Fire driven alien invasion in a fire-adapted ecosystem

Jon E. Keeley · Teresa J. Brennan

Jon E. Keeley
U.S. Geological Survey, Western Ecological Research Center, Sequoia-Kings Canyon Field Station, Three Rivers, CA 93271, USA and Department of Ecology and Evolutionary Biology, University of California, Los Angeles, CA 90095, USA

Teresa J. Brennan
U.S. Geological Survey, Western Ecological Research Center, Sequoia-Kings Canyon Field Station, Three Rivers, CA 93271, USA

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Abstract Disturbance plays a key role in many alien plant invasions. However, often disturbance *per se* is not the main driver of invasion but alterations in the disturbance regime. In fire-adapted California 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 chaparral shrublands. We compared postfire recovery patterns in sites with different prefire stand ages (3 and 24 years), and sites that had burned twice in four years. 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. Following repeat fires 4 years apart on the same sites, annual species increased significantly after the second fire and alien annuals far outnumbered native annuals. Aliens included both annual grasses and annual forbs. Native woody species tended to decline after the second fire and one obligate seeding shrub was extirpated from two sites by the repeat fires. It is concluded that this fire-adapted shrubland is vulnerable to changes in fire regime and this can lead to 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 flashy fuels and changes in carbon storage.

Keywords Alien plants · Disturbance · 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 substantial 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. 2011a). In 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 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 U.S. 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 coupled with these changes have come increased alien plant invasions (Hunter et al. 2006; Keeley et al. 2011b).

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 represents an extreme event that may lead to changes in community composition. Zedler et al. (1983) found that in a California chaparral stand burned twice in three years that native woody species declined or in some instances were extirpated from the site. Jacobsen et al (2004) also found that on landscapes subject to short intervals between fires certain native shrub species were extirpated and this was associated with type conversion from shrublands to alien-dominated grasslands. Similar reductions in woody species were also noted by Haidinger and Keeley (1993) for chaparral sites following short interval fires. They also documented substantial increases in alien grasses and forbs. In a study of postfire recovery over a large portion of southern California shrublands it was found alien invasion of these shrublands was associated with a history of shorter fire intervals (Keeley et al. 2005).

This threat of accelerated fire frequency to native ecosystem sustainability is substantial where population growth is adding to anthropogenic ignitions. Modeling studies point to the potential widespread type conversion of native shrublands to alien dominated grasslands (Syphard et al. 2006). In order to adequately understand the threat, more detailed studies of alien plant response to fires is needed and how these relate to changes in native response to frequent fires. However, studying this invasion process is difficult because young seral stands of chaparral often lack sufficient fuel continuity to carry a fire under experimental prescription burn conditions (typically < 15 kph wind speed and > 30% RH). However, autumn wildfires 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. Here we take advantage of a series of wildfires in southern California that burned a significant portion of the landscape in 2003. This landscape was dominated by the widespread evergreen chaparral shrub *Adenostoma fasciculatum* and in places mixed with lower stature sage scrub.

One edge of the very large 2003 Cedar Fire burned through a 3 year old burn scar of the Viejas Fire. In 2007 another series of wildfires burned through the same region and reburned more than 20,000 ha of the 2003 burn scars (Fig. 1). Two studies of postfire response of native and alien species were undertaken. In the Cedar Fire scar we compared recovery in sites 3 years old at the time of the fire with sites 24 years old at the time of the fire, and followed recovery for 1, 2, 5, & 6 years after fire. On sites burned in 2003, and then reburned in 2007, we compared vegetation recovery for the first two postfire years after each fire. At the time of the 2003 fires all sites were relatively mature stands 1-2 decades old and at the time of the 2007 reburns all stands were immature stands 4 years of age.

Methods

Study sites

In autumn of 2003 several major wildfires burned through San Diego County, California (Fig. 1). 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 3 years of recovery at the time of the Cedar Fire and are 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 at the time of the Cedar Fire. These are here referred to 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 the 1, 2, 5, and 6 years after fire.

In addition, in autumn of 2007 several large wildfires burned through the same region and overlapped in many places with the 2003 fire scar (Fig. 1). In a postfire study of fire severity impacts following the 2003 fires, we had recorded postfire recovery in permanent sites (Keeley et al. 2008), some of which 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 were excluded from analysis. This ad hoc experiment allowed us to compare the first two years postfire recovery in relatively mature stands, 9 - 31 years of age at the time of the 2003 fires, with recovery in immature stands, 4 years of age at the time of the 2004 fires.

Sampling methods

A site comprised a tenth hectare plot 20 x 50 m positioned parallel to the slope contour and subdivided into 10 x 10 m subplots, each with a nested 1 x 1 m quadrat, 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 estimated for higher densities. In the surrounding 10 x 10 m subplot, any additional species were recorded. All plant nomenclature follows Hickman (1993).

For fire severity estimates, the diameter of the smallest twig remaining on the two *Adenostoma fasciculatum* skeletons nearest to each 1-m^2 quadrat was recorded. Another measure of fire severity is 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 last fire due to the rarity of missing or extra rings (Keeley 1993) and the nearly 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 *Adenostoma fasciculatum* skeletons. The foundation for this estimate is the demonstration that higher fire intensities are correlated with the diameter of terminal branches on 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 were organized in an Access database and analyses and graphical displays were conducted with Systat 11.0 (Richmond, CA, USA). For data from the RH sites, comparisons of parameters from the 3 yr and 24 yr 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.

Results

Postfire recovery in 3 and 24 year sites burned in 2003

Sites 3 years old at the time of fire are here referred to as '3 year sites' and those sites 24 years old at the time of fire as '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. 2).

