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BIODIVERSITY RESEARCH

Relating species abundance distributions to species-area curves in two Mediterranean-type shrublands

JON E. KEELEY *U.S. Geological Survey, Western Ecological Research Center, Sequoia National Park, Three Rivers, CA 93271–9651, U.S.A. & Department of Organismic Biology, Ecology and Evolution, University of California, Los Angeles, CA 9009, U.S.A.*

Abstract. Based on both theoretical and empirical studies there is evidence that different species abundance distributions underlie different species-area relationships. Here I show that Australian and Californian shrubland communities (at the scale from 1 to 1000 m^2) exhibit different species-area relationships and different species abundance patterns. The species-area relationship in Australian heathlands best fits an exponential model and species abundance (based on both density and cover) follows a narrow log normal distribution. In contrast, the species-area relationship in Californian shrublands is best fit with the power model and, although species abundance appears to fit a log normal distribution, the distribution is much broader than in Australian heathlands. I hypothesize that the primary driver of these differences is the abundance of small-stature annual species in California and the lack of annuals in Australian heathlands. Species-area is best fit by an exponential model in Australian heathlands because the bulk of the species are common and thus the species-area curves initially rise rapidly between 1 and 100 m^2. Annuals in Californian shrublands generate very broad species abundance distributions with many uncommon or rare species. The power function is a better model in these communities because richness increases slowly from 1 to 100 m^2 but more rapidly between 100 and 1000 m^2 due to the abundance of rare or uncommon species that are more likely to be encountered at coarser spatial scales. The implications of this study are that both the exponential and power function models are legitimate representations of species-area relationships in different plant communities. Also, structural differences in community organization, arising from different species abundance distributions, may lead to different species-area curves, and this may be tied to patterns of life form distribution.

Key words. Chaparral, coastal sage scrub, fire, heathlands, species abundance curves, species-area curves.

INTRODUCTION

In recent years there has been a renewed interest in species-area relationships at local, regional and global scales. Much of this literature has centred on the proper mathematical relationship that describes the species-area curve. Two models have been widely applied (Connor & McCoy, 1979), the power model, typically expressed as the log transformation

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

and the exponential model

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

There is a rich history of ecological studies that have attempted to link species-area curves to species abundance distributions. Fisher *et al.* (1943) proposed that exponential species-area curves would result from species abundance distributions where the most numerous class of species are those that are uncommon and there are very few species that dominate the community (a log

* Corresponding author: E-mail: jon_keeley@usgs.gov

series distribution). Preston (1948, 1962), on the other hand, showed that power function species-area curves were predicted from log normal species abundance distributions in which the most abundant class of species is for those that are neither rare nor exceptionally abundant (log normal distribution).

Here I report that comparisons of plant species-area curves from 1 to 1000 m^2 for two Mediterranean climate regions that support different species-area models and I examine the extent to which species abundance distributions can explain these different species-area relationships.

METHODS

Californian shrublands included coastal and interior associations of evergreen chaparral and the lower-stature semideciduous sage scrub. All stands were 5 years since the last fire and were distributed throughout southern California (Keeley, 1998). Sites were sampled in a nested tenth hectare design (Keeley *et al*., 1995). Briefly, a 20×50 m site was subdivided into 10 contiguous 10×10 m plots and each included two 1×1 m quadrats placed in opposite corners (quadrats on the interior were offset 1 m from the middle of the site). Species richness was recorded in each 1 m^2 quadrat and each 100 m^2 plot and then averaged across the site. Cover and density were estimated for each species in the quadrats. Data for Australian shrublands was with Whittaker plots from Specht (1988) and sites ranged in age from 5 to 20 years since the last fire.

Species-area curves were constructed from the number of vascular plant species in 1, 100 and 1000 m^2. These were nested plots, and thus finer scale measures were not completely independent samples. This lack of independence is less of a factor in this study because each scale is plotted as the mean of multiple sites. For the Californian sites the impact of this potential lack of independence was evaluated by a separate analysis in which the mean species richness at 1 m^2 and 100 m^2 was based on a subset of quadrats and plots from each site that were not nested. Results of the analysis presented in this study, which is based on the full sample design, remained unchanged when these un-nested samples were used.

Species abundance curves were compared with expected values for log series and log normal distributions according to Hayek & Buzas (1997). Californian samples comprised a total of 1760 1 m^2 plots (420, 280, 540, and 520 for coastal sage scrub, coastal chaparral, interior sage scrub, and interior chaparral, respectively). Australian data were from a different data set than that used for the species-area curves and were published by Lamont *et al*. (1976; raw data provided by the first author) and included a total of 500 1 m^2 plots. Data from both regions were standardized by setting the lowest density and cover class to 1. Log 2 octaves as advocated by Preston (1962) were not used because the Californian data were distributed across more than 20 classes, many of more or less equal number of species. Life form distribution for Australia was from George *et al*. (1979).

