



Factors affecting plant diversity during post-fire recovery and succession of mediterranean-climate shrublands in California, USA

Jon E. Keeley^{1,2*}, C. J. Fotheringham² and Melanie Baer-Keeley³

¹US Geological Survey, Western Ecological Research Center, Sequoia-Kings Canyon Field Station, Three Rivers, CA 93271, USA;

²Department of Ecology and Evolutionary Biology, University of California, Los Angeles, CA 90095, USA; ³Resources Division, US National Park Service, Sequoia National Park, Three Rivers, CA 93271, USA

*Correspondence: Jon E. Keeley, US Geological Survey, Sequoia National Park, 47050 Generals Hwy., Three Rivers, CA 93271, USA. Tel.: 559-565-3170; E-mail: jon_keeley@usgs.gov

ABSTRACT

Plant community diversity, measured as species richness, is typically highest in the early post-fire years in California shrublands. However, this generalization is overly simplistic and the present study demonstrates that diversity is determined by a complex of temporal and spatial effects. Ninety sites distributed across southern California were studied for 5 years after a series of fires. Characteristics of the disturbance event, in this case fire severity, can alter post-fire diversity, both decreasing and increasing diversity, depending on life form. Spatial variability in resource availability is an important factor explaining patterns of diversity, and there is a complex interaction between landscape features and life form. Temporal variability in resource availability affects diversity, and the diversity peak in the immediate post-fire year (or two) appears to be driven by factors different from subsequent diversity peaks. Early post-fire diversity is influenced by life-history specialization, illustrated by species that spend the bulk of their life cycle as a dormant seed bank, which is then triggered to germinate by fire. Resource fluctuations, precipitation in particular, may be associated with subsequent post-fire diversity peaks. These later peaks in diversity comprise a flora that is compositionally different from the immediate post-fire flora, and their presence may be due to mass effects from population expansion of local populations in adjacent burned areas.

Keywords

Colonization, core–satellite, dispersal, diversity, growth form, heterogeneity, meta-populations, residual species, resource availability.

INTRODUCTION

Diversity of mediterranean-type ecosystems is of interest because these are hotspots of species richness (Mooney *et al.*, 2001; Myers, 2001). Much of what is known about diversity in these regions concerns patterns of diversity (Bond, 1983; Fox, 1995; Cowling *et al.*, 1996; Keeley & Fotheringham, 2003), and far less is known about processes that determine these patterns (Shmida & Wilson, 1985; Lavorel, 1999).

Globally, disturbance-induced successional changes in species diversity exhibit a variety of patterns. Classical temperate zone old-fields exhibit minimal diversity in the post-disturbance environment and increase monotonically towards a steady-state asymptote after many decades (Bazzaz, 1975; Inouye *et al.*, 1987; Tilman, 1988; *c.f.*, Peet & Christensen, 1988). This pattern runs contrary to some mediterranean shrublands, where diversity often peaks after fire or other disturbance, and succession involves progressive decreases in species richness (Kruger, 1983;

Fox, 1995; Keeley, 2000). These opposite patterns suggest that equilibrium processes are more important in determining richness in temperate old-field succession, and that disequilibrium processes are more important in mediterranean shrubland succession (Huston, 1994).

Particularly important in these shrublands is the predictability of disequilibrium processes such as large-scale crown fires. In temperate forests, such disturbances are less predictable in time and space, and relatively few species can capitalize on resources created by these events. In mediterranean ecosystems, fires are predictable disturbances, and the resources present after fire represent a striking contrast to the more limited resources in undisturbed closed-canopy communities (Carrington & Keeley, 1999; Safford & Harrison, 2004). Many species have mechanisms such as dormant seed banks and resprouting from lignotubers that allow them to capitalize on these enhanced resources in the immediate post-fire environment (Keeley, 1981; Trabaud & Prodon, 1993; Bond & van Wilgen, 1996; Bradstock *et al.*, 2002).

Processes driving species diversity have been the focus of studies in diverse ecosystems, and many important determinants have been delineated (e.g. Tilman, 1988; Huston, 1994; Grace, 1999). Factors most important under conditions of community equilibrium include (i) resource availability, which operates by controlling population sizes; (ii) resource heterogeneity, which affects niche specialization; and (iii) species interactions, which alter competitive relationships, and thus coexistence. Equally important are processes that inhibit equilibrium conditions, such as fires and other disturbances (Petraitis *et al.*, 1989), life-history differences in seed dispersal (Hurt & Pacala, 1995), and influences of regional species pools (Schluter & Ricklefs, 1993). Purely stochastic effects on demographic patterns have also been suggested as an important determinant of diversity in trophically similar species (Chesson & Warner, 1981). It is apparent that species diversity potentially depends on many factors, and diversity patterns likely arise from spatial gradients and temporal variability in multiple controlling variables.

This study investigates factors affecting plant community diversity following wildfires in fire-prone mediterranean-climate shrublands of southern California. We follow the suggestion of Rosenzweig (1995; p. 201) and consider species richness as the clearest measure of species diversity, one that does not confuse other community characteristics such as abundance and dominance. We examine diversity patterns at scales from 1 m² to 1000 m², and how diversity of different life forms varies across broad environmental gradients during the first 5 years after disturbance. Species abundance and distribution patterns within sites and across plant associations were examined to better understand the demographical patterns associated with local vs. widespread species. These patterns were related to dispersal ability based on propagule characteristics. Diversity is also examined within the context of differences in the disturbance event, specifically fire severity, and the effect of spatial and temporal changes in apparent resource availability and in resource heterogeneity.

METHODS

In 1993, massive wildfires burned more than 80,000 ha in 16 different wildfires across southern California, USA. Ninety tenth-acre study sites were selected, and sampling was conducted each spring for the first 5 years (Keeley *et al.*, 2005). Within the 20 × 50 m site were nested 10 non-overlapping 100-m² plots, and within each of these were nested two 1-m² subplots in opposite corners (Keeley & Fotheringham, 2005). Cover and density were recorded in each 1-m² subplot and additional species recorded from the surrounding 100-m² plot. Site factors recorded are described in detail in Keeley *et al.* (2005). Precipitation (September–August) in the first, third and fourth years was approximately 80% of the long-term average, the second year was 175% and the fifth year was an El Niño year of more than 250% of the average.

