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Impact of a high-intensity fire on mixed evergreen and mixed conifer forests in the Peninsular Ranges of southern California, USA

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Abstract

Fire is an important disturbance agent in the southern California landscape and plays a large role in the function and structure of its pine and mixed conifer forests. However, humans have changed the forest fire regime across the western United States by excluding fire. Fire suppression has been blamed for increasing stand densities and a shift from fire-tolerant trees to shade-tolerant but fire sensitive trees. These changes had been observed in Cuyamaca Rancho State Park (CRSP), Peninsular Ranges, San Diego County, California, USA. We surveyed an area in CRSP during the first two post-fire growing seasons following the October 2003 Cedar Fire, a historically large and severe fire, to determine patterns of tree mortality and vegetation recovery. This area is a mosaic of mixed evergreen and mixed conifer forest, oak woodland, chaparral and grassland. Most conifers were killed by the fire, especially smaller trees, and very few pine seedlings have established. Oaks were top-killed but most were resprouting by the second year, although larger oaks were more likely to have died than smaller. A rich herbaceous community of native annuals established in the first post-fire growing season. With a record rainy season during the winter of 2004–2005, all plant functional groups increased in abundance in the second year, including exotic annual grasses. The spread of exotic grasses in CRSP is a plant community change that may be of concern to resource managers. As forest succession is a long term process, it is important to continue monitoring vegetation recovery.

Keywords: *Pinus coulteri*; Tree mortality; Vegetation dynamics; Wildfire

1. Introduction

Fire is an important disturbance agent in the southern California landscape and plays a large role in the function and structure of its pine and mixed conifer forests (Vale, 1979; Talley and Griffin, 1980; Barbour and Minnich, 2000; Taylor, 2000). Fire provides services to conifer forests such as preparing a seedbed, recycling nutrients, regulating successional patterns, and influencing age and species mosaics (Kilgore, 1973; Parsons and DeBenedetti, 1979; Neary et al., 1999; Borchert et al., 2003; Radeloff et al., 2003; Stephens and Fry, 2005). Many shade-intolerant pines depend on these services to persist in the forest.

Although fire history data for southern California are sparse before the early 1900s, fire regimes in the forests of the Transverse and Peninsular Ranges have been studied using fire scar dendrochronology methods, with estimated fire intervals ranging from 4 to 50 years (Kilgore, 1973; McBride and Laven, 1976; Savage, 1994; Sheppard and Lassoie, 1998; Barbour and Minnich, 2000; Stephens et al., 2003; Everett, 2003). A fire interval is the number of years between two successive fire events at a specific site or an area of a specified size (National Park Service, 2004). While there is debate about historic fire regimes in western mixed conifer forest (Minnich et al., 1995, 2000; Baker and Ehle, 2001), studies suggest the intervals under current fire suppression are much longer than they were prior to around 1900. The estimated higher frequency of fire prior to 20th century suppression suggests that historical fires were low intensity surface burns and had minimal effect on large trees, resulting in an open, park-like forest with an uneven aged canopy (Barbour and Minnich, 2000; Minnich et al., 2000; Stephens and Gill, 2005).

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Fire exclusion (Pyne, 1984) has allowed the expansion of shade-tolerant, fire sensitive species, such as *Calocedrus decurrens* (Torrey), Florin (incense-cedar) and *Abies concolor* (Gordon and Glend.), Lindley (white fir), in mixed conifer forests of the west, including the forests of southern California. This has led to a shift in species composition and age structure and increased stem density (Parsons and DeBenedetti, 1979; Swezy and Agee, 1990; Savage, 1997; Minnich et al., 2000; Taylor, 2000). The increased density of small trees (ladder fuels) may have enhanced the potential for stand-replacing crown fires that result in mortality of even large trees (Barbour and Minnich, 2000). This shift in forest structure from shade-intolerant pines (*Pinus jeffreyi*, *P. coulteri*, *P. ponderosa*) to shade-tolerant species, and increased stem density, has been documented in Cuyamaca Rancho State Park (CRSP), in the Peninsular Ranges within San Diego County, California, USA (Krofta, 1995; Stephenson and Calcarone, 1999). For example, four previously mapped fires affected the ‘‘West Mesa’’ area of the Park in the 20th century (prior to 2003) including the Conejos Fire of 1950, Peak Fire of 1986, and a prescribed fire conducted in 1988; areas outside of these fires have not burned since records have been kept, e.g., prior to 1911. Krofta (1995) found more shade-tolerant species (*C. decurrens* and *A. concolor*) in the older fires (Fig. 1) and many small diameter trees throughout West Mesa (Fig. 2).

A large and severe fire occurred in San Diego County in October 2003 when major fires burned throughout southern California (Moritz et al., 2004). The Cedar Fire began October 25 and burned into November, consuming over 113,300 ha of coastal sage scrub (about 10% of the burned area), chaparral (50%), oak woodland (10%) and conifer forest (8%; California Department of Forestry and Fire Protection, 2003a). The Cedar Fire was the largest mapped fire in California history (since ~1911). We investigated patterns of tree mortality and vegetation recovery in CRSP after the Cedar Fire. CRSP (10,000 ha in extent), most of which had not burned since before fire maps were compiled (1911), was entirely burned in the Cedar Fire, most at high severity (California Department of Forestry and Fire Protection, 2003b) as determined by the USDA Forest Service Burn Area Emergency Response Team (http://www.fs.fed.us/biology/watershed/burnareas/). Fire severity is the effect of fire on the ecosystem (plants, soil), while fire intensity is the amount of energy released by a fire (Whelan, 1995; National Park Service, 2004).