RESULTS AND DISCUSSION

Species-area relationships

Evergreen heathlands of both western and eastern Australia provide a slightly better fit to the exponential model as illustrated by the linear relationship of mean richness at 1, 100 and 1000 m^2 on a semilog plot (Fig. 1a,b) and the higher r^2 value for semilog vs. log-log least squares regression (Table 1). In contrast, Californian shrublands of western North America, including coastal and interior populations of semideciduous sage scrub and evergreen chaparral, do not appear to fit a semilog relationship (Fig. 1c–f), and consistently exhibit much higher r^2 values for log-log regressions (Table 1). These differences exist despite marked similarities in species richness of these communities (average per tenth hectare, 48.4–69.0 in Australia and 46.5–59.4 in California for sites in Fig. 1).

Differences in species-area model for these two regions is further suggested by the highly significant difference in slope for 1–100 m^2 vs. 100–1000 m^2 (on a semilog scale) for California, but no significant difference in Australia (Table 2). In Californian shrublands, species richness is relatively depauperate at the 100 m^2 scale but catches up with Australia at the 1000 m^2 scale. Thus, diversity curves in Australian heathlands result from continuous increases in species richness from 1 to 1000 m^2 whereas in Californian shrublands richness at the point scale of 1 m^2 changes

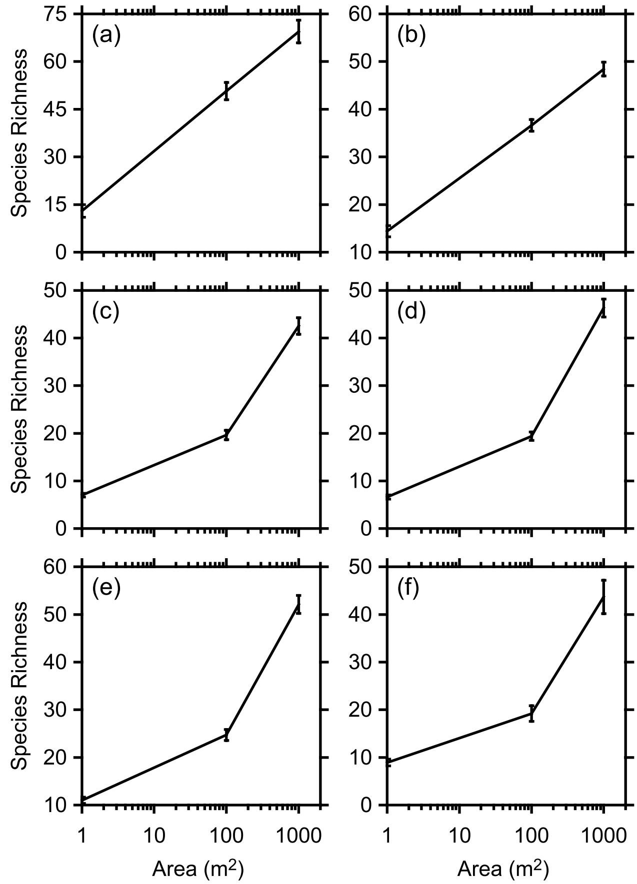

Fig. 1 Semilog species-area curves for (a) Western Australian heathlands, n = 30 sites (b) Eastern Australian heathlands, n = 5 sites (c) Californian coastal sage scrub, n = 21 sites (d) Californian coastal chaparral, n = 14 sites (e) Californian interior sage scrub, n = 27 sites (f) Californian interior chaparral[7], n = 26 sites, means and standard error bars.

relatively little in the surrounding 100 m^2 but increases markedly between 100 and 1000 m^2.

Species abundance distributions

Crawley & Harral (2001) have shown scale dependent changes in slope of the species-area curves similar to those reported for California (Table 2) and they proposed that different processes might operate at different scales. One hypothesis for the shallow slopes from 1 to 100 m^2 and steep slopes between 100 and 1000 m^2 is that species in these Californian shrublands have spatial hierarchies where patches of repeating clusters of species turnover at the scale of 100 m^2.

