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Native and naturalized plant diversity are positively correlated in scrub communities of California and Chile

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Abstract. An emerging body of literature suggests that the richness of native and naturalized plant species are often positively correlated. It is unclear, however, whether this relationship is robust across spatial scales, and how a disturbance regime may affect it. Here, I examine the relationships of both richness and abundance between native and naturalized species of plants in two mediterranean scrub communities: coastal sage scrub (CSS) in California and xeric-sloped matorral (XSM) in Chile. In each vegetation type I surveyed multiple sites, where I identified vascular plant species and estimated their relative cover. Herbaceous species richness was higher in XSM, while cover of woody species was higher in CSS, where woody species have a strong impact upon herbaceous species. As there were few naturalized species with a woody growth form, the analyses performed here relate primarily to herbaceous species. Relationships between the herbaceous cover of native and naturalized species were not significant in CSS, but were nearly significant in XSM. The herbaceous species richness of native and naturalized plants were not significantly correlated on sites that had burned less than one year prior to sampling in CSS, and too few sites were available to examine this relationship in XSM. In post 1-year burn sites, however, herbaceous richness of native and naturalized species were positively correlated in both CSS and XSM. This relationship occurred at all spatial scales, from 400 m^2 to 1 m^2 plots. The consistency of this relationship in this study, together with its reported occurrence in the literature, suggests that this relationship may be general. Finally, the residuals from the correlations between native and naturalized species richness and cover, when plotted against site age (i.e. time since the last fire), show that richness and cover of naturalized species are strongly favoured on recently burned sites in XSM; this suggests that herbaceous species native to Chile are relatively poorly adapted to fire.

Key words. Species richness, exotic, coastal sage scrub, matorral, fire, mediterranean-type climate.

INTRODUCTION

Within the past few hundred years tens of thousands of species have been able to establish themselves outside of their known historical range. This has occurred for many reasons, but the most important of these is undoubtedly human-assisted dispersal (Elton, 1958). Assisted dispersal allows species to cross biogeographical boundaries (such as oceans or deserts) that have previously limited their distributions. Species that have been transported from one region to another are defined as alien or exotic to that newly occupied region (Richardson *et al.*, 2000). Most of these species fail to establish self-perpetuating populations, but those that do have become naturalized (Sax & Brown, 2000). These naturalized species often have profound impacts upon native species and environments as they can cause a reduction in species abundance, they can cause or contribute to species extinctions, and they can modify

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entire ecosystems (e.g. Carlton, 1979; Ebenhard, 1988; Vitousek & Walker, 1989; D'Antonio & Vitousek, 1992; Woods, 1993; Fritts & Rodda, 1998; Mack & D'Antonio, 1998). Of course, not all naturalized species have negative effects on native biota; many show no detectable impact upon native species at all (Simberloff, 1981). Sometimes naturalized species even show a beneficial effect, e.g. by providing a critically limiting resource to native species, such as the overwintering sites that *Eucalyptus globulus* trees provide for monarch butterflies in California (Lane, 1993). Given the variety of effects that alien species may have, it is not surprising that their introduction, varying ability to become naturalized, and impact upon native species has elicited much attention in the ecological literature (e.g. Elton, 1958; Baker & Stebbins, 1965; Groves & Burdon, 1986; Drake *et al.*, 1989; Hengeveld, 1989; Kareiva, 1996; Williamson, 1996; Sax, 2002). Much of this work has focused on the effects of specific alien species upon specific native species or a specific native ecosystem (e.g. Vivrette & Muller, 1977; Mack, 1981; Schierenbeck *et al.*, 1994). Much work has also focused on the presumed differential ability of native systems with certain characteristics (such as biotic diversity or abiotic harshness) to repel the invasion of naturalized species (e.g. Crawley, 1987; Case, 1991; Richardson *et al.*, 1994; Burke & Grime, 1996; Moyle & Light, 1996; Tilman, 1997). Recently, however, researchers have begun to study the nature of these new amalgams of native and naturalized species themselves, by examining the relationship between the richness of the native and naturalized species that compose them (e.g. Lonsdale, 1999).

Most of these studies have compared richness values across regional floras. One drawback to this approach is that areas of different sizes are compared; this complicates analyses because larger areas are expected to have more native and more naturalized species by chance then smaller areas, which creates an artefact that can contribute to positive correlations between native and naturalized richness when the sample units vary in size. Nevertheless, because area does not account for all the variance in these relationships, these studies (with varying levels of confidence) still provide evidence of a positive relationship between richness of native and naturalized species in central California (Knops *et al.*, 1995), Kenya (Stadler *et al.*, 2000), North America and South Africa (Kruger *et al.*, 1989; MacDonald *et al.*, 1989), Europe (Sax, 2001), from various (but primarily continental) sites around the globe (Rejmánek, 1996; Lonsdale, 1999), and on oceanic islands and island archipelagos (Sax *et al.* in review). In a few studies, researchers have standardized the area of their sample units, simplifying interpretations of these patterns. Planty-Tabacchi *et al.* (1996), at multiple landscape-scales, have shown a positive relationship between native and naturalized richness in riparian habitats of the United States and France. Stohlgren *et al.* (1999), at multiple local-scales (1 ha and smaller), have shown a positive relationship between native and naturalized richness in the Rocky Mountains of Colorado, but showed mixed results in the central plains of the United States, where richness of native and naturalized species was positively correlated only at larger scales, and negatively correlated at the 1-m^2 quadrat scale. Levine (2000), at the remarkably small spatial scale of individual tussock patches within a riparian environment of California, has shown that the likelihood of a tussock containing naturalized plants is positively correlated with the number of native species present. From these studies a near-consistent pattern begins to emerge, where native and naturalized richness are positively correlated across sites and regions.

These empirical results are consistent with an emerging body of theoretical research. Huston (1994) suggested that conditions that favoured the growth and establishment of native species should also favour naturalized ones. In particular, he suggested that the process of colonizing a site should not be qualitatively different between the two groups. His work can be extrapolated to predict that species richness of native and naturalized species should often be positively correlated across sites. Recent work by Davis *et al.* (2000) suggests the conditions in which naturalized species should be able to invade communities. Specifically, they propose that communities should be susceptible to invasion when resource availability is increased beyond the ability of resident species to uptake the available resource supply, such as during the period following a disturbance. Therefore, invasion within communities should be episodic and communities that are disturbed should be more susceptible to invasion than those that are not. It remains unclear, however, whether there is an intersection between the theoretical reasoning of Huston (1994) and Davis *et al.* (2000). For example, should native and naturalized species richness be positively correlated across sites that are recently disturbed, or is some type of a time-lag expected? Further, it remains to be determined whether positive correlations between native and naturalized richness are truly expected to be common to many environments, or whether the small number of studies conducted thus far (both empirically and theoretically) have led to spurious conclusions.

