Diversity and Distributions, (Diversity Distrib.) (2011) **17**, 58–67

BIODIVERSITY RESEARCH

Anthropogenic fires increase alien and native annual species in the Chilean coastal matorral

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ABSTRACT

Aim We tested the hypothesis that anthropogenic fires favour the successful establishment of alien annual species to the detriment of natives in the Chilean coastal matorral.

Location Valparaíso Region, central Chile.

Methods We sampled seed rain, seedbank emergence and establishment of species in four paired burned and unburned areas and compared (using GLMM) fire resistance and propagule arrival of alien and native species. To assess the relative importance of seed dispersal and seedbank survival in explaining plant establishment after fire, we compared seed rain and seedbank structure with post-fire vegetation using ordination analyses.

Results Fire did not change the proportion of alien species in the coastal matorral. However, fire increased the number of annual species (natives and aliens) of which 87% were aliens. Fire reduced the alien seedbank and not the native seedbank, but alien species remained dominant in burned soil samples (66% of the total species richness). Seed rain was higher for alien annuals than for native annuals or perennials, thus contributing to their establishment after fire. Nevertheless, seed rain was less important than seedbank survival in explaining plant establishment in burned areas.

Main conclusions Anthropogenic fires favoured alien and native annuals. Thus, fire did not increase the alien/native ratio but increased the richness of alien species. The successful establishment of alien annuals was attributable to their ability to maintain rich seedbanks in burned areas and to the greater propagule arrival compared to native species. The native seedbank also survived fire, indicating that the herbaceous community has become highly resilient after centuries of human disturbances. Our results demonstrate that fire is a relevant factor for the maintenance of alien-dominated grasslands in the matorral and highlight the importance of considering the interactive effect of seed rain and seedbank survival to understand plant invasion patterns in fire-prone ecosystems.

Keywords
Biological invasions, central Chile, disturbance ecology, mediterranean-type ecosystems, plant invasions, propagule pressure, seedling emergence.

INTRODUCTION

Fire is a common driver of alien plant invasion in ecosystems around the world (D'Antonio, 2000). However, general rules on the relationship between fire and non-native species remain elusive. This is because the invasibility of a given ecosystem after fire depends on the interaction of a complex set of factors including historic fire regime, biological characteristics of alien and native species, and propagule supply (Zouhar *et al.*, 2008). Understanding the relative role of such factors in explaining invasion patterns after fire is a major challenge in ecology (D'Antonio *et al.*, 2001) and crucial for effective management

DOI:10.1111/j.1472-4642.2010.00728.x
http://wileyonlinelibrary.com/journal/ddi

and conservation of natural communities. This is particularly relevant in biodiversity hot spots such as mediterranean-type ecosystems, where mild climatic conditions attract people from everywhere (source of aliens) and fire frequency is increasing owing to global climate change (Pausas, 2004; Running, 2006).

It has been suggested that plant communities under novel fire regimes are more susceptible to invasion than those under a natural (historical) fire regime (Trabaud, 1991; D'Antonio, 2000). For example, in most mediterranean-type ecosystems, fire has been an important selective force shaping adaptive traits in native plant species (e.g. Pausas *et al.*, 2006). Under conditions of natural fire frequency, the ability of native species to cope with fire leads to a relatively high resilience to invasion, because alien species that colonize open areas are rapidly excluded from the system (Trabaud, 1991; Keeley, 2006). Conversely, in those ecosystems where fire frequency is higher than the historical fire regimes, it reduces the native vegetation and seedbank, thus generating a more favourable environment for colonization and establishment of alien species (Zouhar *et al.*, 2008). This idea fits to the 'alteration of selection regimes' hypothesis (Byers, 2002), which proposes that anthropogenic disturbances may suddenly put previously well-adapted native species at a competitive disadvantage with non-native species, thus promoting the invasion process.

Unlike other mediterranean-type ecosystems, recurrent fires play a little role in the evolutionary history of the Chilean matorral (Aravena *et al.*, 2003; Villa-Martínez *et al.*, 2003). However, palaeoclimatic records based on fossil charcoal suggest that anthropogenic fires appeared with the first indigenous settlements (14000 yr BP), with several peaks of fire activity between 2000 and 5000 yr BP, and then fire frequency increased exponentially from the time of the Spanish colonization (1536) to the present (Aravena *et al.*, 2003; Villa-Martínez *et al.*, 2003). Although most of the native woody species resprout after fire (Araya & Ávila, 1981), post-fire seed germination of local populations is generally inhibited by the heat shock and smoke produced by fires (Muñoz & Fuentes, 1989; Segura *et al.*, 1998; Gómez-González *et al.*, 2008; Gómez-González & Cavieres, 2009). Some native herbs have a certain resistance to moderate fires (Gómez-González & Cavieres, 2009; Figueroa *et al.*, 2009), but there is no fire-enhanced recruitment as reported in the other mediterranean-type ecosystems (Keeley & Fotheringham, 2000; Moreira *et al.*, 2010).

