Forest Ecology and Management 465 (2020) 118087

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Fire regimes and structural changes in oak-pine forests of the Mogollon Highlands ecoregion: Implications for ecological restoration

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ARTICLE INFO

Keywords:
Historical reference conditions
Dendroecological reconstruction
Land-use changes
Interior chaparral
Transition zone
Southwest United States

ABSTRACT

Ponderosa pine (*Pinus ponderosa*) forests occur at their warmer, drier environmental limits in the Mogollon Highlands ecoregion (MHE) of the Southwestern United States, and are commonly found in stringers or discrete stands that form ecotones with interior chaparral. These "rear edge" forests are likely to be highly vulnerable to rapid changes in structure and composition with climate warming, drought, and wildfire. There is increasing interest in understanding historical conditions, ecosystem changes, and restoration needs for MHE forests. However, comprehensive reconstruction analysis of fire regimes and stand structure has not been done for these systems, which differ from many montane ponderosa pine forests by having an abundance of understory shrubs. In this study we used demographic data from field plots, fire scar samples, and dendroecology to reconstruct historical fire regimes and landscape structure at ponderosa pine-dominated sites that spanned a range of environmental conditions on the Prescott and Tonto National Forests. We found strong evidence of historical surface fire regimes with mean fire intervals ranging 1.3–15.6 years across the five MHE sites during the period 1700–1879. We found very little evidence of historical high-severity fire at any study site. Historical forest structure was open with tree densities ranging 84.7–136.4 trees ha^{-1} and stand basal area (BA) ranging 4.5–8.4 m^2 ha^{-1}. Historical composition showed codominance of ponderosa pine, Arizona white oak (*Quercus arizonica*), Emory oak (*Q. emoryi*), and Gambel oak (*Q. gambelii*). Thus, oak species and likely other hardwoods were important historical components of these ecosystems. Contemporary forests are greater in stand density and BA by 359–703% and 285–502%, respectively, compared to historical estimates. In addition, we observed contemporary shifts in species composition. Changes related to disruption of historical fire regimes have increased susceptibility of ponderosa pine forests in the MHE to rapid shifts in structure and composition that may come about with climate change and high-intensity wildfire. Meeting fuels reduction and ecological restoration goals will be challenging for land managers due to vigorous regeneration responses of shrubs to tree thinning, prescribed burning, or other management activities. Managers will be required to balance attention to historical reference conditions, conservation of biological diversity, and needs for fuels management.

1. Introduction

It is well understood that many forest ecosystems of the western United States have undergone large changes in structure and function due to industrial land uses commencing with Euro-American settlement in the late 19th and early 20th centuries (Covington et al., 1994; Hessburg et al., 2019). Understanding ecological conditions and variability that existed prior to these changes is important to resource managers, who use this information to interpret contemporary ecosystem dynamics and determine best courses of action, which may include ecological restoration (SER, 2004). Managers rely on reference information that characterizes attributes of forest structure, function, and disturbance patterns over timeframes relevant to management activities (Landres et al., 1999; Moore et al., 1999). It is assumed that predegraded forest conditions were resilient to climatic fluctuations and characteristic disturbance, and the best way to conserve species is to manage habitat with the natural range of variation (Gauthier et al., 1996; Bergeron et al., 2004; Romme et al., 2012; Hessburg et al., 2019). In forests of the western United States, various contemporary and historical sources are used to develop reference information. Techniques of

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https://doi.org/10.1016/j.foreco.2020.118087
Received 7 November 2019; Received in revised form 9 March 2020; Accepted 11 March 2020
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dendroecology are especially well-suited for reconstructing disturbance processes, forest structure, and stand composition (Fulé et al., 1997; Swetnam et al., 1999; Huffman et al., 2001; Sánchez Meador et al., 2010). For example, analysis of crossdated fire scars sampled from across a landscape can help to accurately describe several parameters of past fire regimes, including surface fire frequency, size, severity, and season of occurrence (Swetnam and Baisan, 1996). Additionally, analysis of annual growth rings from living trees and dead wood can provide information concerning establishment dates, mortality patterns, growth, and past tree size (Swetnam et al., 1999). In ponderosa pine (*Pinus ponderosa*) forests of the Southwestern United States, low decomposition rates and persistence of dead wood areas that have experienced fire suppression, enhance accuracy of dendroecological reconstructions (Mast et al., 1999; Huffman et al., 2001; Moore et al., 2004).

Fire regime and stand reconstructions have been conducted extensively in southwestern ponderosa pine forests. Pre-Euro-American settlement return intervals have been reported to range from about 4 to 36 years (Swetnam and Baisan, 1996; Reynolds et al., 2013), and tree ring records as well as other paleoecological evidence suggest that dry forests of the region have experienced frequent, recurrent fire for thousands of years (Swetnam et al., 1999; Allen, 2002). Fire regimes in the southwestern ponderosa pine forests are thought to be controlled by bottom-up factors such as fuels and topography at local to landscape scales. In addition, Native Americans in this region utilized fire to meet various resource and social needs, but effects of intentional burning on past fire regimes are poorly understood (see Allen, 2002; Liebmann et al., 2016). Decadal- and multi-decadal climatic patterns, particularly El Nino-Sothern Oscillation, are important in exerting top-down control and synchronizing fire occurrence at regional scales (Swetnam and Brown, 2011; Ireland et al., 2012). Despite this extensive understanding of fire regimes in southwestern ponderosa pine forests, uncertainty remains concerning historical fire regimes and modern anthropogenic changes for some complex southwestern ecoregions such as the Mogollon Highlands.

The Mogollon Highlands ecoregion (hereafter “MHE”) occurs between approximately 1065 m and 2100 m in elevation along the Mogollon Rim of Arizona between the montane and high desert environments of the Colorado Plateau and the lowlands and basins of the Sonoran Desert (Fleischner et al., 2017). The ecoregion roughly corresponds to Arizona’s Transition Zone, a physiographic subdivision and area of geologic transition between the Colorado Plateau and Basin and Range provinces (Peirce, 1985; Hendricks and Plescia, 1991). Here, ponderosa pine forests occur at their environmental limits, particularly with respect to maximum temperature and vapor pressure deficit tolerance, and as such have been described as “fringe” communities (Moir et al., 1997). Such transitional forests have also been referred to as “trailing edge” or “rear edge” ecosystems due to their vulnerability to climate change (Parks et al., 2019; Allen and Breshears, 1998; Savage and Mast, 2005). Forest stands in the MHE commonly form ecotones with interior chaparral, pinyon-juniper woodlands, and the northernmost reaches of Madrean evergreen woodland communities (Brown, 1994). As opposed to the primarily herbaceous understory plant communities found in more montane ponderosa pine forests, MHE forests are presently typified by an abundance of persistent, woody shrubs. Most hardwood shrubs and trees in these communities rapidly reestablish after fire and other disturbance through sprouting and/or dormant seed strategies (Cable, 1975; Pase and Brown, 1994). Limited research has suggested that low-severity surface fire regimes prevailed in some transitional forests prior to Euro-American settlement of the Southwest region in the late 1800s (Dieterich and Hibbert, 1990; Kaib et al., 2000; Sneed et al., 2002). To date, no rigorous reconstructions of these forests have been done, but it has been surmised that frequent fire regimes maintained low shrub cover and open forest structural conditions (Kaib et al., 2000). In this study we used demographic data from systematically collected fire scar samples and field plot measurements to reconstruct historical fire regimes and landscape structure at ponderosa pine-dominated sites that spanned a range of environmental conditions on the Prescott and Tonto National Forests in Arizona’s MHE. We selected sites that typified trailing edge forests where chaparral shrubs and evergreen oaks were abundant in the plant communities. We addressed the following questions: (1) What were the predominant characteristics of the historical fire regimes of these sites? (2) What were the historical forest structural characteristics? (3) How were ponderosa pine trees and stands distributed across landscapes? And, (4) have fire regimes and forest structure changed substantially since Euro-American settlement (late 1800s)? We expected that findings from this research would have implications for management of these complex forest ecosystems.

