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Fire suppression impacts on postfire recovery of Sierra Nevada chaparral shrublands*

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Abstract. A substantial portion of chaparral shrublands in the southern part of California's Sierra Nevada Mountain Range has never had a recorded fire since record keeping began in 1910. We hypothesised that such long periods without fire are outside the historical range of variability and that when such areas burn, postfire recovery is weaker than in younger stands. We predicted that long fire-free periods will result in loss of shrub species and deterioration of soil seed banks, which, coupled with higher fire intensities from the greater accumulation of dead biomass, will lead to poorer postfire regeneration. The 2002 McNally Fire burned ancient stands that were as much as 150 years old, as well as much younger (mature) stands. Based on shrub skeletons in the burned area as a surrogate for prefire density, we found that ancient stands change in structure, owing primarily to the loss of obligate seeding *Ceanothus cuneatus*; other species appear to have great longevity. Despite the reduction in *C. cuneatus*, postfire shrub–seedling recruitment remained strong in these ancient stands, although some seed bank deterioration is suggested by the three-quarters lower seedling recruitment than recorded from mature stands. Total diversity and the abundance of postfire endemic annuals are two other response variables that suggest that these ancient stands are recovering as well as mature stands. The one area of some concern is that non-native species richness and abundance increased in the ancient stands, suggesting that these are more open to alien colonisers. It is concluded that chaparral more than a century old is resilient to such long fire-free periods and fire severity impacts are indistinguishable from those in younger chaparral stands.

Introduction

Today, approximately 45% of the chaparral landscape in the southern Sierra Nevada Mountain Range of California, USA, last burned sometime before record keeping began in 1910 (Fig. 1). In part, this is the result of a century of a highly effective fire suppression policy that has successfully excluded fire over much of the range (Caprio and Graber 2000). This is of particular concern to fire managers because of the fire hazard, and to resource managers because postfire recovery of chaparral shrublands is potentially compromised by long fire-free periods (Zedler 1995). This vegetation always burns in crown fires and long fire-free periods may jeopardise postfire recovery of some species through effects on the deterioration of seed banks and increased mortality from higher fire intensities.

Regeneration of chaparral during the first 5 years has been well studied and is driven largely by residual species present before the fire; colonisation plays a minor role (Keeley *et al*. 2005). Shrubs regenerate either by seedling recruitment and/or by resprouting from basal lignotubers or roots. Some species in the genera *Ceanothus* (California lilac or buckbrush) and *Arctostaphylos* (manzanita) lack resprouting ability and are often referred to as obligate seeders. Others, such as species of *Quercus* (scrub oak) and *Rhamnus* (coffeeberry or redberry), lack a dormant seed bank and regenerate after fire entirely from resprouts and are referred to as obligate resprouters. However, many shrub species combine both modes and are termed facultative seeders. Postfire environments are where chaparral communities exhibit their peak species diversity (Keeley and Fotheringham

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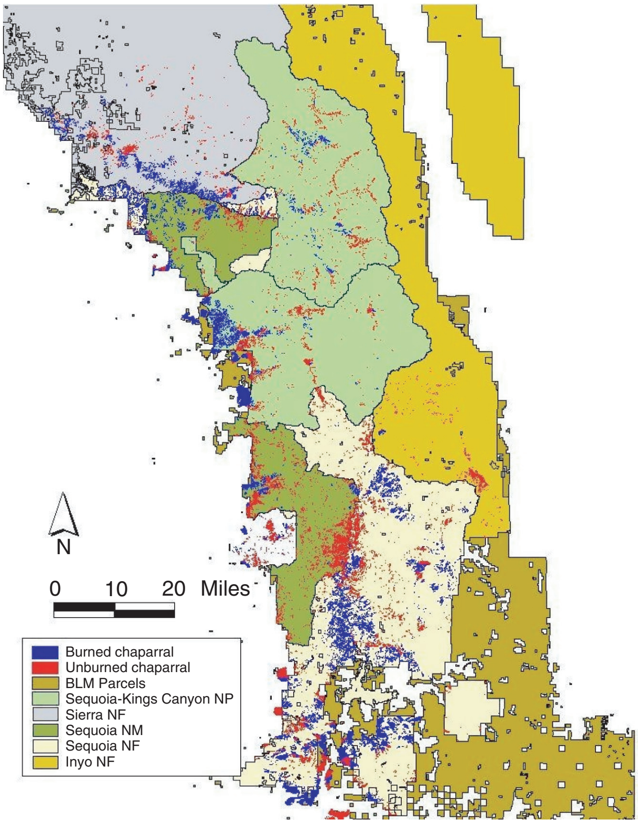

Fig. 1. Chaparral in the southern Sierra Nevada. Approximately 45% of the 138 000 ha of chaparral landscape on US Forest Service, National Park Service and Bureau of Land Management lands has never had a recorded fire (from A. H. Pfaff and J. E. Keeley, unpublished data based on the California Statewide Fire History database maintained by the California Department of Forestry and Fire Protection (CDF) and includes historical data from lands protected by USFS, NPS, BLM and CDF).

2003*b*), and most of this is a result of annuals that establish from deeply dormant seed banks. Many of these species are restricted to these postfire conditions and are known as 'postfire endemics' (Keeley 2000).

Successional change in the absence of fire is largely a process of stand thinning with little change in the composition of most chaparral communities (Keeley 1992*a*). Postfire obligate seeders and facultative seeders have more or less fire-dependent seedling recruitment and so they exhibit no increase during fire-free intervals, except perhaps in certain low-productivity habitats where light incidence at the soil surface is high (Safford and Harrison 2004). In the long-term absence of fire, seed banks may decline owing to diminished seed production and deterioration of the soil-stored seeds, although there is very little evidence for such an effect in stands up to approximately 80 years of age (Keeley and Keeley 1977; Zammit and Zedler 1988, 1994). Conversely, postfire obligate resprouters recruit seedlings during fire-free intervals and, thus, there is some potential for population increase (Keeley 1992*b*). Fire severity does increase with stand age (Keeley *et al*. 2005) and has negative impacts on resprouting success (Rundel *et al*. 1987; Moreno and Oechel 1991; Borchert and Odion 1995).

