

Fire-driven alien invasion in a fire-adapted ecosystem

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Abstract Disturbance plays a key role in many alien plant invasions. However, often the main driver of invasion is not disturbance per se but alterations in the disturbance regime. In some fire-adapted shrublands, the community is highly resilient to infrequent, high-intensity fires, but changes in the fire regime that result in shorter fire intervals may make these communities more susceptible to alien plant invasions. This study examines several wildfire events that resulted in short fire intervals in California chaparral shrublands. In one study, we compared postfire recovery patterns in sites with different prefire stand ages (3 and 24 years), and in another study we compared sites that had burned once in four years with sites that had burned twice in this period. The population size of the dominant native shrub *Adenostoma fasciculatum* was drastically reduced following fire in the 3-year sites relative to the 24-year sites. The 3-year sites had much greater alien plant cover and significantly lower plant diversity than the 24-year sites. In a separate study, repeat fires four years apart on the same sites showed that annual species increased significantly after the second fire, and alien annuals far outnumbered native annuals. Aliens included both annual grasses and annual forbs and were negatively correlated with woody plant cover. Native woody species

regenerated well after the first fire but declined after the second fire, and one obligate seeding shrub was extirpated from two sites by the repeat fires. It is concluded that some fire-adapted shrublands are vulnerable to changes in fire regime, and this can lead to a loss of native diversity and put the community on a trajectory towards type conversion from a woody to an herbaceous system. Such changes result in alterations in the proportion of natives to non-natives, changes in functional types from deeply rooted shrubs to shallow rooted grasses and forbs, increased fire frequency due to the increase in fine fuels, and changes in carbon storage.

Keywords Alien plants · Crown fires · Fire feedbacks · Fire regimes · Type conversion

Introduction

Fire is widely recognized as a disturbance agent contributing to alien plant invasion (D'Antonio 2000). One of the clearest examples is the invasion of fire-sensitive tropical forests where fire has pushed back the forest and promoted the incursion of C_4 grasses (D'Antonio and Vitousek 1992). However, less widely appreciated is the potential for fire-promoting alien invasions into fire-adapted ecosystems. A significant portion of the world comprises fire-prone landscapes (Krawchuk et al. 2009), and there is a substantial fossil record indicating that fire has been a potential selective factor throughout land plant evolution (Pausas and Keeley 2009). In some instances, fire has selected for traits interpreted as fire adaptations, and many Mediterranean-climate forests and shrublands are not only highly resilient to fire but are often dominated by species with fire-dependent reproduction (Keeley et al. 2012). In

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these systems where fire is an important ecosystem process, it seems counterintuitive to picture fire as a disturbance agent leading to alien plant invasion.

Although the fire literature abounds with references to fire-adapted species, it is important to realize that organisms are not adapted to fire per se, but rather to a particular fire regime comprising patterns of fire frequency, fire severity, and fuels consumed, among other things. When these patterns repeat over time they may become important ecosystem processes, and in these systems the biggest disturbance is not fire per se, but alterations in the fire regime. For example, some western US conifer forests have had their historical fire regimes disturbed by a highly successful fire suppression policy that, in conjunction with other land use changes, has excluded fires for unnaturally long periods. This perturbation has changed fire regime parameters such as fire frequency, fuel structure, and fire intensity, and moved these systems from surface fire to crown fire regimes; coupled with these changes have come increased alien plant invasions (Hunter et al. 2006; Keeley et al. 2003, 2011).

Many non-forested ecosystems have had fire regimes perturbed by anthropogenic ignitions that have greatly increased fire frequency (Keeley et al. 2009a). In some fire-prone ecosystems, short intervals between fires represent an extreme event that may lead to changes in community structure. Zedler et al. (1983) found that postfire chaparral heavily seeded by non-native grasses was capable of carrying a repeat fire 11 months later, and this was associated with a marked decline in native woody species. Decline is markedly influenced by life history, as species that are dependent on developing a seed bank prior to fire are the most vulnerable to repeat fires. Zedler et al. (1983) concluded that such repeat fire events would set the stage for the replacement of the native woody flora by non-native annual grasses and forbs, but this was not studied. Similar reductions in woody species were also noted by Haidinger and Keeley (1993) for a localized site where overlapping fire perimeters produced a mosaic of different fire intervals and increased alien grass and forb cover. In coastal California chaparral shrubland, invasion by non-native grasses and forbs correlates with both fire frequency (Keeley et al. 2005) and short intervals between fire (Jacobsen et al. 2004). Similar relationships have been reported for interior fire-prone sagebrush shrublands invaded by the annual non-native cheatgrass (Baker 2006).

These reports suggest that, under the right conditions, fire has the capacity to enhance alien plant invasion in fire-adapted shrublands, but other factors such as grazing and atmospheric nitrogen pollution have also been invoked to explain alien plant invasions in semi-arid shrublands (Padgett and Allen 1999). Although sorting out the roles of pollution, grazing, and fire are not the focus of this study,

it is believed that more detailed studies of fire effects would go a long way towards determining the potential for fire to promote alien plant invasion in fire-prone shrublands. It is evident from the first study by Zedler et al. (1983) that intense management that produces dense growth of grasses can lead to repeat fires within the first year, but under less intensively managed conditions repeat fires are likely to occur at longer intervals. Also, studies performed to date have focused on the immediate postfire response of aliens, and it is assumed that this places communities on a trajectory of increasing alien invasion. Longer-term studies of how fire affects alien invasions, not just immediately after fire but also during subsequent postfire years, are needed to determine the long-term impact of fires on alien invasions.

Understanding the mechanism behind fire-induced alien invasion would help to establish the causal pathway of invasion. In a broad regional study, it was found that postfire shrub cover was negatively correlated with alien grass and forb cover (Keeley et al. 2005). We might expect that with repeat fires, shrubs would be decimated to the point where this relationship weakens.

Controlled experimental studies of this invasion process are difficult because young seral stands of chaparral are the most vulnerable to invasion, and these often lack sufficient fuel continuity to carry a fire under experimental prescription burn conditions (typically <15 kph wind speed and >30% RH). Thus, in order to study this fire-driven invasion phenomenon, we must take advantage of ad hoc experiments set up by autumn wildfires that burn under much more severe fire weather conditions (wind gusts >100 kph and RH <5%) and have little problem carrying fire through young seral stages of chaparral (Halsey et al. 2009). Here we take advantage of a series of autumn wildfires in southern California that burned a significant portion of the landscape in 2003 and again in 2007.