2. Methods

2.1. Study sites

To investigate historical fire regimes and structural characteristics in MHE forests, we looked for sites with ponderosa pine dominance and little evidence of recent disturbance. Ideally, fire regime reconstructions are conducted on large, remote landscapes to ensure historical evidence is intact and to capture spatial variation related to changes in vegetation and topography (Fulé et al., 2003). However, MHE landscapes are heterogeneous in vegetation structure, and fuels reduction activities have been implemented within many of the larger ponderosa pine patches. We examined high-resolution satellite imagery (e.g., National Agriculture Imagery Program (NAIP)) and Terrestrial Ecosystem Survey maps (Robertson, 2000) to search for areas with relatively undisturbed ponderosa pine forest and were able to identify several sites $>$ 100 ha in size for our study. We assumed that sites $\geq$ 100 ha would allow us to quantify landscape fire patterns as well as capture variability in historical overstory characteristics (Swetnam and Baisan, 1996; Van Horne and Fulé, 2006). We identified two study sites (Schoolhouse Gulch (SCH) and Spruce Ridge (SPR)) on the Bradshaw District of the Prescott National Forest and three sites (Ellison Creek (ELL), Horton Creek (HOR), and West Prong of Gentry Creek (PRO)) on the Payson District of the Tonto National Forest (Fig. 1). Although the sites spanned a range of environmental conditions (Table 1), we did not select them to represent a gradient, or in order to address fine-scale questions; rather, we treated sites as independent examples of broad patterns related to fire regimes and historical structure of ponderosa pine forests of the MHE. Sites ranged 1720–2270 m in elevation, and annual precipitation averages ranged 605–818 mm across the five sites. Soils varied across sites with igneous, metamorphic, and sedimentary parent materials represented (Table 1). Vegetation at the sites varied with microclimatic qualities and sub-regional biogeography. On higher, moister sites, oak species that can attain tree form and occur in both chaparral and Madrean evergreen woodland communities include Arizona white oak (*Quercus arizonica*), Emory oak (*Q. emoryi*), and Gambel oak (*Q. gambelii*). Woodland species such as pinyon pines (*P. edulis*, and *P. edulis* var. *fallax*) and junipers (*Juniperus deppeana, J. osteosperma, and J. monosperma*) are also common. Emory oak and Arizona white oak were common overstory associates at the SCH site; whereas, at SPR, Gambel oak was common and Douglas-fir (*Pseudotsuga menziesii*) was found in scattered occurrence. Tonto sites were also comprised of ponderosa pine, Emery oak, and Arizona white oak, with additional notable occurrence of alligator juniper (*J. deppeana*). Emory and white oak grow to be tree form and readily sprout when topkilled by fire (Barton and Poulos, 2018). In addition, understory vegetation at the sites showed species typical of interior chaparral communities and included various shrub species such as shrub live oak (*Q. turbinella*), alder-leaf mountain mahogany (*Cercocarpus montanus*), Fendler’s ceanothus (*Ceanothus fendleri*), Wright’s silktassel (*Garrya wrightii*) and pointleaf and Pringle manzanita (*Arctostaphylos pungens* and *A. pringlei*).

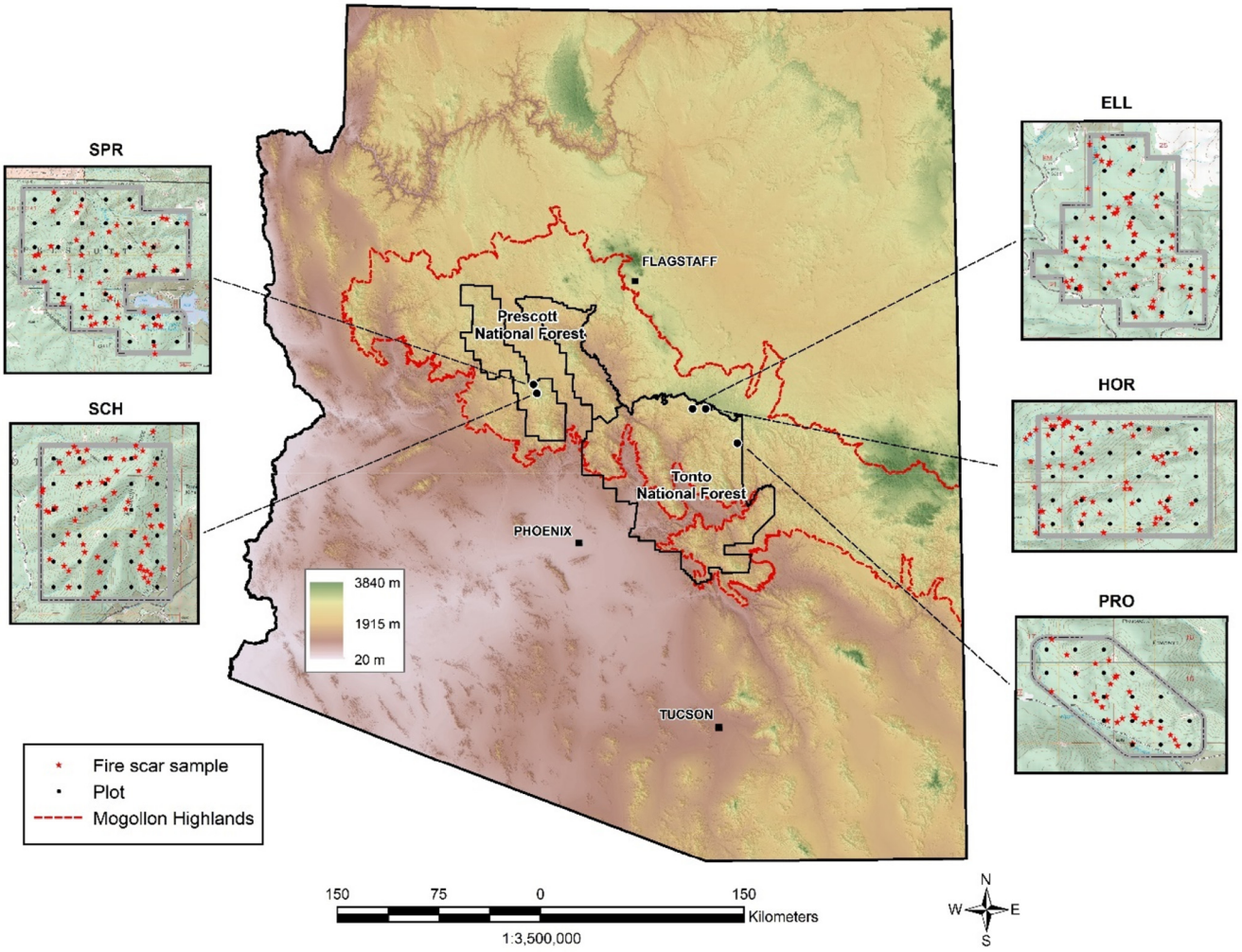

Fig. 1. Study sites used to reconstruct historical fire regimes and stand structure of ponderosa pine forests in the Mogollon Highland ecoregion in Arizona, USA (red dotted boundary). Two sites (SCH, SPR) were located within the Prescott National Forest, and three sites (ELL, HOR, and PRO) were within the Tonto National Forest. Site maps show locations of sample field plots and fire scars. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2.2. Fire scar sampling

Each site was systematically searched for trees with large fire wounds, or "catfaces," wherein multiple fire scars were apparent (Arno and Sneck, 1977). When catfaces were found and the wood appeared sound, partial cross-sections containing fire scars were collected using chainsaws. Such fire scar samples were "targeted" for sampling from spatially distributed locations across each study site. Targeted sampling is commonly used in fire history reconstructions (Farris et al., 2013) and is intended to optimize the number of fire dates included in analysis without excessive collection of wood samples. Accuracy of fire frequency estimates from targeted sampling has been shown to be high (Van Horne and Fulé, 2006; Farris et al., 2013). For each partial cross-section sampled, spatial coordinates were recorded as well as other notes related to tree species and condition (e.g., log, stump, living tree, etc.).

2.3. Forest structure plots

For each study site, we used a geographic information system (GIS)

Table 1
Descriptions of study sites used for reconstruction of fire regimes and stand structure in ponderosa pine forests of Arizona's Mogollon Highlands ecoregion. Climate summaries are 30-year normals (1981–2010). Maximum temperature and maximum vapor pressure deficit are annual maximums derived from daily averages.