Stand age also had a very significant effect on seedling recruitment in the dominant chaparral shrub *Adenostoma fasciculatum*, with very high postfire seedling recruitment in the older stands but relatively little recruitment in the young sites (Fig. 3a). Resprouting success was also affected; 42% in the 3 year sites and 68% in the 24 year sites (P = 0.019). 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 old stands than in the 24 year stands (P = 0.012). The non-resprouting or obligate seeding shrub *Ceanothus greggii* was also apparently extirpated from the 3 year sites as no seedlings were found, whereas that species averaged 7,850 seedlings ha^{-1} on the 24 year sites. This inference is based on the assumption that the species occurred on the 3 year sites prior to the Cedar Fire, something that could not be verified because 3 year old *Ceanothus* would not have left any recognizable skeletons.

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 comprised nearly an order of magnitude lower density and were not significantly different in density from native annuals (P = 0.501). 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 in that consistently each year the native cover significantly exceeded the alien cover (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 5th year after fire *B. madritensis* was still the dominant on 3 year sites, with over 24% cover but the native shrub *A. fasciculatum* was close with 21%. At this time on the 24year 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. 4). 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. On 24 year sites no species was clearly dominant and natives exhibited a broad dominance diversity pattern (Fig. 4d). 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 m^2 (Figs. 5a,c,e) and this pattern remained 5 years after fire (Fig. 5b,d,f).

One difference not readily captured with these data is in the distinct difference in phenology between these sites of different prefire age. The marked dominance of alien annual grasses on the 3 year sites resulted in much earlier drying of the vegetation (Fig. 6a). The greater diversity and cover of natives on the 24 year sites comprised a flora of species with a longer growing season (Fig. 6b).

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

Comparing the first 2 years recovery following the 2003 fires with recovery after the repeat fires in 2007 showed that annuals greatly increased after the second fire (Fig. 7). Immediately after the second fire native and alien annuals had similar densities, but by the second year aliens far exceeded natives. The aliens most abundant after the second fire were *Bromus madritensis* and *Filago gallica* (Fig. 8). Several native annuals were also significantly favored by the second fire (Fig. 9).

Although native herbaceous perennials and shrubs tended to decline and subshrubs increase after the second fire, none of these changes were significant (Fig. 10). Subshrubs *Helianthemum scoparium* and *Lotus scoparius* exhibited large drops in density after the first year seedling recruitment following the 2003 fires (Figs. 11a,b). These fast growing sub-ligneous 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 (Fig. 11d). *Adenostoma fasciculatum* was a dominant at all sites and regenerated by both seedlings and resprouts and had only a slight downward trend in density after the second fire (Fig. 11c).

Discussion

Chaparral shrublands are adapted to a crown fire regime of fires on a frequency of 10^2 to 10^3 years (Keeley et al. 2011a). 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 deeply buried and germinate in response to heat-shock or smoke from fire. These communities are highly resilient to fire and generally reach maturity between one to two decades after fire.

A major perturbation to this ecosystem is an increase in fire frequency that generates short fire intervals and this has been implicated in alien plant invasions (Keeley 2006). As seen in this study short intervals between fires greatly facilities the increase in alien species. This is facilitated by a reduction in native species. Although most native herbaceous and woody species persist in the face of short interval fires, populations often decline and sometimes are extirpated. 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 *Adenostoma 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. 3). However, there is some variability in the impact of short interval fires on this widespread species, as illustrated by Figure 11c. Under such changes in fire regime these chaparral communities suffer a reduction in species diversity and change in community structure (Figs. 4 & 5). This appears to be a common pattern in mediterranean-climate crown fire shrublands such as in Australia, where short fire-intervals are also responsible for losses in biodiversity and 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).

In 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 (Fig. 7). Native annuals have an advantage under longer fire intervals where fire intensity/severity is elevated (e.g., Fig. 2). Native seeds are mostly small and readily buried and deeply dormant, whereas most alien grasses have larger seeds that often remain on the soil surface and have limited dormancy. Under long fire-free periods the alien seed banks diminish and as fuels accumulate they 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 for greatly altering 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 very 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 *Adenostoma 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 (e.g., Fig. 3a). As alien grasses increase on a site it 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 aggessive invader capable of rapidly capitalizing on short fire intervals. This is a widespread pattern in the southwestern US 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 evident by the invasion of the Great Basin sage shrublands by *Bromus tectorum* (Mack 1981). Throughout this extensive area numerous disturbances have played a role in the invasion process, however, these sage scrub systems are adapted to an infrequent crown fire regime, and thus are susceptible to invasion when fire frequency increases. Some of this invasion appears to have started early in the 20th century with the practice of prescription burning of sage scrub for sheep range improvement (Pechanec 1944).

Of course this spread of alien grasses and forbs and type conversion from woody to herbaceous vegetation is not solely dependent on accelerated fire frequency. Other disturbances may stress native shrublands and replace them with more tolerant alien grasses and forbs. 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 leading to conversion from shrublands to grasslands (Keeley 2005), but in the Southwest U.S., mesquite (*Prosopis* spp) shrubs are spiny and deter livestock browsing, often resulting in 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 sort out 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 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 it alone can effect 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 dependent on prior fire history. However, in another study pollution was correlated with alien success on sites with little prior fire history (Talluto & 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 for reducing native cover and enhancing 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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Table 1. Cover of alien and native plants on sites 3 years old 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	6
Alien	19	33	34	23	3	19	24	10
Native	24	19	46	38	26	42	57	42
P	.268	.035	.577	.278	.005	.001	.039	.010

Figure legends

Fig 1. Overlap of fire perimeters for major fires in 2003 and 2007 in San Diego County, California; from north to south the 2003 fires (green shading) were the Paradise, Cedar and Otay fires and the 2007 fires were the Poomacha, Witch, and Harris fires (from Keeley et al. 2009b).

Fig. 2. Measures of fire severity based on (a) the diameter of the smallest twigs on *Adenostoma fasciculatum* skeletons and (b) height of skeletons on the RH sites with different prefire ages burned in the 2003 Cedar Fire.

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

Fig. 4. Dominance diversity patterns on RH sites for aliens (a,b) and natives (c,d) on sites 3 years old or 24 years old at the time of the 2003 Cedar Fire (% GSC = percentage ground surface covered).