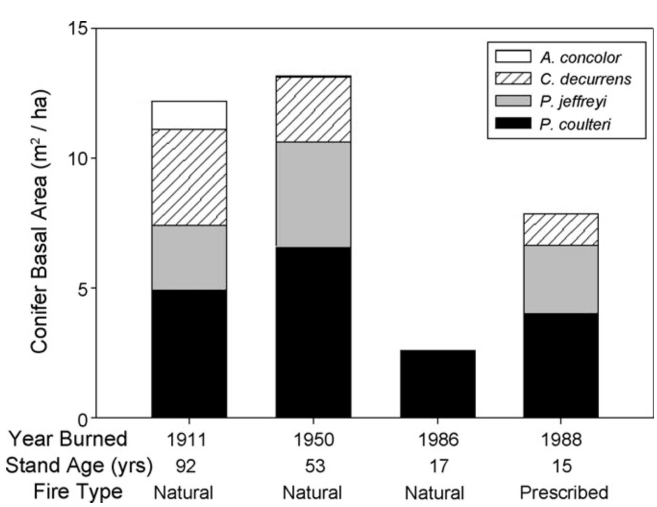


Fig. 1. Basal area ($m^2\ ha^{-1}$) of common conifer species in each mapped fire of West Mesa: 1911, 1950 and 1986 wildfires (natural) and 1988 prescribed fire (prescribed). The most common conifers were *P. coulteri* (Coulter pine; black bars), *P. jeffreyi* (Jeffrey pine, gray bars), *C. decurrens* (incense-cedar, hatched bars), and *A. concolor* (white fir, open bars). Adapted from 1992 survey data by Krofta (1995).

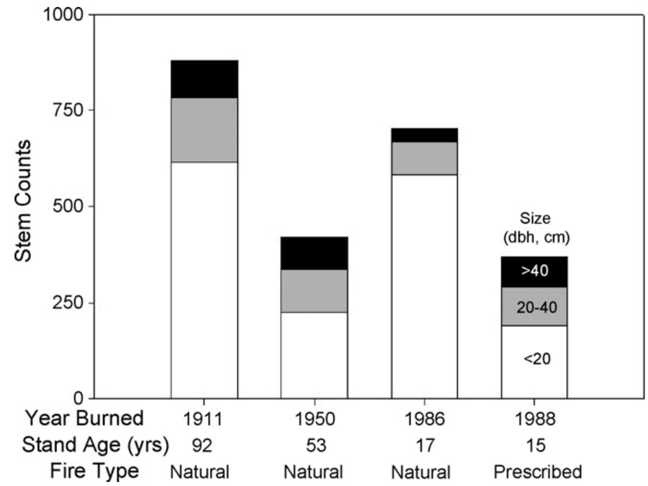


Fig. 2. Proportion of pre-fire size (dbh, in cm) by size classes for four mapped fires surveyed by Krofta (1995) on West Mesa in 1992. Stem count is the total number of trees in 40 stands, total area surveyed 5.016 ha (see text).

This study addressed three questions: (1) what factors were correlated with mortality of tree species in the forests of CRSP after the Cedar Fire? (2) What are the initial patterns of vegetation recovery, e.g., is there early evidence of a type conversion or spread of exotic species? (3) Are there differences between the first (2004) and second (2005) post-fire years in tree mortality or vegetative recovery?

Based on the literature, it was expected that species, fire severity, previous stand age, and tree density would be the most important factors determining tree mortality (Parsons and DeBenedetti, 1979; Swezy and Agee, 1990; Savage, 1997; Stephenson and Calcarone, 1999; Barbour and Minnich, 2000; Minnich et al., 2000; Taylor, 2000). Very recently burned areas are expected to have lower tree densities, and therefore experience lower fire severity, while stands of young trees can be dense and their small trees could be susceptible to higher fire-caused mortality than older stands of larger trees. The few previous fires in CRSP have been attributed to two factors. The first is extreme weather conditions (‘‘Santa Ana’’ or autumn foehn winds; Keeley, 2002). Secondly, chaparral, interspersed with woodland and forest in the study area, may facilitate the spread of high-intensity fires into the forest (Stephenson and Calcarone, 1999). The Cedar Fire was carried into CRSP by extreme weather (not Santa Ana but strong westerly winds). However, weather and the surrounding chaparral are factors affecting the entire study area. Therefore, if stand age and/or tree density are correlated with tree mortality, it suggests that forest structural changes (potentially caused by fire suppression) contributed to the severity of the Cedar Fire in CRSP.

We also expected to find early evidence of a shift in species composition from one plant community to another, e.g., mixed conifer to oak woodland, chaparral or grassland, following the fire. This is sometimes called ''type conversion'' (Stylinski and Allen, 1999; Keeley, 2006). Higher mortality was expected in the fire-sensitive species (*A. concolor*, *C. decurrens*, *P. coulteri*) compared to the fire-tolerant species including pines (*P. jeffreyi*, *P. ponderosa*), oaks (*Quercus kelloggii*, *Q. agrifolia*, *Q. chrysolepis*), and chaparral shrubs. If this occurred, forest structure may ultimately shift back to an open pine-dominated forest as is found in historical descriptions (Kilgore, 1973; Barbour and Minnich, 2000; Minnich et al., 2000). Alternatively, oaks and other resprouting chaparral species may establish before pine seedlings and dominate the site (Minnich, 1988; Savage, 1994). Establishment of exotic plant species is a threat following any disturbance, including fire (Hobbs and Huenneke, 1992; Kotanen, 1997; Wooton, 1998). Of particular concern is the establishment of exotic annual grasses that compete effectively with native species and respond with rapid growth after a fire, affecting both the fire regime and the vegetation composition (D'Antonio and Vitousek, 1992; Keeley, 2006). More exotics were expected where fire was severe.

2. Methods

2.1. Study area

Cuyamaca Rancho State Park (32°56′00″N; 116°57′30″W) comprises several upland vegetation communities including grassland, chaparral, oak woodland and mixed forest. Notably, with an elevation range of about 1000–2000 m, most of the Park is found within the transition zone between foothills mixed evergreen forest (Coulter pine-canyon live oak, black oak) and midmontane forest (mixed conifer, Jeffrey pine) according to Barbour and Minnich (2000). Mixed evergreen and mixed conifer forest stands occur in a fine-grained mosaic with chaparral and montane meadows. The dominant conifers in the forested areas are *P. coulteri* D. Don (Coulter pine), *P. jeffreyi* Grev. & Balf. (Jeffrey pine), *C. decurrens* and *A. concolor*, with a few *P. ponderosa* Laws. (ponderosa pine) which reaches the southern extent of its range in the Park. The dominant oaks are *Q. chrysolepis* Liebm. (canyon live oak), *Q. agrifolia* Nee var. *oxyadenia* (Torrey), J. Howell (coast live oak), and *Q. kelloggii* Newb. (black oak).