Species richness patterns were initially analysed by vegetation type, evergreen chaparral or semideciduous sage scrub stratified by coastal vs. interior populations. When there were significant differences between plant associations, i.e. coastal chaparral,

interior chaparral, coastal sage scrub and interior sage scrub, these were reported. Regression analysis of responses to environmental variables did not stratify by coastal vs. interior. Effect of time since disturbance and plant association on diversity at different scales and for different life forms was tested with a fixed effects two-way ANOVA. The hypothesis of no association between percentage of different life forms and plant association was tested with the λ^2 statistic. Seeds were ranked for dispersability on a scale from 1 to 10, with 1 being seeds with characteristics expected to have low potential for dispersal, and 10 the highest. Species with a score of 10 were animal-dispersed fruits, fleshy or meaty fruits or burs and structures attaching externally. Species with flat seeds or ones with mucilaginous coatings were given a score of 5–7, and species with localized dispersal mechanisms, such as explosive capsules, were scored 3, while all others with passive dispersal were scored as 1. Average dispersal index was compared between satellite and core species (the lowest and highest 25% of abundance classes) and between years 1 and 5 with a two-tailed pooled *t*-test. A surrogate measure of spatial heterogeneity is the mean dissimilarity in species composition among samples within a site (Collins, 1992), where percentage dissimilarity is defined as

$$PD = 1 - \left(1 - 0.5 \sum_{i=1}^s |p_a - p_b| \right)$$

and p_a is the proportional cover of species p in quadrat a , p_b is the proportional cover of species p in quadrat b , and s is the total number of species. We calculated dissimilarity in cover-weighted species composition between all pairwise comparisons of 1-m² subplots at a site. Simulations demonstrated that this measure of heterogeneity does not correlate with average community composition, and thus, we treat heterogeneity as an independent factor affecting diversity.

RESULTS

At all scales (1 m², 100 m² and 1000 m²), total species richness was significantly different ($P < 0.001$) between plant associations and between years with the two-way ANOVA. It was generally greatest in the first or second post-fire year and least in the fourth year (Fig. 1). For both chaparral and sage scrub, interior sites were more diverse at all scales than coastal sites. Yearly variation in richness was not consistently the same for all associations as indicated by the highly significant interaction term at all spatial scales. Both coastal and interior sites for chaparral and sage scrub exhibited an increase in richness in the fifth year (Fig. 1).

In the first post-fire year there was a substantial difference in species richness of life forms, with annuals comprising half of the flora in coastal sites and even more in interior sites (Table 1). Species richness of both annuals and herbaceous perennials exhibited highly significant changes due to year, but the same was not observed for woody species (Table 2). Most of the changes in diversity observed during the first 5 years (Fig. 1) were due to the presence or absence of annuals. In the fourth year there was a 22–57% reduction in richness of annuals, relative to year 1. However, time,

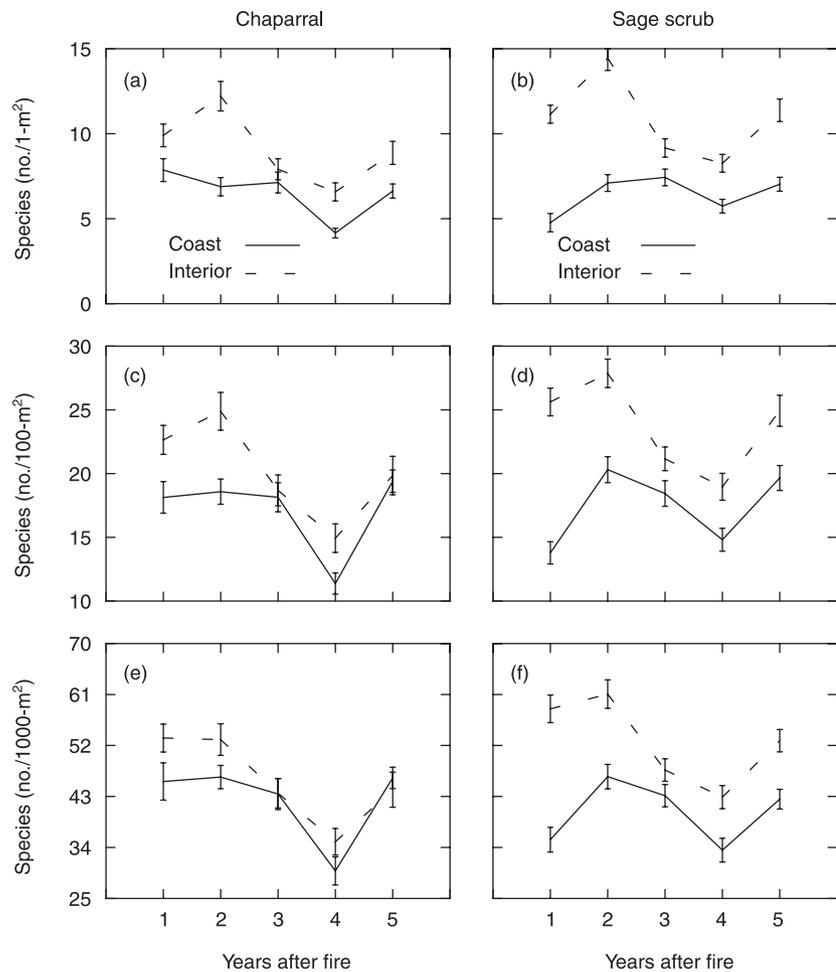


Figure 1 Post-fire changes in species richness at (a, b) 1-m²; (c, d) 100-m²; and (e, f) 1000-m² stratified by vegetation type and coastal vs. interior sites.

Table 1 Species distribution in the major life forms among the four plant associations in the first post-fire year; test of the hypothesis of no association between rows and columns was rejected, $\lambda^2 = 1074$, $P < 0.001$

	No. of sites	Total no. of species	Percentage					Herbaceous perennial	Annual
			Tree	Shrub	Subshrub	Suffrutescent			
Coastal chaparral	14	175	< 1	9	9	5	26	50	
Coastal sage scrub	22	166	0	9	13	5	23	50	
Interior chaparral	26	278	< 1	11	9	4	19	57	
Interior sage scrub	28	265	< 1	5	8	4	25	57	

since disturbance, was apparently not the only factor affecting richness since annuals once again appeared in abundance in year 5, and richness values for annuals were only 2–29% less than year 1.