Fig. 5. Species diversity patterns in the RH sites at different scales in the 3 year old prefer sites (a,c,e) and the 24 year old prefire sites (b,d,f).

Fig. 6. Examples of (a) a site 3 years old and (b) 24 years old at the time of the Cedar Fire at the RH sites taken in July 2 years after the fire (photos by T.J. Brennan).

Fig. 7. (a) Native annuals and (b) alien annuals on sites in the 2003 Cedar and Otay fires reburned by the 2007 Witch and Harris fires, respectively.

Fig. 8. Species responses of (a,b) alien annual grasses and (b) alien annual forbs on sites in the 2003 Cedar and Otay fires reburned by the 2007 Witch and Harris fires.

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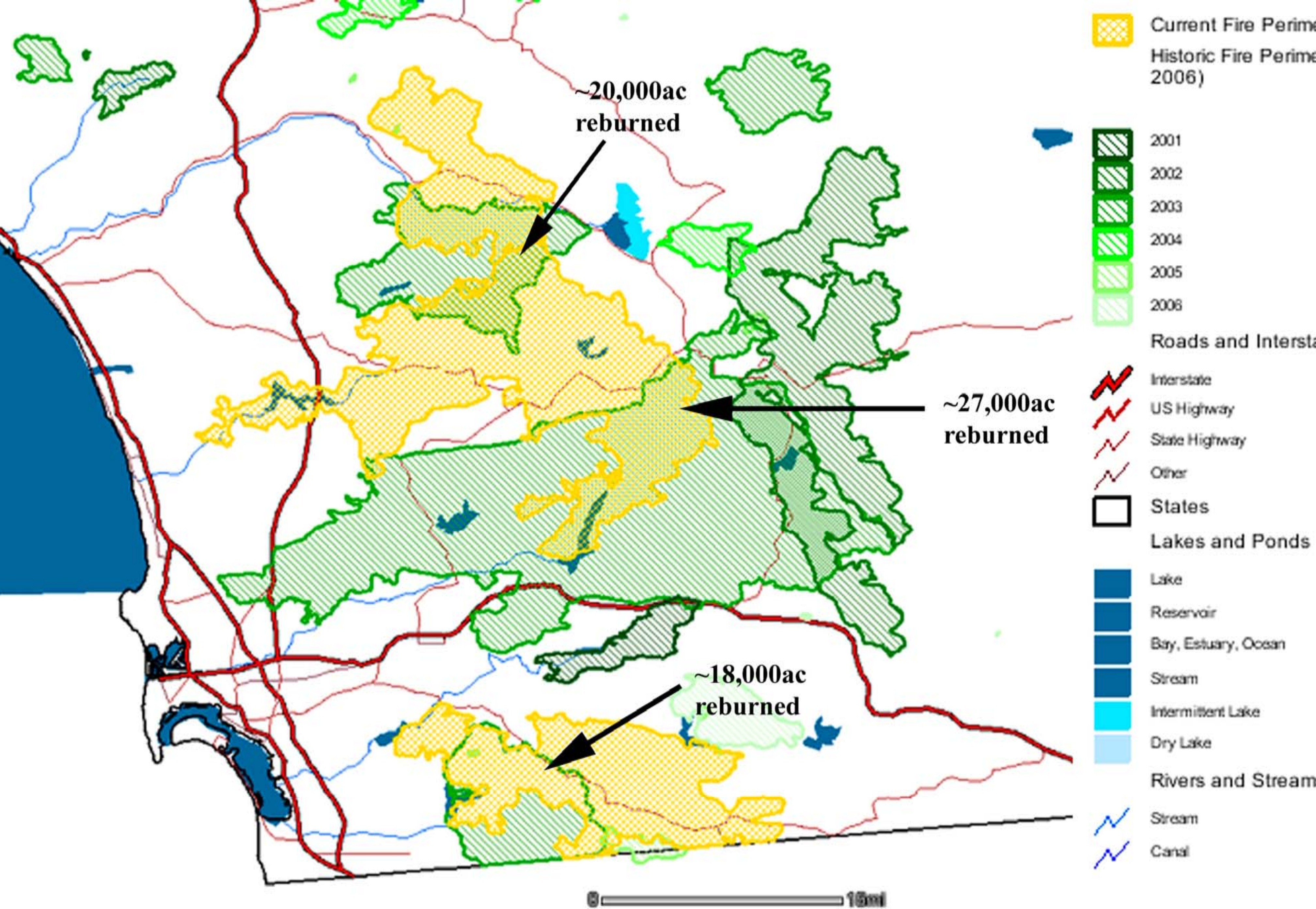
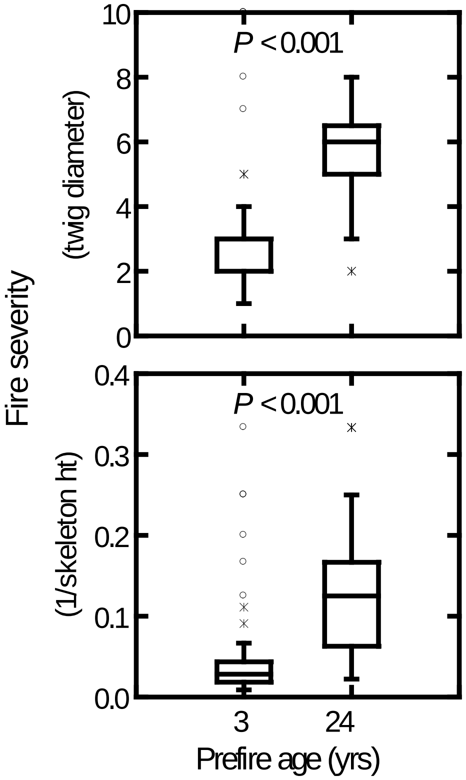
Fig. 9. Species responses of native annual (a,b,c) forbs and (d) grass on sites in the 2003 Cedar and Otay fires reburned by the 2007 Witch and Harris fires.

