ALIEN PLANT DYNAMICS FOLLOWING FIRE IN MEDITERRANEAN-CLIMATE CALIFORNIA SHRUBLANDS

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Abstract. Over 75 species of alien plants were recorded during the first five years after fire in southern California shrublands, most of which were European annuals. Both cover and richness of aliens varied between years and plant association. Alien cover was lowest in the first postfire year in all plant associations and remained low during succession in chaparral but increased in sage scrub. Alien cover and richness were significantly correlated with year (time since disturbance) and with precipitation in both coastal and interior sage scrub associations. Hypothesized factors determining alien dominance were tested with structural equation modeling. Models that included nitrogen deposition and distance from the coast were not significant, but with those variables removed we obtained a significant model that gave an $R^2 = 0.60$ for the response variable of fifth year alien dominance. Factors directly affecting alien dominance were (1) woody canopy closure and (2) alien seed banks. Significant indirect effects were (3) fire intensity, (4) fire history, (5) prefire stand structure, (6) aridity, and (7) community type. According to this model the most critical factor influencing aliens is the rapid return of the shrub and subshrub canopy. Thus, in these communities a single functional type (woody plants) appears to the most critical element controlling alien invasion and persistence. Fire history is an important indirect factor because it affects both prefire stand structure and postfire alien seed banks. Despite being fire-prone ecosystems, these shrublands are not adapted to fire per se, but rather to a particular fire regime. Alterations in the fire regime produce a very different selective environment, and high fire frequency changes the selective regime to favor aliens. This study does not support the widely held belief that prescription burning is a viable management practice for controlling alien species on semiarid landscapes.

Key words: annuals; colonization; disturbance; diversity; invasive species; metapopulations; structural equation modeling.

INTRODUCTION

Disturbance-induced succession comprises a diversity of phenomena, and this complexity presents a challenge to finding broadly applicable generalizations (White and Jentsch 2001). Recently Turner et al. (1998) have outlined certain principles of disturbance impact due to size and intensity. In their view ecosystem recovery is driven by a balance between colonizers and ecosystem ''residuals,'' defined as species that persist on the site. Disturbance intensity or severity plays a primary role by affecting survivorship of residual species. Disturbance size affects the initial densities of colonizers, and as a consequence competitive sorting during early succession may be affected by colonization constraints. These authors conclude that successional trajectories are determined by a balance between colonizers and residuals.

In California shrublands, natural successional processes are dominated by native residual species that are derived from either dormant seed banks or resprouts from dormant bud banks on tubers. Despite this, there are many plant species that colonize burned sites during the early postfire years (Keeley et al. 2005). Alien annual grasses and forbs are a significant part of this colonizing flora, and under some conditions these species may become aggressive invaders that dominate the site for extended periods (Freudenberger et al. 1987, Keeley 1990, Minnich and Dezzani 1998, Stylinski and Allen 1999). Such degradation and type conversion of native shrublands to alien dominated grasslands has been noted by numerous investigators, some of whom contend that increased frequency of disturbance is the primary factor that favors alien annuals over woody native species (Cooper 1922, Wells 1962, Zedler et al. 1983, O'Leary and Westman 1988, Keeley 1990, 2002), while others maintain it is driven by pollution effects arising from ozone that is more toxic to native shrubs (Westman 1979) or nitrogen deposition that favors alien annuals (Padgett et al. 1999, Allen et al. 2000).

Alien plant invasions are encouraged by fire in many ecosystems, regardless of whether or not fire is a natural

part of the ecosystem (D'Antonio 2000, Brooks et al. 2004). In California's fire-type shrublands the primary alien threats are annual forbs and grasses, and shrublands are most vulnerable to invasion in the first few postfire years (Keeley 2001, Keeley et al. 2003). Alien propagule sources are important determinants of alien plant invasion (D'Antonio et al. 2001), and native propagule sources are an important factor in the ability of natives to recolonize invaded sites (Seabloom et al. 2003). When alien propagules are abundant after shrubland fires, they are capable of rapidly expanding their populations at a time when native competition is at its lowest level. Given sufficient time without fire, successional changes in these shrublands typically result in a closed canopy capable of excluding most alien species. However, when fire frequency is high, repeated disturbances exceed the tolerance thresholds of many shrub species, and their demise enhances alien persistance (Haidinger and Keeley 1993, Jacobson et al. 2004, Keeley 2004b). Fires in undisturbed, largely alien-free shrublands usually have limited alien presence after fire because fire intensities from these high fuel volume systems are capable of killing alien seed banks (Keeley 2001). Alien invasion of shrublands is strongly controlled by disturbance history (Zedler et al. 1983, O'Leary and Westman 1988, Minnich and Dizzani 1998); in particular the shortest interval between fires plays a crucial role because it dictates survival of native shrub species (Jacobson et al. 2004). Also, it has been hypothesized that postfire alien invasions are markedly affected by stand structure, which affects fuel volumes, and subsequent fire severity (Keeley 2001). Consequently, it is expected that burning young stands will result in greater alien presence, and thus larger alien seed banks, which contribute to further alien dominance in subsequent years.

Natural successional changes return communities to long-term equilibrial conditions, and thus we might expect with time-since-disturbance, a change in the importance of factors that might provide some level of resistance to invasion. Since the dominant life forms are native shrubs and subshrubs, and the aliens are largely annual grasses and forbs, we predict greater competitive displacement of aliens with succession. Since succession leads to increasing equilibrium, we might also expect diversity will become an increasingly important factor in resisting invasion (Elton 1958).

A crude model of alien invasion in these ecosystems is that following fire "... alien invasion is a drama between the speed at which alien propagules reach a site and the speed at which the shrublands return to their former closed-canopy condition" (Keeley et al. 2003). Here we investigate patterns of alien plant establishment on postfire chaparral and sage scrub sites in southern California in the first five years after fire. The focus of this study was on the relationship between prefire stand age, fire severity, and other environmental factors on immediate postfire establishment of alien

plants, and the role of residual woody species in the alien invasion process during early succession. Since alien invasions are typically species-specific responses (D'Antonio 2000), we investigated the species level changes after fire. This study took advantage of wildfires that burned ~100 000 ha during a two-week period in the autumn of 1993 and included both evergreen chaparral and semi-deciduous sage scrub (described in more detail in Keeley et al. [2005]).

METHODS

This study included 90 sites distributed across 16 fires that burned in the last week of October and/or first week of November of 1993 in southern California, USA. Number of study sites in each burn was based on fire size, range of fire severities, diversity of vegetation types, and accessibility and are described in more detail in Keeley et al. (2005). Fifty sites were in sage scrub and the remaining in chaparral. Since coastal and interior populations of both vegetation types often responded differently, populations were divided into coastal (<10 km from the coast) and interior (20–75 km) associations. Some of the coastal sites were artificially seeded with alien grasses, most prominently *Vulpia myuros* (and possibly *V. bromoides*; Keeley et al. 1995); however, establishment was very poor (Keeley 1996).

Sampling began in the first spring after fire and continued for a total of five growing seasons (two sage scrub sites were lost to development after the second year). In the first postfire year, precipitation averaged 75–84% of the long-term average for coastal and interior sites, respectively. In the subsequent four years it was 195–171%, 85–74%, 84–89%, and 285–231%, for coastal and interior sites, respectively (Keeley et al. 2005).