National Forest	Site	Size (ha)	Sample plots (N)	Elevation (m)	Soil parent material	Precipitation* (mm)	Maximum temperature* (°C)	Maximum vapor pressure deficit* (hPa)
Prescott	SCH	331	36	1720–1950	Granite/gneiss	605	19	20
Prescott	SPR	269	22	2060–2270	Basalt/schist/granite/gneiss	723	17	17
Tonto	ELL	272	30	1720–1780	Sandstone/siltstone	798	20	21
Tonto	HOR	270	30	1755–1960	Sandstone/siltstone	818	20	21
Tonto	PRO	172	18	1840–1975	Diabase/sandstone/limestone	747	19	19

* Data (800-m resolution) from PRISM Climate Group, Oregon State University, http://prism.oregonstate.edu.

to construct a systematic grid (300-m) of sample points within the previously determined site boundary (see *Study sites*). These site maps, along with handheld global positioning system (GPS) units, were used to locate points in the field. At each field point, we established circular sample plots (0.04 ha) and took measurements of live and dead trees and understory shrubs. For each live tree > 10 cm in diameter at breast height (dbh – measured at 1.37 m above ground; Avery and Burkhart (1983)) located on a sample plot, we recorded species and measured dbh to the nearest 0.1 cm. All trees were examined for evidence of past fire such as charring or fire scars. We extracted increment cores from all live trees that met predetermined diameter limits to assure adequate sampling of trees that likely originated prior to Euro-American settlement of the region (Moore et al., 2004). For ponderosa pine, Douglas fir, and most other conifers, the diameter limit for increment core sampling was 37.5 cm dbh. For slower growing conifers (e.g., junipers and pinyon pine) as well as hardwoods, the diameter limit was set to 17 cm dbh. Conifers with diameters smaller than these limits were randomly cored at a rate of 10%, and small hardwoods (< 17 cm dbh) were cored at a rate of 5%. Species, diameter, and condition were recorded for all dead tree structures located on each sample plot. For standing dead trees, condition classes were used that represented stages of decomposition from recently deceased to highly decomposed snags (Thomas et al., 1979). Cut stumps were recorded as "historically cut" or "recently cut." Historically cut stumps were those that appeared weathered, with most of the sapwood decomposed, and were usually > 40 cm in height (Fulé et al., 1997). Trees and shrubs ≤ 10 cm dbh were tallied in size classes by species and condition. Size classes used for these smaller trees and shrubs were the following: (1) ≤ 40 cm height; (2) > 40 and ≤ 80 cm height; (3) > 80 and ≤ 137 cm height; (4) > 137 cm height and ≤ 5 cm dbh; and (5) > 137 cm height and > 5 and ≤ 10 cm dbh.

2.4. Fire regime analysis

We prepared fire scar samples for analysis by gluing them onto plywood when necessary to support the pieces, cutting into thinner cross-sections with a table saw, and sanding with progressively finer grit paper to increase discernibility of annual rings. The rings were crossdated using standard methods of dendrochronology (Stokes and Smiley, 1996) and local master chronologies. We measured annual ring widths, and then verified crossdating using COFECHA computer software (Grissino-Mayer, 2001). Fire dates were identified and a subsample (5%) was independently examined by a second analyst to verify fire scar quality and fire dates. We included only samples with two or more fire scars in analysis, and only one sample was analyzed per tree. We assumed this method would reduce the influence of smaller fires and lightning scars and provide a conservative estimate of surface fire patterns. Few samples showed annual rings or fire dates prior to the late 1600 s and preliminary analysis indicated an abrupt change in fire frequency at all sites in the late 1870 s. Previous studies have explained similar abrupt changes as resulting from intensive livestock grazing and interruption of surface fuel layers associated with Eur-American settlement in the Southwest region (Swetnam and Baisan, 1996, Fulé et al., 1997). Therefore, we identified a fire exclusion date of 1879, and analyzed the two periods of 1700–1879 (i.e. pre-Euro-American settlement) and 1880–2016 (post-settlement) separately for all sites. We focused on the pre-Euro-American settlement period of 1700–1879 for reporting of results. We composited fire dates for all samples that met the above constraints and calculated fire history statistics using the Fire History Analysis and Exploration System (FHAES) computer application (Brewer et al., 2019). We calculated mean fire return interval for all fire dates (MFI_{All}) for each site, and also calculated mean fire interval for fire dates that occurred on 10% (MFI_{10}) and 25% (MFI_{25}) of the samples for each site. The composite analysis provides an estimate of fire occurrence on the landscape but is not spatially explicit. The process of filtering data from MFI_{All} to MFI_{25} provides a range of interval estimates for progressively more widespread fires (Swetnam and Baisan, 1996). We also calculated the ratio MFI_{25}:MFI_{All}, which can be interpreted as the probability of a "smaller" fire ($1/MFI_{All}$) versus the probability of a "larger" fire ($1/MFI_{25}$) occurring in any given year (i.e., $1/MFI_{All} \div 1/MFI_{25} = MFI_{25}:MFI_{All}$). As suggested by Baker and Ehle (2001), we also calculated the mean point fire interval (MPFI), which is not an analysis of composited fire dates but rather is calculated from intervals between scars on individual trees and provides an estimate of fire occurrence at a consistent point on the landscape. Point interval typically yields longer MFI estimates than composited fire dates (Van Horne and Fulé, 2006).

Although filtering composited fire dates provides a way to interpret the relative importance of fires of different sizes, we also quantified fire sizes by mapping fire dates in ArcGIS 10.2.1 and using a convex hull algorithm to build fire polygons. Polygons were constructed from like fire dates found on three or more tree samples and then used as fire size estimates for the given year (North et al., 2005; Shapiro-Miller et al., 2007). This approach may be imprecise as it assumes fires completely burned the area within the polygons and that complete fire perimeters are evidenced by scarred trees.

2.5. Dendroecological reconstruction of forest characteristics

We reconstructed historical stand structure from field plot data and tree increment core samples following procedures outlined in Fulé et al. (1997), Huffman et al. (2001), Bakker et al. (2008), and Rodman et al. (2017). Increment cores collected from live trees on field plots were taken to the laboratory, affixed to wooden mounts, and sanded with progressively finer sandpaper until annual rings could be easily crossdated under a dissection microscope. After crossdating, we measured annual ring increments radially from the most recent complete ring (i.e., 2016) back to 1879 (fire exclusion date) for trees that established or predated this year. Radial increment data as well as field measurements of dbh, diameter at stump height (40 cm; dsh), and tree condition for all trees sampled on plots, were entered into a stand reconstruction model described by Bakker et al. (2008). In this model, a series of routines are applied to estimate tree diameter of live trees, snags, logs, and cut stumps, for a user-defined year in the past. As fire regime characteristics abruptly changed in 1879, we defined this year as the reconstruction date. Core increment values allow estimation of dbh for older trees while species-specific growth equations are used to estimate historical diameter for trees without increment core data. Death dates are estimated for dead structures (snags, logs, stumps) and dbh estimates for these trees are calculated from species-specific growth functions. Details of the reconstruction model routines are provided in Bakker et al. (2008). Huffman et al. (2001) compared outputs from this reconstruction model (Bakker et al., 2008) against actual historical data recorded in 1909–1913, and found that model errors for stand density and tree sizes ranged 7–12%. We used reconstruction model estimates of 1879 tree diameters on each plot to calculate tree density (trees ha^{-1}), basal area (BA; m^2 ha^{-1}), and quadratic mean tree diameter (QMD). QMD is a conventional forestry metric, and is useful as it provides an estimate of the diameter of a tree of average basal area (Davis and Johnson, 1987).

2.6. Analysis

Landscape structure of ponderosa pine stands in 1879 was analyzed for each site using tree density summaries from field plot data. Ponderosa pine tree densities (trees ha^{-1}) were calculated for each plot, and tree density surfaces for each site were created using the inverse distance weighted interpolation (IDW) algorithm in ArcGIS 10.2.1. Surface layers were reclassified into four tree density classes: < 25; 26–75; 76–100; and > 100 tree ha^{-1}, and patch metrics were calculated from these maps to estimate landscape percentage, patch number, and mean patch size.

Means of reconstructed (1879) and contemporary (2017) tree

density and BA were tested for differences at the five sites using Student's t-tests for paired samples. For each site, plot values at each point in time were treated as samples. We also used permutational multivariate analysis of variance (PERMANOVA) to compare differences in overstory composition at each site for each point in time (i.e., 1879 v. 2017). Compositional differences were based on tree densities of overstory species present at the given point in time. We used the PC-Ord computer application (McCune and Mefford 2016) for PERMANOVA, and significance for all statistical tests was indicated if $p < 0.05$.