To examine these relationships, I used ecosystems in two regions with a mediterranean-type climate: southern California and central Chile. These two regions, of the five with this climate type, were chosen because they have the most highly analogous climates (Mooney *et al.*, 1970; Arroyo *et al.*, 1995); both regions are characterized by a temperate climate with winter precipitation and summer drought (Mooney *et al.*, 1970). Both regions have also been invaded by many naturalized plant species, with over 1000 naturalized in California and *c.* 600 naturalized in Chile (Matthei *et al.*, 1995; Randall *et al.*, 1998). One difference between them, however, is the historical presence in California, and the historical absence in Chile, of a disturbance regime dominated by fire (Rundel, 1981; Arroyo *et al.*, 1995; Keeley, 1995). Despite this difference between regions, and despite the largely independent origins of the plants inhabiting them, the closely similar climates shared by these regions have produced floras with many convergent characteristics (e.g. scleropherous leaves) and many convergent vegetation types: drought-deciduous shrublands, evergreen shrublands, and so on (Mooney *et al.*, 1970). Within these regions, however, different vegetation types have been invaded by proportionately different numbers of naturalized species (Kruger *et al.*, 1989). Because most invaders to these regions are species of herbs and grasses, with relatively few shrubby, arborescent, or otherwise woody species, certain types of vegetation, such as grasslands, have been invaded by many species, while other types of vegetation, such as evergreen shrublands have been invaded by fewer species (Kruger *et al.*, 1989; Randall *et al.*, 1998). Examining relationships between native and naturalized species in vegetation types that lack significant variation in the number of native and/or naturalized species is problematic, i.e. it is difficult to make comparisons between native and naturalized species in environments that have been so heavily invaded that few native species persist, or in environments that have been so little invaded that few naturalized species are present. One mediterranean-vegetation type that has been invaded by many naturalized species, but which still retains many native species, is drought-deciduous scrub or shrublands, which contain shrubs as well as a well-developed understorey of herbs and grasses.

Here, I examine the relationships between native and naturalized plant species richness and abundance in two mediterranean-type communities: coastal sage scrub (CSS) in southern California and xeric-sloped matorral (XSM) in central Chile. These two analogous vegetation types have similar environmental characteristics, similar physical structures, largely independent native floras, have been invaded by many naturalized species (while still maintaining high native plant diversity), and differ in their historical association with a fire regime (Mooney *et al.*, 1970; Rundel, 1981; Arroyo *et al.*, 1995; Keeley, 1995; Matthei *et al.*, 1995; Randall *et al.*, 1998). Within these vegetation types, I recorded species richness and foliar cover of vascular plants across local sites that varied in their recent exposure to fire, using a nested sampling design that allowed for an examination of species richness relationships at decreasing spatial scales. To provide a context for this study, I first compare vegetation types and examine their patterns of succession following fires. Second, I compare how species richness, as well as species cover, co-varies between native and naturalized species. Third, I examine the site variables that are predictors of native and naturalized richness. Lastly, I examine how fire differentially affects native and naturalized species in these two vegetation types.

STUDY SITES

California

Sites were located in the Santa Monica Mountains, a coastal mountain range north of Los

Angeles (34°03′N, 118°14′W; mean annual precipitation is 373 mm, mean number of months with less than 1 cm of precipitation is 5, mean annual maximum temperature is 43 °C, mean annual minimum temperature is –2 °C; Court, 1974). Sites were surveyed during a 5-week period in the latter portion of the boreal spring of 1997, from very late April to the end of May. Each site consisted of a single 20 × 20 m plot that was located within coastal sage scrub (CSS) vegetation. A total of 41 plots were selected from areas within CSS vegetation that had burned in different years: 15 in 1996, 13 in 1993, 4 in 1985, 6 in 1982 and 3 in 1978. None of these sites had been subject to any obvious anthropogenic disturbances. Data on fire history of these sites, i.e. the number of years since the most recent fire as well as the frequency of fires over the past 30 years, was provided by the US National Park Service (NPS).

CSS vegetation, also known as soft chaparral, is characterized by the dominance of drought-deciduous shrubs, with inter-shrub gaps filled by a mixture of sub-shrubs, herbaceous species and grasses (Munz & Keck, 1959; Sawyer & Keeler-Wolf, 1995). CSS burns periodically, with fires historically caused by lightening strikes (Keeley, 1986). It is a persistent vegetation type on south-facing slopes and at low elevations, where water is limiting, and is an early successional sere on north-facing slopes and at higher elevations, where it is replaced by hard chaparral (Hanes, 1981).

Chile

Sites were located in the coastal mountains of the Fifth Region, inland from Valparaiso (33°01′S, 71°38′W; mean annual precipitation is 458.9 mm, mean number of months with less than 1 cm of precipitation is 5, mean annual maximum temperature is 36.0 °C, mean annual minimum temperature is 2.0 °C; Miller, 1976). Sites were surveyed during a 5-week period in the latter portion of the austral spring of 1997, from very late October to very early December. Each site consisted of a single 20 × 20 m plot that was located within xeric-sloped matorral (XSM) vegetation. A total of 20 plots were selected from XSM vegetation that had recently burned: 2 in 1997, 6 in 1994, 3 in 1992, 6 in 1989, and 3 in 1985. Six additional sites were surveyed in a coastal vegetation-type that was similar to XSM, but which was not directly comparable because of its lower cover and lower richness of herbaceous species; as such, these six sites were not considered further here. All sites were exposed, at least periodically, to some degree of grazing pressure by domestic animals and many had experienced some selective cutting of woody species. Data on the fire history of these sites, which included the number of years since the most recent fire, was provided by the Corporacion National Forestal (CONAF) of Chile.

XSM vegetation is characterized by the dominance of drought-deciduous shrubs, with inter-shrub gaps filled by a mix of sub-shrubs, herbaceous species and grasses (Armesto & Martínez, 1978; Rundel, 1981). It burns periodically due to anthropogenic fires, but historically was apparently free from regular fires (Rundel, 1981; Arroyo *et al.*, 1995; Keeley, 1995). It is a persistent vegetation type on north-facing slopes, where water is limiting, but is replaced by true matorral on other slopes (Armesto & Martínez, 1978; Rundel, 1981).

METHODS

Plots were surveyed in late spring, when most species with annual life cycles had germinated, but prior to the desiccation and loss of many annual species that occurs in early summer. Species that could not be identified in the field were collected and identified at a herbarium. Voucher specimens of all plant species were collected and deposited at the herbarium of the Universidad de Concepción (Chilean plants) and at the herbarium of the University of New Mexico (Californian and some Chilean plants).

Each 20 × 20 m plot was subdivided into four 5 × 20 m quadrants. In Chile, additional nested subplots, 5 × 5 m and 1 × 1 m, were located in each quadrant (Fig. 1). Species richness was determined by identifying all species present in each plot, quadrant and subplot. Foliar cover was estimated by collecting point intercept data, every 10 cm, along 20 m transects placed on the mid-line of each quadrant. This provided 800 point-estimates per plot. Several site characteristics were recorded for each plot: elevation and Universal Transverse Mercator location from a global positioning system, as well as mean slope,

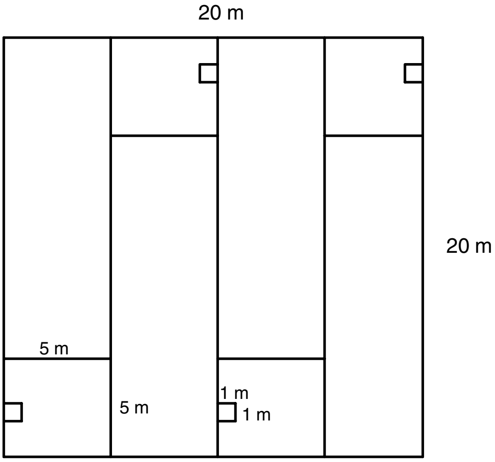

Fig. 1 Plot and subplot dimensions of each site. Note that 5 × 5 m and 1 × 1 m subplots were sampled only in XSM vegetation, not in CSS vegetation.

range in slope, mean aspect, range in aspect, distance to the nearest road, and distance to the coast.

