

Changes in forest structure of a mixed conifer forest, southwestern Colorado, USA

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ARTICLE INFO

Article history:

Received 16 February 2009

Received in revised form 6 June 2009

Accepted 8 June 2009

Keywords:

Ecological restoration

Fuel

Dendrochronology

Fire history

San Juan Mountains

ABSTRACT

We selected a warm/dry mixed conifer forest (ponderosa pine, white fir, Douglas-fir, and aspen) in southwestern Colorado to reconstruct historical conditions of fire regime and forest structure in preparation for an experiment in ecological restoration. Although mixed conifer forests are of high ecological and social value in the Southwest, they have been less studied than ponderosa pine forests. Fire-scar analysis on a 150-ha area showed recurring fires at mean intervals of 24 years (all fires with minimum of 2 sample trees scarred) to 32 years (fire scarring 25% or more of sample trees) from the 16th century until the abrupt cessation of fire after 1868, concurrent with European settlement. There was no evidence in age or species-specific data of severe burning at the scale of the study blocks (approximately 200 ha). The forest remained unharvested throughout most of the 20th century, until a cut in the early 1990s removed approximately equal basal areas of ponderosa pine and white fir. Forest structure had already changed substantially, however. Total basal area increased from an average of 11 m² ha⁻¹ in 1870 to 27 m² ha⁻¹ in 2003, despite harvesting of at least 8.4 m² ha⁻¹. Ponderosa pine declined from representing nearly two-thirds of basal area in 1870 to one-third in 2003. The other species increased dramatically, especially white fir, which went from 12% to 35% of basal area and dominated stand density with an average of 392 trees ha⁻¹. Total tree density increased from 142 trees ha⁻¹ in 1870 to 677 trees ha⁻¹ in 2003. The ecological changes that occurred here since the 19th century have been in exactly the opposite direction considering the warm, fire-favoring climate expected in the 21st century. If warm/dry mixed conifer forests of southern Colorado are to have a reasonable chance for persistence under the future climate regime, restoring conditions more similar to the frequently burned, open forests of the past is likely to be a useful starting point.

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1. Introduction

Mixed conifer forests of the Southwest, characterized by diverse stands of ponderosa pine (*Pinus ponderosa*), white fir (*Abies concolor*), Douglas-fir (*Pseudotsuga menziesii*), quaking aspen (*Populus tremuloides*), and sometimes other species such as limber pine (*Pinus flexilis*), are of great ecological and management interest. These forests occupy intermediate elevations between the lower pine forests and the higher stands of spruce (*Picea*) and fir. Relatively warm, dry mixed conifer at lower elevations or on southerly aspects were characterized by frequent surface fires synchronized by climate, although mean fire intervals of approximately 9–30 years were longer than those observed in ponderosa pine forests (3–14 years) (Brown et al., 2001; Fulé et al., 2003a; Grissino-Mayer et al., 2004; Heinlein et al., 2005; Brown and Wu, 2005). Although warm/dry mixed conifer forests occur in environments that are wet enough

to support mesic trees such as *Abies* and *Populus*, these taxa are also relatively susceptible to fire-caused mortality, as compared to the relatively fire-resistant *Pinus* and *Pseudotsuga*, so species composition was historically regulated by the balance between climate and fire. Relatively cool, moist mixed conifer forests at higher elevations or northerly aspects are distinguished by greater dominance by *Abies* and *Picea*, with limited or no ponderosa pine; cool/moist mixed conifer forests are believed to have burned less frequently and with greater severity than warm/dry forests (Fulé et al., 2003b; Romme et al., 2006) (Table 1).

Both warm/dry and cool/moist mixed conifer forest types (following the terminology of Romme et al., 2006) have been affected by recent human-caused factors. Fire regimes were interrupted in the San Juan Mountains of southwestern Colorado circa 1870, when settlers of European origin introduced livestock grazing that broke the contiguity of surface fuels (Grissino-Mayer et al., 2004; Brown and Wu, 2005). Similar disruptions were observed across the Southwest (Swetnam and Baisan, 1996). On the Kaibab Plateau north of the Grand Canyon, Arizona, the historical mixture of surface and severe fires in mixed conifer and

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Table 1
Species names and codes used in the text.

Species	Common name	Code
<i>Abies concolor</i> (Gordon & Glendinning) Hoopes.	White fir	ABCO
<i>Picea engelmannii</i> Parry ex Engelm.	Engelmann spruce	PIEN
<i>Pinus ponderosa</i> var. <i>scopulorum</i> P. & C. Lawson	Ponderosa pine	PIPO
<i>Populus tremuloides</i> Michx.	Quaking aspen	POTR
<i>Pseudotsuga menziesii</i> (Mirb.) Franco var. <i>glauca</i> (Beissn.) Franco	Rocky Mountain Douglas-fir	PSME

higher forests stopped after 1879 (Fulé et al., 2003b). Under extended fire exclusion, mixed conifer forests have undergone substantial increases in tree density within stands, especially by shade-tolerant white fir and Douglas-fir (Fulé et al., 2004a; Heinlein et al., 2005). Mesic species have become established at lower elevations, and stands have become more homogeneous across landscapes (White and Vankat, 1993; Cocke et al., 2005). In many cases, selective logging of ponderosa pine exacerbated the compositional shift toward mesic species (Cocke et al., 2005).

Interruption of a frequent disturbance regime, such as the frequent surface fire regime of ponderosa pine or warm/dry mixed conifer, will lead to noticeable ecological effects more rapidly than cessation of infrequent fires, because a larger number of disturbance events are skipped in a given period of fire exclusion. Both ponderosa and warm/dry mixed conifer forests have experienced large pulses of tree regeneration following fire cessation in the Southwest, but ponderosa forests have received substantially more attention from researchers and managers (Covington and Moore, 1994). Studies of ponderosa ecology and forest change (White, 1985; Sánchez Meador et al., 2009) have supported the development and testing of ecological restoration treatments (Covington et al., 1997; Roccaforte et al., 2008).

Changes in warm/dry mixed conifer forests are also of concern, however. The dense, low-sweeping canopies of mesic species that have increased following fire exclusion form horizontal and vertical fuel complexes that facilitate the spread of severe wildfires (Fulé et al., 2004a). Meanwhile, climate change in the Southwest is projected to support increasingly common droughts (Seager et al., 2007) and fires (McKenzie et al., 2004). Following the ponderosa pine example, it is logical to suggest that effects of fire exclusion can be reversed by restoration treatments such as re-introduction of surface fire or thinning + burning, as demonstrated in the Sierra Nevada by Stephens and Moghaddas (2005), but the few documented examples in the Southwest show inconsistent results. At Grand Canyon, one example of fire use in mixed conifer led to an escaped wildfire even on gentle slopes (Fulé et al., 2004b) but a second example resulted in landscape-scale burning that generally emulated the effects of historical fires (Fulé and Laughlin, 2007). Forest structure following thinning + burning in a Grand Canyon mixed conifer forest was statistically indistinguishable from burning alone, but the thinning was confined to very small trees (Fulé et al., 2006).

Beginning in 2002, we initiated a study in warm/dry mixed conifer forest of the San Juan Mountains, Colorado, to assess forest change and test restoration alternatives on the overstory and understory (Korb et al., 2007). Here we report on forest measurements and dendroecological reconstructions to address the following questions: (1) what were the reference conditions of historical fire regime and fire–climate relationships, forest composition, and structure? and (2) how have conditions changed to the present?

