 1925–1931. doi:10.1890/0012-9658(2006)87[1925:SIUTGO]2.0.CO;2.

Mogren, E.W. 1956. A site index classification for ponderosa pine in northern Colorado, number 5. School of Forestry and Range Management, Colorado A&M College, Fort Collins, Colorado.

Noss, R.F., Franklin, J.F., Baker, W.L., Schoennagel, T., and Moyle, P.B. 2006. Managing fire-prone forests in the western United States. Front. Ecol. Environ. **4**: 481–487. doi:10.1890/1540-9295(2006)4[481:MFFITW]2.0.CO;2.

Parker, A.J. 1982. The topographic relative moisture index: an approach to soil-moisture assessment in mountain terrain. Phys. Geogr. **3**: 160–168. doi:10.1080/02723646.1982.10642224.

R Core Team. 2014. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from http://www.R-project.org [accessed 14 April 2015].

Rangwala, I., Barsugli, J., Cozzetto, K., Neff, J., and Prairie, J. 2012. Mid-21st century projections in temperature extremes in the southern Colorado Rocky Mountains from regional climate models. Climate Dynamics, **39**: 1823–1840. doi:10.1007/s00382-011-1282-z.

Reynolds, R.T., Sánchez Meador, A.J., Youtz, J.A., Nicolet, T., Matonis, M.S., Jackson, P.L., DeLorenzo, D.G., and Graves, A.D. 2013. Restoring composition and structure in Southwestern frequent-fire forests: A science-based framework for improving ecosystem resiliency. USDA Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, General Technical Report RMRS-GTR-310.

Ripley, B.D. 1977. Modelling spatial patterns. J. R. Stat. Soc. Series B Stat. Methodol. **39**: 172–212.

Sánchez Meador, A.J., Parysow, P.F., and Moore, M.M. 2010. Historical stem-mapped permanent plots increase precision of reconstructed reference data in ponderosa pine forests of northern Arizona. Restor. Ecol. **18**: 224–234. doi:10.1111/j.1526-100X.2008.00442.x.

Savage, M., and Swetnam, T.W. 1990. Early and persistent fire decline in a Navajo ponderosa pine forest. Ecology, **70**: 2374–2378.

Seager, R., and Vecchi, G.A. 2010. Greenhouse warming and the 21st century hydroclimate of southwestern North America. Proc. Natl. Acad. Sci. U.S.A. **107**: 21277–21282. doi:10.1073/pnas.0910856107.

Sherriff, R.L., and Veblen, T.T. 2006. Ecological effects of changes in fire regimes in *Pinus ponderosa* ecosystems in the Colorado Front Range. J. Veg. Sci. **17**: 705–718. doi:10.1658/1100-9233(2006)17%5B705:EEOCIF%5D2.0.CO;2.

Sherriff, R.L., and Veblen, T.T. 2007. A spatially-explicit reconstruction of historical fire occurrence in the ponderosa pine zone of the Colorado front range. Ecosystems, **10**: 311–323. doi:10.1007/s10021-007-9022-2.

Sherriff, R.L., Platt, R.V., Veblen, T.T., Schoennagel, T.L., and Gartner, M.H. 2014. Historical, observed, and modeled wildfire severity in montane forests of the Colorado Front Range. PLoS One, **9**(9): e106971. doi:10.1371/journal.pone.0106971.

Speer, J.H. 2010. Fundamentals of tree-ring research. University of Arizona Press, Tucson.

Stephens, S.L., Skinner, C.N., and Gill, S.J. 2003. Dendrochronology-based fire history of Jeffrey pine – mixed conifer forests in the Sierra San Pedro Martir, Mexico. Can. J. For. Res. **33**(6): 1090–1101. doi:10.1139/x03-031.

Swetnam, T.W., and Baisan. C.H. 1996. Historical fire regime patterns in the southwestern United States since 1700. *In* Fire Effects in Southwestern Forests, Proceedings of the 2nd La Mesa Fire Symposium, 29–31 March (Los Alamos, New Mexico, 1994). *Edited by* C.D. Allen. USDA Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, General Technical Report RM-GTR-286. pp. 11–32.

Touchan, R., Swetnam, T.W., and Grissino-Mayer, H.D. 1995. Effects of livestock grazing on pre-settlement fire regimes in New Mexico. *In* Proceedings: symposium on fire in wilderness and park management, Missoula, Montana, March 30–April 1, 1993. J.K. Brown, R.W. Mutch, C.W. Spoon, and R.H. Wakimoto, technical coordinators. USDA Forest Service, General Technical Report INT-GTR-320, pp. 268–272.

Underhill, J.L., Dickinson, Y., Rudney, A., and Thinnes, J. 2014. Silviculture of the Colorado Front Range landscape restoration initiative. J. For. **112**: 484–493. doi:10.5849/jof.13-092.

Veblen, T.T., and Lorenz, D.C. 1991. The Colorado Front Range: a century of ecological change. University of Utah Press, Salt Lake City.

Veblen, T.T., and Donnegan, J.A. 2006. Historical range of variability of forest vegetation of the National Forests of the Colorado Front Range. USDA Forest Service, Rocky Mountain Region and the Colorado Forest Restoration Institute, Fort Collins, Colorado.

Veblen, T.T., Kitzberger, T., and Donnegan, J. 2000. Climatic and human influences on fire regimes in ponderosa pine forests in the Colorado Front Range. Ecol. Appl. **10**: 1178–1195. doi:10.1890/1051-0761(2000)010[1178:CAHIOF]2.0.CO;2.

Walker, B., Holling, C.S., Carpenter, S.R., and Kinzig, A. 2004. Resilience, adaptability and transformability in social–ecological systems. Ecol. Soc. **9**(2): 5.

Ziegler, J. 2014. Impacts of treatments on forest structure and fire behavior in dry western forests. M.Sc. thesis, Colorado State University, Fort Collins, Colorado.