Data Analysis

Native and naturalized richness values of the 20 × 20 m plots were calculated by tallying all native and naturalized species present. Richness values of 5 × 20 m quadrants were calculated by tallying the species present in the first quadrant at each site. Richness values of 5 × 5 m and 1 × 1 m subplots were calculated by averaging the tallied counts from the replicates at each site. In contrast to richness, foliar cover was only examined at the whole site scale, i.e. within the 20 × 20 m plots. Cover values were calculated by tallying the intercept points for both native and naturalized species, and then dividing these raw values by a factor of eight (as there were 800 points intercepts per plot) to generate percentage cover estimates. Note, however, that estimates of total foliar cover could exceed 100% because a single intercept point could be occupied by multiple species along the same vertical axis, for example when a herb grew beneath a shrub.

Mean differences between the cover and richness of CSS and XSM vegetation were examined with analysis of variance techniques (in this case, *t*-tests of mean differences between native and naturalized species in the two vegetation types). Successional changes in species cover and richness following fires were examined with regression analyses (calculated by the least squares method). Both linear and log-linear fits of the data were examined, as a strictly linear scale was often insufficient to account for the variation in relationships that had asymptotic values, such as with successionally mature CSS sites where foliage cover approaches 100%. The relationships between native and naturalized richness, as well as native and naturalized cover, were also examined with regression analyses, although here strictly linear fits to the data were used. The effect of fire history on the relationship between native and naturalized richness, as well as native and naturalized cover, were examined by comparing these relationships among sites that had last burned at different times in the past: < 1 year, 4–6 years, and > 9 years. A composite of the last two of these temporal classifications was also used, i.e. all sites that had last burned more than 1 year prior to this study. In addition to segregating sites by their fire history, the values within sites were partitioned into two categories: herbaceous and woody species. Woody species here include all sub-shrubs, shrubs, and arborescent taxa, while herbaceous species include all herb and grass species (except for one woody species of grass in Chile, *Chusquea* sp., that was included with the woody species).

Multiple linear regression analyses (using a backward procedure) were performed in JMP (with the *P* value necessary for a variable's removal from the model set at 0.1) to examine the relationship between site variables and the herbaceous richness of both naturalized and native species. All site variables that were not distributed normally were log transformed prior to analysis. The site variables employed in the analysis of naturalized species on Chilean plots included: richness of herbaceous native species, log of foliar cover of herbaceous native species, richness of woody species, log of cover of woody species, log of non-vegetated area, the year a site last burned, elevation, slope, log of slope range (a measure of the variability in slope), aspect, log of aspect range, and distance to the coast. When the dependent variable examined was native species richness (instead of naturalized richness described above) then the independent variables

Table 1 Richness and foliar cover of vascular plant species

	Mean number of species		Mean foliar cover (%)		Total number of species	
	Natives	Aliens	Natives	Aliens	Natives	Aliens
CSS	18.5 (0.96)	5.1 (0.52)	93.3 (5.56)	27.2 (4.86)	131	30
XSM	27.1 (1.90)	23.7 (1.08)	42.3 (4.49)	43.7 (4.43)	116	77
T-stat.	3.62	13.91	6.71	2.33		
d.f.	27	26	50	46		
P value	< 0.01	< 0.001	< 0.001	0.05		

Total number, mean number and mean percentage cover of native and naturalized vascular plant species surveyed at study sites in CSS vegetation (in California) and XSM vegetation (in Chile). Differences between mean values in CSS and XSM were tested for significant differences with *t*-tests that assumed unequal variance between means.

Table 2 Richness and foliar cover of herbaceous species

	Mean number of species		Mean foliar cover (%)		Total number of species	
	Natives	Aliens	Natives	Aliens	Natives	Aliens
CSS	10.2 (0.87)	5.0 (0.52)	33.9 (5.15)	27.2 (4.87)	93	28
XSM	18.5 (1.51)	23.6 (1.09)	18.9 (2.28)	43.6 (4.43)	84	75
T-stat.	4.29	13.76	2.59	2.33		
d.f.	29	26	55	46		
P value	< 0.001	< 0.001	< 0.05	< 0.05		

Total number, mean number and mean percentage cover of native and naturalized herbaceous species (i.e. non-woody herbs and grasses) surveyed at study sites in CSS vegetation (in California) and XSM vegetation (in Chile). Differences between mean values in CSS and XSM were tested for significant differences with *t*-tests that assumed unequal variance between means.

of richness of herbaceous naturalized species and log cover of herbaceous naturalized species were used instead of their native flora counterparts. In California, three additional variables were employed: site distance from a paved road, the frequency of fires since 1981, and the frequency of fires since 1969.

RESULTS

The total number of species observed (the sum of native and naturalized species) was greater in XSM then in CSS, and the number of native species observed was only slightly greater in CSS, despite surveying twice as many sites in CSS (Table 1). Similarly, the mean richness across sites of both native and naturalized species was greater in XSM then CSS (Table 1). The mean foliar cover of native species, however, was significantly greater in CSS, while mean foliar cover of naturalized species was greater in XSM (Table 1). These differences in richness and cover between vegetation types were conserved when herbaceous species were considered in isolation (Table 2). The woody species, however, showed different patterns. Richness of woody species were not significantly different between vegetation types for either native or naturalized species,

Table 3 Richness and foliar cover of woody species

	Mean number of species		Mean foliar cover (%)		Total number of species	
	Natives	Aliens	Natives	Aliens	Natives	Aliens
CSS	8.2 (0.39)	0.1 (0.05)	59.4 (5.74)	0.02 (0.01)	38	2
XSM	8.6 (0.59)	0.1 (0.09)	23.4 (3.56)	0.01 (0.01)	32	2
T-stat.	0.39	0.02	5.10	0.08		
d.f.	32	28	57	35		
P value	0.70	0.98	< 0.001	0.94		

Total number, mean number and mean percentage cover of native and naturalized woody species (i.e. sub-shrubs, shrubs and other arborescent taxa) surveyed at study sites in CSS vegetation (in California) and XSM vegetation (in Chile). Differences between mean values in CSS and XSM were tested for significant differences with *t*-tests that assumed unequal variance between means.

nor was foliar cover of naturalized species significantly different; only the mean foliar cover of native species, which was greater in CSS, was significantly different for woody species (Table 3).

Cover of woody species is positively correlated with the number of years since sites burned. In CSS this relationship is best fit by a log-linear relationship (with log transformed *x*-values) because foliar cover levels off to nearly 100% in successionally mature sites (Fig. 2A). In XSM, cover of woody species is linearly correlated (instead of log-linearly) with the number of years since the last burn because the total span of years compared was less, and oldest sites had not reached 100% cover (Fig. 2B). Cover of herbaceous species was negatively correlated with the number of years since sites had last burned in CSS and XSM; in both cases the best fits were log-linear (Fig. 2C,D). In contrast to cover, richness did not show significant relationships with years since sites last burned, except for herbaceous richness in CSS, which was best fit by a negative log-linear relationship ($R^2 = 0.53$, $P < 0.0001$).