Sampling was conducted in 20×50 m sites with 10 nested 100-m^2 square plots, each with two nested 1-m^2 subplots in opposite corners. Density and cover were recorded for each species within the two subplots, and a list of additional species was recorded from the surrounding 100-m^2 plot. Site factors recorded included distance from the coast, elevation, slope aspect, slope inclination, and annual solar insolation (calculated from slope aspect, inclination, and latitude; Frank and Lee 1966). Surface litter was collected within a 20 cm diameter hoop from three alternate plots at each site, dried, and weighed. Three soil samples from the top 6 cm were collected from alternate plots and combined and dried in paper bags. Texture analysis was done according to Cox (1995). pH was determined on an equal mixture of soil and dH_2O incubated overnight at room temperature. Total soil N, P, and K were determined on a subsample at the Soils Laboratory, USDA Forest Service, Forest Fire Laboratory, Riverside, California. Soil analysis was done in the middle of the first growing season and used in regression analysis with later year's vegetation responses. Plant nomen-

FIG. 1. Initial conceptual model of factors driving alien success in southern California shrublands. Hypothesized effects are represented by arrows connecting conceptual or latent variables (ellipses). Measured variables (rectangles) make up the data matrix that tests these hypotheses with covariance analysis and provides a statistical evaluation of the correspondence between the hypothesized path model and the data. See *Methods* for detailed description of variables.
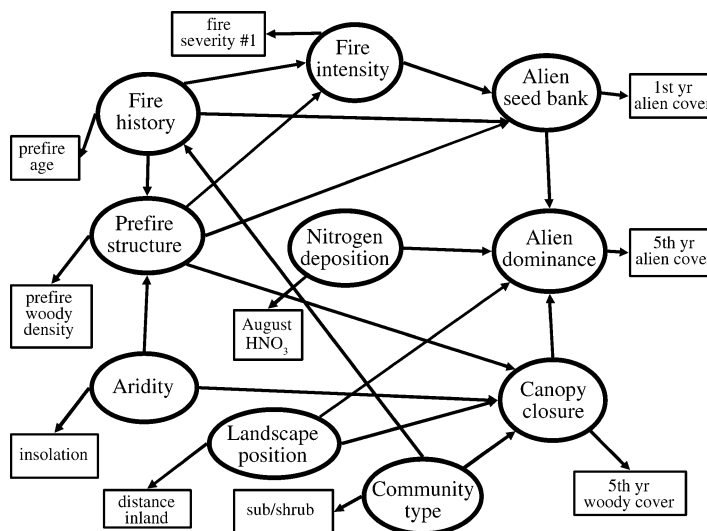
clature follows Hickman (1993). For the structural equation model discussed below we used estimated wet and dry HNO_3 for 1 August 1996 based on models by Tonnesen et al. (2003:317).

Stand age prior to the fire was based on ring counts of stem segments from burned skeletons. Two measures of fire severity were based on skeletal measurements. Fire index number one was based on the diameter of the smallest twig remaining on the two shrub skeletons nearest to each 1-m^2 subplot (Moreno and Oechel 1989). Stem diameters were classified into categories 1–10 with 10 being the largest diameter twigs and thus highest fire severity. A separate scale was used for evergreen chaparral shrubs and semi-deciduous sage scrub (Keeley 1998). Fire severity index number two was based on the height above ground level of five shrub skeletons from each species within each of the 100-m^2 plots.

Data were presented for interior and coastal associations of the two vegetation types (chaparral and sage scrub) when significant differences were present, otherwise data were analyzed by vegetation type. Analysis and graphical display was done with the software SYSTAT 10.2 (SYSTAT 2002). Bivariate relationships between variables were investigated with ordinary least-squares regression. Where bivariate data did not clearly fit an arithmetic relationship, semi-log and log–log transformations were compared and the one giving the highest adjusted R^2 value was presented. Between-treatment comparisons used *t* tests, or one-way or two-way analysis of variance.

Because the relationship between native and alien diversity has been suggested to play a determining role in alien invasions (Elton 1958), we investigate correlations between these two variables and how they changed over the five years of this study. In addition, we developed a null model to determine the probability of such correlations occurring by chance alone. For

each plant association and each year, a pool of species and their alien status were randomly sampled, and the regression between observed native species richness and the number of alien species expected from random samples was determined. This randomization procedure was run 10 000 times with the programming software Python (*available online*)[5] and the proportion of times this *R* value exceeded the observed *R* value was used to assess the significance of the observed relationship.

In order to understand ecosystem impacts of aliens on early postfire succession we examined changes in Jaccard's index relative to changes in alien cover. Jaccard's index for the first and fifth years postfire, weighted by either cover or density as: JI = (MC/[MA + MB]) × 100 where MC is the cover (or density) of species present in the first and fifth years, MA is cover (or density) for species present only in the first year, and MB the same for the fifth year.

Model development

Structural equation modeling or SEM (Grace 2002, Pugesek et al. 2003) was used to analyze a multivariate path model we hypothesized to include the major determinants of alien plant invasion in these shrubland ecosystems (Fig. 1). Structural equation modeling, which is most familiar to ecologists as the specialized case of path analysis, was selected because it has important advantages over more commonly used methods such as multiple regression analysis and ordination. One of SEM's primary features is its ability to statistically evaluate complex hypotheses involving multiple causal pathways. Fig. 1 illustrates our model of the important conceptual or latent variables (ellipses) that determine alien dominance five years after fire. These are theoretical variables that are imperfectly measured

[5] ⟨http://www.python.org⟩

by observed or indicator variables (rectangles). The key concept of a latent variable is that it is not directly measured in the analysis, although some use it in a more restricted sense to mean unmeasurable variables (Bollen 2002). When latent variables are composite variables measured by multiple observed variables, there are certain statistical assumptions of independence. Hypothesized relationships are shown by single headed arrows between conceptual variables, and SEM provides estimates of the strength of these pathways.

One of the features of SEM is that it explicitly recognizes the difference between latent and observed variables, which allows one to evaluate the validity of concepts and the adequacy of our measurements used to represent those conceptual variables. In many respects this is equivalent to the distinction between hypotheses, and predictions that are deduced from those hypotheses, as advocated by the hypothetico-deductive scientific method. For example, the latent variable fire intensity is a measure that requires observations during the fire, and thus can usually only be measured in a study of wildfires by surrogate measures, in this case the diameter of the smallest twig remaining on the shrub skeletons. Thus, the true variable we believe affects alien dominance is fire intensity, but we are forced to use a surrogate measure we call fire severity. One important reason for keeping these variables separate is that if a latent variable is removed from the model, it may be either because it is not an important factor or because the observed variable is a poor measure of that latent variable. As with hypothesis testing in general, falsification is as likely to be due to poor deductions in the generation of predictions as it is to poor hypotheses. Another feature of the SEM approach is that it is possible to make direct estimates of the reliability of these observed variables and include these measurement errors in the model. Finally, SEM analyzes the covariation matrix from the observed variables and provides a statistical evaluation of the correspondence between the hypothesized path model (Fig. 1) and the data. All analyses were conducted with LISREL 8.54 software created by K. Jöreskog and D. Sörbom (SSI Scientific Software International, Lincolnwood, Illinois, USA).

The initial model for our study (Fig. 1) related the response variable (1) alien dominance in the fifth postfire year, to the following latent variables: (2) alien seed bank, which is not necessarily all alien seeds but a specific subset of aggressive alien species that may differ between sites, (3) fire intensity, (4) fire history, specifically the presence of short intervals that may be below the threshold of tolerance for the woody species, (5) prefire woody plant community structure, primarily the density and extent of woody cover, (6) nitrogen deposition, (7) aridity, (8) landscape position relative to coastal marine influence, (9) vegetation stature, reflecting dominance by sage scrub vs. chaparral ele-

ments, and (10) extent of native woody plant canopy closure by year 5.

These latent variables (ellipses) in Fig. 1 were measured by the following observed variables (rectangles): (1) Alien dominance was measured as the cover by alien species in the fifth postfire year. (2) Alien seed bank was represented by the alien cover in the immediate postfire year, which was considered a good relative measure of how sites varied with respect to alien seed production prior to the fire. (3) Fire intensity was measured by fire severity index number one. (4) Fire history was not precisely known because of incomplete coverage and reliability of fire maps, and so time since last fire, which we consider to be a weak measure of this latent variable was the measurement variable. (5) Prefire woody plant community structure was measured as the density of subshrub and shrub skeletons. (6) Nitrogen deposition was not measured at any of our sites but deposition follows a relatively predictable pattern in the southern California air basin (Ulrickson and Mass 1990). We used wet and dry HNO_3 deposition in August from models of Tonnesen et al. (2003), selected because it demonstrated substantially greater differences between regions than other nitrogen forms and on other dates. (7) Aridity is a complex variable that includes characteristics of landscape position, precipitation, and soils, but here is represented by the calculated annual solar insolation. (8) Landscape position is measured by distance from the coast, which is perceived to have a dominant effect on aliens. (9) Vegetation stature, namely sage scrub vs. chaparral, are important determinants of alien success and here is reflected by the ratio of subshrub cover to shrub cover in the fifth postfire year. (10) Native woody plant canopy closure was measured by total cover of woody species in the fifth postfire year.

