Forest Ecology and Management 269 (2012) 10–18

Contents lists available at SciVerse ScienceDirect

Forest Ecology and Management

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

Forest restoration in a surface fire-dependent ecosystem: An example from a mixed conifer forest, southwestern Colorado, USA

Julie E. Korb [a,*], Peter Z. Fulé [b], Michael T. Stoddard [c]

[a] Department of Biology, Fort Lewis College, Durango, CO 81301, USA
[b] School of Forestry, Northern Arizona University, Flagstaff, AZ 86011, USA
[c] Ecological Restoration Institute, Northern Arizona University, Flagstaff, AZ 86011, USA

ARTICLE INFO

Article history:
Received 10 November 2011
Received in revised form 3 January 2012
Accepted 4 January 2012

Keywords:
Adaptive management
Aspen
Ecological restoration
Ponderosa pine
San Juan Mountains
White fir

ABSTRACT

Over a century of fire suppression in warm/dry mixed conifer forests of southwestern Colorado, USA has resulted in changes that have disrupted feedback interactions between vegetation composition and structure and the accompanying natural fire regime. The ecosystem is now more susceptible to high intensity crown fires that were previously rare or absent in this forest type, which can lead to novel ecosystems. We established four replicated blocks of (1) thin/burn, (2) burn alone and (3) control treatments, each approximately 16-ha, to quantify the effects of restoration treatments on forest structure. We sampled in 2003 (pre-treatment) and in 2009 (post-treatment). There were no significant changes in the control and burn alone treatments for tree density, basal area, canopy cover and tree regeneration between pre- and post-treatment. Significant changes in the thin/burn treatments included: tree density declining 82% (582.7 trees ha^{-1}), principally white fir and Douglas-fir; tree canopy cover decreasing 36%; basal area declining 49% (12.5 $m^2\,ha^{-1}$), primarily from white fir; aspen tree regeneration increasing by 362% (582.7 trees ha^{-1}), and white fir regeneration decreasing by 94% (249.1 trees ha^{-1}). Overstory trees that died tended to be younger, shorter, and/or smaller in diameter. Multivariate analysis of tree basal area by species in the thin/burn treatments in 2009 showed a strong directional shift away from 2003 pre-treatment data towards the reconstructed historical (1870) forest structure. Burn alone treatments were distinct from controls after treatment in 2009 but did not resemble reconstructed 1870 forest structure. Thin/burn treatments moved warm/dry mixed conifer forests in southwestern Colorado rapidly along the trajectory toward historical reference conditions by altering forest composition and structure. Burn alone treatments were less effective but also less costly. Forest restoration will make forests more resilient to stand-replacing fires and subsequent transitions to novel ecosystems under a warmer, drier climate.

1. Introduction

There is abundant evidence that 20th century fire suppression in pure ponderosa pine and low elevation mixed conifer forests in the southwestern United States has resulted in changes to forest composition, structure and ecological processes (Brown et al., 2001; Grissino-Mayer et al., 2004; Brown and Wu, 2005; Heinlein et al., 2005; Fulé et al., 2009; Evans et al., 2011). Paleoecological studies in the Southwest (Toney and Anderson, 2006; Allen et al., 2008; Bigio et al., 2010) and other regions with similar vegetation types (Whitlock et al., 2003) have extended the long-term historical fire record to the millennial scale providing further evidence that the absence of fire in the 20th century represents an anomaly in forests where the regular occurrence of low intensity surface burning was previously common.

Mixed conifer forests in the San Juan Mountains of Southwest Colorado occur along a continuum from warm/dry to cool/moist sites (Romme et al., 2009). Moisture and temperature are the primary drivers that influence species composition and fire regimes for these two mixed conifer forest types. Warm/dry mixed conifer is dominated by fire-resistant ponderosa pine (*Pinus ponderosa* var. *scopulorum* P. & C. Lawson) and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *glauca* (Beinssn.) Franco) but also includes species adapted to mesic conditions such as white fir (*Abies concolor* (Gordon & Glendinning) Hoopes.) and aspen (*Populus tremuloides* Michx.). Warm/dry mixed conifer is located adjacent to, but generally higher in elevation than, pure ponderosa pine stands. Surface fires were frequent before 1868, burning with multi- to sub-decadal frequency in the warm/dry mixed conifer (Grissino-Mayer et al., 2004; Fulé et al., 2009). Cool/moist mixed conifer is dominated by white fir and Douglas-fir, as well as aspen and blue spruce (*Picea pungens* Parry ex Engelm.). Historically, fires in cool/moist mixed conifer forests burned at sub-decadal to century frequency with a mixed-severity fire regime, where surface and crown fire

* Corresponding author. Tel.: +1 970 382 6905; fax: +1 970 247 7206.
E-mail address: korb_j@fortlewis.edu (J.E. Korb).

0378-1127/$ - see front matter © 2012 Elsevier B.V. All rights reserved.
doi:10.1016/j.foreco.2012.01.002

behavior could occur during the same fire event (Margolis and Balmat, 2009; Romme et al., 2009). Feedback cycles between vegetation composition and structure and the accompanying disturbance regime (e.g., fire frequency and intensity) are well documented (Miller and Urban, 2000; Beaty and Taylor, 2001; Martin and Kirkman, 2009). Over a century of fire suppression in warm/dry mixed conifer forests has shifted species composition toward more mesic, shade tolerant species such as white fir and Douglas-fir, increased tree density, and increased surface and aerial fuels (Cocke et al., 2005; Crouse, 2005; Fulé et al., 2009), making them more susceptible to stand-replacing fires which can lead to novel ecosystems (Seastedt et al., 2008). For example, in 2011, warmer than average temperatures and drought in the southwestern United States created conditions favorable for wildfire. The Wallow Fire became the largest wildfire in Arizona recorded history (217720 ha) and the Las Conchas Fire became the largest wildfire in New Mexico recorded history (63371 ha). In contrast to historical surface fires, these recent fires burned as both mixed severity and stand-replacing crown fires in ponderosa pine and low-elevation mixed conifer stands. Future stand regeneration in the severely burned areas may represent novel ecosystems on new successional trajectories away from historical stand characteristic. For example, Savage and Mast Nystrom (2005) found conversion of ponderosa pine to non-forested grass or shrub communities in stands that experienced severe crown fires in the southwestern United States.

Novel ecosystems and rapid 21st century environmental change challenge the use of ecological history (reference conditions) as a tool to characterize targets for ecological restoration (Choi, 2007; Jackson and Hobbs, 2009). We argue, however, that under a warmer and drier climate, the use of site-specific reference conditions is a scientifically sound target for forest stand conditions in surface fire-dependent forest ecosystems because they increase resiliency to uncharacteristic fire behavior, increasing the likelihood of maintenance of ecological goods and services these ecosystems provide (Jackson and Hobbs, 2009). Reference conditions are not a snapshot in time but rather represent a range of historical variability and evolutionary adaptations developed over thousands of years (Fulé, 2008). Specifically, ponderosa pine evolutionary adaptations to drought, deep taproots and self-thinning lower branches, and surface fire, thick bark and protected buds, provides a broader definition of reference conditions to include a long-term functional view (Fulé, 2008). As a result, restoring pine dominated surface fire-dependent forest ecosystems to reference conditions can reduce the potential loss of these ecosystems under a warmer and drier climate. One approach to identifying reference conditions is to compare contemporary and pre-European settlement forest conditions and fire regimes (Fulé et al., 1997; Stephenson, 1999) to guide ecological restoration (Brown et al., 2008). Fulé and others (2009) reconstructed past forest conditions ca. 1870 and the historical fire regime for our study site using dendrochronology. In 2002, we initiated a controlled experiment in warm/dry mixed conifer forest of the San Juan Mountains, Colorado, to assess forest change and test restoration alternatives on the overstory and the herbaceous understory (Korb et al., 2007). We established four replicated blocks, each approximately 16 ha, of three treatments: (1) thin/burn, (2) burn alone, and (3) control. The burn alone treatment was included to determine if restoration goals could be achieved without tree thinning. All treatments were tested against site specific dendrochronological reconstructed reference conditions (Fulé et al., 2009). Site reference conditions at our mixed conifer site illustrated total basal area was on average 11 $m^2 ha^{-1}$ with ponderosa pine representing nearly two-thirds of the basal area and total tree density was on average 142 trees ha^{-1} in 1870.