2. Methods

2.1. Study area

The study area is located in the San Juan Mountains on Lower Middle Mountain, approximately 18 km northwest of Pagosa

Springs, in southwest Colorado (N 37.296, W 107.228) on the San Juan National Forest. The site consists of 15–30% slopes on generally south-facing aspects. Elevations range from 2438 to 2743 m. The dominant soil type is Dutton loam, a silty clay loam (USDA Forest Service, 2004). Average daily temperatures range from a maximum of 25.7 °C in July to a minimum of –17 °C in January. Average annual precipitation is 55.4 cm, with the greatest amounts occurring in July and August due to summer thunderstorm activity. Precipitation from November to March is dominated by snowfall, with an average annual snowfall of 326 cm (Western Regional Climate Center, Pagosa Springs, 1906–1998, www.wrcc.dri.edu).

Forest vegetation includes ponderosa pine, Douglas-fir, white fir, and aspen (*P. tremuloides*). The midstory and understory are dominated primarily by white fir and Douglas-fir, with a variety of shrubs including Gambel oak (*Quercus gambelii*), snowberry (*Symphoricarpos rotundifolius*), and serviceberry (*Amelanchier alnifolia*).

Past disturbance history includes sheep grazing beginning in the late 1800s and cattle grazing since the early 1900s on a rest-rotation system annually from June to October with dates varying due to the presence of snow. There are no large meadows, water holes, or tanks in the analysis area so grazing impacts may have been light. Fire suppression has been management policy since the early 20th century. A single timber harvest occurred between 1990 and 1993, using an intermediate harvest system intended to enhance residual tree growth and quality. Approximately 3830 million board feet were harvested in the area, consisting of 51% ponderosa pine, 33% white fir, and 16% Douglas-fir (USDA Forest Service, 2004; S. Hartvigsen, San Juan National Forest, personal communication, 2008).

2.2. Field methods

We collected data in the pre-treatment phase of an experiment in forest ecological restoration. Partial cross-sections were cut from fire-scarred ponderosa pine logs, stumps, and snags and each sample was mapped in an area of approximately 150 ha (1 km × 1.5 km) in the center of the study area (Fig. 1). Because fire scars were not abundant, all fire scars with sound wood were taken. The fire history collection was done before the forest structure units were laid out, so the fire scar sampling area did not completely overlap with the experimental units. However, the study area is continuous forest with no physical barriers to fire spread so the fire history collection is still relevant to the experimental units.

Forest structure was measured in each of twelve, 16-ha experimental units. We established 20 study plots on a 60-m grid per unit to characterize vegetation (total $N = 12$ units × 20 plots = 240 plots). Plot centers were permanently marked with iron stakes and were geo-referenced. Overstory trees and saplings taller than breast height (137 cm) were measured in a 400 m² (11.28 m radius) circular plot. Species, condition (living or snag/log classes, Thomas et al., 1979), diameter at breast height (dbh), height, and a preliminary field classification of presettlement or postsettlement origin were recorded for each tree encountered in the plot. Potentially presettlement ponderosa pine trees were identified based on size (>40 cm diameter at “stump height” [dsh], 40 cm above ground level) or yellow bark (White, 1985). Other conifers were also considered as potentially presettlement if dsh > 40 cm; aspen were noted as potentially presettlement if dsh > 20 cm. All potentially presettlement trees, as well as a random 10% subsample of other trees, were cored with an increment borer at 40 cm above ground level. Diameter at stump height was recorded for all cored trees. Tree regeneration (trees below breast height) was measured on a nested 100 m² circular

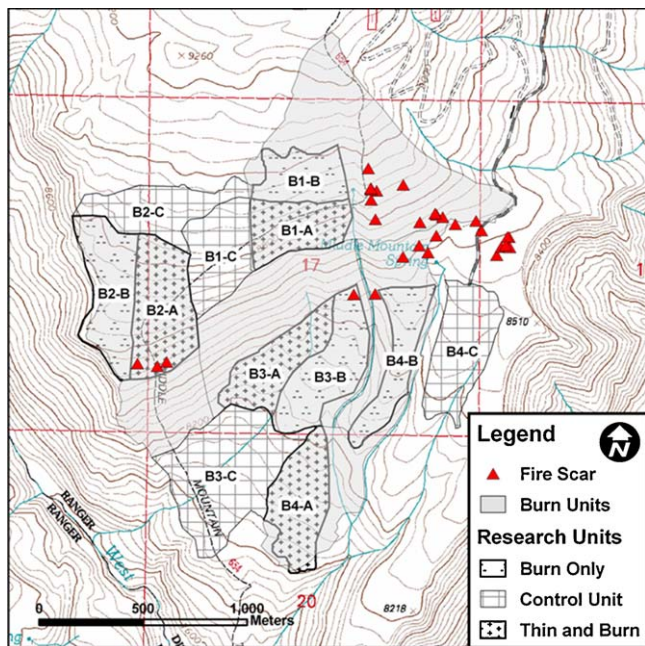


Fig. 1. Study site layout at Lower Middle Mountain, San Juan National Forest, Colorado. Fire-scarred samples, research blocks and planned treatments are shown.

plot (5.64 m radius); species, condition, and height class (<40 cm; 40.1–80 cm; 80.1–137 cm) were recorded for each seedling or sprout. Understory vegetation was also measured and has been described elsewhere (Korb et al., 2007).

2.3. Laboratory, statistical, and modeling analysis

Fire-scarred samples were surfaced with increasingly finer grits of sandpaper until cells were clearly visible under magnification. We visually crossdated all samples against a master chronology for Lower Middle Mountain. We used FHX2 software (Grissino-Mayer, 2001) to analyze the fire history data and calculate mean, median, and Weibull median fire interval statistics. The fit of the Weibull functions to the fire interval distributions was tested; only results that fit the data are reported. We analyzed spatial and temporal fire patterns statistically with percent-scarred filters, a relative measure of fire extents assuming that larger fires will have scarred more trees than smaller ones (Swetnam and Baisan, 1996). We used a 2-scar minimum to represent fires of any size while minimizing the chance of including false positives and the 25%-scarred level to represent the subset of larger fires. The time frame for our fire history analysis was 1500–1868. The beginning date was selected where we had a minimum of at least five recording sample trees. The ending date was the last fire date; the study area had not burned since 1868.

Fire-climate relationships were tested using superposed epoch analysis (in FVS version 3.02; Grissino-Mayer, 1995) on fires that scarred a minimum of 2 sample trees. SEA compares climate of the years leading up to the fire and the fire year itself. Our test window, or epoch, was 11 years taking into account 6 years before the fire year, the fire year, and 4 years after the fire. Following the approach used at a nearby site by Brown and Wu (2005), we used two independently derived tree-ring based climate reconstructions for the SEA: (1) an annual precipitation reconstruction from northern New Mexico (Grissino-Mayer, 1996), and (2) a summer Palmer Drought Severity Index (PDSI) reconstruction from the area (Cook et al., 2004). We also assessed the relationship between fire dates and the Niño3 sea surface temperature (SST) index (Cook, 2000), a reconstruction of the El

Niño/Southern Oscillation. Significance was determined with bootstrapped confidence intervals ($\alpha = .01$).

Increment cores were surfaced and visually crossdated (Stokes and Smiley, 1968) with local tree-ring chronologies. Rings were counted on cores that could not be crossdated. For cores that missed the pith, additional years to the center were estimated with a pith locator consisting of concentric circles matched to the curvature and density of the inner rings. Presettlement forest structure was reconstructed at the time of disruption of the frequent fire regime, circa 1870, following dendroecological methods described in detail in Fulé et al. (1997). We used 1870 as the general fire regime disruption date for the region (Grissino-Mayer et al., 2004). Tree diameters in 1870 were reconstructed for all living trees by subtracting the radial growth measured on increment cores since 1870. For dead trees, the date of death was estimated based on tree condition class using diameter-dependent snag decomposition rates (Thomas et al., 1979). These models are widely used in ponderosa pine and have been tested in the Southwest (Fulé et al., 1997). To estimate growth between 1870 and death date, we developed local species-specific relationships between tree diameter and basal area increment.