We test the following hypotheses. (1) Early seral stages produce less severe fires when reburned. This is due to the lower fuel volumes, and it has the potential to enhance alien invasion because it increases survivorship of alien seed banks. (2) Under short fire return intervals, shrubs that recruit after fire will have greatly diminished seedling recruitment. This is because short fire return intervals have a direct effect on shrub life histories that require a decade or more to reach maturity and replenish the soil seed bank. (3) Under short fire return intervals, resprouting shrubs will exhibit lower resprouting success. This is presumed to be due to the shorter period of carbohydrate accumulation in woody underground storage organs and the exhaustion of bud banks. (4) When early seral stage stands are reburned, they will have a greater alien species presence than older stands that burn at the same time. The apparent reasons for this are that alien seed banks are favored by the lower fire

severities and the depression of potential competitors such as native woody species by short fire-return intervals. (5) Higher postfire alien presence puts communities on a trajectory towards alien invasion that predicts alien persistence for five or more years after fire. (6) These direct effects of short fire-return intervals on native and alien species translate into changes in community structure and diversity. (7) In addition to the differential effects of short fire return intervals on the regenerative capacity of natives and aliens, there is an interaction that predicts a negative relationship between alien cover and native woody species.

Methods

Study sites

In the autumn of 2003, several major wildfires burned through San Diego County, CA, USA. The biggest of these was the Cedar Fire, that consumed over 110,000 ha of largely shrubland-dominated landscape and burned through a mosaic of age classes ranging from 3 to more than 30 years of age (Keeley et al. 2004). Along the southern edge, it overlapped with the Viejas Fire from January of 2001. This zone of overlap comprised vegetation with only three years of recovery at the time of the cedar fire, and is discussed in more detail in Halsey et al. (2009). Sites were selected within the zone of overlap for comparison with nearby sites that were 24 years old at the time of the Cedar Fire. These are referred to here as the RH sites, and comprised three sites that had a prefire age of 3 years and three sites with a prefire age of 24 years. Vegetation recovery was recorded for 1, 2, 5, and 6 years after fire.

In addition, in the autumn of 2007, several large wildfires burned through the same region and overlapped in many places with the 2003 fire scars, and this provided a second opportunity to study the effect of short fire intervals on plant invasion. This study took advantage of a previous investigation of the impact of fire severity on plant recovery following the 2003 fires (Keeley et al. 2008), which included sample sites that were reburned in 2007. Thirteen sites were included, nine from the 2003 Cedar fire scar, which were reburned by the 2007 Witch Fire, and four within the 2003 Otay Fire scar, which were reburned by the 2007 Harris Fire (Keeley et al. 2009b). In a few cases, some subplots were not completely reburned, and these were excluded from analysis, so some site averages are based on ten subplots and others on fewer. Where analysis is based on subplots, the final sample size will be given. This ad hoc experiment allowed us to compare the first two years of postfire recovery in relatively mature stands

(9–31 years of age at the time of the 2003 fires) with the recovery in immature stands (4 years of age at the time of the 2007 fires).

Sampling methods

A site comprised a tenth hectare plot of size 20×50 m positioned parallel to the slope contour and subdivided into 10×10 m subplots, each with a nested 1×1 m quadrat, as described in more detail in Keeley and Fotheringham (2005). Briefly, within each quadrat, number and percentage ground surface covered were recorded for each species. Exact counts were made for species with densities of approximately 30 m^{-2} , but counts were estimated for higher densities. Any additional species in the surrounding 10×10 m subplot were recorded. All plant nomenclature follows Hickman (1993).

We used two surrogate measures of fire intensity. One of these fire severity estimates was the diameter of the smallest twig remaining on the two *Adenostoma fasciculatum* skeletons nearest to each 1 m^2 quadrat. Another measure of fire severity was skeleton height, and this was measured on the same two *Adenostoma* skeletons. Prefire stand age was determined from stem sections of burned skeletons for the non-resprouting obligate-seeding *Ceanothus* species. These provide an accurate estimate of the time since the last fire due to the rarity of missing or extra rings (Keeley 1993) and the near-exclusive restriction of seedling recruitment to the first postfire year in these taxa (Keeley et al. 2006).

Data analysis

Fire severity was based on the diameter of the smallest twig remaining on *A. fasciculatum* skeletons. The foundation for this estimate is the demonstration that higher fire intensities are correlated with terminal branch diameter for burned skeletons of a number of species (Moreno and Oechel 1989). Another potential measure of fire intensity is skeleton height, as it is assumed that as intensity increases there will be greater biomass consumption.

Data analyses and graphical displays were conducted with Systat 11.0 (Systat Software, Inc., Richmond, CA, USA). For data from the RH sites, comparisons of parameters from the 3-year and 24-year prefire treatments were made with a two-tailed Student's *t* test. For sites burned in 2003 and 2007, vegetation was monitored in 2004, 2005, 2008, and 2009, and individual parameters were compared across all four years of study with a mixed effects ANOVA. Heteroscedasticity was tested with Levine's test, and a few instances of departure from equal variance were detected, and these means were tested with the non-parametric Kruskal–Wallis test.

Results

Postfire recovery in 3- and 24-year sites burned in 2003 (“RH sites”)

Sites 3 years old at the time of fire are referred to here as “3-year sites” and those sites that were 24 years old at the time of fire are termed “24-year sites.” This difference in prefire stand age had a significant effect on both measures of fire severity, with higher severities recorded following fire in the 24-year stands (Fig. 1), as predicted by our first hypothesis.

