

Abundance and distribution of desert annuals: are spatial and temporal patterns related?

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Summary

1 Spatial distribution–abundance relationships have been intensively studied. Workers have now begun to study temporal relationships but little is known about how these are related to spatial patterns. We examined these relationships both over space and time using 15 years of data from permanent quadrats in the Chihuahuan Desert.

2 Winter and summer annual communities were analysed. Within single years, the species in each community exhibited a positive relationship between distribution and abundance at two spatial scales, 0.25-ha plots and 0.25-m² quadrats. Over 15 years, the species in each community also exhibited a positive relationship between abundance and the number of years in which they were present. Species frequency distributions, both in space and over time, were scale-dependent.

3 Over space, the frequency distribution was bimodal at large (plot) scales, but unimodal at small (quadrat) scales in both communities. Over time, the frequency distribution was bimodal for winter annuals but unimodal for summer annuals, a difference we attribute to the marked difference between the two communities in the temporal consistency of rank abundance of species. We conclude that both niche and metapopulation models can be used in explaining the distribution patterns of species but at different scales. The factors and processes in these models are not mutually exclusive in determining the overall abundance and distributions of these species in space and over time.

Key-words: abundance, Chihuahuan Desert, distribution, long-term study, spatial-temporal relationships

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Introduction

Positive relationships between abundance and distribution (number of sites occupied) have been observed by many investigators at many spatial scales (Hanski 1982a,b; Brown 1984; Gotelli & Simberloff 1987; Collins & Glenn 1990, 1991; Maurer 1990; Nee *et al.* 1991; Hanski & Gyllenberg 1993, 1997; Guo *et al.* 2000; but see Gaston 1996) and similar patterns are usually seen for all species in the same guild, functional group or higher taxon. Despite the ubiquity of these relationships, however,

the mechanisms that produce them remain poorly understood (e.g. Burgman 1989; Gaston *et al.* 1997). Another commonly but by no means universally observed pattern is the bimodal frequency distribution when occurrence (again measured as number of sites occupied) is plotted for a group of co-occurring species (e.g. Hanski 1982a,b; Brown 1984; Bock 1987; Gotelli & Simberloff 1987; Gaston & Lawton 1989). Many ecological patterns that are expressed over space are also observed over time (e.g. Blackburn *et al.* 1998) and this might also be true for abundance–distribution relationships. In this case, is the species frequency distribution bimodal and do abundant species occur frequently and less abundant species (or rare species) occur infrequently over time as well as over space? If so, such observations could lead to a better understanding both of the relationship between abundance and distribution and of the causes of commonness and rarity.

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Several abundance-distribution models provide different, but not mutually exclusive, explanations for these empirical patterns. For example, the niche-based model (Brown 1984) proposes that both local abundance within sites and the extent of spatial distribution between sites reflect the extent to which local environments meet the ecological requirements of a species. In addition to a positive relationship between local distribution and abundance, this model predicts that at most spatial scales there will be a unimodal species frequency distribution in which most species (the rare ones) have restricted distributions, while a few (common) species are widely distributed. This model also predicts that similar patterns of abundance and distribution will be observed over time, such that abundant species are more consistently present than rare ones. Metapopulation models (Hanski 1982a), on the other hand, assume that patterns of distribution and abundance reflect stochastic processes of local colonization and extinction. Like the niche-based model, these metapopulation models predict a positive relationship between distribution and abundance. Further, the stochastic nature of colonization and extinction processes predicts that even in a constant environment, the distribution and abundance of a species will fluctuate randomly over time, i.e. core species may become satellites, and vice versa.

There has been much debate over the empirical applications of these models, particularly with respect to the assumptions of each and the spatial scales over which they may operate (Levin 1976; Collins & Glenn 1991, 1997; Wright 1991; Scheiner & Rey-Benayas 1997). In addition, sampling and other aspects of data collection and analysis can influence the apparent patterns of distribution and abundance, and thus affect interpretations of the applicability of the models (Williams 1950; McIntosh 1962; Hanski *et al.* 1993). Finally, although the relative ability of species occurring in new locations is likely to have a strong influence on colonization and extinction probabilities, and therefore the scale at which they in turn affect abundance and distribution, this has rarely been examined empirically or theoretically (but see Hanski *et al.* 1993; Rees 1995).

Both because annual plants have generally similar ecologies and life histories (Gaston & Lawton 1990) and because their abundance and distribution can be measured accurately in small quadrats, they are an ideal system for empirical study. Here, we analyse 15 years of data for both summer annuals (1981–95) and winter annuals (1982–96) collected from a large number of permanent quadrats at a long-term experimental site in the northern Chihuahuan Desert. The study site receives a distinctly bimodal distribution of annual precipitation and supports diverse communities of both winter and summer annuals (> 30 species in each). On one

hand, these communities are distinct: there is essentially no overlap in species composition and no temporal overlap in vegetative life cycles. Winter annuals tend to have a longer period of vegetative growth and to have larger seeds which are subject to selective seed predation (Davidson *et al.* 1985). On the other hand, the two communities are similar in many respects: they occur together in the same macroenvironment, coexist in the soil seed bank, and are potentially exposed to similar biotic and abiotic conditions (Guo & Brown 1997).

The availability of significant quantities of both spatial and temporal data provides an ideal opportunity to compare abundance-distribution relationships for the same set of species over both these scales. We (i) analyse the relationship between abundance and spatial distribution at two spatial scales within a single season (summer 1990 and winter 1992), (ii) examine the relationship between abundance and distribution over time using 15 years of data, and (iii) both analyse the combined patterns of abundance and distribution over space and the pattern of distribution over time to assess whether abundant species are more widely distributed in both space and time than rare ones.