The Chilean matorral has been strongly modified by human activities (logging, burning, grazing, etc.) and currently consists of clumps of shrubs and trees surrounded by a seasonal herbaceous matrix dominated by alien plants (Keeley & Johnson, 1977; Fuentes *et al.*, 1984; Montenegro *et al.*, 1991; Holmgren *et al.*, 2000). The percentage of alien species ranges from 20 up to 50% in the coastal range (Figueroa *et al.*, 2004), and most of them are annual grasses and forbs coming from the Mediterranean Basin (Montenegro *et al.*, 1991). Annuals from the Mediterranean Basin are successful invaders in ecosystems with frequent, human-made fires (D'Antonio & Vitousek, 1992; Norton *et al.*, 2007), because they are very competitive in the open spaces created after fire (high irradiance, mortality of native species, high resource availability, etc.). Probably, this is because the Mediterranean Basin had long history of (natural and anthropogenic) disturbances such as fire (Daniau *et al.*, 2007; Pausas & Keeley, 2009) and livestock grazing (Perevolotsky & Seligman, 1998). The contrast in the fire history between the Chilean matorral and the original habitats of alien species suggests that fire could favour the invasion process by producing more negative effects on native species. For example, there is evidence that the seedbank of native matorral species is more sensitive to high-intensity fires than the seedbank of coexisting alien species (Gómez-González & Cavieres, 2009). Some field studies have reported that alien species are favoured over natives in recently burned sites (Ávila *et al.*, 1981; Sax, 2002), while other studies found no effects (Keeley & Johnson, 1977; Holmgren *et al.*, 2000). This discrepancy may be related to differences between sites in terms of seedbank composition, level of grazing and propagule availability; therefore, field studies where these confounding factors are controlled are needed.

Invasion success after fire also depends on the availability and mobility of propagules from adjacent unburned areas. In ecosystems where fire is not a historical natural disturbance (such as the Chilean matorral), the resistance to invasion after fire should be relatively low and alien plant establishment may be favoured even in conditions of low propagule supply (D'Antonio *et al.*, 2001). Despite the fact that propagule availability is regarded as an important factor affecting ecosystem invasibility (Lockwood *et al.*, 2005; Von Holle & Simberloff, 2005), it has rarely been considered in studies of biological invasions (Colautti *et al.*, 2006). Furthermore, few studies have quantitatively evaluated the relative influence of propagule supply and biotic resistance in determining invasion patterns after fire (D'Antonio *et al.*, 2001; Zouhar *et al.*, 2008).

We tested the hypothesis that fire increases the establishment of alien annual plants (in relation to native species) and that this process is attributable to a more resistant seedbank in aliens than in native species. Alternatively, the increase in alien annuals may be driven by a larger seed rain. To test this hypothesis, we studied seed rain, emergence and establishment of alien and native species in paired burned and unburned areas in four coastal matorral communities of Chile.

METHODS

Study sites

This study was carried out during 2006 and 2007 on the western foothills of the coastal range in the Region of Valparaíso (central Chile). The climate is mediterranean, with a rainy cold season from May to September and a longer warm dry season from October to April (DiCastri & Hajek, 1976). During the study period, from January to November 2006 and 2007, the accumulated precipitation was 238 and 204 mm (respectively), and the mean temperature was 14.5 and 13.9°C

(Dirección Meteorológica de Chile, http://www.meteochile.cl/climatologia.html; Accessed 2006–2007).

We focused on secondary-type matorral communities (the most common successional stage today), which are characterized by patches of native shrubs and trees, such as *Lithraea caustica*, *Peumus boldus*, *Retanilla trinervia* and *Quillaja saponaria*, and a seasonal herbaceous layer. We localized four sites with the following characteristics: (1) within a given site, there was a recent burned area next to an unburned area with similar slope and aspect (paired design); (2) vegetation structure (which varies depending on historical human activities) was similar among different sites; and (3) sites had relatively high canopy cover (≥ 50%), indicating no severe land use. Three of the sites (Lo Orozco, Los Perales and Los Molles) burned in January–February 2006 and were sampled in 2006/2007, while El Álamo burned in January 2007 and was sampled in 2007/08. None of these sites burned in the previous 20 years, except Lo Orozco, which burned twice in that period (in 1985 and 1989; C. Echeverría, personal communication) (See Table S1 in Supporting Information for more details on study sites).