Our study encompassed areas of West Mesa and East Mesa in CRSP (characteristics of these areas are summarized in Table 1). West Mesa (1140 ha) was selected because of the previous study of forest structure conducted there a decade prior to the Cedar Fire (Krofta, 1995), providing the potential to revisit established plots. However, fire history and environment (for example the elevation gradient) are not independent in West Mesa. In our second survey year (2005) we expanded our sampling to include a ~500-ha area on East Mesa, about half of which (211 ha) had been burned in a prescribed fire, the Tragedy burn, conducted during the first 2 weeks of June 2003 (total area about 480 ha, half inside and half outside CRSP). This allowed us to also examine the effects of a very recent prescribed burn on patterns of forest mortality and vegetation recovery.

2.2. Survey design and data collection

Surveys were conducted in the first and second growing seasons following the Cedar Fire (May–June 2004 and 2005). The initial survey served to capture tree mortality soon after the disturbance. The second year of survey identified delayed fire-caused mortality and captured early vegetation recovery patterns. Although forest succession is a long-term process, important patterns may be established in the first few years. Precipitation preceding the 2004 survey was much lower than preceding the 2005 survey (Fig. 3).

In 1992, Krofta (1995) selected a random sample of 40 stands in West Mesa, from a systematic grid with points at intervals of 250 m, stratified across the four previous fire dates with 10 stands in each fire perimeter (the extent of the 1140-ha area he sampled is shown in Fig. 4). However, only 18 of the original 40 stand locations had been recorded using a global positioning system (GPS) and could be relocated. We established the remaining stand locations by navigating to

Table 1
Summary of study area characteristics for two regions of Cuyamaca Rancho State Park (10,000 ha in total extent)

Study area	West Mesa	East Mesa
Location	West of Highway 79, north of Arroyo Seco Fire Road and south of Lookout Fire Road, east of the Cuyamaca Peak ridgeline	East of Highway 79, at the end of East Mesa Fire Road near Granite Springs Primitive Camp, about 5 km east of West Mesa
Topography	Most of the area is a plateau (Mesa) at about 1400–1500 m, gently sloping towards the southeast, with steeper slopes in the lower elevation south and to the northwest below the 2000 m Cuyamaca Peak	Most of the area is a plateau (Mesa) at about 1450–1500 m, gently sloping towards the south
Area	1140 ha	~500 ha
Elevation	1250–1700 m	1400–1550 m
Vegetation	Coulter pine-canyon live oak forest and woodland on the plateau; live oak woodland at lower elevations on south-facing slopes, chaparral on steep rocky slopes, mixed conifer forest at higher elevations and on north facing slopes; small montane dry meadows interspersed on flatter sites	Jeffrey pine-black oak forest and woodland on the plateau interspersed with a large complex of montane dry meadows (0.5 km across at the widest places, more than 3 km long north to south)
Study plots	37 stands in 2004; 32 of those repeated in 2005	None in 2004; eight stands in 2005

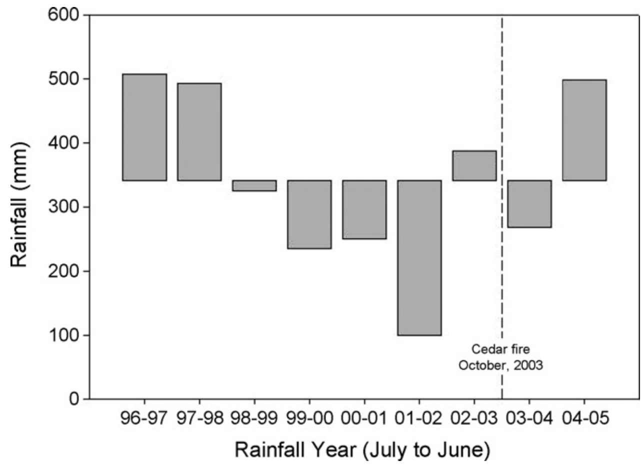


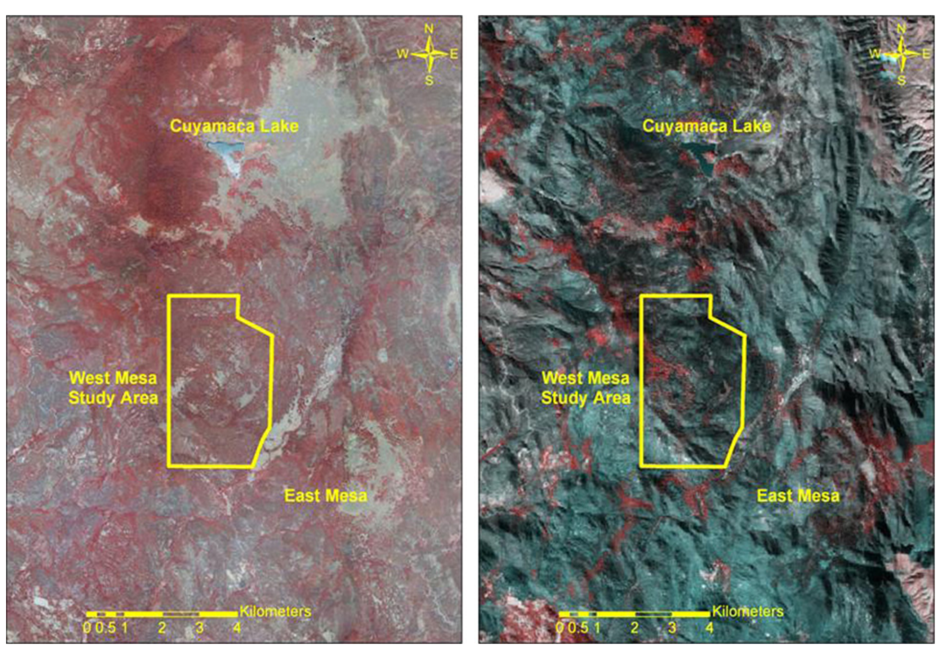
Fig. 3. Rainfall anomalies for nearby Mt. Laguna Weather Station 1996–2005 (data from http://www.wrcc.dri/edu/cgi-bin/rawMAIN.pl?caCLAG). Rainfall is presented as deviations from the mean (343.5 mm y^{-1}) using a July 1–June 30 rainfall year. The dashed line denotes the time of the Cedar Fire, California's largest mapped fire which began in October 2003.

the originally assigned grid points using a high precision GPS (Trimble GeoXM) and installing new rebar. It is important to note that, because all stands could not be precisely relocated, direct comparisons could not be made at the scale of the individual stand across the entire study area. Five of the original 40 stands were dropped because they fell entirely within chaparral. Two new stands were selected from among the unsampled grid points in an area of lower fire severity once it was determined that most of the original stands fell within areas of high fire severity.