We have two objectives for this paper: (1) quantify post-treatment differences in forest composition and structure among treatments and compare post-treatment stands with site specific reference conditions; and, (2) quantify changes in untreated controls over a six year period (2003–2009) to assess the stability of warm-dry mixed conifer stands.

2. Methods

2.1. Study area

The study area is located in the San Juan Mountains, in southwest Colorado (N 37.296, W 107.228) on the San Juan National Forest. The site consists of 15–30% slopes on 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. Precipitation from November to March is dominated by snowfall, with an average annual total of 326 cm (Western Regional Climate Center, Pagosa Springs, 1906–1998, <http://www.wrcc.dri.edu>). Forest vegetation includes ponderosa pine, Douglas-fir, white fir, and aspen. The midstory and understory are dominated primarily by white fir and Douglas-fir, with a variety of shrubs including Gambel oak (*Quercus gambelii*), snowberry (*Symphoricarpus rotundifolius*), and serviceberry (*Amelanchier alnifolia*). Past disturbance history includes sheep grazing beginning in the late 1800s and cattle grazing since the early 1900s. Fire suppression has been management policy since the early twentieth century. A single timber harvest occurred between 1990 and 1993, using a selective system that removed 51% ponderosa pine, 33% white fir, and 16% Douglas-fir evenly across the study area (USDA Forest Service, 2004).

2.2. Experimental design

We established four replicate blocks of three randomly assigned treatment units, each approximately 16 ha in size (Fig. 1). Existing roads were used to delineate the blocks because the roads served as safe firelines, causing the blocks to be irregular in shape. The three treatments were (1) thin/burn, (2) burn alone, and (3) an untreated control. We did not include a thin alone treatment because the goal of forest restoration is to restore ecological function, which is not possible without a burn treatment in ecosystems that historically were dominated by surface fires. The thinning prescription retained all living trees that established in 1870 or earlier as identified by size, bark color, and canopy architecture (Fulé et al., 2009). If remnants (e.g., snags, logs, and stumps) were present in 1870 but were no longer alive, we kept live post-settlement trees as a substitute for those remnants. An average of two younger trees of the same species, within 20 m of the remnant if possible, was retained for each dead remnant encountered (see Fulé et al., 2001 for a detailed description of the thinning prescription). Because of past cutting of ponderosa pine and 20th century establishment of non-pine species (Fulé et al., 2009), there was a relatively high number of pine remnants and a relatively low density of potential pine replacements. Therefore, the trees designated for thinning were mostly white fir and some Douglas-fir. Aspen are highly susceptible to fire so none were thinned, because we assumed that many would be killed by burning. Crews thinned the thin/burn units with chain saws during the summer and fall 2004 with a cost of $926/hectare. Wood was not removed due to restrictions on road access, so logs and limbs were lopped and scattered. Old-growth trees were not raked to remove fuels around tree boles. Fire crews did prescribed burning in fall 2007 (Blocks 1 and 2) and fall 2008 (Blocks 3 and 4) using strip headfires with a cost of $370/hectare. Fire crews were unable to burn all units during the same time period because of regulations on smoke output.

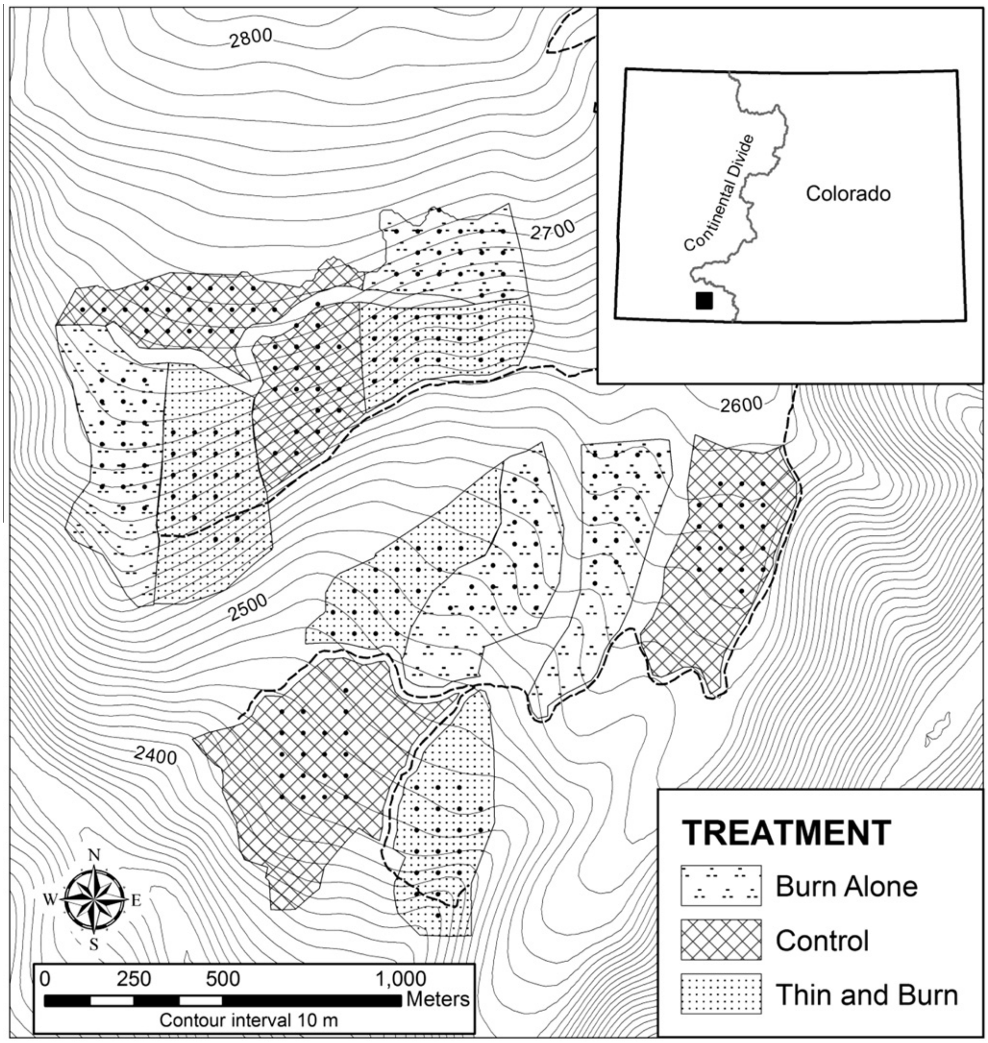

Fig. 1. Study site at Lower Middle Mountain, San Juan National Forest, Colorado. Research blocks (1–4) and restoration treatments (Control, Thin/Burn, Burn Alone) are shown. Black circles represent individual plots (N = 20/treatment unit).

The maximum temperature during 2007 burning was 17.8 °C with a minimum relative humidity of 24%; maximum temperature during 2008 burning was 20.5 °C with a minimum relative humidity of 18. Average flame lengths were 0.3–0.9 m in needle duff, 1–2.4 m in tree thinning slash and up to 7.6 m from torching trees with a very low rate of spread for both years.