Fig. 10. Perennial life form responses on sites in the 2003 Cedar and Otay fires reburned by the 2007 Witch and Harris fires.

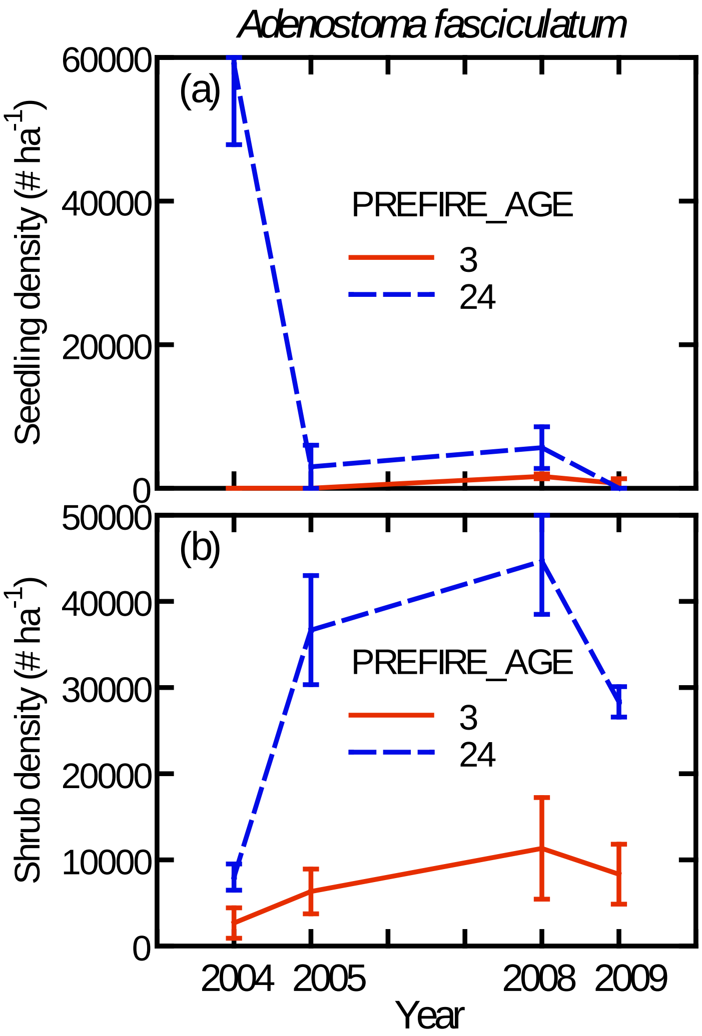
Fig. 11. Species responses of native perennial (a,b) subshrubs and (c,d) shrubs on sites in the 2003 Cedar and Otay fires reburned by the 2007 Witch and Harris fires.


~20,000ac reburned
~27,000ac reburned
~18,000ac reburned
Current Fire Perime
Historic Fire Perime
2006)
2001
2002
2003
2004
2005
2006
Roads and Intersta
Interstate
US Highway
State Highway
Other
States
Lakes and Ponds
Lake
Reservoir
Bay, Estuary, Ocean
Stream
Intermittent Lake
Dry Lake
Rivers and Stream
Stream
Canal
0
15mi



Fire severity
(twig diameter)
(1/skeleton ht)
P < 0.001
P < 0.001
10
8
6
4
2
0
0.4
0.3
0.2
0.1
0.0
3
24
Prefire age (yrs)

Figure 2



Adenostoma fasciculatum
(a)
Seedling density (# ha-1)
60000
40000
20000
0
PREFIRE_AGE
3
24
(b)
Shrub density (# ha-1)
50000
40000
30000
20000
10000
0
PREFIRE_AGE
3
24
2004
2005
2008
2009
Year