Stand age also had a very significant effect on seedling recruitment in the dominant chaparral shrub *A. fasciculatum*, with very high postfire seedling recruitment in the older stands but relatively little recruitment in the younger sites (Fig. 2a), consistent with hypothesis 2. Resprouting success was also affected; it was 42% in the 3-year sites and 68% in the 24-year sites ($P = 0.019$), consistent with

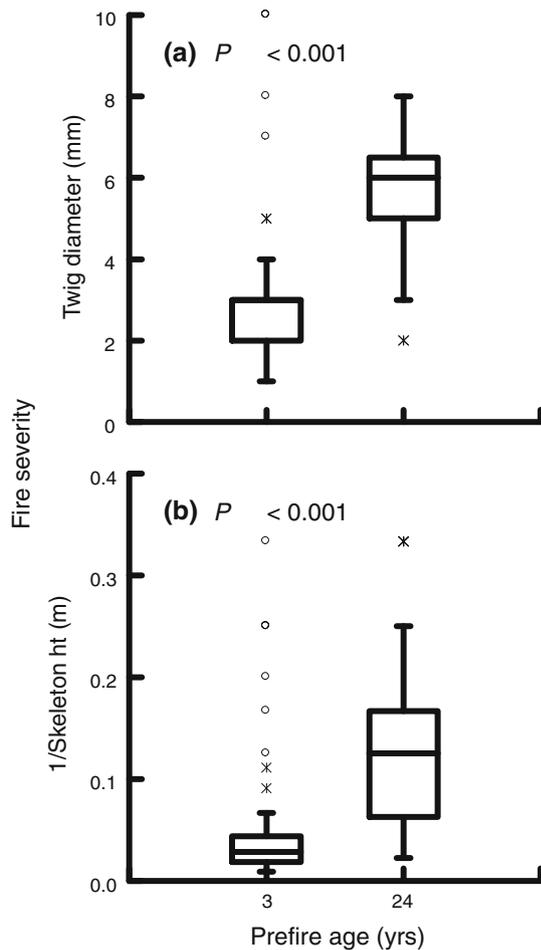


Fig. 1 Estimates of fire severity, based on **a** the diameters of the smallest twigs on *Adenostoma fasciculatum* skeletons and **b** the heights of skeletons, at RH sites with different prefire ages that were burned in the 2003 Cedar Fire; each bar is the mean \pm SE, P values are from Student’s t test

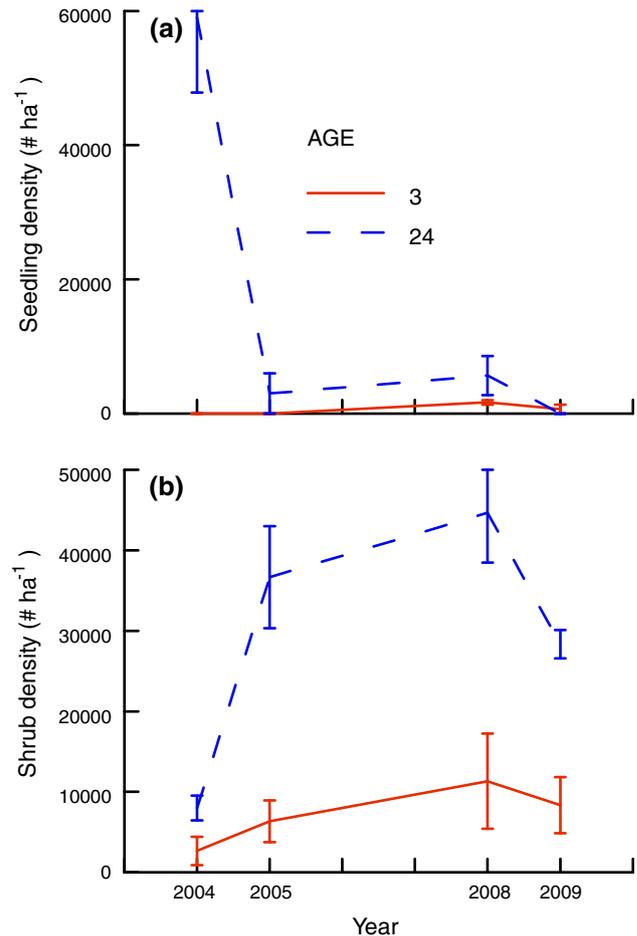


Fig. 2 Postfire *Adenostoma fasciculatum* **a** seedling density and **b** total shrub density in RH sites that were 3 years or 24 years old at the time of the 2003 Cedar Fire (note: after their first year, the surviving seedlings become part of the total shrub population); vertical bars are standard errors

hypothesis 3. Prefire stand age had significant effects on the longer-term recovery of this shrub. Six years after the 2003 Cedar Fire, *A. fasciculatum* populations were substantially smaller in the 3-year stands than in the 24-year stands ($P = 0.012$). The non-resprouting or obligate seeding shrub *Ceanothus greggii* had no seedlings in the 3-year sites but averaged 7,850 seedlings ha^{-1} on the 24-year sites, as predicted by hypothesis 2.

Alien plants were all annuals. In the first postfire year they outnumbered native annuals by more than 5:1 on sites 3 years old at the time of fire ($P = 0.019$). The same alien species were present on the 24-year sites but at a density that was almost an order of magnitude lower, and they were not significantly different in density from native annuals ($P = 0.501$), consistent with hypothesis 4. In the first year after fire, cover of aliens was significantly higher on 3-year sites than on 24-year sites ($P < 0.001$), and remained significantly higher in the second year ($P = 0.009$). The 24-year sites were unlike the 3-year sites

Table 1 Cover of alien and native plants on sites 3 or 24 years old at the time of the 2003 Cedar Fire for 1, 2, 5, and 6 postfire years

	Plant cover (% ground surface covered)							
	Prefire age: 3 years				Prefire age: 24 years			
	Year	1	2	5	6	1	2	5
Alien	19	33	34	23	3	19	24	10
Native	24	19	46	38	26	42	57	42
<i>P</i>	0.268	0.035	0.577	0.278	0.005	0.001	0.039	0.010

P values compare alien and native cover at each time period

in that the native cover significantly exceeded the alien cover every year (Table 1).