In 2005, the 250-m sample grid was expanded to include East Mesa and eight stands were randomly selected from among those grid points that fell in the low burn severity area, identified by post-fire digital color infrared orthorectified aerial imagery (Fig. 4). Four of these were inside the perimeter of the June 2003 prescribed fire and four were in an adjacent area of East Mesa, outside the perimeter but burned with low severity in the October 2003 Cedar Fire. Five stands in West Mesa that yielded redundant information for the statistical analysis (almost identical in composition, burn severity, and vegetation response to plots that were retained) were not revisited in 2005 to allow resources to be allocated to the extra sampling on East Mesa. In summary, 37 stands were surveyed on West Mesa in 2004 and 40 stands were surveyed on West (32) and East Mesa (8) in 2005 (Table 1).

Following Krofta (1995) a ''stand'' was defined as a 100 m × 100 m (1 ha) area, with the center point marked by rebar. In each stand, four subplots were established at azimuths of 45°, 135°, 225°, and 315°, centered 36 m from the center rebar. Each subplot was 20 m in diameter, and for all trees in a subplot species, dbh (diameter at 1.3 m height), and mortality (dead or alive) were recorded (in a total area of 1254 m^2 per stand). Aspect, slope, and fire severity were measured, while elevation and previous stand age were noted from topographic and fire history maps (Krofta, 1995).

Fire or burn severity is a measure of the ecological effects of a fire. It is related both to the physical intensity of the fire and the characteristics of the ecosystem. Spatially explicit data on fire line intensity and burning duration do not exist for most fires. Fire severity is sometimes estimated using single factors, such as canopy consumption or charring of soil organic matter, or multiple factors (discussed by Epting and Verbyla, 2005), but no common standard yet exists. The choice of variables depends both on ecological and resource management



Fi g. 4. Digital color infrared images of Cuyamaca Rancho State Park (provided by SDSU, Department of Geography). Left: pre-Cedar Fire, forests are intermingled with meadows (digital orthophotographic scanned CIR aerial photograph, 2002). Right: post-Cedar Fire, red (lighter) patches show live vegetation or low fire severity areas (Leica ADS 40 pushbroom multispectral sensor, 2003) (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.).

objectives. Fire severity was determined in this study using the composite burn index (CBI) which has been proposed as a common standard by US federal land management agencies especially for use in conjunction with remotely sensed mapping of burn severity (van Wagtendonk et al., 2004; Cocke et al., 2005). The CBI is a visual field-based assessment of fire severity that represents the magnitude of fire effects across all canopy strata and considers multiple variables including color of the soil, amount of vegetation and substrate consumed, resprouting from burned plants, and mortality or scorching of trees (FIREMON, 2003). The CBI scale ranges from 0 to 3 with 0–1 being low severity, 1–2 moderate, and 2–3 high. For each subplot we visually assessed scorch height, percent green, black or brown canopy (average for all trees in two strata, subcanopy and canopy), proportion of plants altered, living or resprouting in the herb and shrub layers, soil color change, and proportion of litter and duff consumed, according to the ordinal scale defined for each of these components in the CBI protocol. Their average provides the CBI for each subplot, and these were then averaged for each stand.

The east to west diameter of every subplot delineated a transect from which five 1-m^2 quadrats placed at meters 0, 4, 8, 12, and 16, on alternating sides, were sampled for species, density (counts), and percent cover of all resprouts (trees, shrubs, perennials), tree and shrub-seedlings, and herbs. Species were later assigned to the following functional groups for analysis: shrubs-seedlings, shrubs-sprouts, exotic annuals, native annuals, and native perennials (Appendix A).

2.3. Data analysis

Logistic regressions identified those characteristics—size and species group (conifer versus oak)—related to mortality of individual trees (e.g., Ryan and Reinhardt, 1988; Regelbrugge and Conard, 1993; Stephens and Finney, 2002; Franklin et al., 2004). To determine those factors influencing tree mortality at the stand level, multiple regression was used to analyze average stand mortality, as well as the abundance of each functional group in relation to other functional groups and abiotic factors (2004 and 2005 data analyzed separately). Bootstrapping was performed on all regressions. Linear regressions were performed on 1000 bootstrap samples of size $n = 37$ (2004) or $n = 40$ (2005) for each model. Bootstrap estimates, standard errors, and 95% confidence intervals were constructed and compared to the parametric regression. In all regressions, the bootstrap estimates were similar to the parametric estimates so both significance tests and rank order of predictors were unchanged. Paired t-tests were used to examine between-year differences in tree mortality and functional group abundance for the 32 stands on West Mesa that were surveyed in both 2004 and 2005.

3. Results

3.1. Tree mortality and regeneration

In 2004, of 2155 trees measured in 37 stands on West Mesa, 1162 (54%, 250 ha^{-1}) were conifer species that experienced 95% mortality and 993 (46%, 214 ha^{-1}) were oak species that experienced 14% mortality (Table 2 and Fig. 5). Oaks were counted as alive if they had any living resprouting stems. Almost all above-ground biomass of the oak species was killed. Although species group (conifers versus oaks) was the most important predictor of survival ($n = 2172$, $\rho^2 = 55.6\%$, $\chi^2 = 1654$ with 1 d.f., $p < 0.001$), tree size (dbh) was a significant mediating factor ($\Delta\rho^2 = +3.3\%$, $\chi^2 = 74$ with 2 d.f., $p < 0.001$; Table 2). For example, a 10-cm dbh oak had an estimated mortality rate of 12.5% compared to 23.9% for a 75-cm dbh oak. The opposite pattern was observed with conifers. A small conifer (10 cm dbh) had an estimated mortality rate of 98.2% compared to 76.2% for a 75-cm dbh conifer.

