



# Species–area relationships in Mediterranean-climate plant communities

Jon E. Keeley<sup>1,2,\*</sup> and C. J. Fotheringham<sup>2</sup> <sup>1</sup>US Geological Survey, Western Ecological Research Center, Sequoia National Park, Three Rivers, CA, USA and <sup>2</sup>Department of Organismic Biology, Ecology and Evolution, University of California, Los Angeles, CA, USA

## Abstract

**Aim** To determine the best-fit model of species–area relationships for Mediterranean-type plant communities and evaluate how community structure affects these species–area models.

**Location** Data were collected from California shrublands and woodlands and compared with literature reports for other Mediterranean-climate regions.

**Methods** The number of species was recorded from 1, 100 and 1000 m<sup>2</sup> nested plots. Best fit to the power model or exponential model was determined by comparing adjusted  $r^2$  values from the least squares regression, pattern of residuals, homoscedasticity across scales, and semi-log slopes at 1–100 m<sup>2</sup> and 100–1000 m<sup>2</sup>. Dominance–diversity curves were tested for fit to the lognormal model, MacArthur's broken stick model, and the geometric and harmonic series.

**Results** Early successional Western Australia and California shrublands represented the extremes and provide an interesting contrast as the exponential model was the best fit for the former, and the power model for the latter, despite similar total species richness. We hypothesize that structural differences in these communities account for the different species–area curves and are tied to patterns of dominance, equitability and life form distribution. Dominance–diversity relationships for Western Australian heathlands exhibited a close fit to MacArthur's broken stick model, indicating more equitable distribution of species. In contrast, Californian shrublands, both postfire and mature stands, were best fit by the geometric model indicating strong dominance and many minor subordinate species. These regions differ in life form distribution, with annuals being a major component of diversity in early successional Californian shrublands although they are largely lacking in mature stands. Both young and old Australian heathlands are dominated by perennials, and annuals are largely absent. Inherent in all of these ecosystems is cyclical disequilibrium caused by periodic fires. The potential for community reassembly is greater in Californian shrublands where only a quarter of the flora resprout, whereas three quarters resprout in Australian heathlands. Other Californian vegetation types sampled include coniferous forests, oak savannas and desert scrub, and demonstrate that different community structures may lead to a similar species–area relationship. Dominance–diversity relationships for coniferous forests closely follow a geometric model whereas associated oak savannas show a close fit to the lognormal model. However, for both communities, species–area curves fit a power model. The primary driver appears to be the presence of annuals. Desert scrub communities illustrate dramatic changes in both species diversity and dominance–diversity relationships in high and low rainfall years, because of the disappearance of annuals in drought years.

**Main conclusions** Species–area curves for immature shrublands in California and the majority of Mediterranean plant communities fit a power function model. Exceptions that fit the exponential model are not because of sampling error or scaling effects, rather structural differences in these communities provide plausible explanations. The

\*Correspondence: Jon E. Keeley, US Geological Survey, Western Ecological Research Center, Sequoia National Park, Three Rivers, CA 93271, USA.  
E-mail: jon\_keeley@usgs.gov (or) seajay@ucla.edu

exponential species–area model may arise in more than one way. In the highly diverse Australian heathlands it results from a rapid increase in species richness at small scales. In mature California shrublands it results from very depauperate richness at the community scale. In both instances the exponential model is tied to a preponderance of perennials and paucity of annuals. For communities fit by a power model, coefficients  $z$  and  $\log c$  exhibit a number of significant correlations with other diversity parameters, suggesting that they have some predictive value in ecological communities.

### Keywords

Diversity, chaparral, coniferous forests, desert scrub, dominance–diversity, exponential model, fynbos, geometric model, heathland, MacArthur’s broken stick model, maquis, power model, sage scrub, savannas, shrublands.

## INTRODUCTION

Biodiversity of Mediterranean-climate ecosystems is of particular interest, not only because all five of these regions are hotspots of plant diversity, but all are also hotspots of human population growth (Cowling *et al.*, 1996; Rundel, 1998; Mooney *et al.*, 2001). Thus, factors driving plant diversity patterns in these regions are of both theoretical and practical concern.

One approach to understanding drivers of species diversity is through comparative study of species–area relationships. In recent years, these relationships have attracted a great deal of attention, perhaps because the rule that the number of species increases with increasing area may be viewed as one of the few ‘laws’ in ecology (Schoener, 1976). However, there are exceptions to this rule because of the fact that dissimilar areas may have very different species densities (Dunn & Loehl, 1988), although in the case of nested samples the species–area relationship does indeed approach the status of an ecological law. Research in this field has pursued two questions. What is the most appropriate mathematical model to describe species–area relationships and what are the underlying ecological explanations for different models.

It is widely held that for most landscapes the relationship is best described by a power function (Connor & McCoy, 1979; Wright, 1981; Rosenzweig, 1995), which is usually presented as the log transformation

$$\log S = \log c + z \log A \quad (1)$$

where  $S$  is the number of species,  $A$  the area, and  $c$  and  $z$  are coefficients. Alternatively, Gleason (1922) argued that this model was inappropriate and he suggested a better fit to empirical results was the exponential model, expressed as the semi-log equation

$$S = c + z \log A \quad (2)$$

This model provides a better fit for some plant communities (Kilburn, 1966; Connor & McCoy, 1979; Rydin & Borgegard, 1988; Rejmanek & Rosen, 1992), including two Mediterranean-climate ecosystems, South African fynbos (Bond, 1983) and Australian heathlands (Keeley, 2003).

In an extensive comparison of data sets fitting the exponential versus the power model, Connor & McCoy (1979) could discern no apparent pattern to the factors determining a fit to one model or the other. Others, however, contend that there is a strong theoretical basis for expecting a power model fit, and some have suggested that empirical fits to the exponential model are the result of sampling error at small scales (Rosenzweig, 1995, 1998; He & Legendre, 1996).

Most of the interest in the species–area relationship has focused on regional and global scales where  $\beta$ -diversity is an important determinant, and far less work has concerned more local  $\alpha$ -diversity patterns. Indeed, it has even been proposed that species–area curves at the community scale (e.g. tenth-hectare) do not reveal any fundamental diversity properties about the organisms or their environment (Rosenzweig, 1995, p. 279). This proposition, however, remains to be tested.

Part of the reason for discounting the importance of community level species–area curves is that most of the proposed drivers of the species–area relationship, e.g. island area, habitat diversity, distance to source populations, may not be important determinants of local community-level species–area relationships. However, recently it was shown that two Mediterranean-climate shrub communities fit different species–area models and that these differences are tied to patterns of species abundance (Keeley, 2003).

The purpose of this study was to investigate community scale species–area curves for Mediterranean-climate plant communities, and determine which model best describes this relationship. We then investigate the extent to which community structure, as reflected in dominance–diversity distributions, may explain different species–area curves. Dominance–diversity curves have been fit to a wide variety of models, including the lognormal, MacArthur’s broken stick, geometric and harmonic series, and these have been interpreted in terms of what they reflect about community structure (Whittaker, 1965, 1972).

The primary focus here is on diversity patterns in Californian shrublands (both evergreen chaparral and semi-deciduous sage scrub) and these patterns were contrasted with published literature on other Mediterranean-type

shrublands. Since comparisons with other regions requires use of published data, not all Mediterranean-climate regions are equally represented. For example, comparable species–area data are available for California, the Mediterranean basin, South Africa and Australia but are missing for Chile (see Methods). Dominance–diversity data, coupled with species–area curves, are even more limited, being available for only California (from this study) and Australia (from Lamont *et al.*, 1976, Specht, 1988). Matching sites with respect to time since disturbance is problematic as well. Prior studies have focused on comparisons of mature communities (Cowling *et al.*, 1996), however, Mediterranean regions differ markedly in the timing of peak diversity. South African fynbos and Australian heathlands exhibit relatively small increases in diversity after disturbances such as fire and maintain high diversity in mature stands (Kruger, 1983; Bell *et al.*, 1984). In contrast, Californian and Mediterranean basin shrublands exhibit dramatic increases in vascular plant diversity following disturbance and diversity declines as the shrub canopy returns (Pausas *et al.*, 1999; Keeley, 2000). The primary focus here was to capture the patterns during periods close to the peak diversity for each region. Thus, data collected for California shrublands were from early successional years; however, published data on mature chaparral and sage scrub are included for comparison. Data from other Mediterranean-climate regions included both recently disturbed as well as relatively undisturbed mature communities. While the concentration here is on shrublands, data were also collected from other communities in Mediterranean-climate parts of California, including coniferous forests, oak savannas and desert scrub, for comparison with Californian chaparral and sage scrub shrublands, as well as comparable communities in other Mediterranean-climate regions.

## METHODS

### Data collection

Shrubland data from California, USA sites represent unpublished data from a 5-year postfire study of 90 tenth-hectare sites (two sites lost after the second year) distributed between 60 m and 1225 m elevation across 300 km along the southern coast and interior (see Keeley, 1998). All sites burned in October 1993 and data for vegetation recovery in the second and fourth postfire years were used. On average, across all sites, precipitation was 180% of normal in the second year and 90% of normal in the fourth year (Climatological Annual Summary, National Oceanic and Atmospheric Administration, Ashville, NC, USA).

For comparison with other Mediterranean-type shrublands, published data for plots at the scales of 1, 100 and 1000 m<sup>2</sup> were used (sources listed in Appendix 1). Data were available for shrublands in South Africa, Australia and the Mediterranean Basin. Such data were unavailable for Chile. Chilean data from Specht (1988) were based on separate 100 m<sup>2</sup> plots combined to give 1000 m<sup>2</sup> samples (G. Montenegro, Universidad de Catolica, Santiago, Chile,

July 2002, pers. comm.) and this sort of data generates cumulative (collector's) curves that are inappropriate for comparison as the 1000 m<sup>2</sup> samples are taken over a total area in excess of 1000 m<sup>2</sup>. This is apparently why an earlier comparison of Mediterranean plant communities concluded that Chilean diversity was 'anomalously high' (Fox, 1995). Disturbance history for sites in the literature varied and were noted when reported.

In order to compare shrubland patterns with other vegetation types in Mediterranean-climate parts of California, sampling was also conducted in coniferous forests, oak savannas and desert scrub. Montane coniferous forests were between 1400 m and 2400 m elevation in Sequoia-Kings Canyon National Parks in the southern Sierra Nevada Range, and were dominated by white fir (*Abies concolor*), incense cedar (*Calocedrus decurrens*), and sugar pine (*Pinus lambertiana*). Blue oak savannas were between 440 m and 680 m in the foothills of the southern Sierra Nevada, and were dominated by annual grasses and forbs with *c.* 20% cover by blue oak (*Quercus douglasii*). Desert scrub sites were distributed in the Colorado (< 100 m elevation) and Mojave (> 1000 m) deserts of southern California. To best characterize diversity patterns, each of these community types were sampled under conditions that presented the greatest contrasts in diversity. For forest sites, unburned and high intensity-burned sites 3 years postfire were sampled. The oak savannas sites included ones with no livestock grazing for more than a century and sites currently grazed by either cattle or horses. Desert scrub sites were sampled in a year of modest rainfall (2001; sites ranged from 90% to 130% of normal) and a year of drought (2002; 30–70% of normal). Data for woodlands in some other Mediterranean regions were available from the literature and these included both hardwood-dominated and softwood-dominated sites.

### Sample design

The number of vascular plant species from samples of 1, 100 and 1000 m<sup>2</sup> were used to construct species–area curves. In most cases, these were nested plots, an approach that has both positive and negative attributes. The primary criticism of this technique is that lower scale measures do not represent completely independent samples and this may present problems in certain statistical analyses. This lack of independence, however, is one of the positive attributes of the method when addressing community patterns because it ensures that one is not sampling different community types at different scales. In addition, nested designs have the property that they always give a positive species–area slope, whereas this is not always true of unnested designs. Lack of independence is less of a problem in the present study because all statistical analyses utilized means of species richness at each scale calculated from multiple sites over broad areas. Evidence that the statistical analysis here is not affected by the nested design is a comparison of standard errors (SEs) generated from complete data sets against sub-sampled data where each scale is represented by a different set of sites.

All California data were collected with a tenth-hectare nested sample design described in Keeley *et al.* (1995) and Keeley (1998). It is a highly modified version of the classic Whittaker plot and samples a 20 × 50 m site with the long axis usually parallel to the slope contour. This tenth-hectare site is subdivided into 10 non-overlapping 100-m<sup>2</sup> square plots, each containing two 1-m<sup>2</sup> subplots in opposite corners (interior subplots offset 1 m from the centre). In addition to recording species lists from each plot, density and cover were estimated for each species in the 1-m<sup>2</sup> subplots. One variation on this design was that in the savanna sites only one subplot was sampled per 100-m<sup>2</sup> plot. Data from the literature were collected with Shmida's (1984) version of a 'Whittaker plot,' where a single 100-m<sup>2</sup> square plot is sampled from the centre of the 20 × 50 m tenth-hectare site and only ten 1-m<sup>2</sup> subplots are sampled and they are arranged contiguously in the centre of the site, and density and cover are not usually recorded. In California shrublands the heterogeneity of species distributions does not lend itself to the Whittaker method, which implicitly assumes homogeneity at the tenth-hectare scale.

### Data analysis

Data were first plotted on a semi-log scale (equation 2) in order to compare all communities with a common model. The primary reason for picking the exponential model for comparisons was because previously it was reported as the appropriate model for some Mediterranean shrublands, and depicting species richness on an arithmetic scale is more amenable to interpretation. In addition, substantial attention was given to comparing slopes of this semi-log relationship at different scales.

Each data set was tested for the best fit with least squares regression to both this exponential model and the power model (equation 1). Magnitude of the adjusted  $r^2$  was one measure of fit and is a reasonable and tractable means of comparing these models (Connor *et al.*, 1983), although Lomolino (2001) warns that these are not true measures of the explained variation because of different transformations. Another indicator of fit was the pattern of the distribution of residuals, and homoscedasticity was evaluated by comparing residuals across scales with one-way ANOVA (Wilkinson *et al.*, 1996). An additional measure of fit to the semi-log model was the difference in slopes between 1 and 100 m<sup>2</sup> vs. 100 and 1000 m<sup>2</sup> (Crawley & Harral, 2001), with a two-tailed  $t$ -test.

Dominance–diversity curves (Whittaker, 1965) were constructed for all California sites using areal coverage. These curves were generated by plotting the log of cover for each species in sequence from the most to the least dominant. Other measures of dominance such as biomass have sometimes been used and when curves based on both measures have been compared they have been shown to produce broadly similar distributions (Chiarucci *et al.*, 1999), although biomass appears to be more sensitive to subtle environmental differences (Guo & Rundel, 1997). The present study, however,

makes no assumptions about the relationship between cover and biomass. Quantitative data were not available for most other Mediterranean climate regions, with one exception, the study by Lamont *et al.* (1977) for Western Australian heath.