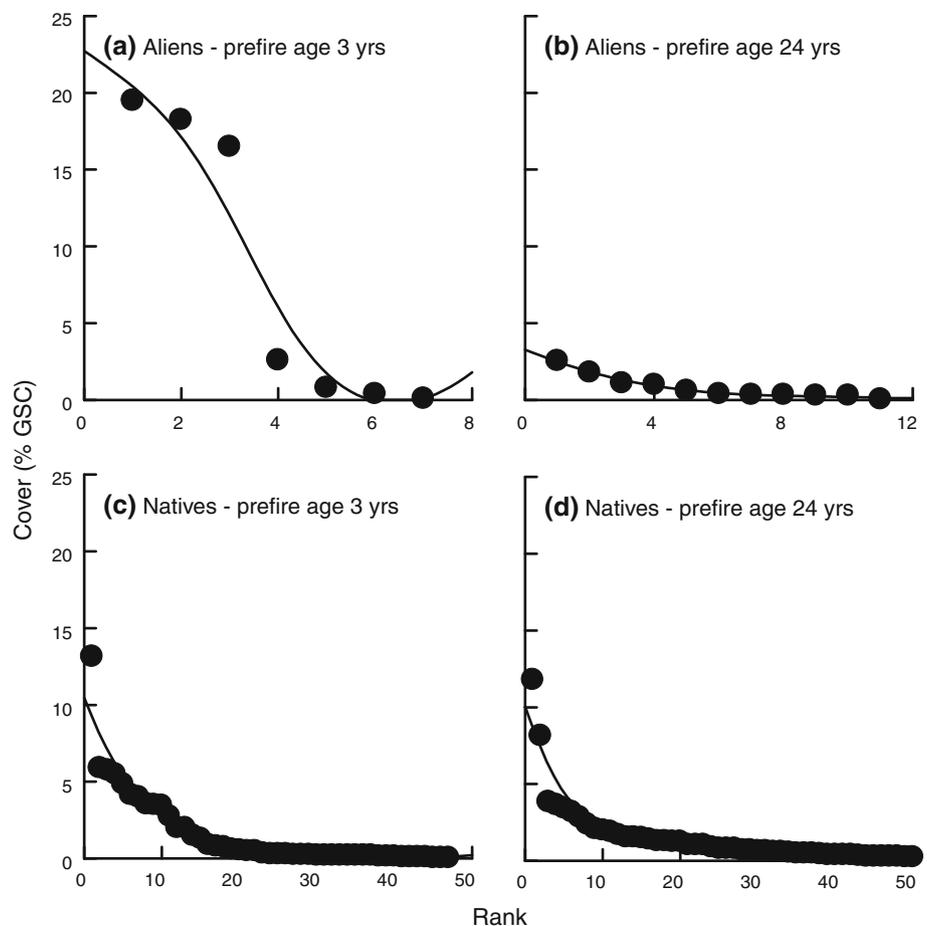
On the 3-year sites, the dominant species was the alien annual grass *Bromus madritensis*, and it averaged 18% cover in the first postfire year and 30% in the second year. In contrast, on the 24-year sites, this species had only 0.4% cover immediately after fire, and in year two it comprised only 4.9% cover. By the fifth year after fire, *B. madritensis* was still dominant on 3-year sites with over 24% cover, consistent with hypothesis 5, but the native shrub *A. fasciculatum* was close with 21%. At this time on the 24-year sites, *A. fasciculatum* had the same cover but *B. madritensis* was half of what it was on the 3-year sites.

Community structure was also affected by prefire stand age (Fig. 3), as predicted by hypothesis 6. On 3-year sites,

cover was dominated by one alien species, and most of the other aliens contributed much less to postfire cover during the first year. No species was clearly dominant on 24-year sites, and natives exhibited a broad dominance diversity pattern (Fig. 3d). Species diversity was also greatly affected by prefire age. Immediately after fire, diversity was significantly greater on 24-year sites than on 3-year sites at scales of 1, 100, and 1000 m² (Fig. 4a, c, e), and this pattern remained 5 years after fire (Fig. 4b, d, f).

One difference that was not readily captured with these data is the distinct difference in phenology between these sites of different prefire ages. The marked dominance of alien annual grasses on the 3-year sites resulted in much earlier drying of the vegetation. The greater diversity and

Fig. 3 Dominance diversity patterns in the second postfire year on RH sites for **a, b** aliens and **c, d** natives on sites 3 or 24 years old at the time of the 2003 Cedar fire (% GSC = percentage ground surface covered)



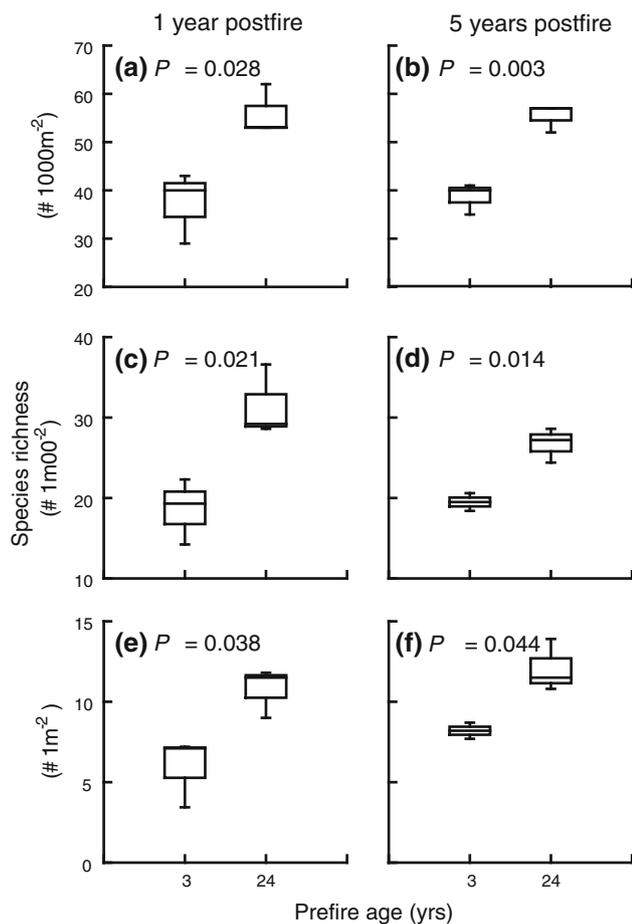


Fig. 4 Species richness 1 and 5 years postfire in the RH sites at different spatial scales in the **a, c, e** 3 year old prefire sites and the **b, d, f** 24 year old prefire sites; *P* values are for Student *t*-test comparisons and vertical bars are standard errors

cover of natives on the 24-year sites comprised a flora of species with a longer growing season.