The path coefficients between latent and measurement variables can be biased by measurement error, and SEM allows for incorporation of this measurement error. Most of the measurement variables were not considered to be biased by measurement error, including prefire stand age, prefire woody plant density, calculated annual solar insolation, distance from the coast and ratio of subshrubs to shrubs. In other words repeated sampling of these variables would not be expected to vary. However, for fire severity index number one, first year alien cover, fifth year alien cover, and fifth year woody plant cover we did expect measurement error, and thus we estimated reliability through a bootstrap estimate of variation among the 20 random subplots. The average correlation among bootstrap samples gave a measure of reliability and this was used to specify error variances. This reliability value was specified as a fixed parameter in the structural equation model, along with the estimated error variances (error variance = (1 − reliability squared) times the variance.

Model fit was made using the chi-square statistic, and a series of models (Fig. 1) were tested that sys-

tematically excluded variables whose inclusion resulted in a significant departure between data and the model. In addition, hypothesized paths in the model that did not produce significant effects as assessed by the chi-square statistic were eliminated from the final model.

RESULTS

Over 75 species of alien plants were recorded from these sites during the first five years after fire (Table 1). The vast majority were annuals from the Mediterranean Basin of Europe and included species from 16 families. In general the dominant alien species were the same in chaparral and sage scrub. Aliens present at two-thirds or more of the sites included the Asteraceae forbs *Centaurea melitensis*, *Conyza bonariensis*, *Filago gallica*, *Hypochoeris glabra*, *Lactuca serriola*, and *Sonchus* spp., the Brassicaceae forb *Hirschfeldia incana*, the Geraniaceae forb *Erodium* spp., and the Poaceae grasses *Avena* spp., *Bromus diandrus*, *B. hordaceus*, *B. madritensis*, and *Vulpia myuros*. These density measures were significantly correlated with plant cover, but there was a great deal of variation due to differences in plant size, e.g., in the first postfire year cover and density gave an $R^2 = 0.216$ ($P < 0.01$, $n = 40$ sites) for chaparral and an $R^2 = 0.173$ ($P < 0.01$, $n = 50$) for sage scrub. On average the species most abundant at a site were also the most widely distributed; the positive correlation between number of sites and average density was $R^2 = 0.387$ ($P < 0.001$, $n = 51$) for chaparral and $R^2 = 0.511$ ($P < 0.001$, $n = 62$) for sage scrub.

During the first five years postfire there were marked shifts in the dominant alien species (Table 2). In the two coastal associations, *Vulpia myuros*, which had been artificially seeded on many coastal sites, dominated for the first two years but was eventually replaced by *Hirschfeldia incana* and species of *Avena* and *Bromus*. In the interior associations *Hirschfeldia* dominated the first year but by year 5, sites were dominated by *Bromus madritensis* and species of *Avena*.

Both cover and richness of aliens varied significantly between years and plant association, and there was a significant interaction between postfire year and association (Table 3). Alien cover was lowest in the first postfire year in all plant associations (Fig. 2a, b) and remained low during succession in chaparral but increased in sage scrub. Both alien cover and species richness peaked in the second postfire year in all four plant associations (Fig. 2a–d). As a proportion of the total cover, alien cover differed significantly between associations, but not between years (Table 3). In other words, between year variation was small compared to between plant associations; for the five years, coastal chaparral ranged 8–16%, coastal sage scrub 9–19%, interior chaparral 15–20%, and interior sage scrub 27–39%.

Alien cover and richness was significantly correlated with year (time since disturbance) and with precipitation in both coastal and interior sage scrub associations (Table 4). In coastal chaparral alien cover and richness was not correlated with year or with precipitation, whereas in interior chaparral there was a significant correlation with precipitation. In all four associations alien cover changed in concert with changes in native cover, and this is reflected in the lack of correlation between percentage alien cover and year or precipitation.

Ordinary least-squares regression of individual bivariate relationships is presented because of marked colinearities between most environmental parameters used in this study (Keeley et al. 2005). In postfire chaparral the only significant relationship between alien cover and environmental parameters was a negative relationship with percentage rock in the surface soil (Table 5). By year 5 this relationship was no longer evident but at that time there was a slightly significant positive correlation with elevation. In contrast there were many environmental correlates with alien cover in sage scrub, with the strongest being a negative relationship with fire severity that was still evident five years after the fire. In a majority of years distance from the coast was positively tied to alien cover. Nitrogen deposition is not included in Table 5 since it was not directly measured in this study. However, estimated wet and dry deposition of HNO_3 from models was not significantly correlated with alien cover in any of the five years ($P > 0.05$, $R^2 < 0.047$ for all years). Estimated deposition, however, was negatively correlated with measured soil nitrogen ($P < 0.01$, $R^2 = 0.076$).

Alien species richness at the 1-m² scale increased significantly with distance from the coast in both chaparral and sage scrub, and this relationship continued for the duration of the study (Table 5). Both chaparral and sage scrub also showed a negative relationship between total soil nitrogen and carbon and alien species richness in a majority of years. In chaparral there was also a consistent negative relationship with percentage rock in the soil, and this persisted through the five years of study. In sage scrub solar insolation, fire severity and prefire stand age were also negatively correlated with postfire alien richness. Prefire woody plant density was also negatively correlated with alien richness in the majority of years in sage scrub. At the largest scale of 1000 m² many of these same relationships were evident immediately after fire but did not persist through early succession (not shown).

Plant associations differed in the relationship between alien richness and alien cover, and it was more closely tied to coastal vs. interior sites than to vegetation type. Coastal chaparral and coastal sage scrub showed a significant correlation between alien richness and alien cover ($R^2 = 0.472$, 0.396, $P < 0.01$, respectively). In contrast, alien richness was not linked to

TABLE 1. Alien species population density during the first five years after fire in chaparral and sage scrub in southern California, USA.

| | | | Total density over years 1–5 (no./ha) | | | | | |
| | | | Chaparral | | | Sage scrub | | |
Species	Origin†	LF‡	No. sites	$\bar{X}$	SE	No. sites	$\bar{X}$	SE
Alien forbs								
Apiaceae								
Conium maculatum	Eur	Bie	2	500	500	2	19 000	19 000
Asteraceae								
Carduus pycnocephalus	MedEur	Ann	5	1 800	1 000	5	307 600	236 400
Carthamus 'leucocaulos'	MedEur	Ann	0			1	50	
Centaurea melitensis	MedEur	Ann	27	16 300	6 900	41	285 800	79 400
Cirsium vulgare	Eur	Ann	4	300	100	7	35 400	22 200
Conyza bonariensis	S Am	Ann	35	81 600	32 400	50	56 100	14 800
Cynara cardunculus	MedEur	HP	0			5	2 400	1 700
Filago gallica	MedEur	Ann	25	665 000	232 500	36	138 900	38 500
Gazania linearis	S Af	HP	0			1	50	
Gnaphalium luteo-album	EurAs	Ann	4	1 900	1 000	6	9 000	8 600
Hypochoeris glabra	Eur	Ann	25	554 100	445 400	44	409 200	127 200
H. radicata	Eur	HP	1	50 000		0		
Lactuca serriola	Eur	Ann	32	4 200	1 500	34	2 900	1 000
Picris echioides	Eur	Ann	1	50		8	700	300
Senecio vulgaris	EurAs	Ann	10	1 400	1 000	8	200	100
Silybum marianum	MedEur	Bie	4	20 000	15 600	3	900	600
Sonchus asper, *S. oleraceus*, and *S. tenerrimus*	MedEur	Ann	39	20 300	6 100	50	34 500	8 300
Brassicaceae								
Brassica nigra	Eur	Ann	8	86 700	54 700	19	271 600	184 100
Hirschfeldia incana	Eur	Ann	23	358 300	113 400	32	209 800	65 900
Lobularia maritima	Eur	Ann	1	50		1	3 000	
Sinapis arvensis	Eur	Ann	4	3 300	2 600	1	4 500	
Sisymbrium altissimum, *S. erysimoides*, *S. irio*, and *S. orietale*	Eur	Ann	18	6 000	2 000	14	6 200	3 700
Caryophylaceae								
Cerastium glomeratum	Eur	Ann	9	161 700	80 600	11	112 900	97 800
Herniaria hirsuta	MedEur	Ann	0			1	1 000	
Silene gallica	Eur	Ann	8	800	200	18	58 900	34 500
Spergularia villosa	S Am	Ann	0			1	1 000	
Stellaria media	MedEur	Ann	17	326 100	160 200	12	166 600	154 800
Chenopodiaceae								
Atriplex semibaccata	Aus	Suff	0			1	50	
Chenopodium album	Eur	Ann	1	50		2	400	200
Salsola tragus	EurAs	Ann	4	3 500	2 400	12	1 000	500
Euphorbiaceae								
Euphorbia peplus	Eur	Ann	2	20 800	20 700	4	600	300
Ricinus communis	Eur	Shrub	1	2 200		0		
Fabaceae								
Acacia melanoxylon	Aus	Shrub	0			1	50	
Medicago polymorpha	MedEur	Ann	1	1 000		22	49 100	44 300
Melilotus indica	MedEur	Ann	3	900	400	19	6 900	5 000
M. officinalis	EurAs	Bie	0			1	50	
Trifolium hirtum	EurAs	Ann	9	25 700	9 500	26	82 400	35 800
T. pratense	Eur	Ann	0			1	6 000	
Vicia tetrasperma	Eur	Ann	0			1	2 000	
Geraniaceae								
Erodium botrys, *E. cicutarium*, and *E. moschatum*	MedEur	Ann	29	117 000	84 900	44	341 200	106 400
Lamiaceae								
Marrubium vulgare	Eur	HP	2	1 100	500	6	900	500
Malvaceae								
Malva pariviflora	EurAs	Ann	1	100		1	50	