Figure 3

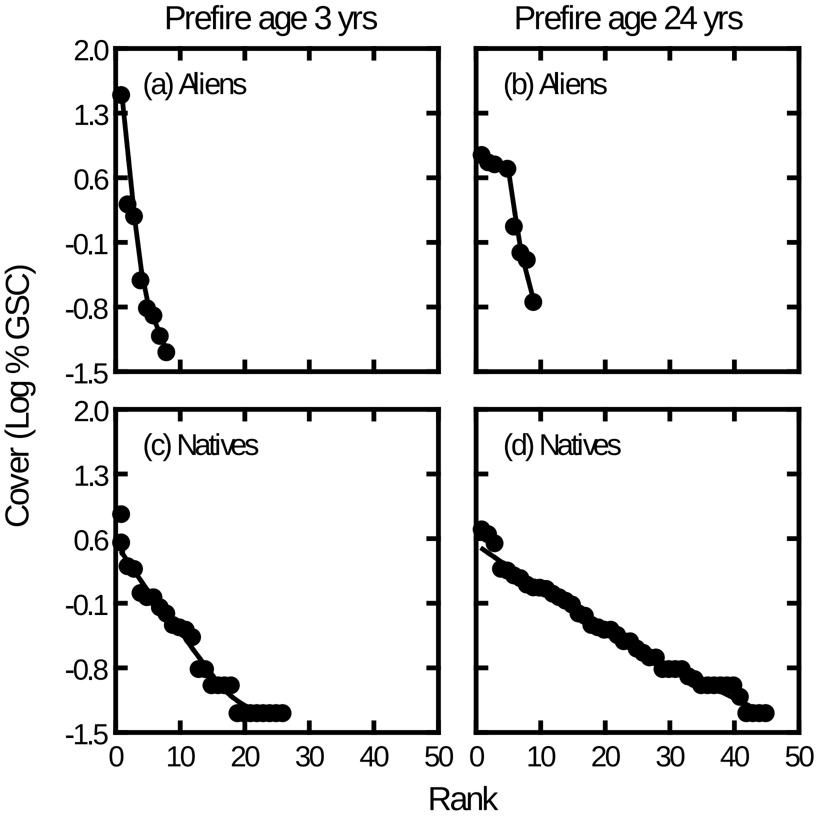
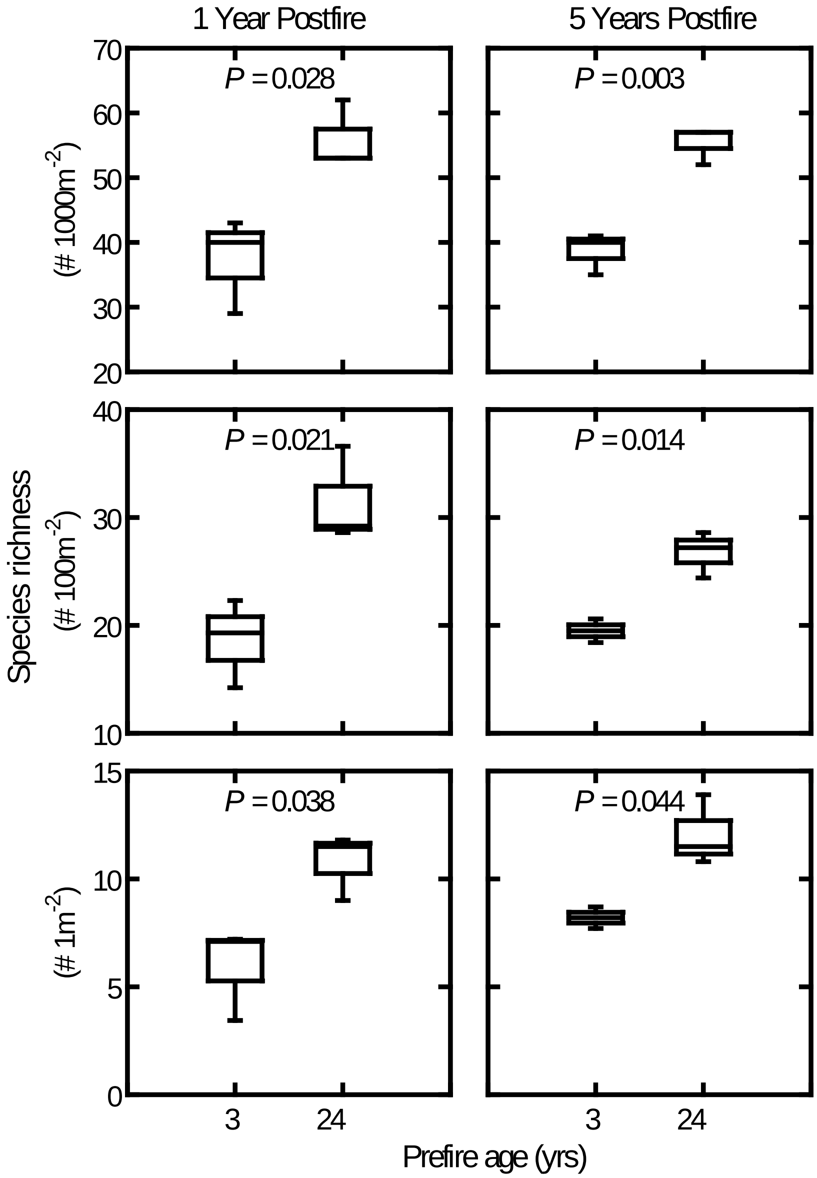

Prefire age 3 yrs
Prefire age 24 yrs
(a) Aliens
(b) Aliens
(c) Natives
(d) Natives
Cover (Log % GSC)
2.0
1.3
0.6
-0.1
-0.8
-1.5
0
10
20
30
40
50
Rank

Figure 4



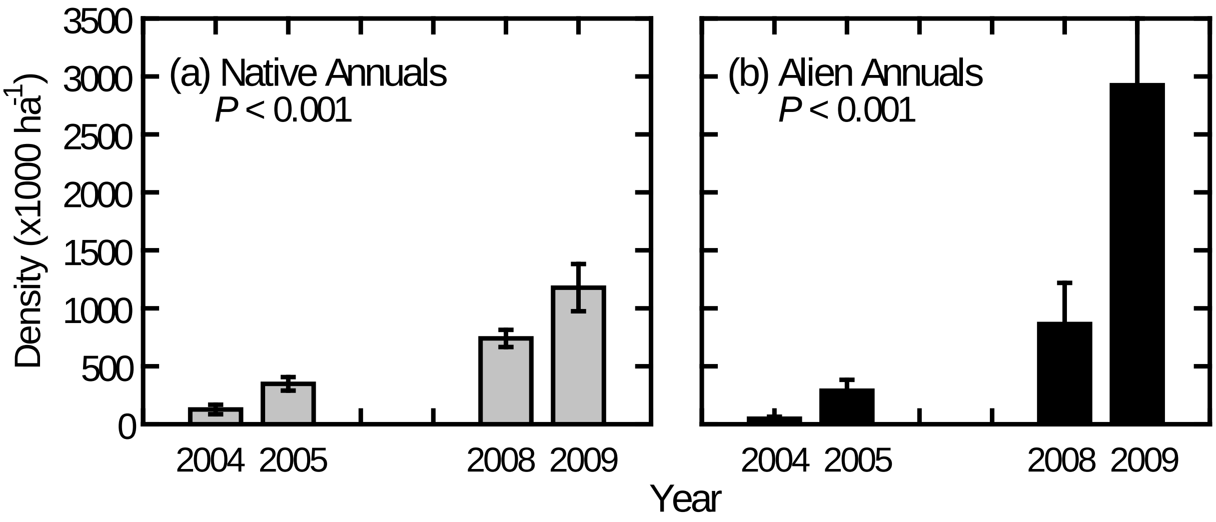
1 Year Postfire
5 Years Postfire
P = 0.028
P = 0.003
P = 0.021
P = 0.014
P = 0.038
P = 0.044
70
60
50
40
30
20
40
30
20
10
15
10
5
0
(# 1000m-2)
Species richness
(# 100m-2)
(# 1m-2)
3
24
3
24
Prefire age (yrs)