Postfire recovery following fires in 2003 and 2007 at the same sites

Comparing the first two years of recovery following the 2003 fires with recovery after the repeat fires in 2007 showed that annuals greatly increased after the second fire (Fig. 5), consistent with hypothesis 5. Immediately after the second fire, native and alien annuals had similar densities, but by the second year aliens far exceeded natives. The aliens that were most abundant after the second fire were *Bromus madritensis* and *Filago gallica* (Table 2). Several native annuals were also significantly favored by the second fire (Table 2).

Although native herbaceous perennials and shrubs tended to decline and subshrubs increase after the second fire, none of these changes were significant (Fig. 6). The

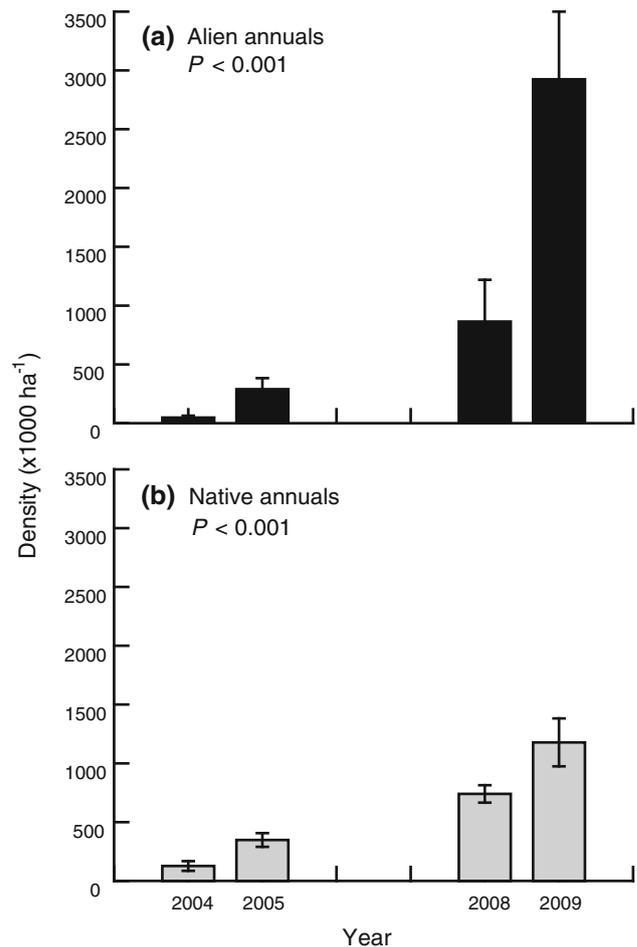


Fig. 5 Densities of **a** alien annuals and **b** native annuals on sites in the 2003 Cedar and Otay fires reburned by the 2007 Witch and Harris fires, respectively; bars are standard errors and *P* values are for ANOVA comparison across years

subshrubs *Helianthemum scoparium* and *Lotus scoparius* exhibited large drops in density after the first year seedling recruitment following the 2003 fires (Table 2). These fast-growing subligneous species were able to replenish the soil seedbank so that they exhibited substantial seedling recruitment after the second fire in 2007. However, the non-resprouting obligate seeding shrub *Ceanothus tomentosus* is slower to reach reproductive maturity and was extirpated from these sites (Table 2), as predicted by hypothesis 2. *A. fasciculatum* was a dominant shrub at all sites and regenerated by both seedlings and resprouts, and had only a slight downward trend in density after the second fire (Table 2), which was inconsistent with hypothesis 2.

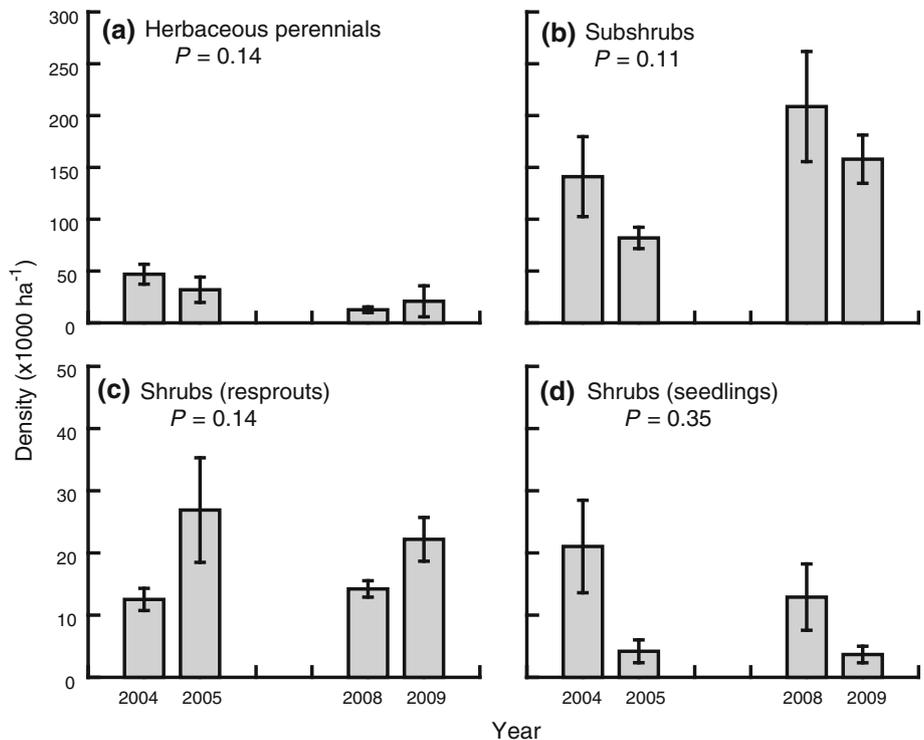
Two years after the first fire there was a significant negative relationship between woody density and alien density at the 1 m² scale ($r^2 = 0.13$, $P < 0.001$) as predicted by hypothesis 7. This relationship was much weaker years after the second fire ($P = 0.21$).