2.3. Field methods

We established 20 permanent study plots on a 60-m grid per unit to characterize forest structure and vegetation (total $N = 12$ U $\times$ 20 plots = 240 plots). We collected pre-treatment data in the summer of 2003 and post-treatment data in the summer of 2009. We measured overstory trees and saplings taller than breast height (137 cm) in a 400 m^2 (11.28 m radius) circular plot. Species, condition (living or snag/log classes Thomas et al., 1979), diameter at breast height (dbh), total height, crown base height, and a preliminary field classification of presettlement or postsettlement origin were recorded for each tree encountered in the plot. We identified potentially presettlement ponderosa pine trees 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. A random 10% subsample of all trees and any trees classified as potentially presettlement were cored. Cored trees were dated and have been described elsewhere (Fulé et al., 2009). Tree regeneration (trees below breast height) was measured on a nested 100 m^2 circular 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. We recorded tree canopy cover using a vertical projection densiometer every 3 m along a permanently marked 50-m line transect oriented upslope through the plot center. We measured dead woody biomass and forest floor (litter and duff) depth on a permanently marked 15.2-m planar transect in a random direction from each plot center (Brown, 1974). Understory vegetation was also measured and has been described elsewhere (Korb et al., 2007).

2.4. Statistical analysis

We compared forest structural variables, including tree density, basal area, canopy cover, regeneration density, and mortality among treatments with a Kruskal–Wallis test ($\alpha \leqslant 0.05$). We conducted post hoc tests with pairwise Kruskal–Wallis two-sample tests following a statistically significant result for a total variable and then adjusted alpha levels by the number of pairwise comparisons using a Bonferroni correction (Kuehl, 1994). We used Wilcoxon signed-ranks tests to quantify changes over time between

2003 and 2009 data to include the repeated measurements on the permanent plots.

We used nonmetric multidimensional scaling (NMS) to examine changes in basal area of all tree species over time and among treatments (Clark, 1993). We used basal area because it is the most accurate variable to reconstruct with dendroecological data (Moore et al., 2004). 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 ran the NMS ordination in PC-ORD software [version 5.10, McCune and Mefford, 2006] using a Bray–Curtis distance measure, 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 examined differences between reconstructed 1870, 2003 pre-treatment, and 2009 post-treatment forest structure using a permutational multivariate analysis of variance (PERMANOVA) (Anderson, 2001) to quantify differences in basal area and trees ha^{-1} across time and among treatments. We used a one fixed-factor and one-level nested design with time as our main effect [PC- software version 5.10, McCune and Mefford, 2006]. We used indicator-species analysis to identify species that were particularly faithful (i.e., consistent indicators) to the analysis dates of 2003 or 2009. 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 $P \leqslant 0.05$ and indicator values (INDVAL) > 25 (INDVAL = relative abundance × relative frequency; range 0–100) were accepted as indicator species (Dufrêne and Legendre, 1997; Bakker, 2008).

3. Results

3.1. Forest structure

There were no differences in total tree density ($U = 2.81$, $P = 0.25$) or basal area ($U = 2.44$, $P = 0.29$) among treatment units prior to restoration in 2003. In 2009, following treatments, total density ($U = 9.27$, $P = 0.01$) and basal area ($U = 9.85$, $P = 0.007$) were lower in thin/burn units than the control and burn alone units (Table 1). Thin/burn units had the only significant ($Z = 2.17$, $P = 0.03$) change in tree density with an 82% decline between pre (709.6 trees ha^{-1}) and post-treatment (126.9 trees ha^{-1}) largely from decreases, 96%, in white fir ($Z = 2.17$, $P = 0.03$) and 76%, in Douglas-fir ($Z = 2.03$, $P = 0.03$) (Table 1). In 2009, total basal area differences among treatments were driven by Douglas-fir basal area ($U = 8.8$, $P = 0.013$). Thin/burn units had the only significant decrease in basal area ($Z = 2.17$, $P = 0.03$) declining 49% between pre- (25.6 $m^2 ha^{-1}$) and post-treatment (13.1 $m^2 ha^{-1}$) with white fir having the largest decrease, 86% ($Z = 2.17$, $P = 0.03$) (Table 1).

Diameter distributions in 2003 for all treatment units prior to restoration followed a reverse-J distribution with strong dominance by small trees, especially aspen and white fir (Fig. 2). All units had trees at least through the 85-cm diameter class with most of the trees ⩾45-cm class being ponderosa pine (Fig. 2). After treatment, diameter distributions in the controls were relatively unchanged except for a decrease of small aspen ramets (Fig. 2).

Diameter distributions post-treatment in the burn alone units were unimodal with a peak at the 25-cm diameter class. The main shifts were decreases in white fir in the 5, 15, and 25-cm diameter classes (Fig. 2). Diameter distributions post-treatment in the thin/burn units were bimodal (Fig. 2). After treatment, all units maintained trees at least through the 85-cm diameter class with ponderosa pine still dominating trees ⩾45-cm (Fig. 2).

Table 1
Forest structure (trees taller than breast height (137 cm) for Control, Thin/Burn, and Burn Alone treatments.

Treatment	Total	ABCO	PIEN	PIPO	POTR	PSME
Tree density (tree ha^{-1})						
Control (pre-treatment)	735.0	364.7		48.8	180.9	140.6
Percent change	−22	−20		−3	−39	−9
Thin/Burn (pre-treatment)	706.9	444.7	0.3	60.9	174.1	26.6
Percent change	**−82**	**−96**	**−100**	−32	−65	**−76**
Burn (pre-treatment)	590.0	366.6	0.6	57.2	83.1	82.5
Percent change	−37	−42	0	−8	−48	−22
Basal area ($m^2 ha^{-1}$)						
Control (pre-treatment)	29.6	9.3		9.5	3.8	7.0
Percent change	−9	−21		5	−23	−8
Thin/Burn (pre-treatment)	25.6	10.3	0.04	10.6	3.0	1.6
Percent change	**−49**	**−86**	**−100**	−8	**−64**	**−45**
Burn (pre-treatment)	25.8	9.1	0.1	9.4	1.8	5.3
Percent change	−16	−29	9	−0.2	−22	−21
Canopy cover (%)						
Control (pre-treatment)	46.6					
Percent change	7					
Thin/Burn (pre-treatment)	48.5					
Percent change	**−36**					
Burn (pre-treatment)	40.2					
Percent change	1					

Species codes: ABCO (*Abies concolor*), PIEN (*Picea engelmannii*), PIPO (*Pinus ponderosa*), POTR (*Populus tremuloides*), and PSME (*Pseudotsuga menziesii*). Data values are shown from measurements carried out prior to treatments in 2003, followed by percentage change (positive or negative) as measured after treatment in 2009. $N = 4$. Significant percent change within a treatment between 2003 and 2009 is denoted by bold text ($\alpha \leqslant 0.05$).

3.2. Canopy cover

There were no differences among treatment units in tree canopy cover ($U = 3.18$, $P = 0.17$) prior to restoration treatments in 2003 (Table 1). Tree canopy was different ($U = 9.85$, $P = 0.007$) post-treatment with the controls having the highest average canopy cover (49%), followed by burn alone (40.3%), and thin/burn treatments (30.8%) (Table 1). In the thin/burn treatment, tree canopy cover ($Z = 2.17$, $P = 0.03$) decreased 36% between 2003 and 2009 (Table 1). There were no differences in canopy cover between pre/post-treatment for the control or burn alone units ($Z = 0.144$ and 0.7222, $P = 0.89$ and $P = 0.47$, respectively).