In these semi-arid land ecosystems it is not surprising that for all four plant associations, species richness during the first 5 years was positively correlated with precipitation at some or all scales (Table 3). This positive relationship with precipitation is overlaid on another trend of negative species richness with time since fire for all but the coastal populations of sage scrub (Table 3).

Life forms were further broken into 18 growth forms (Appendix S1). The dominant shrubs were evergreen, subshrubs were

mostly summer-deciduous and the bulk of herbaceous perennial and annual species were caulescent forbs. Growth form richness was significantly different between plant associations and between years, but the lack of a significant interaction term suggested the differences between associations remained the same over time (Table 2).

Environmental filters

Total species richness at the 1-m² scale in the first post-fire year was positively correlated with distance inland from the coast and

Table 2 Two-way ANOVA tenth hectare form diversity vs. post-fire year and plant association (coastal sage scrub, interior sage scrub, coastal chaparral, interior chaparral); *n* = 440

Dependent variable	d.f.	<i>F</i>	<i>P</i>
Shrub species richness			
Year	4	3.033	< 0.05
Association	3	27.762	< 0.001
Year × association	12	0.463	> 0.05
Subshrub species richness			
Year	4	2.700	< 0.05
Association	3	6.591	< 0.001
Year × association	12	0.921	> 0.05
Suffrutescent species richness			
Year	4	1.640	> 0.05
Association	3	4.880	< 0.01
Year × association	12	0.873	> 0.05
Herbaceous perennial species richness			
Year	4	7.255	< 0.001
Association	3	3.073	< 0.05
Year × association	12	0.539	> 0.05
Annual species richness			
Year	4	30.412	< 0.001
Association	3	53.693	< 0.001
Year × association	12	2.42	< 0.01
Growth form richness*			
Year	4	16.445	< 0.001
Association	3	22.059	< 0.001
Year × association	12	1.411	> 0.05

*Growth forms in Appendix S1.

negatively with fire severity in both chaparral and sage scrub (Table 4). In this first year, richness did not correlate with other parameters in chaparral, but in sage scrub it was correlated with prefire stand age and various soil characteristics. In subsequent post-fire years, distance inland from the coast remained a significant

factor in most years for both sage scrub and chaparral (Table 4). A detailed overview of how richness is varied through time for individual life forms is shown in Appendix S2.

Multiple regression models incorporating the significant variables in Table 4 and Appendix S2 invariably produced higher regression coefficients (data not shown). However, these models included variables that exhibited significant collinearity (Keeley *et al.*, 2005). When collinear variables were eliminated, the remaining models either failed to produce a significant relationship, or the adjusted *R*² was no greater than that exhibited by simple bivariate relationships.

Species distribution patterns

At all scales there were highly significant relationships between average density and number of sites, plots or subplots in which the species was distributed (Table 5). Thus, widely distributed species (within regions or within sites) were those that were most abundant. This could reflect on niche breadth differences or greater colonizing potential in widespread species, and is potentially sorted out by examining patterns of species abundance.

Species abundance distribution followed a unimodal pattern at the spatial extremes of 1000-m² (Fig. 2a,b) and 1-m² (Fig. 2e,f). For sites across the region, and for 1-m² subplots within tenth-hectare sites, the vast majority of species are best regarded as satellite species, being recorded from only a few sites, and very few qualified as core species, here very liberally defined as present in 75% or more of the samples (Fig. 2). However, an apparent bimodal pattern, which included both core and satellite species, was evident at the intermediate scale of 100-m² plots within tenth-hectare sites (Fig. 2). These patterns were robust across years (Fig. 2) and plant associations (Appendix S3).

If metapopulation theory and colonizing ability explain these patterns of satellite and core species, then we should see some relationship with dispersal capacity. We examined the extent to which dispersal characteristics correlated with abundance

	Species richness					
	1-m ²		100-m ²		1000-m ²	
	<i>R</i>	<i>P</i>	<i>R</i>	<i>P</i>	<i>R</i>	<i>P</i>
Coastal chaparral (<i>n</i> = 70)						
vs. year	-0.324	< 0.01	-0.140	> 0.05	-0.194	> 0.05
vs. ppt	0.050	> 0.05	0.313	< 0.01	0.265	< 0.05
Coastal sage scrub (<i>n</i> = 107)						
vs. year	0.193	< 0.05	0.177	> 0.05	0.020	> 0.05
vs. ppt	0.226	< 0.05	0.391	< 0.001	0.283	< 0.01
Interior chaparral (<i>n</i> = 130)						
vs. year	-0.279	< 0.001	-0.299	< 0.001	-0.342	< 0.001
vs. ppt	0.197	< 0.05	0.152	> 0.05	0.076	> 0.05
Interior sage scrub (<i>n</i> = 137)						
vs. year	-0.217	< 0.01	-0.228	< 0.01	-0.318	< 0.001
vs. ppt	0.336	< 0.001	0.273	< 0.001	0.194	< 0.05

Table 3 Regression coefficients between species richness at different scales vs. post-fire year or precipitation (ppt)

Table 4 Regression coefficients for total species richness (no. of species/m²) vs. environmental parameters for the first 5 post-fire years for both vegetation types; *n* = 40 for chaparral and *n* = 50 (year 1 and year 2) and *n* = 48 (years 3–5) for sage scrub; ****P* < 0.001, ***P* < 0.01, **P* < 0.05, *R* not shown for *P* > 0.05.†

	<i>R</i>				
	Year 1	Year 2	Year 3	Year 4	Year 5
Chaparral					
Distance inland	0.315*	0.487***	0.378*	0.362*	
Insolation					
Rock cover					
Soil:					
% rock		-0.487***		-0.362*	-0.321*
% clay					
pH					
% P		-0.478**	-0.434**	-0.322*	-0.454**
% N		-0.473**		-0.364*	-0.322*
% C		-0.392*			
Prefire stand age					
Fire severity no. 1	-0.359*				
Sage scrub					
Distance inland	0.709***	0.724***	0.352*	0.553***	0.666***
Insolation					
Rock cover	0.288*				
Soil:					
% rock					
% clay		-0.407**		-0.289*	-0.292*
pH	0.350*				0.405**
% P	-0.284*	-0.458***		-0.384**	-0.416**
% N	-0.377**	-0.390**		-0.376**	-0.619***
% C				-0.321*	-0.515***
Prefire stand age	-0.652***	-0.404**	-0.287*		
Fire severity no. 1	-0.589***				

†Presentation was simplified by eliminating parameters that were strongly collinear with other parameters; e.g. elevation exhibits colinearity with distance inland, sand with clay and fire index 2 and index 1 (Keeley *et al.* 2005).