Table 2 Densities of alien and native species in the two years following the Cedar or Otay fires in 2003 and in the two years following the Witch or Harris fires in 2007

Density ($\times 1000 \text{ ha}^{-1}$)	Growth forms	Year				P
		2004	2005	2008	2009	
Alien annuals						
<i>Bromus madritensis</i>	Grass	5	35	115	747	<0.001
<i>Centaurea melitensis</i>	Forb	1	34	139	1406	<0.001
<i>Filago gallica</i>	Forb	21	111	240	651	0.282
<i>Gastridium ventricosum</i>	Grass	32	133	346	252	0.271
<i>Hypochaeris glabra</i>	Forb	3	18	13	191	0.089
<i>Vulpia myuros</i>	Grass	10	43	251	690	0.013
Native annuals						
<i>Chaenactis artemisiifolia</i>	Forb	6	31	68	68	<0.001
<i>Cryptantha muricata</i>	Forb	32	83	214	368	0.030
<i>Navarretia hamata</i>	Forb	40	132	266	163	0.175
<i>Phacelia parryi</i>	Forb	6	3	69	83	0.186
<i>Pterostegia drymarioides</i>	Forb	13	10	7	85	<0.001
<i>Vulpia octoflora</i>	Grass	15	49	120	538	0.023
Native perennials						
<i>Adenostoma fasciculatum</i>	Shrub	30	24	23	19	0.757
<i>Ceanothus tomentosus</i>	Shrub	6	6	0	0	<0.001
<i>Helianthemum scoparium</i>	Subshrub	109	29	116	69	<0.001
<i>Lotus scoparius</i>	Subshrub	57	48	103	70	0.279
<i>Quercus berberidifolia</i>	Shrub	4	4	4	2	0.703

P values for ANOVA comparison across years, except where Levine's test demonstrated non-homogeneity of variances and thus comparisons were made with the Kruskal–Wallis test

Fig. 6 Density of perennial life forms on sites in the 2003 Cedar and Otay fires reburned by the 2007 Witch and Harris fires; bars are standard errors and P values are for ANOVA comparison across years



Discussion

Many semi-arid shrublands are adapted to a crown fire regime of fires at a frequency of 30–150 years (Keeley

et al. 2009a). These are high-intensity fires that kill all aboveground biomass. Belowground stems and lignotubers typically survive and rapidly resprout on many dominant woody species. In addition, many taxa have dormant seeds

that are buried deeply and germinate in response to heat shock or smoke from fire. These communities are highly resilient to fire and generally reach maturity between two to three decades after a fire.

One major perturbation to fire-prone shrublands is an increase in fire frequency that generates short fire intervals, and this has been implicated in alien plant invasions in many parts of the western USA (Keeley 2006). As seen in this study, short intervals between fires greatly facilitates the increase in alien species, all of which are annuals from the Mediterranean Basin. We propose there are two factors at work. One is the lower fire intensity in young immature shrublands, and this enhances alien seed bank survivorship. In addition, short fire-return intervals directly inhibit the regeneration of some native woody species, and this reduces the competitive inhibition of alien species. Although most native herbaceous and woody species persist in the face of short-interval fires, populations often decline, and sometimes species are extirpated from sites. Most sensitive are obligate seeding shrubs that lack the capacity to vegetatively resprout after fire, and persistence following fire is dependent on a dormant seed bank. These taxa often require a decade or more to replenish the seed bank, and thus they are extirpated when fire intervals are short. Such a fate is implicated for two *Ceanothus* species in this study, and similar results have been reported for two other *Ceanothus* species (Zedler et al. 1983; Jacobsen et al. 2004). Model simulations suggest this is a particular ecosystem threat on landscapes with high anthropogenic ignitions (Syphard et al. 2006; Lawson et al. 2010; Regan et al. 2010).

Resprouting species such as the widespread *A. fasciculatum* persist in the face of repeat fires but do suffer reductions in population size. Zedler et al. (1983) reported a 75% reduction in this species with two fires in 3 years, and that is comparable to our results (Fig. 2). However, there is some variability in the impact of short-interval fires on this widespread species, as illustrated by demographic patterns (Table 2). Under such changes in fire regime, these chaparral communities suffer a reduction in species diversity and a change in community structure (Figs. 3, 4). This appears to be a common pattern in Mediterranean-climate crown fire shrublands such as those in Australia, where short fire intervals lead to increased resprouting mortality (Enright et al. 2011) and are also responsible for losses in biodiversity and the extirpation of some species (Bradstock et al. 1995).

In California shrublands, this change in fire regime towards more frequent fires greatly accelerates alien plant invasion. Factors responsible for this high invasibility are similar to those widely recognized as important factors in invasions: altered disturbance regimes, high resource availability, and diminished competition (Alpert et al.

2000). Equally important, however, is the presence or close proximity of an alien seedbank (D'Antonio et al. 2001).

Upon modeling the alien success 5 years after fire across 90 chaparral sites, it was found that two factors directly affected aliens: the alien seedbank at the time of fire and the rate of shrub canopy closure (Keeley et al. 2005). As shown in the present study, altered disturbance regimes in the form of short fire intervals will greatly thin the woody plant populations, opening up resources to life forms that can exploit the postfire conditions. Annuals, both native and non-native, are capable of taking advantage of these conditions. The alien annuals, however, appear to have an advantage under short fire intervals. Native annuals have an advantage under longer fire intervals, where fire intensity/severity is elevated (e.g., Fig. 1). Native seeds are mostly small and readily buried and deeply dormant, whereas most alien grasses have larger seeds that often remain on or near the soil surface and have limited dormancy. The alien seed banks diminish under long fire-free periods, and as fuels accumulate alien seeds are more susceptible to being killed by the higher fire intensity fires. This is evident in a study of 250 postfire chaparral sites that showed an inverse relationship between fire severity and alien success (Keeley et al. 2008).

This discussion illustrates that short-interval fires have the potential to greatly alter the balance between native and alien composition in fire-prone landscapes. Numerous studies have contended that this represents the initial stages in type converting native shrublands to alien-dominated “grasslands” comprising both non-native annual grasses and native and non-native annual forbs (Cooper 1922; Wells 1962; Hamilton 1997; Keeley 2006). Early “range improvement” studies have shown that repeated burning is a highly effective means of type converting chaparral to alien-dominated annual grasslands (Sampson 1944; Burcham 1955).