TABLE 1. Continued.

Species	Origin†	LF‡	Total density over years 1–5 (no./ha)					
			Chaparral			Sage scrub		
			No. sites	$\bar{X}$	SE	No. sites	$\bar{X}$	SE
Polygonaceae								
Polygonum arenastrum	Eur	Ann	0			1	50	
Primulaceae								
Anagalis arvensis	Eur	Ann	18	61 800	23 600	33	82 700	32 100
Solanaceae								
Nicotiana glauca	S Am	Shrub	0			5	7 800	4 700
Rubiaceae								
Galium parisiense	MedEur	Ann	0			1	3 500	
Verbenaceae								
Lantana montevidensis	S Am	Subs	2	1 500		0		
Alien Grasses								
Poaceae								
Avena barbata and *A. fatua*	Eur	Ann	22	6 900	2 300	47	525 800	207 700
Brachypodium distachyon	MedEur	HP	0			3	20 000	10 100
Bromus diandrus	Eur	Ann	25	401 200	319 200	44	366 000	152 000
B. hordaceus	EurAs	Ann	29	2 034 800	955 300	44	2 525 200	837 700
B. inermis	Eur	HP	1	1 000		0		
B. japonicus	EurAs	Ann	2	2 500		0		
B. madritensis	Eur	Ann	39	5 408 800	1 657 700	50	5 066 900	812 900
B. stamineus	S Am	Ann	0			1	137 500	
B. sterilis	EurAs	Ann	10	39 500	30 400	18	858 700	428 900
B. tectorum	EurAs	Ann	10	1 477 100	655 700	4	40 400	39 000
Dactylis glomerata	EurAs	HP	0			1	50	
Echinochloa crus-galli	EurAs	Ann	2	1 000	500	0		
Gastridium ventricosum	Eur	Ann	10	166 500	88 200	21	82 900	47 400
Hordeum marinum	Eur	Ann	6	100	100	7	300	100
Lamarckia aurea	MedEur	Ann	6	1 300	700	17	9 800	5 200
Lolium multiflorum	Eur	Ann	8	449 500	330 000	16	1 360 500	826 000
Phalaris minor	MedEur	Ann	0			1	50	
Poa annua	Eur	Ann	1	50		1	1 000	
P. infirma	MedEur	Ann	1	371 500		0		
Polypogon monspeliensis	MedEur	Ann	0			4	1 000	500
Schismus barbatus	MedEur	Ann	21	516 800	337 300	23	278 800	93 100
Vulpa bromoides and *V. myuros*	Eur	Ann	33	5 791 800	1 506 800	46	6 066 600	1 246 500

† Aus, Australia; Eur, Europe; EurAs, EuroAsia; MedEur, southern Europe; S Af, South Africa; S Am, South America.
‡ Life-form: Ann, annual; bie, biennial; HP, herbaceous perennial; suff, suffrutescent; subs, subshrub; shrub, shrub.

alien cover for interior chaparral and sage scrub ($R^2 = 0.150, 0.001, P > 0.05$, respectively).

Across all sites in the first postfire year alien species richness was weakly and positively correlated with native species richness (1000 m², $R^2 = 0.098, P < 0.01$), but by the fifth year there was no significant relationship. When analyzed separately for each plant association, there was a highly significant relationship between native and alien diversity in both the first and fifth years, but in all cases the coefficient of variation explained only 3–9% of the variation. Randomization tests revealed that these correlations were not significantly different from that expected by chance alone.

Alien cover in the first year was not related to native plant cover, but by the fifth year there was a weak but significant negative relationship between alien and native cover ($R^2 = 0.191, P < 0.001$), and a somewhat negative relationship between woody plant cover and alien cover ($R^2 = 0.325, P < 0.001$). In the fifth postfire year there was a significant negative relationship between native woody cover and alien cover in all four plant associations (Fig. 3).

Using Jaccard's index as a measure of community similarity between the first and fifth postfire years showed a significant positive relationship with alien cover (Fig. 4). Sage scrub communities with high alien cover in the first year exhibited less change in community composition and structure in the subsequent postfire years. In chaparral this relationship only held for the density-weighted Jaccard's index.

Alien plant distribution in year 5 at different scales is illustrated in Fig. 5. The bulk of all alien species were restricted to just one or two sites (Fig. 5a–d). Within a site at the 100-m² scale, particularly on interior

TABLE 2. Relative dominance of the three alien species with the highest cover each year (years 1–5) for the four plant associations.

Association	Coastal chaparral					Coastal sage scrub				
	1	2	3	4	5	1	2	3	4	5
Avena spp.	0.05									0.78
Brassica nigra						0.72		0.40	1.00	0.61
Bromus diandrus					0.92					
B. hordaceus		0.36	0.76	0.62						
B. madritensis				0.88	1.00		0.56	0.92	0.88	1.00
Centaurea melitensis						0.09				
Erodium cicutarium										
Hirschfeldia incana	0.10	0.36		1.00						
Hypochoeris glabra										
Sonchus spp.							0.56			
Stellaria media			1.00		0.68					
Vulpia myuros	1.00	1.00	0.76			1.00	1.00	1.00	0.76	

sites, two peaks were evident, one for aliens occurring in very few plots and one for species occurring in nearly all plots (Fig. 5e–h). At the 1-m^2 scale most aliens were found in only one or two subplots (Fig. 5i–l).

Structural equation model

Examination of bivariate relationships of all relevant parameters led us to the decision that all latent variables were best represented by a single measurement variable and these are shown along with our final model in Fig. 6. These measurement variables each approximated a normal distribution and so we used maximum likelihood procedures for the analyses. For the observed variables expected to have measurement error we determined the average correlation between bootstrap samples for fifth year alien cover to have an estimate of reliability of 0.96, for alien cover in year 1 an estimate of reliability of 0. 94, and for fifth year woody plant cover of 0.89. These reliability values and the estimated error variances were then specified as fixed parameters in the structural equation model.

Our initial model (Fig. 1) yielded a chi square of 42.1 with 20 degrees of freedom and a *P* value of 0.0027, indicating a highly significant discrepancy between our data and the model. By dropping landscape position as a latent variable the chi square dropped to 31.9 with 17 degrees of freedom and a *P* value of 0.0156, indicating still a significant discrepancy between data and model. By further removing nitrogen deposition as a latent variable the chi square dropped to 19.4 with 12 degrees of freedom and a nonsignificant *P* value of 0.0804. Further improvement in the model was obtained by eliminating direct effects of aridity and community type on alien dominance, giving the final model a chi square of 19.9, 13 degrees of freedom, and a *P* value of 0.1000. The nonsignificant *P* value shows that in terms of absolute fit there was no indication of major discrepancies between our data and the model. Fig. 6 portrays the final model based on our structural equations and presents for each path between latent variables the standardized path coefficients that represent the influences expressed in terms of standard deviation units.