Table 5 Regression coefficients between species distribution (i.e., number of 1000-m² sites, 100-m² plots or 1-m² subplots) and log of average density and cover

	Year 1				Year 5					
	<i>n</i>	Log density		Log cover		<i>n</i>	Log density		Log cover	
		<i>R</i>	<i>P</i>	<i>R</i>	<i>P</i>		<i>R</i>	<i>P</i>	<i>R</i>	<i>P</i>
Sites	381	0.443	< 0.001	0.443	< 0.001	359	0.449	< 0.001	0.458	< 0.001
Plots	4414	0.785	< 0.001	0.717	< 0.001	4107	0.710	< 0.001	0.766	< 0.001
Subplots	3079	0.854	< 0.001	0.650	< 0.001	3038	0.765	< 0.001	0.641	< 0.001

distribution patterns. At the scale of sites within a region, there was no significant difference in dispersal ability of core or satellite species or between years 1 and 5 (Table 6). At the scale of plots within a site the widespread core species in the first post-fire year had significantly lower dispersal scores than satellite species in three of the four plant associations. In all four plant associations the dispersal index was significantly higher for core species in year 5 than in year 1 and not different from satellite

species (Table 6). Similar patterns were also evident for 1-m² subplots.

An alternative explanation for core species could be longevity of persistence, in other words residual species present for multiple fire cycles may have a longer period for dispersal and establishment. This is evaluated for year 5 floras where species also present in year 1 are considered residual species, whereas new species are considered post-fire colonizers. Consistent with the

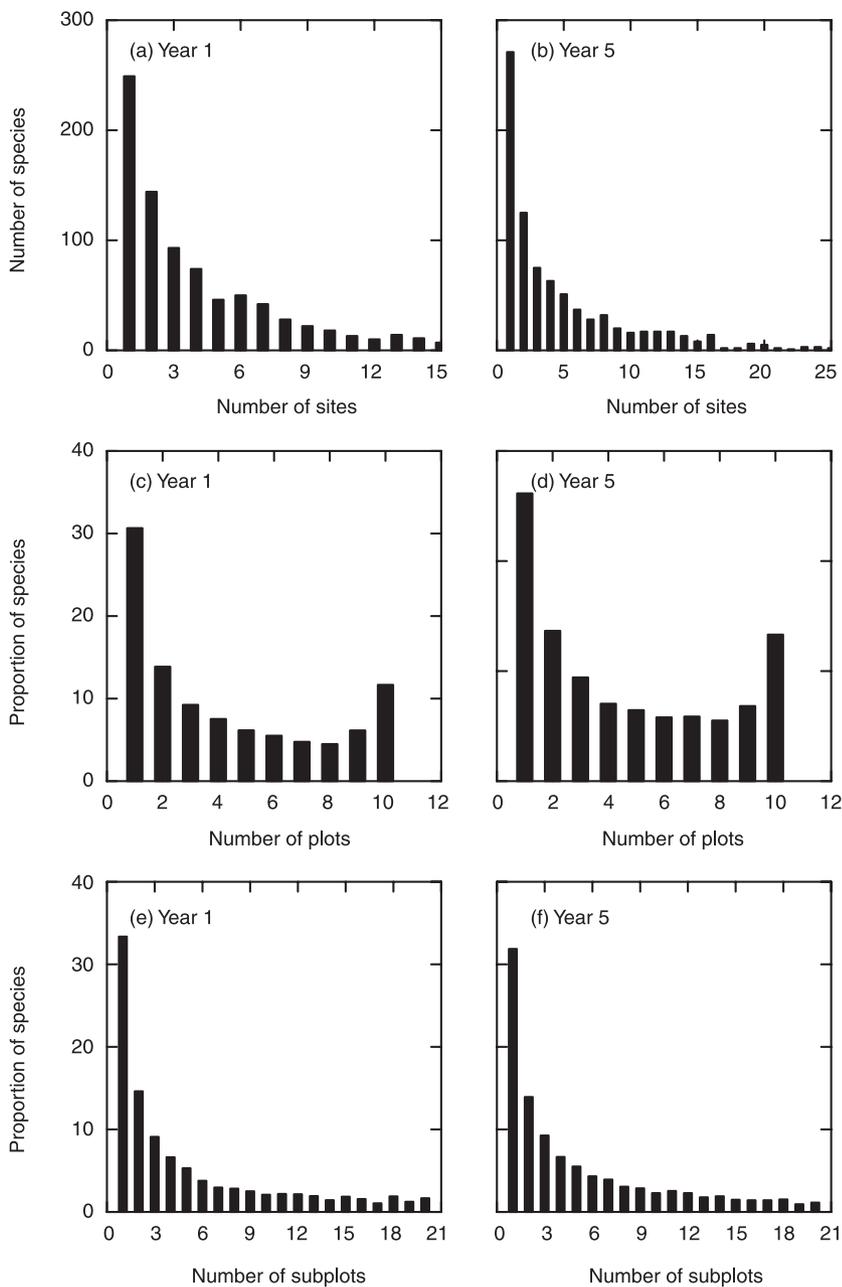


Figure 2 Core satellite analysis showing number of species occupying tenth hectare sites in the (a) first and (b) fifth post-fire years; (c, d) proportion of species occupying 100-m² plots within a site; and (e, f) proportion occupying 1-m² subplots within a site occupied. Breakdown by plant association shown in Appendix S2.

lack of a strong difference in dispersal index for core vs. satellite species (Table 6) is the fact that in the fifth year (Table 7) core species were typically residual species that were present from the immediate post-fire environment.

Resource availability

Considering all sites together, there was a highly significant positive relationship between richness and our surrogate measure of resource availability in the first year, which accounted for 21% of the variation but substantially less in subsequent years (Table 8). Examining this relationship by life form, we see that for herbs, both annuals and herbaceous perennials, as much as a half of the variation in richness was accounted for by resource availability,

except in the below average rainfall years, 3 and 4. Woody species richness followed a similar pattern, except the relationship between richness and density was not sensitive to the below average rainfall of years 3 and 4.

