Fire as a Threat to Biodiversity in Fire-Type Shrublands[1]

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Abstract

Chaparral and coastal sage scrub communities have a disproportionately high number of rare and endangered plants and thus are of particular conservation concern. Unnaturally high fire frequency has been a leading cause of degradation of chaparral and coastal sage scrub ecosystems. Although these shrublands are fire-adapted, below a certain threshold of fire frequency, resilience is inversely related to the fire return interval: this threshold is 3-5 years in coastal sage scrub and 10-20 years in chaparral, with the higher values more typical of interior sites. High fire frequency depletes the native flora and increases the proportion of non-native herbaceous species. Resilience to different fire regimes varies across growth forms, and thus it is of particular significance that the growth form distribution of rare species is significantly different from the proportions of growth forms in these communities.

Key words: chaparral, endangered species, high fire frequency, resilience, sage scrub

Introduction

The California landscape has been altered in many ways, with the potential for profound impacts on biodiversity and ecosystem functioning (Keeley and Swift 1995). Other than direct development, one of the more important changes in shrubland ecosystems has been the anthropogenic alteration of the natural fire regime. Despite a long-standing policy of fire suppression, the primary impact has been a dramatic acceleration of fire occurrence (Keeley and Fotheringham 2002, Keeley and others 1999, Moritz 1997). Although species in these shrublands are "fire adapted," they are not adapted to all fire regimes, and one can distinguish species differences and broad growth form differences in resilience to increased fire occurrence. This is of particular concern because both chaparral and coastal sage scrub communities have a disproportionately high number of rare and endangered plants.

Shrubland Biodiversity

The California Native Plant Society (CNPS) list of rare and endangered plant species (Skinner and Pavlick 1994) places chaparral first in number of taxa that are of concern (*table 1*). Although coastal sage scrub ranks fifth, both shrub communities have a much higher number of rare taxa than expected based on their area occupied. If all the rare and endangered taxa in the top five habitats were distributed randomly,

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Table 1—*Top-ranking habitats of California's rare plants according to all CNPS lists (data from Skinner and Pavlik 1994). These observed values are contrasted with the values expected based upon the amount of land area occupied by each habitat (data from Jones and Stokes 1987).*

Rank	Habitat	Taxa	
		Observed	Expected
1	Chaparral	516	432
2	Lower coniferous forests	359	294
3	Cismontane woodland	311	362
4	Valley/foothill grassland	247	431
5	Coastal scrub	211	132
		($p < 0.001$; $\Pi^2 = 164.2 >>> \Pi^2_{0.999[3]} = 16.3$)	

one would expect chaparral to top the list based just on areal extent of this vegetation, but chaparral contains 18 percent more species than expected. Coastal sage scrub contains nearly 40 percent more taxa than predicted by its areal extent.

In both chaparral and coastal sage scrub, herbaceous perennials, typically geophytes, top the list of growth forms that are rare or endangered (Skinner and Pavlick 1994). If we contrast these numbers just for southern California chaparral and coastal sage vegetation with those expected, based on extensive surveys of postfire peak of diversity (Keeley 1998a), we see that rarity is not randomly distributed across growth forms (*table 2*). Annuals are very under-represented. If rarity were randomly distributed with respect to growth form we would expect three times as many annuals as observed in the lists. On the other hand, there are three times as many herbaceous perennials as expected and double the number of shrub species.

Resilience to different fire regimes varies across growth forms (Keeley 2000), and thus it is of interest to consider rarity in terms of fire specialization. Fire is a frequent ecological factor and has played an obvious evolutionary role in these communities. Most non-woody plant species reach their greatest population sizes, and thus greatest potential for spread, in the postfire environment. However, not all species or even all growth forms are equally specialized towards fire. Annuals comprise a rich diversity of species that range from extreme specialization—strictly fire-stimulated germination (Keeley and Fotheringham 1998)—to generalized opportunistic species that occupy many types of disturbance. Cursory examination of the rare annuals listed in Skinner and Pavlick (1994) indicates they are not highly restricted to burned sites. Herbaceous perennials, particularly geophytes, in these shrublands lack obvious specialization to fire, and their life cycle is not substantively different from that of geophytes in other less fire-prone habitats (Rundel 1996). At the time of fire most geophytes are dormant and nearly all have transient seed banks that do not require specialized fire cues (Keeley1991). Thus, most rare herbaceous species do not appear to be highly specialized for postfire recruitment.