This model (Fig. 6) showed that 60% of the variance in alien dominance in the fifth postfire year was explained by the model and that the important direct effects were shrub cover in year 5 and the seed bank present immediately postfire. Alien success was also affected by indirect effects. Shrub cover was negatively influenced by local site aridity and the extent to which subshrubs vs. shrubs dominated the site, and positively influenced by the prefire density of shrubs. Our surrogate measure of alien seed bank was negatively affected by fire severity, prefire stand age, and prefire shrub density.

Discussion
Shrubland alien invasion model

Complex temporal and spatial patterns in alien plant dominance of postfire chaparral and sage scrub (Tables 3–5) demonstrate a need for multivariate models that can evaluate the relative contributions of the multitude of variables found to correlate with alien dominance. Our model (Fig. 6) explains a substantial amount of the variation in alien dominance five years after fire, and allows us to partition the contribution of different factors. In terms of standardized total effect, the ranking of variables in importance are, direct effects of (1) woody plant canopy closure in year 5 and (2) postfire alien seed banks, and indirect effects of (3) fire intensity, (4) fire history, (5) prefire stand structure, (6) site aridity, and (7) community type.

The strongest direct factor affecting alien dominance is the negative effect of postfire recovery of the woody plant canopy (Fig. 6). Since the bulk of the alien cover comprises annual grasses and forbs (Table 1), this negative relationship (Fig. 3) suggests the hypothesis that the woody plants competitively displace aliens. Indirectly, canopy closure is affected by the type of shrub community, because subshrub dominated sage scrub vegetation naturally forms more open communities. Another indirect factor is aridity, which is a significant

TABLE 2. Extended.

	Interior chaparral					Interior sage scrub				
	1	2	3	4	5	1	2	3	4	5
								0.46	1.00	1.00
	0.28	0.89	1.00	1.00	1.00	0.60	1.00	1.00	0.66	0.48
										0.48
	0.29					0.95	0.55			
	1.00	1.00	0.38	0.29	0.45	1.00			0.36	
		0.60			0.30		0.59			
			0.41	0.36				0.63		

control on the rate and extent of shrub canopy recovery. Canopy closure is also influenced by prefire stand structure, which is controlled by fire history, and other disturbances (e.g., grazing) not considered here. In terms of fire history the key factor is not the average frequency of fires, but the occurrence of extremely short fire return intervals (Zedler et al. 1983, Giessow and Zedler 1996), which can have persistent effects on stand structure evident decades later (Jacobsen et al. 2004).

The other direct factor strongly controlling alien dominance is the positive effect of the alien seed bank available immediately after fire (Fig. 6). One important factor affecting seed banks is fire intensity. Our indicator variable for fire intensity was a measure of fire severity, i.e., diameter of the smallest twig remaining

on skeletons. This measure has been demonstrated to be closely tied to fire temperatures (Moreno and Oechel 1994), but its relationship to fire line intensity, which is considered a better measure of fire intensity (Borchert and Odion 1995), is unknown. Fire intensity negatively affects alien seed banks and it is likely due to high temperatures that are more lethal to alien seed banks than to native seed banks. This is because our most aggressive alien annuals have large seeds, which makes them more sensitive to high temperatures (Keeley 1991). In addition, most all have transient seed banks, and thus the bulk of the seed bank comprises recently dispersed seeds that are likely on or near the soil surface. Alien seed banks are also affected by fire history, particularly through the effects of fire history on stand structure, with frequent fires opening the stands and making them more vulnerable to alien invasion.

Once the woody species have been displaced, alien grasses and forbs can dominate sites for very long pe-

TABLE 3. Two-way ANOVA for alien cover and diversity vs. postfire year and vegetation type (coastal sage scrub, interior sage scrub, coastal chaparral, interior chaparral; n = 88 sites over five years, n = 440).

| Dependent variable	df	F	P
Alien cover			
Year	4	5.149	<0.001
Plant association	3	27.824	<0.001
Year × association	12	1.864	<0.05
Percentage alien cover			
Year	4	0.998	>0.05
Plant association	3	31.671	<0.001
Year × association	12	0.625	>0.05
Alien species richness at 1 m^2			
Year	4	15.790	<0.001
Plant association	3	98.567	<0.001
Year × association	12	2.563	<0.01
Alien species richness at 100 m^2			
Year	4	14.989	<0.001
Plant association	3	56.711	<0.001
Year × association	12	2.083	<0.05
Alien species richness at 1000 m^2			
Year	4	25.790	<0.001
Plant association	3	49.566	<0.001
Year × association	12	1.973	<0.05
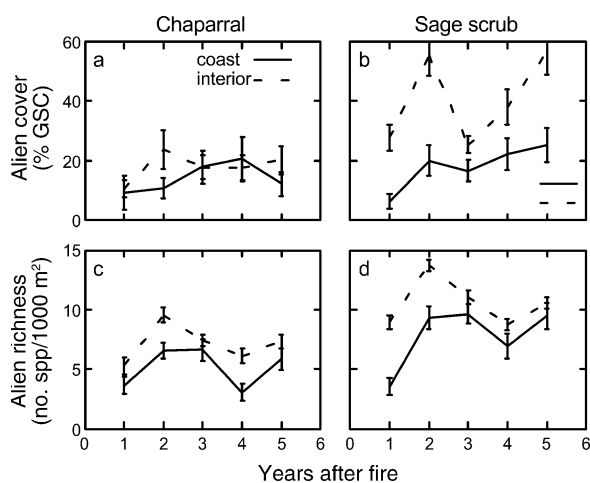
FIG. 2. Postfire changes in (a, b) alien cover and (c, d) alien species richness in coastal and interior associations of (a, c) chaparral and (b, d) sage scrub. GSC, ground surface covered.

TABLE 4. Regression coefficients and adjusted R^2 values between alien cover and richness vs. postfire year and precipitation (Ppt).

Associa-tion†	Alien cover			Alien cover (%)			Alien species richness			Alien species (%)		
	R	R^2	P	R	R^2	P	R	R^2	P	R	R^2	P
Coastal chaparral												
Year	0.115	0.000	NS	0.038	0.000	NS	0.040	0.000	NS	0.042	0.000	NS
Ppt	0.093	0.000	NS	0.129	0.002	NS	0.232	0.040	NS	0.105	0.000	NS
Coastal sage scrub												
Year	0.263	0.60	**	0.128	0.007	NS	0.286	0.073	**	0.382	0.137	***
Ppt	0.198	0.030	*	0.136	0.009	NS	0.285	0.073	**	0.236	0.047	*
Interior chaparral												
Year	0.075	0.000	NS	0.005	0.000	NS	0.028	0.000	NS	0.290	0.077	***
Ppt	0.110	0.040	*	0.044	0.000	NS	0.277	0.044	**	0.167	0.020	NS
Interior sage scrub												
Year	0.173	0.023	*	0.047	0.000	NS	−0.075	0.000	NS	0.177	0.024	*
Ppt	0.379	0.137	***	0.148	0.015	NS	0.262	0.062	**	0.078	0.000	NS

 * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; NS, $P > 0.05$.
 † Coastal chaparral, $n = 14$ sites over five years, $n = 70$; coastal sage shrub, $n = 21$ sites over five years, $n = 105$; interior chaparral, $n = 26$ sites over five years, $n = 130$, interior sage shrub, $n = 27$ sites over five years, $n = 135$.

riods. Two mechanisms appear to be sufficient to maintain these invaded sites. One is resource preemption, particularly competition for water, since annual grasses are more competitive for soil water (Davis and Mooney 1985, Eliason and Allen 1997). Another factor is propagule limitation of the native species (Seabloom et al. 2003). Sage scrub species have light wind-dispersed seeds (Wells 1962) and will recolonize alien dominated sites if disturbance frequency diminishes (Hobbs 1986, Hobbs and Mooney 1986, Freudenberger et al. 1987). Chaparral recolonizes much more slowly because of limited propagule dispersal (Keeley 1992), and seedlings that are poor competitors against alien annuals (Davis and Mooney 1985).

Alternative model

An alternative to our model (Fig. 6) of alien invasion of shrublands argues that air pollution is the primary driver. This model was first proposed by Westman (1979), who reported a correlation between estimated oxidant (mostly ozone) levels and alien dominance, and suggested that native shrubs were more vulnerable to this atmospheric toxin. However, this study has been criticized because it did not adequately consider disturbance history (Haidinger and Keeley 1993).