One means of comparing dominance–diversity curves is Whittaker's (1972) equitability index, defined as

$$Ec = S/(\text{Log } C_1 - \text{Log } C_N) \quad (3)$$

where  $S$  is the total species,  $C_1$  and  $C_N$  the cover for the first and last species, respectively. This is a crude measure of slope and refers to the average number of species per log-cycle of cover value, steep slopes have few species per log cycle and low values for  $Ec$  and the opposite applies to shallow curves.

Dominance–diversity curves were tested for fit to Preston's (1948) lognormal model, MacArthur's broken stick model, and the geometric and harmonic series. This was carried out for each site in California and on Lamont *et al.*'s (1977) data for Australia.

Expected lognormal values were calculated as described by Hayek & Buzas (1997) for cover classes where the expected number of species for an interval along the species rank axis is given by

$$n_R = n_{MO} + \exp(-\hat{a}^2 R^2) \quad (4)$$

and  $R$  is the cover class,  $n_{MO}$  the number in the modal class and  $\hat{a}$  is a proportionality constant estimated by

$$\hat{a} = \text{SQR}[\log_2(n_{MO}/n_{R_{\max}})/R_{\max}^2] \quad (5)$$

Expected cover values for MacArthur's broken stick model were modified by Hayek & Buzas (1997), where

$$C_i = C/S[\ln(S/i)] \quad (6)$$

where  $C_i$  is the cover for the  $i$ th species,  $C$  the total cover,  $S$  the number of species, and  $i$  the species sequence.

Expected values for the geometric and harmonic models were derived from

$$\text{Exp}_{(\text{geometric})} = C_1[1 - (C_1/C)]^{(i-1)} \quad (7)$$

$$\text{Exp}_{(\text{harmonic})} = C_1/i \quad (8)$$

where  $C_1$  is the cover for the first species in the sequence.

The chi-square test for goodness of fit was used to compare observed and expected dominance–diversity distributions (Pielou, 1975) and curves were considered good fits if  $\chi^2_{(\text{calculated})} < \chi^2_{(\text{table})}$  at  $P = 0.05$ . Tokeshi (1993) warns that this model may not be reliable at small sample sizes and advocates use of the Kolmogorov–Smirnov test; however, Sokal & Rohlf (1969) caution that that test is only properly applied to continuous frequency distributions.

Other measures that relate to dominance–diversity include the Simpson concentration index, defined as

$$\lambda = \sum p_i^2 \quad (9)$$

where  $p$  is the proportion of total cover for each species. This index is strongly affected by the first few dominant

species and thus it is a measure of community dominance (Peet, 1974). Another measure used was the Shannon information index, defined as

$$H = \sum p_i (\log p_i) \quad (10)$$

and increases as the evenness of species cover increases.

All statistical analyses and graphical presentations were done with SYSTAT Version 10.0 (Evanston, IL, USA).

Life form distribution was presented for the different regions based on the Raunkiaer life form system (Raunkiaer, 1934).

## RESULTS

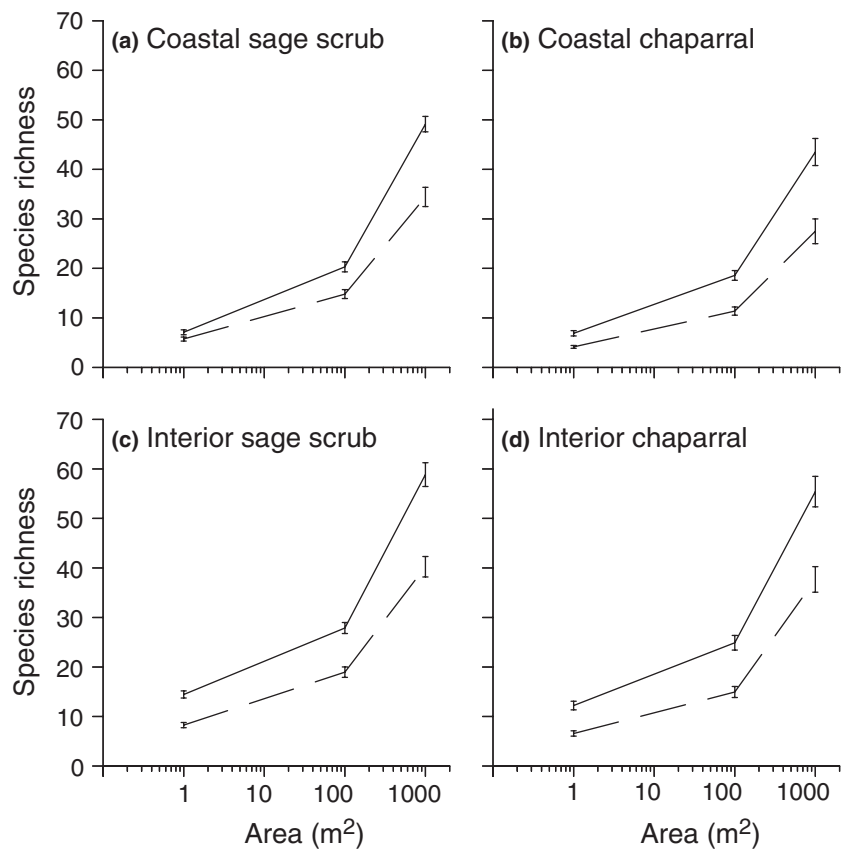
### Shrubland species–area relationships

Piecewise plots of species–area relationships in semi-log space for the four postfire Californian shrubland associations do not exhibit a linear relationship across the full scale from 1 m<sup>2</sup> to 1000 m<sup>2</sup> and this was true for high diversity and low diversity years (Fig. 1). The patterns were similar between semi-deciduous sage scrub and evergreen chaparral and coastal and interior sites. This is in contrast to the patterns observed for shrublands in many other Mediterranean-climate regions (Fig. 2). Both western and eastern Australian heathland communities (Fig. 2c & d) appear to fit a linear relationship in semi-log space and other

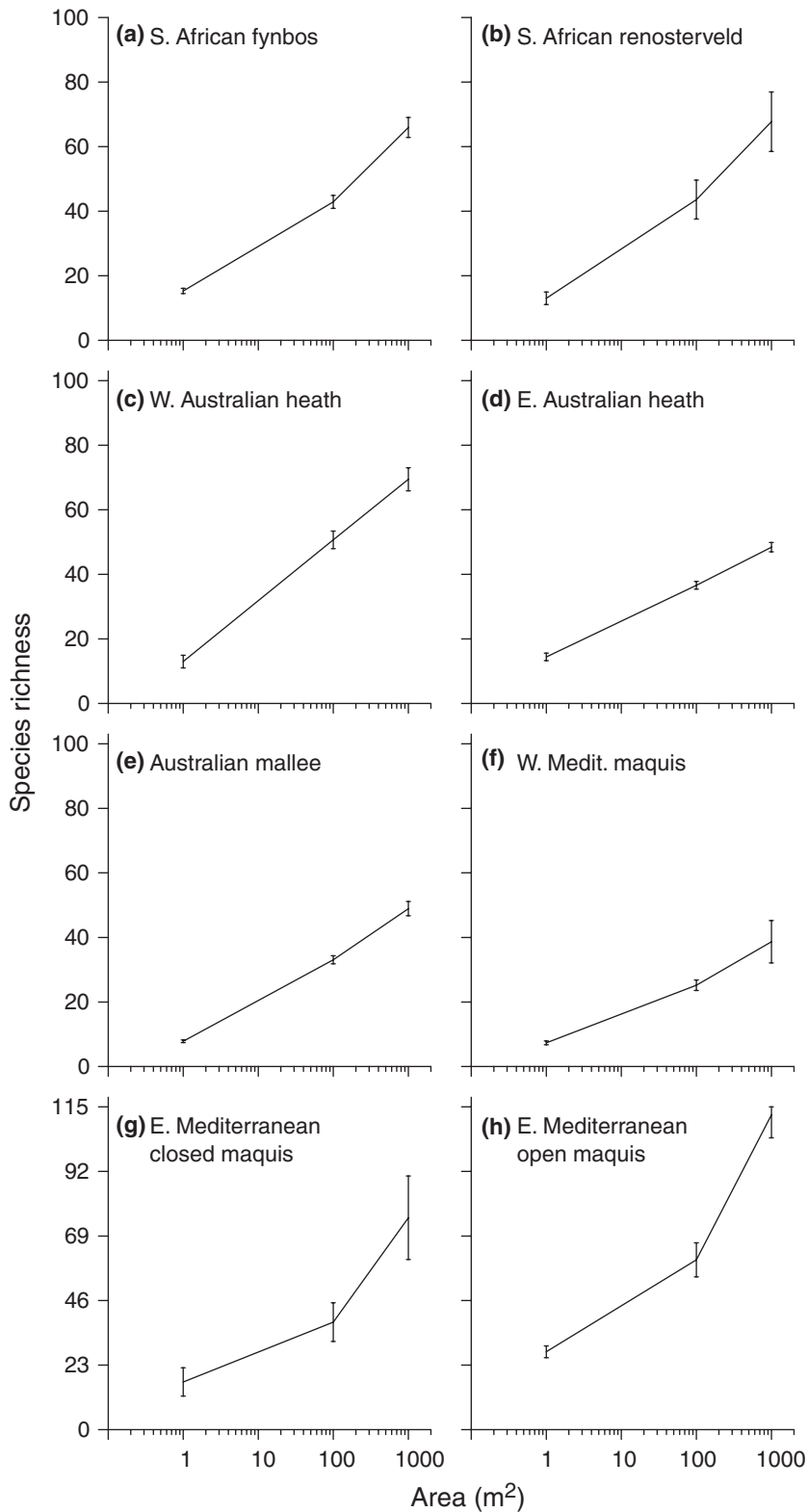
Mediterranean-climate shrublands (Fig. 2) fall somewhere between this and the California pattern (Fig. 1).

The adjusted  $r^2$  comparisons show that Californian shrublands exhibited a better fit to the power model than to the exponential model (Table 1), and is consistent with our visual interpretation of Fig. 1. In contrast, Australian heathlands were a slightly better fit to the exponential model (Table 1), consistent with the patterns evident in Fig. 2. Most other Mediterranean shrublands fell somewhere in between the California and Australian patterns with respect to both the shapes of the curves (Fig. 2) and  $r^2$ -values (Table 1).

Another measure of fit to the exponential model is the distribution of residuals for this model (Fig. 3). The preponderance of points at 100 m<sup>2</sup> in California shrublands fell below the regression line indicating a poor fit to this exponential model. Further demonstration of this heteroscedasticity is the highly significant difference in mean residuals at the different scales (Table 2). None of the other Mediterranean shrublands exhibited a significant departure from homoscedasticity (Table 2). Thus, relative to other Mediterranean shrublands, Californian shrublands were depauperate in species richness at the scale of 100 m<sup>2</sup> (Fig. 3). This is also illustrated by examining slopes from the semi-log plots for different spatial scales. Comparing the ratios of slope<sub>(1–100 m<sup>2</sup>)</sub> vs. slope<sub>(100–1000 m<sup>2</sup>)</sub> we found a significant difference between Californian and other Mediterranean shrublands (Table 3). In California the slopes between 1 m<sup>2</sup>



**Figure 1** Piecewise semi-log species–area plots for California shrublands including (a) semi-deciduous coastal sage scrub, (b) evergreen coastal chaparral, (c) interior sage scrub and (d) interior chaparral sites. Each point is the mean of multiple sites with vertical SE bars (see Table 1 for sample sizes). Solid lines are the second year postfire and dashed lines are the 4th year postfire.



**Figure 2** Piecewise semi-log species–area plots for shrublands in other Mediterranean-climate regions, including (a) and (b) South African fynbos and renosterveld (c), (d) and (e) Western and Eastern Australian heath and mallee, (f) Western Mediterranean Basin maquis, and (g) and (h) Eastern Mediterranean Basin maquis closed canopy and disturbed open canopy communities. Each point is the mean of multiple sites with vertical SE bars (see Table 1 for sample sizes and data sources).

and 100 m<sup>2</sup> were shallow and the slopes between 100 m<sup>2</sup> and 1000 m<sup>2</sup> were significantly steeper. Most other Mediterranean type ecosystems exhibited no significant difference

in slopes between 1 and 100 m<sup>2</sup> vs. 100 and 1000 m<sup>2</sup>, e.g. South African renosterveld, Australian heathlands, and western and eastern Mediterranean maquis.

**Table 1** Comparison of species–area curves for 1, 100, and 1000 m<sup>2</sup> nested subplots across Mediterranean type ecosystems for:  $S = c + z \log A$ ;  $\log S = \log c + z \log A$ , where  $S$  = number of species,  $A$  = area,  $z$  describes the slope and  $c$  or  $\log c$  describes its intercept. When raw data were available there were three data points for each site, but in some cases the literature only reported means for multiple sites, thus  $n$  may be less than the number of sites. Data sources listed in Appendix I

