

Forest change on a steep mountain gradient after extended fire exclusion: San Francisco Peaks, Arizona, USA

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Summary

1. More than a century of forest management, including fire exclusion, livestock grazing and tree harvesting, may have affected forest structure and composition in south-western USA. Dendroecological techniques were used to reconstruct an 1876 baseline against which modern conditions could be compared. We assessed the magnitude of changes on the San Francisco Peaks in five distinct forest types: ponderosa, mixed conifer, aspen, spruce–fir and bristlecone.

2. We established a systematic grid of 135 plots, each 0.1 ha in size, over a 1117-m altitudinal band.

3. In the contemporary forest, density was greatest in spruce–fir and least in bristlecone whereas basal area was greatest in spruce–fir and lowest in ponderosa. In 1876, all forest types had significantly lower densities and basal areas.

4. The period since 1876 was associated with increased forest density, a shift in species composition as a result of invasion of shade-tolerant conifers, and a trend for mesic species to migrate to lower altitudes. Changes were least evident in the highest altitude forests. Climate and human-caused and natural biotic disturbance factors probably all played a role in forest change, but we argue that the most prominent factor was probably exclusion of the thinning effect of fire, especially on fire-susceptible mesic species.

5. *Synthesis and applications.* Mesic species have encroached to lower altitudes and forest density has increased since 1876. These changes have created to conditions opposite to those suitable for warmer, drier future climates that will display increased fire risk, setting the stage for sudden and severe change. Management is complex because of heavy fuel loading, administrative constraints and high public visibility. However, ‘sky island’ landscapes such as the Peaks represent protected ecosystems of great importance in arid regions. Testing of wildland fire use and other management interventions to restore composition and fuel structures more resilient to warmer climate should proceed.

Key-words: dendrochronology, altitudinal gradient, fire exclusion, fire management, wilderness management

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Introduction

Patterns of recent (20th century) forest change vary with forest type (Bekker & Taylor 2001; Whitlock, Shafer & Marlon 2003). In the south-western USA, the role of surface fire regimes and the effects of fire exclusion associated with Euro-American settlement have been well studied in low altitude forests (c. 2000–2600 m a.s.l.)

dominated by ponderosa pine and mixed conifers (scientific names of species are given in Table 1). In these areas, fire exclusion beginning in the late 19th century, accompanied by grazing and tree cutting, has resulted in high tree density, fuel accumulations and increased risk of crown fire (Cooper 1960; Covington *et al.* 1994; Swetnam & Baisan 2003). High altitude forests (> 2600 m a.s.l.) comprise only about 3% of Arizona forests (O’Brien 2002) but are ecologically critical sites for landscape diversity (Dahms & Geils 1997). The role of fire and the effects of fire exclusion have not been well studied in these rare forests.

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Table 1. Tree species found on study plots. White fir *Abies concolor* (Gordon & Glendinning) Hoopes, and Gambel oak *Quercus gambelii* Nutt. were found sparsely in the study area but were not encountered on sampling plots. We called the low-altitude white pine *Pinus flexilis* following Mitton, Kreiser & Latta (2000) but there is uncertainty about the presence of *Pinus strobiformis* or a zone of hybridization between *P. flexilis* and *P. strobiformis* on the San Francisco Peaks

Latin name and authority	Common name	Code
<i>Abies lasiocarpa</i> var. <i>arizonica</i> (Hook.) Nutt	Corkbark fir	<i>Abies</i>
<i>Pinus aristata</i> Engelm.	Bristlecone pine	<i>P. aristata</i>
<i>Picea engelmannii</i> Parry ex Engelm.	Engelmann spruce	<i>Picea</i>
<i>Pinus flexilis</i> James	Limber pine	<i>P. flexilis</i>
<i>Pinus ponderosa</i> var. <i>scopulorum</i> P. & C. Lawson	Ponderosa pine	<i>P. ponderosa</i>
<i>Populus tremuloides</i> Michx.	Quaking aspen	<i>Populus</i>
<i>Pseudotsuga menziesii</i> (Mirb.) Franco var. <i>glauca</i> (Beissn.) Franco	Douglas-fir	<i>Pseudotsuga</i>

Forest changes associated with fire exclusion vary widely between forest types. Because ponderosa and some mixed conifer stands have estimated fire return intervals of 2–12 years and 4–25 years, respectively (Wolf & Mast 1998; Swetnam & Baisan 2003), structure and composition have been dramatically altered as a result of fire exclusion (Covington *et al.* 1994; Fulé *et al.* 2002). Shade-tolerant mesic trees that would be most readily killed by fire are able to survive below the existing canopy. In contrast, overall aspen cover may be declining (Loope & Gruell 1973; Johnson 1994; Renkin & Despain 1996; Kay 1997; Ripple & Larsen 2000) as most sprouting occurs vegetatively following large disturbances. Finally, because mesic spruce–fir forests experience naturally long fire intervals, estimated at 70–400 years (Aplet, Laven & Smith 1988; White & Vankat 1993; Grissino-Mayer, Baisan & Swetnam 1995; Fulé *et al.* 2003), it is possible that a century of fire exclusion has not had as large an impact as in lower altitude forests (Romme 1982). Little is known about bristlecone forests (Schubert & Rietveld 1970; Baker 1992).