3.3. Tree mortality

Overstory trees that died were relatively young, short, and/or smaller in diameter. There were no differences in overstory tree mortality for young ($U = 5.69$, $P = 0.06$) or old-growth ($U = 1.38$, $P = 0.5$) trees post-treatment. Old-growth trees for this study are defined as trees established by 1870. The thin/burn treatments had the highest variability in tree mortality. Overstory old-growth aspen had the highest species mortality in the thin/burn units, 10.1 trees ha^{-1}, followed by ponderosa pine, 3.29 trees ha^{-1}, with white fir and Douglas-fir each having just over 1 tree ha^{-1} mortality (Table 2). In contrast, overstory old-growth Douglas-fir had the highest species mortality in the burn alone units, 4.95 trees ha^{-1}, followed by aspen, 3.19 trees ha^{-1}, and white fir and ponderosa pine had sequentially lower mortality (Table 2). Mortality was dominated by old-growth aspen in the controls, 6.71 trees ha^{-1}, followed by Douglas-fir, 2.32 trees ha^{-1}, with white fir and ponderosa pine having low mortality (Table 2).

3.4. Regeneration

Total tree regeneration (seedling >40 cm in height) density (seedling ha^{-1}) was not different before ($U = 1.19$, $P = 0.55$) or after ($U = 2.92$, $P = 0.23$) treatments. Tree regeneration density after

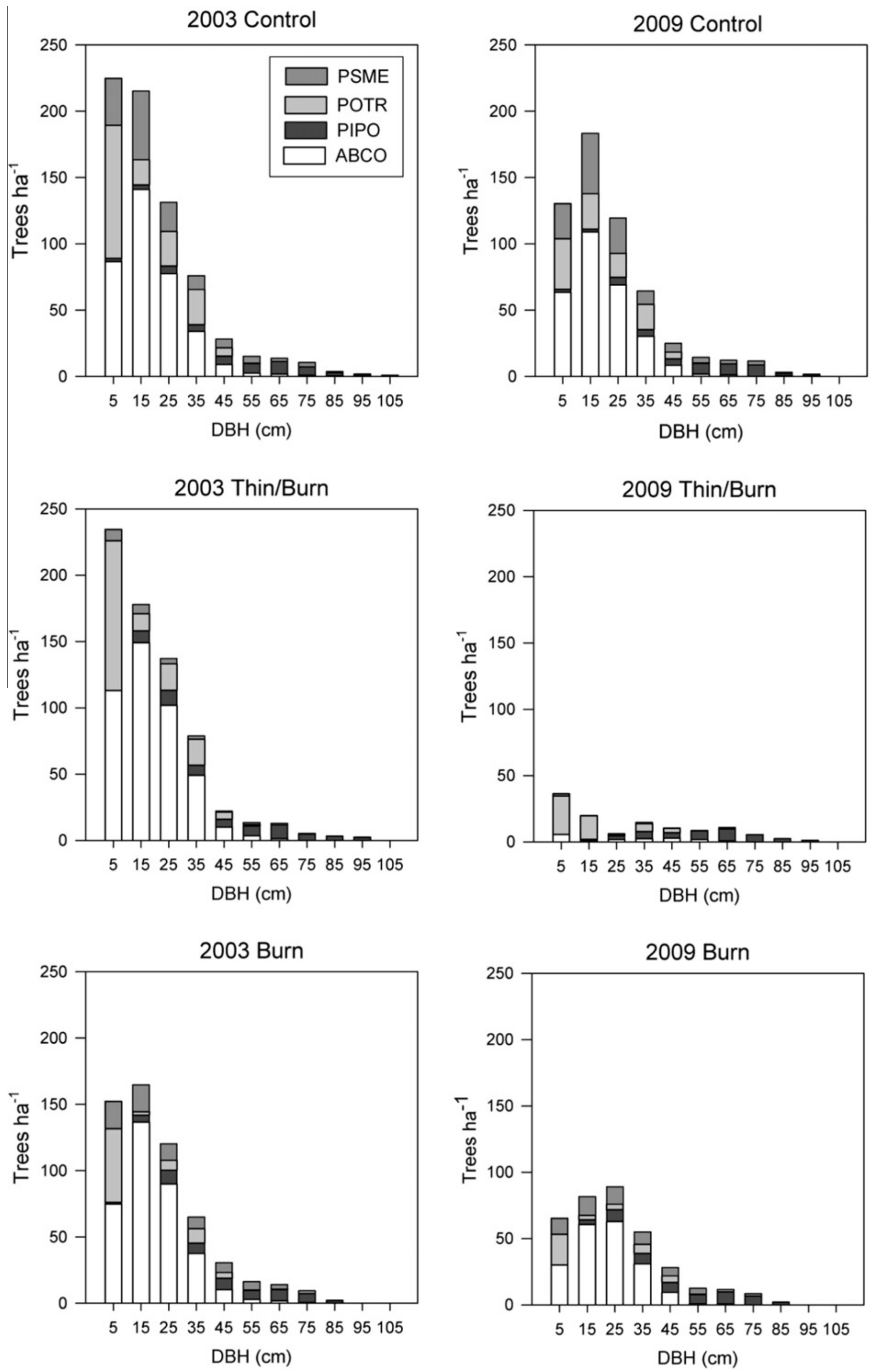

Fig. 2. Changes in diameter distribution by species for Control, Thin/Burn and Burn Alone treatments. Diameter class midpoints are shown on *x*-axis. Tree survival is shown in both prior to (2003) and after treatment (2009).

restoration treatments was different for white fir and Douglas-fir ($U = 7.88$ and 7.14, $P = 0.02$ and $P = 0.03$, respectively) (Table 3). Total tree regeneration for individual treatments between pre/post-treatment were not different, but some individual species' regeneration did differ in thin/burn treatments pre/post-treatment. Aspen regeneration density increased ($Z = 2.17$, $P = 0.03$) from 237.5 seedlings/ramets ha^{-1} to 1097.5 seedlings/ramets ha^{-1} (Table 3), while white fir and Douglas-fir decreased ($Z = 2.37$ and 2.165, $P = 0.2$ and $P = 0.3$, respectively) (Table 3).

3.5. Surface fuels

There were no differences in forest floor depth (litter plus duff) ($U = 1.38$, $P = 0.5$) prior to restoration treatments. In 2009 following treatments, forest floor depth ($U = 8.11$, $P = 0.02$) decreased (Table 4). In the thin/burn and burn treatments, forest floor decreased ($Z = 2.17$, $P = 0.03$) from 4.24 to 1.3 cm in the thin/burn and from 4 to 1.9 cm in the burn alone treatments (Table 4). Fine woody debris ($\leqslant$7.62 cm diameter) was not different ($U = 0.75$, $P = 0.3$) before

Table 2
Old-growth (trees established ⩽1870) tree density (trees ha^{-1}) and mortality (percentage) for Control, Thin/Burn, and Burn Alone treatments.

Treatment	Total	ABCO	PIPO	POTR	PSME
Control (pre-treatment)	68.4	8.1	26.6	17.2	16.6
Percent mortality	17	14	1	39	14
Thin/Burn (pre-treatment)	43.4	2.2	25.3	13.8	2.2
Percent mortality	28	61	13	73	53
Burn (pre-treatment)	57.8	4.4	28.1	10.3	15.0
Percent mortality	20	42	3	31	33

Species codes: ABCO (*Abies concolor*), PIEN (*Picea engelmannii*), PIPO (*Pinus ponderosa*), POTR (*Populus tremuloides*), and PSME (*Pseudotsuga menziesii*). Data values are shown from measurements carried out prior to treatments in 2003, followed by percent mortality as measured after treatment in 2009. $N = 4$. There was no significant percent mortality within a treatment between 2003 and 2009.