We hypothesised that extended fire-free periods pose two risks to postfire recovery of chaparral: (1) progressive loss of viability of seeds in the soil reduces postfire seedling recruitment of obligate and facultative seeding shrubs and also reduces community diversity, much of which is dependent on dormant seed banks; and (2) greater fire intensities from potentially higher fuel loads in ancient stands of chaparral (Paysen and Cohen 1990; Conard and Regelbrugge 1994; Riggan *et al*. 1994) contribute to lower seedling establishment, lower resprouting success and lower diversity.

The very large 2002 McNally Fire in the southern Sierra Nevada burned 15 000 ha of chaparral, half of which had never had a recorded fire (Fig. 2), and, thus, provided an opportunity to test these hypotheses. Those stands without a recorded fire were at least 90 years of age, and likely much older, and are referred to here as ancient stands. Within the perimeter of the McNally Fire, there were areas that had burned within the past 50–60 years, which is likely within the historical fire rotation interval for chaparral (Keeley in press), and these are referred to here as mature stands.

Methods

Study area

The McNally Fire burned 25 100 ha during July 2002 in the lower Kern River watershed of the Sequoia National Forest. Slightly more than 60% was chaparral between 1000 and 1700 m elevation and half this landscape had not burned since record keeping began in 1910 (Fig. 2). These ancient stands are presumed to have been at least 90 years of age at the time of the McNally Fire. Stand age maps based on fire records (Fig. 2) were used to select ancient sites and, for comparison, mature sites that had burned in the past 50–60 years. There is the potential for error in using these fire records because they map fires over approximately 40 ha in size. This is not likely to be a problem in chaparral because these crown fire shrublands generally burn in large fires. Sites that were selected within areas mapped as unburned before the McNally Fire all had large shrub skeletons consistent with them being rather ancient. Determining precise ages for all ancient stands was not possible because only obligate seeding species with skeletons that survived the fire could be used (Keeley 1993). On selected ancient sites with standing skeletons of the obligate seeding *Arctostaphylos visicida*, stem sections were cut and age determined. In many cases, much of the stem was rotted; however, stem sections at two sites with the smallest rotted centres were counted. One site recorded 127 rings and we estimated the final age was between 140 and 150 years. Another site recorded 107 rings and the estimated age was 130–150 years. It is likely this represents the age for all ancient sites because chaparral fires often cover large areas.

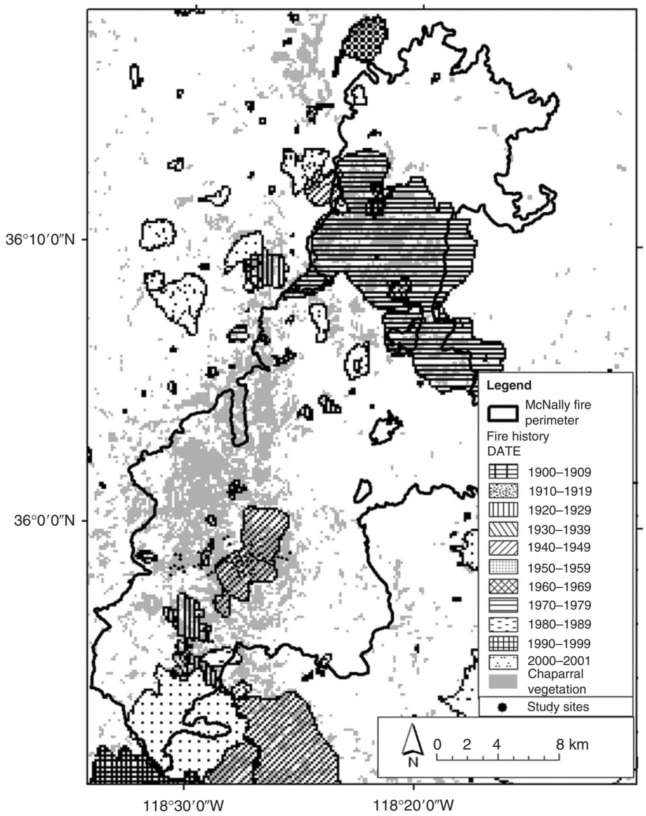

Fig. 2. McNally Fire perimeter and prior fire history for the study area and distribution of chaparral study sites according to fire history before the McNally Fire (from A. H. Pfaff and J. E. Keeley, unpublished data based on the California Statewide Fire History database maintained by the California Department of Forestry and Fire Protection).

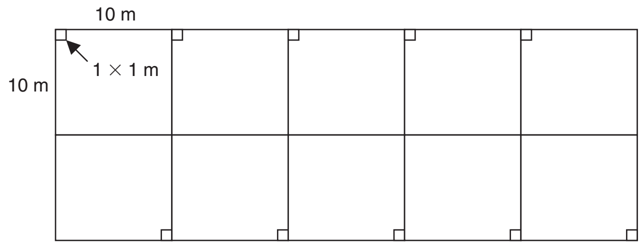

Fig. 3. Sample plot design with nested subplots (see Keeley and Fotheringham 2005 for comparison with other sample designs).

Sixty-seven sites were selected, approximately half in areas with no prior recorded fire and half with a fire in the past 50–60 years. Site selection was based on accessibility and a goal of sampling all slope aspects more or less equally for both ancient and mature stands.

The burned area in the lower Kern River watershed is on dry interior slopes that are more arid than the west-facing foothills of the Sierra Nevada. The nearest climate station is the Kern River #3 at an elevation of 825 m, which records a 54-year average precipitation of 938 mm and average temperatures of 7.7°C in January and 26.4°C in August (NOAA 2004). The McNally Fire covered an area of some geological complexity with both metasedimentary (including limestone and marble) and granite substrates. We restricted our sampling to just the granitic soils so as to avoid the confounding effects of including soils of markedly differing productivities and floras (see Safford and Harrison 2004).