In 2005, the 32 West Mesa stands surveyed in both years ($n = 2039$ trees) showed significantly increased conifer mortality of 99%, a 4% increase from 2004, due to delayed mortality. Oak mortality decreased significantly to 6.5%, due to delayed resprouting of nearly half of the oaks scored as dead in

Table 2
Results of logistic regression of mortality for individual trees as a function of species group (conifer vs. oak) and tree size (log of diameter) in 2004 and 2005

Variable	$\Delta\rho^2$ (%)	$\Delta\chi^2$	p-Value
2004 logistic regression model ($n = 2155$)			
Tree type[a]	55.6	1654	<0.001
Tree size[b]	3.3	74	<0.001
Model	58.9	1728	<0.001
Tree type/size[c] (%)			
Predicted mortality			
Small oak			12.5
Large oak			23.9
Small conifer			98.2
Large conifer			76.2
Change in sampling 2004–2005			
Trees dropped from sampling			116 (4.9%)
Trees added to sampling			210 (8.9%)
Trees sampled in both years[d]			2039 (86.2%)
Variable	$\Delta\rho^2$ (%)	$\Delta\chi^2$	p-Value
2005 logistic regression model ($n = 2249$)			
Tree type	65.6	2038	<0.001
Tree size	5.3	166	<0.001
Model	70.9	2204	<0.001
Tree type/size[c] (%)			
Predicted mortality			
Small oak			3.3
Large oak			32.5
Small conifer			98.7
Large conifer			74.5

Change in sampling occurred because five West Mesa plots sampled in 2004 were dropped in 2005 and eight new plots were added in East Mesa in 2005 (Table 1).

[a] Tree type: oak vs. conifer (1 d.f.).

[b] Tree size: ln(dbh), main effect and interaction (2 d.f.).

[c] Small and large trees were defined as 10 and 75 cm dbh for illustrative purposes.

[d] Concordance between 2004 and 2005 tree mortality was high (Cohen's $k = 0.89$), oaks showed some delayed resprouting (6.7% of live 2005 oaks), conifers showed some delayed mortality (4.3% of dead 2005 conifers).

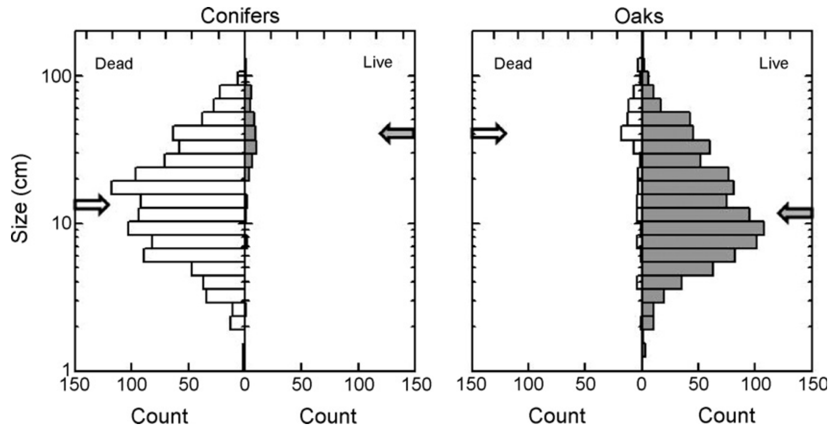


Fig. 5. Mirrored histograms showing the fate of individual trees measured in 2004 as a function of tree size (dbh, in cm) for conifers (left panel) and oaks (right panel). Bar shading denotes fate (dead trees are open bars, live trees are gray bars). The median tree size for each group is denoted on the axis with a block arrow. Note the $\log_{10}$ scale on the *y*-axis.

2004. In the eight East Mesa stands surveyed in 2005 conifer mortality was only 31% and oak mortality was 13%. The four East Mesa sites inside the 2003 prescribed fire perimeter had an average CBI of 0.82 (low severity); conifer mortality was only 17% and oak mortality was 9%. Outside the prescribed-fire perimeter the average CBI for the four stands was 1.92 (moderate severity); conifer mortality was 39% and oak mortality was 25%.

In 2005, of 2249 trees in 40 stands on East and West Mesas, 1162 were conifer species and 1087 were oak species. The patterns of mortality observed in 2005 were similar to those observed in 2004 with the two tree types differing dramatically in mortality. The importance of tree size was more pronounced in 2005 (Table 2) because delayed resprouting of small oaks and delayed mortality of small pines amplified the difference between small and large trees. This increased difference due to tree size is enhanced by the addition of the plots on East Mesa that experienced less intense burns and included large surviving conifers.

This Cedar Fire-caused mortality can be compared with 303 conifers ha^{-1}, 43% of them dead, and 285 oaks ha^{-1}, 8% of them dead, measured in 1992 (Krofta, 1995). Krofta attributed the high proportion of dead conifers to drought and bark beetle infestation as well as the prescribed fire of 1988 and wildfire of 1986 (only 4 and 6 years prior to his observations). Further, Krofta's survey included a large number of living small trees (<5 cm dbh), both oaks (119 ha^{-1}) and conifers (51 ha^{-1}). We encountered comparatively fewer small trees in 2004, either oaks (only 25 ha^{-1}) or conifers (26 ha^{-1}), and our figures include both dead (12%) and living small trees. This suggests that, although there was undoubtedly some stand thinning as well as tree establishment from 1992 to 2003, a large number of small trees (up to 116 ha^{-1}, mainly oaks) vaporized without a trace on West Mesa in the Cedar Fire. Therefore, our mortality estimates apply to trees $\geq$5 cm dbh.

Only five pine seedlings were found on vegetation transects within stands on West Mesa during the 2004 field season. Pine seedlings could not all be identified to species, but most adult conifers killed in the stands were *P. coulteri* (see Fig. 1 and Spears, 2005 for details). In total, 342 pine seedlings were noted while hiking to stand locations. In 2005, 59 large (2 years growth) seedlings were observed on West Mesa that had survived from the first year. In addition, 181 new pine seedlings (germinated in 2005) were counted on West Mesa. These opportunistic observations do not allow density to be estimated.

In 2005, thousands of *C. decurrens* seedlings were observed in Stand 41 on West Mesa; 1039 were counted along the transects (density of 6.5 m^{-2}). This stand had surviving, adult *C. deccurens* trees and was one of only two stands with living *C. decurrens* individuals.

3.2. Tree mortality at the stand level

Because conifer versus oak was shown to be the most significant factor in tree mortality in both 2004 and 2005, factors related to stand mortality were analyzed separately for these two groups of species. For conifers, fire severity (CBI) was a significant predictor of stand mortality in 2004 and 2005 (Table 3). Species was not a significant predictor for these data in spite of known species difference in fire tolerance. The Cedar Fire was high severity across almost all of West Mesa where CBI only ranged from 2.28 to 3.0. The only stands where any live conifers were found were the five stands that had a CBI less than 3.0 (Fig. 6). However, in 2005, with the addition of eight stands on East Mesa, all of which had live conifer trees (Fig. 6), CBI was still found to be the single most important predictor of conifer mortality (Table 3).