It is clear from our studies and those discussed earlier that a single short-interval fire is insufficient to effect this type conversion in *A. fasciculatum* chaparral, although it appears possible in obligate seeding *Ceanothus* stands (Jacobsen et al. 2004). However, by thinning the native shrub density and opening up the canopy, which enhances annual plant expansion, the community is placed on a trajectory towards more frequent fires. Annuals provide flashy fuels that are more likely to ignite under a wider range of weather conditions than native woody fuels, and alien grasses from the Mediterranean Basin dry very early in the growing season. The increase of alien grasses on a site has the effect of greatly expanding the fire season and the probability of a repeat fire. Indeed, in an examination of fire starts in southern California, it was found that the majority of fires begin in grassy fuels (A. Syphard, unpublished data). Thus, the initial short-interval fire

regime initiates the introduction of sufficient fine fuels to provide a positive feedback that further accelerates the invasion process (D'Antonio et al. 1999).

In this study, the alien grass *Bromus madritensis* was a very aggressive invader capable of rapidly capitalizing on short fire intervals. This is a widespread pattern in the southwestern USA, where this species is known to be an aggressive invader of disturbed desert ecosystems (Salo 2005). Other annual brome grasses are even more aggressive, as evidenced by the invasion of the Great Basin sage shrublands by *Bromus tectorum* (Mack 1981). Numerous disturbances have played a role in the invasion process throughout this extensive area, but these sage scrub systems are adapted to an infrequent crown fire regime, and are thus susceptible to invasion when fire frequency increases (Allen 2004). Some of this invasion appears to have started early in the twentieth century with the practice of prescription burning of Great Basin sage scrub for sheep range improvement (Pechanec 1944).

A necessary condition for alien invasion into closed-canopy shrublands is some form of disturbance that opens the canopy and provides establishment sites for annuals. Multiple fires can initiate this process, but other disturbances may suffice. It is apparent that in some cases intensive livestock grazing has played a role in type conversions, although the direction of change is a function of innate community characteristics. In California shrublands, woody species are readily browsed and trampled by livestock that can lead to alien invasion (Keeley 2005), but in the southwestern USA, mesquite (*Prosopis* spp.) shrubs are spiny and deter livestock browsing, often resulting in the conversion of grasslands to shrublands (Archer 1994). Atmospheric pollutants are another potential stressor that could enhance alien invasion at the expense of native shrublands. Ozone was proposed by Westman (1979) as a major determinant of alien invasion in California shrublands. He examined landscape patterns of alien species and correlated them with ozone levels; however, his failure to consider fire history makes it impossible to disentangle the role of ozone from correlated traits such as high human presence and accelerated fire ignitions in regions of high ozone concentration. Nitrogen pollutants have also been hypothesized to play a role in the type conversion of shrublands to grasslands (Padgett and Allen 1999). Nitrogen appears to favor annual growth forms over shrubs. This effect is most evident in open desert scrub communities, but there is little evidence that nitrogen alone can effect the type conversion of intact chaparral and sage scrub in the absence of physical disturbance that opens up the shrub canopy. Regional studies of aliens and nitrogen pollution have produced conflicting conclusions. In a study across southern California shrublands, alien presence 5 years after fire was unrelated to nitrogen pollution but it was dependent on prior fire history

(Keeley et al. 2005). However, in another study, pollution was correlated with alien success on sites with little prior fire history (Talluto and Suding 2008). That study, though, focused on a region of extremely high fire frequency, and their database considered only large fire events, which comprised about 5–10% of all fires in the region (Keeley, unpublished data), making it impossible to rule out fire as an important driver of alien invasion on all sites.

In conclusion, fire-adapted ecosystems are vulnerable to fire when fire regime characteristics are altered. In this California example, the crown fire shrubland regime is one of infrequent, high-intensity fires. Increasing the frequency of fires has the potential to reduce native cover and enhance invasion by alien annual grasses and forbs. This creates conditions that further favor high fire frequency, and this positive feedback may lead to complete type conversion from shrublands to annual grasslands dominated by alien grasses and forbs.

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References

- Allen EB (2004) Restoration of *Artemisia* shrublands invaded by exotic annual *Bromus*: a comparison between southern California and the Intermountain Region. In Hild AL, Shaw NL, Meyer SE, Booth DT, McArthur ED (eds) Seed and soil dynamics in shrubland ecosystems (proceedings RMRS-P-31). USDA Forest Service, Fort Collins, pp 9–17
- Alpert P, Bone E, Holzapfel C (2000) Invasiveness, invasibility and the role of environmental stress in the spread of non-native plants. *Perspect Plant Ecol Evolu Systematics* 3:52–66
- Archer S (1994) Woodland plant encroachment into southwestern grasslands and savannas: rates, patterns and proximate causes. In: Vavra M, Laycock WA, Pieper RD (eds) Ecological implications of livestock herbivory in the west. Society for Range Management, Denver, pp 13–68
- Baker WL (2006) Fire and restoration of sagebrush ecosystems. *Wildl Soc Bull* 34:177–185
- Bradstock RA, Keith DA, Auld TD (1995) Fire and conservation: imperatives and constraints on managing for diversity. In: Bradstock RA, Auld TD, Keith DA, Kingsford RT, Lunney D, Sivertsen DP (eds) Conserving biodiversity: threats and solutions. Surrey Beatty and Sons, Chipping Norton, pp 323–333
- Burcham LT (1955) Recent trends in range improvement on California foothill ranges. *J Range Manag* 8:121–125
- Cooper WS (1922) The broad-sclerophyll vegetation of California. An ecological study of the chaparral and its related communities. Carnegie Institution of Washington, Washington, DC
- D'Antonio CM (2000) Fire, plant invasions, and global changes. In: Mooney HA, Hobbs RJ (eds) Invasive species in a changing world. Island, Covelo, pp 65–93