Because it is impossible in a field study to keep all variables constant except the variable of interest, in this case stand age, it is important to have some confidence that other site factors are not determining the outcome of our comparison between ancient stands and mature stands. Ideally, one would select sites randomly across the landscape of interest; however, because fire perimeters of different age are rather coarse scale and spatially constrained (Fig. 2), that was not possible. Our approach was to select ancient and mature stands that were in close proximity and broadly similar with respect to the range of elevations, slope aspects and slope inclines represented. These were compared with a two-tailed *t*-test. Sites were placed in stands of seemingly homogeneous prefire vegetation, defined as having burned skeletons of similar stature, species composition and dispersion throughout the plot.

Sampling

Vegetation was sampled in 20 × 50 m (0.10 ha) sites with nested subplots, similar to the widely cited ‘Whittaker plot’ method (Shmida 1984). However, the highly clumped distribution of subplots in the Whittaker design is only appropriate for sites where the vegetation is homogeneous at the tenth ha scale and this does not hold for chaparral (Keeley 2004). In the present study, we used a design with greater dispersion of nested subplots, where the tenth ha plot was subdivided into 10 non-overlapping 100-m^2 square plots, each containing one 1-m^2 subplot in opposite corners (Fig. 3). Observations in chaparral suggest that an important determinant of community scale species turnover is related to differences in drainage patterns. Because water drains parallel to the slope incline, we expected the greatest variation in community composition to be perpendicular to the incline and so we positioned our tenth ha plots with the long axis along the elevational contour (Keeley and Fotheringham 2005).

Within each 1-m^2 subplot, cover was visually estimated for each species and density was determined precisely for all perennial species and for annuals with densities less than approximately 25, but higher densities of annuals were estimated. Within the 100-m^2 subplots, a list was made of additional species not recorded from the 1-m^2 quadrats. In addition, within each 100-m^2 subplot, we recorded for each shrub skeleton the species, height and whether or not it resprouted. A few species, such as *Eriodictyon crassifolium*, produced both seedlings and root suckers that could be confused. Sufficient excavations (outside the plots) and examination of morphological characteristics were performed to be certain we correctly differentiated seedlings from these resprouts. Plant nomenclature follows Hickman (1993).

Shrub skeletons in the first postfire year were used to estimate prefire populations. In these communities, skeletons can be identified to species based on the branching pattern and bark characteristics (Keeley *et al*. 2005). These skeleton populations are inferred to represent the prefire shrub population density; however, we lack a measure of the amount of error associated with this method. On most sites, large skeletons at densities and spacings similar to those in unburned stands were observed and, so, we assumed that they represented the prefire population of living shrubs. It seems likely that this represents largely living shrubs before the fire, because dead shrubs would be more likely to be completely consumed by fire and not leave a recognisable skeleton. On some sites, skeletons were burned to ground level, but there still persisted characteristics of root–crown shape that allowed us, in most cases, to assign a species name.

For each site, elevation, slope aspect and inclination were recorded. Potential annual direct incident solar radiation was calculated for each slope using latitude, aspect and incline, as described by McCune and Keon (2002). This parameter has a range of 0.03–1.11 MJ cm^{-2} $year^{-1}$.

Analysis

All tests between ancient and mature sites were performed with the pooled *t*-test on site averages obtained from the 10 nested subplots. Data were initially plotted to verify that they approximated a normal distribution and hypotheses of greater or lesser values for ancient *v.* mature sites were tested with the one-tailed *t*-test.

We first evaluated successional changes that had occurred between the mature and ancient stands before the McNally Fire. Shrub skeletons were used to reconstruct the prefire shrub communities. We hypothesised that the density of postfire obligate and facultative seeders would be lower in ancient stands compared with mature stands owing to shorter life spans often attributed to these species, greater thinning owing to weak shade tolerance and their lack of seedling recruitment during the fire-free interval (Keeley 2000). We hypothesised that postfire obligate resprouting species would have much less of a decline in density owing to longer life spans, less thinning as a result of greater shade tolerance and seedling recruitment during the fire-free interval.

To test whether fire-dependent ecosystems lose resilience to fire when subjected to very long fire-free intervals, we examined a variety of postfire vegetative response variables. Postfire cover, density, species diversity and seedling recruitment by obligate and facultative seeding shrubs were all hypothesised to be less in the ancient stands than in the mature stands.

To help interpret patterns of postfire recovery, we also examined how regeneration varied in response to site variables, such as fire intensity. Owing to the accumulation of dead fuels, fire intensity is considered to be one of the main site variables that is likely to change with stand age. Our surrogate measure of fire intensity was the height of shrub skeletons (e.g. Keeley *et al*. 2005), because higher fire intensity is likely to consume more biomass, and this metric is best referred to as our fire severity measure. The species found at the most number of sites (*Cercocarpus betuloides*) was selected and its average height recorded for each site was standardised to the maximum skeleton height recorded across all sites. Because we are assuming skeleton height is inversely related to fire severity, this value was subtracted from 1 to represent the relative fire severity for each site. Differences in stand age are unlikely to have any effect on height because these species reach their mature height in the first few decades after fire. However, slope aspect and other site conditions could affect shrub height and our only means of controlling for this source of error was to include a roughly comparable number of each slope aspect in both ancient and mature sites.

Fire severity, as well as other site variables, such as incident solar radiation, which combines attributes of both aspect and inclination, are hypothesised to affect postfire recovery. We tested this by combining data from all sites and testing whether there was a significant correlation between these variables and different response variables, such as cover and density, using least-squares regression.