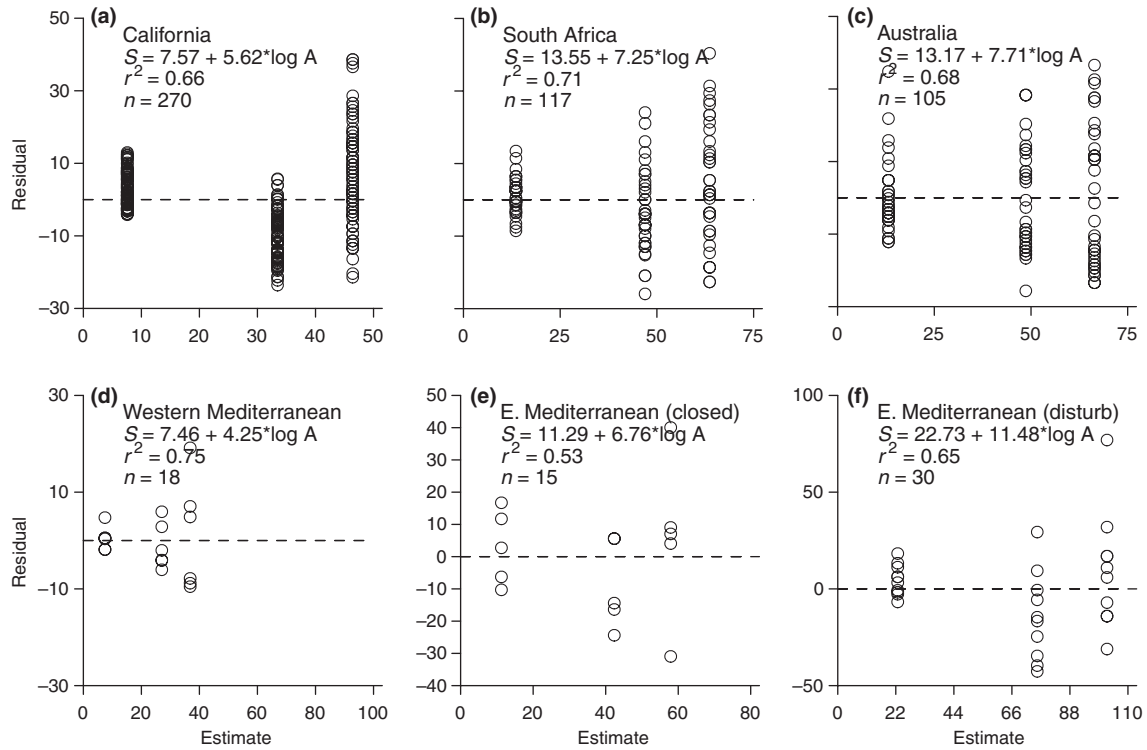
Country	Vegetation	Age*	No. of sites/ $n$	Semi-log	Log-log			Data source
				Adj. $r^2$	Adj. $r^2$	$z$	$\log c$	
<b>(a) Shrublands</b>								
California								
	Coastal sage scrub	2	22/66	0.74	0.87	0.270	1.87	1
		4	21/63	0.67	0.86	0.249	1.66	1
	Coastal chaparral	2	14/42	0.76	0.90	0.271	1.83	1
		4	14/42	0.64	0.88	0.274	1.33	1
	Interior sage scrub	2	28/84	0.69	0.78	0.202	2.56	1
		4	27/81	0.68	0.81	0.234	2.00	1
	Interior chaparral	2	26/78	0.64	0.75	0.209	2.38	1
		4	26/78	0.58	0.71	0.234	1.74	1
	Mature chaparral	> 20	10/6	0.91	0.89	0.247	1.92	24
	Mature coastal sage	7–?	3/9	0.59	0.59	0.174	2.45	30, 31
South Africa								
	Fynbos	1–30	32/96	0.73	0.79	0.215	2.69	3, 8, 29, 30
	Renosterveld	1–15	7/21	0.64	0.75	0.243	2.52	3, 8, 30
Australia								
	Western heath	6–15	30/90	0.70	0.66	0.299	2.28	30
	Eastern heath	10–32	5/15	0.97	0.94	0.181	2.68	30
	Mallee	25–50	13/39	0.91	0.94	0.273	2.09	30, 36
Mediterranean basin								
	Western maquis	1–5	6/18	0.75	0.87	0.232	2.06	3, 26, 30
	Eastern maquis (closed canopy)	?	4/12	0.60	0.54	0.307	1.87	18, 24, 30
	Eastern maquis (open canopy)	1–10	12/36	0.67	0.79	0.197	3.25	18, 24, 30
<b>(b) Other communities</b>								
California								
	Conifer forest							
	Unburned	> 50	19/57	0.71	0.89	0.310	0.71	1
	Burned	3	27/81	0.48	0.68	0.351	0.68	1
	Oak savanna							
	Ungrazed	?	5/15	0.75	0.90	0.218	2.29	1
	Grazed	?	10/30	0.75	0.90	0.203	2.47	1
	Desert scrub							
	High ppt	?	15/45	0.64	0.80	0.225	0.293	1
	Low ppt	?	15/45	0.66	0.80	0.352	0.025	1
South Africa								
	Afromontane forest	> 50	6/18	0.98	0.92	0.277	2.14	3
	Strandveld	?	9/27	0.52	0.59	0.234	2.71	30
Australia								
	Woodland	2–32	30/90	0.69	0.77	0.227	2.36	5
Mediterranean basin								
	Western woodland	1–34	27/81	0.57	0.77	0.302	1.69	23, 30
	Eastern woodland	?	4/12	0.50	0.70	0.257	2.72	6, 13, 30
	Eastern desert	–	3/9	0.39	0.56	0.328	1.15	33

\*Years since last fire.

The patterns observed in Californian shrublands appear to change with successional age as closed canopy mature stands reported from the literature were linear in semi-log space (Fig. 4) and these sites showed an equal or better fit with the semi-log model (Table 1). The effect of canopy closure on

the species–area relationship was also observed with open and closed canopy maquis sites in the eastern Mediterranean basin (Table 1).

Much has been written on the significance of the power model coefficients,  $\log c$  and  $z$ . There is substantial variation



**Figure 3** Residuals for the exponential model ( $S = c + z \log A$ ) for all shrublands from (a) California, (b) South Africa, (c) Australia, (d) Western Mediterranean Basin, and (e) and (f) Eastern Mediterranean Basin.

**Table 2** Test of homoscedasticity for residuals to the semi-log model for Mediterranean shrublands (from Fig. 3). Superscript indicates value is significantly different from other values in a row

	Semi-log regression mean residuals at:			F	P-value
	1 m <sup>2</sup>	100 m <sup>2</sup>	1000 m <sup>2</sup>		
California	3.250	-9.751 <sup>a</sup>	6.501	79.83	0.000
South Africa	1.313	-3.938	2.626	2.75	0.068
Australia	0.004	-0.012	0.008	0.00	1.000
W. Mediterranean Basin	0.412	-1.237	0.825	0.133	0.876
E. Mediterranean Basin					
Closed canopy	2.929	-8.786	5.857	0.945	0.416
Disturbed	4.671	-14.014	9.343	3.062	0.063

across sites in these parameters, however, inspection of these values (Table 1) does not suggest any obvious relationship between parameter range and vegetation type. A more detailed examination of these parameters is presented in a later section.

In short, species–area curves were similar among the different California shrublands considered here and were best fit by a power model (Fig. 5a). In contrast certain other Mediterranean shrublands were best fit by an exponential model (e.g. Australian heathlands, Fig. 2c & d).

**Nested vs. unnested statistical analysis**

Least squares regression analysis assumes that samples at different scales are independent. While it is intuitive that nested designs would comprise less independent samples than unnested designs, it is not a given that this alters statistical conclusions. To test the effect of the nested design on the species–area curves we randomly sub-sampled without replacement from the 90 sites (second year), such that each scale comprised a different subset of 30 sites. By grouping all California shrubland types and using the power function model, it is apparent that little changes whether or not one uses all of the nested data (Fig. 5a) or a sub-sample of unnested data (Fig. 5b). Lack of independence may lead to an underestimate of the true SE, however, in this case the SE of estimate is remarkably similar between the nested and unnested samples; SE = 0.375 and 0.369, respectively.

**Other communities**

In California, data from other vegetation types included coniferous forest, oak savanna and desert scrub; none of which exhibited a clear linear relationship across the full scale when plotted piecewise in semi-log space, although desert scrub during a drought year does approach a linear relationship (Fig. 6). Adjusted  $r^2$  values suggest a better fit to a power model than the exponential model for all of these community types (Table 1). This is also supported by the

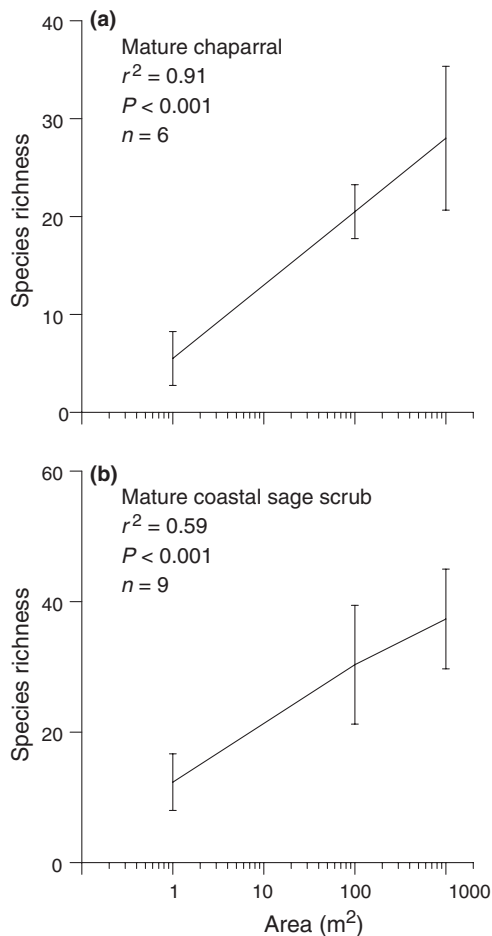


**Table 3** Comparison of slopes between 1–100 m<sup>2</sup> and 100–1000 m<sup>2</sup> for semi-log relationship in Mediterranean-climate shrublands and other vegetation types. Ratios of slope from 1 to 100 m<sup>2</sup> over slope from 100 to 1000 m<sup>2</sup> were compared across all vegetation types with a one-way ANOVA and superscripts indicate ratios not different at  $P > 0.05$ . Sample size and sources of data as in Table 1

Country	Vegetation	Slope (z)			Slope <sub>(1–100 m<sup>2</sup>)</sub> Slope <sub>(100–1000 m<sup>2</sup>)</sub>
		1–100 m <sup>2</sup>	100–1000 m <sup>2</sup>	P-value (d.f.)	
<b>(a) Shrublands</b>					
California					
	Coastal sage scrub				
	Second year	2.868	11.375	0.000 (42)	0.255 <sup>a</sup>
	Fourth year	1.970	8.128	0.000 (42)	0.242 <sup>a</sup>
	Coastal chaparral				
	Second year	2.540	12.095	0.000 (26)	0.210 <sup>a</sup>
	Fourth year	1.567	8.028	0.000 (26)	0.195 <sup>a</sup>
	Interior sage scrub				
	Second year	2.914	14.420	0.000 (50)	0.202 <sup>a</sup>
	Fourth year	2.324	10.391	0.000 (50)	0.224 <sup>a</sup>
	Interior chaparral				
	Second year	2.754	12.225	0.000 (55)	0.226 <sup>a</sup>
	Fourth year	1.815	8.714	0.000 (54)	0.209 <sup>a</sup>
	Mature chaparral	3.247	3.257	0.999 (4)	1.000 <sup>b</sup>
	Mature sage scrub	3.909	3.040	0.469 (6)	1.315 <sup>b</sup>
South Africa					
	Fynbos	5.992	10.015	0.000 (62)	0.598 <sup>b</sup>
	Renosterveld	6.639	10.485	0.150 (12)	0.633 <sup>b</sup>
Australia					
	Western heathland	8.180	8.153	0.964 (58)	1.003 <sup>b</sup>
	Eastern heathland	4.800	5.125	0.318 (8)	0.937 <sup>b</sup>
	Mallee	5.480	6.882	0.042 (24)	0.796 <sup>b</sup>
Mediterranean basin					
	Western garrigue	3.893	5.147	0.535 (10)	0.756 <sup>b</sup>
	Eastern maquis (closed)	4.180	10.966	0.098 (6)	0.569 <sup>b</sup>
	Eastern maquis (open)	7.112	22.439	0.000 (22)	0.317 <sup>a</sup>
<b>(b) Other communities</b>					
California					
	Conifer forest				
	Unburned (>50 years)	0.735	3.358	0.000 (36)	0.219 <sup>a</sup>
	Burned (3 years)	1.382	6.037	0.000 (52)	0.229 <sup>a</sup>
	Oak savanna				
	Ungrazed	2.445	12.985	0.000 (8)	0.188 <sup>a</sup>
	Grazed	2.931	12.234	0.000 (18)	0.240 <sup>a</sup>
	Desert scrub				
	High ppt year	3.568	10.669	0.000 (28)	0.338 <sup>a</sup>
	Low ppt year	1.019	2.300	0.000 (28)	0.443 <sup>a</sup>
South Africa					
	Afromontane forest	5.863	7.383	0.465 (2)	0.794 <sup>b</sup>
	Strandveld	8.179	10.857	0.540 (4)	0.753 <sup>b</sup>
Australia					
	Woodland	5.604	7.750	0.005 (26)	0.720 <sup>b</sup>
Mediterranean basin					
	Western woodland	4.279	8.885	0.000 (52)	0.482 <sup>b</sup>
	Eastern woodland	9.772	13.680	0.547 (6)	0.714 <sup>b</sup>
	Eastern desert	3.547	4.922	0.533 (4)	0.721 <sup>b</sup>
					$F = 63.027$
					$P < 0.001$

fact that these communities had a rather shallow slope between 1 m<sup>2</sup> and 100 m<sup>2</sup> and a significantly steeper slope from 100 m<sup>2</sup> to 1000 m<sup>2</sup> (Table 3). Considering the latter

scale, savannas exhibited the steepest slopes, followed by burned forests and desert scrub in a year of high precipitation. Disturbance had a variable effect on the species–area



**Figure 4** Piecewise semi-log species–area plots for (a) mature chaparral and (b) mature coastal sage scrub from California. Each point is the mean of multiple sites with vertical SE bars (see Table 1 for sample sizes and data sources).

relationship. Grazing of oak savannas had little impact on the shapes of these curves, whereas burning in coniferous forests altered these curves, and drought in desert scrub produced dramatic changes in their shape (Fig. 6).

### Comparison of species richness

Species richness at the point scale of 1 m<sup>2</sup> and the community level of 1000 m<sup>2</sup> for these vegetation (Table 4) can be summarized as follows. At the point scale, communities with the highest average values (*c.* 12–16 or more species per m<sup>2</sup>) include California shrublands on interior sites, South African fynbos and renosterveld, western and eastern Australian heathland, and eastern Mediterranean basin open canopy maquis and woodlands. Moderate values (6–11 species per m<sup>2</sup>) include California coastal shrublands and desert scrub in high rainfall years, Australian mallee, Chilean matorral, and western Mediterranean basin maquis and woodlands. Low point diversity (1–5 species per m<sup>2</sup>) is exhibited in mature closed canopy shrublands in California and the

Mediterranean basin, California coniferous forests and California desert scrub in years of below normal rainfall as well as eastern Mediterranean desert scrub in a year of unspecified rainfall.

Across all sites considered here (Table 4) there was a modest but significant relationship between richness at 1 m<sup>2</sup> and 1000 m<sup>2</sup> ( $r^2 = 0.587$ ,  $P < 0.001$ ,  $n = 427$ ). Despite this significant relationship, there is much variance in the relationship between richness at the point scale and the community scale. A number of communities with high richness at the point scale fell to rather modest richness at the 1000 m<sup>2</sup> scale, these included South African fynbos and Australian heathlands. At the community scale of 1000 m<sup>2</sup> the open canopy shrublands and woodlands in the eastern Mediterranean Basin stood out as exceptionally diverse, often averaging more than 100 species per tenth-hectare (Table 4).