Cover of woody species is also correlated with the richness of herbaceous species. In CSS, cover of woody species is negatively correlated with the richness of herbaceous native species ($R^2 = 0.65$, $P < 0.001$), negatively correlated with richness of herbaceous naturalized species ($R^2 = 0.21$, $P < 0.01$), and negatively correlated with total herbaceous richness ($R^2 = 0.60$, $P < 0.001$). In XSM, cover of woody species is negatively correlated with richness of herbaceous naturalized species ($R^2 = 0.35$, $P < 0.05$), but is not significantly correlated with richness of herbaceous native species or with total herbaceous richness.

Native and naturalized cover of herbaceous species were not significantly correlated across sites in CSS, nor were these relationships correlated when sites were segregated by years since they had last burned. However, in XSM there was a nearly significant ($P < 0.06$), negative correlation between native and naturalized cover of herbaceous species across all sites, a significant negative correlation on sites 4- to 6-years old ($R^2 = 0.60$, $P < 0.05$), and a nearly significant ($P < 0.07$) negative correlation on all post 1-year burn sites.

Native and naturalized richness of herbaceous species were significantly and positively correlated across sites in CSS and XSM (Fig. 3A,B). In CSS and XSM these significant correlations were conserved for all sites segregated by successional age, except in pre 1-year burn sites, where there was no significant relationship in CSS and too few points to evaluate in XSM (Fig. 3). Note, however, that on 4- to 6-year and post 9-year burn sites the positive correlations in XSM were nearly significant ($P < 0.11$ and 0.07, respectively; Fig. 3F,H). The strongest relationships were observed in both CSS and XSM when all post 1-year burn plots were considered together (Fig. 4A,B). These positive correlations between native and naturalized richness were conserved at

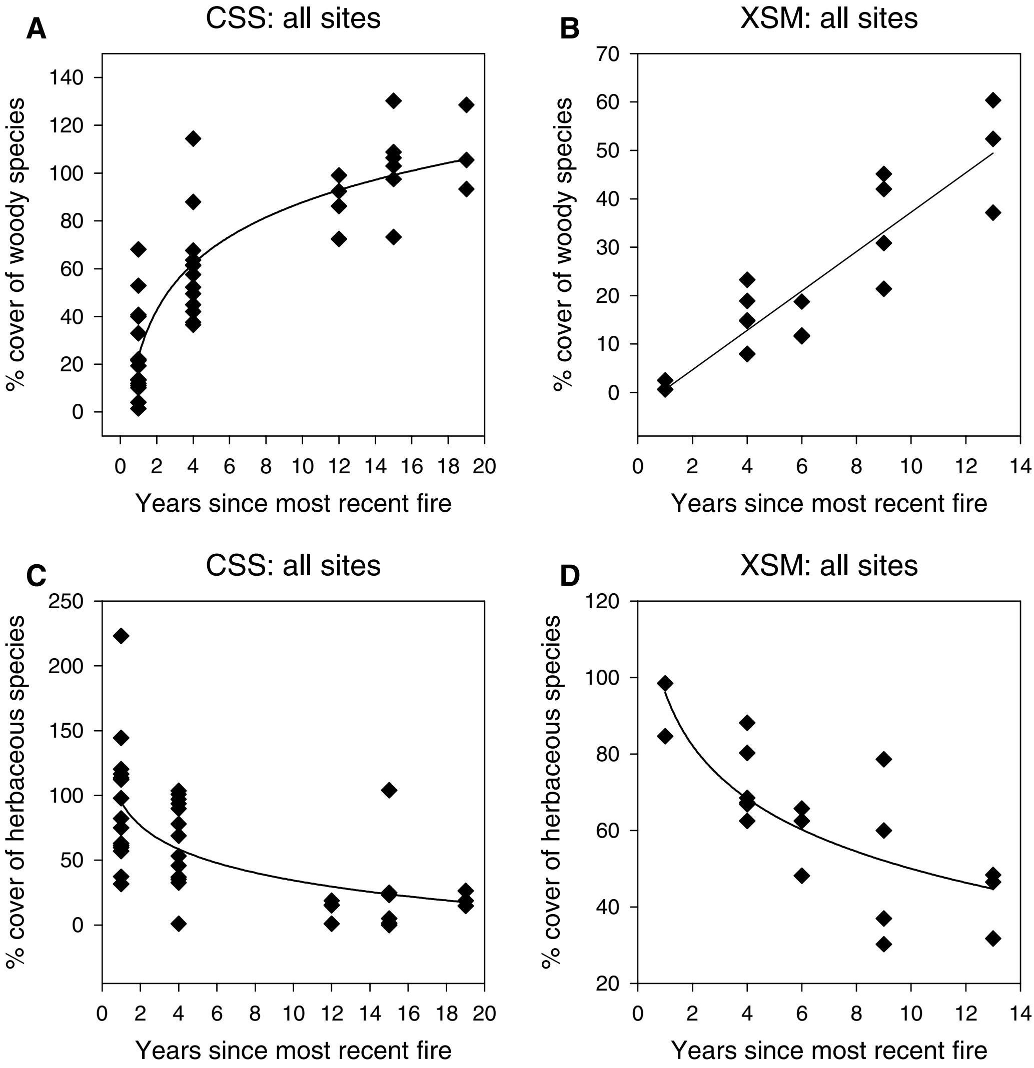

Fig. 2 Relationships between the successional age of sites (measured as years since they last burned) and percentage cover of woody and herbaceous species (measures that include both native and naturalized species). Relationships were examined for the best fit of linear and log-linear regressions. (A) Log-linear fit: $R^2 = 0.75$, $P < 0.0001$. (B) Linear fit: $R^2 = 0.80$, $P < 0.0001$. (C) Log-linear fit: $R^2 = 0.39$, $P < 0.0001$. (D) Log-linear fit: $R^2 = 0.60$, $P < 0.001$.

Fig. 3 Relationship between richness of native and naturalized species, (A) in all CSS sites, $R^2 = 0.23$, $P < 0.01$; (B) in all sites in XSM, $R^2 = 0.21$, $P < 0.05$; (C) in sites that burned less than 1 year prior to the study in CSS, $P = 0.22$; (D) in sites that burned less than one 1 year prior to the study in XSM (here there were too few points to determine if a relationship exists); (E) in sites that burned approximately 4 years prior to the study in CSS, $R^2 = 0.56$, $P < 0.01$; (F) in sites that burned approximately 4–6 years prior to the study in XSM, $R^2 = 0.32$, $P = 0.11$; (G) in sites that burned approximately 9 or more years prior to the study in CSS, $R^2 = 0.40$, $P < 0.05$; and (H) in sites that burned approximately 9 or more years prior to the study in XSM, $R^2 = 0.39$, $P = 0.07$.