Results

Prefire comparison of ancient and mature stands

In order to attribute age effects to our results, it is important that we have some confidence the sites being studied are broadly similar, except with respect to stand age, before the McNally Fire. Ancient sites comprised a similar range of the elevations and slope aspects as the mature sites (Table 1).

Table 1. Comparison of site conditions for ancient and mature stands of chaparral before the McNally Fire

P-values for two tailed *t*-tests of the null hypothesis that ancient sites = mature sites (–, no test)

Variable	Ancient	Mature	*P*
Sample size (0.1-ha plots)	33	34	–
Elevation (m)			
Mean	1447	1413	0.274
Range	1134–1756	1292–1609	–
Slope aspect			
North	6	6	–
South	10	11	–
East	9	7	–
West	8	10	–
Mean incline (°)	21.4	21.6	0.866
Incident radiation (MJ cm^{-2} $year^{-1}$)			
Mean	0.878	0.891	0.705
Range	0.600–1.064	0.583–1.065	–

There was no significant difference in average elevation, slope incline or calculated incident radiation.

Estimated prefire shrub composition was broadly similar between ancient and mature sites (Table 2). Total prefire density was significantly lower on the ancient sites and this was largely due to the much lower density of the obligate seeding *Ceanothus cuneatus* (buckbrush) in mature sites, consistent with our hypothesized changes in ancient chaparral. However, none of the other obligate or facultative seeding species were significantly less abundant on ancient sites.

Prior to the McNally Fire, the resprouting shrubs *C. betuloides* (mountain mahogany), *Fremontodendron californicum* (fremontii) and *Garrya flavescens* (silk tassel bush) were more abundant on the ancient sites (Table 2). The prefire density of most other species was not significantly different between ancient and mature sites. *Pinus sabiniana* (foothill pine), a common pine throughout the chaparral zone in this area, was sporadically present on these sites, as was the shrub *Rhamnus ilicifolia* (redberry). Another pine, *Pinus monophylla* (singleleaf pinyon), and two oaks, *Quercus chrysolepis* (canyon live oak) and *Q. kelloggii* (California black oak), were present on a few sites. Although not related to our hypotheses about change, it is of particular interest that *Adenostoma fasciculatum* (chamise), a nearly ubiquitous chaparral shrub throughout the state, was absent from all sites. Our study site falls in a gap in chamise distribution that stretches along the interior drainages of the southernmost Sierra Nevada and Tehachapi Mountains (Keeley and Davis in press).

The largest shrub skeletons were those of *Arctostaphylos viscida* (manzanita), which, on the ancient sites, had trunks with basal diameters from 30 to 50 cm. This suggests that this obligate seeding shrub is rather long lived. The smallest and least woody shrub was *E. crassifolium* (yerba santa), which was the only one that sprouted from rhizomes rather than the base, as in the other resprouting shrubs.

Postfire community comparison

Surprisingly, total vegetative cover after fire was significantly greater in ancient stands than in younger stands (Fig. 4*a*) and this was largely due to greater herbaceous cover (Fig. 4*b*) because woody cover was not significantly different (Fig. 4*c*). Although total herb cover was greater, there was no significant difference for herbaceous perennials or annuals alone (Table 3). In contrast with patterns of cover, the postfire density of woody plants other than suffrutescents was greater in mature stands (Table 4) and there was no difference in the density of either herbaceous perennials or annuals. Total density for native species was significantly less on ancient sites, but non-native density, although somewhat higher, was not significantly greater on ancient sites. Cover (data not shown) exhibited the opposite pattern, with no significant difference for natives ($P > 0.05$), but non-native cover was significantly different ($P < 0.01$): 14% (s.e. = 2) and 6% (s.e. = 1) for ancient and mature sites, respectively.

Species diversity was not significantly different between ancient and mature sites at the scale of 1 m^2 (Fig. 4*d*), but, at larger scales, the ancient sites were significantly more diverse than the younger mature sites (Fig. 4*e*,*f*). These patterns were basically the same for native and non-native species, except at the lowest scale (Table 5). In ancient stands, there was, on an average, one non-native species in every 1-m^2 subplot,

Table 2. Comparison of estimated prefire shrub density in ancient and mature stands of chaparral before the McNally Fire

P-values for one-tailed *t*-tests of the null hypothesis that: (1) total density, obligate seeder and facultative seeder density in ancient sites is greater than that in mature sites; or (2) obligate resprouter density in ancient sites is less than in mature sites ($n = 33$ ancient and 34 mature sites for each species). os, obligate seeder; fs, facultative seeder; or, obligate resprouter

	Regeneration mode	Prefire shrub density (no. ha^{-1})		
		Ancient	Mature	*P*
Total[A]		1160	1666	0.002
Arctostaphylos viscida	os	19	12	0.536
Ceanothus cuneatus	os	185	1008	0.000
Cercocarpus betuloides	or	487	209	0.000
Eriodictyon crassifolium	fs	44	84	0.378
Fremontodendron californicum	fs	164	102	0.037
Garrya flavescens	fs	57	11	0.038
Pinus sabiniana	os	6	12	0.233
Quercus berberidifolia	or	58	21	0.488
Q. garryana var. *breweri*	or	89	111	0.761
Q. wizlizenii var. *frutescens*	or	38	76	0.191
Rhamnus ilicifolia	or	10	8	0.651

[A]Total density includes a few other species not listed here.