In recent years the hypothesis of pollution-driven alien displacement of native shrublands has been resurrected, but it is now hypothesized that nitrogen deposition is the factor responsible for alien displacement of native shrubs (Allen et al. 1999, Padgett et al. 1999). When nitrogen deposition was included in our model (Fig. 1) it resulted in a significant departure between the model and data, and thus it was excluded from the final model (Fig. 6). It is possible that this outcome would change with direct measures of nitrogen deposition at our sites, in place of the estimated values given by Tonneson et al. (2003). However, we doubt this because alien invasion and type conversion of shrublands to annual alien grasslands has occurred throughout the southern California region (Keeley 2002). Although the interior basins are highly polluted relative to more coastal sites, our observations reveal that substantial alien invasion has occurred in low pollution coastal regions (e.g., Appendix), as well as in highly polluted interior regions. While our study showed interior sage scrub sites had substantially higher alien cover than coastal sage scrub (Fig. 2), interior sites were broadly distributed (20–90 km from the coast), and included a substantial range in nitrogen deposition.

Much of the support for the pollution model is based on extensive alien invasion of shrublands in the most heavily polluted interior basins (Minnich and Dizzani 1998). However, the interior part of the Los Angeles Basin has had extensive disturbance (including grazing; O'Leary and Westman 1988) and has experienced an exponential rise in fire frequency during the 20th century (Keeley 2004a). This increased fire frequency is tied to a similar rise in human population density and perhaps is affected by the much drier conditions during the latter half of the century as measured by the Palmer Drought Severity Index (Keeley 2004a). Increased drought severity would have enhanced the alien invasion by slowing woody plant recovery (Fig. 6) and would have been exacerbated on interior sage scrub sites because of weaker resprouting capacity and greater dependence on seedling recruitment than coastal sage scrub (O'Leary and Westman 1988, Keeley 2004b).

Of course it is possible that alien dominance is a function of both disturbance and pollution, but there are still unresolved issues with the mechanism driving the nitrogen deposition model. Total soil nitrogen is not tied to alien cover (Padgett et al. 1999; see also Table 5), and in fact on our sites soil nitrogen was

TABLE 5. Regression coefficients for alien cover and richness vs. environmental parameters for the first five postfire years.

Variable and association	R				
	Year 1	Year 2	Year 3	Year 4	Year 5
Alien cover					
Chaparral					
Distance inland					0.311*
Elevation					0.313*
% rock	−0.403**	−0.305*			−0.303*
Sage scrub					
Distance inland	0.371**	0.582***			0.315*
Elevation	0.434**	0.561***			0.381*
Surface litter	0.521***	0.309*			
% N	−0.292*				
% C				−0.291*	−0.292*
Prefire stand age	−0.400**				
Prefire density†		−0.333*	−0.317*		−0.354*
Fire severity number one	−0.556***				−0.313*
Fire severity number two		−0.298*		−0.298*	
Postfire resprout cover					−0.297*
Alien richness at 1 m²					
Chaparral					
Distance inland	0.425*	0.516***	0.355*	0.591***	0.422**
Elevation				0.368*	
% rock	−0.496***	−0.551***	−0.363*	−0.419**	−0.396*
% N		−0.448**	−0.391*	−0.374*	
% C		−0.426**	−0.336*	−0.366*	−0.308*
Sage scrub					
Distance inland	0.697***	0.755***	0.513***	0.581***	0.622***
Elevation	0.638***	0.661***	0.395***	0.489***	0.553***
Insolation	−0.577***				
% rock					−0.290*
% sand		0.379**			
% clay		−0.326*	−0.294*		
% P		−0.405**		−0.339*	−0.323*
% N	−0.282**	−0.398**		−0.377**	−0.567***
% C	−0.325*	−0.320*		−0.366*	−0.563***
Prefire stand age	−0.464***				
Prefire density†		−0.325*	−0.406**	−0.472***	−0.488***
Fire severity number one	−0.564***				
Fire severity number two					
Postfire resprout cover			−0.293*	−0.295*	
Alien richness at 1000 m²					
Chaparral					
Distance inland	0.438**	0.469**		0.336*	
Elevation					−0.329*
% rock		−0.488***		−0.611***	−0.334*
% N	−0.332*	−0.411**		−0.466**	
% C	−0.374*	−0.418**		−0.447***	
Prefire stand age					0.343*
Fire severity number one			0.315*		
Sage scrub					
Distance inland	0.512***				
Elevation	0.335*				
Rock cover		−0.362**			
Surface litter			0.309*		0.287*
% rock		−0.361**		−0.381**	−0.311*
% sand			−0.382**		
pH	0.325*				
% P		−0.313*			
% N			0.335*		
Prefire stand age	−0.333*				0.389**
Prefire density†				−0.393**	
Fire severity number one	−0.396**				
Fire severity number two			0.323*		

Notes: Sample sizes were *n* = 40 sites for chaparral, and *n* = 50 sites (years 1 and 2) or *n* = 48 sites (years 3–5) for sage scrub.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; *R* not shown for $P > 0.05$.
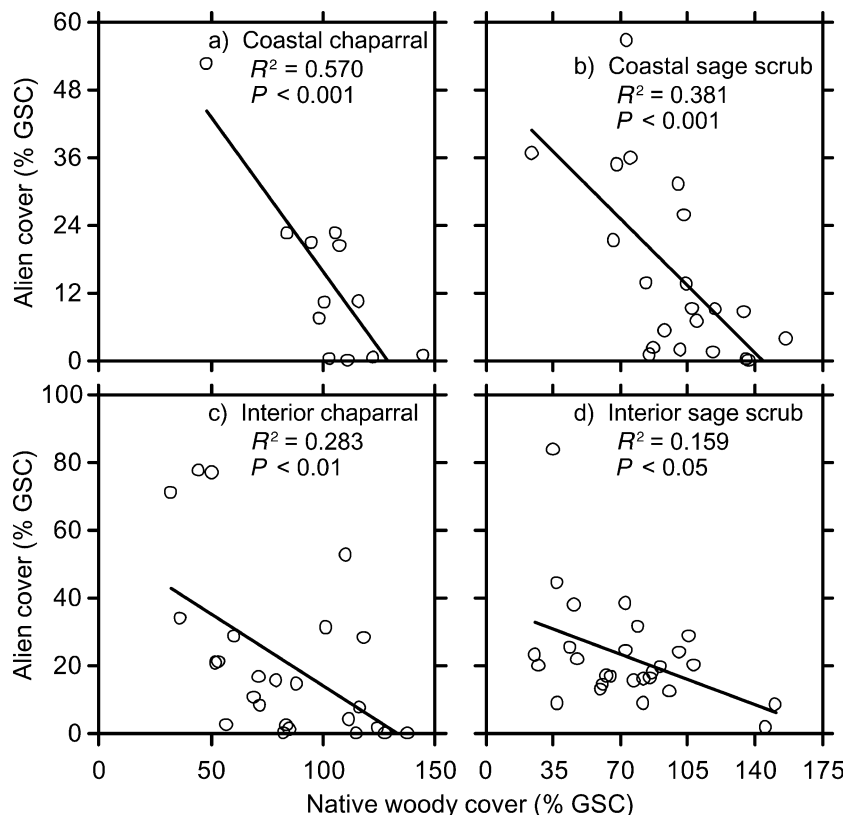
† Shrub and subshrub.

FIG. 3. Relationship between alien cover and native woody cover in the fifth postfire year for the four plant associations.

negatively correlated with nitrogen deposition. It has been hypothesized that annual aliens gain a competitive advantage not from nitrogen per se, but from increased nitrogen availability in the form of nitrate and ammonium. However, the seasonal distribution of these pollutants follows a pattern that is inconsistent with this mechanism. These more readily available nitrogen sources fluctuate markedly through the year in soils and are at their peak during the summer dry season, when the alien annuals are dead, and are close to background levels during the winter–spring growing season (Padgett et al. 1999). In addition, experimental studies have failed to provide evidence of differential yield responses to elevated nitrogen between alien annuals and native shrubs (Padgett and Allen 1999), although there is some evidence that elevated nitrogen may inhibit the growth of native shrubs (Allen et al. 2000). While pollution may have some effect on the balance of aliens to natives, there is little evidence that in the absence of disturbance it could drive the alien invasion of shrublands.