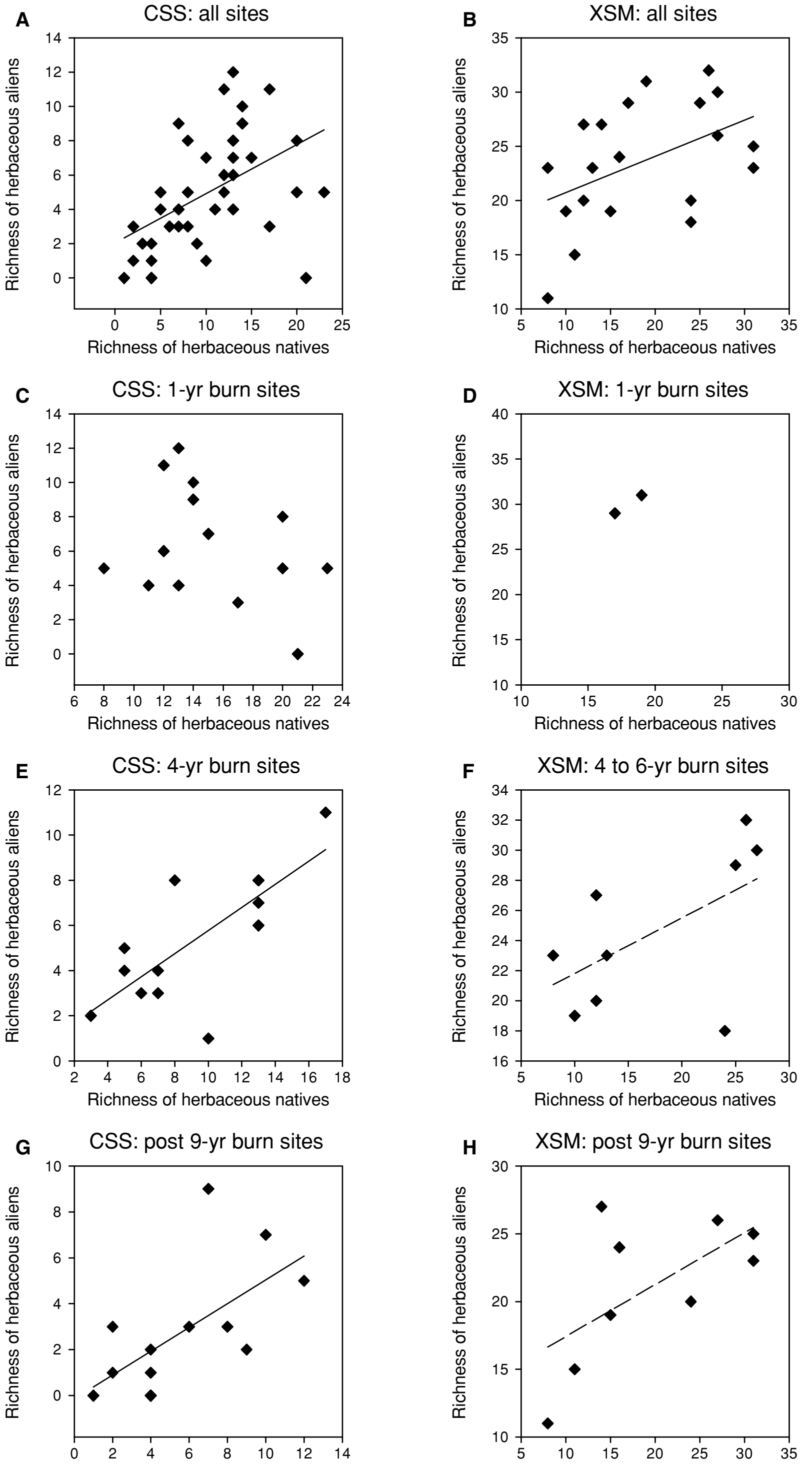
A
CSS: all sites
B
XSM: all sites
C
CSS: 1-yr burn sites
D
XSM: 1-yr burn sites
E
CSS: 4-yr burn sites
F
XSM: 4 to 6-yr burn sites
G
CSS: post 9-yr burn sites
H
XSM: post 9-yr burn sites
Richness of herbaceous aliens
Richness of herbaceous natives
0 2 4 6 8 10 12 14
0 5 10 15 20 25
10 15 20 25 30 35
5 10 15 20 25 30 35
6 8 10 12 14 16 18 20 22 24
10 15 20 25 30 35 40
10 15 20 25 30
0 2 4 6 8 10 12
2 4 6 8 10 12 14 16 18
16 18 20 22 24 26 28 30 32 34
5 10 15 20 25 30
0 2 4 6 8 10
0 2 4 6 8 10 12 14
10 15 20 25 30
5 10 15 20 25 30 35

Table 4 Relationship between site characteristics and the number of alien and native species in CSS and XSM sites

Habitat	Dependent variable	Independent variable	Coefficient	*F*	*P*
CSS	No. alien spp.	No. native spp.	0.57	60.01	0.001
		No. woody spp.	0.28	3.06	0.098
		Year of last burn	0.18	7.94	0.012
		Elevation	0.01	10.64	0.005
		Slope	−0.08	6.11	0.024
		Slope range	0.51	5.17	0.036
		Log aspect range	−3.97	13.16	0.002
CSS	No. native spp.	No. alien spp.	1.27	62.40	0.001
		No. woody spp.	−0.64	6.48	0.021
		Burn freq. post 1981	−1.63	4.72	0.044
		Elevation	−0.01	6.06	0.025
		Slope	0.12	5.61	0.030
		Slope range	−0.89	6.99	0.017
		Log aspect range	6.68	16.82	0.001
XSM	No. alien spp.	No. native spp.	0.53	48.59	0.001
		No. woody spp.	−1.36	21.83	0.002
		Year of last burn	−1.17	45.91	0.001
		Elevation	−0.01	29.33	0.001
		Slope	−0.42	32.50	0.001
		Log slope range	8.13	15.72	0.005
		Log aspect range	4.25	16.96	0.005
XSM	No. native spp.	No. alien spp.	1.65	48.59	0.001
		No. woody spp.	2.54	39.97	0.001
		Year of last burn	1.92	21.02	0.003
		Elevation	0.01	26.61	0.001
		Slope	0.73	31.09	0.008
		Log slope range	−14.97	21.76	0.002
		Log aspect range	−6.82	10.02	0.016

Multiple linear regression analysis was used to determine site characteristics that predict native and naturalized richness of herbaceous species in CSS and XSM. Data from 400 m^2 plots were used that had last burned more than 1 year prior to the study. Predictors were removed with a backwards procedure when *P*-values were < 0.10; these non-significant variables are not presented here. The independent variables 'Number of alien species' and 'Number of native species' refer specifically to the herbaceous components of the vegetation, i.e. they exclude species that are woody.

the reduced spatial scale of 100 m^2 (the size of site quadrants; Fig. 4C,D). Finally, in Chile, where additional nested subplots of 25 m^2 and 1 m^2 were sampled, these relationships were also significant for 25 m^2 subplots (Fig. 4E), and nearly so on 1 m^2 subplots ($P < 0.10$; Fig. 4F).