3. Results

3.1. Historical fire regimes

All study sites on the Prescott (SCH and SPR) and Tonto (ELL, HOR, and PRO) National Forests showed strong evidence of historical surface fire regimes. On the Prescott National Forest, we collected 49 partial cross-section samples at SCH and 64 samples at SPR. At SCH, all samples were collected from ponderosa pine with the majority (82%) coming from old cut stumps. At SPR, all samples except one (Gambel oak) were collected from ponderosa pine and most (57%) came from standing dead snags. Only 2–8% of the samples were collected from live trees across the two sites. For samples from SCH, we crossdated 428 individual fire scars with earliest fire date being 1641 and the latest was 1946. For samples at SPR, we crossdated 565 fire scars with 1621 and 1994 being the earliest and latest fire dates, respectively. For the period 1700–1879, we identified 90 unique fire dates at SCH and 94 at SPR. We identified only one fire date for the period 1880–2017 at SCH and nine fire dates for this period at SPR (Fig. 2). Mean fire interval for all crossdated fires (MFI_{All}) was < 2.0 years for both sites (Table 2). Weibull median probability interval for all fires (WMPI) was 4% less than MFI_{All} at SCH and 6% less than MFI_{All} at SPR. Mean fire intervals for more widespread fires that scarred at least 10% (MFI_{10}) and at least 25% (MFI_{25}) of the samples, ranged 2.7–8.4 years across both sites. The probability of smaller versus larger fire occurrence (MFI_{25}:MFI_{All}) was higher for SCH than SPR, and < 5.0 for both sites (Table 2). Estimated mean fire size based on polygons constructed for fires that scarred three or more trees at a given site was not significantly lower ($p = 0.165$) for SCH (61.4 ha) than SPR (75.0 ha) (Fig. 3). Mean point fire interval was less than 8.5 years at both SCH and SPR (Table 2).

On the Tonto National Forest, we collected 54, 59, and 24 partial cross-section samples on ELL, HOR, and PRO, respectively. All samples were collected from ponderosa pine, and were mainly found on cut stumps (81% ELL and 75% PRO) or snags (46% HOR). A small fraction of samples was collected from live trees at ELL (5%) and HOR (9%), whereas no samples were collected from live trees at PRO. We crossdated 583 fire scars at ELL, 485 at HOR, and 202 at PRO. The earliest fire dates identified on samples were 1624, 1652, and 1660, and the latest fire dates were 1990, 1900, and 1890 for ELL, HOR, and PRO sites, respectively. For the period 1700–1879, we found 139 unique fire dates at ELL, 113 at HOR, and 80 at PRO. We identified two fire dates for the period 1880–2017 at ELL, one fire date for this period at HOR, and one fire date post-1879 at PRO (Fig. 2). Composite fire scar analysis showed that MFI_{All} ranged 1.29–2.13 years across the Tonto National Forest sites (Table 2). Weibull median probability interval ranged 1.25–1.81 years. Mean fire interval for widespread fires (MFI_{10} and MFI_{25}) ranged 2.39–15.55 years (Table 2). Probabilities for smaller fire occurrence versus large fires (MFI_{25}:MFI_{All}) were 11.18 and 10.16 for ELL and HOR, respectively; however, MFI_{25}:MFI_{All} for PRO was 3.59. Estimated mean fire sizes were 53.0 ha (CV = 83%) and 57.4 ha (CV = 76%) for ELL and HOR, respectively, whereas mean fire size for PRO was 12.8 ha (CV = 102%) (Fig. 3). Mean point fire intervals for the three sites ranged 10.19–10.87 years.

3.2. Fire synchrony

At individual sites, we identified 3–11 fire years that occurred on > 20% of the collected samples (Fig. 4). The most important fire years (i.e., found on the highest proportion of samples) at SCH, SPR, ELL, HOR, and PRO were 1765, 1818, 1861, 1879, and 1808, respectively. We identified 59 sub-regional fire years that were shared by the two PNF sites (SCH and SPR) (Fig. 4). The most common sub-regional PNF fire year, which was found on 28% of samples, was 1829. Other fire years occurring on more than 20% of combined samples at SCH and SPR were 1765, 1794, 1803, 1827, 1840, 1845, and 1851. For TNF, we found 56 fires shared sub-regionally across the three sites (ELL, HOR, and PRO). The most important fire year on TNF sites was 1879, which was identified on 23% of the combined samples. One other fire year, 1808, was found on > 20% of the TNF combined samples. Other important years that occurred on > 15% of TNF samples were 1794, 1817, 1818, 1840, 1851, and 1855. Regionally, we found 22 fire years shared by all sites (Fig. 4). Two fire years, 1829 and 1849, were found on > 20% of the combined PNF and TNF samples. Other important years that occurred on > 15% of all samples were 1794, 1827, and 1851.

3.3. Historical stand conditions

Dendroecological reconstruction of 1879 forest structure at PNF sites indicated that mean total tree densities at SCH and SPR were 84.7 trees ha^{-1} and 136.4 trees ha^{-1}, respectively, in 1879 (Fig. 5). Mean BA in 1879 of all species combined at the two PNF sites was 4.5 m^2 ha^{-1} and 6.7 m^2 ha^{-1} for SCH and SPR, respectively (Fig. 5A). Quadratic mean diameter (QMD) was 26.1 cm and 24.6 cm on average for all tree species combined at SCH and SPR, respectively. At SCH, tree density was almost evenly comprised of ponderosa pine (55% of stems on average) and tree-form oaks (Gambel oak, Arizona white oak, and Emory oak) (42% of stems); however, ponderosa pine made up 70% of stand BA. At SPR, oak was historically dominant both in terms of tree density (70% of stems) as well as stand BA (59% of total BA) (Fig. 5B). Ponderosa pine was completely absent on 28% of reconstructed SCH plots and 27% of SPR plots. No trees of any species were found in reconstructions of 5% of SCH plots and 4% of SPR plots. Alligator juniper comprised a minor fraction of tree density and BA at both PNF sites, and no other species were indicated in our historical reconstructions.

Mean reconstructed tree densities at TNF sites ranged 84–100 trees ha^{-1}, and BA ranged 5.8–8.4 m^2 ha^{-1} (Fig. 5A and 5B). QMD in 1879 for all species combined at the three PNF sites ranged 24.5–29.0 cm. Ponderosa pine comprised 27–36% of tree numbers on average, and density at all sites was dominated by oak species (43–59% of stems). Ponderosa pine trees were historically absent on 30–37% of sample plots, and no trees of any species were found on up to 7% of sample plots across the three TNF sites. Although juniper made up a small percentage of stem density (3–13%), this species was more important at TNF sites in terms of BA (26–41% of total BA).

3.4. Historical ponderosa pine landscape patterns

Interpolated patterns of tree densities indicated that ponderosa pine primarily occurred on PNF and TNF sites in patches < 25 and 26–50 trees ha^{-1}, which comprised 18%-63%, and 24%-69%, respectively, of site areas (Fig. 6A). Less than 7% of any site was made up patches 76–100 trees ha^{-1}, or > 100 trees ha^{-1}, in 1879. In addition, there were more low-density patches than high-density patches of ponderosa pine historically. For example, number of patches < 25 trees ha^{-1} ranged 1–10, number of patches 26–50 trees ha^{-1} ranged 1–4, and number of higher density patches (i.e., classes > 50 trees ha^{-1}) ranged up to 3 across all sites (Fig. 6B). Interestingly, mean patch sizes appeared to be larger for low-density patches than higher density patches, For example, mean ponderosa pine patch size ranged up to 187 ha