Sampling design

We established a block design, where each of the four sites was regarded as a block. Within each site (block), we delimited a burned plot (20 × 100 m) and a close unburned plot (same dimensions) with similar slope and aspect. The distance between these paired plots (burned and unburned) ranged from 100 to 200 m depending on the site, but in all cases, burnt plots were close (< 50 m) to unburned areas. We established 20 sampling points along the longest side of each plot at intervals of 5 m, which were randomly located in the 20 m width of the plot. Preliminary analysis suggested that this number of sampling points per area (20) was appropriate for the variability in the species composition of the herbaceous layer at this spatial scale. At each sampling point, we established a permanent 0.5 × 0.4 m subplot (0.2 m^2) from which we sampled the following: (1) soil seedbank immediately after fire (summer), (2) seed rain in burned plots during the dispersal season (late summer to late autumn) and (3) vegetation established (in 0.25 × 0.50 m) during the flowering season (next spring). To avoid the confounding effects of granivory and herbivory during the sampling, all subplots were protected by a wire mesh cage (0.50 m long × 0.40 m wide × 0.40 m high) with openings of 2 cm diameter, so birds and rodents were excluded but the seed rain was not impeded (the largest seeds in the system are from the tree *Q. saponaria*, which passed through the holes perfectly).

Soil seedbank

Soil seedbank was sampled during the first week following the fire so as to avoid collecting seeds coming from post-fire dispersal processes. Soil samples were collected with a metal soil core (5 cm in diameter and 10 cm in depth), sealed in paper bags and transported to the laboratory. Then, each sample was spread on a 500-cm^3 plastic tray, placed in a greenhouse, and watered and checked daily for seedling emergence. After 90 days, soil samples were disturbed by turning the soil, so as to stimulate further seedling emergence. Germination was then monitored for five additional months (i.e. when no additional seedlings emerged). Finally, we calculated the species richness and abundance of all native and alien species in each soil sample. To correctly identify all of the species, several seedlings per species were grown until flowering (nomenclature follows Marticorena & Quezada, 1985).

Propagule arrival at burned areas (seed rain)

While we collected soil seedbank samples, we also placed a seed trap at each sampling point ($n = 20$) of the burned plots. Seed traps were plastic dishes (12 cm diameter; 0.013 m^2) impregnated with waterproof glue (Tanglefoot®, Contech Enterprises Inc., Victoria, Canada). They were collected and replaced by new traps every 2 weeks, during the whole dispersal period after fire (i.e. from late summer to late autumn). In the laboratory, seed traps were carefully checked with a stereoscopic microscope. Only seeds that looked healthy (unburned) and filled with an embryo were regarded as viable. Seeds were identified by comparing with seeds and fruits collected in mature plants in the study sites. When the identification was not possible, seeds were germinated and seedlings grown in a growth chamber until they flowered. Then, we calculated the species richness and the abundance of alien and native propagules that accumulated at each burned subplot at the end of the dispersal season.

Plant establishment after fire

Plant establishment was sampled the next spring following the fire (8 months after fire). Given that plant phenology is not synchronic, we performed two complementary samplings, one in late September and the other in late November. We counted and identified all established plant individuals in the herbaceous layer (i.e. grasses, forbs, bulbs and seedlings of shrubs and trees) within each subplot (0.125 m^2) (the full species list is provided in Appendix S1). As we were interested in those plants established from seeds after fire, we marked all the resprouting individuals at the beginning of the rainy season (autumn) to discard them during the following sampling visits.

Data analysis

Because almost all alien species were annuals (we found only two alien perennials in a few samples) and native species include both annuals and perennials, all statistical analyses were performed for alien annuals (grasses and forbs), native annuals (grasses and forbs) and native perennials (i.e. grasses, geophytes and seedlings of shrubs and trees), separately. We evaluated the effect of fire on the species richness and abundance of each of these three functional groups using generalized linear mixed models (GLMM) (lm4 library; R 2.8.0 software, R Development Core Team, 2008), where fire was considered as fixed factor and site (block) as random factor. Then, considering only the annual species, we compared the response to fire of native and alien species using two-factor GLMM, where fire and the species origin (native or alien) were the fixed factors, site was the random factor, and the species richness and abundance were the dependent variables (with Poisson error distribution). Additionally, we evaluated the effect of fire on the percentage of alien species (GLMM with binomial distribution), first considering only annual species and then including the whole species pool (annuals and perennials). All these GLMM were performed for vegetation data (establishment) and for seedbank data (emergence). Differences in propagule arrival at burned plots of native species (annuals and perennials) and alien species were analysed also using a GLMM (Poisson error distribution). In the latter, the fixed factor was the functional group. In all GLMM, the effect of the fixed factors was evaluated by model selection and likelihood ratio (LR) test (estimate parameters of the final models are provided in Tables S2 and S3), while the random factor (site) was included as a variance component and not as a factor of interest (Crawley, 2007).