The roles of species and scale

The most aggressive and widespread aliens are grasses, and most alien species are not specific to either chaparral or sage scrub (Table 1). While several species of *Bromus* are very widespread, the most abundant,

both in density and breadth of distribution is *B. madritensis*, being found at all but one site in this study. The only other grass that dominated in all four plant associations was *Vulpia myuros*, and the very close *V. bromoides* (Table 2). These latter grasses were nearly as important postfire species as *Bromus madritensis*, but unlike that species, *V. myuros* was seeded at many sites as part of postfire management activities (e.g., Keeley et al. 1995, Keeley 1996). These seeded species dominated the alien flora early in succession but were replaced by the fifth year with other aliens (Table 2).

During the first five years the most abundant alien species are also the most widely distributed ones, comprising mostly species of *Bromus* and a few Asteraceae forbs (Table 1). However, by the fifth year, within each of the four plant associations, most aliens were restricted to just one or two sites (Fig. 5a–d). Thus, while the most successful aliens are able to occupy many sites in the immediate postfire years, eventually they become restricted to relatively few sites. At this scale it seems unlikely that Hanski's (1982) metapopulation model can explain these patterns. This is based on the observation that there is marked species-specific variation in habitat differentiation in these shrublands (O'Leary and Westman 1988, DeSimone and Burk 1992), particularly differences between slope aspects (Keeley et al. 2005), which makes it apparent that this regional
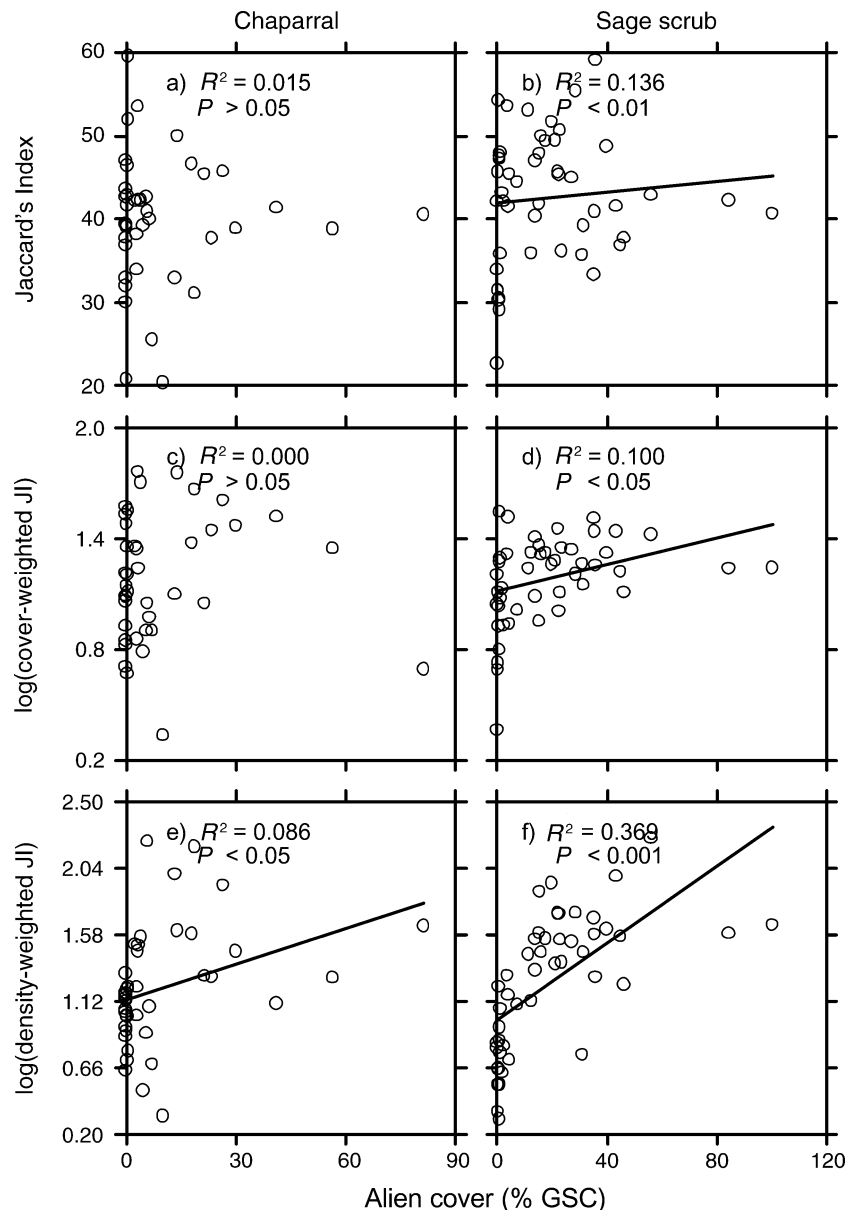
FIG. 4. Jaccard's index (JI) comparing community composition and structure in the first postfire year with the same site in the fifth year for the four plant associations.

comparison violates the homogeneity assumption of Hanski's metapopulation model. A likely explanation for the preponderance of satellite species across sites in the region (Fig. 5a–d) is that the bulk of the aliens exhibit marked niche specialization (Brown 1984), and this becomes increasingly more accentuated by the fifth postfire year.

However, at the community scale of 100 m², alien distribution is bimodal, with a significant number of core species that are found in the majority of plots, particularly on interior sites (Fig. 5e–h). Under equilibrial conditions niche differentiation might explain this (Brown 1984), but in these successional commu-

nities they are more likely tied to metapopulation dynamics involving colonization and extinction dynamics (Hanski 1982). Consistent with the differences between regional and community scales is the likelihood that assumptions of homogeneity in the Hanski model are met at the lower scale of 100 m² (Gaston and Blackburn 2000:109). Thus, within a site, colonization and extinction patterns may play important roles in determining alien patterns. However, it would appear that the metapopulation dynamics are different at the 1-m² (Fig. 5i–l) scale. Lack of core species at this point scale could derive from recruitment limitations to these colonizing species (e.g., Harrison et al. 2001), or to habitat
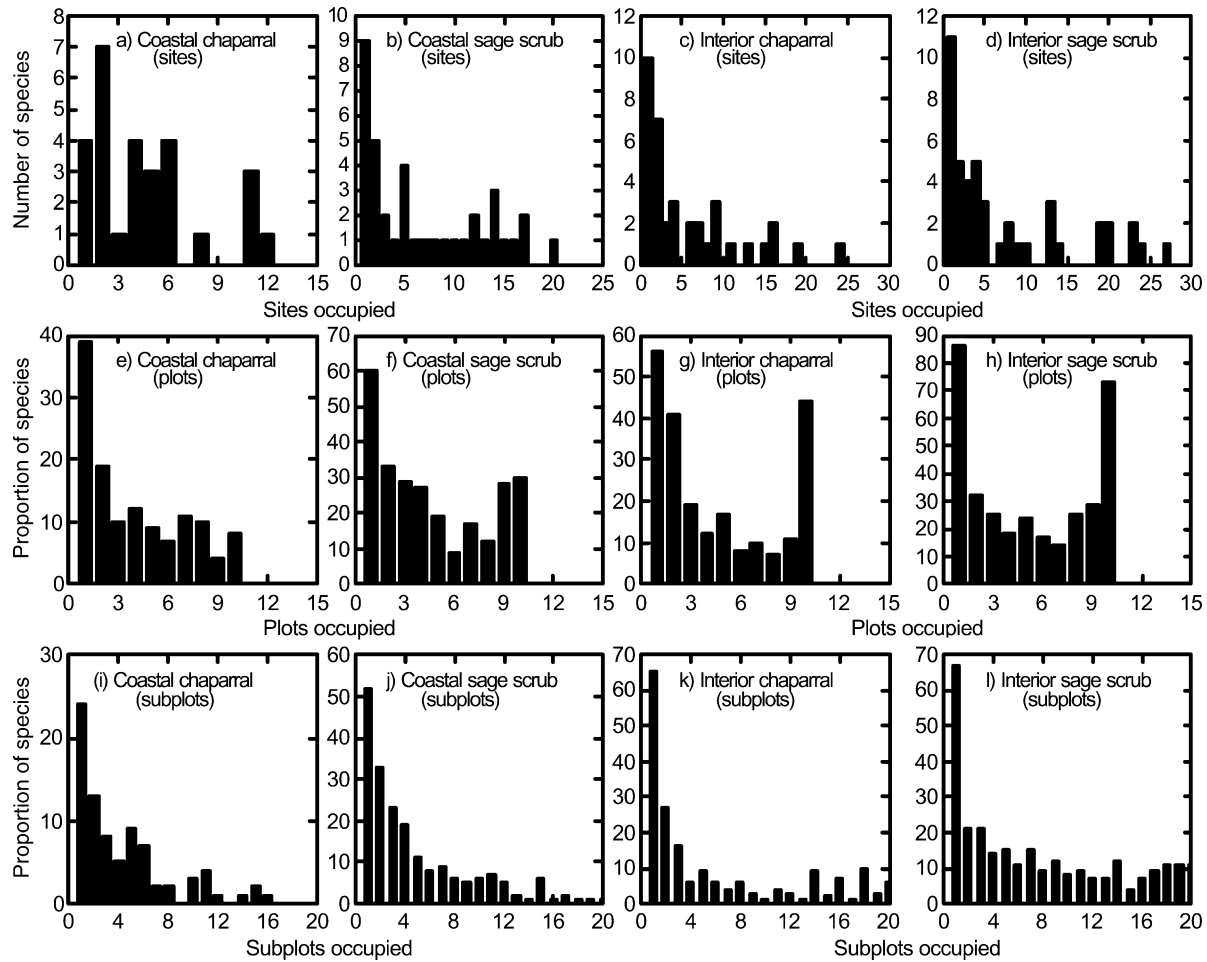
FIG. 5. Distribution of alien species (a–d) in 0.1-ha sites across the region under study, (e–h) in 100-m² plots across 0.1-ha sites, and (i–l) in 1-m² subplots across 0.1-ha sites.
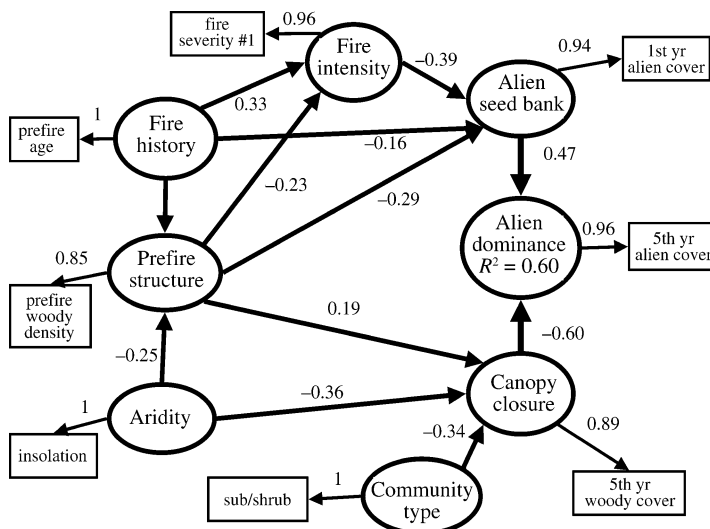