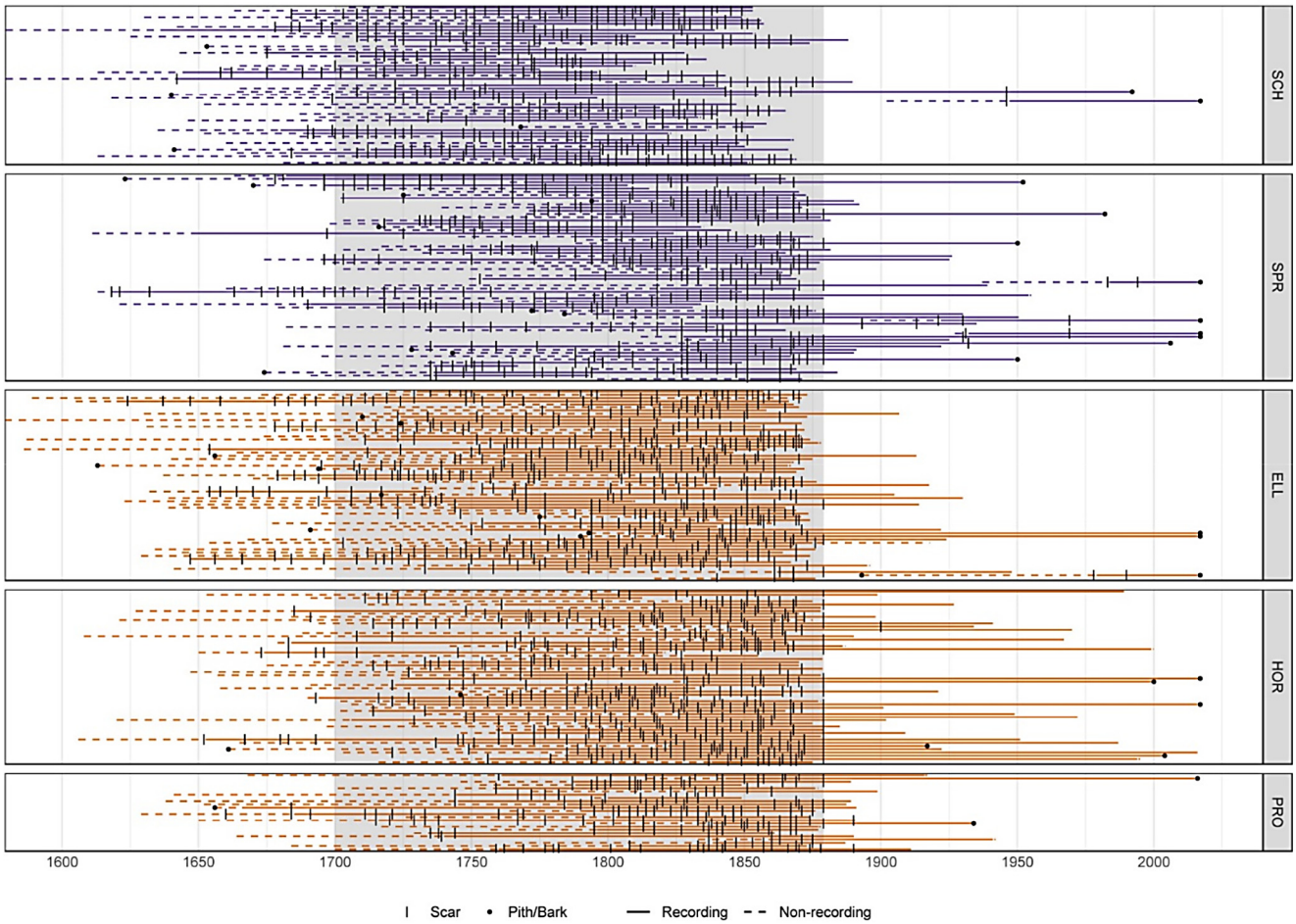

Fig. 2. Composite fire history chart for two study sites (SCH and SPR) on the Prescott National Forest and three sites on the Tonto National Forest (ELL, HOR, and PRO) in Arizona. Charts show each individual fire scar sample (horizontal lines) and crossdated fire dates (vertical tick marks) observed on samples. Solid horizontal lines indicate recording periods for fire scar samples whereas dotted horizontal lines show non-recording periods (e.g., before the first scar formed on a sample, or periods when scars cannot be identified due to decay or charring). Shaded area indicates analysis period of interest (1700–1879) prior to modern shift in fire regime patterns (post-1880).

in 1879 for density class 26–50 trees ha^{-1}, whereas the largest mean patch size for any density class above 50 trees ha^{-1} was just 20 ha (Fig. 6C).

3.5. Contemporary stand conditions

In 2017, tree densities and BA at both PNF sites were significantly greater ($p < 0.001$) than reconstructed conditions. Tree density means were 389 trees ha^{-1} at SCH and 870 trees ha^{-1} at SPR, and mean BA means were 20.6 m^2 ha^{-1} and 35.3 m^2 ha^{-1} at the two sites, respectively (Fig. 5). Tree density changes represented increases of 359% and 538%, and increases in BA were 357% and 427% for SCH and SPR, respectively. Permutational multivariate analysis of variance (PERMANOVA) showed that composition based on species densities was significantly different ($p < 0.001$) between 1879 and 2017 at both sites. The main compositional changes were increases in oak species that comprised 50% of stems at SCH and 67% of stems at SPR in 2017 (Fig. 5C).

In addition, we observed higher numbers of white fir (*Abies concolor*) and Douglas-fir in 2017 at SPR compared with reconstructed conditions.

Similar to PNF sites, tree densities at the three TNF sites were all

Table 2
Historical (1700–1879) fire regime parameters for Mogollon Highlands ecoregion study sites in ponderosa pine forests of the Prescott and Tonto National Forests, Arizona. Shown are the number of catface samples crossdated, mean fire interval in years for all fire dates (MFI_{All}), fire dates occurring on 10% of samples (MFI_{10}), and those occurring on 25% of samples (MFI_{25}). Larger values of the index MFI_{25}:MFI_{All} suggest greater tendency for smaller historical fire sizes. Also shown is Weibull median probability interval for all fires (WMPI) and mean point fire interval (MPFI) in years for each site.

			Fire regime parameter					
National Forest	Site	Samples (N)	MFI_{All}	WMPI	MFI_{10}	MFI_{25}	MFI_{25}:MFI_{All}	MPFI
Prescott	SCH	49	1.97	1.88	2.73	8.35	4.24	8.09
Prescott	SPR	64	1.92	1.80	3.38	5.59	2.91	8.45
Tonto	ELL	59	1.29	1.25	2.39	14.42	11.18	10.45
Tonto	HOR	54	1.53	1.42	2.76	15.55	10.16	10.19
Tonto	PRO	24	2.13	1.81	2.71	7.64	3.59	10.87

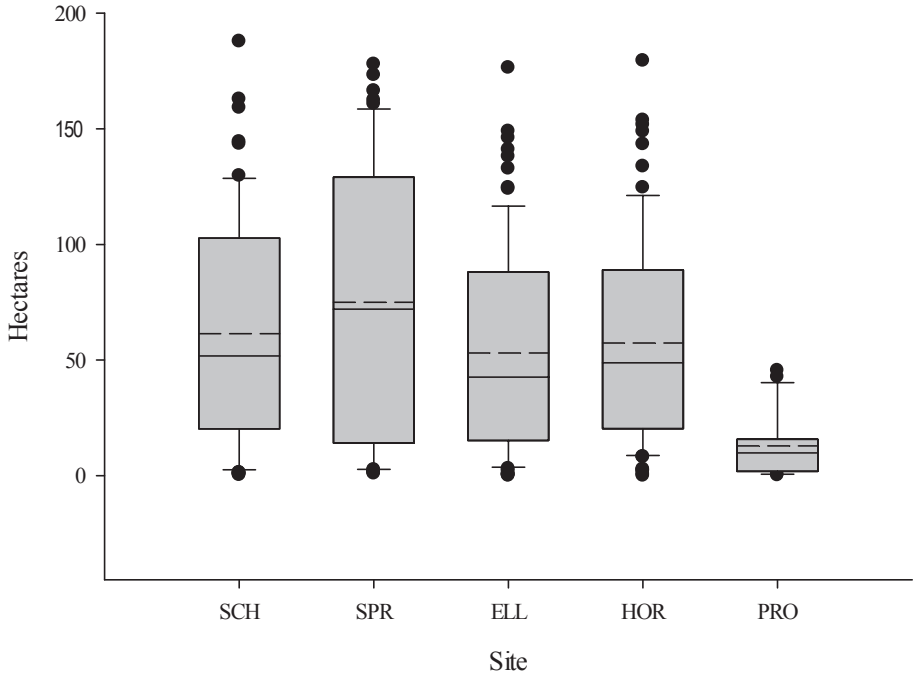

Fig. 3. Box plots of surface fire size estimates based on fire scar locations at study sites on the Prescott (SCH and SPR) and Tonto (ELL, HOR, and PRO) National Forests in Arizona. Dashed lines within boxes indicate fire size means, and solid lines in boxes are fire size medians.

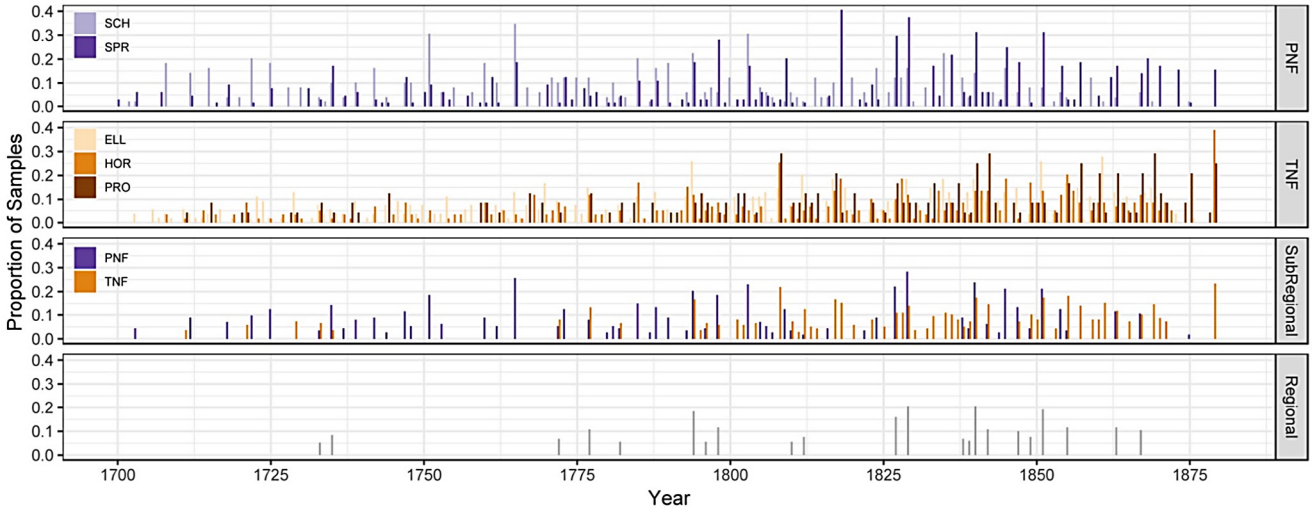

Fig. 4. Fire dates observed on samples all sites (top), sub-regional (middle), and regional (lower). Y-axis is proportion of total samples within each scale of observation (all sites, sub-regional, regional).