### Dominance–diversity relationships

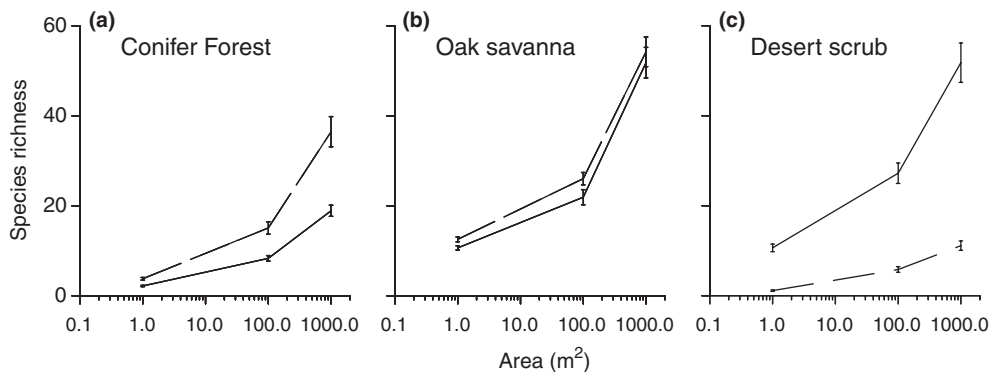
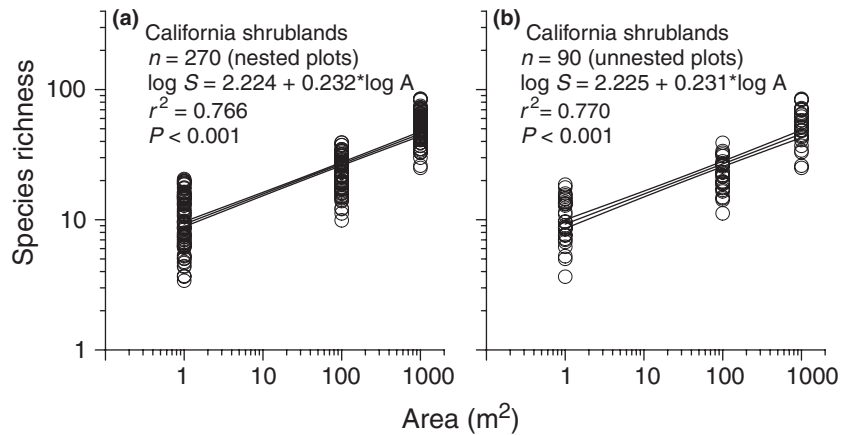
Dominance–diversity curves based on cover are presented for different shrublands in California (Figs 7–9) and Australia (Fig. 10). A subset of sites were selected as examples and the dominance–diversity curves for all sites are presented in an electronic appendix available on the World Wide Web (see Supplementary Material section). All curves were examined in three ways: by inspection of dominance–diversity patterns, examining Whittaker's equitability index, and by comparing distributions with parametric models.

Particularly striking is the difference in curves between the Australian and Californian shrublands, the former (Fig. 10) having much broader dominance–diversity curves, indicating greater evenness of cover distribution. Most California sites were dominated by a few species with the bulk of the flora having two to four orders of magnitude less cover (Figs 7 & 8). In these California shrublands, dominance–diversity curves dropped more sharply in the later successional year (Figs 7 & 8) and very steeply in older chaparral (Fig. 9).

Dominance–diversity curves for other Californian vegetation types are illustrated in Figs 11–13. They show that unburned coniferous forests (Fig. 11a & b) and desert scrub in a year of low precipitation (Fig. 13c & d) were similar to later successional and mature Californian shrublands in that they were dominated by a very few species, with subordinates several orders of magnitude lower. In oak savannas (Fig. 12), forests after burning (Fig. 11c & d) and desert scrub during high rainfall years (Fig. 13a & b) dominance–diversity curves were more similar to early successional shrublands in that the curves were broader, indicating a somewhat more equitable distribution of cover. None of the California communities, however, approached the broad dominance–diversity curves observed for Australian heathlands (Fig. 10).

Whittaker's equitability index (Table 4) appears to be a useful index for distinguishing the different curves described above. California shrubland sites dominated by a few species had *Ec*-values ranging from 6 to 10, whereas Australian heathlands, with more equitable distribution of cover, had

**Figure 5** Log-log species–area plots for all California shrublands combined at 2 years postfire (a) including all nested data (each scale represented by data from all 90 sites) and (b) unnested subsets (data at each scale sampled from a random subset of sites without replacement).



**Figure 6** Piecewise semi-log species–area plots for other vegetation types in Mediterranean-climate California, including (a) montane coniferous forests, solid line is unburned and dashed line is 3 years postfire, (b) foothill oak savannas, solid line is ungrazed by livestock for more than a century and dashed line is grazed, and (c) desert scrub, solid line is above average rainfall year and dashed line is below average rainfall year.

$E_c$ -values four to five times higher. Several other Mediterranean regions had published  $E_c$ -values or data from which this parameter could be calculated (Table 4). South African fynbos had a relatively high  $E_c$ -value, more comparable with Australian heathlands than with California. Mediterranean maquis values were comparable with California shrublands with the exception of one very high value reported for a disturbed maquis site.

Each of the California sites and the Australian sites of Lamont *et al.* (1977) were tested for fit to models that cover the range of dominance–diversity relationships (Table 5). The majority of sites within each Californian shrubland type exhibited a significant fit to the geometric model in both early and later successional years. Other models were significant; however, MacArthur's broken stick model was seldom significant and exhibited the highest average  $\chi^2$  values, indicating the largest departure between data and the model. The fit between these data and the geometric model is illustrated for examples from each of the four shrubland associations in California (Figs 7 & 8).

The California shrubland patterns contrasted markedly with the patterns observed for the Australian heathlands, which exhibited a significant fit to MacArthur's broken stick

model, and the average  $\chi^2$  value was substantially smaller than that calculated for other models (Table 5). This fit is illustrated for four sites in Fig. 10.

In California coniferous forests, a majority of unburned sites fit both the geometric and the lognormal models (Table 5), and the former curve is illustrated in Figs 11a and b. Nearly all of the burned sites exhibited a significant fit to the lognormal model although a majority still showed a significant fit to the geometric model; however, by inspection (Figs 11c & d) it would appear the lognormal provides a closer approximation for the sites illustrated.

California oak savanna sites, both grazed and ungrazed, exhibited a significant fit in nearly all cases to the lognormal model (Table 5, Fig. 12). None of these sites exhibited a significant fit to the MacArthur model and only a minority of sites fit other models. Goodness-of-fit tests exhibited an average  $\chi^2$ -value that was substantially smaller for the lognormal model relative to the other models tested.

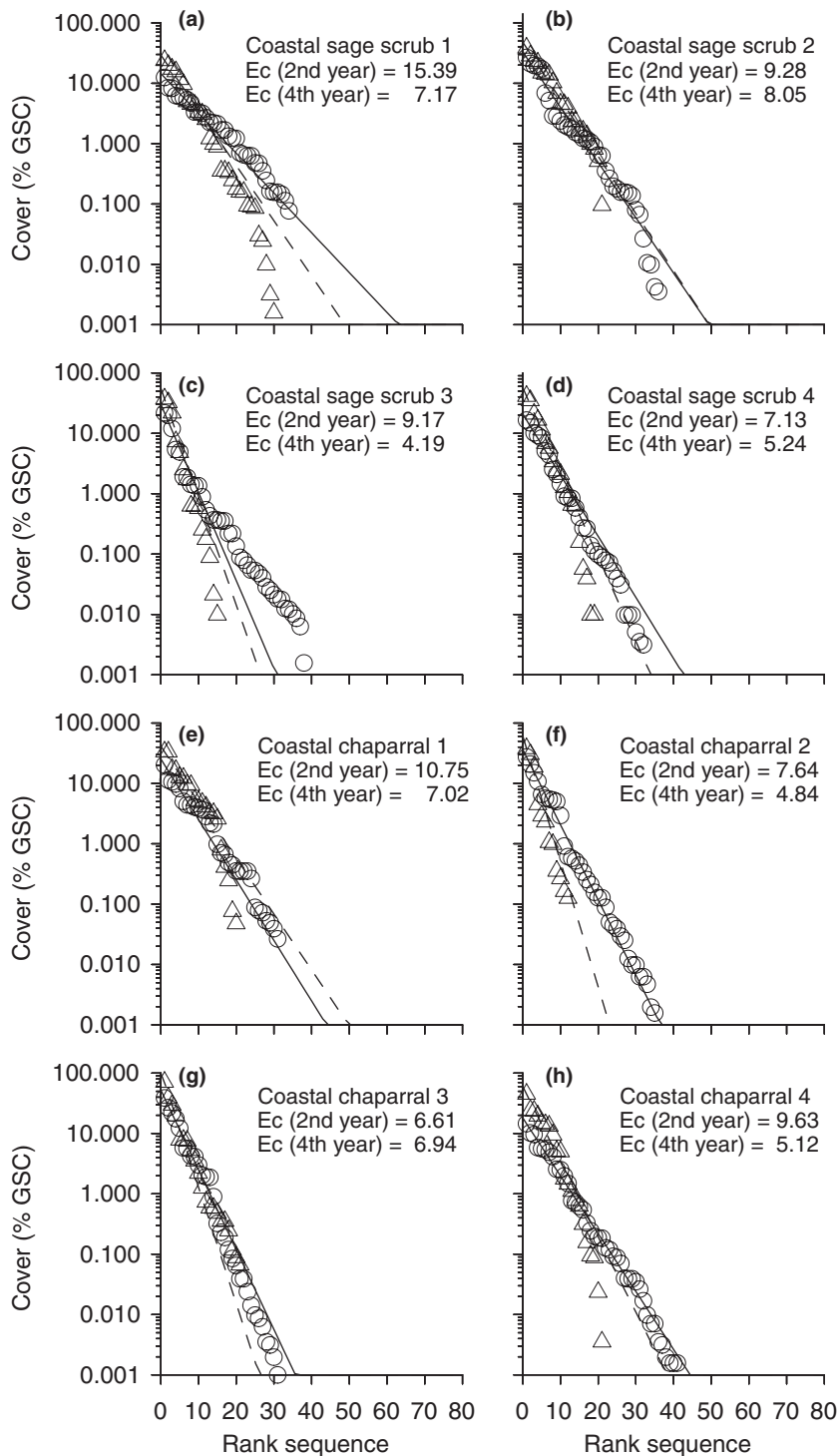
Desert scrub during a year of moderately high precipitation exhibited a significant fit to the geometric, harmonic and the MacArthur models (Table 5). Examination of Figs 13a and b suggests that these sites fit the geometric model for the dominant species, but subordinates deviate from this model in

**Table 4** Comparison of species richness, the Whittaker Equitability Index ( $E_c$ ), the Simpson Concentration Index ( $\lambda$ ) measure of dominance, and Shannon Index ( $H'$ ) measure of equitability in Mediterranean shrublands and associated vegetation. Data sources listed in Appendix I

Country	Vegetation	Species richness		Whittaker's equitability ( $E_c$ ) $\bar{X}$ (SE)	Simpson's concentration ( $\lambda$ ) $\bar{X}$ (SE)	Shannon-Weiner information ( $H'$ ) $\bar{X}$ (SE)	Number of sites/ $n$	Data source
		1 m <sup>2</sup> $\bar{X}$ (SE)	1000 m <sup>2</sup> $\bar{X}$ (SE)					
Shrublands California	Coastal sage scrub							
	Second year	7.1 (0.5)	46.5 (2.1)	7.93 (0.63)	0.187 (0.023)	2.22 (0.10)	22/22	1
	Fourth year	2.0 (0.1)	33.5 (2.1)	6.03 (0.46)	0.203 (0.020)	2.04 (0.08)	21/21	1
	Coastal chaparral							
	Second year	6.9 (0.5)	46.4 (2.0)	7.67 (0.44)	0.182 (0.027)	2.20 (0.09)	13/13	1
	Fourth year	4.2 (0.3)	29.9 (2.5)	5.08 (0.41)	0.199 (0.023)	2.00 (0.07)	13/13	1
	Interior sage scrub							
	Second year	14.5 (0.7)	61.1 (2.5)	10.82 (0.48)	0.132 (0.011)	2.53 (0.07)	28/28	1
	Fourth year	8.3 (0.5)	42.9 (2.0)	6.99 (0.45)	0.183 (0.022)	2.20 (0.09)	27/27	1
	Interior chaparral							
	Second year	12.2 (0.9)	53.0 (2.8)	9.28 (0.55)	0.161 (0.014)	2.34 (0.08)	26/26	1
	Fourth year	6.6 (0.5)	35.0 (2.3)	6.11 (0.35)	0.221 (0.015)	1.92 (0.06)	26/26	1
	Mature chaparral	1.4 (0.0)	8.8 (1.7)	—	0.970 (0.205)	0.68 (0.51)	2/2	3
	Mature chaparral	5.5 (1.5)	28.0 (4.0)	—	0.570 (0.010)	—	10/2	24
Mature chaparral	—	—	—	0.587 (0.218)	0.55 (0.09)	3/3	16	
Mature sage scrub	—	—	—	0.300 (0.021)	—	67/67	34	
Mature sage scrub	11.5 (1.5)	37.0 (10.0)	—	0.300 (0.021)	—	2/2	30	
South Africa	Fynbos	15.2 (1.1)	63.8 (4.0)	25.91 (4.66)*	0.144 (0.015)	3.07 (0.09)	20/20	3
	Fynbos	16.1 (1.7)	66.4 (6.2)	—	0.106 (0.011)	1.31 (0.10)	9/9	8
	Fynbos	16.7 (—)	75.0 (—)	—	0.220 (—)	1.31 (0.09)	10/1	24
	Fynbos	13.3 (1.9)	78.6 (5.2)	—	—	—	3/3	29
	Renosterveld	6.2 (—)	28.0 (—)	—	0.620 (—)	1.55 (—)	1/1	3
	Renosterveld	13.6 (2.9)	80.0 (10.4)	—	0.140 (0.029)	1.12 (0.09)	3/3	8
	Western heathland	—	—	41.19 (0.86)	0.030 (0.001)	3.86 (0.03)	10/10	20
	Western heathland	12.9 (2.0)	69.4 (3.6)	—	—	—	30/30	30
Australia	Western heathland	13.3 (—)	65.0 (—)	—	0.210 (—)	—	7/1	24
	Eastern heathland	14.4 (1.2)	48.4 (1.4)	—	—	—	5/5	30
	Mallee	7.8 (0.4)	48.9 (2.2)	—	—	—	13/13	30, 36
	Mallee	6.1 (—)	49.0 (—)	—	0.300 (—)	—	6/1	24
	Matorral	7.7 (0.9)	—	—	—	—	3/3	30
	Matorral	—	—	—	—	—	—	—
Mediterranean basin	Western maquis	8.9 (3.3)	35.6 (8.3)	—	0.290 (0.010)	2.56 (0.25)	2/2	3
	Western maquis	—	—	5.74 (0.35)	0.514 (0.067)	1.47 (0.18)	7/7	2
	Western maquis	7.4 (0.5)	38.7 (6.6)	—	—	—	8/4	30, 26