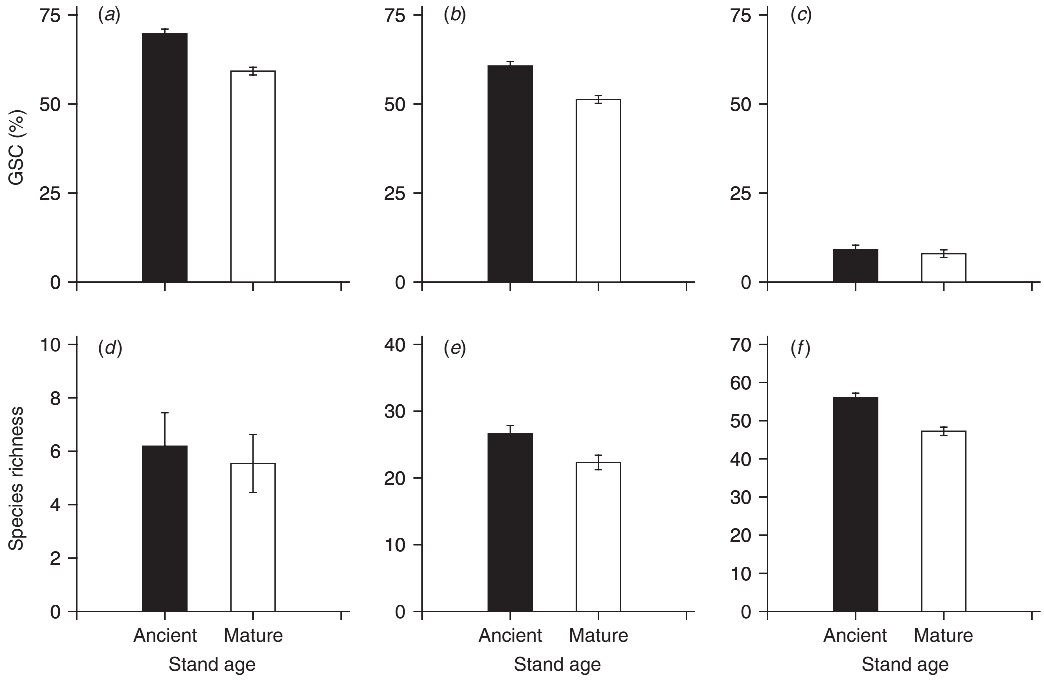

Fig. 4. Plant cover (*a–c*) and species richness (*d–f*) on ancient and mature sites in the McNally burned area. For one-tailed *t*-tests of the null hypothesis that values for ancient sites are greater than those for mature sites: (*a*) $P < 0.001$ for total cover, (*b*) $P > 0.05$ for herbaceous cover, (*c*) $P < 0.01$ for woody cover, (*d*) $P > 0.05$ at 1 m^2, (*e*) $P < 0.001$ at 100 m^2 and (*f*) $P < 0.01$ at 1000 m^2 ($n = 33$ ancient and 34 mature sites). GSC, ground surface covered.

Table 3. Cover for different life forms in ancient and mature stands in the McNally burned area in the first postfire growing season

P-values for one-tailed *t*-tests of the null hypothesis that cover is greater in ancient sites than in mature sites ($n = 33$ ancient and 34 mature sites). Life forms most important in these shrublands (and the Raunkiaer equivalents) are: shrubs and occasional trees (phanerophytes), subshrubs (chamaephytes that exhibit little annual dieback), suffrutescents (diminutive chamaephytes that exhibit substantial annual dieback), herbaceous perennials (cyptophytes and hemicryptophytes) and annuals (therophytes)

	Cover (% ground surface covered)		
	Ancient	Mature	*P*
Shrub	0.5	1.1	0.164
Subshrub	7.3	5.3	0.248
Suffrutescent	1.0	1.2	0.709
Herbaceous perennial	8.3	4.8	0.090
Annual	52.4	46.8	0.139

Table 4. Density by life form and native status after fire in ancient and mature stands in the McNally burned area in the first postfire growing season

P-values for one-tailed *t*-tests of the null hypothesis that density is greater in ancient sites than mature sites ($n = 33$ ancient and 34 mature sites). See Table 3 for life form definitions

	Density (no. ha^{-1})		
	Ancient	Mature	*P*
Total	350 000	454 000	0.040
Shrub	32 000	81 000	0.000
Subshrub	5000	26 000	0.000
Suffrutescent	3000	3000	0.979
Herbaceous perennial	55 000	52 000	0.786
Annual	255 000	292 000	0.389
Native	278 000	410 000	0.001
Non-native	72 000	45 000	0.197

whereas in mature stands the average was one every other subplot.

There was a total of 238 species recorded for all sites. Collectively, ancient sites had 210 species, of which 71 were unique to the those sites. Mature sites had 167 species, of which 28 were unique. Those species unique to ancient or mature sites were relatively rare species and did not contribute greatly to cover. That is, the ancient and mature sites shared 139 species in common and these comprised the bulk of cover and density (97.5% and 98.2%, respectively).

Postfire demographic patterns

One important measure of ecosystem resilience is the ability to regenerate following fire. Prior to the fire, species likely differed in abundance from site to site, thus, it is expected that soil-stored seed pools differed and this could affect postfire seedling recruitment. One can factor out some of the variability in seedling abundance by using seedling/prefire parent plant ratios. However, because seedbanks can accumulate and persist long after the parent plant dies, this ratio could be distorted if a species dies out in older stands. With these caveats, we compared seedling/parent ratios (Table 6). Considering only species with seedling recruitment after fire, four patterns were evident: (1) *A. viscida* and *G. flavescens* showed no significant difference in the seedling/parent ratio (Table 6) or in absolute density (1151 *v.* 455 seedlings ha^{-1} for *A. viscida* ($P = 0.291$) and 197 *v.* 74 seedlings ha^{-1} for *G. flavescens* ($P = 0.168$)); (2) *C. cuneatus* had a substantially greater seedling/parent ratio in ancient stands (Table 6), but absolute seedling density was significantly less in ancient stands compared with mature stands (14 575 *v.* 68 545, respectively; $P < 0.001$); (3) *E. crassifolium* had a significantly lower ratio in ancient stands compared with mature stands and absolute density was lower as well (4712 *v.* 25 867, respectively; $P < 0.001$); and (4) *F. californicum* had a significantly greater ratio in ancient stands (Table 6) and its absolute density was also greater in ancient compared with mature stands (13 742 *v.* 4661, respectively; $P < 0.001$).