Figure 5

a) Prefire age 3 years

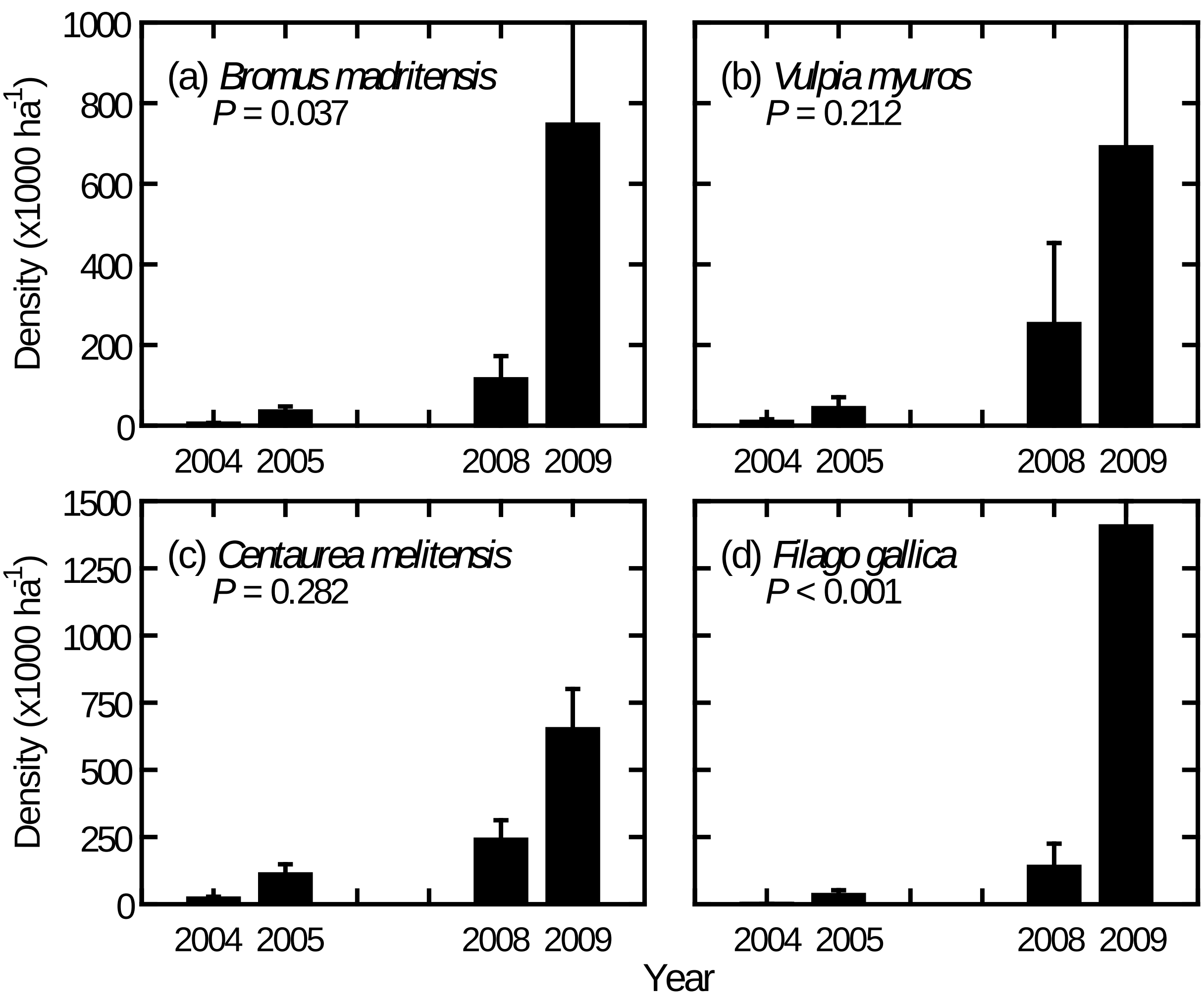
b) Prefire age 24 years

Figure 6



(a) Native Annuals
$P < 0.001$
(b) Alien Annuals
$P < 0.001$
Density (x1000 ha^{-1})
3500
3000
2500
2000
1500
1000
500
0
2004
2005
2008
2009
2004
2005
2008
2009
Year

Figure 7



(a) *Bromus madritensis*
P = 0.037
(b) *Vulpia myuros*
P = 0.212
(c) *Centaurea melitensis*
P = 0.282
(d) *Filago gallica*
P < 0.001
Density (x1000 ha^{-1})
0
200
400
600
800
1000
0
250
500
750
1000
1250
1500
2004
2005
2008
2009
Year