significantly ($p < 0.001$) higher in 2017 than in 1879 (Fig. 5C). At ELL, HOR, and PRO, mean tree densities ranged 491.7–680.0 trees ha^{-1} and represented increases of 392–703%. Mean BA was also significantly ($p < 0.001$) greater in 2017 than 1879 at all three TNF sites, and ranged 23.1–36.1 m^2 ha^{-1} (Fig. 5D). These values represented BA increases of 285–502%. PERMANOVA indicated that species composition in terms of tree densities was significantly ($p < 0.001$) different at all three TNF sites between 1879 and 2017 conditions, but, in contrast to PNF sites, ponderosa pine importance increased from 1879 to 2017 and was 37–51% of total stem density on average across the three TNF sites in 2017. Alligator juniper also increased across all TNF sites and made up 22–38% of stem density in 2017. Oak, however, decreased in importance from 1879 to 2017, and comprised 10–26% of tree density on average across the three TNF sites in 2017 (Fig. 5C). At HOR, Douglas-fir, white fir, boxelder (*Acer negundo*), maple (*Acer* spp.), and manzanita combined made up 17% of stems on average in 2017 (Fig. 5C).

4. Discussion

4.1. Fire regimes

Frequent surface fire regimes predominated for at least 200 years before the 20th century at all five MHE sites. Results of composite fire scar analysis showed mean fire intervals ranging 1.3–15.6 years, and these findings were supported by analysis of mean point fire intervals, which ranged 8.1–10.9 years across all sites (Table 2). Frequent fire regimes in MHE ponderosa pine forests have been described previously in less intensive studies and unpublished reports (Dieterich and Hibbert, 1990; Kaib et al., 2000; Sneed et al., 2002). For example, Dieterich and Hibbert (1990) analyzed seven fire-scarred samples collected from dead material at Battle Flat, an 87-ha ponderosa pine-Arizona white oak site, located about 21–23 km from our PNF sites and reported a composite MFI of 1.89 years (1700–1874). Similarly, in an

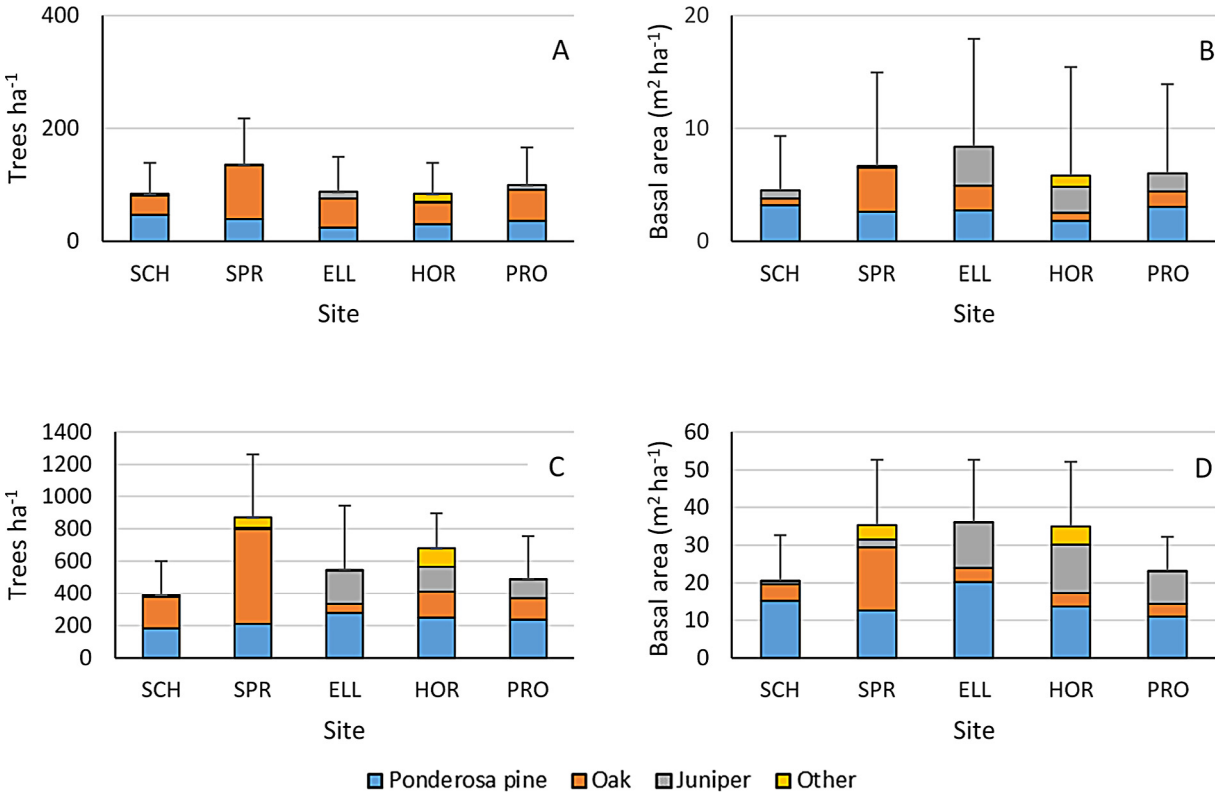

Fig. 5. Historical and contemporary tree densities (A and C, respectively) and basal area (B and D, respectively) for ponderosa pine as well as oak and juniper species groups at study sites on the Prescott (SCH and SPR) and Tonto (ELL, HOR, and PRO) National Forests in Arizona. Note: y-axis scale differences between historical and contemporary periods.

unpublished report, Sneed et al. (2002) analyzed 12 samples collected from our SCH site and found MFI to be 2.53 years. This mean interval was slightly longer than our findings (Table 2), and may reflect fewer samples as well as a long frame of analysis (1615–1996) that included both early dates with no fire records (pre-1650) and the post-fire-exclusion period (post 1875) (Sneed et al., 2002). On the Tonto National Forest, Kaib et al. (2000) reported that MFI ranged 1–10 years for smaller fires (all fire dates) to more widespread fires (25% filter; ≥ 8 of 32 fire-scarred trees) at Webber Creek, a ponderosa pine site about 13 km west of ELL and 27 km west of HOR. Similarly, frequent fire regimes have been documented for ponderosa pine or related forests forming ecotones with other shrub-dominated communities in the Southwest U.S. and Mexico (Swetnam et al., 1992; Fulé and Covington, 1997; Grissino-Mayer et al., 2004; Iniguez et al., 2009; O'Connor et al., 2014; Guiterman et al., 2015). For example, Swetnam et al. (1992) found MFI to be 3.9 years at a ponderosa pine (and Arizona pine; *P. arizonica* var. *arizonica*) site in Chiricahua National Monument in southeastern Arizona, where Madrean evergreen woodland was the primary associated vegetation community, and interior chaparral and semi-desert grassland communities also occurred on the landscape. Kaib et al. (1996, 1999) reported similar fire regimes at sites in southeast Arizona. In ponderosa pine-dominated forests of the Santa Catalina Mountains, historical MFI ranged 9.0–9.8 years (Iniguez et al., 2008), and WMPI ranged 3.6–8.4 years for the period 1689–1880 at three sites in the Huachuca Mountains (Danzer, 1998). Frequent historical fire regimes have also been reported for pine forests in Madrean evergreen woodlands of the Sierra Madre Occidental, Mexico (Fulé and Covington, 1997). Few studies have documented noteworthy high-severity fire occurrence in these ecosystems; however, Iniguez et al. (2009) found evidence of both frequent surface fires as well as a stand-replacing fire (60 ha) that occurred in 1867 at a dry mixed-conifer–ponderosa pine–oak site adjacent to chaparral and oak-scrub communities on Rincon Peak in Arizona. Reynolds et al. (2013) suggested that ponderosa pine dominance in southwestern forests is a reliable indicator of historical frequent fire regimes, regardless of understory characteristics. However, this hypothesis has not been systematically tested. We did not attempt to disentangle the role of Native American burning on fire frequency at our sites, but it is well understood that indigenous peoples used fire on these landscapes for a variety of purposes (Allen, 2002). Although Allen (2002) suggests that an abundance of lightning ignitions, and climate patterns that include seasonal drought, would be sufficient to produce frequent surface fire regimes in these forests regardless of Native American burning practices, Liebmann et al. (2016) found that fire frequency in the Jemez Province of northern New Mexico increased due to reforestation after decline of Native American populations between 1620 and 1640. Very little is known about Native American burning and land management practices of peoples that inhabited lands near our study sites (e.g., Yavapai, Apache, etc.).