This pattern is not evident in the rare shrubs, where a large proportion are species of *Ceanothus* and *Arctostaphylos* that have seedling recruitment strictly tied to postfire conditions (Keeley 1998b). Thus, it is to be expected that the direct effects of alterations in fire regime would affect some components of the rare plant flora more than others.

Table 2—*Growth form distribution of CNPS rare and endangered taxa in southern California chaparral and coastal sage scrub (data from Skinner and Pavlik 1994). Expected values based on distribution of growth forms following fire in 90 0.1 ha sites in southern California (Keeley 1998a)*

	Annual	Herbaceous perennial	Suffrutescent	Subshrub/ shrub/tree
Observed	43	79	17	63
Expected	131	27	16	28

($p < 0.001$; $\Pi^2 = 202.5 >>> \Pi^2_{0.999[2]} = 13.8$)

This is well illustrated by the extreme event of back-to-back wildfires studied by Zedler and others (1983). At four *Adenostoma fasciculatum* dominated sites, postfire frequency of this shrub increased following a fire in mature vegetation but decreased dramatically following the second fire. The impact was most profound on the non-resprouting shrub *Ceanothus oliganthus*, which was present from seed in three-fourths of the plots after the first fire but nearly absent after the second fire. In contrast, these repeat fires had little impact on the herbaceous perennials *Calochortus weedii* and *Dichelostemma pulchella.*

Fire suppression has been frequently cited as a major threat to fire type rare species, for example, the rare locoweed *Astragalus brauntonii* that is restricted to sites around the Los Angeles Basin (Skinner and Pavlick 1994). This idea is a logical extension of the well-documented threat of fire suppression in many western coniferous forests (SNEP 1996). However, fire records show that in southern California fire suppression has not effectively excluded fire (Conard and Weise 1998, Keeley and others 1999). Indeed, urban mountain ranges such as the Santa Monica Mountains in Los Angeles and Ventura Counties have a fire rotation interval of less than 15 years, and this is likely many times shorter than the natural regime (Keeley 2002a). Lack of fire is not likely a threat to the persistence of these shrublands or rare species within them. A far greater threat in many areas, particularly the Los Angeles Basin, is habitat degradation due to increased fire frequency.

Fire-Induced Habitat Degradation

Unnaturally high wildfire frequency has long been a leading cause of degradation of chaparral and coastal sage scrub ecosystems, second only to land development. While these shrublands are fire-adapted, below a certain threshold of fire frequency resilience is inversely related to the fire return interval. This threshold is probably about 3 years in coastal sage scrub (but longer for interior sage scrub sites) and 10-20 years in chaparral (Keeley 2000). Generally speaking, as fire frequency increases, herbaceous vegetation is favored over woody growth forms (Sauer 1975, Wells 1962). Numerous studies have shown that unnaturally high fire frequency depletes the native flora and increases the proportion of non-native herbaceous species (Haidinger and Keeley 1993, Zedler and others 1983). In California it is quite likely that, except on fine-textured argillaceous soils, grasslands are degraded shrubland sites (Cooper 1922, Keeley 1990, 1993; Wells 1962), and even grasslands on certain argillaceous soils may have been dominated by the shallow rooted summer-deciduous coastal sage scrub (Kirkpatrick and Hutchinson 1980, Wells 1962).

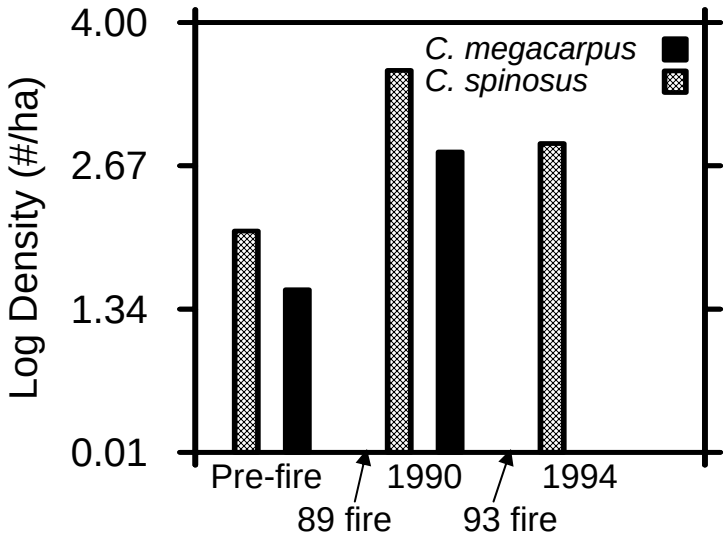

Figure 1—Effect of repeat fires on the populations of an obligate-seeding shrub, *Ceanothus megacarpus*, and a facultatively-seeding shrub*, C. spinosus*, in the Santa Monica Mountains. The first fire occurred in mature chaparral in 1989, the second in 1993 (from Keeley 2000).