We used non-metric multidimensional scaling (NMS) to examine changes in basal area of all tree species over time and among blocks (Clark, 1993). We used basal area instead of tree density because basal area is likely to have higher accuracy than reconstructed tree density using dendroecological data (Moore et al., 2004). We conducted NMS analyses using PC-ORD software (version 5.10, McCune and Mefford, 2006). We ran the NMS ordination using a Bray–Curtis distance measure (Faith et al., 1987), random starting configurations, 50 runs with real data, a maximum of 200 iterations per run and a stability criterion of 0.00001. We compared the stress value of the final solution to 50 random solutions using a Monte Carlo test. We filtered out two species, *Pinus edulis* (piñon pine) and *Juniperus scopulorum* (Rocky Mountain juniper), because they did not occur on a minimum of 5% of the plots (McCune and Grace, 2002). We determined the relationships between plant species and ordination axes using the main matrix Pearson's r correlations (McCune and Grace, 2002). We considered tree species with the highest correlation coefficients to have the strongest weight on the axes.

We examined differences between reconstructed 1870 and 2003 forest structure using a permutational multivariate analysis of variance (PERMANOVA) (Anderson, 2001; McArdle and Anderson, 2001). PERMANOVA uses common ecological distance measures (Bray–Curtis for this study) to examine multivariate datasets and calculates P -values using permutations, rather than tabled P -values that assume normality. We used PERMANOVA to quantify differences in basal area and trees ha^{-1} across time and among blocks. We used a one fixed factor and one level nested design with time as our main effect (PC-ORD software version 5.10, McCune and Mefford, 2006). We analyzed species that were present in a minimum of 5% of the plots as recommended by McCune and Grace (2002).

We used indicator-species analysis (McCune and Grace, 2002), which uses species richness and associated abundance values of species, to identify species that were particularly consistent indicators for the analysis dates of 1870 or 2003. A comparison between the maximum indicator value (0–100) and random trials for occurrence of a given species (1000 Monte Carlo randomizations) provided an approximate P -value (McCune and Grace, 2002). Species with $P \leq 0.05$ and indicator values (INDVAL) > 25 (INDVAL = relative abundance \times relative frequency; INDVAL ranges from 0 to 100) were accepted as indicator species for a particular time period (Dufrene and Legendre, 1997).

We used simple linear regression to examine the relationship between tree basal area and tree canopy cover using JMP IN software (version 7.0.1, SAS Institute, 2007).

3. Results

Surface fires were frequent before 1868, burning with multi to sub-decadal frequency (Fig. 2), as reconstructed from the fire-scarred samples. We were able to date 20 of the 31 fire-scarred samples collected. Ring complacency was the chief reason samples could not be dated. Twenty-nine fire years were dated in the period from 1500–1868. Two long fire-free periods were notable: no fires burned from 1685 to 1735 and again from 1824 to 1861. Comparison to climate reconstructions shows that the fire free or quiescent

periods coincided with wet periods (Fig. 2). Fire return intervals prior to fire exclusion ranged from 3 to 50 years with a MFI of 24.3 (± 11.5) years (Table 2). Fires scarring 25% or more of the samples occurred at longer intervals (MFI 32.3 ± 23.4 years). Fires tended to occur in significantly dry years, as shown by superposed epoch analysis (Fig. 3). Significantly low precipitation, dry PDSI values, and La Niña conditions were all associated with fire years. Antecedent climate conditions were not statistically significantly dry or wet, but preceding years do show a 1–2-year drying pattern before the fire year. There were statistically significant wet or dry years at 3 or 5 years after or before the fire years in one of the three analyses (Fig. 3); there is no logical reason to link these patterns with fire occurrence.

Unlike the case of ponderosa pine forests that have been “invaded” by mesic conifers, forest reconstruction showed that the