While frequencies of surface fires at our MHE sites resemble those of other southwestern ponderosa pine forests, multiple lines of evidence indicate that historical fires at these sites were relatively small in extent. For example, comparison of MFI_{25} with MFI_{All} indicated that widespread fires were less probable than smaller fires, particularly at the ELL and HOR sites on the Tonto National Forest (Table 2). Although few fire history studies report this ratio (MFI_{25}:MFI_{All}), our findings contrast with those of Fulé et al. (2003), who reported $WMPI_{25}$:$WMPI_{All}$ (note: Weibull median probability interval) ranged 1.4–2.9 for montane ponderosa pine forests in northern Arizona near Grand Canyon National Park. At a pinyon-juniper-ponderosa pine ecotone site in northwestern Arizona, MFI_{25}:MFI_{All} values ranged 2.12–4.98 (Ireland et al., 2012). Thus, historical fire sizes at our sites in Arizona's MHE may have been particularly small compared with other southwestern ponderosa pine sites. We found fire size estimates based on spatially explicit delineations were not commonly greater than 100 ha, and most fires were less than 75 ha (Fig. 3). Fire synchrony analysis suggested that smaller

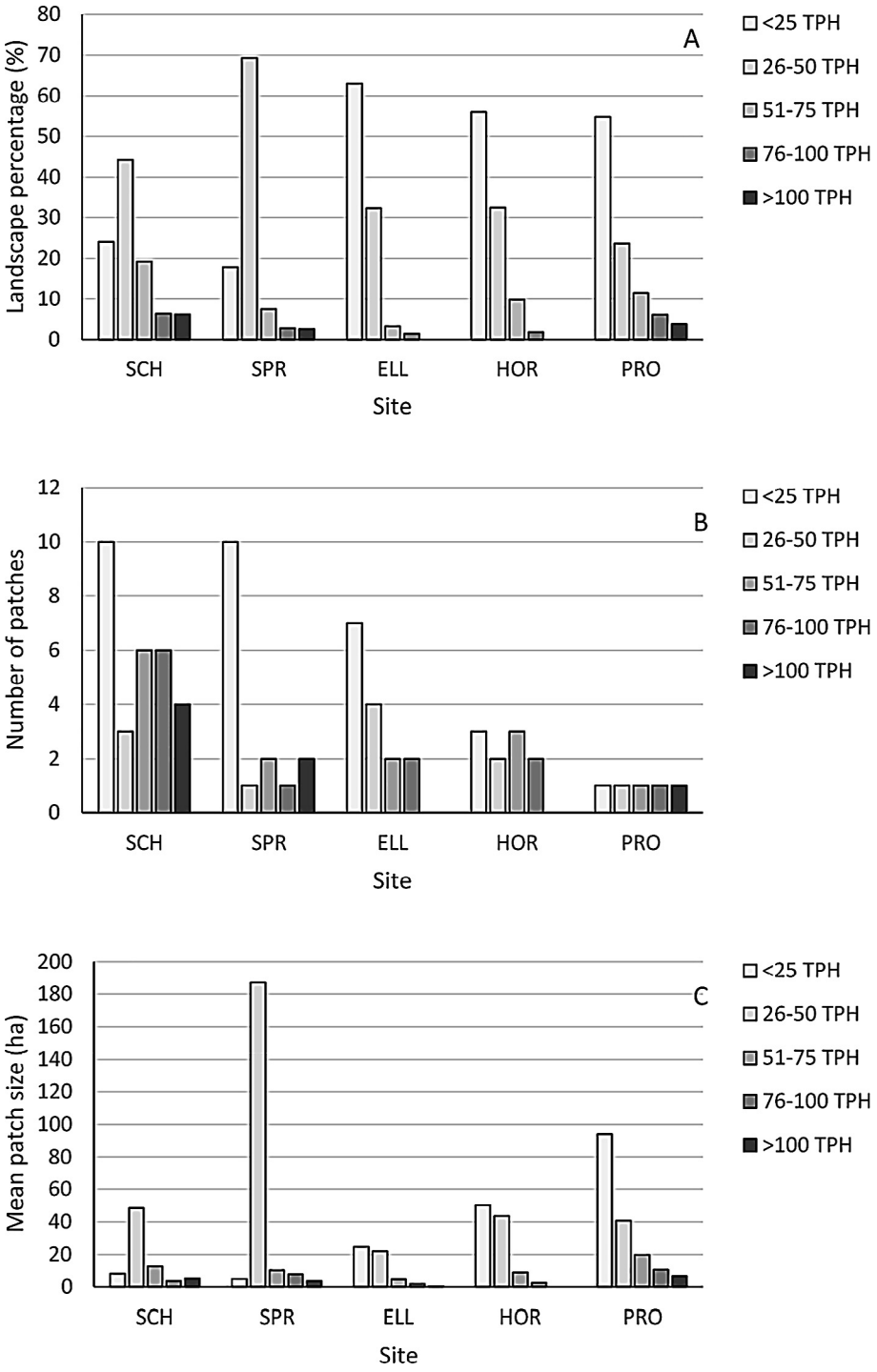

Fig. 6. Landscape metrics for reconstructed (1879) ponderosa pine tree density (trees ha^{-1} (TPH)) in five density classes at study sites on the Prescott (SCH and SPR) and Tonto (ELL, HOR, and PRO) National Forests in Arizona. Shown are percentage of the landscape made up by ponderosa pine patches (A), number of ponderosa pine patches (B), and mean size of ponderosa pine patches (C) at each site.

historical fires at our MHE sites were likely driven by local, bottom-up factors, although regional climatic drivers were important in determining some fire events. For example, all sites showed fire events in 1851, a year identified as a regionally important fire year by Swetnam and Brown (2011), who examined common fire dates from 120 sites in Arizona and New Mexico. Other dates we identified that also have been reported as regionally important were 1765, 1861, and 1879. Interestingly, we did not identify 1748 as a regionally important fire date, although this has been found by others to be the single most prevalent fire date in Southwest fire chronologies (Swetnam and Brown, 2011). This suggests that fires at ponderosa sites with Arizona's MHE were strongly influenced by fine-scale factors such as variability in fuel type (e.g. shrubs versus grasses) and connectivity (Falk et al. 2007, Ireland et al. 2012). Major fuel breaks such as rock outcrops, cliffs, and canyons were not present on our sites.

4.2. Structural patterns

Forests of our MHE sites were historically open in structure, and heterogeneous in ponderosa pine density. Our reconstruction analysis

indicated that these landscapes were made up of low density (< 50 trees ha^{-1}) patches of ponderosa pine with denser patches occurring infrequently (Fig. 6A). Tree-form oak species were co-dominant in terms of tree numbers in forest overstories. Historical forest stand densities at our MHE sites were within the natural range of variation reported for ponderosa pine systems across the Southwest. For example, Reynolds et al. (2013) compiled results from dendroecological reconstructions as well as early survey records and found historical tree densities in ponderosa pine forests across Arizona and New Mexico ranged 28.9–306.3 trees ha^{-1}, and BA ranged 5.1–20.5 m^2 ha^{-2}, prior to fire exclusion. Although, Reynolds et al. (2013) considered all plant associations for ponderosa pine, including ponderosa pine/Gambel oak, ponderosa pine/Arizona white oak, and ponderosa pine/Emory oak, few historical data for these associations are available. One exception came from Woolsey (1911), who described an "average" yellow [ponderosa] pine stand (i.e., dominated by mature ponderosa pine trees) on the Prescott National Forest with 68.4 trees ha^{-1}, somewhat lower than our estimates for our PNF sites (Fig. 5). It should be noted that, although ponderosa pine dominated in terms of BA, tree-form oaks were historically more numerous at all of our study sites except SCH. Earlier studies have surmised that frequent fires in ponderosa pine forests of MHE were likely supported primarily by fine fuels, and shrub abundance was assumed to be low (Kaib et al., 2000), but there have been no prior dendroecological reconstruction of stand conditions. Thus, our study expands understanding of the natural range of variation for ponderosa pine forests in the Southwest and provides new information concerning fringe forests occupying ecotones with chaparral and evergreen woodlands.