In 2004, elevation was significantly related to the average stand mortality of the oak group but the regression explained little variance (Table 3). Although the oak species tended to be found at different elevations, there were not significant differences in mortality among species. Elevation was most likely found to be statistically significant because of two outliers found at higher elevations with very few oak trees (four and five) but very high mortality (100% and 80%). In 2005, none of the variables examined were found to be significant predictors of oak mortality.

Table 3
Multiple regression analysis of factors related to stand-level tree mortality and plant group abundance for stands measured in 2004 and 2005 (see Table 1)

Dependent variable	Explanatory	2004 (37 stands)				2005 (40 stands)			
		β	t	p-Value	R^2	β	t	p-Value	R^2
Mortality-conifers	CBI	1.008	14.214	<0.001	0.871	0.528	21.572	<0.001	0.940
Mortality-oaks	Elevation × 1000 m	0.343	2.076	0.045	0.113	–	–	–	0.000
Shrub-seedling	CBI	18.513	3.216	0.003	0.527	3.721	4.003	<0.001	0.498
	Native annual cover	−20.129	−2.591	0.015		−10.649	−3.007	0.004	
	Tree density	−98.208	−2.413	0.022		–	–	–	
	Stand age	−0.074	−2.339	0.026		–	–	–	
Shrub-sprout	Slope	0.007	2.803	0.008	0.460	–	–	–	
	Exotic annual cover	–	–	–		−0.340	−4.615	<0.001	0.503
	Stand age	–	–	–		−0.002	−3.448	0.002	
	Native annual cover	–	–	–		−0.392	−3.297	0.002	
Native Perennial	Elevation × 1000 m	−0.185	−3.409	0.002	0.353	−0.135	−2.500	0.017	0.211
Native annual	Tree density	−2.487	−4.733	<0.001	0.796	–	–	–	
	Slope	−0.014	−4.154	<0.001		−0.012	−2.602	0.014	0.601
	Stand age	−0.002	−2.751	0.01		−0.003	−3.71	0.001	
	CBI	0.232	2.582	0.015		–	–	–	
	Exotic annual cover	0.338	2.514	0.018		−0.26	−2.544	0.016	
	Shrub-seed count	−0.005	−2.013	0.053		−0.016	−3.163	0.003	
Exotic annual	Native annual cover	0.274	2.706	0.011	0.298	−0.884	−4.162	<0.001	0.656
	Shrub-seed count	−0.005	−2.128	0.041		−0.023	−3.434	0.002	
	Shrub-sprout cover	–	–	–		−0.68	−3.102	0.004	
	Stand age	–	–	–		−0.003	−2.631	0.013	
	Slope	–	–	–		−0.017	−2.333	0.026	
	Native perennial cover	–	–	–		−0.473	−2.282	0.03	

Dependent variable is proportion dead for mortality, density for shrub-seedling and cover for other plant groups. Stand age is years since previous burn, CBI is composite burn index.

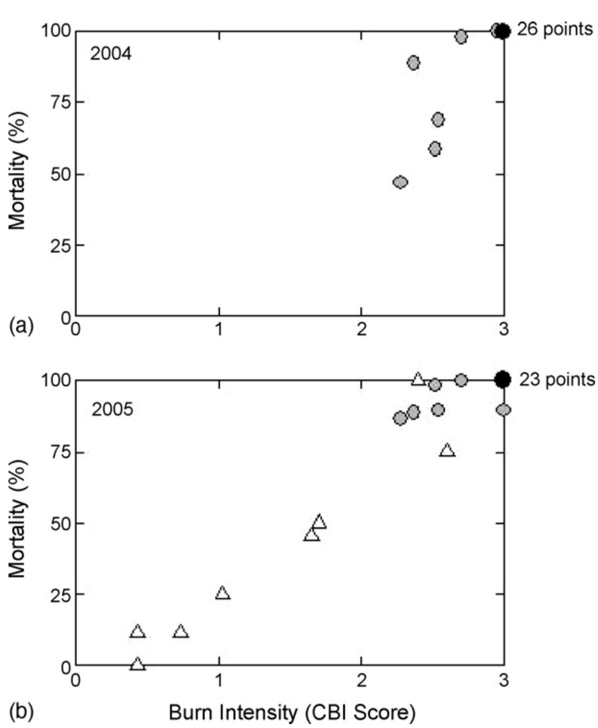


Fig. 6. Stand-level mortality of conifers (proportion) by fire severity (CBI) for (a) 2004, $n = 37$ West Mesa stands and (b) 2005, $n = 40$ West and East Mesa stands. Location is denoted with a circle (West Mesa) or a triangle (East Mesa). Notice the large number of stands with fire severity of 3.0 (maximum possible score) and 100% conifer mortality.

3.3. Shrub regeneration

On West Mesa more shrub-seedlings were found in younger stands, with high fire severity, low tree density, and low native annual cover in the first year (2004; Table 3). In 2005, when more stands with low CBI were included (East Mesa), only CBI and native annual cover were significant factors with more shrub-seedlings found, again, in stands with high fire severity and in areas with low native annual cover (Table 3). Shrub-seedling abundance (density) decreased while cover dramatically increasing from 2004 to 2005 (Table 4).

Table 4
Changes in plant group abundance in the 32 West Mesa stands sampled in both 2004 and 2005

Variable	Mean (S.D.)		Paired t-test, p-value
	2004	2005	
Conifer mortality	95.19 (13.38)	98.38 (3.98)	0.068
Oak mortality	17.13 (16.51)	12.46 (14.85)	<0.001
Shrub-seedling count	0.525 (0.365)	0.375 (0.215)	<0.001
Shrub-seedling cover	1.65 (1.91)	11.24 (10.90)	<0.001
Shrub-sprout cover	1.38 (2.08)	5.54 (7.26)	<0.001
Native annual cover	17.2 (13.98)	32.92 (14.95)	<0.001
Native perennial cover	6.43 (5.88)	9.68 (8.76)	0.008
Exotic annual cover	3.02 (5.28)	15.02 (13.10)	<0.001

Mortality and cover are percentages. Seedling count is average number per m^2.