Predictions for increased global temperatures may threaten the sustainability of high-altitude forests (Malcolm *et al.* 2002). Because of changes in forest composition, structure and fuel loading, these forests may be relatively severely impacted by increased temperatures, drought and fire (Flannigan, Stocks & Wotton 2000). Rapid changes in climate may result in certain species being incapable of surviving in their present locations (Loehle 2000; Shafer, Bartlein & Thompson 2001).

The San Francisco Peaks (hereafter Peaks) in northern Arizona, USA, reach 3855 m a.s.l. and comprise a unique environment that represents all of the important high-altitude forest types of south-western USA. Forests of ponderosa pine, aspen and bristlecone pine are dominated by a single species (Table 1). Co-dominant species exist in mixed conifer forests (Douglas-fir and limber pine) and in Engelmann spruce–subalpine fir forests (an endemic south-western USA variety, corkbark fir). Fire was nearly completely excluded after the 1870s as a result of livestock grazing and fire suppression practices introduced by European settlers (Dieterich 1980; Heinlein 1996), with minimal areas burnt since

then (P.Z. Fulé, unpublished data). In 1984, a large portion of the Peaks was set aside as a designated Wilderness Area.

The objectives of this study were to compare current and reconstructed historical forest structure over the Peaks altitudinal gradient to address the following questions. (i) How has forest structure changed within each forest type since Euro-American settlement? After approximately 124 years of fire exclusion, we hypothesized that forests adapted to frequent surface fire would be the most altered, while high-altitude forests, adapted to an infrequent fire regime, would show minimal change. (ii) Has forest composition shifted over the landscape? Fire-susceptible mesic species populations, with characteristics such as thin bark, low crown base height and low resistance to scorch, were considered likely to have been held in check by frequent fires at low altitude. We expected to find downward encroachment of such species in the altitudinal gradient in the absence of fire. (iii) Finally, how can these data be applied to the management and conservation of these rare habitats?

Materials and methods

LOCATION

We sampled 3500 ha on the south face of the Peaks within the Coconino National Forest, north of Flagstaff, Arizona, USA. Study plots were within or directly adjacent to the Kachina Peaks Wilderness Area. Past sheep and cattle grazing occurred at all altitudes but timber harvesting only occurred up to roughly 2700 m. Study plot altitudes ranged from 2442 m to 3559 m. Plots were measured from the year 2000 until 2003. Weather from the Fort Valley weather station (www.wrcc.dri.edu), located approximately 5 km south-west of the study site, was summarized from 1909 to 2001. Mean January temperatures were 5.2 °C maximum and –12.3 °C minimum. Mean July temperatures were 26.7 °C maximum and 7.1 °C minimum. Mean annual precipitation was 56.9 cm. The Fort Valley weather data are applicable only to the lower altitudes of our study. The cooler conditions at higher altitudes may be inferred from measurements taken at weather stations established by Pearson (1920) in 1917 and 1918 in the

following forest types on the Peaks: ponderosa pine (2043–2530 m), Douglas-fir (2530–2896 m), Engelmann spruce (2896–3506 m) and alpine (above 3506 m). Mean annual temperatures ranged from 5.8 °C in ponderosa, 5.4 °C in Douglas-fir, 3.1 °C in Engelmann spruce and –0.05 °C in alpine zones.

In this study, we stratified forest types into five categories: ponderosa, mixed conifer, aspen, spruce–fir and bristlecone. Henceforth, these terms will be used to indicate the forest type. To minimize confusion between forest type names and the names of species, individual tree species will be referred to by genus (and species for *Pinus*) for the remainder of the paper (Table 1).

FIELD SURVEY

To measure forest structure and composition proportional to occurrence over the landscape, 135 sample plots were located on a systematic grid 300 m north–south and 300 m or 600 m east–west, with greater sampling density along the prevailing altitude gradient, north–south. The grid spacing was designed to assess forest structure at a large spatial scale. If a grid point fell in a non-forested location, we checked 50 m to the north, east, south and west to locate a substitute plot. Only if all those locations were also non-forested was the grid point eliminated from assessment. The 500-ha Leroux Fire burned over part of the study area in 2001, but we had already collected ground data before the fire (Cocke, Fulé & Crouse 2005) in all but nine plots. These nine plots had surface fire and mortality was low, although the density of recently dead trees was slightly higher here than overall across the Peaks.

Sampling plots, modified from the National Park Service's fire monitoring protocol (NPS 2003), were 0.1 ha (20 × 50 m) in size and were orientated with the 50-m sides uphill–downhill. All trees were tagged and tree measurements included species, diameter at breast height (d.b.h.), height, crown base height and tree condition. Trees larger than 15 cm d.b.h. were measured on the entire plot; trees between 2.5 and 15 cm d.b.h. were measured on a 0.025-ha subplot. Trees smaller than 2.5 cm d.b.h. (regeneration) were tallied by species and height class on a 50-m² subplot.