Eastern maquis (–)	–	96.3 (22.5)	–	–	0.282 (0.063)	0.90 (0.16)	6/6	24, 30
Eastern maquis (mature)	–	21 (–)	8.99 (–)	–	–	–	1/1	24
Eastern maquis (disturbed)	–	119 (–)	31.33 (–)	–	–	–	1/1	24
Eastern maquis (closed canopy)	10.8 (4.9)	55.3 (9.5)	–	–	–	–	12/4	18, 24, 30
Eastern maquis (open canopy)	27.8 (2.1)	105.2 (10.3)	–	–	–	–	36/12	18, 24, 30
Eastern maquis (2 years)	–	101.0 (14.0)	–	–	0.295 (0.015)	1.76 (0.06)	2/2	18
Eastern maquis (8 years)	–	107.5 (3.5)	–	–	0.215 (0.045)	2.31 (0.16)	2/2	18
Eastern maquis (mature)	–	94.0 (10.3)	–	–	0.167 (0.011)	2.19 (0.08)	6/6	18
Other communities								
California								
Conifer forest								
Unburned (>50 years)	2.2 (0.2)	18.9 (1.2)	2.66 (0.21)	–	0.453 (0.043)	1.16 (0.10)	19/19	1
Burned (3 years)	3.8 (0.2)	38.8 (3.6)	5.04 (0.46)	–	0.260 (0.029)	1.83 (0.10)	27/27	1
Oak savanna								
Ungrazed	10.6 (0.5)	51.2 (3.4)	7.56 (0.25)	–	0.210 (0.023)	1.99 (0.12)	5/5	1
Ungrazed	12.3 (1.6)	52.5 (5.5)	–	–	–	–	12/2	24
Grazed	12.5 (0.5)	54.2 (3.3)	7.68 (0.80)	–	0.206 (0.012)	2.01 (0.08)	10/10	1
Grazed	15.6 (–)	64.0 (–)	–	–	–	–	5/1	24
Desert scrub								
High ppt year	10.8 (0.8)	51.8 (4.4)	8.63 (0.63)	–	0.295 (0.041)	1.79 (0.10)	15/15	1
Low ppt year	1.5 (0.1)	11.1 (1.0)	4.40 (0.59)	–	0.395 (0.058)	1.27 (0.14)	15/15	1
Mediterranean basin								
Western woodland	–	–	–	–	0.300 (–)	2.00 (–)	1/1	2
Western woodland	–	–	–	–	0.271 (0.022)	2.31 (0.12)	8/8	21
Western woodland	5.9 (0.5)	46.0 (4.0)	–	–	–	–	49/27	6, 13, 23, 30
Eastern woodland	–	136.0 (1.0)	6.76 (–)†	–	0.030 (0.001)	1.69 (0.06)	2/2	24
Eastern woodland	15.8 (3.6)	92.2 (25.3)	–	–	–	–	4/4	30
Eastern desert	4.3 (2.4)	32.0 (11.9)	–	–	–	–	9/3	33
	$F = 18.42$	$F = 18.94$	$F = 14.86$	$F = 10.97$	$F = 27.27$			
	$P < 0.001$	$P < 0.001$	$P < 0.001$	$P < 0.001$	$P < 0.001$			

\* $n = 5$  † $n = 1$ .Values are given as  $\bar{X}$  (SE).

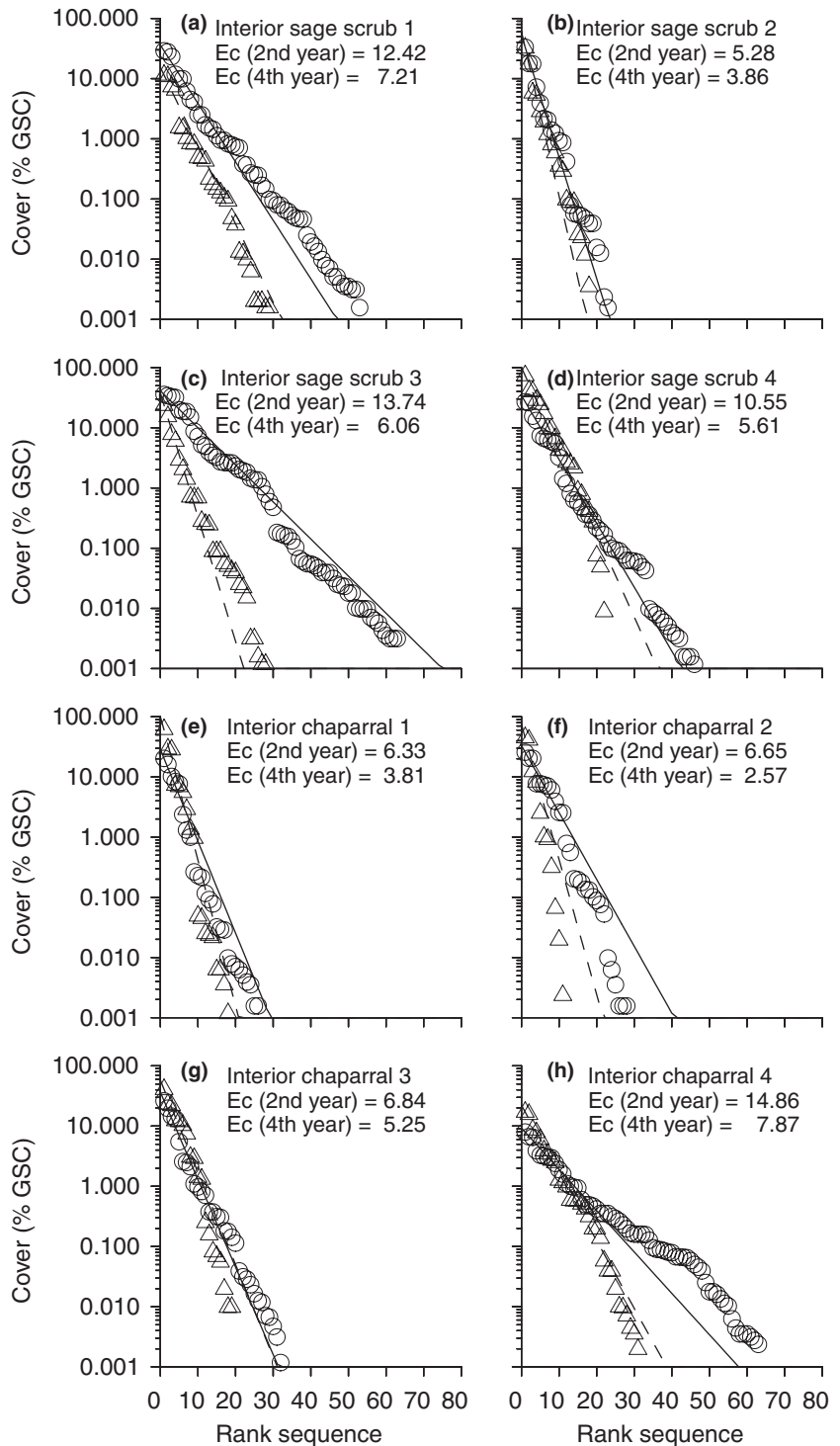


**Figure 7** Dominance–diversity curves based on percentage ground surface covered for single sites of coastal California shrublands. Circles are from the second year postfire and triangles from the fourth year postfire. Each site showed a significant fit to the geometric model, solid line is second year postfire and dashed line is fourth year postfire.  $E_c$  = Whittaker's equitability index, which is derived from the slope of the dominance–diversity curve. These four sage scrub sites and four chaparral sites were selected to represent the range of observed responses. The full set of dominance–diversity curves for all sites may be viewed online (see Supplementary Material section).

the direction of the MacArthur broken stick model. During the drought year, species richness was so low it was not possible to apply the  $\chi^2$  test to test the distributions (Table 5), although it would appear from inspection (Fig. 13c & d) that cover values were approximated by the geometric distribution.

### Dominance vs. equitability

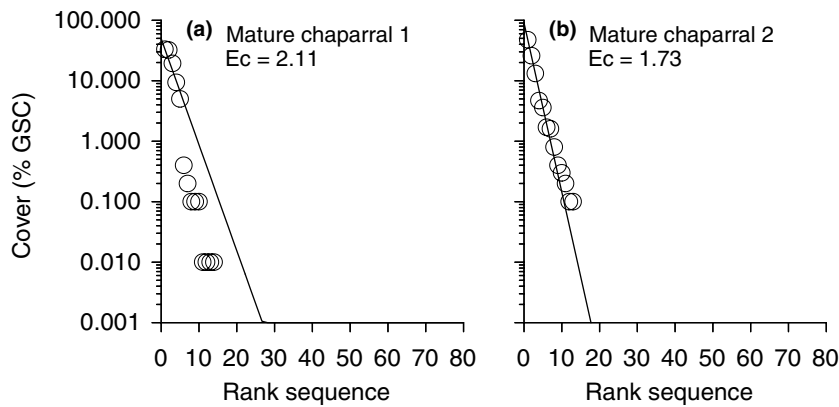
Beyond comparing these parametrical distributions, another approach to examining dominance–diversity relationships is through comparison of non-parametric measures. Both Simpson's index ( $\lambda$ ) and the Shannon



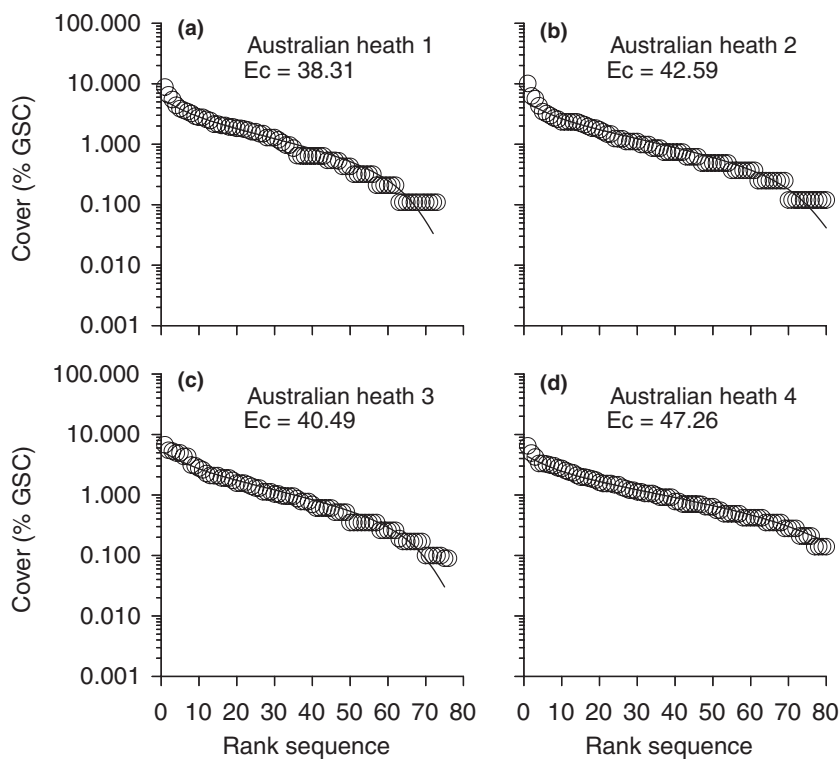
**Figure 8** Dominance–diversity curves based on percentage ground surface covered for single sites of interior California shrublands. Circles are from the second year postfire and triangles from the fourth year postfire. Each site showed a significant fit to the geometric model, solid line is second year and dashed line is fourth year.  $Ec$  = Whittaker's equilibrium index. These four sage scrub sites and four chaparral sites were selected to represent the range of observed responses. The full set of dominance–diversity curves for all sites may be viewed online (see Supplementary Material section).

information index ( $H'$ ), showed significant differences across sites (Table 4). In Californian shrublands, Simpson's measure of dominance increased during postfire succession, indicating increased dominance, from the second to the fourth year to mature shrublands (Table 4). The lowest value observed was  $\lambda = 0.030$  for western Australian

heathlands studied by Lamont *et al.* (1977), indicating far less species dominance than for the California shrublands. Shannon's index increased with the evenness of species distribution and not surprisingly this decreased with maturity in California shrublands, but was highest for Australian heathlands.



**Figure 9** Dominance–diversity curves based on percentage ground surface covered for mature chaparral in interior California; (a) > 30 years and (b) > 90 years. Each site showed a significant fit to the geometric model.  $E_c$  = Whittaker's equitability index.



**Figure 10** Dominance–diversity curves based on percentage ground surface covered for single sites of Western Australian heathland. Each site showed a significant fit to MacArthur's broken stick model.  $E_c$  = Whittaker's equitability index. The full set of dominance–diversity curves for all sites may be viewed online (see Supplementary Material section).

Least squares regression analysis was used to relate dominance–diversity measures to species–area parameters (Table 6). Whittaker's equitability index  $E_c$  showed a strong positive relationship with species richness at both small and large scales (Table 6). In other words, as dominance declined, richness increased. Interestingly this equitability index was positively related to the species–area curve slopes from 1 to 100 m<sup>2</sup> and 100 to 1000 m<sup>2</sup> in the semi-log plots, but negatively related to the overall slope in the log-log model.

Since Simpson's  $\lambda$  is a measure of dominance it is not surprising that it was negatively related to  $E_c$  and to species richness (Table 6). Less intuitive, however, is the negative relationship between this dominance index and the slope of the semi-log model from small and large spatial scales. In

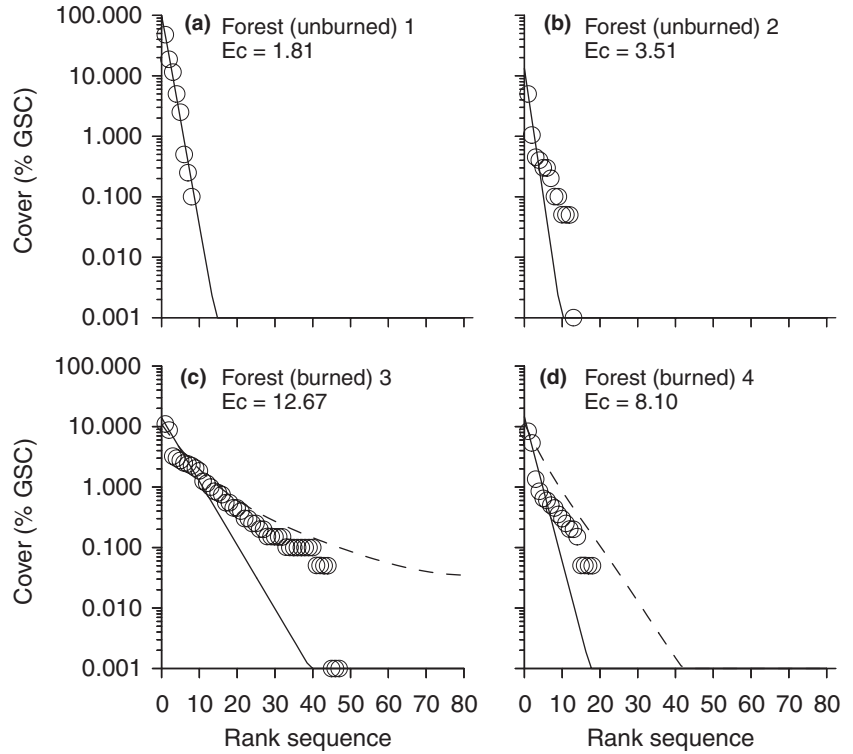
other words, sites with a steeper increase in species richness from 1 to 100 m<sup>2</sup> and 100 to 1000 m<sup>2</sup> were sites with a lower dominance value.