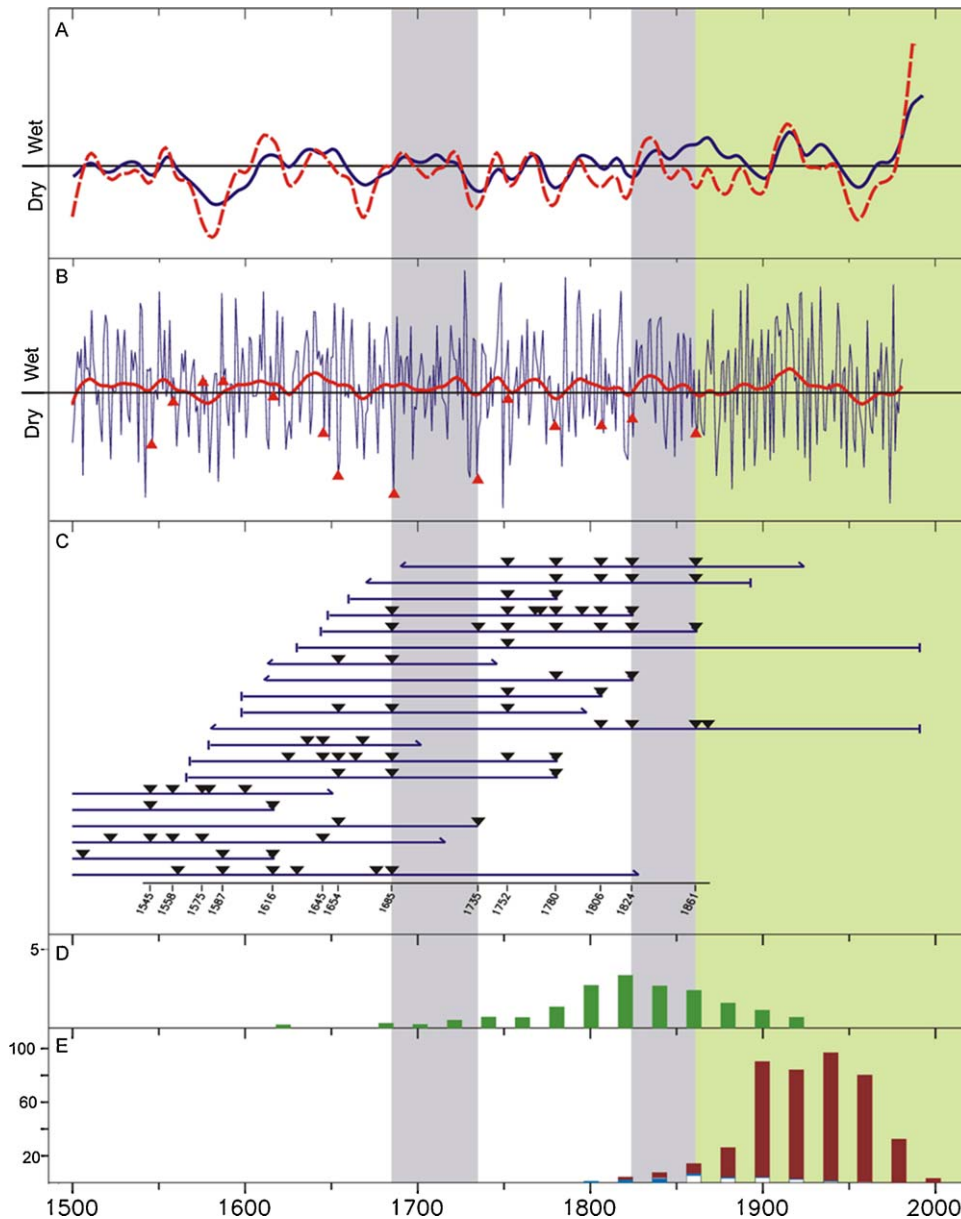


Fig. 2. Comparison of precipitation and ENSO indices with fire history and age structure. (A) PDSI for the four-corners area (Cook et al., 2004) in dashed red. Annual precipitation reconstruction from El Malpais, NM (Grissino-Mayer, 1996) in solid blue. Both hydroclimate series have been smoothed with 20-year cubic splines. (B) Niño3 SST index (Cook, 2000) representing ENSO conditions. Unsmoothed data (blue) and 20-year cubic splined data (red) are displayed. (C) Fire history for Lower Middle Mountain. Horizontal lines mark the time span of each sample. Inverted triangles designate fire years. Fire dates listed below plot were fires that scarred ≥ 2 trees and were used in SEA analysis in Fig. 3. (D) Tree recruitment dates of ponderosa pine (green) in 20-year age classes (y-axis: number of trees). (E) Tree recruitment dates of all other trees in 20-year age classes: red: ABCO; blue: PSME; and white: POTR (y-axis: number of trees). Shaded areas highlight periods lacking fire. Wetter climatic conditions underlie fire quiescent periods in gray bars. Lack of fire in green bar is due to fire exclusion. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

Table 2

Mean fire interval statistics in the 10%- and 25%-scarred filter class for the time period 1500–1868 in a 150-ha study area. Standard deviation (SD) is reported for the mean (MFI). Because fire interval data are not normally distributed, the Median and Weibull Median Probability (WMPI) are also reported to better represent the central tendency of skewed data. The range shows minimum and maximum fire interval for the data set.

Filter	MFI \pm SD	Median	WMPI	Range
10%	24.3 \pm 11.5	16.0	17.1	3–50
25%	32.3 \pm 23.4	27.0	28.6	7–79

Lower Middle Mountain area was a true mixture of species both at the time of fire exclusion and today. However, forest composition and structure changed substantially, and statistically significantly, between 1870 and 2003 (Table 3). Forest structural data are presented by experimental block (Table 3, Figs. 4 and 5) to illustrate variability and to facilitate future comparisons after the restoration treatments are completed. There was a significant difference between reconstructed 1870 and 2003 tree basal area ($F = 49.6$; $P = 0.029$) (Table 4). There was also a significant difference between reconstructed 1870 and 2003 tree density ($F = 42.3$; $P = 0.03$) (Table 4). There were no differences among blocks across time for tree basal area ($F = 1.21$; $P = 0.28$) or tree density ($F = 1.52$; $P = 0.12$) (Table 4).

Ponderosa pine made up an average 64% of basal area in the 1870 forest (range 54–69%) but only 36% in the 2003 forest (range 27–46%) (Table 3). White fir and Douglas-fir were similar in their average proportion of basal area in 1870, 15% and 17%, respectively. By 2003, the Douglas-fir basal area increased by approximately two times, but the relative contribution of the species to stand basal area was unchanged at 17%. White fir, on the other hand, increased in basal area by approximately six times and made up an average of 35% of total basal area by 2003. White fir also became the numerically dominant tree species, with an

average of 392 trees ha^{-1} , more than twice the average density of the next species, aspen (146 trees ha^{-1}), and far higher than Douglas-fir (83 trees ha^{-1}) or ponderosa pine (56 trees ha^{-1}).

The magnitude of the early 1990s tree harvest, estimated from cut stumps, is a minimal estimate because some tree bases had deteriorated from decay or the impact of harvesting machinery to the point that it was not possible to determine if the tree had been cut or had died and broken at the base. Only confirmed cut stumps were included in the following figures: an average of 49 trees ha^{-1} were cut, representing 8.4 $\text{m}^2 \text{ha}^{-1}$ of basal area. For comparison, this value constitutes 76% of the 1870 average basal area (11.0 $\text{m}^2 \text{ha}^{-1}$) but only 31% of the 2003 average (27.0 $\text{m}^2 \text{ha}^{-1}$). White fir trees were the most commonly cut (26 trees ha^{-1} , representing 3.5 $\text{m}^2 \text{ha}^{-1}$). Consistent with the silvicultural goal of the harvest to reduce white fir dominance, white firs <45 cm in diameter made up 68% of the cut trees. Ponderosa pine was less heavily harvested in terms of density (14 trees ha^{-1}) but made up the largest fraction of basal area removed (3.8 $\text{m}^2 \text{ha}^{-1}$) and cut trees were generally large; ponderosa pines >45 cm in diameter made up 76% of the cut pines. Douglas-fir harvest averaged 7 trees ha^{-1} and 1.1 $\text{m}^2 \text{ha}^{-1}$.

Historical diameter distributions in 1870 were unimodal with a peak at 15 or 25 cm, varying among blocks, and a relatively gentle decline of the diameter distribution curve to higher values; all sites had trees at least through the 85-cm diameter class (Fig. 4). Almost all of the trees \geq the 45-cm class were ponderosa pines. By 2003, diameter distributions on all four blocks followed the reverse-J distribution, indicating strong dominance by small trees, most of them white fir. However, all blocks still had trees at least through the 85-cm diameter class and most of the trees \geq the 45-cm class were still ponderosa pines. Age distributions showed that tree establishment was dominated by ponderosa pine prior to 1870 but white fir established strongly and consistently through most of the decades after 1870 (Fig. 5). Aspen and Douglas-fir established