Increment cores were taken at 40 cm above ground level for all trees that were considered to have established before the time of fire exclusion and for 10% of trees that had established after this period. Conifers with d.b.h. 37 cm, aspens with d.b.h. 20 cm and ponderosa pine trees of any size with yellowed bark were likely to pre-date fire exclusion (Mast *et al.* 1999). Origin date was corrected later in the laboratory using age data.

Along the 50-m sidelines of the plot, canopy cover was recorded with a vertical densiometer (Ganey & Block 1994); in 2000 this was measured every 30 cm, and in 2001–03 it was measured every 3 m. Forest floor and woody debris were measured along four 15.24-m planar intersect transects (Brown 1974) located every

10 m along the plot centreline. Transect directions were randomly chosen. Litter and duff depths were measured every 1.52 m along each transect, and woody debris was measured by time-lag classes (equivalent to diameter categories; Anderson 1982) of 1 h, 10 h, 100 h and 1000 h along each transect. Fuel loadings were calculated from the planar transect data (Brown 1974; Sackett 1980).

LABORATORY METHODS

Tree increment cores were surfaced and visually cross-dated (Stokes & Smiley 1968; Graybill 1987). Rings were counted on cores that could not be cross-dated. Past forest structure was reconstructed for the year 1876, the time of disruption of the frequent fire regime (Dieterich 1980; Heinlein 1996), following methods described in detail by Fulé *et al.* (2002) and summarized here: (i) the tree diameter in 1876 was reconstructed for all living trees by subtracting the radial growth measured on increment cores since fire exclusion; (ii) for dead trees, the date of death was estimated based on tree condition class using diameter-dependent snag decomposition rates (Thomas *et al.* 1979; Rogers *et al.* 1984) or historical harvesting dates for stumps; (iii) decomposition rates were calculated for average conditions (the 50th percentile tree) as well as for fast decomposition (25th percentile) and slow decomposition (75th percentile) in order to assess the sensitivity of reconstruction results to decomposition rate; and (iv) to estimate growth between the fire exclusion date and death date, we developed local species-specific growth relationships between tree diameter and basal area increment (r^2 for the growth models ranged from 0.38 to 0.92, depending on the species).

We used Landsat 7 Enhanced Thematic Mapper Plus (ETM+) imagery from 6 June 2000 to develop a forest type map to assess whether our plots adequately represented the landscape. A supervised classification using a minimum distance algorithm was undertaken with ERDAS Imagine (Atlanta, GA). Sampling plot data were used as training sites for the classification process where species labels were based on importance values (Taylor 2000) calculated as the sum of the relative frequency (density) and relative abundance (basal area).

Statistical analysis included descriptive statistics and correlation–regression to explore relationships between variables. Differences in structural characteristics on the same plots over time were compared with paired *t*-tests after data were transformed using the equation $X' = \log(X + 1)$ (Zar 1984) to meet assumptions of normality and equality of variance for parametric tests. The alpha level for all analyses was 0.05.

Results

The ground plot distribution was a faithful representation of the landscape. According to the classified imagery, ponderosa was the predominant forest type on the landscape, with roughly 30.1% of the study area.

Table 2. Characteristics of forest types and sample plots on an altitudinal gradient on the San Francisco Peaks, Arizona, USA

Forest type	Area (ha)	Average altitude (m a.s.l.)	Number of sample plots	Average slope (%) on plots	East aspect	South-east aspect	South aspect	South-west aspect	West aspect
Aspen	1020.2	2867	42	31	1	8	15	11	7
Bristlecone	432.5	3287	23	53	1	8	10	3	1
Mixed conifer	633.2	2781	30	31	2	3	17	5	3
Ponderosa	1042.6	2604	30	16	0	2	20	8	0
Spruce–fir	330.5	3197	10	41	0	1	0	7	2
Subtotal	3459		135		4	22	62	34	13
Grass	152.6								
Rock	135.4								
Total	3747								

This was followed closely by aspen (29.5%), then mixed conifer (18.3%), bristlecone (12.5%) and spruce–fir (9.6%). The field plots were distributed similarly (Table 2): 31.1% of the field plots were dominated by aspen, followed by ponderosa (22.2%), mixed conifer (22.2%), bristlecone (17.0%) and spruce–fir (7.4%). Thus the largest discrepancy between field plot sampling and landscape forest types was < 8%.

Average altitudes ranged from ponderosa (2605 m) to bristlecone (3288 m). Slopes increased at higher altitudes, with ponderosa averaging 15.9% slope to bristlecone averaging 53.3%. Altitude and slope were highly positively correlated (Pearson, $r = 0.75$, $P = 0.00$). Most plots (45.9%) had a southerly aspect (Table 2).

Most tree species occurred in all forest types, although one species clearly dominated in both density (trees per hectare) and basal area in most forest types. For example, in ponderosa, 87% of the density and 88% of the basal area were composed of *P. ponderosa*. Compositional mixing was highest in mixed conifer, where *Populus* was 22% of the density and 19% of the basal area. *Picea* also comprised a large percentage of the density in bristlecone (31%), although *Picea* trees were relatively small, making up only 14% of the basal area in this forest type.