Across all regions, the Shannon index  $H'$  was positively correlated with the rate of increase in semi-log species–area curves (Table 6).  $H'$  exhibited the same, albeit weaker, relationship with species richness and species–area parameters as did  $E_c$ .

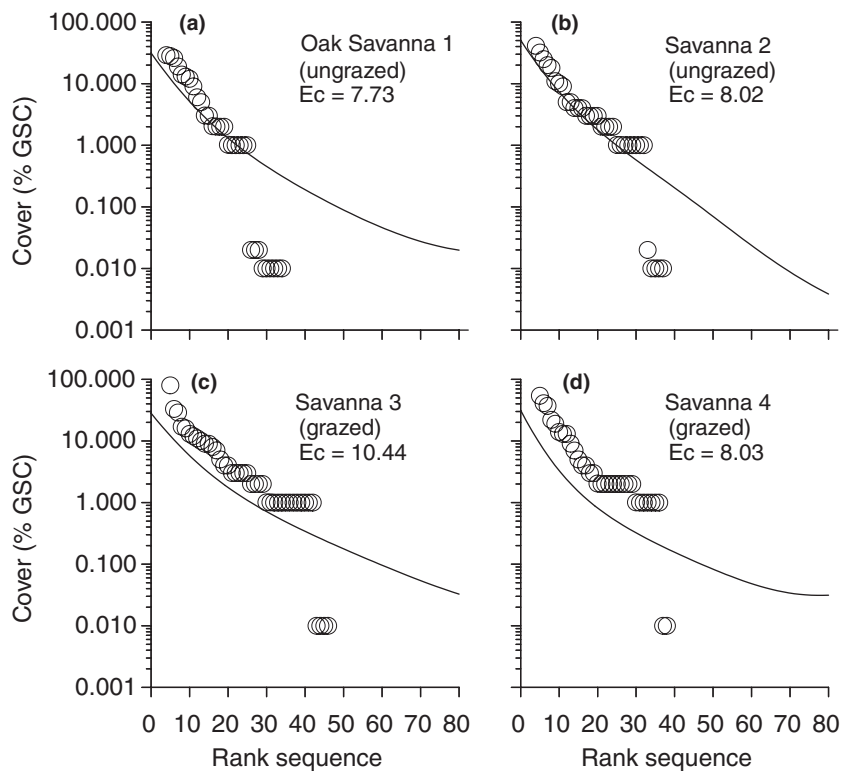
Power model coefficients for the log-log regressions, slope  $z$  and  $y$ -intercept  $\log c$  exhibited correlations with dominance and equitability indices in opposite directions. Whittaker and Shannon's measures of equitability were positively correlated with log-log intercepts, whereas Simpson's dominance measure was positively correlated

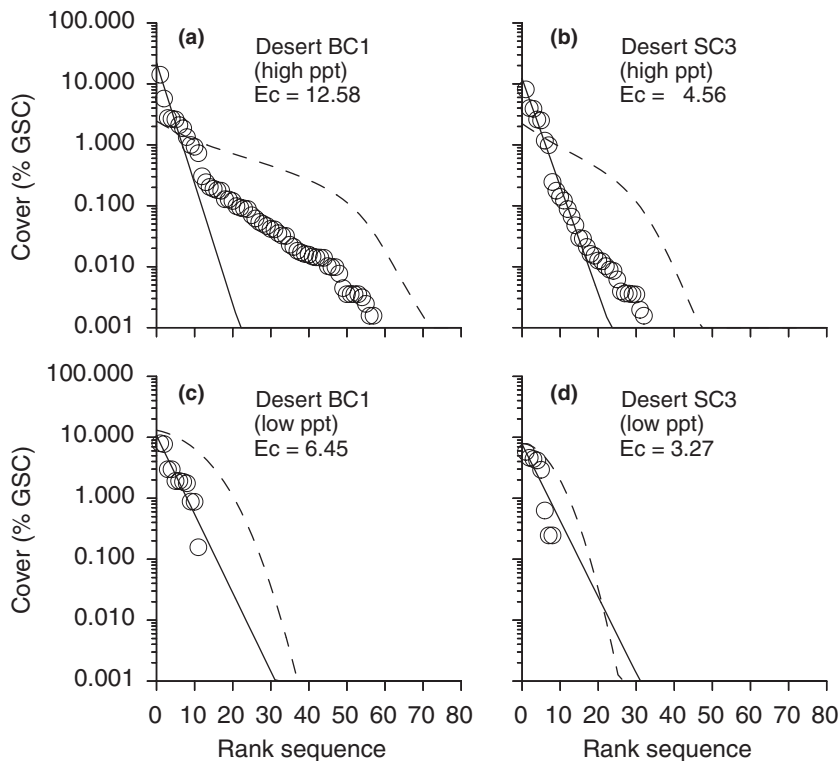


**Figure 11** Dominance–diversity curves based on percentage ground surface covered for single sites of California conifer forests (a) and (b) unburned and (c) and (d) third year postfire. Each site showed a significant fit to the geometric model (solid line) and the burned sites (c) and (d) also had a significant fit to the lognormal model (dashed line).  $E_c$  = Whittaker's equitability index. The full set of dominance–diversity curves for all sites may be viewed online (see Supplementary Material section).



**Figure 12** Dominance–diversity curves based on percentage ground surface covered for single sites of California oak savanna, (a) and (b) ungrazed and (c) and (d) grazed. Each site showed a significant fit to the lognormal model.  $E_c$  = Whittaker's equitability index. The full set of dominance–diversity curves for all sites may be viewed online (see Supplementary Material section).





**Figure 13** Dominance–diversity curves based on percentage ground surface covered for two California desert scrub sites (a) and (b) in a year of above average precipitation and (c) and (d) in a year of below average precipitation. Each site showed a significant fit to the geometric model (solid line). High precipitation years (a) and (b) also had a significant fit to MacArthur's broken stick model (dashed line) and low precipitation years (c) and (d) also had a significant fit to the lognormal model (dashed line).  $E_c$  = Whittaker's equitability index. The full set of dominance–diversity curves for all sites may be viewed online (see Supplementary Material section).

with the slope  $z$  of log-log transformations (Table 6). The log-log model slope  $z$  exhibited a strongly negative relationship with the y-intercept  $\log c$  ( $r^2 = 0.60$ ,  $F = 633.36$ ,  $P < 0.001$ ,  $n = 421$ ).

### Life forms

Viewing species–area curves in the context of the different life forms that generate them may be instructive. In Californian shrublands (Fig. 14), forest (Fig. 15a & b) and desert scrub (Fig. 5c & d), in semi-log space, herbs showed a much steeper increase in species richness from 100 m<sup>2</sup> to 1000 m<sup>2</sup> than woody plants. Woody species on the other hand more closely approached a linear relationship across the full scale from 1 m<sup>2</sup> to 1000 m<sup>2</sup>. Oak savannas were not presented because woody species comprised a minor portion of their flora. This type of breakdown was not available for most other Mediterranean regions. One exception was the western Mediterranean maquis or garrigue, where similar curves have already been published (see Pausas *et al.*, 1999) and revealed curves remarkably similar to those presented here. Namely, woody species more closely approached a linear relationship in semi-log space and herbaceous species exhibited a marked change in slope with a scale change from 100 m<sup>2</sup> to 1000 m<sup>2</sup>.

In order to evaluate to what extent differences in species–area curves may be driven by differences in life forms, we have compiled data from most Mediterranean plant communities (Table 7). Several patterns are evident. In

California, the floras in early successional chaparral and coastal sage scrub stands were dominated by annuals (therophytes), however this was less consistently the case with older stands. In contrast, South African fynbos and Australian heath consistently had relatively few annuals. Of all the Mediterranean shrublands, annual species comprised the greatest proportion of the flora in eastern Mediterranean maquis.

Considering other Californian vegetation types, we found that annuals were relatively uncommon in coniferous forests but comprised more than three-fourths of the lower elevation oak savanna flora (Table 7). California desert scrub illustrates the powerful influence of precipitation in annual species-rich systems – annuals comprised 74% of the life forms in a high rainfall year and this dropped by over an order of magnitude in a low rainfall year (Table 7).

Comparing life forms in woodlands between Australia and the Mediterranean basin illustrates that there was a greater affinity between shrublands and woodlands in the same region than between similar vegetation types in different regions. Australian woodlands were relatively depauperate in annual species and had a very substantial herbaceous perennial component, as was the case with Australian heathlands. In contrast, woodlands in the Mediterranean basin had a moderate to high proportion of annual species, as was the case with maquis shrublands. Thus, in general, annuals were a minor part of shrubland and woodland floras in Australia and South Africa, but a major component in California, Chile and the Mediterranean basin.

**Table 5** Dominance–diversity curves fitted to lognormal, broken stick, geometric and harmonic models. Percentage of sites within a vegetation type with  $P < 0.05$  significant fit to each model and mean  $\chi^2$  value; number of sites listed in Table 4. Geometric expected truncated at 0.01

Country	Vegetation	Percentage of sites fitting model				Mean $\chi^2$ (SE)			
		Log-normal	Broken-tick	Geometric	Harmonic	Log-normal	Broken-stick	Geometric	Harmonic
<b>(a) Shrublands</b>									
California									
	Coastal sage scrub								
	Second year	36	22	68	50	23.7 (2.9)	77.1 (10.5)	53.2 (27.8)	51.3 (6.1)
	Fourth year	48	19	71	10	20.4 (2.2)	91.5 (15.4)	62.8 (22.3)	65.9 (5.8)
	Coastal chaparral								
	Second year	21	29	57	64	75.5 (38.3)	78.9 (12.6)	57.7 (21.8)	42.4 (5.6)
	Fourth year	71	14	79	14	12.7 (2.1)	59.4 (11.7)	49.0 (22.0)	48.6 (5.9)
	Interior sage scrub								
	Second year	11	29	89	71	23.7 (2.5)	124.1 (11.2)	51.7 (20.1)	63.8 (9.3)
	Fourth year	33	15	89	56	23.7 (2.5)	86.5 (10.6)	28.2 (8.3)	53.9 (8.5)
	Interior chaparral								
	Second year	19	19	73	54	26.5 (2.1)	112.1 (14.8)	61.9 (20.8)	53.8 (4.7)
	Fourth year	27	4	85	27	23.1 (2.4)	105.9 (14.2)	46.9 (17.6)	50.1 (5.0)
	Mature	66	0	100	0	8.8 (4.5)	63.2 (1.3)	10.1 (4.4)	48.0 (3.1)
Australia									
	Western heathland	10	100	90	10	20.6 (2.3)	4.9 (0.5)	59.4 (18.5)	148.9 (12.8)
<b>(b) Other communities</b>									
California									
	Conifer forest								
	Unburned	84	31	63	31	10.9 (1.5)	53.4 (11.5)	8.5 (2.2)	37.0 (7.2)
	Burned	96	59	67	78	11.1 (1.1)	34.3 (7.8)	17.5 (4.8)	18.6 (4.4)
	Oak savanna								
	Ungrazed	100	0	40	40	13.6 (1.6)	512.4 (92.9)	25.9 (7.9)	54.2 (8.8)
	Grazed	90	0	30	50	13.5 (1.9)	461.4 (59.9)	30.7 (7.2)	44.7 (4.6)
	Desert scrub								
	High precipitation year	0	80	100	100	43.4 (4.6)	44.9 (9.6)	5.2 (1.7)	16.5 (3.5)
	Low precipitation year	n.d.*	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.

\*n.d. = Not determined because of insufficient number of species.

Across all of these vegetation types, annuals appeared to play a significant role in driving species–area relationships and other species diversity patterns, and were positively correlated with species richness at all scales (Table 6). Annuals were weakly correlated with the slope of the semi-log plot between 1 m<sup>2</sup> and 100 m<sup>2</sup> but much more strongly correlated with the slope between 100 m<sup>2</sup> and 1000 m<sup>2</sup>. On a log-log plot annuals were positively correlated with the y-intercept log  $c$ , or in other words as the proportion of annuals increased, the richness at the point scale increased. The slope  $z$  of this line, however, declined with increasing presence of annuals.

## DISCUSSION

There have been numerous attempts to discern the most appropriate model to describe the species–area relationship. Some (e.g. Connor & McCoy, 1979) have suggested an empirical approach that determines for each community the ‘best-fit’ to different models, predominantly either the power model (equation 1) or the exponential model (equation 2). In contrast, theoretical approaches have sought to link

ecological meaning to the power model, and sampling error or scale effects have been invoked to explain empirical results that run contrary to predictions (Rosenzweig, 1995, 1998; He & Legendre, 1996).

### Mediterranean-climate shrublands

Species–area relationships for shrublands of Australia and California provide an interesting contrast as there is strong support for the exponential model as a best fit for the former, and the power model as a best fit for the latter. This conclusion is based on visual inspection of species–area curves, magnitude of  $r^2$ -values, distribution of residuals and changes in slope between 1 m<sup>2</sup> and 1000 m<sup>2</sup>. Sampling error is an unlikely explanation for the differences. Both regions sampled tenth-hectare sites at the same scales, total richness was similar between regions, Australian curves were the average of 30 sites and each of the four Californian shrubland curves were based on 14–28 sites. We hypothesize that structural differences in these communities account for the different species–area curves. The important differences are tied to patterns of dominance, equitability and life form distribution.