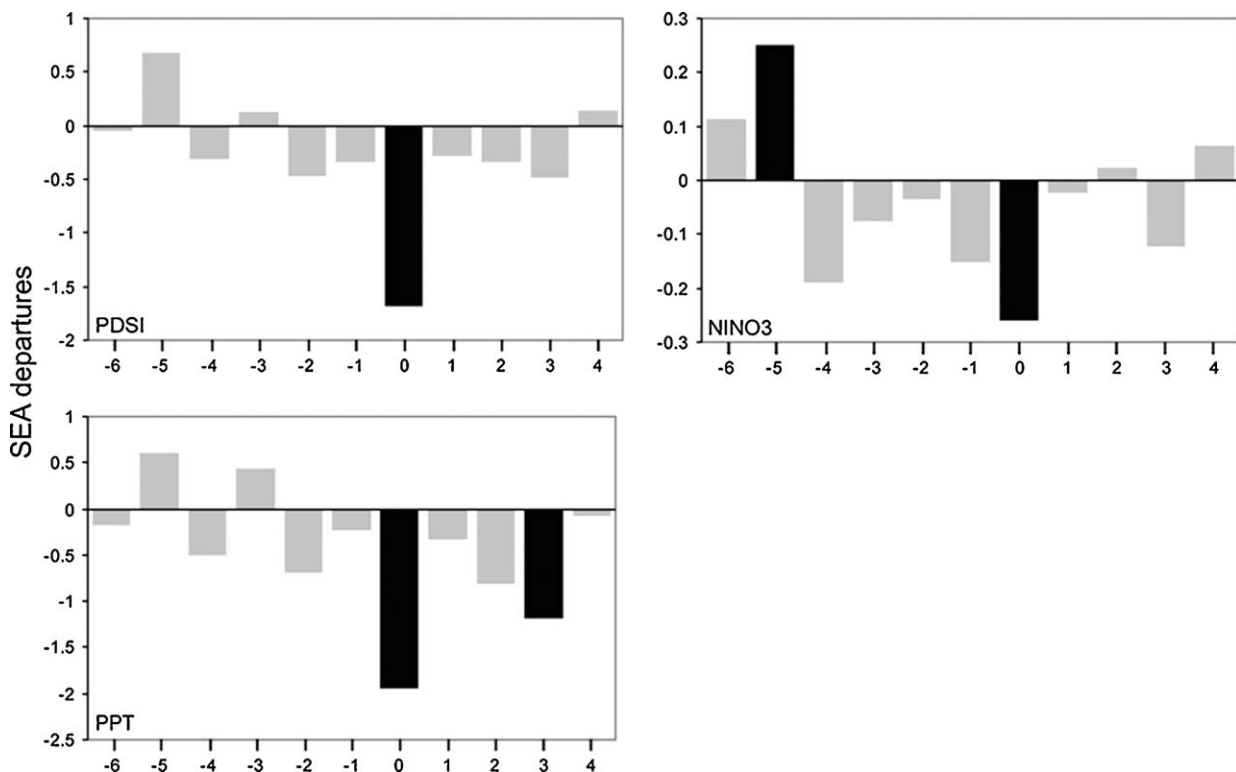


Fig. 3. Superposed epoch analysis comparing fire years and preceding and succeeding years with same three climate indices displayed in Fig. 2 (clockwise from upper left): Palmer Drought Severity Index (PDSI), Niño3 SST index, annual precipitation. Dark bars indicate statistical significance ($\alpha = .01$). Dry conditions are indicated by negative values in all indices. The fire year (0) was always significantly dry. The lack of significance in antecedent years indicate LMM forests were moisture limited and not fuel limited.

Table 3

Forest structure of the four study blocks reconstructed in 1870 and measured in 2003. Standard errors are shown in parentheses. Species codes are shown in Table 1.

	Basal area 1870 (m ² ha ⁻¹)	Basal area 2003 (m ² ha ⁻¹)	Trees ha ⁻¹ 1870	Trees ha ⁻¹ 2003
Block 1				
ABCO	1.4 (0.4)	8.6 (0.8)	25.8 (4.9)	319.6 (24.5)
PIEN	0	0	0	0
PIPO	7.1 (1.0)	6.6 (1.1)	61.3 (7.2)	30.8 (4.5)
POTR	0.5 (0.2)	4.8 (0.9)	40.0 (9.2)	300.8 (86.2)
PSME	1.6 (0.5)	4.1 (1.0)	19.6 (4.6)	82.5 (15.3)
Total	10.7 (1.1)	24.3 (1.4)	146.7 (11.2)	734.2 (88.5)
Block 2				
ABCO	1.6 (0.34)	7.7 (0.6)	20.8 (3.3)	310.0 (23.4)
PIEN	0	0.0002 (0.0002)	0	0.4 (0.4)
PIPO	8.8 (1.0)	11.0 (1.4)	78.8 (6.8)	52.9 (6.6)
POTR	0.6 (0.3)	2.1 (0.5)	20.4 (5.4)	142.1 (28.1)
PSME	2.3 (0.5)	5.3 (0.8)	26.7 (4.4)	79.2 (11.6)
Total	13.3 (1.1)	26.1 (1.6)	146.7 (9.4)	584.6 (42.8)
Block 3				
ABCO	2.2 (0.4)	13.2 (1.2)	40.8 (6.1)	580.8 (42.3)
PIEN	0.07 (0.07)	0.2 (0.2)	0.8 (0.8)	0.8 (0.6)
PIPO	5.5 (0.7)	8.5 (1.1)	60.8 (7.7)	36.7 (4.8)
POTR	0.4 (0.1)	2.8 (0.5)	25.0 (4.7)	71.3 (12.3)
PSME	2.0 (0.6)	4.0 (0.8)	18.3 (3.7)	82.9 (14.2)
Total	10.1 (0.9)	28.7 (1.3)	145.8 (8.6)	772.5 (50.5)
Block 4				
ABCO	1.3 (0.3)	8.8 (1.0)	24.2 (3.9)	357.5 (32.0)
PIEN	0	0	0	0
PIPO	6.8 (0.9)	13.2 (1.4)	68.8 (7.6)	102.1 (11.3)
POTR	0.3 (0.1)	1.8 (0.6)	15.8 (4.6)	70.0 (18.6)
PSME	1.6 (0.6)	5.1 (1.1)	18.3 (5.1)	88.3 (14.8)
Total	9.9 (1.1)	29.0 (1.7)	127.1 (10.3)	617.9 (38.8)

periodically throughout the post-1870 period. The most recent period in Fig. 5, centered on 1990 (covering tree center dates from 1980 to 2000), included the early 1990s harvest and was dominated by aspen regeneration.

Tree basal area by species in 2003 showed a strong directional shift away from reconstructed 1870 forest structure (Fig. 6). Changes along the time gradient (Axis 1) were driven by changes in basal area and trees ha⁻¹ (Fig. 6). White fir had the strongest positive correlation with the time gradient ($r = 0.82$) (Table 5). Ponderosa pine had the strongest negative correlation with the time gradient ($r = -0.24$) (Table 5). Conversely, white fir had the weakest positive correlation with Axis 2 ($r = 0.04$) and ponderosa pine had the strongest correlation ($r = 0.47$). Indicator species analysis detected species that were particularly consistent

Table 4

PERMANOVA based on Bray–Curtis dissimilarities of basal area and tree density for four tree species (ponderosa pine, Douglas-fir, white fir, and aspen) for reconstructed 1870 and 2003 data.

Source	df	MS	F	P (perm)
Basal area (m² ha⁻¹)				
Time	1	2.4585	49.55	0.0294
Block	6	0.4962	1.215	0.2846
Residual	16	0.4083		
Total	23			
Tree density (trees ha⁻¹)				
Time	1	2.5053	42.29	0.0296
Block	6	0.5924	1.524	0.1216
Residual	16	0.3887		
Total	23			

Table 5

Pearson's r correlation coefficients from the main matrix for tree species along NMS ordination axes.

	Species	Correlation coefficient
Axis 1 (time)		
Positive	<i>A. concolor</i>	0.824
	<i>P. menziesii</i>	0.348
	<i>P. tremulooides</i>	0.267
Negative	<i>P. ponderosa</i>	-0.242
Axis 2 (time)		
Positive	<i>P. ponderosa</i>	0.474
	<i>P. tremulooides</i>	0.243
	<i>P. menziesii</i>	0.187
	<i>A. concolor</i>	0.040

Table 6

Indicator species associated with time for 1870 reconstructed and 2003 data.

Time	Species	Indicator value	P
1870	<i>P. ponderosa</i>	45.4	0.0138
2003	<i>A. concolor</i>	93.4	0.0002
2003	<i>P. menziesii</i>	56.4	0.0002
2003	<i>P. tremulooides</i>	46.5	0.0002

indicators for time (Table 6). Ponderosa pine was the only indicator species for the reconstructed 1870 data. White fir had the highest indicator value for 2003 data (Table 6).

The linear regression analysis showed poor correlation between tree canopy cover and tree basal area ($r = 0.11$) and therefore we were unable to reconstruct tree canopy cover in 1870 from the relationship between tree canopy cover and tree basal area in 2003.