In 2004 higher shrub-sprout cover was found on steeper slopes. In the second year, shrub-sprout cover was highest in younger stands with low native and exotic annual cover (Table 3). There was a large increase in shrub-sprout cover between the years (Table 4).

3.4. Herbaceous vegetation in the forest understory

Higher native perennial cover was found at lower elevations in both years (Table 3), and cover increased in 2005 (Table 4), except in one stand (27) that had a 29% decrease. Fifty-nine species of native annuals (Appendix A) were found in the understory in one or both years. In 2004, more native annuals were found in younger stands on flatter sites, in lower severity areas with low tree density and with high exotic annual cover but low density of shrub-seedlings (Table 3). The factors seem to describe a meadow environment. Dry meadows occur in a fine scale mosaic with forest, woodland and chaparral in the study area (Fig. 4). Native annual cover increased in 2005 (Table 4) when there was more native annual cover in younger stands with gentle slopes and low shrub-seedling density. Native annual cover was high where exotic annual cover was low in the second year (Table 3). Total species richness of native annuals in quadrats was 46 in 2004 (area surveyed 740 m^2) and 50 (800 m^2) in 2005.

In 2004, exotic annuals were abundant in stands with high native annual cover and low shrub-seedling density, while in 2005, there were more exotic annuals in younger stands with lower cover of native annuals—but also with fewer shrub-seedlings, native perennials and shrub resprouts, and with gentle slopes (Table 3). Exotics made up 23% of the total cover in 2005 compared with only 8% in the first year (Table 4).

4. Discussion

4.1. Tree mortality and regeneration

The Cedar Fire was a high severity crown fire and conifer mortality was high everywhere on West Mesa, even more so in the second year (2005) with the additional mortality. A tree that was not killed directly by the fire but was weakened and succumbed between the two sampling periods experienced delayed mortality. Small conifers were especially susceptible to mortality and delayed mortality. For western conifers, it is likely a tree with crown kill greater than 70% will die within 5 years (Ryan, 1982; Weatherby et al., 2001). However, there are many interrelated factors that ultimately determine an individual tree's survival such as size, fire injury, susceptibility to insect and pathogens, pre-fire vigor, size, weather, and site conditions (Ryan and Reinhardt, 1988; Scott et al., 1996). In 2004, a conifer tree was designated "alive" if there were any green needles present but most of these trees had substantial fire injury with greater than 70% crown kill. Although the region received record amounts of rain over the 2004–2005 winter, these trees did not survive to the second year.

Fire exclusion and associated, documented (Krofta, 1995) changes in forest structure could have contributed to the high fire severity experienced during the Cedar Fire. Along with the shifts in forest structure, tree mortality produced by recent drought (Fig. 3) and bark beetle infestations could have added to the fuel load (Savage, 1997; Guarin and Taylor, 2005), and drought also reduces fuel moisture.

Oak mortality was generally low on West Mesa with most oak trees that were top-killed resprouting in the first spring, and additional individuals resprouting by the second year. Oaks are known to resprout after the first growing season, with *Q. agrifolia* able to resprout from the root crown up to 2–3 years after a fire (Steinberg and Howard, 2002). Site variables, such as elevation, slope, aspect, and the abundance of other plant groups, were not significant predictors of oak mortality. Nor was fire severity, consistent with the findings of Stephens and Finney (2002) for *Q. kelloggi*. All the oaks species present can resprout after a disturbance such as fire (Tirmenstein, 1989; Howard, 1992; Steinberg and Howard, 2002). Interestingly, it was large oaks that were less likely to have resprouted, suggesting that the ability to resprout declined with age.

With so many adult conifers killed by the fire, the low number of regenerating pines may affect forest composition in future decades. *P. coulteri* had been abundant in West Mesa except at the highest elevations. *P. coulteri* is partially serotinous (Borchert, 1985; Cope, 1993), e.g., retains seeds in some cones on some trees that are then released after exposure to heat, normally fire. Cone serotiny in this species is variable and related to the fire regime of the surrounding vegetation (Borchert, 1985). *P. coulteri* trees surrounded by chaparral have a high proportion of serotinous cones, attributed to the high mortality risk by fire. *P. coulteri* in these stands have episodic reproduction in the first few years following a fire. Borchert found *P. coulteri* in *Q. agrifolia* stands had very few serotinous cones and reproduction was sporadic and continuous; this was attributed to the low mortality risk by fire. *P. coulteri* pine seeds (300 mg with large wings) may be dispersed by wind (Wells, 2001) or rodents (Borchert et al., 2003), but in either case recolonization from unburned patches may occur.

Very few pine seedlings were observed on West Mesa in the first post-fire year. *P. coulteri* is capable of producing 0.21 seedlings/m^2 (Borchert et al., 2003). It was promising to see some seedlings had survived the first year and that there was additional germination in the second year (from either serotinous trees or dispersal from unburned trees), but the total number of first plus second year seedlings seen in 2005 was even lower than the number of first year seedlings seen in 2004. *P. coulteri* first bears cones at 10–15 years of age with good seed crops occurring every 3–6 years (Cope, 1993). Without restoration efforts, it will probably be many years before Coulter pines are again a substantial part of the forests of West Mesa.

C. decurrens seedlings were counted in the thousands the second year in a single stand. *C. decurrens* is not serotinous, is shade-tolerant and susceptible to fire when small, and has fluctuating seed production with prolific production every 3–6 years alternating with years of no seed production (Habeck, 1992a). In a heavy seed production year, almost one million seeds per ha can be produced; 2005 appears to have been a year of prolific seed production. This highlights the importance of even small patches of unburned trees to *C. decurrens* regeneration following the Cedar Fire.

All of East Mesa was also burned in the Cedar Fire but patches of it experienced a much lower severity fire than West Mesa (Fig. 6). One possible factor may be the meadows that surround these patches of forest on East Mesa. The fire had to burn through the meadows before reaching the forest, which may have caused the fire to ''lay down'' and burn as a surface fire through the forested areas. This is speculative as the behavior of the Cedar Fire on East Mesa is not known. Different pine species dominate the two areas—*P. coulteri* on West Mesa and *P. jeffreyi* on East Mesa. Species characteristics may be related to observed differences in fire severity. These species differ in their response to fire. While *P. coulteri* is partially cone-serotinous but self-prunes poorly and tends to be killed by fire (Borchert et al., 2002), *P. jeffreyi* typically has low mortality when large because of its thick insulating bark; incense-cedar is also fire-sensitive when small and resistant when large, and white fir is sensitive to fire (Habeck, 1992a,b,c; Keeley and Zedler, 1998; Zouhar, 2001). Stand structure differences could also have affected fire severity. The prefire tree size distribution on East Mesa is not known.