To quantitatively determine the relative importance of soil seedbank and seed rain in explaining plant establishment after fire, we used non-metric multidimensional scaling (NMS) ordination analyses on samples of soil seedbank, seed rain, and established vegetation (MASS library; R 2.8.0 software, R Development Core Team, 2008) (see Figs S1 and S2). For each site, we applied one NMS for presence/absence data (using a similarity matrix for binary data) and another NMS for abundance data (using the Sorensen index). Then, we calculated the mean distance ($n = 4$ sites) between vegetation and seedbank ordination centroids and the mean distance between vegetation and seed rain ordination centroids for the two NMS ordinations (occurrence and abundance). Finally, we evaluated the differences in these two distances (by a paired t-test) to determine whether the structure of the established vegetation is more similar to that of the seedbank or of the seed rain.

RESULTS

Effect of fire on the establishment of native vs. alien species

Eight months following the fires, we found (in all sites and fire conditions) a total of 57 species successfully established in the herbaceous layer: 29 (50.9%) natives and 28 (49.1%) aliens. Among the natives, 13 species (44.8%) were annuals and 16 (55.2%) were perennials. Among the aliens, 26 species (98.2%) were annuals and only two (1.8%) were perennials. That is, overall, 26 out of the 39 annual species were aliens (2/3), while only 2 out of the 18 perennials were alien. In unburned sites, the more frequent alien species were the annual grasses *Bromus hordeaceus* (20.5% of the total plant abundance, on average, n = 4), *Aira caryophyllea* (11.1%) and *Vulpia myuros* (10.9%) and the forb *Euphorbia peplus* (11.40%), while the more frequent native species were the annuals *Bromus berteroanus* (4.8%), *Pectocarya linearis* (1.2%) and *Oxalis micrantha* (0.9%). In burned areas, the alien *A. caryophyllea* becomes more frequent (21.3%) together with *V. myuros* (12.5%) and the annuals *Hypochaeris glabra* (9.9%) and *Briza minor* (5.6%). The annual grass *B. berteroanus* (5.1) remains as the more frequent native species in burned areas, with the geophyte *Dioscorea humifusa* (1.8%) and the annual forb *Plantago firma* (0.9%).

Fire significantly increased the number of annual species, both alien and native, but did not affect the number of native perennial species (Table 1; Fig. 1a) (see mean values in Table S4). Alien and native annual species showed the same response to fire (no significant *fire × origin* interaction; Table 1), and, as a consequence, there was no change in the proportion of alien annual species established after fire (87% in unburned plots and 86.8% in burned plots, on average, $n = 4$ sites) (Tables 1 and S4). Similarly, fire did not change the proportion of alien species when considering the whole species pool (71.3% and 74% in burned and unburned plots, respectively, $n = 4$ sites) (Tables 1 and S4). Fire did not affect plant abundance of any functional group (Table 1).

Effect of fire on native vs. alien seedbanks

Regarding all sites and fire conditions, we found a total of 58 species in the soil seedbank, of which 28 (48.3%) were natives and 30 (51.7%) were aliens. Among the natives, 14 species (50%) were annuals and 14 (50%) were perennials, while alien species were all annuals. That is, 30 out of the 46 annuals species were aliens (65%), while none of the perennials were aliens. The main alien species in the seedbank of the unburned areas were the grasses *V. myuros* (18.1% of the total seedling abundance, on average, $n = 4$ sites), *A. caryophyllea* (13.4%) and *B. minor* (9.6%), and the main native species were the annual grass *B. berteroanus* (4.8%) and *O. micrantha* (3.9%). In burned areas, the same alien and native species dominated the seedbank, but they changed their relative importance (*A. caryophyllea* 28.4%; *B. minor* 9.2%; *B. berteroanus* 8.6%; *O. micrantha* 6%; *V. myuros* 5.9%).

Fire significantly reduced the number of annual species in the soil seedbank (Table 1), but this tendency was driven by the negative effect on alien annual species, so that there were no effects on native annual species (significant *fire × origin* interaction; Table 1, Fig. 1b). Despite this, the proportion of alien annual species in the soil seedbank did not change significantly by fire (81.8% in unburned plots and 77.8% in burned plots, on average, $n = 4$ sites) (Tables 1 and S4). Fire did not change the number of native perennial species in the soil seedbank (Fig. 1b, Table 1). When considering all native species together, fire did decrease the proportion of alien species in the soil seedbank (from 74.5% in unburned plots to

Table 1 Likelihood ratio test results for vegetation and seedbank species richness and abundance.