4. Discussion

4.1. Alteration of fire regime

The historical regime of frequent surface fires at Lower Middle Mountain had similar frequency (mean fire interval 24 years) to other mixed conifer forests in the San Juan Mountains (average fire return intervals 21–30 years, Grissino-Mayer et al., 2004), somewhat longer than fire return intervals in mixed conifer forests of northern Arizona (6–9 years, Fulé et al., 2003a; 8.7 years, Fulé et al., 2003b; 9–10 years, Heinlein et al., 2005), and northern New Mexico (7–17 years, Touchan et al., 1996) (ranges cover all-scarred to 25%-scarred filters). In contrast to more northerly, higher, or wetter mixed conifer forests where variable-severity fire regimes have been reported (Fulé et al., 2003b; Hessburg et al., 2007), at the scale of individual blocks (64+ ha each) we did not see evidence of historical severe burning in terms of even-agedness or abrupt establishment of severe-fire-following species such as aspen. At a finer scale, the presence of aspen which established in the same decades as the fires that ended the quiescent periods (1735 and 1861) suggest that patches of lethal fire behavior may have occurred when the quiescent periods were ended. Fire cessation at our study area after 1868 was also consistent with general fire exclusion in the San Juan Mountains after 1871 (Brown and Wu, 2005) to 1880 (Grissino-Mayer et al., 2004). The onset of fire exclusion occurred abruptly between 1870 and 1900 throughout the mountains of the Southwest (Swetnam and Baisan, 1996), coinciding with European settlement and the introduction of livestock, except for the Chuska Mountains in Arizona where sheep were introduced in the early 19th century (Savage, 1991) and northern Mexico where intensive land use was delayed till the early to mid-20th century (Fulé et al., 2005).

Prior to fire exclusion, dry climatic patterns were significantly associated with fire years at Lower Middle Mountain. Similar

relationships were observed in ponderosa pine forests nearby by Brown and Wu (2005) and elsewhere throughout the Southwest (Swetnam and Baisan, 1996; Swetnam and Betancourt, 1998). However, years preceding fire were not significantly wet, unlike the wet/dry pattern that was often significant at southwestern ponderosa pine sites (Swetnam and Betancourt, 1998). The fact that the preceding years are not significantly dry leads us to surmise that mixed conifer forests are not fuel limited like ponderosa pine forests, in which fire spread was encouraged by the flush of fine fuels in the form of herbaceous plants accumulating during one or two wet years before a dry major (spatially extensive) fire year. Mixed conifer forests are probably productive enough that the herbaceous and litter fuels are typically present in sufficient quantities to support fire, but whether they are available to burn depends on moisture conditions.

4.2. Drivers of forest structural change

Fire exclusion is the most common factor associated with recent increases in density of mixed conifer forests. However, fire-free

gaps even prior to European settlement may already have begun to effect change. The two extended fire-free periods observed at Lower Middle Mountain before 1868 were also documented at Archuleta Mesa (Brown and Wu, 2005), roughly 15 km away, and the second gap appears in at least two of the San Juan sites studied by Grissino-Mayer et al. (2004). At Archuleta Mesa, Brown and Wu (2005) showed that episodic ponderosa pine recruitment was favored during unburned intervals. Our data from Lower Middle Mountain are less temporally precise than those of Brown and Wu (2005) because we cored trees at a higher point on the stem in order to develop accurate reconstructions of past diameter. The Lower Middle Mountain age distributions do not indicate a recruitment pulse associated with the first fire gap (1685–1735), although it is logical that greater survival of non-pine recruitment could have occurred during this period, only to be thinned by the 1735 and 1752 fires. A substantial proportion of the non-pine recruitment at all blocks began during the second period (1824–1861). White firs and other trees that established in this unburned gap had only to survive the 1861 and 1868 fires before entering the 135+ year fire-free period to the present.

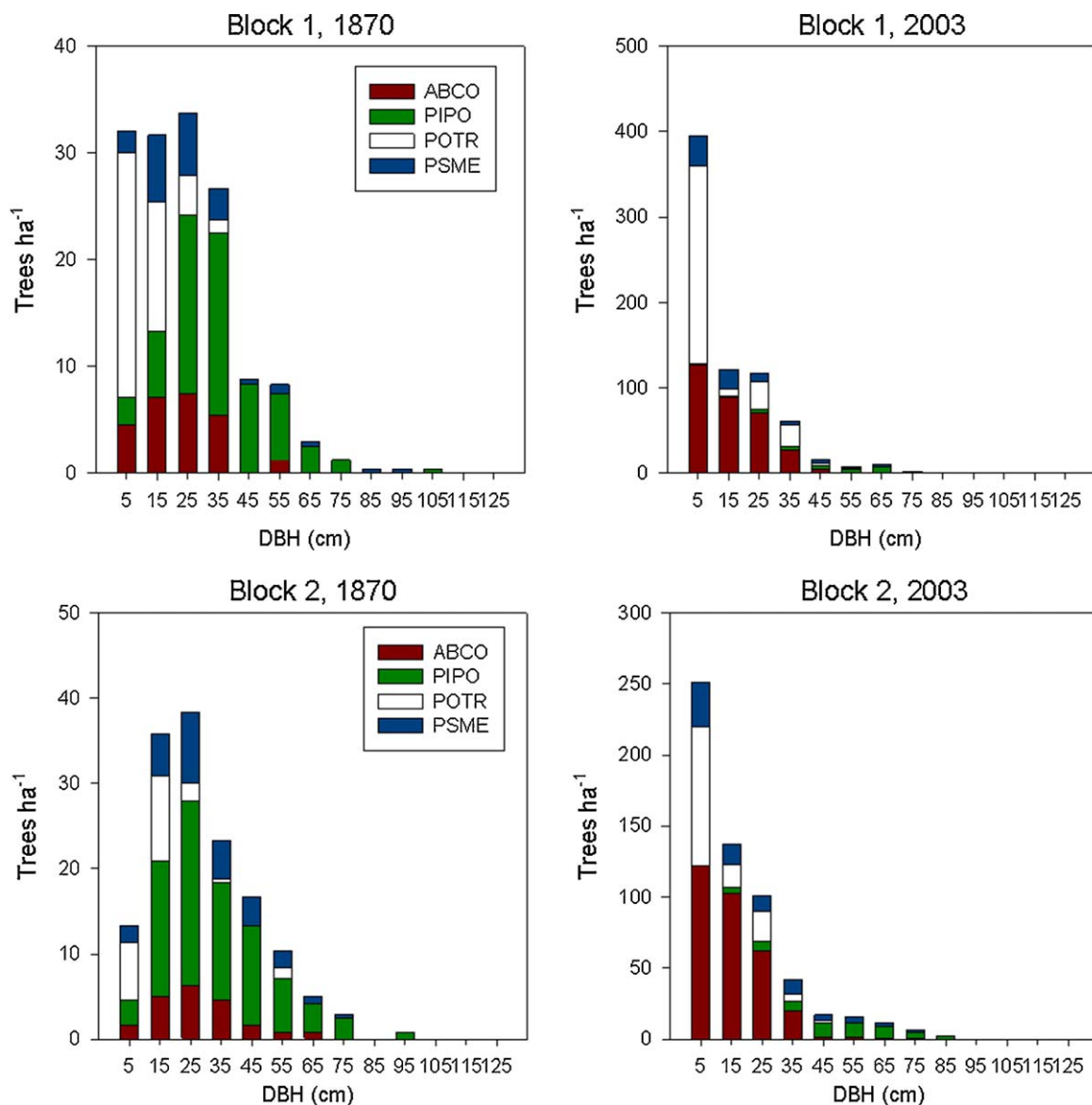


Fig. 4. Diameter distributions by species on the four study blocks reconstructed in 1870 and measured in 2003 show a consistent increase in forest density by approximately an order of magnitude and a shift toward dominance by mesic conifers and aspen.