Alternatively, there is a rich history of ecological studies that have attempted to link species-area curves to species abundance distributions. These studies suggest an alternative to the process-based hypothesis proposed above. Namely, that the exponential species-area relationship in Australian heathlands results from species of similar abundance with few dominants, whereas the power function for Californian shrublands results from a broad range of abundances that include significant numbers of uncommon or rare species, which are more likely to be encountered

Table 1 Comparison of species-area relationships for 1, 100, and 1000 m^2 between Australian heathlands and Californian sage scrub and chaparral on coastal and interior sites; semilog: S = c + z log A, and log-log: log S = log c + z log A, where S = number of species, A = area in m^2, and z describes the slope and c describes its intercept

			adjusted r^2	
Country	Vegetation	*n*	Semilog	Log-log
Australia				
	Western heathland	90	0.70	0.66
	Eastern heathland	15	0.97	0.94
California				
	Coastal sage scrub	66	0.78	0.91
	Coastal chaparral	42	0.79	0.94
	Interior sage scrub	81	0.73	0.83
	Interior chaparral	78	0.54	0.65

Table 2 Comparison of slopes between 1 and 100 m^2 and 100–1000 m^2 for the semilog relationship in Australian and Californian shrublands and compared with the paired *t*-test. Ratios of slope from 1 to 100 m^2 divided by slope from 100 to 1000 m^2 were compared across all vegetation types with a one-way ANOVA

		Slope (z)			$\text{Slope}_{(1-100)}$
Country	Vegetation	1–100 m^2	100–1000 m^2	*P*(d.f.)	$\text{Slope}_{(100-1000)}$
Australia					
	Western heathland	8.186	8.150	= 0.964 (52)	1.051
	Eastern heathland	4.821	5.125	= 0.318 (8)	0.941
California					
	Coastal sage scrub	2.742	9.933	= 0.000 (40)	0.279
	Coastal chaparral	2.104	12.537	= 0.000 (6)	0.243
	Interior sage scrub	2.981	14.119	= 0.000 (16)	0.248
	Interior chaparral	1.643	15.640	= 0.000 (12)	0.227
					$F = 22.897$
					$P < 0.001$

at coarser spatial scales, such as from 100 to 1000 m^2.

Patterns of species abundance can distinguish between the competing hypotheses of repeating clusters of species vs. rare species accounting for the species-area curves (Fig. 1). I predict that in Californian shrublands, if there is a turnover of species clusters at the scale of 100 m^2, then at the 1000 m^2 site level there will be few highly dominant species, and the abundance distribution for all species will be narrow. In contrast, if the alternative hypothesis is true, then there will be many uncommon species and a broad range of abundance classes.

Species abundance curves based on either density or cover illustrate marked differences between Australia (Fig. 2a,b) and California (Fig. 2c–j), although all appear to better fit a log normal than a log series distribution (Table 3). In Australia the bulk of the species occupy a narrow range of density and cover classes (classes based on log 10 not log 2, see Methods), with the peak in the mid-classes (Fig. 2). In Californian shrublands species density curves are much broader and peak in the lowest class. It may be that these represent log normal distributions truncated due to limited sampling that failed to detect rare species (May, 1974; Rosenzweig, 1995; Hubbell,