The impact of frequent fires on the native shrub populations is well illustrated by the back-to-back wildfires that Zedler and others (1983) discussed, above. This extreme event resulted in the near extirpation of one obligate-seeding shrub population, and this can occur with even longer intervals between fires. *Figure 1* shows the extirpation of a non-sprouting shrub with fires four years apart, whereas a resprouting congener survived this high fire frequency, albeit at a lower density.

As native shrub cover is reduced due to high fire frequency, there is typically a type conversion to an herbaceous community dominated by non-native species. This is illustrated in the study by Haidinger and Keeley (1993) showing vegetation changes on adjacent sites experiencing different fire regimes. For example, two fires in six years reduced shrub populations of *Adenostoma fasciculatum* and *Salvia mellifera* but favored the suffrutescent *Lotus scoparius* (*fig. 2*). Three fires in six years were detrimental to most natives but conducive to the spread of non-native invasives such as *Brassica nigra* and species of *Bromus*. The results of this chronosequence study are corroborated by similar observations on a single site over time (*fig. 3*). In this study a mature coastal sage scrub site burned in 1993, and over the following three growing seasons the exotic cover declined as the native shrubs recovered. Following a second fire in 1996 the exotics exploded; within two years they dominated the site.

Such type conversions of shrublands to grasslands are not always the result of wildfires but have long been a goal of prescription burning programs (CDF 1978, Sampson 1944). Sometimes these are done for “range improvement,” to increase deer and livestock range, but other times for reducing fire hazard. These herbaceous (grassland) associations generate far less intense fires than shrub associations, and these grassland fires are more safely suppressed than chaparral fires (Keeley 2002a).