Although we could not reconstruct historical understory composition, we hypothesize that shrubs were present at our sites historically, while grasses and fine fuels that are more favorable to spread of surface fire were more abundant. We base this hypothesis on our understanding of shrub responses to fire as described in the relevant literature. For example, following an initial burn, recovering interior chaparral shows reduced flammability and may not reburn for 10–20 years (Cable, 1975; Dieterich and Hibbert, 1990). Further, natural fire rotations of interior chaparral in Arizona are thought to be about 30–40 years (Sneed et al., 2002), and coastal chaparral burns with high severity at intervals of 50–100 years (Conard and Weise, 1998). Juvenile tissues of sprouting chaparral shrubs tend to be fire resistant, but as they age stems become rich in epicuticular waxes and support low fuel moistures, characteristics which can accelerate wildfire intensity, severity, and spread in older stands (Rothermel and Philpot, 1973; Nagel and Taylor, 2005; Keeley, 2006). In addition, frequent surface fires may over time reduce shrub abundance by depleting resources and bud banks required for sprouting and persistence, and favor fine fuels such as grasses and other herbaceous plants. This process was suggested by Fulé and Covington (1998), who found lower resprouting hardwood abundance in pine-oak forests where fires continued to burn with expected frequency compared with forests where fire had been excluded for about 50 years in the Sierra Madre Occidental, Mexico. Indeed, similar landscapes of the Sierra Nevada range in California show distinct fire regimes and related feedback mechanisms of chaparral and mixed conifer forests that appear to maintain stable, distinct systems (Lauvaux et al., 2016).

Although stand-replacing fire occurrence is difficult to reconstruct using our methods, we expected historical high-severity fire to be evidenced by large fire-scar-free areas on the landscapes, plots showing no ponderosa pine in dendroecological reconstructions (i.e., only younger trees (post-1879) present in 2017), and/or charred tree remnants observed in our field plot measurements. However, in our study, these lines of evidence did not clearly converge and we cannot conclude that stand-replacing fire behavior was important historically. For example, we found fire scars indicative of repeated surface fire abundant and distributed evenly across all study sites (Fig. 1), but we also found ponderosa pine was absent in reconstructions of 27–37% of sample plots. Although only a small fraction (up to 7%) of plots was completely absent of trees, it is plausible that tree-form oaks may have originated from sprouting after severe fire on plots where ponderosa pine was absent. Charred tree structures were noted during field plot sampling but we found no extensive patches indicating large stand-replacing fire.

4.3. Contemporary conditions

Ecological conditions in contemporary ponderosa pine forests of Arizona's MHE are substantially different from those prior to fire regime disruption. Overall, tree density increases found in our study, and recruitment of shade-tolerant and fire-intolerant species, parallel those widely reported for frequent-fire forests across the western US (Covington et al., 1994; Reynolds et al., 2013; Strahan et al., 2016; Rodman et al., 2017; Hessburg et al., 2019). Major landscape changes due to historical livestock grazing, mining, and timber harvesting have been described for central Arizona landscapes. For example, Prescott, Arizona was formally established as the Territorial Capital in 1864, and forests in the area as well as other landscapes of the MHE experienced intensive livestock grazing and timber harvesting (Croxen, 1926; Dieterich and Hibbert, 1990). Leopold (1924) described early landscape changes in central Arizona, and observed widespread soil erosion, cessation of spreading surface fires, and increases in "brush" (chaparral) cover and tree reproduction. Similarly, Croxen (1926), gathered anecdotes from early settlers within the Tonto National Forest, and recounted stories of general decreases in grasses within pine forests and increases of chaparral throughout these landscapes. In relatively cooler montane ponderosa pine forests, intensive grazing associated with Euro-American settlement of northern Arizona reduced herbaceous fuel layers and limited spread of natural surface fires (Covington and Moore, 1994; Covington, 2003). Cessation of the frequent fire regime along with active fire suppression by forest managers later in the 20th century resulted in establishment of substantial cohorts of tree regeneration (Savage et al., 1996; Mast et al., 1999; Sánchez Meador et al., 2009; Schneider et al., 2016). Increases in forest density and buildup in woody surface fuels and forest floor layers led to radical changes in fire behavior as well as ecosystem function in montane forests (Moore et al., 1999). In addition to fire exclusion and reduction of grass competition, shrub proliferation in MHE forests was also likely aided by early timber harvests for mining, fuel, and forage (Croxen, 1926). For example, use of pine, oak, and juniper for mining activities on the Prescott National Forest resulted in some areas being mostly cutover by 1880 (Dieterich and Hibbert, 1990). Reduction in forest cover and disturbance associated with harvesting would be expected to stimulate shrub regeneration, particularly that of sprouting species. Fire exclusion beginning around 1879 likely allowed shrub survival and facilitated development of long-term shrub persistence mechanisms.

5. Management implications

Ecological changes related to disruption of historical fire regimes have increased susceptibility of ponderosa pine forests in Arizona's MHE to rapid shifts in structure and composition that may come about with climate change and high-intensity wildfire (Parks et al., 2019). Overall, forests of the Southwest have recently experienced increases in high-severity fire due to climate warming, drought, and land use factors (O'Connor et al., 2014; Singleton et al., 2019). Increases in tree density, reduction of grasses in understory communities, and development of persistent shrub layers all increase potential for stand replacing fires. Increasing warming and drought conditions following high-severity fire can result in limited tree regeneration and conversion to persistent shrubfields (Barton, 1999, 2002; Savage and Mast, 2005; Savage et al., 2013; Ouzts et al., 2015; Guiterman et al., 2018). Susceptibility to type conversion is amplified for ponderosa pine forests occurring at their environmental limits within Arizona's MHE, where conifer regeneration after wildfire can be negligible (Ouzts et al., 2015).

Our findings suggest that MHE forests were resilient to climate

fluctuations and fire for at least 200 years prior to Euro-American settlement. These historical conditions help managers understand processes that contributed to ecological resilience, which in turn can be used to frame strategies for management with climate change (Gauthier et al., 1996; Bergeron et al., 2004). Prescriptions aimed at restoring resilience, treating hazardous fuels, and reducing crown fire potential in these systems will follow basic principles described for frequent fire forests (Agee and Skinner, 2005). However, meeting fuel reduction goals is certain to be challenging for land managers due to vigorous sprouting responses of shrubs to tree thinning, prescribed burning, or other management activities such as mastication focused on shrub control (Pond and Cable, 1960; Kane et al., 2010; Brennan and Keeley, 2015). In addition, our study indicated that tree-form oak species and likely other hardwoods were important components of these ecosystems prior to fire regime disruption. Thus, managers will be required to balance attention to historical reference conditions, conservation of biological diversity, and needs for fuels management. Restoration treatments should be focused on reducing overstory density while maintaining ponderosa pine seed trees and tree-form oaks such as Arizona white oak, Emory oak, and Gambel oak. Multiple entries with prescribed fire or mastication to reduce sprouting understory shrubs and encourage establishment and growth of herbaceous species, limiting livestock grazing, and perhaps seeding with native grasses may all lower crown fire potential and help restore ecosystem function. In some cases, maintaining forest cover while treating understories may help dampen shrub sprouting responses. Drought tolerant shrubs and other sprouting woody species are likely to be favored with a rapidly warming and drier climate. Because of heightened risk of conversion due to climate-driven tree mortality as well as wildfire, fringe forests such as those within Arizona's MHE should be considered high priority for conservation.

CRediT authorship contribution statement

David W. Huffman: Conceptualization, Methodology, Writing - original draft. **M. Lisa Floyd:** Conceptualization, Writing - review & editing. **Dustin P. Hanna:** Dendrochronology. **Joseph E. Crouse:** Writing - review & editing. **Peter Z. Fulé:** Conceptualization, Writing - review & editing. **Andrew J. Sánchez Meador:** Writing - review & editing. **Judith D. Springer:** Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We thank staff and students of the Ecological Restoration Institute for assistance in field data collection, logistics and data management. In particular, we thank Scott Curran, Don Normandin, John Paul Roccaforte, and Caleb Stotts. We thank US Forest Service staff, particularly Keith Borghoff, Deb Cress, Pete Gordon, Chris Welker, and Danny Whatley for assistance with field reconnaissance coordination and permitting. We are grateful to the late Dr. Paul Sneed whose insights into the fire dynamics of Prescott forests were foundational for this study. We thank two anonymous reviewers for their comments on an earlier manuscript draft. This work was funded by a grant from the US Forest Service. Northern Arizona University is an equal opportunity provider.

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2020.118087.

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