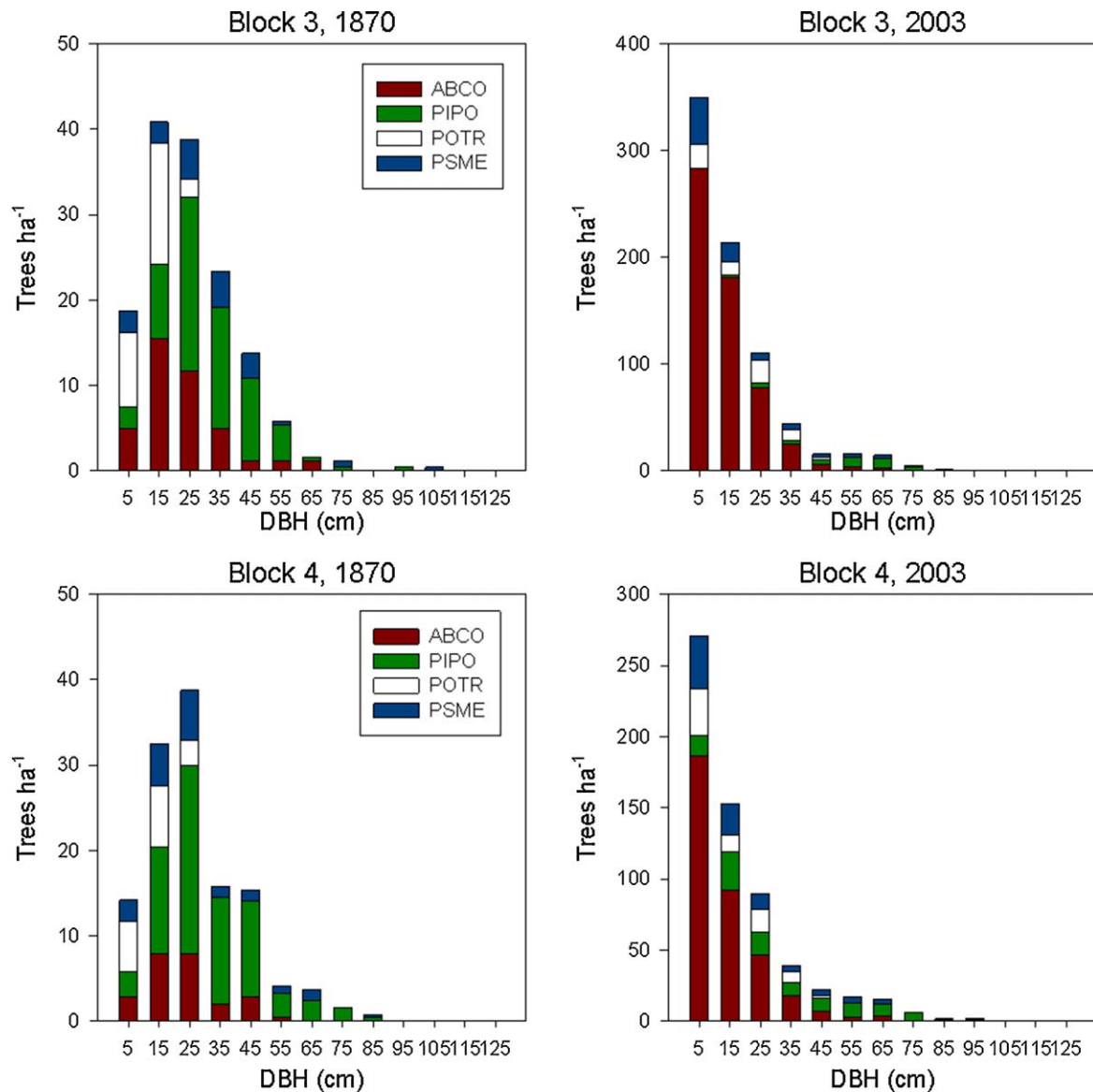


Fig. 4. (Continued).

Frequent-fire periods in mixed conifer gave ponderosa pine a competitive advantage, allowing them to establish dominance. During past periods of less frequent fire, ponderosa pines were still able to persist. After surface fire disturbance was completely removed from Lower Middle Mountain, however, tree density increased rapidly and non-pine species dominated. The shade tolerance of white fir and Douglas-fir gave these species a competitive advantage for regeneration. Similar changes were observed in mixed conifer forests of the Grand Canyon where basal area increased 128%, tree density 380%, and white fir basal area proportion went from 12% to 35% after fire exclusion beginning in 1880 (Fulé et al., 2002). On a site in the San Francisco Peaks, northern Arizona, where white fir was rare, basal area still increased 252% and tree density 510% after fire exclusion beginning in 1877 (Cocke et al., 2005). In the absence of white fir, it was Douglas-fir, aspen, and limber pine that replaced ponderosa pine as the dominant species. Although increased forest density at Lower Middle Mountain was similar in relative terms to the changes at the Arizona sites, the absolute value of basal area in 1870 (9.9–13.3 m² ha⁻¹) was lower than previously reported in mixed conifer (17.6–28.5 m² ha⁻¹; Fulé et al., 2002, 2003b; Cocke et al., 2005).

Tree harvesting is a common factor affecting forest structure by removing large-tree biomass and often facilitating vigorous regeneration. For example, Sánchez Meador et al. (2009) found that an 1894 harvest in an Arizona ponderosa pine forest removed 2/3 of the basal area, but by 2002 tree density had increased by a factor of six and basal area had more than doubled. Comparisons between logged vs. fire-excluded forests in Montana led Naficy and Sala (2007) to suggest that logging may have been the more important cause of increased tree densification. In the Southwest, however, there are numerous examples of never-logged ponderosa pine and some mixed conifer forests that have undergone extended fire exclusion and have become equally as dense over the 20th century as logged forests (Covington et al., 1997; Fulé et al., 2002).

Logging at Lower Middle Mountain occurred nearly a century later than at many southwestern sites (Sánchez Meador et al., 2009), so tree harvest did not play a role in most of the post-1870 forest changes. However, the removal of approximately 28% of the ponderosa pine basal area, primarily from larger trees, contributed to the long-term reduction in pine influence. Managers also removed a comparable basal area of white fir, but this species had