Table 3
Tree regeneration (seedling >40 cm in height) density (seedling ha^{-1}) for Control, Thin/Burn, and Burn Alone treatments.

Treatment	Total	ABCO	PIPO	POTR	PSME
Control (pre-treatment)	740	105.0	2.5	595.0	37.5
Percent change	50	4.8	150	61	−10
Thin/Burn (pre-treatment)	515	265.0	1.3	237.5	11.3
Percent change	116	**−94**	0	**362**	**−100**
Burn (pre-treatment)	502.5	81.3	6.3	380.0	35.0
Percent change	39	−68	−40	69	−25

Species codes: ABCO (*Abies concolor*), PIEN (*Picea engelmannii*), PIPO (*Pinus ponderosa*), POTR (*Populus tremuloides*), and PSME (*Pseudotsuga menziesii*). POTR regeneration is defined as seedling/ramet since data on whether regeneration is sexual or asexual was not determined. Data values are shown from measurements carried out prior to treatments in 2003, followed by percent change (positive or negative) measured after treatment in 2009. $N = 4$. Significant percent change within a treatment between 2003 and 2009 is denoted by bold text ($\alpha \leqslant 0.05$).

treatments (Table 4). Following treatments, fine woody debris decreased ($Z = 2.17$, $P = 0.03$) in the thin/burn treatments from 7.2 to 4.2 mg ha^{-1} (Table 4). In burn alone treatments, fine woody debris decreased ($Z = 2.17$, $P = 0.03$) from 9.6 to 5.6 mg ha^{-1} (Table 4). Coarse woody debris (⩾7.64 cm diameter) did not differ before ($U = 0.04$, $P = 0.98$) or after ($U = 0.81$, $P = 0.67$) restoration treatments (Table 4).

3.6. Comparisons with reconstructed 1870 forest structure

There was a difference in tree basal area between reconstructed 1870, 2003 pre-treatment and 2009 post-treatment data ($F = 9.6$; $P = 0.001$) (Table 5). There was also a difference between reconstructed 1870, 2003 pre-treatment and 2009 post-treatment data for tree density ($F = 14.4$; $P = 0.0002$) (Table 5). There were no differences among blocks across time for tree basal area ($F = 1.53$; $P = 0.07$) or tree density ($F = 1.12$; $P = 0.35$) (Table 5).

Tree basal area by species in 2009 in the thin/burn treatments showed a strong directional shift away from 2003 pre-treatment data towards the reconstructed 1870 forest structure (Fig. 3). Burn treatments in 2009 were separated from controls in the same year but did not resemble reconstructed 1870 forest structure (Fig. 3). Indicator species analysis detected species that were particularly consistent indicators for time (Table 6). Ponderosa pine was the only indicator species for the reconstructed 1870 data. White fir, Douglas-fir, and aspen were all indicator species for the pre-treatment units in 2003, but there were no indicator species in 2009 post-treatment, indicating that the units in 2003 had higher dominance of white fir, Douglas-fir and aspen than in 2009 (Table 6).

Table 5
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, pre-treatment 2003, and post-treatment 2009 data.

Source	*df*	MS	F	P (perm)
Basal area ($m^2 ha^{-1}$)				
Time	2	0.5199	9.5516	0.0014
Block	9	0.5443	1.5337	0.0710
Residual	24	0.3139		
Total	35			
Tree density (trees ha^{-1})				
Time	2	1.2926	14.385	0.0002
Block	9	0.8985	1.1221	0.3518
Residual	24	0.8008		
Total	35			

4. Discussion

This experiment is the first to apply dendrochronologically reconstructed data (Fulé et al., 2009) on historical reference conditions to the design and testing of replicated ecological restoration treatments (thin/burn and burn-only) in a mixed-conifer forest representing the transition between the Southwest and Southern Rocky Mountains. Neither the mixed-conifer forest type nor the biogeographical location has received much research attention related to restoration, despite the large geographic area of this forest type and its ecological and economic importance. In contrast, replicated ecological restoration treatments have been more thoroughly tested in ponderosa pine in this biogeographical location.

4.1. Forest compositional and structural changes

Restoring ecological integrity to altered ecosystems often requires bold management to reinitiate feedback cycles and overcome the constraints of degraded systems (Suding et al., 2004). In our study, the combination of thinning and burning moved degraded warm/dry mixed conifer forests in southwestern Colorado close to the historical reference condition, whereas burn alone treatments simply moved forests in the same direction towards the historical range. Thin/burn treatments had an average of 129.6 trees ha^{-1}, which was close to the historical reference

Table 4
Changes in forest floor and woody debris for Control, Thin/Burn, and Burn Alone treatments.

Treatment	Forest floor depth (cm)	Fine woody debris (mg ha^{-1})	Coarse woody debris (mg ha^{-1})
Control (pre-treatment)	4.18	7.08	65.89
Percentage change	−31	−4	−10
Thin/Burn (pre-treatment)	4.24	7.18	59.69
Percentage change	**−69**	**−41**	−27
Burn (pre-treatment)	4.00	9.61	63.56
Percentage change	**−53**	**−43**	−29

Fine woody debris is defined as wood ⩽7.64 cm and coarse woody debris is defined as wood ⩾7.64 cm diameter. Data values are shown from measurements carried out prior to treatments in 2003, followed by percentage change (positive or negative) as measured after treatment in 2009. $N = 4$. Significant percent change within a treatment between 2003 and 2009 is denoted by bold text ($\alpha \leqslant 0.05$).