Even more remarkable than the difference between East and West Mesa are the differences within East Mesa, between the stands inside or outside the perimeter of the 2003 prescribed fire. It is possible that environmental site conditions differed between these locations (although they appeared similar) or that fire behavior was affected by factors other than prescribed fire effects on fuel load (e.g., terrain, wind speed and direction). However, the purpose of the prescribed burn in 2003 was to lower fuels loads by 40–80% while minimizing damage to mature trees, and other studies have reported that prescribed burning lowers fire severity in pine forests (e.g., Pollet and Omi, 2002). The much lower tree mortality of both oaks and conifers inside the perimeter is hard to ignore and should be considered when fire management plans are implemented for CRSP.

4.2. Shrub regeneration

Ceanothus palmeri Trel., the most abundant shrub-seedling in both years, is a facultative seeder (Halsey, 2005)—it can resprout after a fire and its seeds have fire-cued germination. High fire severity, found to be positively related to its abundance both years, may have been necessary to cue germination of these shrub-seedlings. The negative relationship found between both native and exotic annuals and shrub-seedlings may be related to competition between shrub-seedlings and these annuals, preference for different environmental conditions, or simply to what was present on a site before the fire. The significant decrease in shrub-seedling density between years, as well as the increase in seedling cover, is expected as growth and thinning occur (Tyler and D'Antonio, 1995), especially given the high precipitation received in the winter of 2004–2005.

4.3. Herbaceous vegetation in the forest understory

Several of the abundant native perennials were geophytes—perennial herbaceous plants whose overwintering buds are below the soil surface—including *Calochortus albus* Benth., *Calochortus splendens* Benth., *Dichelostemma capitatum* (Benth.) A.W. Wood, and *Bloomeria crocea* (Torrey) Cov. Geophytes are able to survive fire because their bulbs are buried in the soil and high surface temperatures do not kill them. Nearly all geophytes bloom profusely the first spring after a burn and are thought to be mostly dormant in the years between fires (Keeley and Keeley, 1988). Tyler and Borchert (2002) studied the geophyte, *Zigadenus fremontii* (Torrey) S. Watson, and found that most flowering and all seed production occurred in the first winter and spring after fire followed by lowered leaf area and number of leaves in subsequent years. This pattern was followed in CRSP by the most abundant native geophyte in 2004, *C. splendens*. In the first year post-fire, many stands were blanketed by dense areas of *C. splendens* but in the second year (2005) there were hardly any *C. splendens* flowering.

In 2004, native and exotic annuals both had high cover in the same stands. However, in 2005 natives had low cover in stands where exotic cover was high. This suggests an increase in competition between the two annual plant groups, although the negative relationship may also be the result of demographic differences such as higher seed output, lower seed predation, and the buildup of a large seed bank by exotics (D'Antonio and Vitousek, 1992) rather than direct competition. Both annual groups had a large increase in cover between the years, again probably related to the high precipitation received. Increases in water availability can facilitate establishment and dominance of exotic species (Dukes and Mooney, 1999).

The Cedar Fire was severe over much of CRSP and completely removed the tree canopy in many places. Both of these factors increase the susceptibility of CRSP to the spread of exotic invasive species within the Park. An intense fire reduces native competition (Harrod and Reichard, 2001) and the longer a canopy takes to close, the longer the area is open for post-fire colonization (Keeley et al., 2003; Keeley, 2006). Once established, exotic species can change the fire regime by increasing or decreasing fire frequency and intensity (Harrod and Reichard, 2001). *Bromus tectorum* L., an exotic that we found in our surveys, is a common exotic grass found across the western USA that has increased the fire hazard by changing fuel continuity (Veblen, 2003). Using prescribed fire to restore natural fire regimes and fuel loads to mixed-conifer forests is a common management practice, but prescribed fire can be a potential facilitator of exotic species like *B. tectorum* (Merriam et al., 2004; Keeley, 2006).

Brooks et al. (2004) suggest a multiphase conceptual model to understand the impacts of exotic species on the plant-fire regime cycle. They recognize several phases of the cycle where management action can take place. The first phase is excluding exotic species to prevent a fire regime from being altered. Prevention of establishment is the most effective management strategy. The second phase considers exotic species that have naturalized in an area but have not significantly impacted the ecosystem. Phase three deals with exotic species that have significantly impacted the ecosystem but not yet changed the fire regime. The last phase refers to exotic species that are establishing an invasive plant-fire regime cycle. The results of this study suggest CRSP is in phase two. Several exotic species have established themselves in the park and the potential fire-regime altering *B. tectorum*, along with the other invasive grasses such as *B. diandrus*, should be targeted as priority for exotic control.

5. Conclusion

The Cedar Fire was a high severity fire that changed the structure of the forests of Cuyamaca Rancho State Park for decades to come. Conifer mortality was very high on West Mesa with few live adults or seedlings. It will be many years before conifers dominate the landscape again without active restoration efforts. However, the plant community is regenerating. Oaks are resprouting and experienced fairly low mortality. Shrubs, native perennials, and native annuals are establishing rapidly after the record rain the area received during the 2004–2005 winter. Unfortunately, so are exotic annuals.

It was anticipated that tree mortality would vary with time since previous fire. However, the high-severity Cedar Fire erased any potential stand age affects on West Mesa and the greatest differences were found in a 1-year old prescribed burn on East Mesa. These differences could potentially be due to other factors besides those induced by the prescribed burning. Although this natural experiment is unreplicated, the sharp difference is hard to ignore.

Conifer forest can occur as ‘‘sky islands’’ on mountain peaks (Stephenson and Calcarone, 1999) in southern California, as it does throughout much of the arid southwestern USA and northwestern Mexico. Extreme disturbance events can affect large proportions of these small, forested areas, as the Cedar Fire affected CRSP. As forest managers in the region develop strategies to protect biodiversity while reducing fire hazard at the expanding wildland–urban interface (Radeloff et al., 2005), it is important to continue monitoring the long-term patterns of forest succession following this historical fire event.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.foreco.2006.07.023.

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