Overall, density was greatest in spruce–fir and least in bristlecone (Table 3). Basal area was also highest in

Table 4. Canopy cover (%) by forest type on an altitudinal gradient on the San Francisco Peaks, Arizona, USA

Forest type	Mean	SE	Minimum	Maximum
Aspen	63.6	2.9	25	97.6
Bristlecone	39.3	4.2	0	75
Mixed conifer	65.7	3.5	18.8	96.9
Ponderosa	50.9	3.3	18.8	86
Spruce–fir	58.2	4.6	28.1	80.1

spruce–fir but lowest in ponderosa because of the large number of small diameter trees. The highest percentage canopy cover was in mixed conifer followed by aspen; the lowest was bristlecone (Table 4). Litter depths ranged from an average of 0.73 cm in bristlecone to 1.62 cm in ponderosa. Duff was lowest in bristlecone (1.79 cm) but highest in spruce–fir (4.32 cm). Total woody debris was quite variable by forest type, ranging from 62 to 132 Mg ha⁻¹ (Table 5).

Regeneration density ranged from highest in aspen (2580 stems ha⁻¹, mostly *Populus*) to lowest in bristlecone (301.5 stems ha⁻¹, mostly *P. aristata*; Table 6). These two species followed the same trend regardless of forest type, with *Populus* regenerating the most (775 stems ha⁻¹) and *P. aristata* the least (25 stems ha⁻¹). Total regeneration was highest for all species in the height class less

Table 3. Density and basal area, for trees greater than 2.5 cm d.b.h., by forest type on an altitudinal gradient on the San Francisco Peaks, Arizona, USA. Standard error is in parentheses. Tree species codes are given in Table 1

Forest type	<i>Abies</i>	<i>P. aristata</i>	<i>Picea</i>	<i>P. flexilis</i>	<i>P. ponderosa</i>	<i>Populus</i>	<i>Pseudotsuga</i>	Total
Tree density (trees ha ⁻¹)								
Aspen	52.15 (30.3)	35.07 (16.2)	46.29 (31.7)	83.71 (20.6)	8.51 (3.3)	432.9 (37.2)	110.04 (38.6)	768.67 (94.0)
Bristlecone	0.95 (0.7)	342.61 (34.6)	169.49 (43.4)	12.84 (4.1)	0	20.13 (17.3)	0	546.02 (69.8)
Mixed conifer	9.08 (6.0)	9.64 (8.5)	2.18 (1.9)	272.45 (40.3)	28.24 (10.7)	176.57 (321)	322.78 (51.5)	820.94 (76.7)
Ponderosa	0	0.35 (0.35)	0.34 (0.3)	29.93 (6.4)	626.32 (96.5)	18.07 (14.3)	49.08 (23.8)	724.07 (116.5)
Spruce–fir	297.92 (89.3)	95.56 (51.1)	368.44 (81.9)	6.47 (4.6)	0	66.28 (34.1)	5.59 (5.6)	840.26 (138.0)
Basal area (m ² ha ⁻¹)								
Aspen	1.969 (1.0)	1.705 (0.9)	1.25 (0.7)	4.019 (0.8)	0.856 (0.3)	30.221 (2.0)	4.031 (0.9)	44.055 (2.5)
Bristlecone pine	0.131 (0.1)	38.324 (4.1)	6.46 (1.4)	0.523 (0.3)	0	0.767 (0.7)	0	46.207 (4.8)
Mixed conifer	1.094 (0.7)	0.407 (0.3)	0.151 (0.1)	15.675 (2.2)	1.877 (0.6)	8.69 (1.1)	17.36 (3.0)	45.254 (4.2)
Ponderosa	0	0.007 (0.007)	0.012 (0.012)	1.506 (0.4)	30.394 (2.9)	0.532 (0.3)	1.99 (0.8)	34.439 (3.0)
Spruce–fir	20.963 (5.5)	7.173 (3.0)	24.965 (4.9)	0.119 (0.09)	0	2.891 (1.5)	1.667 (1.7)	57.776 (4.2)

Table 5. Forest floor (litter and duff) depth and woody debris on an altitudinal gradient on the San Francisco Peaks, Arizona, USA. Woody materials are listed by time-lag class (1H, 1 h time lag) corresponding to diameter categories (Anderson 1982). Standard error is in parentheses

Forest type	Litter depth (cm)	Duff depth (cm)	1H (Mg h ⁻¹)	10H (Mg h ⁻¹)	100H (Mg h ha ⁻¹)	1000H sound (Mg ha ⁻¹)	1000H rotten (Mg ha ⁻¹)	Total woody debris (Mg ha ⁻¹)
Aspen	1.09 (0.1)	2.64 (0.2)	0.22 (0.03)	1.6 (0.2)	6.46 (0.6)	41.05 (6.2)	44.88 (13.0)	94.21 (16.6)
Bristlecone	0.73 (0.1)	1.79 (0.3)	0.38 (0.06)	1.03 (0.2)	2.99 (0.7)	26.87 (7.2)	30.78 (14.6)	62.04 (19.5)
Mixed conifer	1.23 (0.1)	3.82 (0.3)	0.33 (0.04)	2.82 (0.5)	7.42 (1.1)	32.24 (9.3)	29.61 (6.4)	72.41 (13.2)
Ponderosa	1.62 (0.2)	2.46 (0.3)	0.23 (0.04)	1.46 (0.2)	3.03 (0.5)	28.01 (16.3)	36.84 (17.1)	69.57 (25.0)
Spruce–fir	1.05 (0.2)	4.32 (0.8)	0.69 (0.1)	2.29 (0.8)	5.07 (1.1)	55.49 (24.3)	68.66 (38.8)	132.19 (51.9)