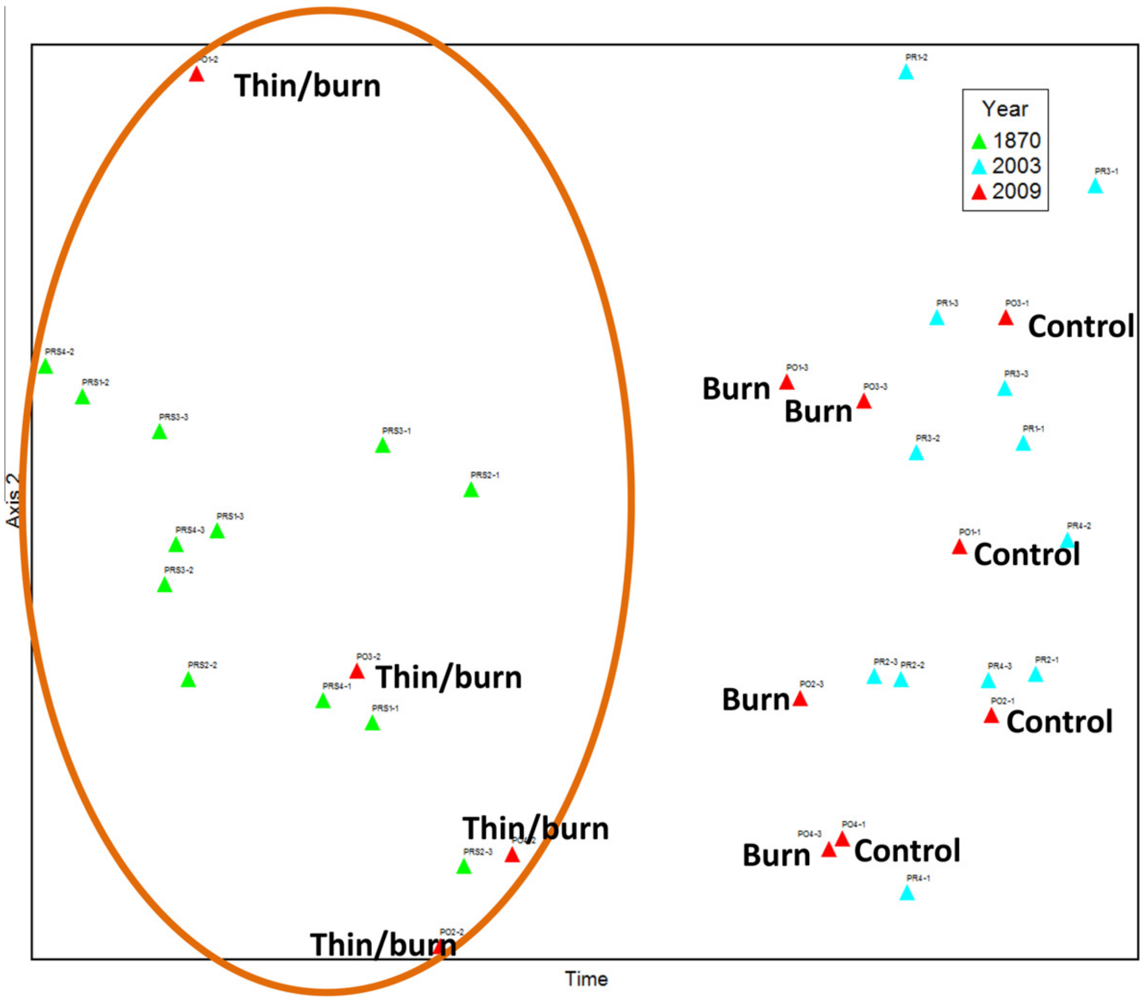

Fig. 3. Non-metric multidimensional scaling ordination of untransformed tree basal area of species reconstructed for 1870 (reference condition), pre-treatment 2003 and post-treatment 2009. Each symbol represents one unit for 1 year (N = 12/year). The final solution had three dimensions, stress = 14.52 and P = 0.02.

Table 6
Indicator species associated with time for reconstructed 1870 and pre-treatment 2003 data.

Time	Species	Indicator value	P
1870	*Pinus ponderosa*	45.4	0.0138
2003	*Abies concolor*	71.0	0.0002
2003	*Pseudotsuga menziesii*	36.4	0.0154
2003	*Populus tremuloides*	29.7	0.0010

There were no indicator species for post-treatment 2009.

condition of 142 trees ha^{-1} ± 9.9 (Fulé et al., 2009). Fire had a thinning effect in the sense that younger and smaller trees were most likely to be heavily charred and die (Fig. 2), but the fire thinning was less effective than mechanical thinning, as indicated by the relatively high residual density in burn treatments, averaging 373.4 trees ha^{-1}. For basal area, thin/burn treatments moved close to the historical reference condition of 11 m^2 ha^{-1} ± 1.1 (Fulé et al., 2009), having an average 13.1 m^2 ha^{-1} basal area in comparison to burn alone treatments (21.6 m^2 ha^{-1}).

Forest composition also shifted in the thin/burn treatments. Ponderosa pine represented nearly 63% of the basal area in the historical reference condition (Fulé et al., 2009), comparable to 73% of the basal area in thin/burn treatments but only 44% in burn alone treatments. White fir represented 11% of the basal area in both the historical reference condition (Fulé et al., 2009) and the thin/burn treatments where white fir was targeted in the hand thin, but 30% of the basal area in burn alone treatments.

Old-growth trees were considered a priority for retention in the treatments, because they represent a genetic and structural legacy that has largely vanished (Abella et al., 2007). Mortality was low in absolute terms (<7 trees ha^{-1}) but ranged as high as 73% in relative terms because many units had low pre-treatment densities of old trees. The mortality of old aspen trees, the species with the greatest decline, was similar to old aspen mortality in a mixed conifer forest at Grand Canyon National Park, Arizona (Fulé et al., 2006). Mortality of old ponderosa pines, the most fire-resistant species in the forest, ranged from 1% (control) to 13% (thin/burn), substantially less than the 34% old ponderosa pine mortality observed in similar treatments in a drier site in Arizona (Fulé et al., 2007). The differences in species-specific mortality at our experimental site were consistent with fire-resistant traits such as bark thickness (Ryan and Reinhardt, 1988). Differential mortality implies that the reintroduction of the repeated surface fire regime on south facing slopes will continue to shift composition away from the less fire-resistant species over time.

There was no net change in ponderosa pine regeneration in the thin/burn treatments and a 40% decrease in burn alone treatments. Despite limited ponderosa pine seedling establishment in the first years following treatments, restoration treatments did significantly decrease forest floor (litter plus duff) and fine woody debris by over 70% and 40%, respectively in the thin/burn treatments.

These changes should favor ponderosa pine regeneration because litter prevents seeds from imbibing water due to poor contact with moist mineral soil and litter provides habitat for damping-off fungi, which cause seedling wilting and mortality (Farmer, 1997). In addition, direct microsite changes from fire such as scorched needles on blackened mineral soil have been shown to favor ponderosa emergence and establishment (Bonnet et al., 2005). Aspen regeneration in thin/burn treatments increased almost fivefold over pre-treatment levels while aspen regeneration in burn alone treatments did not even double. These responses are most likely due to old-growth aspen mortality being twice as high in thin/burn versus burn alone treatments and variation in fire behavior because aspen trees were not harvested in any treatments.

4.2. Tree mortality

Our findings support restoration studies in mixed conifer at other biogeographic locations where limited treatments such as burning alone or burning with minimal thinning did not restore stand composition and structure within historical reference conditions over the short-term (Stephens and Moghaddas, 2005; Fulé et al., 2006; Mason et al., 2009; Rambo and North, 2009; Schwilk et al., 2009; Stephens et al., 2009). Specifically, a comprehensive synthesis of hazardous fuel treatments in western mixed conifer by Stephens and others (2009) showed that thin and burn treatments were the most resistant to simulated active and passive crown fire; however, they recommended land managers utilize a variety of treatments to create forest stand structures that are resistant to wildfires. Creating forest conditions that increase forest heterogeneity at the landscape scale to emulate historical reference conditions will make forests more resilient to altered fire regimes under a warmer, drier climate (Stephens et al., 2009; Evans et al., 2011; Johnson et al., 2011). In addition, thin and burn treatments decrease other stress induced mortality from forest insects, pathogens and drought stress due to increased competition among trees for nutrients, water, and growing space (Hessburg et al., 1994).

Van Mantgem et al. (2009) found that widespread increases in mortality of old trees across the western United States was linked to regional warming. In our study, untreated controls experienced a 22% decrease in total tree density over a six-year period between pre/post-treatment measurements from 735 to 573 trees ha^{-1}. The majority of this decrease was small (<25 cm dsh) white fir and (<20 cm dsh) aspen but older, larger trees also had a moderate contribution. While this difference in mortality was not significant, the mortality still has management implications because of the potential impact that insects and pathogens may have on drought stressed systems. It is critical that restoration ecologists incorporate natural mortality into restoration treatment design because of the ensuing implications that background tree mortality has on forest stand structure and thus restoration goals.

4.3. Implications for management

Numerous climate models have projected significant anthropogenic climate change by the end of the 21st century (IPCC, 2007). In the southwestern United States, both historical data and climate models reflect earlier spring snow melt, increased spring and summer temperatures, and drier summers (Westerling et al., 2006; Seager et al., 2007; Barnett et al., 2008). Fires are easier to ignite and spread, the fire season is longer, and extreme fire behavior is more common with warmer temperatures, drier soils and longer growing seasons (McKenzie et al., 2004; IPCC, 2007; Lui et al., 2010).