Figure 8

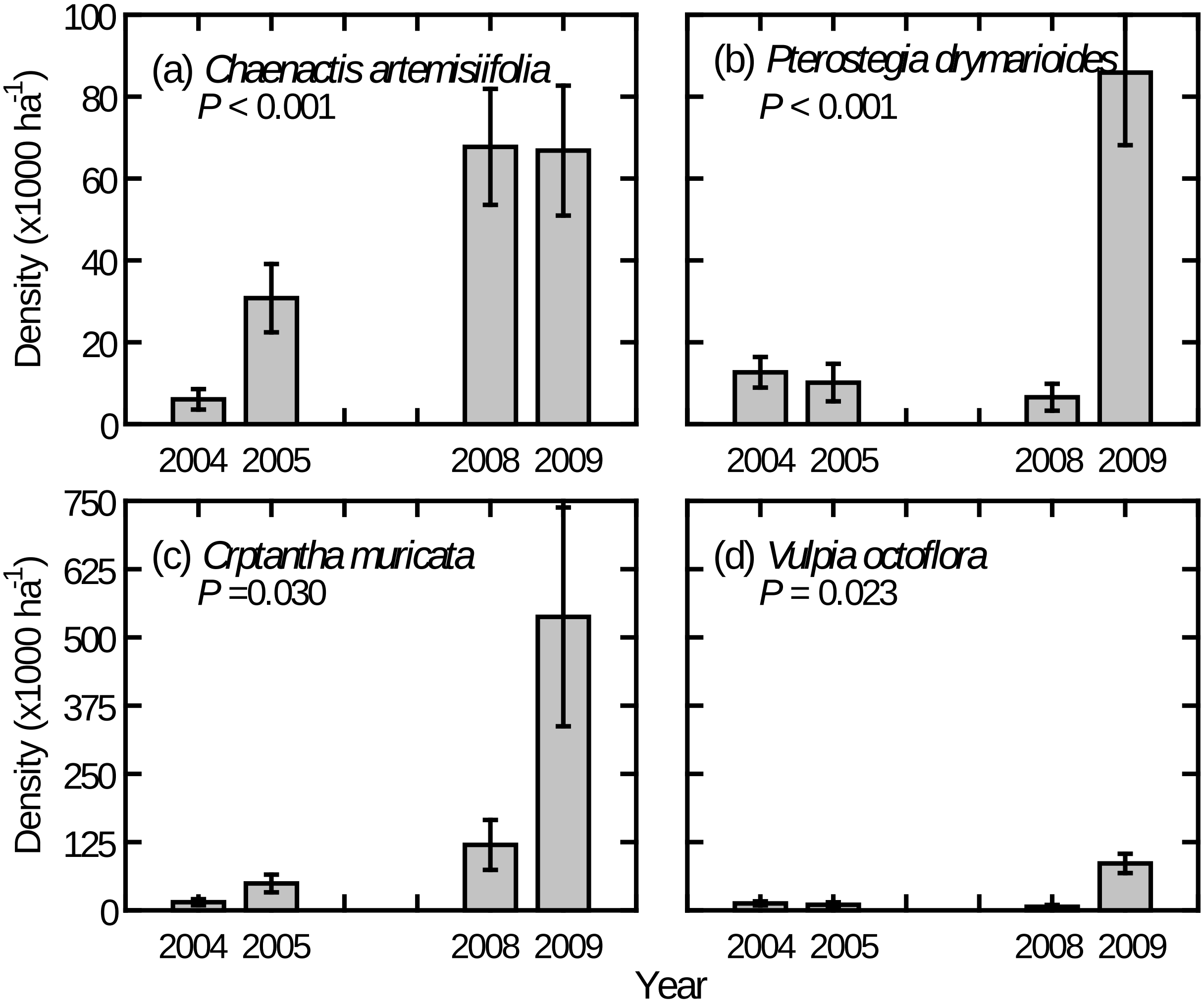

(a) *Chaenactis artemisiifolia*
$P < 0.001$
(b) *Pterostegia drymarioides*
$P < 0.001$
(c) *Crptantha muricata*
P =0.030
(d) *Vulpia octoflora*
$P = 0.023$
Density (x1000 ha^{-1})
0
20
40
60
80
100
0
125
250
375
500
625
750
2004
2005
2008
2009
Year