than 30 cm, ranging from 127 stems ha⁻¹ in bristlecone to 1766 stems ha⁻¹ in aspen. Densities were lowest for all stems taller than 2 m. No stems in this height class occurred in bristlecone or spruce–fir, and other values were 72 stems ha⁻¹ for mixed conifer, 35 stems ha⁻¹ for ponderosa and 44 stems ha⁻¹ for aspen. All stems in the aspen type greater than 2 m were either *P. flexilis* or *Pseudotsuga*. Therefore, although *Populus* sprouts made up the highest density of all species, all were smaller than 2 m.

Age distributions were calculated in 20-year intervals by species (Fig. 1). *Pinus aristata* trees have been steadily establishing for the last 400 years. The spruce–fir (*Picea* and *Abies*) and mixed conifer species (*Pseudotsuga* and *P. flexilis*) also experienced continuous establishment. In contrast, *Populus* experienced a large increase around 1880 followed by a decline; few have established since the 1940s. *Pinus ponderosa* experienced a large increase in establishment around the 1920s and 1940s.

All forest types had significantly lower densities and basal areas in 1876 than in 2000 (paired *t*-test, $P = 0.0001$; Tables 7 & 8). Tree densities in 1876 ranged from 61.7 trees ha⁻¹ in ponderosa to 283.9 trees ha⁻¹ in bristlecone. Basal areas ranged from 7.3 m² ha⁻¹ in aspen to 27.3 m² ha⁻¹ in bristlecone. Density increases were largest in ponderosa (1073%) and lowest in bristlecone (92%). However, changes in basal area were greatest in aspen (456%) and lowest in bristlecone (69%) (Table 8). Several species now occur in forest types in which they previously did not occur. In the 1876 forest, *Abies*, *P. aristata*, *Picea* and *P. flexilis* were absent from the ponderosa type and *P. ponderosa* was absent from bristlecone and spruce–fir types. By 2000, *P. ponderosa* was still absent from bristlecone and spruce–fir types but *Abies* was the only species absent from ponderosa. By matching 1876 and modern distributions with plot altitudes, we found that *P. aristata* had descended by 150 m, *Picea* by 400 m, *P. flexilis* by 25 m and *Pseudotsuga* by 55 m. In 1876 *P. ponderosa*'s upper limit was 3029 m, but currently the

Table 6. Tree regeneration (stems ha⁻¹) by forest type on an altitudinal gradient on the San Francisco Peaks, Arizona, USA. All classes of regeneration up to saplings (trees < 2.5 cm d.b.h.) are grouped together. Standard error is in parentheses

Forest type	<i>Abies</i>	<i>P. aristata</i>	<i>Picea</i>	<i>P. flexilis</i>	<i>P. ponderosa</i>	<i>Populus</i>	<i>Pseudotsuga</i>	Total
Aspen	390.4 (339.4)	0	0	92.6 (49.8)	4.8 (4.8)	1975.1 (461.4)	117.3 (57.1)	2580.24 (557.1)
Bristlecone	0	118.6 (53.8)	133.5 (70.9)	20.3 (14.0)	0	29.2 (29.2)	0	301.49 (93.8)
Mixed conifer	0	7.4 (7.4)	0	217.6 (124.9)	27.6 (27.6)	1431 (510.0)	180.6 (57.6)	1864.14 (499.5)
Ponderosa	0	0	0	33.7 (23.9)	533.7 (284.6)	221.6 (152.6)	40.7 (15.1)	829.61 (321.7)
Spruce–fir	218.8 (98.0)	0	173.2 (89.6)	0	0	217.9 (148.7)	153.5 (153.5)	763.37 (294.5)

Table 7. Reconstructed forest structure in 1876, based on dendro-ecological sampling and decomposition modelling. Standard error is in parentheses