Resource heterogeneity

Two direct measures of environmental variability were used to examine the relationship between environmental heterogeneity and species richness, coefficient of variation in fire severity (index no. 1) and in rock cover. Collectively, across all sites there was no significant (or very weak with $R^2 < 0.03$) relationship between richness and these two measures, for all species, or species by life form. However, when stratified by vegetation type, two

Table 6 Average dispersal index for satellite and core species in years 1 and 5 for different spatial scales; tenth-hectare sites across region, 100-m² plots across sites, and 1-m² subplots across sites. Satellite species were defined as those occurring in (approximately) 25% or fewer of the sites, plots or subplots and core species those occurring in 75% or more; Kruskal–Wallis test *P*-values, ns > 0.05, * < 0.05, ** < 0.01, *** < 0.001

	Average Dispersal Index								
	Sites Satellite	Core	Plots Satellite	Core	Subplots Satellite	Core			
Coastal chaparral									
Year 1	6.2	4.8	ns	6.6	5.2	***	6.4	4.3	**
Year 5	5.9	7.3	ns	6.9	7.0	ns	6.9	5.5	ns
	ns	ns		ns	***		*	ns	
Coastal sage scrub									
Year 1	5.9	5.3	ns	6.7	5.7	***	5.9	4.5	*
Year 5	5.5	6.8	ns	6.9	6.9	ns	7.2	5.8	ns
	ns	ns		ns	***		***	ns	
Interior chaparral									
Year 1	5.6	8.2	ns	6.4	5.5	***	6.2	5.5	ns
Year 5	6.1	7.0	ns	6.5	6.7	ns	6.6	7.0	ns
	ns	ns		ns	***		ns	**	
Interior sage scrub									
Year 1	5.1	6.8	ns	6.3	6.1	ns	6.5	5.4	*
Year 5	5.8	7.2	ns	6.6	6.8	ns	6.3	7.5	**
	ns	ns		ns	**		ns	***	

Table 7 Year 5 distribution of satellite and core species by residual (present in year 1) or colonizing status for different spatial scales; tenth-hectare sites across region, 100-m² plots across sites and 1-m² subplots across sites. Satellite species were defined as those occurring in (approximately) 25% or fewer of the sites, plots or subplots and core species those occurring in 75% or more. Test of the hypothesis of no association between rows and columns is presented for each 2 × 2 contingency table

	Frequency					
	Sites Satellite	Core	Plots Satellite	Core	Subplots Satellite	Core
Coastal chaparral						
Residual	78	10	133	112	154	11
Colonizer	38	1	202	18	155	1
	$\chi^2 = 2.65, P > 0.05$		$\chi^2 = 81.07, P < 0.001$		$\chi^2 = 8.09, P < 0.01$	
Coastal sage scrub						
Residual	72	9	146	169	162	18
Colonizer	45	1	277	62	273	2
	$\chi^2 = 3.23, P > 0.05$		$\chi^2 = 81.07, P < 0.001$		$\chi^2 = 22.26, P < 0.001$	
Interior chaparral						
Residual	140	4	282	252	291	63
Colonizer	43	0	302	42	292	9
	$\chi^2 = 1.22, P > 0.05$		$\chi^2 = 116.76, P < 0.001$		$\chi^2 = 36.45, P < 0.001$	
Interior sage scrub						
Residual	134	10	317	355	340	92
Colonizer	51	0	363	40	367	6
	$\chi^2 = 3.75, P < 0.05$		$\chi^2 = 199.49, P < 0.001$		$\chi^2 = 72.57, P < 0.001$	

significant relationships were evident. In sage scrub, first year richness at the 1-m² level increased significantly with variation in fire severity (Fig. 3b). In chaparral there was a significant increase in richness with site variation in rock cover (Fig. 3a).

An indirect measure of spatial heterogeneity is the dissimilarity in cover-weighted species composition between 1-m² subplots at a site. It is expected that this relationship should be expressed in both chaparral and sage scrub, and so to increase the sample size, this regression analysis was done for all sites

together. When the average dissimilarity value for a site was regressed against first year species richness, there was a highly significant positive relationship at both the 1-m² and the 1000-m² scales, explaining between 10% and 20% of the variation, respectively (Fig. 4a,c). In the fifth year this relationship was still evident at the largest scale (Fig. 4d).

Heterogeneity is thought to increase richness by providing greater opportunities for niche specialization. One indication of this would be a significant correlation between growth form

		Post-fire year				
		1	2	3	4	5
All species	R^2	0.209	0.091	0.002	0.007	0.026
	P	< 0.001	< 0.001	< 0.05	< 0.001	< 0.001
Annuals	R^2	0.288	0.333	0.035	0.037	0.208
	P	< 0.001	< 0.001	< 0.05	< 0.05	< 0.001
Herb. perennials	R^2	0.502	0.323	0.051	0.068	0.129
	P	< 0.001	< 0.001	< 0.05	< 0.05	< 0.001
Woody species	R^2	0.459	0.204	0.360	0.267	0.028
	P	< 0.001	< 0.001	< 0.05	< 0.001	> 0.05

Table 8 Regression analysis of 1-m² species richness vs. coefficient of variation for resource availability ($n = 1800$ for year 1 and year 2 and $n = 1760$ for years 3–5). Because of limited species richness for shrubs, subshrubs and suffrutescents individually these are presented collectively as all woody species

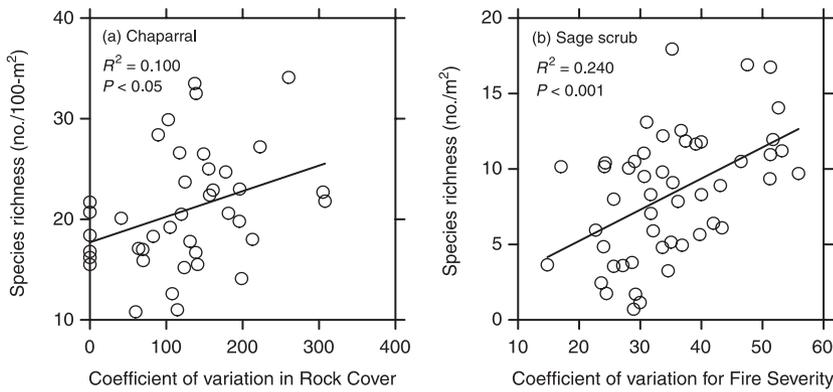


Figure 3 Relationship of species richness to heterogeneity in (a) fire severity in sage scrub and (b) rock cover in chaparral.