Multiple linear regression analyses of herbaceous species in post 1-year burn sites identified a number of site characteristics that were significant in predicting the richness of native and naturalized species (Table 4). The single best predictor of the richness of herbaceous native species, in both CSS and XSM, was richness of herbaceous naturalized species (Table 4). Conversely, the best predictor for richness of herbaceous naturalized species was richness of herbaceous native species (Table 4). The other significant variables in both CSS and XSM included: richness of woody plant species, number of years since a site last burned, elevation, slope, range in slope, and range in aspect (Table 4). For native species in CSS, the frequency at which sites had burned since 1981 (i.e. in the previous 17 years) was also significant

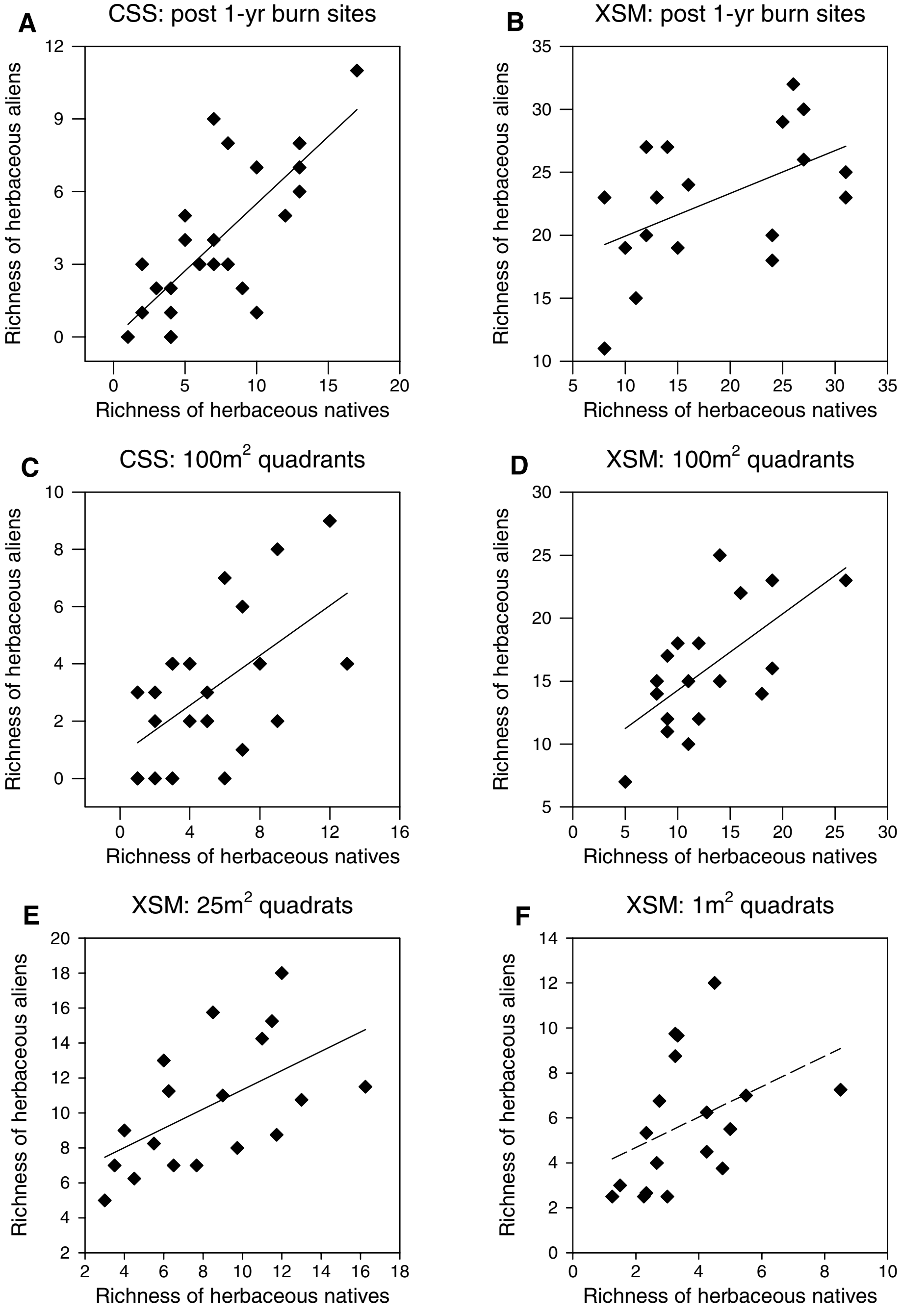

Fig. 4 Relationship between richness of native and naturalized species in sites that last burned more than 1 year prior to the study, (A) in CSS using entire study plots (400 m^2), $R^2 = 0.57$, $P < 0.001$; (B) in XSM using entire study plots (400 m^2), $R^2 = 0.26$, $P < 0.05$; (C) in CSS using 100 m^2 quadrants, $R^2 = 0.33$, $P < 0.01$; (D) in XSM using 100 m^2 quadrants, $R^2 = 0.41$, $P < 0.01$; (E) in XSM using 25 m^2 quadrats, $R^2 = 0.31$, $P < 0.05$; and (F) in XSM using 1 m^2 quadrats, $R^2 = 0.16$, $P = 0.10$.