		Vegetation		Seedbank	
Source of variation	Factor	χ^2	*P*	χ^2	*P*
Native perennials					
Species richness	Fire	0.01	0.925	0.05	0.819
Abundance	Fire	1.28	0.256	0.01	0.899
Native annuals					
Species richness	Fire	4.24	0.039	2.76	0.096
Abundance	Fire	0.01	0.918	0.54	0.460
Alien annuals					
Species richness	Fire	12.14	< 0.001	5.37	0.020
Abundance	Fire	1.33	0.248	1.87	0.171
Annual species					
Species richness	Fire	14.16	< 0.001	46.07	< 0.001
	Origin	8.6	0.003	19.7	< 0.001
	Fire × origin	0.03	0.857	9.8	0.002
Abundance	Fire	0.01	0.914	2.35	0.125
	Origin	240.93	< 0.001	109.43	< 0.001
	Fire × origin	3.10	0.078	2.94	0.086
Proportion of alien annual species (relative to all annual species)	Fire	0.330	0.565	1.05	0.306
Proportion of alien species (relative to all species pool)	Fire	0.08	0.775	10.37	0.001

The effect of fire on each functional group separately is shown (alien annuals, native annuals and native perennials). For annual species (natives and aliens), the interaction fire by origin is also shown. See the estimate parameters of the best-fitted models (generalized linear mixed model) in Table S2.

65.8% in burned plots, on average, $n = 4$ sites) (Fig. 1b, Tables 1 and S4).

There were no significant differences in the abundance of seedling that emerged from burned and unburned soil samples for any functional group (Table 1).

Seed rain into burned areas of alien vs. native species

We found a total of 33 species in the seed traps located in the burned areas, of which 16 species were natives, 14 species were aliens and 3 species were not identified. Among the natives, 5 species were annuals and 11 were perennials. All alien species were annuals. That is, 14 of the 19 annuals were alien (74%), and all perennials were native. The grasses *V. myuros*, *A. caryophyllea* and *B. hordeaceus* and the forb *H. glabra* were more abundant alien species in the seed rain (17.7%, 17.4%, 6.8%, and 5.3%, respectively). These alien species are mainly dispersed by animals (epizoochory; see Appendix S1). Among the natives, the more frequent species were the geophyte *Sisyrinchium* sp. (9.7%), the annual *Chaetanthera linearis* (6.8%), the tree *Q. saponaria* (3.4%) and the shrubby *Baccharis linearis* (3.2%); these species are mainly dispersed by wind (Appendix S1).

There were not clear differences in the number alien and native species that arrived at burned areas ($\chi^2 = 3.58$, $P = 0.058$, LR test), but the abundance of alien propagules was significantly higher than the abundance of native propagules ($\chi^2 = 145.98$, $P < 0.001$, LR test). When considering the functional groups separately, the richness and the abundance of alien annual species were significantly higher than those of native annuals and perennials ($\chi^2 = 9.98$, $P = 0.006$ and $\chi^2 = 11.60$, $P = 0.003$ for richness and abundance, respectively, LR test) (Fig. 2, see also Table S4).

The relative importance of seedbank and seed rain in explaining plant establishment after fire

The distance between the vegetation and the seed rain composition (ordination centroids; Figs S1 and S2) tended to be higher than the distance between the vegetation and the seedbank composition in the NMS ordinations, although this difference was more evident when considering species abundance (Fig. 3). That is, the structure of the herbaceous layer 8 months following fire better reflected the soil seedbank than the seed rain.

DISCUSSION

Fire did not favour the establishment of alien species over natives in the Chilean coastal matorral. Both native and alien species became successfully established in burned as well as in unburned areas. This suggests that the herbaceous community of the coastal matorral is highly resilient to fire, which could be explained by the disturbance history of the Chilean matorral (Rundel, 1998). After centuries of intense human activity (grazing, clearing, burning, etc.), a great number of alien species have successfully invaded the matorral becoming dominant in the herbaceous layer, but these aliens coexist with many ruderal native species, which have also been filtered by anthropogenic disturbances.

Indeed, we found that native seedbank (including annual and perennial species) was more resistant to fire than alien