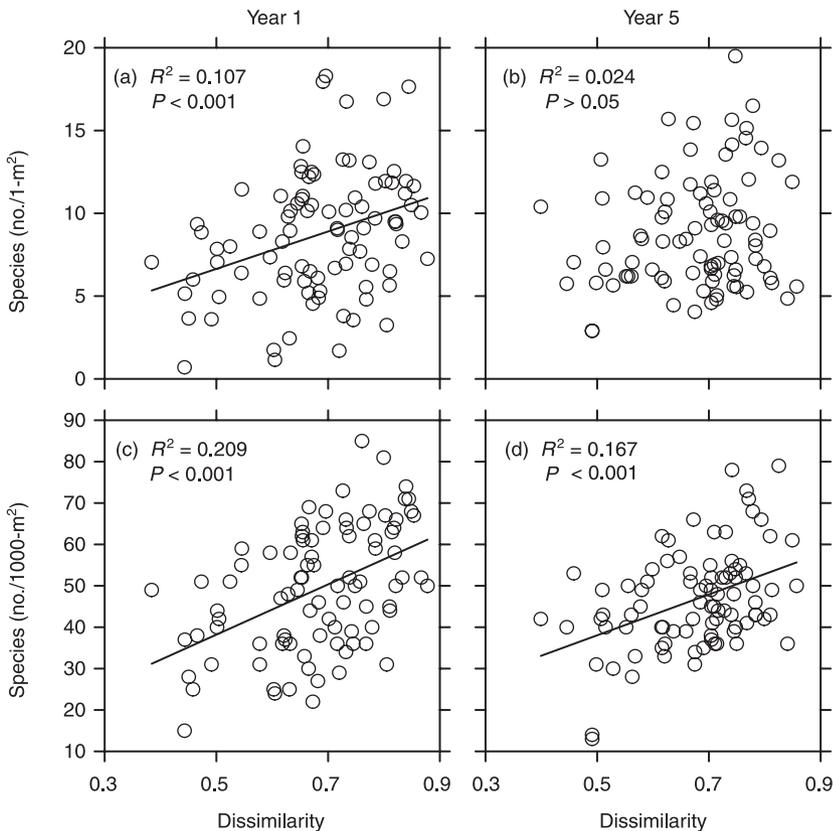


Figure 4 Relationship of species richness to spatial heterogeneity measured by percentage dissimilarity in species composition weighted by cover in (a, c) year 1 and year 5 (b, d) at two different scales for all sites combined.

(Appendix S1) richness and species richness, particularly at the 1-m² point scale where competitive displacement is most likely to occur, and in the fifth post-fire year when competition would be expected to be more intense. At the 1-m² scale the relationship between species richness and growth form richness was highly significant ($P < 0.001$) for each of the four plant associations and in all five years. To evaluate the ecological significance of this relationship we tested these relationships against a null model based on random sampling of the species pools within each plant association. This randomization procedure was run 10,000 times and the proportion of times this R -value exceeded the observed R -value was used to assess the significance of the observed relationship. In year 1, coastal chaparral came close to showing a significant departure from random expectation ($P = 0.064$), but for the other three associations there was no significant difference in the R -value for the observed vs. that obtained from random samples. In year 5, both chaparral associations exhibited a significant relationship between species and growth form richness (Fig. 5), and the observed R -values were significantly greater than those expected by chance alone ($P < 0.001$ and $P < 0.01$ for coastal and interior associations, respectively). However, the two sage scrub associations gave R -values that were not significantly different from those expected by chance.

DISCUSSION

Plant diversity in California shrublands has long been known to follow a marked temporal pattern with the greatest diversity concentrated in the first post-fire year or two (Sweeney, 1956; Keeley *et al.*, 1981; Guo, 2003). This pattern stands in contrast to the generalizations about successional patterns of diversity based on temperate forests where diversity tends to increase with time since disturbance and is heavily dependent on rates of colonization (Bazzaz, 1975; Inouye *et al.*, 1987). In California shrublands, the post-fire flush of species is due almost entirely to residual species present prior to the fire in various vegetative stages or as dormant soil-stored seed banks (Keeley *et al.*, 2005). The successional decline in diversity culminates in mature communities with an order of magnitude fewer species than in the immediate post-fire flora (Keeley & Fotheringham, 2003). This successional decline in diversity is tied to increases in size, cover and biomass of woody plants (Guo & Rundel, 1997; Keeley *et al.*, 2005), and results in the displacement of herbaceous species. This inverse relationship of plant biomass and diversity is commonly observed in other communities as well, and may represent competitive effects of the dominant life forms (Tilman, 1988; Grace, 1999).

The present study demonstrates how these successional trajectories in diversity can be altered by exceptional climatic events. In California shrublands the commonly observed successional decline in species diversity is reversible by exceptional rainfall events such as the extraordinary El Niño rains prior to the fifth growing season. However, this rainfall-induced flush of species does not entirely mirror the immediate post-fire flush of species diversity. Eighteen of the most common post-fire annuals were endemic to these recently burned sites and were no longer