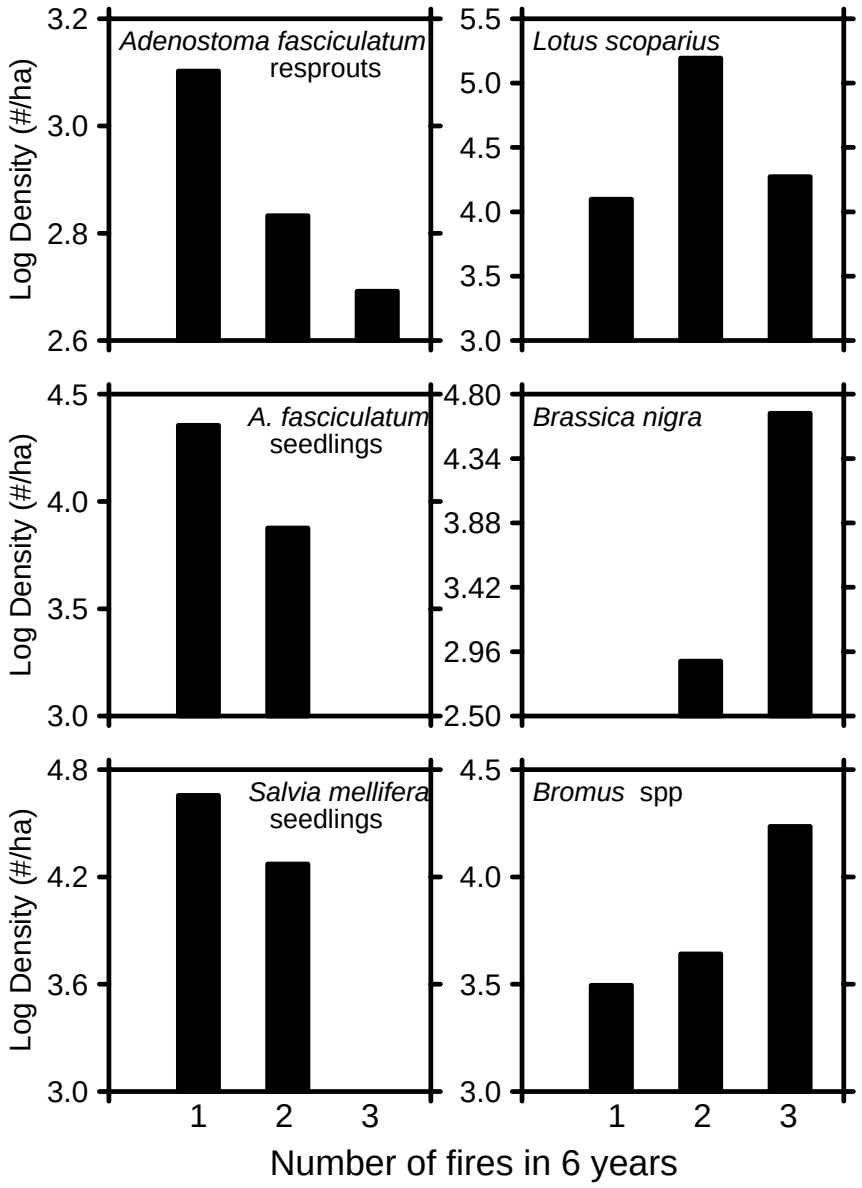

Figure 2—First growing season shrub and herb density in adjacent stands of mixed chaparral and coastal sage scrub burned once, twice, and three times in 6 years (redrawn from Haidinger and Keeley 1993).

Type conversion not only alters fire intensity, but also it often leads to increased fire frequency (Keeley 2002a). This results from several factors. These herbaceous species dry rapidly during the late spring and thus greatly expand the seasonal window of opportunity for fire. In addition, they constitute fine fuels that ignite readily and spread fire both horizontally through the stand and vertically into the shrubs with little wind. As the extent of herbaceous cover increases, it sets the stage for repeat fires in a self feed-back process where more fires thin the shrub overstory and increase the presence of a persistent herbaceous layer. Over time, repeating this process will type-convert shrublands to annual grasslands dominated by non-native species, which in turn alters the fire regime by increasing further expansion of

the seasonal window for fire because non-native species dry earlier in the spring than most native herbaceous species (Keeley and Fotheringham 2003).

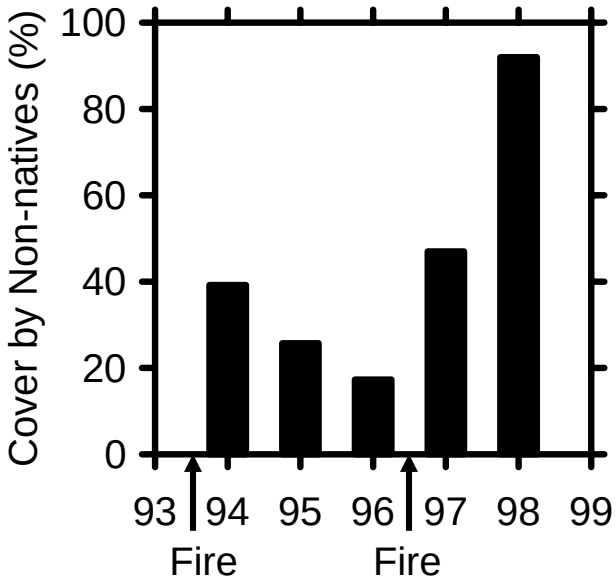

Figure 3—Percentage ground surface covered by non-native species on a coastal sage scrub site in the Santa Monica Mountains burned at 21 years of age in 1993 and reburned three years later in 1996 (data from Keeley and Fotheringham, unpublished data).

Sites differ greatly in their propensity for repeat fires. In general, interior sites are far more vulnerable to frequent fires than coastal sites due to the slower rate of shrub recovery (*fig. 4*). In another study of 90 sites burned during the same week in 1993, total herbaceous cover was positively correlated with parameters such distance from the coast, soil phosphorous, organic matter, and sand content (*table 3*). Postfire herbaceous cover was negatively correlated with stand age prior to the fire and estimated annual insolation. In short, herbaceous cover sufficient to carry a repeat fire is most likely when fires occur in young stands on fertile sites in the interior.

History of Type Conversion

Cooper (1922) believed there was abundant evidence, based upon his observations in the Coast Ranges, to say that burning by Indians accounted for a shift from woody vegetation to grasslands. He contended that this process of type conversion continued with the colonization by Europeans. Bauer (1930) believed the same applied to the grasslands of the Tehachapi Mountains farther south and cited examples of relictual patches of shrubland as evidence.