Half the shrub dominants were obligate resprouters that seldom ever recruit seedlings after fire and that was certainly the case in the present study (Table 6). These shrubs all exhibited very high resprouting success that did not differ greatly between ancient and mature stands. For two species, resprouting success was significantly less in ancient stands (Table 6), but the mature stands were only 4–10% higher.

One component of the flora likely to be most sensitive to ageing effects consists of annual species with deeply dormant seed banks that (at least in closed-canopy shrublands) restrict establishment to the immediate postfire environment and are commonly called postfire endemics. Based on prior information on postfire endemics (Keeley 2000; Keeley *et al.*, unpublished data), we selected eight species or closely related species that were known to be postfire endemics or specialists in other regions. These included: *Allophyllum divaricatum*, *A. glutinosum*, *Emmenanthe penduliflora*, *Malacothrix clevelandii*, *Mentzelia dispersa*, *M. pectinata*, *Nicotiana attenuata* and *Phacelia imbricata*. All eight species were found in both ancient and mature sites and, collectively, neither the density ($P = 0.528$) nor cover ($P = 0.645$) of these postfire

Table 5. Species richness for ancient and mature stands in the McNally burned area in the first postfire growing season

P-values for one-tailed *t*-tests of the null hypothesis that species richness is greater in ancient sites than mature sites ($n = 33$ ancient and 34 mature sites)

	Species richness		
	Ancient	Mature	*P*
Native species			
1 m^2	5.2	5.1	0.832
100 m^2	23.2	20.3	0.007
1000 m^2	50.7	42.8	0.002
Non-native species			
1 m^2	1.0	0.5	0.000
100 m^2	3.4	2.1	0.000
1000 m^2	5.3	4.4	0.033

Table 6. Seedling/parent ratios and resprouting success for woody shrubs in ancient and mature stands in the McNally burned area in the first postfire growing season

Calculated only for those sites with parent skeletons. *P*-values for one-tailed *t*-tests of the null hypothesis that: (1) obligate seeder ratios for ancient sites are greater than for mature sites; or (2) obligate resprouter and facultative seeder ratios for ancient sites are less than for mature sites. NA, not applicable

Species	Seedling/parent ratio (ancient)		Seedling/parent ratio (mature)		*P*	Resprouting succes (%)		
	n	Ratio	*n*	Ratio		Ancient	Mature	*P*
Arctostaphylos viscida	6	19.3	12	23.0	0.835	NA	NA	
Ceanothus cuneatus	29	267.6	31	76.3	0.012	NA	NA	
Cercocarpus betuloides	32	0.1	31	0.2	0.769	91.1	95.1	0.050
Eriodictyon crassifolium	8	104.4	18	1702.8	0.017	66.6	69.0	0.885
Fremontodendron californicum	32	130.5	29	50.8	0.040	85.6	96.4	0.026
Garrya flavescens	19	10.9	10	2.5	0.315	93.0	100.0	0.901
Quercus berberidifolia	6	0.0	7	0.5	0.356	81.7	97.1	0.393
Q. garrayana	11	<0.1	8	<0.1	0.940	94.2	99.0	0.326
Q. wislizenii	12	<0.1	17	0.0	0.339	87.5	97.6	0.287
Rhamnus crocea	10	0.0	9	0.0	0.942	100.0	88.9	0.287

Table 7. Regression analysis of fire severity effects on postfire recovery across both ancient and mature sites

Fire severity is based on the height of *Cercocarpus betuloides* skeletons and is presumed to be a surrogate measure of fire intensity; this species was selected because it occurred at the greatest number of sites

Parameter	*R*	*P*	*n*
Total density	0.163	0.201	63
Cover			
Total	−0.346	0.005	63
Shrub	−0.379	0.002	63
Herbaceous perennial	−0.381	0.002	63
Annual	0.030	0.817	63
Arctostaphylos viscida seedling density	−0.122	0.607	11
Ceanothus cuneatus seedling density	0.330	0.009	61
Cercocarpus betuloides resprouting success	−0.102	0.425	63
Eriodictyon crassifolium seedling density	0.519	0.000	50
Eriodictyon crassifolium resprouting success	0.189	0.367	25
Fremontodendron californicum seedling density	−0.184	0.178	57
Fremontodendron californicum resprouting success	0.022	0.871	58
Garrya flavescens seedling density	−0.395	0.258	10
Garrya flavescens resprouting success	0.304	0.109	29

ephemerals were significantly different between ancient and mature stands.

Fire severity effects

Fire severity was measured by the height of shrub skeletons. In mature stands, this is a likely measure of fire severity because shrubs generally reach their mature height after several decades. Postfire skeleton height is largely influenced by biomass loss from the fire. Owing to inherent differences in height and fuel consumption between species, we restricted our surrogate measure of fire intensity to a single species. *Cercocarpus betuloides* was the obvious choice because it was found at the greatest number of sites: 32 ancient sites and 31 mature sites. Our fire severity index ranged from 0 to 0.880. Using regression analysis on all sites combined, we found several significant relationships between fire severity and postfire recovery parameters (Table 7). We had expected the fire severity index to increase following fires in older stands; however, ancient stands had a significantly lower score than mature sites ($P < 0.05$), namely 0.394 and 0.490, respectively.

Fire severity tended to be greater on the sunnier, more-exposed slopes, as indicated by the significant relationship between incident radiation and fire severity (Fig. 5). Fire severity was positively related to the density of the prefire shrub population ($r^2 = 0.168$; $P < 0.001$). However, species differed in their effect on fire severity. For example, the obligate resprouting *Quercus garryana* showed a slightly negative relationship between prefire population density and fire severity (Fig. 6*a*). Conversely, the obligate seeding *C. cuneatus* showed a highly significant positive relationship with fire severity (Fig. 6*b*). Seedling recruitment by both this species and *E. crassifolium* was also positively correlated with fire severity ($r^2 = 0.120$ and 0.276, with $P < 0.01$ and < 0.001, respectively).