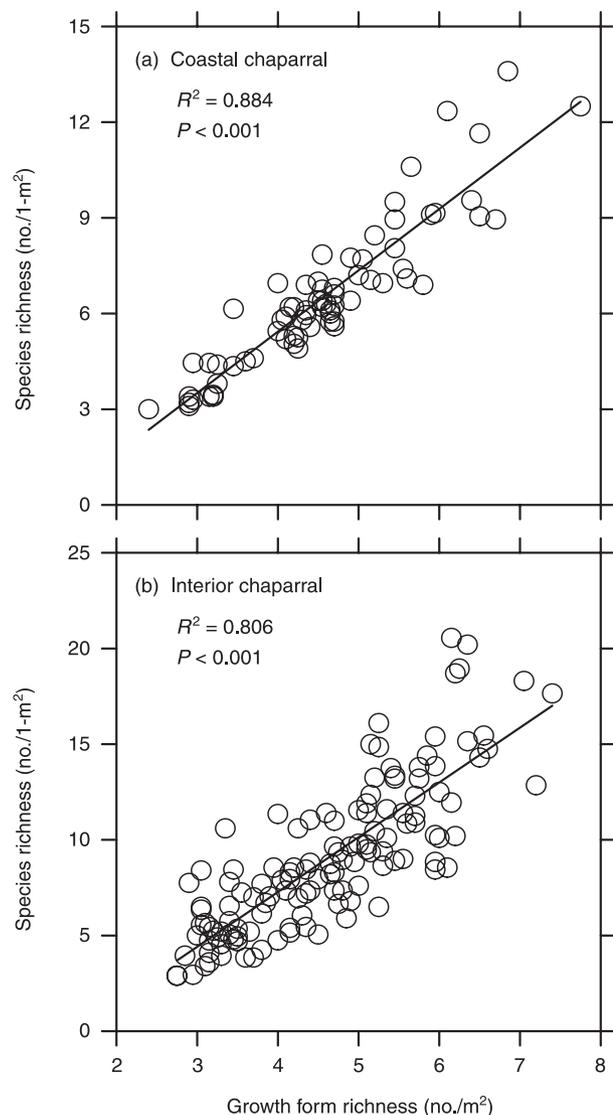


Figure 5 Relationship between growth form richness and species richness at the 1-m² scale in the fifth post-fire year for the (a) coastal and (b) interior chaparral sites. These two associations exhibited a significant departure from random expectation when growth form richness was determined by randomly sampling from the plant association pool of species ($P < 0.001$ and $P < 0.01$ for coastal and interior chaparral, respectively).

present after the second year (Keeley *et al.* in review). In addition, for most sites, 40–50% of the species present in year 5 were not present in year 1 and thus were colonizers (Keeley *et al.*, 2005). Consistent with this interpretation is the fact that the dispersal index of year 5 species is, with rare exceptions, higher than for year 1 species (Table 6).

These temporal patterns of diversity suggest a sort of ‘regulation’ of species diversity driven by colonization and extinction as outlined by Brown *et al.* (2001), however, with important differences. The fourth year decline in diversity is not likely driven by extinction, rather it is due to enforced dormancy of seed banks, many of which will remain entirely dormant until the next round

of the fire cycle (Keeley, 2000). This is an important distinction since it implies that the 'loss' of fourth year species is independent of population size, as would be the case with extinction (Hanski, 1982). The fifth year colonization of sites appears to be the result of rather localized metapopulation dynamics due to species in the surrounding burned landscape that expand their populations into the tenth hectare study sites. It may arise from a 'mass effect' where individuals flow from core areas of high success to less favourable areas (Shmida & Wilson, 1985) or to a more stochastic population turnover (Harrison, 1998). Regardless, colonization does not appear to be due to long-distance dispersal from outside the burned areas, as burned areas tend to be rather large, on the order of tens of thousands of hectares, and, although differences in dispersal capacity are evident (Table 6), very few of the species in the early successional flora have highly developed dispersal ability. In addition, most all species colonizing a site after the first post-fire year, were present on other, often nearby, burned sites in the first year (Keeley *et al.* in review).

Environmental filters

These broad patterns of disturbance and climate-driven successional changes in diversity are complicated by variations in the disturbance event and landscape position. Also, sorting out the factors determining overall diversity patterns requires examining these effects in the context of different life forms.

First year plant diversity is negatively affected by fire severity (Table 4), however, this is not uniformly experienced by all life forms since shrub diversity increases under higher severity fires (Appendix S2). Landscape position likewise affects diversity and plays a different role in different life-history types. For example, distance from the coast is an important determinant of diversity, however, while annual diversity increases, herbaceous perennial diversity decreases (see also Ammirati, 1967). Calculated solar insolation, which across these sites is largely influenced by slope aspect, is also an important determinant of diversity, with drier sunnier slopes decreasing diversity of some perennial life forms but increasing diversity of other life forms. Factors associated with diversity patterns become even more complicated when soil parameters are included.

Grubb (1977) outlined four components of a species niche, the habitat niche, life form niche, phenological niche and regeneration niche, all of which are highly relevant to post-fire conditions in California shrublands. When one considers the multitude of combinations of fire severities, landscape position, soil type and life forms and recruitment strategies, it is apparent that there that there is an '*n*-dimensional' (Hutchinson, 1957) combination of factors driving diversity patterns. Thus, in these shrublands, a significant part of the explanation of landscape level diversity patterns is that plants are segregating along various environmental niche axes (Silvertown, 2004).

Resource availability

One potential driver of species diversity is the availability of resources. Direct measures of resource availability are difficult

because they represent numerous parameters weighted differently for each species. However, it is expected that as resource availability increases, density of similar sized individuals increases (Brown, 1984), and this may be an appropriate surrogate measure for resource availability (Diamond, 1988).

In California shrublands, richness is strongly correlated with this measure of resource availability in the first year, which accounted for up to 50% of the variation for certain life forms (Table 8). However, during early succession this relationship varied with life forms.

In woody species, resource availability appears to affect diversity through the first four post-fire years. We hypothesize the primary reason for this relationship breaking down at this point is due to the intense thinning of woody plant seedling populations during the fourth year (Keeley, *et al.* in review), when the annual summer drought was likely more intense due to the sub-normal precipitation, coupled with the greater demand for water by the growing shrub saplings. This suggests that once shrubs are established, intense thinning does not greatly alter diversity.

Herbs, on the other hand, exhibited a strong correlation between diversity and our surrogate measure of resource availability in all but the two driest years, 3 and 4. Thus, in the two highest rainfall years, resource availability appears to exhibit some control on diversity, but in drought years, factors other than resource availability appear to be involved. This presents something of a conundrum because in these semi-arid land systems soil moisture is expected to be a limiting resource, and we did find a strong relationship between diversity and precipitation (Table 3). We hypothesize that the answer lies in a minimum threshold of precipitation required to trigger germination and sprouting of herbs. In dry years, many fewer species are present and those that do recruit are better adapted to drier conditions and expand their populations to fill the available space. In support of this explanation is the observation that in our sites, herb diversity was lowest during the third and fourth years, but for about 25% of the herbs this was the time of peak abundance (Keeley, *et al.* in review).

Resource heterogeneity

One of the major drivers of plant diversity in California shrublands is the temporal heterogeneity in resources. Life-history studies provide abundant evidence that a large portion of the flora has some degree of seed dormancy that times recruitment to post-fire conditions (Keeley, 1991). There are several dozen species that are so highly restricted to post-fire conditions that they disappear after the first or second year and don't reappear until the next fire. It has been hypothesized that limiting resources including light, water and nutrients in undisturbed shrublands, coupled with the high predictability of fire disturbance, have selected for deep seed dormancy, which is broken by fire cues such as heat and smoke (Keeley & Fotheringham, 2000). We see cyclical disturbances and life-history evolution have acted in concert to produce non-equilibrium coexistence that contributes to plant diversity in these shrubland communities.