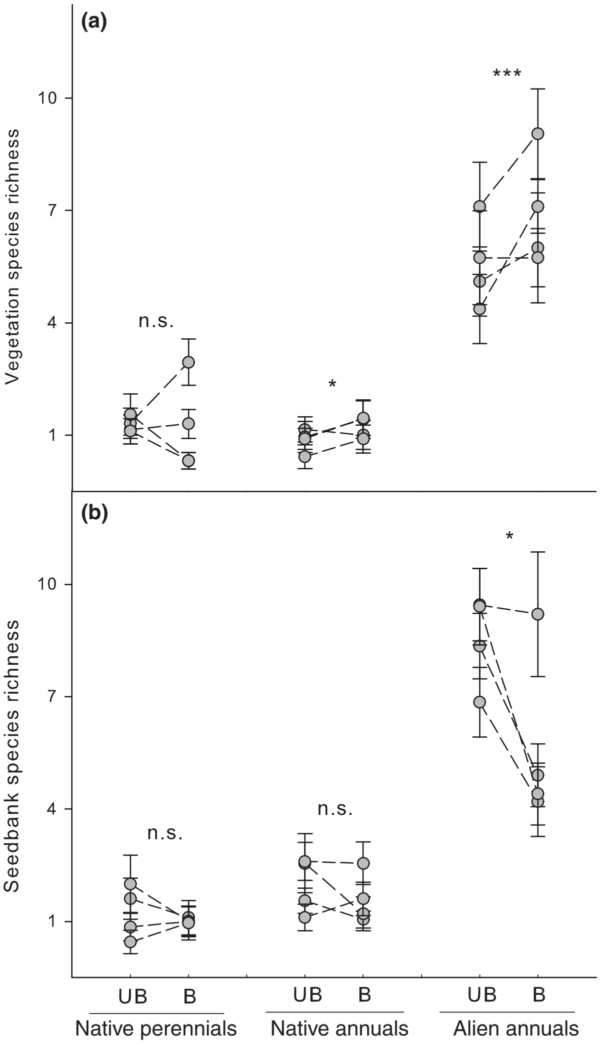

Figure 1 Species richness of native perennials, native annuals and alien annuals in the established vegetation (a) and in the soil seedbank (b). B = Burned plots; UB = Unburned plots. Dots represent the average of the 20 subplots within each site, and error intervals are ±2SE. Dashed lines join dots of the same site (block). Asterisks denote significant fire effect (generalized linear mixed model; *$P < 0.05$, ***$P < 0.001$, n.s. = not significant; see Tables 1 and S2 for statistical details).

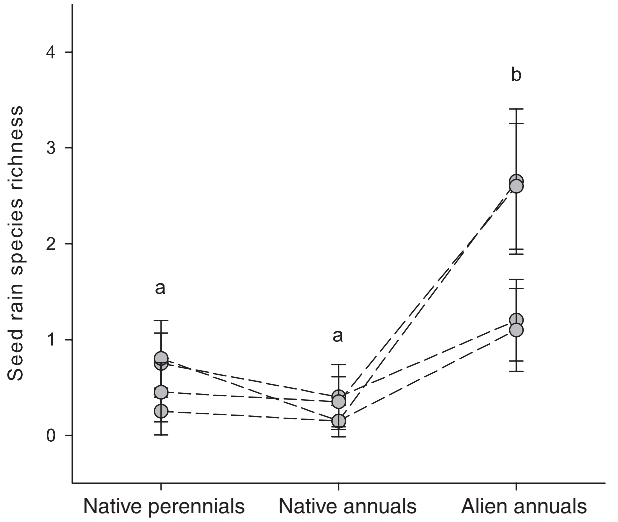

Figure 2 Species richness of native perennials, native annuals and alien annuals in the seed rain of burned plots. Dots represent the average of the 20 subplots within each site, and error intervals are ±2SE. Dashed lines join dots of the same site (block). Different letters denote significant differences ($P < 0.05$; generalized linear mixed model). See estimate parameters in Table S3.

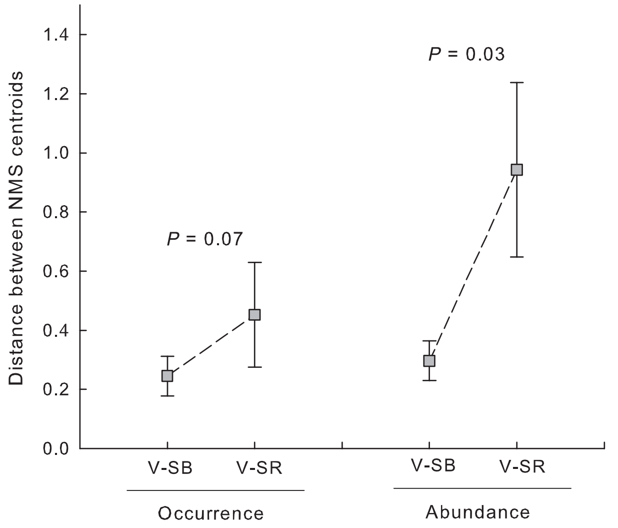

Figure 3 Differences in the distance between vegetation and seedbank centroids (V-SB) and the distance between the vegetation and seed rain centroids (V-SR) in non-metric multidimensional scaling (NMS) ordinations applied to occurrence and abundance data from burned plots. Square dots represent the mean distance ($n = 4$ sites), and error intervals are ±2SE. Significant differences are $P < 0.05$ (paired t-test). See NMS ordinations in Figs S1 and S2.