- D'Antonio CM, Vitousek PM (1992) Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Ann Rev Ecol Syst* 23:63–87
- D'Antonio CM, Dudley TL, Mack M (1999) Disturbance and biological invasions: direct effects and feedbacks. In: Walker LR (ed) *Ecosystems of disturbed ground*. Elsevier, New York, pp 413–452
- D'Antonio C, Levine J, Thomsen M (2001) Ecosystem resistance to invasion and the role of propagule supply: a California perspective. *J Mediterr Ecol* 2:233–245
- Enright NJ, Fontaine JB, Westcott Lade JC, Miller BP (2011) Fire interval effects on persistence of resprouter species in Mediterranean-type shrublands. *Plant Ecol*. doi:10.1007/S11258-011-9970-7
- Haidinger TL, Keeley JE (1993) Role of high fire frequency in destruction of mixed chaparral. *Madroño* 40:141–147
- Halsey RW, Keeley JE, Wilson K (2009) Fuel age and fire spread: Natural conditions versus opportunities for fire suppression. *Fire Manag Today* 69:22–28
- Hamilton JG (1997) Changing perceptions of pre-European grasslands in California. *Madroño* 44:311–333
- Hickman JC (1993) *The Jepson manual: higher plants of California*. University of California Press, Los Angeles
- Hunter ME, Omi PN, Martinson EJ, Chong GW (2006) Establishment of non-native plant species after wildfires: effects of fuel treatments, abiotic and biotic factors, and post-fire grass seeding treatments. *Int J Wildland Fire* 15:271–281
- Jacobsen AL, Davis SD, Fabritius SL (2004) Fire frequency impacts non-sprouting chaparral shrubs in the Santa Monica Mountains of southern California. In: Arianoutsou M, Panastasis VP (eds) *Ecology, conservation and management of Mediterranean climate ecosystems*. Millpress, Rotterdam
- Keeley JE (1993) Utility of growth rings in the age determination of chaparral shrubs. *Madroño* 40:1–14
- Keeley JE (2005) Fire history of the San Francisco East Bay region and implications for landscape patterns. *Int J Wildland Fire* 14:285–296
- Keeley JE (2006) Fire management impacts on invasive plant species in the western United States. *Conserv Biol* 20:375–384
- Keeley JE, Fotheringham CJ (2005) Plot shape effects on plant species diversity measurements. *J Veg Sci* 16:249–256
- Keeley JE, Lubin D, Fotheringham CJ (2003) Fire and grazing impacts on plant diversity and alien plant invasions in the southern Sierra Nevada. *Ecol Appl* 13:1355–1374
- Keeley JE, Fotheringham CJ, Moritz MA (2004) Lessons from the 2003 wildfires in southern California. *J For* 102:26–31
- Keeley JE, Baer-Keeley M, Fotheringham CJ (2005) Alien plant dynamics following fire in Mediterranean-climate California shrublands. *Ecol Appl* 15:2109–2125
- Keeley JE, Fotheringham CJ, Baer-Keeley M (2006) Demographic patterns of postfire regeneration in Mediterranean-climate shrublands of California. *Ecol Monogr* 76:235–255
- Keeley JE, Brennan T, Pfaff AH (2008) Fire severity and ecosystem responses following crown fires in California shrublands. *Ecol Appl* 18:1530–1546
- Keeley JE, Aplet GH, Christensen NL, Conard SG, Johnson EA, Omi PM, Peterson DL, Swetnam TW (2009a) Ecological foundations for fire management in North American forest and shrubland ecosystems (Gen Tech Rep PNW-GTR-779). USDA Forest Service, Pacific Northwest Research Station, Portland, p 92
- Keeley JE, Safford H, Fotheringham CJ, Franklin J, Moritz M (2009b) The 2007 southern California wildfires: lessons in complexity. *J For* 107:287–296
- Keeley JE, Franklin J, D'Antonio C (2011) Fire and invasive plants on California landscapes. In: McKenzie D, Miller C, Falk DA (eds) *The landscape ecology of fire*. Springer, New York, pp 193–221
- Keeley JE, Bond WJ, Bradstock RA, Pausas JG, Rundel PW (2012) *Fire in Mediterranean climate ecosystems: ecology, evolution and management*. Cambridge University Press, Cambridge
- Krawchuk MA, Moritz MA, Parisien MA, Dorn JV, Hayhoe K (2009) Global pyrogeography: the current and future distribution of wildfire. *PLoS ONE* 4:e5102
- Lawson DM, Regan HM, Zedler PH, Franklin J (2010) Cumulative effects of land use, altered fire regime and climate change on persistence of *Ceanothus verrucosus*, a rare, fire-dependent plant species. *Glob Change Biol* 16:2518–2529
- Mack RN (1981) Invasion of *Bromus tectorum* L. into Western North America: an ecological chronicle. *Agro-Ecosystems* 7:145–165
- Moreno JM, Oechel WC (1989) A simple method for estimating fire intensity after a burn in California chaparral. *Acta Oecologica* 10:57–68
- Padgett PE, Allen EB (1999) Differential responses to nitrogen fertilization in native shrubs and exotic annuals common to Mediterranean coastal sage scrub of California. *Plant Ecol* 144:93–101
- Pausas JG, Keeley JE (2009) A burning story: the role of fire in the history of life. *Bioscience* 59:593–601
- Pechanec JE (1944) Sagebrush burning—good and bad. USDA, Washington, DC
- Regan HM, Crookston JB, Swab R, Franklin J, Lawson DM (2010) Habitat fragmentation and altered fire regime create trade-offs for an obligate seeding shrub. *Ecology* 91:1114–1123
- Salo LF (2005) Red brome (*Bromus rubens* subsp. madritensis) in North America: possible modes for early introductions, subsequent spread. *Biol Invasions* 7:165–180
- Sampson AW (1944) *Plant succession and burned chaparral lands in northern California*. University of California, Agricultural Experiment Station, Berkeley
- Syphard AD, Franklin J, Keeley JE (2006) Simulating the effects of frequent fire on southern California coastal shrublands. *Ecol Appl* 16:1744–1756
- Talluto MV, Suding KN (2008) Historical change in coastal sage scrub in southern California, USA in relation to fire frequency and air pollution. *Landsc Ecol* 23:803–815
- Wells PV (1962) Vegetation in relation to geological substratum and fire in the San Luis Obispo quadrangle, California. *Ecol Monogr* 32:79–103
- Westman WE (1979) Oxidant effects on Californian coastal sage scrub. *Science* 205:1001–1003
- Zedler PH, Gautier CR, McMaster GS (1983) Vegetation change in response to extreme events: the effect of a short interval between fires in California chaparral and coastal scrub. *Ecology* 64:809–818