Given these projected changes, it is crucial to implement management actions to mitigate altered trajectories in species composition, structure, and ecological processes by restoring the self-regulating attributes of surface-fire-dependent forests. The general approach in ecological restoration of surface fire-dependent forests has been to carry out initial treatments and then seek to maintain the treatment effects over time with recurring surface fires at intervals close to the historical mean (Allen et al., 2002; Roccaforte et al., 2010). This approach is logical to some extent even as climate warms, because frequently burned southwestern forests were quite resilient to drought and disturbance (Fulé, 2008), but continued warming may push habitats across ecological thresholds (Millar et al., 2007). The uncertainty of site-specific climate changes makes detailed planning difficult but it is wise for managers to evaluate likely trends. In warm/dry mixed conifer forests, which already represent the transition from ponderosa pine to cool/moist mixed conifer, a logical expectation is that the species adapted to more xeric conditions (ponderosa pine, Douglas-fir) will increase in dominance while *Abies* and *Populus* decline. The ecological role of frequent surface fire to maintain open structure is likely to continue to be important, but fire may cause higher-than-expected mortality in drought-stressed trees (Diggins et al., 2010). To address possible increased mortality due to fire in a warmer, drier climate, managers might consider reapplying fire at longer-than-historical intervals in an adaptive future-orientated restoration framework (Choi, 2007; Seastedt et al., 2008). In addition, burn alone treatments are a viable restoration option for forest managers in Wilderness areas where mechanized equipment is prohibited and in areas not adjacent to vulnerable infrastructure where a manager's goal is simply to get forests on a trajectory toward a more sustainable historical condition as suggested by Allen et al. (2002) for ponderosa pine surface-fire-dependent ecosystems (Evans et al., 2011). Finally, management funding for fuels and restoration treatments are limited making burn alone treatments a feasible option because they are less expensive per hectare than thin/burn treatments.

Acknowledgements

We thank the Ecological Restoration Institute, William Romme, Sara Brinton, Steve Hartvigsen and Scott Wagner. This manuscript was greatly improved by reviewer comments.

References

Abella, S.R., Covington, W.W., Fulé, P.Z. Lentile, L.B., Sánchez Meador, A.J, Morgan, P., 2007. Past, present, and future old growth in frequent-fire conifer forests of the western United States. Ecology and Society 12, 16. [online] URL: <http://www.ecologyandsociety.org/vol12/iss2/art16/>

Allen, C.D., Savage, M., Falk, D.A., Suckling, K.F., Swetnam, T.W., Schulke, T., Stacey, P.B., Morgan, P., Hoffman, M., Klingel, J.T., 2002. Ecological restoration of southwestern ponderosa pine ecosystems: a broad perspective. Ecological Applications 12, 1418–1433.

Allen, C.D., Anderson, R.S., Jass, R.B., Toney, J.T., Baisan, C.H., 2008. Paired charcoal and tree-ring records of high-frequency Holocene fire from two New Mexico bog sites. International Journal of Wildland Fire 17, 115–130.

Anderson, M.J., 2001. A new method for non-parametric multivariate analysis of variance. Austral Ecology 26, 32–46.

Bakker, J.D., 2008. Increasing the utility of indicator species analysis. Journal of Applied Ecology 45, 1829–1835.

Barnett, T.P., Pierce, D.W., Hidalgo, H.G., Bonfils, C., Santer, B.D., Das, T., Bala, G., Wood, A.W., Nozawa, T., Mirin, A.A., Cayan, D.R., Dettinger, M.D., 2008. Human-induced changes in the hydrology of the western United States. Science 319, 1080–1083.

Beaty, R.M., Taylor, A.H., 2001. Spatial and temporal variation of fire regimes in a mixed conifer forest landscape, Southern Cascades, California, USA. Journal of Biogeography 28, 955–966.

Bigio, E., Swetnam, T.W., Baisan, C.H., 2010. A comparison and integration of tree-ring and alluvial records of fire history at the Missionary Ridge Fire, Durango, Colorado, USA. The Holocene, doi:10.1177/0959683610369502.

Bonnet, V.H., Schoettle, A.W., Shepperd, W.D., 2005. Postfire environmental conditions influence the spatial pattern of regeneration for *Pinus ponderosa*. Canadian Journal of Forest Research 35, 37–47.