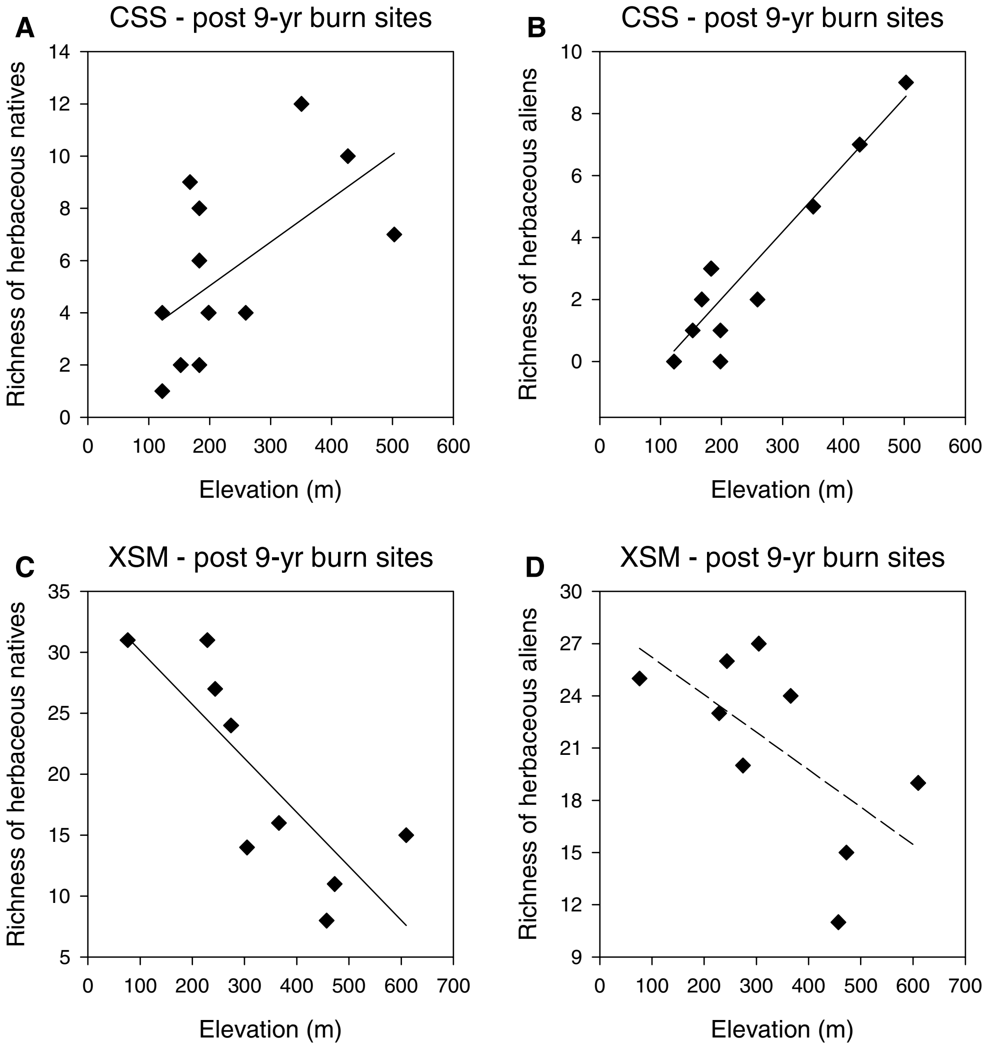

Fig. 5 Relationship between elevation and species richness of native and naturalized herbaceous species in sites that burned approximately 9 or more years prior to the study. (A) Native richness in CSS, $R^2 = 0.35$, $P < 0.05$. (B) Naturalized richness in CSS, $R^2 = 0.86$, $P < 0.001$. (C) Native richness in XSM, $R^2 = 0.65$, $P < 0.01$. (D) Naturalized richness in XSM, $R^2 = 0.40$, $P = 0.07$.

(Table 4). Together these variables explained much of the variation in native and naturalized richness of herbaceous species, with adjusted R^2 values of 0.84 (naturalized species in CSS), 0.80 (native species in CSS), 0.93 (naturalized species in XSM) and 0.88 (native species in XSM) (Table 4). Standard pair-wise regressions between species richness and the variables identified above were also informative. One correlation in particular, between elevation and richness for post 9-year burn sites, was found to be positive in CSS for both native and naturalized species, but negative for XSM for native species, and close to significance ($P = 0.07$) for naturalized species (Fig. 5).

The residuals from native vs. naturalized cover (using data from all sites) were negatively correlated with years since sites had last burned in

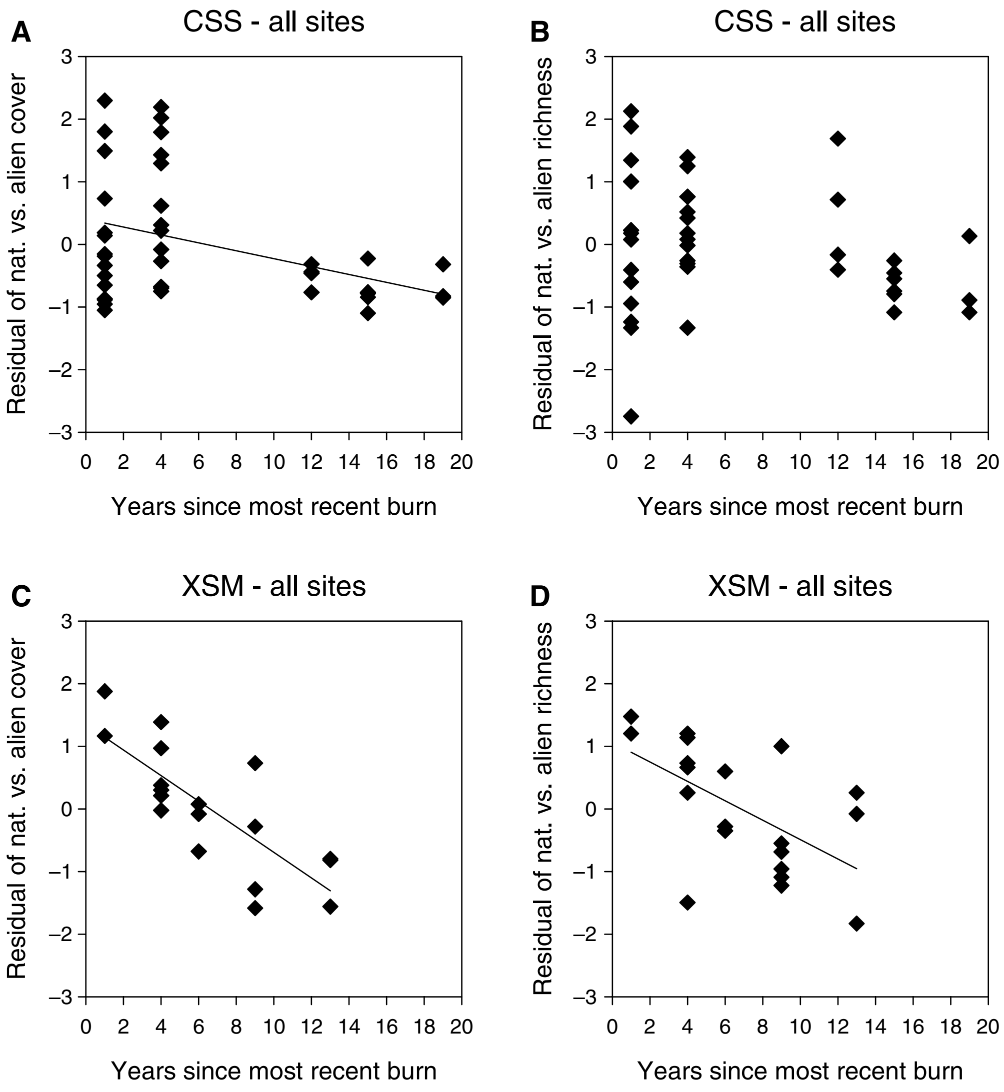

Fig. 6 Relationship between standardized residuals of native vs. naturalized cover, or native vs. naturalized richness, and years since sites last burned. (A) Cover residuals in CSS, $R^2 = 0.16$, $P < 0.05$, slope = −0.063. (B) Richness residuals in CSS, $P = 0.14$. (C) Cover residuals in XSM, $R^2 = 0.61$, $P < 0.001$, slope = −0.204. (D) Richness residuals in XSM, $R^2 = 0.33$, $P < 0.01$, slope = −0.155.

CSS and XSM, with one-sixth and two-thirds of the variation explained, respectively (Fig. 6A,C). The residuals from native vs. naturalized richness (using data from all sites, i.e. from Fig. 3A for CSS, and 3B for XSM) were negatively correlated with years since sites had last burned in XSM, but not significantly so in CSS (Fig. 6B,D).