seedbank. This suggests that native matorral species are more resistant to fire than previously thought. Previous studies showing the intolerance of matorral species to fire had been focused only on woody species (Armesto & Gutiérrez, 1978; Muñoz & Fuentes, 1989; Segura *et al.*, 1998; Gómez-González *et al.*, 2008), while this study has been mainly directed to annual and perennial herbs. Past fires have reduced the diversity and cover of the matorral through time (Armesto & Gutiérrez, 1978), and only the few that resist fires (and probably also grazing) remain in the community today. Despite the current lack of a natural fire regime in central Chile, the high frequency of anthropogenic fires during the last centuries (Aravena *et al.*, 2003; Villa-Martínez *et al.*, 2003) could have selected favourable traits to fire among the native species, such as a hard seed coat (seed persistence) or an efficient resprouting ability (Pausas *et al.*, 2004). This is particularly likely for herbaceous species, because their evolutionary rate is generally higher than that of woody species (Levin & Wilson, 1976). Even some pioneering woody species such as *Muehlenbeckia hastulata* and *R. trinervia* have shown to have heat-stimulated germination (Muñoz & Fuentes, 1989). However, we have found no evidence of adaptations like fire-dependent recruitment among native matorral species (data not shown). This contrasts with the wide variety of adaptive traits to fire reported in other mediterranean-type ecosystems (Keeley & Fotheringham, 2000; Pausas *et al.*, 2004), and therefore, we support the idea of a low fire frequency in the evolutionary history of the Chilean matorral (Armesto & Gutiérrez, 1978; Villa-Martínez *et al.*, 2003). Fire resistance of native species' seeds could be consequence of exaptation. In other words, plant traits that are currently adaptive to fire might have been generated by other selective pressures (e.g. endozoochory or drought).

Fire increased the establishment of species with annual life cycle in general (natives and aliens), but most of them (mean = 87%) were aliens. Thus, fire contributed to increase the species richness of alien annuals (in absolute terms) even in a community where alien species were already dominant (71.3%). These results support the idea that fire is a relevant factor for the maintenance of the seasonal, alien-dominated grassland that surrounds the remnant patches of native shrubs (Fuentes *et al.*, 1984). Holmgren (2002) suggested that the shrubs and the herbaceous patches represent alternative stable states and that the introduced herbivores are the main responsible for the switch from mature matorral to invaded grasslands, while the role of fire remained unclear owing to contrasting evidences (e.g. Keeley & Johnson, 1977; Araya & Ávila, 1981; Holmgren *et al.*, 2000; Sax, 2002). By excluding herbivory, we have demonstrated that fire alone can favour the establishment of annuals, including both alien and native species, thus promoting the maintenance of invaded grasslands in the system.

In many forest and shrubland ecosystems, fire generates a favourable environment for the colonization and establishment of alien annual plants by opening the canopy, reducing competition with woody native species and increasing resource availability (Zouhar *et al.*, 2008). In the Chilean matorral, fire produces strong negative effects on the population dynamic of late-successional woody species (Muñoz & Fuentes, 1989; Segura *et al.*, 1998; Gómez-González *et al.*, 2008), and the recovery of the canopy after fire is very slow. In addition, native annual species are relatively scarce (e.g., 16% in central Chile against 30% in California; Arroyo *et al.*, 1995), and thus, novel disturbances like fire are particularly favourable for the establishment of alien annuals, which find an 'empty niche' (Elton, 1958) in the open spaces generated by fire. Once alien annuals are abundant enough, then they can change the natural fire regime and generate a positive feedback between fire and their establishment (D'Antonio & Vitousek, 1992; Brooks *et al.*, 2004). In the Chilean matorral, this positive feedback could be happening because (1) seasonal grasslands are extensive and highly flammable in summer, which probably leads to a rising fire frequency in the system, and (2) as our results indicated, fire increases the establishment of alien annuals.

Fire characteristics (size, frequency and severity) and vegetation structure are factors that directly affect the patterns of survival, dispersal and establishment of alien and native species (Keeley *et al.*, 2005). There was a variation of all these factors across our study sites (e.g., fire severity, size and frequency; Table S1), which was manifested as a site × fire effect (random effect on the slopes in the GLMM) in a considerable number of the variables analysed (see Tables S2 and S3). This indicates there is variability in the effects of fire depending on site and fire characteristics. For example, Gómez-González & Cavieres (2009) found differential effects of fire on native and alien seedbank depending on the microhabitat within a given site (beneath canopy vs. open grasslands), which was caused by differences in fuel load and fire intensity. Thus, future studies should evaluate the effects of fire severity on alien plant invasion at a wide spatial scale in the Chilean matorral.