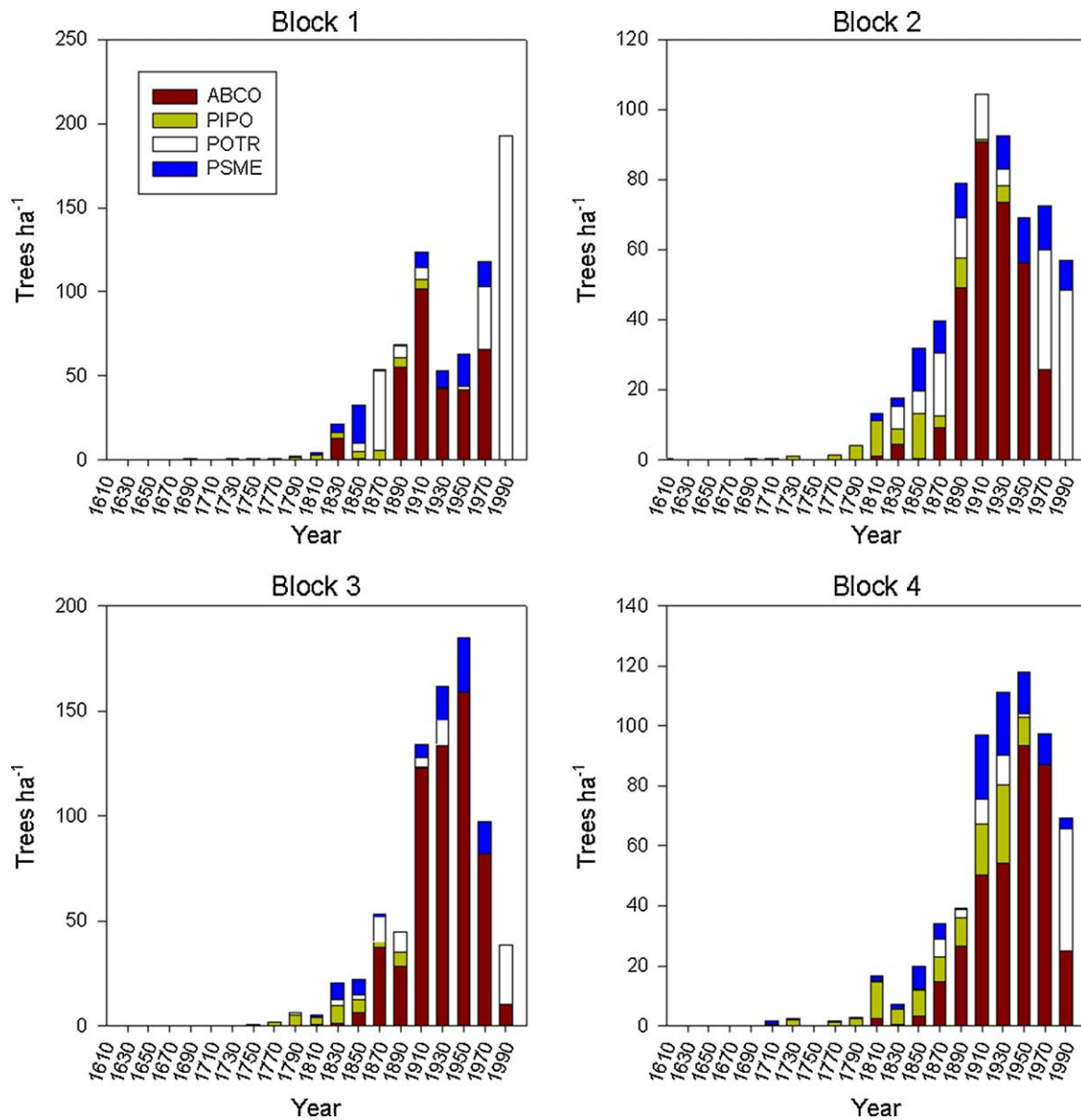


Fig. 5. Tree establishment was dominated by ponderosa pine prior to 1870, although white fir, Douglas-fir, and aspen were all present. Dates shown are tree center dates at coring height (40 cm above ground). Two other species, Engelmann spruce and Rocky Mountain juniper, were so infrequently encountered that they could not be represented at the scale of the graphs.

become so dominant that the harvest did not restore the historical balance nor substantially reduce the high fir densities.

4.3. Implications for forest sustainability

In the 135-year period of fire exclusion from 1868 to 2003, the warm/dry mixed conifer ecosystem at Lower Middle Mountain changed from a relatively open, frequently burned forest dominated by large ponderosa pines to a relatively dense, unburned forest. White fir has tripled in relative basal area and is now the numerically dominant species; together with Douglas-fir and aspen, the mesic species predominate and ponderosa pine has been reduced to less than 40% of total basal area. Most of these changes happened in the absence of harvesting, but a recent harvest in the early 1990s removed large pines. Even though many firs were also cut, the overall effect of harvest was to exacerbate the already altered species composition. The changes at Lower Middle Mountain are consistent with those at other mixed conifer forests

in southern Colorado and the Southwest (Fulé et al., 2002; Coker et al., 2005; Romme et al., 2006) and the Sierra Nevada of California (Minnich et al., 1995; Stephens, 2000; Taylor, 2000). What are the implications of these changes for forest conservation and restoration?

The sustainability of dense fire-excluded forests has been questioned across western North America because of their high vulnerability to disturbance (Covington and Moore, 1994; Youngblood et al., 2004). Increased forest density is associated with reduced growth and greater moisture stress (Stone et al., 1999). Contiguous canopy fuels in mixed conifer support increased crown fire activity not only because of higher canopy bulk density but also because the long crowns and shade-tolerant regeneration of the mesic species form fuel ladders to conduct fire to the canopy (Fulé et al., 2004a). Interactions among the disturbance factors of fire, bark beetles and other insects, and fungal pathogens can accelerate the process of large-scale mortality (Parker et al., 2006). These challenges are raised to higher levels by anticipated climate change

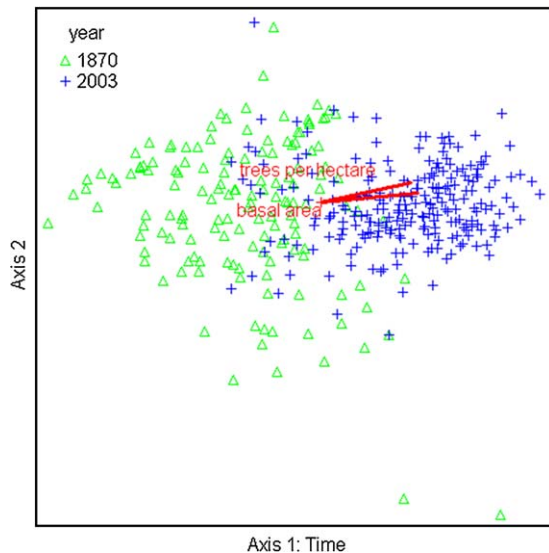


Fig. 6. Non-metric multidimensional scaling ordination of untransformed tree basal area of species reconstructed for 1870 (reference condition) and 2003 data. Each symbol represents one plot for 1 year ($N=240/\text{year}$). Vector lengths are proportional to correlations with community composition. The final solution had three dimensions, stress = 14.07 and $P=0.02$.

effects including increased severity and length of droughts (Seager et al., 2007), longer and more severe fire seasons (Westerling et al., 2006), and mild winters that extend the annual number of bark beetle generations (Waring et al., submitted for publication). Although not all the tree species at Lower Middle Mountain have been studied, Shafer et al. (2001) showed that the range of Douglas-fir was projected to contract in southern Colorado under three modeled climate scenarios.

The forest restoration experiment initiated at Lower Middle Mountain is designed to draw upon historical reference information while considering future ecosystem resilience. The obstacles to success are high because the ecological changes that occurred here since the 19th century have been in exactly the wrong direction considering the warm, fire-favoring climate expected in the 21st century. If warm/dry mixed conifer forests of southern Colorado are to have a reasonable chance for persistence under the future climate regime, restoring conditions more similar to the historical characteristics of the frequently burned, open forests of the past is likely to serve as a useful starting point: introducing surface fire to reduce fire intervals from centuries to decades, consuming accumulated surface fuels, thinning dense canopy fuels and ladder fuels, and counteracting the trend toward reduced influence by fire-resistant ponderosa pines.

Acknowledgements

Thanks to Bill Romme, Colorado State University, and faculty and staff of the Ecological Restoration Institute, Northern Arizona University, especially Doc Smith, W. Wallace Covington, Mark Daniels, and Matt Tuten. Peter M. Brown of Rocky Mountain Tree-Ring Research provided help and suggestions. Sara Brinton and Steve Hartvigsen of the San Juan National Forest provided historical information and logistical assistance. Larissa Yocom, Emily Heyerdahl, and an anonymous reviewer gave helpful comments on the draft manuscript.

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