Forest type	<i>Abies</i>	<i>P. aristata</i>	<i>Picea</i>	<i>P. flexilis</i>	<i>P. ponderosa</i>	<i>Populus</i>	<i>Pseudotsuga</i>	Total
Tree density (trees ha ⁻¹)								
Aspen	2.2 (1.25)	9.1 (4.74)	0.8 (0.44)	9.0 (2.83)	9.5 (4.00)	96.15 (12.40)	9.8 (2.76)	136.5 (11.74)
Bristlecone	0.51 (0.51)	258.7 (33.3)	19.3 (7.2)	0.5 (0.51)	0	3.9 (3.89)	0	282.9 (35.77)
Mixed conifer	2.4 (1.64)	2.4 (1.44)	0.4 (0.4)	43.8 (8.18)	18.0 (5.20)	43.3 (7.29)	50.6 (10.03)	160.88 (16.70)
Ponderosa	0	0	0	0	57.9 (6.38)	2.27 (1.38)	1.1 (0.83)	61.4 (6.53)
Spruce–fir	62.0 (21.64)	87.8 (39.62)	98.92 (27.00)	2.2 (2.24)	0	7.44 (3.08)	4.5 (4.47)	262.9 (40.86)
Basal area (m ² ha ⁻¹)								
Aspen	0.26 (0.15)	0.75 (0.39)	0.03 (0.02)	1.14 (0.58)	1.12 (0.50)	2.44 (0.59)	2.17 (0.68)	7.92 (1.15)
Bristlecone	0.01 (0.01)	26.53 (3.58)	0.71 (0.34)	0.003 (0.003)	0	0.03 (0.03)	0	27.30 (3.71)
Mixed conifer	0.24 (0.24)	0.26 (0.17)	0.001 (0.001)	4.64 (0.85)	2.06 (0.60)	0.65 (0.13)	10.03 (2.71)	17.89 (2.94)
Ponderosa	0	0	0	0	7.20 (1.09)	0.06 (0.04)	0.31 (0.22)	7.57 (1.13)
Spruce–fir	2.63 (0.97)	8.05 (3.62)	3.67 (1.04)	0.05 (0.05)	0	0.11 (0.06)	0.97 (0.97)	15.47 (3.28)

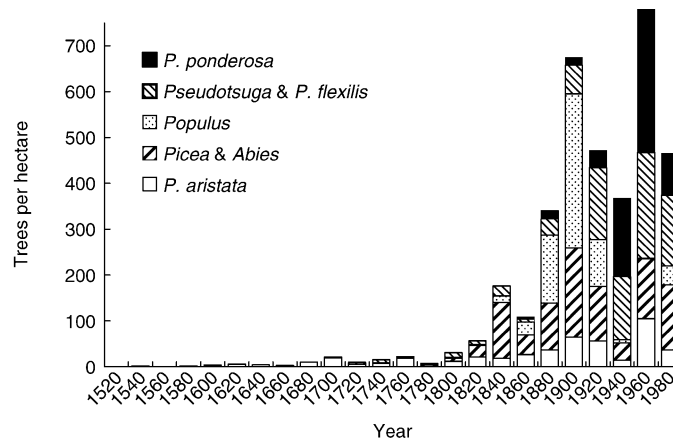


Fig. 1. Centre date at 40-cm coring height in 20-year intervals of trees; ≥ 2.5 -cm diameter on an altitudinal gradient on the San Francisco Peaks, Arizona, USA.

Table 8. Matrix of percentage change in tree density and basal area by forest types between 1876 and 2000

Forest type	<i>Abies</i>	<i>P. aristata</i>	<i>Picea</i>	<i>P. flexilis</i>	<i>P. ponderosa</i>	<i>Populus</i>	<i>Pseudotsuga</i>	Total
Density change (%)								
Aspen	2241	285	5 887	807	10	327	1024	442
Bristlecone	93	32	753	2 425	0	417	0	92
Mixed conifer	284	301	452	522	53	290	537	403
Ponderosa	0	0	0	0	980	581	4233	1072
Spruce–fir	380	8	268	189	0	588	25	215
Basal area change (%)								
Aspen	648	126	4 494	252	23	1138	85	456
Bristlecone	959	44	803	18 585	0	2284	0	69
Mixed conifer	347	55	10 907	237	8	1227	73	152
Ponderosa	0	0	0	0	337	852	564	371
Spruce–fir	698	10	579	145	0	2558	72	273

upper limit for this species is 2860 m. In contrast, *Abies* and *P. flexilis* are currently found 200 and 156 m higher, respectively, than in 1876.

Discussion

Potential sources of error in the 1876 stand reconstruction include loss of evidence, variability between species in time to reach coring height and the use of decomposition models. Loss of evidence would be largest if a fire had occurred in the study site after the reconstruction date. Fire scars and age data collected in a companion study show that almost no fires occurred in the study site after 1880 (P.Z. Fulé, unpublished data). Loss of evidence could also occur if small trees decayed completely, which could occur within a 124-year period. However, the methods we applied on the Peaks have been tested in other northern Arizona forests. Mast *et al.* (1999) showed that old tree material could be reliably dated to pre/post-1876 status in the field. Moore *et al.* (2004) compared historical tree records (1909) to reconstructed ponderosa density, finding that roughly 3 trees ha^{-1} were lost in the reconstruction, most probably as a result of decay. Fulé *et al.* (2003) compared reconstructed forest structure, including ponderosa, Douglas-fir, cork-bark fir and Engelmann spruce, to data from a detailed

survey conducted by Lang & Stewart (1910) on the North Rim of Grand Canyon. Tree density in the 1910 survey data averaged within 5–9% of the reconstructed data and no species exceeded a 25% difference.

Establishment year uncertainty exists because of a lack of knowledge of time to reach coring height and how this varies between species. On the Peaks, Heinlein (1996) found that ponderosa ranged from 11 to 17 years to attain a 40-cm height, whereas limber pine took as long as 25 years to reach the same height. To compensate for uncertainty, we grouped trees into 20-year intervals and assessed data as the age at coring height and not by year of establishment.