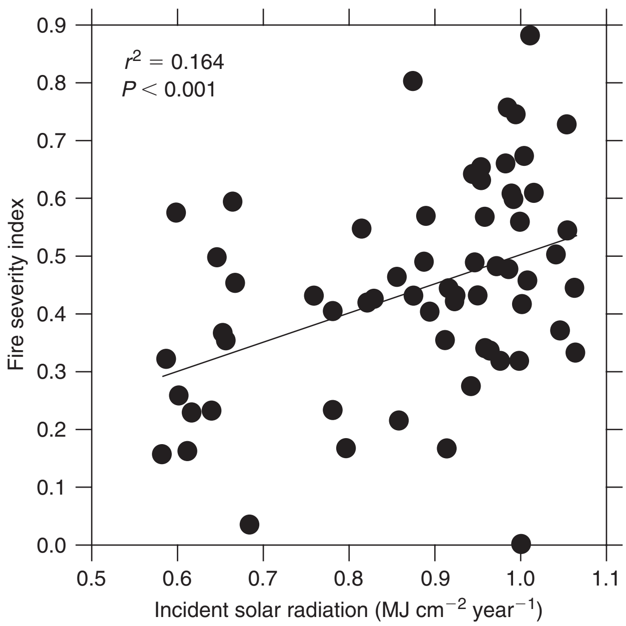

Fig. 5. Relationship between incident solar radiation and fire severity for all sites combined.

Other factors affecting postfire recovery

On these dry interior slopes, there is good reason to expect that incident solar radiation has a marked effect on the postfire response, such that patterns on steep shady north-facing slopes are likely to differ greatly from those on shallow-soiled, sunny south-facing slopes. Radiation exhibited little correlation with overall community patterns, including

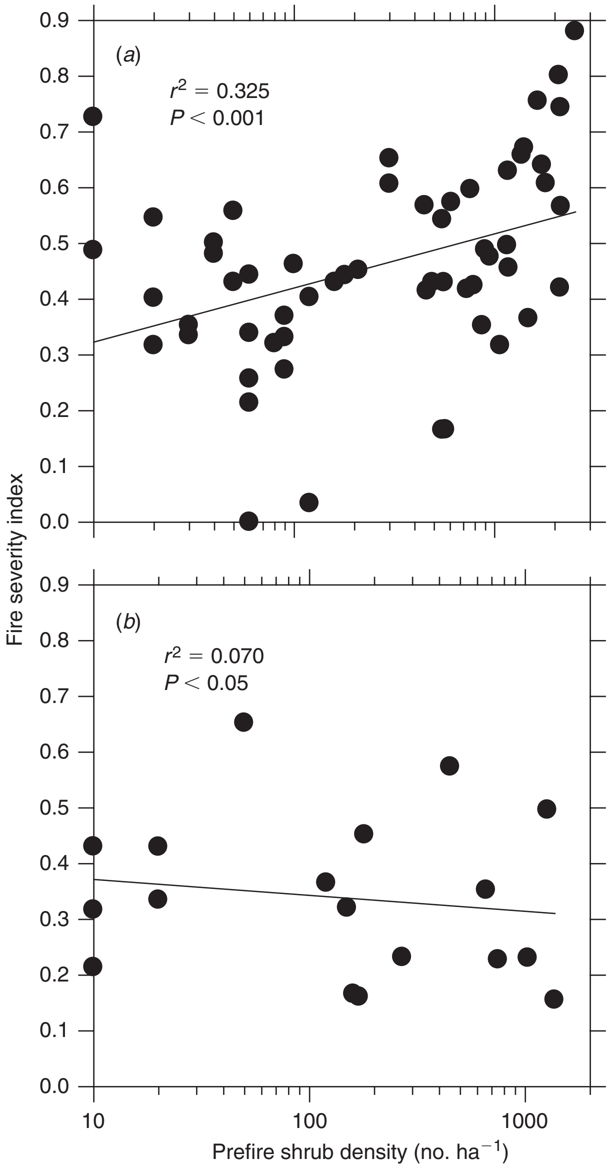

Fig. 6. Relationship between prefire shrub density and fire severity for (*a*) the obligate seeding *Ceanothus cuneatus* and (*b*) the obligate resprouting *Quercus garryana*.

density, cover and species richness; however, individual life forms sorted out differently according to radiation load. Shrub cover, which was largely due to resprouts, declined sharply with increasing radiation (Fig. 7*a*). Herbaceous perennial cover, which was almost entirely due to resprouts from bulbs and rhizomes, also declined with increasing radiation (Fig. 7*b*). In contrast, annuals increased significantly with incident radiation (Fig. 7*c*).

Considering the prefire populations of the dominants, most showed no significant relationship with incident radiation. However, *C. betuloides*, *G. flavescens*, *Q. garryana* and *P. sabiniana* populations were all negatively related to