DISCUSSION

The greater mean richness of species in XSM was caused by a greater number of herbaceous species, as the mean number of woody species was not significantly different between vegetation types (Tables 1–3). In contrast to richness patterns, the total mean cover of herbaceous species were similar between vegetation types (61.1% in CSS and 62.5% in XSM; data from Table 2), while mean cover of woody species was greater in CSS (Table 3). The difference in cover of woody species between vegetation types was apparent in similar aged sites, e.g. 4-year burn sites in CSS averaged close to 50% cover, while 4- to 6-year burn sites in XSM averaged under 20% cover (Fig. 2). This greater cover of woody species in CSS is notable because of the negative influences that woody cover may have on herbaceous richness. This contention is supported indirectly in CSS by the increase of woody cover and the decrease in herbaceous cover with site age (Fig. 2A,C), while it is supported directly in CSS by the negative correlation between the cover of woody species and the richness of herbaceous ones. These results are consistent with the hypothesis that in CSS increasing cover of woody species causes a decrease in herbaceous richness. In XSM, however, the relatively low cover of woody species, as well as the lack of a significant relationship between woody cover and herbaceous richness, is consistent with the hypothesis that herbaceous richness is greater in XSM because of a reduced importance of woody cover in structuring these systems. This reduced importance of woody cover could be due to an inherent difference in the woody species present (e.g. to differences in the production of allelopathic chemicals), or to the lower quantity of cover itself, which would necessarily have less of an affect upon the availability of resources. However, besides the reduced cover of woody species in XSM (which may be due to the introduction of fire into this system), other explanations for the higher species richness in Chilean sites have also been proposed, such as differences in precipitation and anthropogenic disturbance (Parsons, 1976; Gulmon, 1977; Keeley & Johnson, 1977).

In CSS there were no significant relationships between the herbaceous cover of native and naturalized species. This suggests that herbaceous native and naturalized species may not be regularly competing with each other in CSS, and that their distributions and abundance may be determined by other factors, such as the abundance of woody species. In XSM, however, a significant negative correlation between herbaceous cover of native and naturalized species was found for 4- to 6-year burn sites (as well as a nearly significant relationship across all sites). In XSM then, it appears that competition between herbaceous native and naturalized species may be affecting their abundance. This is consistent with the hypothesis that woody species are not structuring XSM sites with sufficient strength to prevent competitive interactions between herbaceous species.

In contrast to cover relationships, richness relationships were consistent between vegetation types. In pre 1-year burn sites there were no significant trends between herbaceous richness of native and naturalized species. The absence of a relationship in pre 1-year burn sites in CSS (where sufficient sites existed to detect a pattern) could be due to a time-lag associated with the colonization of these sites, or to a lack of significant competitive interactions in these sites, which are resource rich and biomass poor. In post 1-year burn sites the strong positive relationships between richness of native and naturalized species are striking in their consistency, both across space (in Chile and California), and across spatial scales (400 m^2, 100 m^2, 25 m^2 and 1 m^2) (Fig. 4). These results are consistent with previously published empirical work (Kruger *et al.*, 1989; MacDonald *et al.*, 1989; Knops *et al.*, 1995; Planty-Tabacchi *et al.*, 1996; Rejmánek, 1996; Lonsdale, 1999; Stohlgren *et al.*, 1999; Levine, 2000; Stadler *et al.*, 2000; Sax, 2001) and with the theoretical work of Huston (1994), who suggested the possibility of positive relationships between native and naturalized species. These results also provide a context for the work of Davis *et al.* (2000), by showing that although disturbance may facilitate the coexistence of native and naturalized species within communities, that a time-lag following disturbance may be necessary before this relationship is present or detectable. Further, the consistency of these results across decreasingly small spatial scales, even at 1 m^2 (where the correlation was nearly significant), raises the question of whether this relationship between native and naturalized richness will break down at any spatial scale less than that at which any two individuals of the same trophic level, regardless of their designation as a native or naturalized species, would be expected to exclude each other (e.g. Yoda *et al.*, 1963). Finally, these results expand the known occurrence of these positive relationships between native and naturalized species to coastal scrub vegetation, to South America, and to systems in which the relative numbers of native and naturalized species are more equitably distributed.

Greater than 80% of the variation in the herbaceous richness of native and naturalized species in post 1-year burn sites was explained by multiple linear regression models (Table 4). Several variables were significant, but none were as important in explaining the variance in these models as native and naturalized richness; a result that is consistent with the strong correlations found between these two groups, and one that suggests that these two groups are responding similarly to environmental conditions. Some of the other significant variables in these models were also informative, particularly when they were segregated by successional maturity and regressed directly against native or naturalized richness. In mature CSS sites, i.e. in post 9-year burn sites, elevation was positively correlated with richness of native species, and positively correlated with richness of naturalized species (Fig. 5A,B). In the Santa Monica Mountains, where the CSS data were collected, elevation should be roughly correlated with precipitation because of the orographic lifting of moist air masses that are pushed over these coastal mountains in the winter (e.g. Barros & Lettenmaier, 1994). Therefore, sites with the highest elevation should receive the most precipitation and should in turn have the most productivity, as precipitation is the principal limiting factor in this environment (Hanes, 1981). This suggests that in CSS, sites with the most productivity support the greatest richness of both native and naturalized species, and that conditions that are beneficial to native species may also be beneficial to naturalized species.

In XSM, however, in post 9-year burns sites, elevation was negatively correlated with richness (Fig. 5C,D), instead of positively correlated as in CSS. This contrasting finding may be due to differences in the productivity of the sites sampled in these two vegetation types. If a curvilinear relationship exists between productivity and richness, and if these XSM sites are further along the gradient of productivity, then increasing productivity in these sites should lead to decreasing richness (for a review of this topic see Mittelbach *et al.*, 2001). Unfortunately, no independent measure of site productivity is available, and the merits of this hypothesis in explaining the patterns observed here are difficult to evaluate. An alternative explanation for the decline in richness with elevation in XSM sites is that water was not limiting (at least in the year preceding sampling), and that some other variable associated with elevation is responsible for the decline in richness. This hypothesis is supported by the initiation of an ENSO (in this case an El Nino) event in the austral winter of 1997, when much greater then average precipitation occurred in Chile (e.g. Jaksic, 1998); this may have temporarily lessened the normally limiting role of water in this system, and allowed other variables that co-vary with elevation to have an increased importance in structuring this system. Note also that the differences in precipitation in the boreal and austral winters of 1997 (an El Nino year in Chile and a 'normal' year in California) strengthen the results of this study, as they suggest that positive correlations between native and naturalized richness are still detectable despite inter-annual variation in precipitation.

Finally, CSS and XSM vegetation appear to respond differently to fire. After controlling for the strong covariance between native and naturalized cover, or the covariance between native and naturalized richness, it is clear that naturalized species are favoured by recent fires in XSM to a much greater extent then in CSS (Fig. 6). This may be due to the historical absence of fire in Chile, and/or to the historical presence of fire in the other regions with mediterranean-type climates, which are the predominant sources of naturalized species in Chile (Mooney *et al.*, 1970; Fox, 1990). Therefore, naturalized species in Chile may be better adapted than native species to a disturbance regime that is dominated by fire. Of course, woody species in Chile are thought to be 'pre-adapted' for fire, as seen by their ability to stump-sprout after fires (Mooney, 1977; Rundel, 1981). However, these woody species still appear to regenerate after fire more slowly in Chile than in California (Fig. 2). While the potential role of confounding factors, such as grazing pressure and wood cutting, cannot be discounted, it nevertheless appears that fire may have done much to modify vegetation in Chile: by reducing the cover of woody species, by increasing herbaceous cover and richness, and by differentially favouring naturalized species.

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