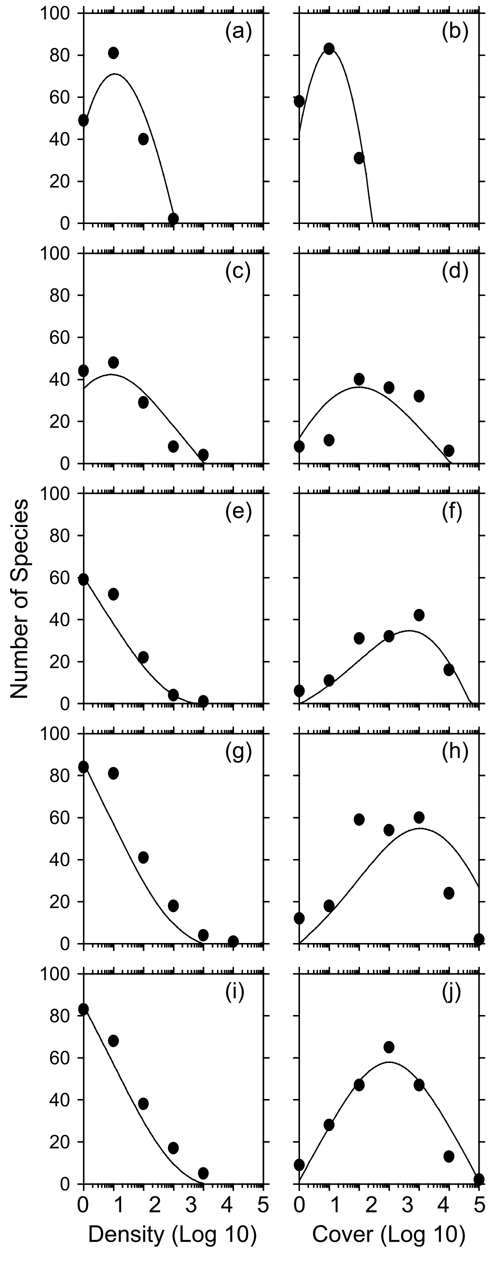

Fig. 2 Species abundance curves for density and cover of (a,b) Western Australian heathlands, n = 500 1 m² quadrats and 173 species (c,d) Californian coastal sage scrub, n = 420 quadrats and 133 species (e,f) Californian coastal chaparral, n = 280 quadrats and 138 species (g,h) Californian interior sage, n = 540 quadrats and 229 species (i,j) Californian interior chaparral, n = 520 quadrats and 211 species.

2001). However, the pattern in coastal chaparral (Fig. 2e) with 280 m² sampled and 138 species included was similar to that for interior sage scrub (Fig. 2g) with 540 m² sampled and 229 species included. The distributions contrast markedly with that observed for Australian shrublands (Fig. 2a,b) with 500 m² sampled and 173 species encountered, making it seem unlikely that the differences between California and Australia are due simply to sampling error.

Distribution by cover class in Australia (Fig. 2b) showed an extremely narrow distribution with total cover for a species differing by only two orders of magnitude and all classes well represented. In contrast, Californian shrublands exhibited very broad distributions (Fig. 2d,f,h,j).

Species abundance curves for both density and cover indicate that in Australian heathlands the bulk of the species have similar abundances, whereas in Californian shrublands the bulk of the species are uncommon. These data support the hypothesis that different species-area relationships derive from different species abundance distributions.

Life form distribution

The factors driving these different patterns of abundance distributions are unknown. One likely contributor, however, is the striking difference in life forms. The Californian shrublands comprise a mixture of large woody shrubs (2–5 m in height), and commonly half of the diversity is composed of small stature annuals, whereas Australian heathlands typically comprise similar stature perennial shrubs and subshrubs, and annuals are largely absent (Specht, 1988). In Californian shrublands the high proportion of species in the lowest abundance classes is due to the large number of small annual species. These patterns (Table 4) are likely driven by regional differences in soils and species pools (Rundel, 1983). Fire, which is a common disturbance in both regions, does not appear to explain these different patterns as both data sets represent similar-aged stands; Australian heathlands were all 7 years postfire and Californian shrublands were all 5 years postfire.

CONCLUSIONS

Exponential and power function models are both legitimate representations of species-area

Table 3 Chi-square test of fit for log 10 classes of species abundance to the log normal and log series distributions for Australian and Californian shrublands

Country	Vegetation	Abundance measure	d.f.	Chi-square log normal	Chi-square log series
Australia					
	Western heathland	Density	3	4.09*	1763
		Cover	2	8.53	476
California					
	Coastal sage scrub	Density	4	6.69*	1785
		Cover	5	52.47	2440
	Coastal chaparral	Density	4	2.61*	183
		Cover	5	41.28	1860
	Interior sage scrub	Density	5	48.35	439
		Cover	6	102.31	2858
	Interior chaparral	Density	4	35.13	319
		Cover	6	13.39	908

* 95% probability that the distribution fits the log normal.

Table 4 Life form comparison of plant species in Australian and Californian shrublands

Country Vegetation	(#of sites)	Percentage of species: Phanero-phytes	Chamae-phytes	Hemicrypto-phytes & geophytes	Thero-phytes	Percentage cover by annuals (therophytes)
Australia[13]						
Western heathland	(33)	62	7	30	< 1	< < 1
California						
Coastal sage scrub	(21)	16	9	20	55	19
Coastal chaparral	(14)	17	10	23	50	13
Interior sage scrub	(27)	11	9	21	59	53
Interior chaparral	(26)	15	9	18	58	27

relationships in different plant communities. The implications of this study are that structural differences in community organization resulting from different species abundance distributions may lead to different species-area curves, and this may be tied to patterns of life form distribution. The exponential model is a better fit to Australian heathlands because the bulk of the species are common and thus the species-area curves initially rise rapidly between 1 and 100 m^2. Annuals in Californian shrublands generate very broad species abundance distributions with many uncommon species. Here the power function is a better model because richness increases slowly at the finest scales, but more rapidly between 100 and 1000 m^2 due to the abundance of rare or uncommon species that are more likely to be encountered at coarser scales.

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