Figure 9

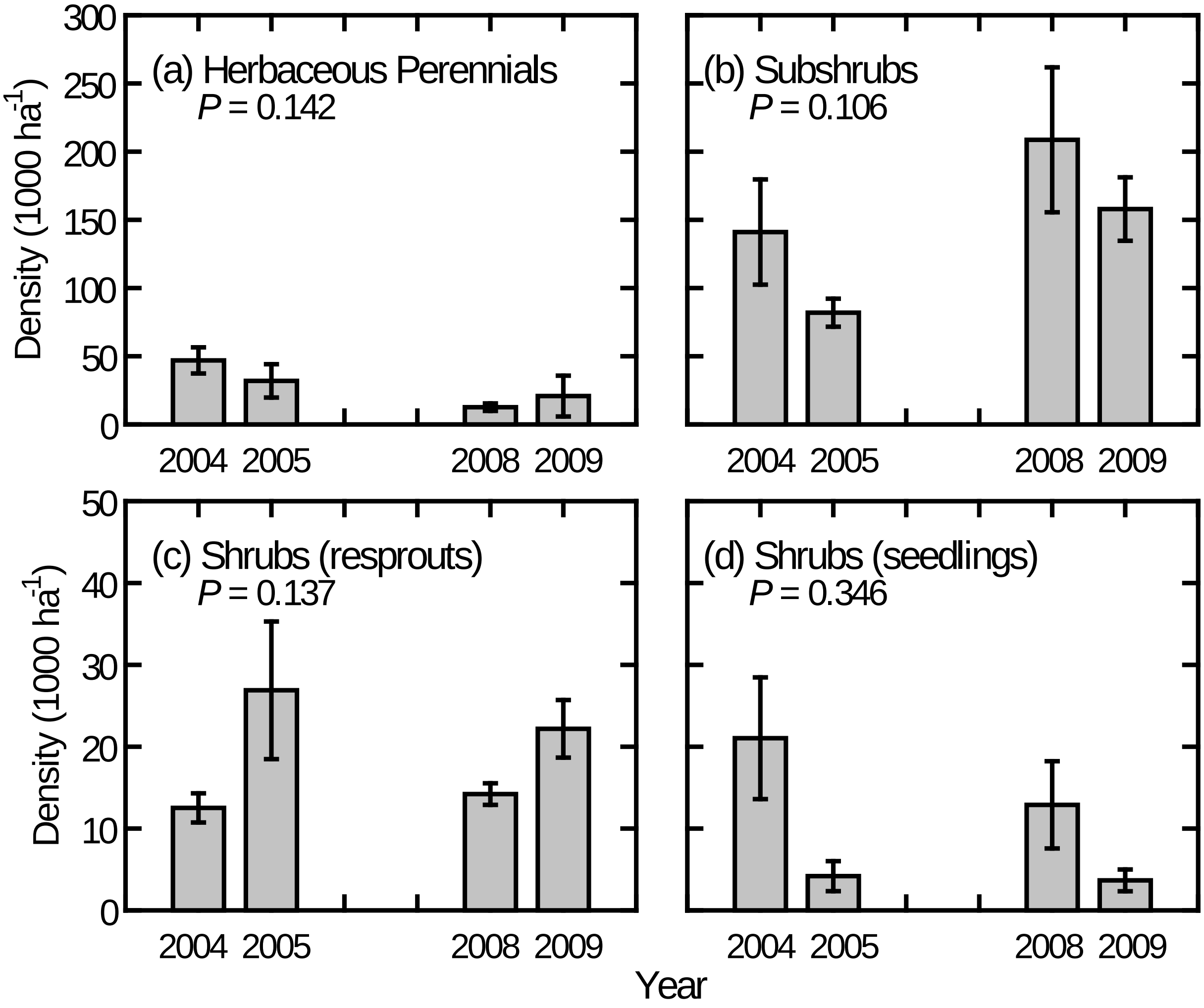

(a) Herbaceous Perennials
P = 0.142
(b) Subshrubs
P = 0.106
(c) Shrubs (resprouts)
P = 0.137
(d) Shrubs (seedlings)
P = 0.346
Density (1000 ha-1)
Density (1000 ha-1)
300
250
200
150
100
50
0
50
40
30
20
10
0
2004
2005
2008
2009
Year

Figure 10

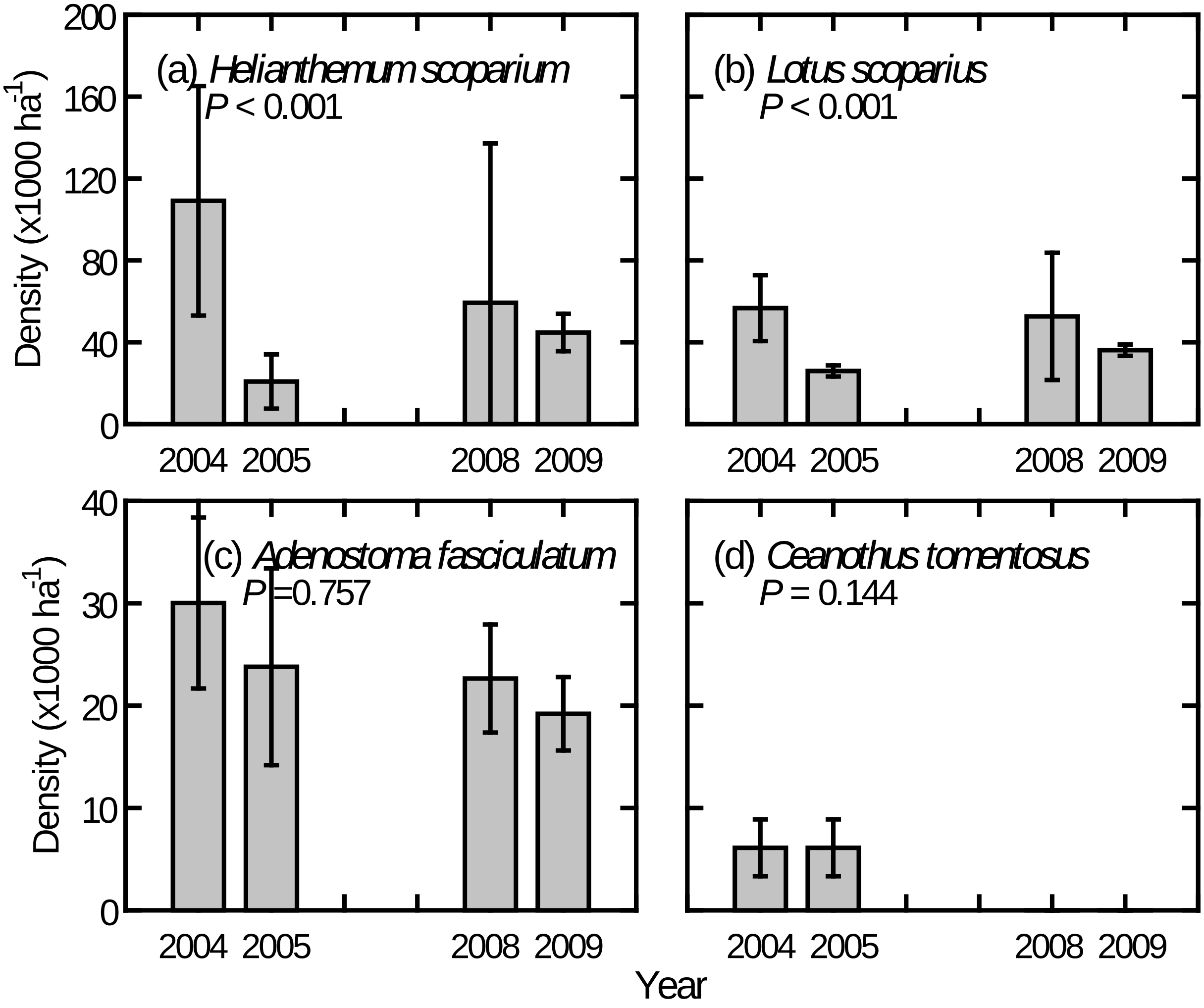

(a) *Helianthemum scoparium*
P < 0.001
(b) *Lotus scoparius*
P < 0.001
(c) *Adenostoma fasciculatum*
P =0.757
(d) *Ceanothus tomentosus*
P = 0.144
Density (x1000 ha^{-1})
200
160
120
80
40
0
40
30
20
10
0
2004
2005
2008
2009
Year

Figure 11