Independent	Dependent	Slope	adj. $r^2$	F	P-value	n
Whittaker's $E_c$	Species $m^{-2}$	Positive	0.468	241.66	0.000	275
Whittaker's $E_c$	Species 1000 $m^{-2}$	Positive	0.568	362.60	0.000	276
Whittaker's $E_c$	Semi-log: $z_{(1-100m^2)}$	Positive	0.671	559.11	0.000	275
Whittaker's $E_c$	Semi-log: $z_{(100-1000m^2)}$	Positive	0.387	174.24	0.000	275
Whittaker's $E_c$	$z$ -Ratio $_{(1-100/100-1000)}$	Positive	0.122	38.99	0.000	275
Whittaker's $E_c$	Log-log: $\log c$	Positive	0.389	175.69	0.000	275
Whittaker's $E_c$	Log-log: $z$	Negative	0.115	36.75	0.000	275
Whittaker's $E_c$	Simpson's $\lambda$	Negative	0.212	79.06	0.000	292
Whittaker's $E_c$	Shannon's $H'$	Positive	0.544	348.65	0.000	292
Simpson's $\lambda$	Species $m^{-2}$	Negative	0.201	80.14	0.000	316
Simpson's $\lambda$	Species 1000 $m^{-2}$	Negative	0.224	96.57	0.000	332
Simpson's $\lambda$	Semi-log: $z_{(1-100m^2)}$	Negative	0.130	47.35	0.000	310
Simpson's $\lambda$	Semi-log: $z_{(100-1000m^2)}$	Negative	0.250	104.12	0.000	310
Simpson's $\lambda$	$z$ -Ratio $_{(1-100/100-1000)}$	Negative	0.000	0.08	0.780	310
Simpson's $\lambda$	Log-log: $\log c$	Negative	0.325	149.51	0.000	310
Simpson's $\lambda$	Log-log: $z$	Positive	0.134	49.51	0.000	310
Simpson's $\lambda$	Shannon's $H'$	Negative	0.556	438.28	0.000	350
Shannon's $H'$	Species $m^{-2}$	Positive	0.220	87.55	0.000	308
Shannon's $H'$	Species 1000 $m^{-2}$	Positive	0.137	52.25	0.000	324
Shannon's $H'$	Semi-log: $z_{(1-100m^2)}$	Positive	0.111	39.52	0.000	308
Shannon's $H'$	Semi-log: $z_{(100-1000m^2)}$	Positive	0.143	52.39	0.000	308
Shannon's $H'$	$z$ -Ratio $_{(1-100/100-1000)}$	Positive	0.027	9.56	0.002	308
Shannon's $H'$	Log-log: $\log c$	Positive	0.342	160.47	0.000	308
Shannon's $H'$	Log-log: $z$	Negative	0.153	56.46	0.000	308
Annual species (%)	Species $m^{-2}$	Positive	0.247	95.66	0.000	289
Annual species (%)	Species 1000 $m^{-2}$	Positive	0.143	51.71	0.000	289
Annual species (%)	Semi-log: $z_{(1-100m^2)}$	Positive	0.051	16.36	0.000	289
Annual species (%)	Semi-log: $z_{(100-1000m^2)}$	Positive	0.209	77.26	0.000	289
Annual species (%)	$z$ -Ratio $_{(1-100/100-1000)}$	Positive	0.054	17.36	0.000	289
Annual species (%)	Log-log: $\log c$	Positive	0.349	155.33	0.000	289
Annual species (%)	Log-log: $z$	Negative	0.213	78.96	0.000	289
Annual species (%)	Whittaker's $E_c$	Negative	0.004	2.17	0.142	281
Annual species (%)	Shannon's $H'$	Positive	0.029	10.26	0.002	309
Annual species (%)	Simpson's $\lambda$	Negative	0.026	9.14	0.003	309

**Table 6** Regressions using all Mediterranean sites with appropriate data. Independent variables are the Whittaker Index based on dominance–diversity curves, the Simpson Index of plant dominance, the Shannon index of evenness, and the percentage of species in the flora that were annuals. Independent variables include species richness at the point and community scales, the slope of the line for the semi-log plots ( $S = c + z \log A$ ) between 1 and 100  $m^{-2}$  and between 100 and 1000  $m^{-2}$

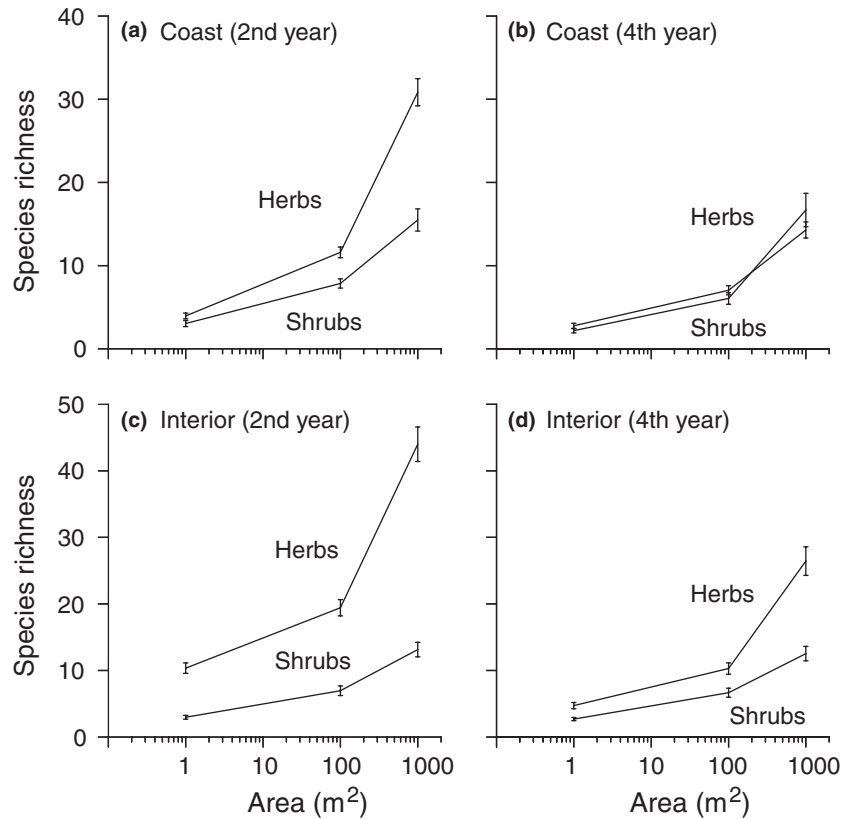
Dominance–diversity curves have long been used to illustrate community structure. For Western Australian heathlands these curves provide a strikingly close fit to MacArthur's broken stick model (Table 5, Fig. 10). This model is based on the concept of  $n$  species of equal competitive ability contesting each other in the determination of niche boundaries (MacArthur, 1960). The implication of this model is that populations of different species in a community reach a stable equilibrium without the development of dominance by any one species (Whittaker, 1972). This conclusion is also supported for the Australian sites by a very low Simpson index and evenness of species distribution, as reflected in high values for Whittaker's equitability index and the Shannon index (Table 4).

In contrast, dominance–diversity curves for Californian sites show a better fit to a geometric series. Also known as the niche-preemption model, it has been hypothesized that this model best describes communities where a single species dominates a substantial fraction of resources and subordinate species in sequence occupy a similar fraction of the remaining resources (Whittaker, 1972). In all four Californian shrubland associations, strong dominance is indicated

by relatively high values for the Simpson index, and less equitable distribution of species cover is illustrated by the low values for the Whittaker and Shannon indices (Table 4).

These interpretations are based on equilibrium conditions; however, cyclical disequilibrium is inherent in the fire cycle of these Mediterranean shrublands. What role disturbance has played in generating these species–area and dominance–diversity patterns requires close examination.

In Australian heathlands, there are postfire ephemerals (Pate *et al.*, 1985), however species richness at 1  $m^2$  or 1000  $m^2$  remains high in older stands and species–area curves fit the exponential model in both young and old stands (Bell *et al.*, 1984; Specht, 1988). Dominance–diversity curves for Australian heathlands were based on young stands 7 years postfire (Fig. 10) and there is little reason to believe the evenness of distribution patterns would change with age (George *et al.*, 1979). Part of the explanation for this is the fact that two-thirds of the community comprises woody species, and annual species are essentially absent (Table 7). Long-term persistence of this entirely perennial flora potentially contributes to formation of stable competitively determined boundaries that persist in maturity. These



**Figure 14** Piecewise semi-log species–area plots for herbs and shrubs separately in California shrublands. (a) coastal 2<sup>nd</sup> year; (b) coastal 4<sup>th</sup> year; (c) interior 2<sup>nd</sup> year; and (d) interior 4<sup>th</sup> year. Each point is the mean of multiple sites with vertical SE bars (see Table 1 for sample sizes).

patterns persist after fire because over 70% of the species resprout (Bell *et al.*, 1984).

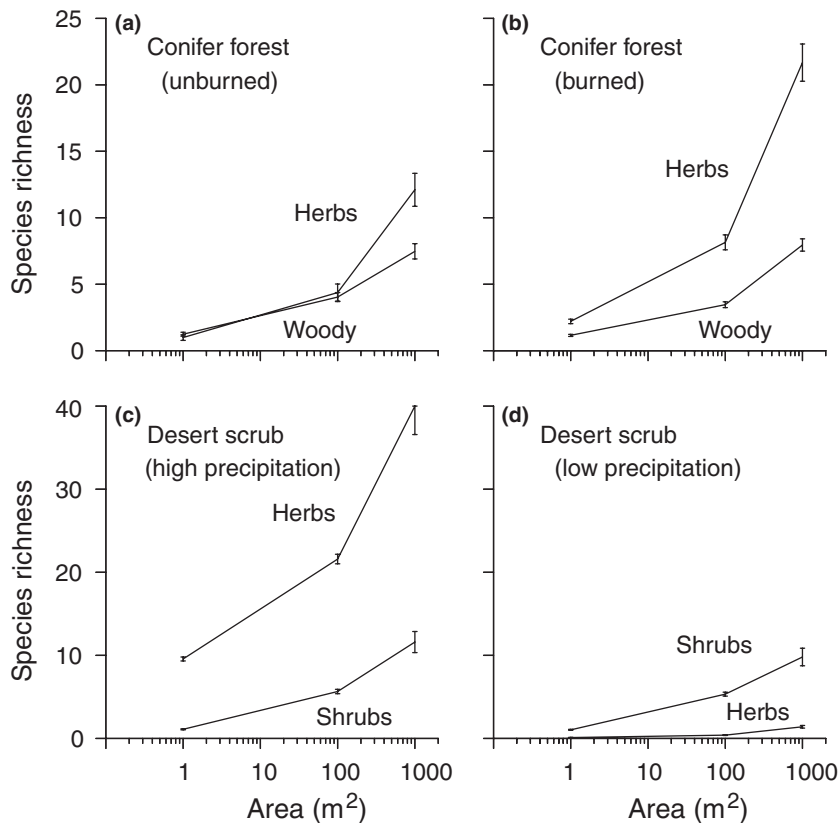
This is in marked contrast to Californian shrublands where there are substantial differences in richness with time since fire (Table 4) and species–area relationships change from a power model early in succession to an exponential model in mature stands (Table 1; Figs 1 & 4). The primary change in dominance relationships with successional age is towards increased dominance. This is reflected by a small drop in the Whittaker and Shannon equitability indices between the second and fourth years postfire and a marked drop in mature stands, and the opposite pattern with the Simpson index (Table 4, Figs 7–9). This Californian shrubland pattern of high richness and moderate dominance moving towards reduced diversity and increased dominance is in striking contrast to temperate latitude old field/forest succession (Bazzaz, 1975), and reflects a long evolutionary relationship with predictable stand-replacing fires in Californian shrublands (Keeley, 2000).

Dominance in these Californian shrublands is driven by the fact that a substantial portion of postfire resources are immediately occupied by resprouts from large root crowns and lignotubers, even though these resprouters comprise only about a quarter of the flora (Keeley, 1998). Additionally, some of these same species recruit from fire-stimulated seed banks and thus are poised for expanding dominance with age. The annual life history results in unstable competitive boundaries that are continually readjusted each year,

eventually being all but completely crowded out as the shrub canopy closes. The role of ephemeral herbaceous species in driving these patterns is reflected in Fig. 14.

The important role of disturbance in successional patterns of California shrublands, coupled with evidence of a power model fit for species–area relationships, supports Connor & McCoy's (1979) contention that there is little reason to assume a strict adherence between the power model and equilibrium conditions. In short, the equilibrium theory of species diversity (MacArthur & Wilson, 1967) predicts a power model describing species–area relationships; however, empirical data for Californian shrublands demonstrate that disequilibrium processes may also generate these models.

In sum, the more even competitive relationships of the entirely perennial flora in Australian heathlands generates species–area relationships that do not change with scale and lead to community level exponential species–area curves. These patterns persist over time because of the extreme soil nutrient deficiency (Rundel, 1983) that limits the formation of closed canopy conditions (Bond & Ladd, 2001). The lack of canopy closure has likely reduced selection for large woody species with the potential for canopy dominance. After fire, three-fourths of the flora resprout, which reduces the structural reassembly of the community. Californian shrubland diversity is largely concentrated in early successional stages because the bulk of the diversity comprises fire specialist annuals that are eliminated with canopy closure. In early successional communities the yearly turnover of spatial



**Figure 15** Piecewise semi-log species–area plots for herbs and shrubs separately in California (a) conifer forests unburned, (b) conifer forests third year postfire, (c) desert scrub in year of high precipitation, and (d) desert scrub in year of low precipitation. Each point is the mean of multiple sites with vertical SE bars (see Table 1 for sample sizes).

boundaries of annuals works against the formation of equilibrational competitive relationships and enhances the influence of stochastic effects, e.g. unpredictable rainfall. A substantial proportion of the diversity comprises small stature annuals that often persist at low levels, perhaps because of mass effects *sensu* Shmida & Wilson (1985). The probability of encountering these uncommon species is scale dependent, being small at fine scales and increasing markedly between 100 m<sup>2</sup> and 1000 m<sup>2</sup>, thus leading to a power model of species–area relationships.

Patterns evident in mature chaparral (Fig. 9) illustrate that the exponential species–area model may arise in more than one way. In the highly diverse Australian heathlands it results from a rapid increase in species richness at small scales. In mature chaparral it results from very depauperate richness at the community scale. In both instances the exponential model is tied to a preponderance of perennials and paucity of annuals.

Other Mediterranean-climate shrublands fall between the Australian and Californian patterns. South African fynbos would appear to fit either the power or the exponential model, the former based on comparison of the adjusted  $r^2$  values and the latter based on the relatively even distribution of residuals from semi-log plots (Fig. 3). However, studies report different species–area relationships (cf., Bond, 1983 vs. Schwilk *et al.*, 1997) and a causal explanation is wanting. Although South African fynbos shares the distinc-

tion with Australian heathlands of extremely limited soil nutrients, life form distribution comprises a larger herbaceous element (Table 7).