Generalized decomposition equations also add uncertainty to the reconstruction model, leading us to carry out a sensitivity analysis using three different decomposition rate percentiles, 25%, 50% and 75%. Changes in stand densities in the five forest types ranged from 1.3% to 16.6% between the 25th and 50th percentiles. Differences were between 7.0% and 14% between the 50th and 75th percentile. Changes in basal area ranged from 0.1% to 21.2% between the 25th and 50th percentiles. Differences were between 10.8% and 22.6% between the 50th and 75th percentiles. Aspen and spruce–fir forest types were the most sensitive (Table 9). While the variability associated with the reconstruction is substantial, covering

Table 9. Results of sensitivity analysis on tree decomposition modelling. Percentage changes between 25% and 50% decomposition rates and percentage changes between 50% and 75% decomposition rates

Forest type	% difference 25% to 50% rate		% difference 50% to 75% rate	
	Density	Basal area	Density	Basal area
Aspen	16.6	15.6	13.0	18.4
Bristlecone	2.4	5.8	7.0	10.8
Mixed conifer	4.9	0.1	14.0	17.9
Ponderosa	1.3	12.8	9.7	15.5
Spruce–fir	2.7	21.2	10.7	22.5

an approximate range of -20% to $+20\%$, this variability is still substantially less than the overall increase in tree density and basal area between the 1870s and today: range 69% to $> 1000\%$.

Between 1876 and the present, changes in tree density and basal area were lowest in higher altitude forests. Changes in the bristlecone type were lower than all other forest types on the Peaks. This type also has minimal fuel loadings. Bristlecone pine has a high fire tolerance rating (USDA 2004; <http://www.fs.fed.us/database/feis/index.html>, accessed 4 June 2005) but was classified in the 'no predictable fires' group by Keeley & Zedler (1998). Mature *P. aristata* trees on the Peaks may have survived fires over the last several centuries, as current forests are characterized by large and old trees, several with multiple fire scars (P.Z. Fulé, unpublished data). While Baker (1992) determined that bristlecone in Colorado established primarily following fire, we found continuous establishment of *P. aristata* for more than 400 years, even at the plot level. Preliminary fire regime data from bristlecone pine on the study area indicated evidence of both surface and small patches of stand replacing fire (P.Z. Fulé, unpublished data).

Density changes in the spruce–fir type were also low compared with lower altitude forests. Because *Abies* and *Picea* are relatively fire-susceptible, ages of old trees may indicate fire-free intervals. From the ages of trees on the Peaks, it appears that a stand-replacing fire has not occurred for at least 200 years in most of the spruce–fir type. These forests had high duff and coarse woody debris accumulation. Litter depths and fine woody fuel loadings were low, which could be the result of a compact litter layer under these short-needed species (Burns & Honkala 1990) and retention of dead branches (Brown & Bevins 1986).

Mid-altitude forests had moderate structural changes. The mixed conifer type had moderate density increase and relatively low increase in basal area. The aspen type showed large density increases, but mostly from conifers. More than 84% of dead trees within aspen types were actually *Populus*, underscoring the decline of the aspen forest type.

Ponderosa types of forest changed the most in density. Current ponderosa types on the Peaks have high densities but low basal areas, indicating establishment of many small trees. Ponderosa establishment was low but continuous until around 1880, when establishment escalated, similar to patterns in nearby stands (Mast *et al.* 1999). Meadow invasion has occurred in many lower altitude parks in the south-western USA (Dyer & Moffett 1999). Plots where oldest trees established after 1920 on the Peaks were along dry grassland meadows.

The whole landscape is affected by forest change, even though the degree of change has varied among forest types. Because changes were lowest in high altitude forests where fire frequency was historically lower (Wolf & Mast 1998), fire exclusion has probably had less impact on these areas (Romme 1982) although even limited effects might be ecologically meaningful (Taylor 2000). Fulé *et al.* (2003) found that fire years in higher altitudes were also fire years in lower altitudes, as many ignitions in lower forests were carried upslope. In cedar groves, Habeck (1985) found that although stands that experience fire infrequently may have had few direct effects of fire exclusion, these forests were often adjacent to forest types that had been highly affected by exclusion, creating more fuel continuity. White & Vankat (1993) noted that the continuity of dense stands in a high-altitude forest could lead to larger fires, perhaps creating landscapes with less patch diversity. Grissino-Mayer, Baisan & Swetnam (1995) suggested that the mixed conifer type acted as a buffer around the spruce–fir type.

Climate change also causes forest change (Shafer, Bartlein & Thompson 2001) and can interact with fire exclusion effects. Past climatic events have strong relationships with regional fire years in south-western USA (Swetnam & Baisan 2003). The role of climate change in the 20th century on the Peaks is not entirely clear. Salzer's (2000) dendroclimatological reconstruction from the Peaks found that periods in the early and late 20th century were relatively wet, but Biondi (1999) observed no trend in 20th century weather records from Fort Valley, at the base of the Peaks. While it may not be possible to disentangle the past influences of climate from those of fire exclusion, the predicted future climate is likely to pose a sharply different environment with negative effects on current forest conditions, as described below.