Spatial heterogeneity is also linked to diversity patterns, both through the inherent variability of the disturbance event and variability in landscape features. Variation in fire severity (Fig. 3a) is the result of prefire variations in biomass age and volume as well as topography and weather. Species diversity is affected by variations in fire severity due to species-specific differences in heat tolerance of seeds (Keeley, 1991), and to prefire heterogeneity in seed bank distribution related to species-specific microhabitat preferences (Davis *et al.*, 1989). In addition, since severity is positively related to prefire stand age (Keeley *et al.*, 2005), severity may be negatively correlated with diversity due to seed bank attrition in older stands (Zammit & Zedler, 1988). Variability in landscape features such as rock cover also can influence diversity (Fig. 3b) by increasing microhabitat variation in soil moisture.

There is a temporal component to habitat heterogeneity in that the scale changes during early succession. This is evident in California shrublands by a significant relationship between site heterogeneity and diversity at both 1-m² and 100-m² scales during the first post-fire year (Fig. 4). But by the fifth post-fire year, heterogeneity at the lowest scale is no longer correlated with diversity.

Spatial heterogeneity is generally regarded as affecting diversity by allowing greater niche specialization, which would reduce competitive exclusion under equilibrium conditions (Diamond, 1988). There are two lines of evidence that indicate niche specialization may be tied to diversity in California shrublands: patterns of growth form diversity and distribution of species abundances.

Growth form diversity would be expected to promote niche specialization, and increase species diversity by promoting greater coexistence (Cody, 1991). In chaparral there is a highly significant relationship between growth form richness and species richness (Fig. 5), although this is not evident in sage scrub.

Species abundance and distribution patterns may also reflect on niche specialization as well as other factors that could drive species richness patterns. Brown (1984) interpreted abundance and distribution patterns as reflective of niche breadth characteristics. His model predicted a unimodal distribution where the bulk of the species are found at relatively few sites because most species are adapted to a relatively narrow subset of environmental conditions and widely distributed species are accounted for by a broad niche breadth.

Although this model was originally proposed to account for species abundance patterns over very large geographical areas (Collins & Glenn, 1991), there is no necessary reason it wouldn't apply to smaller scales where niche separation occurs at microhabitat scales. Also, at these scales, as microhabitat heterogeneity increases, unimodal distribution patterns are more likely (Gotelli & Simberloff, 1987). At the smallest scale in our study it is clear that at least a third of all species are only found in one of the 20 1-m² subplots at each site (satellite species) and very few occur in the majority of subplots (core species). This suggests that microhabitat niche partitioning is commonplace in our sites. At the intermediate scale these sites consistently showed a bimodal pattern with both satellite and core species. The fact that these widespread core species were not present in the much smaller nested subplots makes it likely that the microhabitat niche specialization is repeated at a scale closer to 100-m² than to 1-m².

This scale is consistent with patterns of microcommunity associations proposed by Westman (1983). At the regional scale a unimodal pattern shows a third or more of all species are restricted to just a single site, suggesting gradients in species-specific habitat requirements.

Alternatively, Hanski (1982) has offered a very different explanation for species abundance and distribution patterns that relies on metapopulation dynamics of colonization and extinction. His core-satellite model predicts a bimodal distribution something like that shown at the intermediate scale in our sites. This model would predict a relationship between the density or cover of a species and the number of sites it occurs at. In our study, at all three scales considered, there were very significant relationships between these two parameters, which is consistent with Hanski's core-satellite model, but also is consistent with resource availability controlling diversity patterns as well. However, Hanski's model applies only to homogenous environments where species are equally adapted to all sites considered. At the scale of sites within plant associations this is certainly not true as there is much species-specific variation in habitat differentiation (O'Leary, 1988; Desimone & Burk, 1992; Keeley, 2000). Habitat homogeneity is more likely within the tenth hectare sites than between these tenth hectare sites, even when analysed separately within plant association.

We contend that if metapopulation dynamics account for these species abundance and distribution patterns, then we should expect core species to have better developed dispersal ability than satellite species. This, however, does not appear to be the case and in fact just the opposite would seem to be true. Another test of this model would be the prediction that residual species present in the first year after fire would be more likely to be extirpated by year 5 in satellite species, and in year 5 more of the core species would be colonizer species not present in the first year after fire. These predictions are not upheld and it appears that in our study, at scales from 1-m² to sites within the region, a much greater proportion of the uncommon satellite species are present in year 5 as colonizers than as residual species present immediately after fire. Widespread core species do not owe their origin to colonization. Also not supportive of the metapopulation explanation for species abundance and distribution patterns is the fact these patterns appear stable during the first 5 years after fire.

CONCLUSIONS

Determining the factors responsible for community-scale plant diversity in California shrublands is a multifaceted problem. Important factors include: (1) life-history specialization to temporal heterogeneity in resources created by fire; (2) species-specific responses to characteristics of disturbance events, e.g. fire severity; (3) niche specialization between life forms; (4) growth forms that further subdivide resources along other axes such as soil characteristics, phenology, etc.; (5) species-specific differences in response to annual fluctuations in resource availability, in particular precipitation; and (6) mass effects due to metapopulation dynamics whereby fluctuations in disturbances

and resource availability result in occasional localized expansion of highly successful core species populations. While diversity in these shrublands appears to be driven by disequilibrium processes, the important role of residual species suggests a long-term equilibrium, whereby composition has stabilized according to species-specific niche specialization.

SUPPLEMENTARY MATERIAL

The following material is available from www.blackwell-synergy.com/loi/ddi

Appendix S1 Growth form distribution of species present in the first post-fire year. These 18 growth form categories captured much of the structural variability in our sites, although embedded within them is some potentially significant phenological variability such as caulescent annuals that included both spring flowering and summer flowering annuals.

Appendix S2 Regression coefficients for species richness (no. of species/1-m²) of life-history types vs. environmental parameters for the first 5 post-fire years

Appendix S3 Core satellite analysis showing (first figure) the number of species occupying sites in the (a–d) first and (e–h) fifth post-fire years for each of the four plant associations; (second figure) proportion of species occupying 100-m² plots within a site; and (third figure) proportion occupying 1-m² subplots within a site occupied.

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