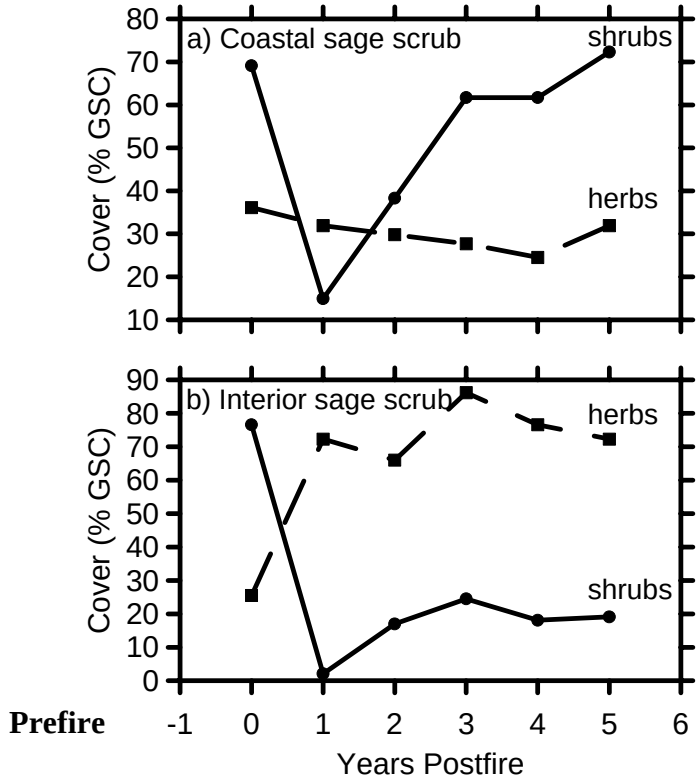

Figure 4—Foliar cover before and after fire at coastal and interior sage scrub sites (redrawn from O'Leary and Westman 1988).

Today the coastal ranges south of San Francisco have 25 percent of their landscape dominated by alien grasses, and there is reason to believe this derives from shrubland type conversion beginning with Native Americans (Keeley 2002b). Brown and Show (1944) recounted the history of rural land use in California, which included the use of fire to convert "useless" brush to "more productive" grasslands. This type conversion process accelerated in the latter part of the 19th century with increasing competition for suitable grazing land. During the latter part of the last century such type conversion was officially sanctioned by the issuing of brush burning permits for "range improvement" by the California Division of Forestry (CDF 1978). Throughout the 20th century, type conversion of shrublands occurred from other types of disturbance as well (Stylinksi and Allen 1999).

Presently, we have relatively limited information on the extent of such type conversions. However, there are reasons to believe this was done on a massive scale. One is the extensive distribution of non-native grasslands in the Coast Ranges of central California and the lack of any obvious correlation with environmental parameters such as soil type or slope exposure (Wells 1962). Another is the widespread distribution of grasslands in the foothills east of San Francisco and the demonstration of their rapid conversion to woody vegetation upon cessation of grazing (McBride and Heady 1968). Finally, quantitative measures of type conversion in southern California coastal sage scrub indicate that over the past 60 years more than half of the vegetation has been partially or completely type converted to grassland (Minnich and Dezzani 1998).

Table 3—*Stepwise multiple regression of postfire herbaceous cover vs. environmental variables at 90 sites of coastal sage scrub and chaparral (from Keeley and Fotheringham unpublished data).*

$r^2 = 0.42$ $P < 0.001$	
	2-tail *P*
Positively correlated:	
Distance from coast	0.000
Percentage sand	0.002
Soil phosphorus level	0.003
Soil organic matter	0.009
Negatively correlated:	
Prefire stand age	0.002
Annual solar insolation	0.033

Conclusions

Besides human development, the greatest threat to biodiversity in Mediterranean-climate shrublands of California is changes in the natural fire regime. Fire suppression alters the fire regime by increasing the fire return interval and potentially threatens the persistence of species with fire-dependent recruitment. However, this impact is offset by the abnormally high number of fire occurrences due to human-caused ignitions. Consequently, the fire return intervals in southern California shrublands are higher than was historically the case, and the greatest threat to the persistence of these vegetation types is type conversion to herbaceous species more resilient to and more conducive to frequent fires. In general, non-native grasses and forbs are most favored by the current fire regime of frequent fires.

In general the majority of rare herbaceous species show no specialized response to fire. However, areas heavily affected by human-induced acceleration of fire return intervals may not be suitable sites for these natives because of the intense competition from non-native invasives that are favored by high fire frequency.

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