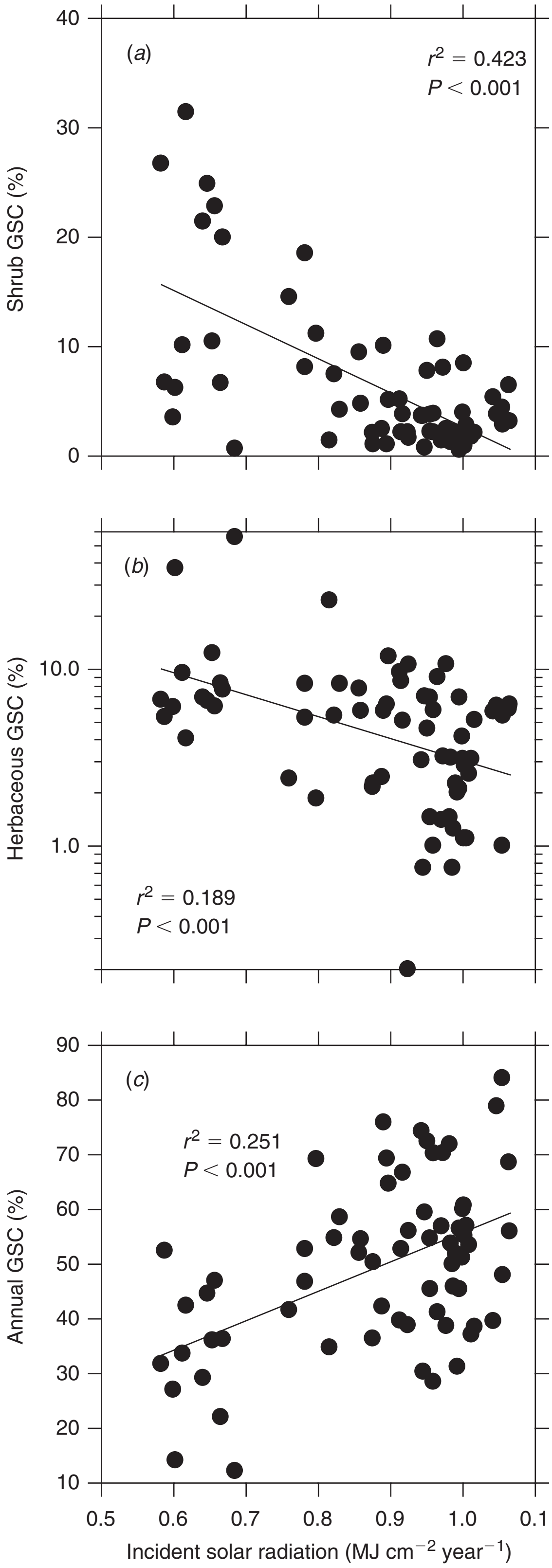

Fig. 7. Relationship between postfire recovery and calculated incident solar radiation for (*a*) shrub cover, (*b*) herbaceous perennial cover and (*c*) annual cover for all sites combined. GSC, ground surface covered.

incident radiation ($r^2 = 0.122$, 0.236, 0.375 and 0.110, with $P < 0.01$, < 0.001, < 0.001, and < 0.01, respectively).

Discussion

Natural crown fire regimes include diverse ecosystems from California shrublands to Rocky Mountain petran chaparral, lodgepole and subalpine forests, and pose special problems for fire and resource managers (Johnson *et al*. 2001; Keeley 2002). California chaparral is of particular concern because it is the most extensive vegetation type in California, covering one-twentieth of the state (Jones and Stokes 1987). Much of what is known about fire history of chaparral is for southern and central coastal California (Minnich 1983; Keeley *et al.* 1999; Moritz *et al*. 2004). Relatively little of this landscape has escaped burning during the 20th century and much of it is considered to be at the lower end of the range of historical variability (Keeley and Fotheringham 2003*a*; Keeley in press). This is in striking contrast to the patterns in the southern Sierra Nevada chaparral belt, where 45% of the landscape has never had a recorded fire (Fig. 1). These ancient stands are at least 90 years of age and some are substantially older.

We hypothesised that this was outside the historical range of variability for this type, but we have no way of directly testing this hypothesis. Crown fire ecosystems by their very nature lack a clear mechanism for recording historical fire regimes, as is the case with fire-scarred trees in surface fire regimes. As a consequence, chaparral ecologists have been forced to make inferences based on other data. For example, life history characteristics have been used to infer that the lower threshold for tolerable fire return intervals is in the range of two to three decades (Keeley 1986; Zedler 1995). Putting an upper bound on historical fire regimes in this type is more difficult, but studies such as the present one may provide an answer.

The potential ecosystem impacts of long fire-free periods in chaparral are described by Zedler (1995). He referred to this threat as 'senescence risk' and it arises from the fact that postfire regeneration is largely from soil-stored seed banks and vegetative structures. Germination of this seedbank is fire dependent and, in the long absence of fire, there is a natural attrition of seeds. Theoretically, soil-stored seed pools should deteriorate to the point where postfire recovery is jeopardised. One study in the southern Sierra Nevada hypothesised this may be a factor in postfire regeneration following fire in a 125-year-old stand of chaparral (Keeley *et al*. 2003).

In the present study, we hypothesised that if older chaparral stands were unburned for as much as 150 years, which is likely outside their historical range of variability, then postfire recovery would be jeopardised. We found relatively little support for this hypothesis. The primary changes we observed were an apparent reduction in prefire populations of the obligate seeding *C. cuneatus* (Table 2) and a reduction in the absolute density of postfire seedling recruitment by this species (Table 6). Nonetheless, the densities of seedlings in these ancient stands were potentially at replacement level; ancient stands averaged over 14 000 seedlings ha^{-1}, which was an order of magnitude larger than the average prefire *C. cuneatus* population in the mature stands.

Total diversity and the abundance of postfire endemic annuals are two other response variables that suggest that these ancient stands of chaparral are within the historical range of variability. The one parameter of some concern is that non-native species richness and abundance increased in the ancient stands. We hypothesise that with the decline in total density, these stands become more open and receptive to colonisers. In a historical landscape where non-native species were not present, this posed little problem for long-term sustainability of chaparral. However, in the current landscape, non-native species are readily able to exploit changes in the structure of very old chaparral. Presumably they invaded these sites before the recent McNally Fire and there was good seed bank survivorship during this fire, perhaps assisted by the reduced fire severity in these older stands, resulting from substantial thinning of *C. cuneatus*.

In conclusion, we found that chaparral is resilient to long fire-free periods. It is not known with certainty whether the long fire-free period currently experienced by foothill chaparral in the southern Sierra Nevada is outside the historical range of variability. We can say that this long fire-free period has had little impact on the ability of these shrublands to recover following fire. In this respect, they are similar to other crown fire ecosystems (e.g. Schoennagel *et al*. 2004).

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