We observed a shift in species composition, resulting in greater dominance by mesic species at lower altitudes compared with 1876. Certain species were able to survive where establishment was previously prevented, most probably by the historical surface fire regime. In 1876 *Abies*, *P. aristata*, *Picea* and *P. flexilis* did not exist within the ponderosa type, while in 2000 all of these species except *Abies* occurred there. Shade-tolerant conifers also increased in mid-altitude forests. Not only have *P. flexilis* and *Pseudotsuga* become more dominant in the mixed conifer type, but the aspen types are also being invaded by conifers, consistent with numerous studies that have suggested that aspen cover is declining in the west. Johnson (1994) estimated that

aspen stands declined by 46% in a 24-year period in New Mexico and Arizona. Because *Populus* regenerates best following disturbances (Dahms & Geils 1997) and poorly without disturbances (Andrejak & Barnes 1969), fire exclusion has probably had a negative impact on these stands. On the other hand, high numbers of elk *Cervus elaphus* may decimate any regeneration (Bartos, Brown & Booth 1994; Kay 1997; Ripple & Larsen 2000; Hessler & Graumlich 2002). Age data showed that within 50 years of fire exclusion, *Populus* establishment severely decreased and invasion of conifers occurred. Most establishment of *Populus* on the Peaks occurred before 1920. Overstorey mortality may result in more sprouting (Bartos, Brown & Booth 1994; Bailey & Whitham 2002), although areas of most re-growth may receive heavier elk browsing.

Climate interacts with disturbance, influencing how and when forests burn (Turner *et al.* 1994; Swetnam & Baisan 2003). Many studies suggest that global temperatures will increase (Hanson & Weltzin 2000; Flannigan, Stocks & Wotton 2000), leading to increases in fire frequency and severity because of more extreme temperature days, increased drought (Hanson & Weltzin 2000) and longer fire seasons (Flannigan, Stocks & Wotton 2000).

Climate changes combined with fire exclusion have major implications for south-western USA forests. Increased temperatures cause lower altitudes to become too dry to support some species (Shafer, Bartlein & Thompson 2001), which may migrate to higher altitudes if natural and/or human-aided migration rates are fast enough (Malcolm *et al.* 2002). High-altitude forests, which usually retain higher moisture content (Pearson 1920), will become drier and more likely to burn. Without fire exclusion, mesic species would probably not have migrated down in altitude and would not be as susceptible to increased fire. However, because species have moved down in altitude, fire threatens more forest types and their dependant species. Rapid climate change may already be difficult for plant communities to cope with (Shafer, Bartlein & Thompson 2001; Malcolm *et al.* 2002) and, coupled with the results of fire exclusion, will potentially lead to substantial shifts in vegetation.

Ecosystem management on the Peaks is done in the context of the 1964 Wilderness Act's mandate for protected lands to be 'untrammeled by man'. However, many wilderness areas, including the Kachina Peaks, were designated in recent decades after sustained manipulation through fire exclusion, grazing and logging by humans. Prior to Euro-American settlement, alterations by indigenous people occurred for thousands of years (Pyne 1982). But in south-western USA forests that were remote from intensive Native American use, such as the Peaks, the recent changes in forest structure and process are much faster and broader in spatial scale (Allen 2002). Fire exclusion on the Peaks is associated with compositional shifts that may increase stand homogeneity and in turn could increase susceptibility to fire and other disturbance agents such as pathogens.

Management in wilderness areas should be orientated towards certain key objectives. One objective may be to minimize management, maximizing the characteristics that Cole (2001) referred to as 'wildness'. Under this option, larger fires are likely to spread through all forest types in the next few decades but aspen could still decline as a result of herbivory (Kay 1997; Bailey & Whitham 2002). These effects may seem negative in the short term but eventually will result in lands that are in a 'wild' state.

An alternate objective might be to manage for 'naturalness' (Cole 2001) by restoring and maintaining, to the extent possible, forest structures, composition and disturbance regimes similar to historical patterns. Several studies throughout the south-western USA have examined ponderosa pine and lower mixed conifer forest restoration through combinations of thinning and burning (Covington *et al.* 1997; Lynch, Romme & Floyd 2000; Fulé *et al.* 2002). There is also evidence that relatively severe prescribed burning without thinning could also serve restorative goals in some circumstances (Miller & Urban 2000; Fulé *et al.* 2004). If the lower altitude forests were targeted for restoration management, reestablishment of open forest and meadows could mitigate the size and intensity at which high-severity burns could enter higher altitudes, maintaining a pattern of stand-replacing fires in the aspen and spruce-fir similar to historical patterns.

Merriam (1890) used the Peaks' forests to illustrate the relationship between latitudinal and altitudinal climate patterns, explaining the post-glacial 'distribution of life in North America' as the result of the Holocene mixing of northern (boreal) and southern (Sonoran) taxa. The concept of climatically regulated 'life zones' was readily accepted by ecologists but it took longer to recognize the critical role of disturbance. Now that a brief 130-year period of fire exclusion and other human-caused factors has led to substantial changes in forest structure, especially at lower altitudes, and future climate appears likely to turn favourable for increased fire activity, Merriam's (1890: pp. 23–24) observation regarding post-glacial migration takes on new urgency: 'when the physiographic conditions of a region are in a process of change, those forms of life which are sufficiently plastic to adapt themselves to the rapidly changing conditions survive, while those which cannot so adapt themselves become extinct'.

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