The Mediterranean Basin shrublands share many features in common with Californian shrublands. Species–area curves in open-canopy disturbed communities in the eastern portion of the basin are best fit with a power model, whereas mature closed canopy maquis in the western portion of the basin tend towards the exponential model (Tables 1–3; Figs 2 & 3). As with Californian shrublands, annuals dominate disturbed sites and become increasingly uncommon in closed canopy shrublands (Table 7). Indeed, even within the same community, shrubs appear by inspection to fit an exponential model, whereas herbs a power model (Pausas *et al.*, 1999).

The Mediterranean basin is remarkably distinct from California as well as Southern Hemisphere Mediterranean-climate shrublands in having extraordinarily high levels of community richness; eastern-basin disturbed communities often have 100 or more species per tenth-hectare (Table 4). Although the point has not been well explored, it seems likely that this arises from regional influences on local diversity patterns, suggested by the fact that the flora comprises floristic elements derived from Europe, Asia and Africa.

No comparable data on species–diversity relationships exist for Mediterranean shrublands of central Chile. Based on the similarity in life form distribution between Chile and

**Table 7** Life form comparison of plant species in Mediterranean-type shrublands and associated vegetation types. Data sources listed in Appendix I

Country	Vegetation	Age*	Percentage of species				Data source
			Phanerophytes	Chamaephytes	Hemicryptophytes and geophytes	Therophytes	
<b>(a) Shrublands</b>							
California							
	Coastal sage scrub	2	16	14	16	54	1
		4	21	19	18	42	1
	Coastal chaparral	2	24	12	18	46	1
		4	35	19	21	25	1
	Interior sage scrub	2	10	10	15	65	1
		4	14	13	18	55	1
	Interior chaparral	2	16	10	13	61	1
		4	24	14	13	49	1
	Coastal chaparral	> 40	23	23	46	8	7
	Coastal chaparral	> 50	21	14	18	48	10
	Interior chaparral	> 25	41	16	30	13	22
	Interior chaparral	42	42	27	8	23	32
	Interior chaparral	Mature	25	7	19	46	36
	Coastal and interior Sage scrub	Mature	24	7	30	39	34, 35
South Africa							
	Fynbos	–	41	6	52	1	17
	Fynbos	–	32	15	52	1	27
	Fynbos	–	48	5	41	6	9
	Renosterveld	–	47	9	31	13	4
Australia							
	Western heathland	5–20	62	7	28	< 1	14
	Western heathland	7	68	6	26	0	20
	Eastern heathland	–	46	13	41	0	28
	Eastern mallee	Immature	29	3	41	28	36
	Eastern mallee	Mature	28	2	35	35	36
	Eastern scrub	–	68	8	24	0	27
Chile							
	Matorral	–	12	15	26	46	22
	Matorral	20–25	29	–	39	32	30
Mediterranean basin							
	Western garrigue	1	10	3	36	51	12
	Western maquis	1	7	14	37	42	12
	Western garrigue	10	13	5	46	36	12
	Western maquis	10	10	23	39	28	12
	Western garrigue	12	11	–	42	47	25
	Western garrigue	12	11	–	42	47	25
	Western maquis	1	12	–	46	42	11
	Western maquis	5	18	–	43	39	11
	Western maquis	15	14	–	41	45	11
	Eastern maquis	30	8	5	24	63	24
	Eastern maquis	–	10	5	23	62	25
<b>(b) Other communities</b>							
California							
	Conifer forest						
	Unburned	> 50	22	7	45	26	1
	Burned	3	18	9	41	32	1
	Oak savanna						
	Ungrazed	–	8	3	12	77	1
	Grazed	–	6	1	7	86	1

Table 7 continued

Country	Vegetation	Age*	Percentage of species				Data source
			Phanerophytes	Chamaephytes	Hemicryptophytes and geophytes	Therophytes	
Australia	Desert scrub						
	High ppt	Mature	19	3	4	74	1
	Low ppt	Mature	81	8	5	6	1
Mediterranean basin	Western woodland	–	9	55	34	2	5
	Eastern woodland	–	64	9	26	< 1	27
Mediterranean basin	Western woodland	1	13	13	34	40	12
	Western woodland	10	24	20	36	20	12
	Western woodland	1	26	29	33	12	23
	Eastern woodland	–	5	9	15	71	24
	Eastern woodland	2	23	–	25	52	19
	Eastern woodland	8	32	–	22	46	19
	Eastern woodland	Mature	34	–	28	38	19
	Eastern woodland	Mature	40	–	43	17	15

\*Years since last fire when known.

California (Table 7) and the analysis above, we predict that closed canopy matorral will resemble mature chaparral stands and follow an exponential model. The patterns in postfire matorral are not as readily predicted since these communities appear to have had a different evolutionary relationship with fire and lack a fire-endemic ephemeral component (Keeley & Johnson, 1977).

#### Other Mediterranean-climate associations

The bulk of data for other Mediterranean vegetation types comes from Californian forests, savannas and desert scrub. Based on visual inspection of species–area curves (Fig. 6) and comparison of  $r^2$  values it is apparent that these communities do not fit the exponential model and the power relationship is more appropriate. In this regard they share much in common with early successional Californian shrublands; however, these communities exhibit structural differences from chaparral and coastal sage scrub.

Mixed conifer forests are fire-prone communities, but unlike associated shrublands, the natural regime has not historically been dominated by stand replacing crown fires, but rather by mixed intensity stand-thinning fires. Not surprisingly, the dominance–diversity patterns support the niche-preemption (geometric) model (Figs 11a & b). Following fire, particularly in high intensity gaps where overstorey trees have been thinned, species are more equitably distributed (Figs 11c & d), some sites even fitting the broken stick model (Table 5). However, unlike the Australian heathlands, these assemblages are more ephemeral, being populated by herbaceous species that soon diminish in importance as the mature forest recovers. In contrast to shrublands where canopy closure is accompanied by the loss of understory species, mixed coniferous forests retain these

species in gaps. Consequently, the species–area relationship remains unchanged between mature forests and recently burned forests (Fig. 6a).

Species–area relationships in oak savannas share many features in common with associated shrublands. The power model is clearly a better fit than the exponential, as reflected in the  $r^2$ -values (Table 1) and change in slope from 1 to 100 m<sup>2</sup> vs. 100 to 1000 m<sup>2</sup> on a semi-log plot (Fig. 6b; Table 3). However, dominance–diversity relationships are decidedly different, with 100% of the sites exhibiting a significant fit to the lognormal model (Table 5; Fig. 12c & d), a pattern not observed in other associations.

Although Preston's (1948) original lognormal model was statistical rather than biological in origin, various ecological interpretations have been deduced from it. Preston (1962) himself proposed a causal relationship between the lognormal abundance distribution and the power function species–area relationship. Whittaker (1972) suggested that communities comprising a large number of species not closely related in resource use would form a lognormal distribution. In contrast, Sugihara (1980) contended that the lognormal model applies to species assemblages with a significant measure of ecological homogeneity or similarity, and used this to argue for a biological basis for this model. Following Preston's (1962) lead, MacArthur & Wilson (1967) used the linkage between the lognormal abundance distribution and the power function species–area relationship to support their equilibrium model of island biodiversity.

Preston (1962) suggested that lognormal distributions were inevitable when samples of large numbers of species are considered. This of course cannot account for differences in dominance–diversity patterns between savannas and other vegetation types in California. Indeed, the tenth-hectare



species counts in savannas fall within the range observed for shrublands (Table 4), yet dominance–diversity curves bear little resemblance (Figs 7–9 & 12). Whittaker's (1972) suggestion that dissimilar resource utilization leads to a lognormal model is an unlikely explanation in these savannas that are dominated by species of similar life form (Table 7). MacArthur & Wilson's (1967) equilibrium explanation may apply with the following qualification: while these species may represent an equilibrium between colonization and extinction, it needs to be recognized this is a new quasi-equilibrium of relatively recent origin as the majority of species are neophytes to the California flora, having invaded only within the last 200 years. The fact that these savannas are dominated by annuals with radical recruitment fluctuations from year to year does not invoke the notion of an equilibrium.

Desert scrub patterns illustrate the critical need for multiple observations over years of different precipitation in ecosystems with a strong annual species presence (Fig. 6c). Unlike the pattern in Californian shrublands, the range of high and low diversity is not accompanied by a change in the species–area curves (Tables 1 and 2). Dominance–diversity curves demonstrate interesting patterns. During years of high precipitation it is almost as if there are two separate assemblages: the dominants that clearly fall along a geometric curve, and the subordinants (mostly annual species) that follow the shape of the MacArthur broken stick model (Fig. 13a & b). In years of low precipitation, the annuals disappear and the few species remaining all appear to follow a geometric series (Fig. 13c & d).

From a practical standpoint, diversity studies that focus on systems dominated by annual species, e.g. Mediterranean-climate associations other than South African and Western Australian systems, need to consider pre- and post-disturbance patterns as well as high and low precipitation years. Studies that fail to do so should be suspect and will have limited applicability to the range of potential patterns in species–area relationships.

### Power model coefficients

A large proportion of Mediterranean-climate plant communities considered here appear to provide a best fit to the power model (Tables 1 & 2, Figs 2–5), consistent with the pattern in many, but not all, plant communities (Connor & McCoy, 1979). Preston (1962) attempted to assign meaning to coefficients of the power function least squares regression model, suggesting a range for values of slope  $z$  dictated by constraints of the lognormal abundance distribution. In contrast, Connor & McCoy (1979) provided analysis suggesting that species–area power function coefficients have little or no biological meaning.

According to the equilibrium theory (MacArthur & Wilson, 1967), the coefficient  $z$  represents the rate of accumulation of species with area that is caused by differences in immigration and extinction. In support of this conclusion, MacArthur and Wilson observed that mainland samples gave  $z$ -values in the range of 0.12–0.17 whereas island samples were around 0.27. They surmised

that on continental landmasses, small samples were flooded with 'transient species that maintain themselves in ecologically different areas nearby'. Modern translation: metapopulation dynamics are different on mainland vs. islands. Although never specified, it is obvious that this conclusion is highly scale dependent. The  $z$ -values in most of the communities studied here fell within the range typically observed on islands. This may result from mass effects (Shmida & Wilson, 1985) at the community scale of 1000 m<sup>2</sup>, which should have the impact of increasing  $z$ . In the context of this model, the very high  $z$ -values observed for Mediterranean basin woodlands may derive from the regional influences resulting from the convergence of three continental floras.

When examining Mediterranean-climate vegetation we see that in log-log space, both regression coefficients, the  $y$ -intercept  $\log c$  and the slope  $z$ , vary systematically in statistically significant ways (Table 6). The coefficient  $\log c$  is positively related to indices of equitability (Whittaker's and Shannon's) and negatively correlated with the Simpson index of dominance. In short, the  $y$ -intercept of the species–area curve appears to be influenced by dominance–diversity patterns and is best interpreted as demonstrating that as the dominance of a selected few species increases in a community, the point diversity decreases. This is reflected in the strong relationship between  $\log c$  and the proportion of the flora comprising annuals, suggesting that it is possible to cram more annual species into 1 m<sup>2</sup> than perennials. However, as the number of species increases at the point scale there is an inhibitory effect on the slope  $z$ .

Across the Mediterranean-climate vegetations considered here, the power function slope  $z$  is negatively correlated with equitability measurements and positively correlated with the Simpson measure of dominance (Table 6). In ecological terms, as species dominance increases, point diversity decreases and the diminishment of dominant species on richness is not as great at higher scales because of the greater patchwork of suitable habitat for uncommon species.

### CONCLUSIONS

Most Mediterranean-climate ecosystems are subject to predictable stand-replacing fires, creating cyclical disequilibrium. Geological and phylogenetic history, combined with contemporary environmental differences, have selected for quite different life form compositions in these regions, resulting in different patterns of community assembly.

Plant communities with a strong annual species component have species–area curves that invariably fit the power function model (equation 1, e.g. Fig. 5). Shrublands and woodlands on low nutrient soils in South Africa and Australia largely lack a significant annual component and the exponential model (equation 2, e.g. Fig. 2) often provides the best fit to species–area relationships. Dominance–diversity patterns between these regions reflect differences in life form and hypotheses are proposed on how these can be related mechanistically to species–area relationships.

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## SUPPLEMENTARY MATERIAL

The following material is available from <http://www.blackwellpublishing.com/products/journals/suppmat/JBI/JBI950/JBI950sm.htm>

**Appendix SI** Dominance–diversity curves for all study sites.

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## APPENDIX I. DATA SOURCES

1. This study
2. Basanta *et al.* (1989)
3. Bond (1983)
4. Boucher & Moll (1981)
5. Bridgewater & Backshall (1981)
6. Chiarucci *et al.* (2001)
7. Christensen (1973)
8. Cowling (1983)
9. Cowling (1990)
10. Davis *et al.* (1988)
11. De Lillis & Testi (1992)
12. Espirito-Santo & Capelo (1998)
13. Fernandez-Gonzalez *et al.* (unpublished data)
14. George *et al.* (1979)
15. Kazanis & Arianoutsou (1996)
16. Keeley (1973)
17. Kruger (1983)
18. Kutiel (1997)
19. Kutiel (2000)
20. Lamont *et al.* (1977)
21. Mazurek & Romane (1986)
22. Mooney (1997)
23. Moreno *et al.* (1997)
24. Naveh & Whittaker (1979)
25. Nevo *et al.* (1999)
26. Pausas (1999)
27. Rice & Westoby (1983)
28. Russell & Parsons (1978)
29. Scwhilk *et al.* (1997)
30. Specht (1988)
31. Troeger (1983)
32. Vogl & Schorr (1972)
33. Ward & Olsvig-Whittaker (1993)
34. Westman (1981)
35. Westman (1983)
36. Whittaker *et al.* (1979)

**BIOSKETCHES**

**Jon Keeley** is leader of the US Geological Survey research station at Sequoia National Park, in California, USA, adjunct Professor of Organismic Biology, Ecology and Evolution at the University of California, Los Angeles, CA, USA, and Research Associate at the Rancho Santa Ana Botanical Garden. He has published on the fire ecology of California chaparral and coastal sage scrub vegetation over a period of 30 years and is author of the chaparral chapter in the *Terrestrial Vegetation of North America* and the upcoming edition of *California Terrestrial Vegetation*. Other research interests include ecophysiology of smoke-stimulated seed germination and photosynthetic pathways of aquatic plants and biosystematics of *Arctostaphylos* and *Ceanothus*. Dr Keeley is a Fellow of the Southern California Academy of Sciences, a Guggenheim Fellow, and Honorary Lifetime member of the California Botanical Society.

**C. J. Fotheringham** is currently a Doctoral Student in the Organismic Biology, Ecology and Evolution Department at the University of California, Los Angeles, CA, USA. She has interests in the evolutionary patterns of species response to fires. Main field research locations include Mediterranean shrublands and adjacent deserts in California and South Africa, and non-Mediterranean sclerophyllous shrublands of the south-western USA.