FIG. 6. Final conceptual model of alien dominance in the fifth postfire year. Latent variables (ellipses) and observed variables (rectangles) are described in the *Methods*. Two latent variables in the original model (Fig. 1), nitrogen deposition and landscape position, did not produce significant models, either combined or excluding one at a time, and were removed. Path strength is indicated with standardized regression coefficients, and R^2 is given for the response variable of alien dominance.

differentiation that occurs at patches >1 m², since as habitat heterogeneity increases, unimodal distribution patterns are more likely (Gotelli and Simberloff 1987).

Broader implications

Disturbance is widely recognized as a major factor in alien invasions (D'Antonio 2000), and recovery of a critical functional type in the community is often the primary factor in sustaining alien dominance (Holle and Simberloff 2004). On our landscapes the critical functional type leading to alien dominance is the loss of woody species. This functional type is the only native component capable of competitively displacing the alien annuals. Other functional types such as native annuals appear to be rather weak competitors, and this likely derives from their specialization on postfire environments, which due to higher resources and more open conditions (Keeley et al. 2005) would not have provided strong selection for competitive ability. The lack of a native annual grass functional type may be a contributing factor as suggested by Fox's (1987) assembly rule.

Altered selection regimes has also been suggested as a widely applicable explanation for invasive species dominance in disturbed habitats (Byers 2002). Although California shrublands are commonly described as fire-adapted ecosystems, they in fact are not adapted to fire per se, but rather to a particular fire regime. Alteration in the frequency of fires results in a new selection regime, which selects against native species and favors alien annuals, and thus supports the "altered selection regime" hypothesis.

Once aliens have established they can alter ecosystem properties (Robles and Chapin 1995). One of the means by which aliens on these landscapes alter ecosystem processes is by slowing the rate of successional change following fire (Fig. 4). Another, and widely documented mechanism in fire prone ecosystems is the ability to alter fire regimes, in particular the feedback effects on subsequent fire frequency (Zedler et al. 1983, D'Antonio and Vitousek 1992) resulting from a change in fuel structure (Brooks et al. 2004). In our ecosystems, alien species are largely short-lived annuals that are generally more ephemeral than native annuals. As a result they die earlier in the spring, and thus extend the length of the fire season. They also comprise fine fuels and are more likely to ignite and carry fire than much of the native flora. As the frequency of fires increases above a certain threshold, there is a type conversion of these native shrublands to alien dominated grasslands (Haidinger and Keeley 1993, Jacobsen et al. 2004). In contrast, as the shrubs recolonize these alien dominated sites there is evidence they in turn can act to diminish fire frequency (Cione et al. 2002).

Natural diversity patterns are considered to play a role in providing ecological communities resistance to invasion, but the relationship between invasion and native diversity is debatable (Levine and D'Antonio 1999). In the present study there was no significant relationship between native diversity and alien diversity or alien cover that could not be accounted for by factors other than differences in regional alien species pool size.

Management implications

The dominant influence of shrub and subshrub canopy recovery on controlling alien invasions raises serious issues about the use of prescription burning and other fuel manipulations in these shrubland ecosystems. These landscapes currently experience an unnaturally high frequency of fire, and thus much of it is at risk for alien invasion. Fire managers need to consider this risk, and the potential effects of prescription burning and other prefire fuel manipulations, which decrease woody plant cover and expose sites to alien invasion. In managing these landscapes it might be helpful to consider the fact that the vast majority of alien species in California are opportunistic species that capitalize on disturbance. Adding additional disturbance through prescription burning (or grazing) will only exacerbate the alien problem.

This is contrary to the model proposed in several recent reviews that contend prescription burning is a viable means of controlling noxious aliens on California landscapes. Confidence in this prescribed burning treatment is based on the results of annual burning for three consecutive years that demonstrated >90% reduction in yellow starthistle, *Centaurea solstitialis*, a major pest widely distributed from Idaho to California. However, long-term study shows that this species rapidly reestablishes once burning is halted, and thus prescribed burning does not provide a sustainable solution to the control of this noxious alien thistle, and in fact probably exacerbates the alien situation (DiTomaso et al. 1999).

Management agencies are beginning to recognize that there are potential conflicts between control of aliens and fuel manipulations, and they are incorporating this understanding into their management actions. This is reflected in the recent U.S. Forest Service draft management plan for southern California forests (USDA Forest Service 2004) and the U.S. National Park Service draft fire management plan for the Santa Monica Mountains (USDI National Park Service 2004). These plans call for greatly limiting or abandoning such fuel treatments in the lower elevations of the southern California landscape that already experiences an unnaturally high frequency of fires.

Seeding of alien grasses has long been a controversial issue in California (Beyers 2004). In addition to being of questionable value in slowing soil erosion, this practice has the potential for negatively affecting postfire recovery by competitive displacement of natives. Some managers contend that use of the alien *Vulpia myuros* is less damaging because it persists for a relatively short time after fire and this is supported

by our results (Table 2). However, much of the damage may be done early in succession, since the bulk of shrubland diversity comprises postfire endemics that are weak competitors against aggressive alien grasses. Competitive inhibition of native annual seed production may have cascading effects, resulting in diminished postfire populations during subsequent fire cycles. In addition, the rapid decline of this seeded alien grass may leave an ecological vacuum that is readily filled by other aggressive aliens (Table 2).

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APPENDIX

A photograph of alien dominated shrublands at Mission Trails Park in coastal San Diego County, California, is available in ESA's Electronic Data Archive: *Ecological Archives* A015-064-A1.