The establishment of plant species during the first year following fire is driven by propagule dispersal from unburned areas and by the ability of the resident species to survive fire by means of persistent seedbanks or resprouting structures (Turner *et al.*, 1998). The relative importance of dispersal and survival processes in explaining plant invasion patterns after fire has been rarely addressed in a quantitative manner under field conditions (Zouhar *et al.*, 2008). In the coastal matorral, we found that plant establishment after fire was strongly determined by seedling emergence from the soil seedbank, while propagule arrival was a less important factor. In other mediterranean-type ecosystems, like the Californian chaparral, severe crown fires reduce the alien seedbank, and hence, plant invasion during the first year after burn is mainly attributable to propagule sources from unburned areas, while alien seedbanks can survive and contribute substantially to invasion success after low-intensity fires (Keeley *et al.*, 2005). In the Chilean matorral, fires generally have lower severity than chaparral crown fires (Keeley & Johnson, 1977), which may explain the greater importance of seedbank survival in relation to propagule dispersal for plant invasion patterns in this system.

Although the alien seedbank was significantly reduced by fire and more affected than the native seedbank, the proportion of alien species and their relative abundance was above 65% in burned soil samples (Table S4), so that they remained dominant over natives in the soil seedbank after fire. This elevated survival of alien seedbank in burned plots might be the main factor determining their dominance during the next spring, while post-fire dispersal processes would play a less relevant role. Despite this, seed rain can also contribute (although to a less degree) to invasion success because alien annuals dispersed more propagules into burned areas than native species. This pattern can be explained by differences in the distribution of dispersal modes between both groups; alien annuals are mainly grasses dispersed by the movement of animals (epizoochory) or by wind (anemochory), while most native species are dispersed at short distances (e.g. barochory, autochory; see Appendix S1). Only a few anemochorus native species significantly contributed to the seed rain into burned areas. Also, the huge abundance of alien annuals in the surrounding unburned areas could explain the seed rain pattern. Therefore, there is a 'mass effect' (Rouget & Richardson, 2003) determining the successful establishment of alien annual plants after fire in the Chilean matorral.

It is known that alien grasses and forbs dominate the herbaceous layer in the matorral (Keeley & Johnson, 1977; Montenegro *et al.*, 1991; Holmgren *et al.*, 2000). Nevertheless, we found that the proportion of alien species was above 70% in unburned sites. This value is much higher than any previously reported value for other coastal matorral communities of the same region (Sax, 2002; Figueroa *et al.*, 2004). This highlights the advanced stage of the invasion process and the great need for implementing management tools to protect plant diversity in this mediterranean-type ecosystem. Fire has been used as a tool for controlling invasive plants in other ecosystems (Di Tomaso *et al.*, 2006); however, this method would not be recommendable for the coastal matorral, because some alien annuals, such as *Aira caryophyllea*, are particularly successful in burned areas. Furthermore, fire could contribute to the vegetation-type transformation from matorral to grassland, because it produces positive effect on native and alien annuals but strong negative effects on mature matorral species.

ACKNOWLEDGEMENTS

We thank L. Bacigalupe and A. Fajardo for helping with statistical analyses, L. Suárez and M. Apablaza for field assistance, and W. Ridenour for English edition. The Department of Fire Management of CONAF cooperated with the searching of study sites. Plant species were identified by A. Marticorena and M. Negritto. Information on dispersion syndrome of alien plants was extracted from the database generated by the ALARM Project (Assessing LArge scale environmental Risks for biodiversity with tested Methods; GOCE-CT-2003-506675; http://www.alarmproject.net). Susana G.-G. holds a postdoctoral grant FONDECYT-3090018. This study was funded by MECESUP (UCO-0214), CONICYT (AT-24060008), and the Institute of Ecology and Biodiversity (IEB; P05-002 F ICM).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Full list of alien and native species recorded.

Figure S1 NMS ordinations for occurrence data.

Figure S2 NMS ordinations for abundance data.

Table S1 Additional information on study sites.

Table S2 Estimate parameters of the best-fitted GLMM for seedbank and vegetation data.

Table S3 Estimate parameters of the best-fitted GLMM for seed rain data.

Table S4 Mean values of the response variables for each functional group in the vegetation, the seedbank and the seed rain.

BIOSKETCH

Susana Gómez-González's research interests are focused on ecology and evolution of mediterranean plants, fire ecology and biological invasions.

Author contributions: S.G.-G. and L.A.C. conceived the ideas; S.G.-G., C.T.-D., P.T.-M. and G.V. collected the data; S.G.-G. and J.G.P analysed the data and wrote the final version of the manuscript. All authors contributed to the writing of the first draft of the manuscript, which was led by S.G.-G.

Editor: Marcel Rejmanek