Brown, J.K., 1974. Handbook for inventorying downed woody material. USDA Forest Service General Technical Report INT-16. Intermountain Forest and Range Experiment Station, Ogden, Utah.
Brown, P.M., Wu, R., 2005. Climate and disturbance forcing of episodic tree recruitment in a southwestern ponderosa pine landscape. Ecology 86, 3030–3038.
Brown, P.M., Wienk, C.L., Symstad, A.J., 2008. Fire and forest history at Mount Rushmore. Ecological Applications 18, 1984–1999.
Brown, P.M., Kaye, M.W., Huckaby, L.S., Baisan, C.H., 2001. Fire history along environmental gradients in the Sacramento Mountains, New Mexico: influences of local and regional processes. Ecoscience 8, 115–126.
Choi, Y.D., 2007. Restoration ecology to the future: a call for a new paradigm. Restoration Ecology 15, 351–353.
Clark, K.R., 1993. Non-parametric multivariate analysis of changes in community structure. Australian Journal of Ecology 18, 117–143.
Cocke, A.E., Fulé, P.Z., Crouse, J.E., 2005. Forest change on a steep mountain gradient after extended fire exclusion: San Francisco Peaks, Arizona, USA. Journal of Applied Ecology 42, 814–823.
Crouse, J., 2005. Fuels and fire behavior modeling using remotely sensed data on the San Francisco Peaks, Arizona. Master Thesis, Northern Arizona University, Flagstaff, Arizona.
Diggins, C., Fulé, P.Z., Kaye, J.P., Covington, W.W., 2010. Future climate affects management strategies for maintaining forest restoration treatments. International Journal of Wildland Fire 19, 903–910.
Dufrêne, M., Legendre, P., 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecological Monographs 67, 345–366.
Evans, A.M., Everett, R.G., Stephens, S.L., Youtz, J.A., 2011. Comprehensive fuels treatment guide for mixed conifer forests: California, Central and Southern Rockies, and the Southwest. Forest Guild and USDA Forest Service, Santa Fe, New Mexico.
Farmer Jr., R.E., 1997. Seed Ecophysiology of Temperate and Boreal Forest Zone Trees. St. Lucie Press, Delray Beach Florida, p. 253.
Fulé, P.Z., Moore, M.M., Covington, W.W., 1997. Determining reference conditions for ecosystem management in southwestern ponderosa pine forests. Ecological Applications 7, 895–908.
Fulé, P.Z., McHugh, C., Heinlein, T.A., Covington, W.W., 2001. Potential fire behavior is reduced following forest restoration treatments. RMRS-P-22. Fort Collins, CO: U.S. Department of Interior, Forest Service, Rocky Mountain Research Station. Proc: 28–35.
Fulé, P.Z., Covington, W.W., Stoddard, M.T., Bertolette, D., 2006. ‘‘Minimal-impact’’ restoration treatments have limited effects on forest structure and fuels at Grand Canyon, USA. Restoration Ecology 14, 357–368.
Fulé, P.Z., Roccaforte, J.P., Covington, W.W., 2007. Post-treatment tree mortality after forest ecological restoration, Arizona, United States. Environmental Management 40, 623–634.
Fulé, P.Z., 2008. Does it make sense to restore wildland fire in a changing climate? Editorial opinion. Restoration Ecology 16, 526–531.
Fulé, P.Z., Korb, J.E., Wu, R., 2009. Changes in forest structure of a dry mixed conifer forest, southwestern Colorado USA. Forest Ecology and Management 258, 1200–1210.
Grissino-Mayer, H.D., Romme, W.H., Floyd, M.L., Hanna, D., 2004. Climatic and human influences on fire regimes in the southern San Juan Mountains, Colorado, USA. Ecology 85, 1708–1724.
Heinlein, T.A., Moore, M.M., Fulé, P.Z., Covington, W.W., 2005. Fire history of two ponderosa pine-mixed conifer sites: San Francisco Peaks, Arizona, USA. International Journal of Wildland Fire 14, 307–320.
Hessburg, P.F., Mitchell, R.G., Filip, G.M., 1994. Historical and current roles of insects and pathogens in eastern Oregon and Washington forested landscapes. General Technical Report PNW-GTR-327. USDA Forest Service, Portland, Oregon, USA.
IPCC, 2007. Climate change 2007: the physical science basis. In: Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K.B., Tignor, M., Miller, H.L. (Eds.), Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge, Cambridge University Press.
Jackson, S.T., Hobbs, R.J., 2009. Ecological restoration in the light of ecological history. Journal of Science 325, 567–569.
Johnson, M.C., Kennedy, M.C., Peterson, D.L., 2011. Simulating fuel treatment effects in dry forests of the western United States: testing the principles of a fire-safe forest. Canadian Journal of Forest Research 41, 1018–1030.
Korb, J.E., Daniels, M.L., Laughlin, D.C., Fulé, P.Z., 2007. Understory communities of warm/dry mixed conifer in southwestern Colorado. Southwestern Naturalist 52, 493–503.
Kuehl, R.O., 1994. Statistical principles of research design and analysis. Wadsworth Publishing Company, Belmont, CA, USA.
Lui, Y., Stanturf, J., Goodrick, S., 2010. Trends in global wildfire potential in a changing climate. Forest Ecology and Management 259, 685–697.
Margolis, E., Balmat, J., 2009. Fire history and fire–climate relationships along a fire regime gradient in the Santa Fe Municipal Watershed, NM, USA. Forest Ecology and Management 258, 2416–2430.
Martin, K.L., Kirkman, L.K., 2009. Management of ecological thresholds to re-establish disturbance-maintained herbaceous wetlands of the south-eastern USA. Journal of Applied Ecology 46, 906–914.
Mason, G.J., Bakker, T.T., Cram, D.S., Boren, J.C., Fernald, A.G., Van Leeuwen, D.M., 2009. Mechanical fuel treatment effects on vegetation in a New Mexico dry mixed conifer forest. Forest Ecology and Management 257, 868–875.
McCune, B., Grace, J.B., 2002. Analysis of Ecological Communities. MjM Software Design, Gleneden, Oregon, USA.
McCune, B., Mefford, M.J., 2006. PCORD. Multivariate Analysis of Ecological Data. Version 5.10. MjM Software, Gleneden Beach, Oregon, USA.
Millar, C.I., Stephenson, N.L., Stephens, S.L., 2007. Climate change and forests of the future: managing in the face of uncertainty. Ecological Applications 17, 2145–2151.
Miller, C., Urban, D., 2000. Connectivity of forest fuels and surface fire regimes. Landscape Ecology 15, 145–154.
McKenzie, D., Gedalof, Z., Peterson, D.L., Mote, P., 2004. Climatic change, wildfire, and conservation. Conservation Biology 18, 890–902.
Moore, M.M., Huffman, D.W., Fulé, P.Z., Covington, W.W., Crouse, J.E., 2004. Comparison of historical and contemporary forest structure and composition on permanent plots in southwestern ponderosa pine forests. Forest Science 50, 162–176.
Rambo, T.R., North, M.P., 2009. Canopy microclimate response to pattern and density of thinning in a Sierra Nevada forest. Forest Ecology and Management 257, 435–442.
Roccaforte, J.P., Fulé, P.Z., Covington, W.W., 2010. Monitoring landscape-scale ponderosa pine restoration treatment implementation and effectiveness. Restoration Ecology 18, 820–833.
Romme, W.H., Floyd, M.L., Hanna, D., 2009. Historical range of variability and current landscape condition analysis: South Central Highlands section, Southwestern Colorado & Northwestern New Mexico. Colorado Forest Restoration Institute, Fort Collins, CO, USA.
Ryan, K.C., Reinhardt, E.D., 1988. Predicting post-fire mortality of seven western conifers. Canadian Journal of Forest Research 18, 1291–1297.
Savage, M., Mast Nystrom, J., 2005. How resilient are southwestern ponderosa pine forests after crown fires? Canadian Journal of Forest Research 35, 967–977.
Schwilk, D.W., Keeley, J.E., Knapp, E.E., McIver, J., Bailey, J.D., Fettig, C.J., Fiedler, C.E., Harrod, R.J., Moghaddas, J.J., Outcalt, K.W., Skinner, C.N., Stephens, S.L., Waldrop, T.A., Yaussy, D.A., Youngblood, A., 2009. The national Fire and Fire Surrogate study: effects of fuel reduction methods on forest vegetation structure and fuels. Ecological Applications 19, 285–304.
Seager, R., Ting, M.F., Held, I.M., Kushnir, Y., Lu, J., Vecchi, G., 2007. Model projections of an imminent transition to a more arid climate in southwestern North America. Science 316, 1181–1184.
Seastedt, T.R., Hobbs, R.J., Suding, K.N., 2008. Management of novel ecosystems: are novel approaches required? Frontiers in Ecology & the Environment 6, 547–553.
Stephens, S.L., Moghaddas, J.J., 2005. Experimental fuel treatment impacts on forest structure, potential fire behavior, and predicted tree mortality in a California mixed conifer forest. Forest Ecology and Management 215, 21–36.
Stephens, S.L., Moghaddas, J.J., Edminster, C., Fielder, C.E., Haase, S., Harrington, M., Keely, J.E., Knapp, E.E., McIver, J.D., Metlen, K., Skinner, C.N., Youngblood, A., 2009. Fire treatment effects on vegetation structure, fuels, and potential fire severity in western US forests. Ecological Applications 19, 305–320.
Stephenson, N.L., 1999. Reference conditions for giant sequoia forest restoration: structure, process, and precision. Ecological Applications 9, 1253–1265.
Suding, K.N., Gross, K.L., Houseman, G.R., 2004. Alternative states and feedbacks in restoration ecology. Trends in Ecology and Evolution 19, 46–53.
Thomas, J.W., Anderson R.G., Maser C., Bull E.L., 1979. Snags. In: Wildlife Habitats in Managed Forests–the Blue Mountains of Oregon and Washington. USDA Agricultural Handbook 553, Washington, DC, USA, pp. 60–77.
Toney, J.L., Anderson, R.S., 2006. A post-glacial paleoecological record from the San Juan Mountains of Colorado: fire, climate and vegetation history. The Holocene 16, 505–517.
USDA Forest Service, 2004. Lower Middle Mountain Research Project Environmental Assessment. San Juan National Forest, Durango, CO.
Van Mantgem, P.J., Stephenson, N.L., Byrne, J.C., Daniels, L.D., Franklin, J.F., Fulé, P.Z., Harmon, M.E., Larson, A.J., Smith, J.M., Taylor, A.H., Veblen, T.T., 2009. Widespread increase of tree mortality rates in the western United States. Science 323, 521–524.
Westerling, A.L., Hidalgo, H.G., Cayan, D.R., Swetnam, T.W., 2006. Warming and earlier spring increase spring increase western US forest wildfire activity. Science 313, 940–943.
White, A.S., 1985. Presettlement regeneration patterns in a southwestern ponderosa pine stand. Ecology 66, 589–594.
Whitlock, C., Shafer, S.L., Marlon, J., 2003. The role of climate and vegetation change in shaping past and future fire regimes in the northwestern US and the implications for ecosystem management. Forest Ecology and Management 178, 5–21.