Methods

The field data were collected from a 20-ha, long-term experimental study site established in 1977 near Portal, Arizona (Brown & Munger 1985). At a coarse scale, the alluvial soil is a fairly homogeneous mixture of small boulders mixed with and overlaid by finer particles, but there is considerable small-scale heterogeneity related to microtopography, soil structure, shrub cover, animal disturbance, and other factors (Guo 1994). The vegetation is primarily upper elevation Chihuahuan Desert scrub, consisting of scattered shrubs (common genera include *Acacia*, *Ephedra*, *Flourensia* and *Prosopis*), half-shrubs (including *Gutierrezia sarothrae* (Pursh) Britt. & Rusby, *Haplopappus tenuisectus* (Greene) Blake and *Zinnia* spp.) and perennial grasses (including *Eragrostis* spp., *Aristida* spp. and *Muhlenbergia porteri* Scribn.). Livestock have been excluded from the site since 1977.

The study site contains 24 plots, each 0.25 ha in area. Within each plot are 16 permanent, regularly spaced quadrats each 0.25 m² in area (Fig. 1). The bimodal distribution of precipitation (maxima in January and July) led us to census annual species and perennials twice each year, during April–May and August–September, beginning in 1981. Each census was conducted during a 1 to 3-week period of peak flowering and maximum biomass (for details, see Davidson *et al.* 1985). The 24 experimental plots have been subjected to replicated experimental manipulations that involved primarily removal of some or all species of rodents or ants

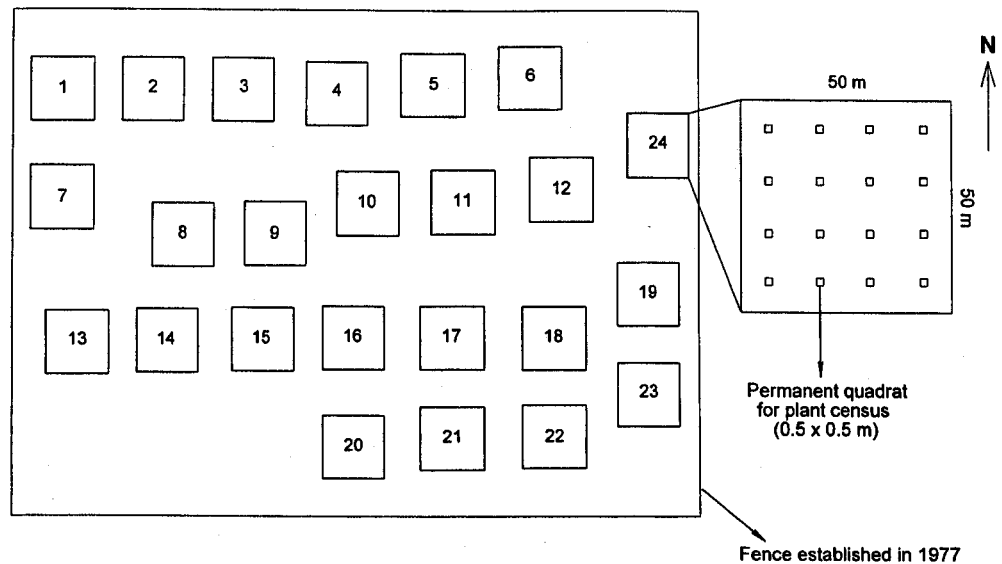


Fig. 1 Layout of experimental site. Plots 11 and 14 have been used as controls since 1977, plots 2 and 24 as controls since 1988, and all other plots have been subjected to experimental manipulation of herbivory.

(see Brown & Munger 1985; Heske *et al.* 1993). Effects of these treatments on the abundance and species composition of the annuals were sometimes substantial (see Brown *et al.* 1986; Samson *et al.* 1992). Although the effects of experimental treatments are not the focus of this paper, abundance-distribution relationships could be confounded with the effects of seed predators and we therefore used only data from control plots, to which all kinds of seed-eating animals have equal access, when conducting spatial analyses at the quadrat level. The number of such control plots changed over the course of the study from two (1977–87) to four (1988–present). We used data only from the two long-term control plots (32 quadrats in plots 11 and 14, Fig. 1) in the temporal analyses. For spatial analyses we used only data from all four control plots (adding plots 2 and 22 to give 64 quadrats); we chose two censuses in which both species richness and plant abundance were high: summer 1990 and winter 1992. Data from other years gave similar results, although there were, of course, differences in the total and relative abundances of species.

When characterizing relationships between distribution and abundance of species within a community, two methods are commonly employed (C.B. Williams 1950, 1964; M.R. Williams 1996). Most typically, abundance is characterized by the mean density of a species using only sites on which the species is present. Less commonly, workers calculate the mean density of species using all sites, and therefore include values of zero in the calculation of average or total abundance. We used both methods in this study and the results were compared. We used

data from 32 or 64 quadrats on control plots (see above) for the quadrat-scale analyses and from 384 quadrats on 24 plots for the plot-scale analyses.

We defined temporal distribution as the number of years that a species was present and used the total abundance of a species over the entire duration of the study (but only from control plots) as our measure of abundance. Then we examined the 3-dimensional space-time relationships by plotting the total abundance of each species as a function of both the number of years in which it occurred and the mean number of quadrats in which it occurred over the entire 15-year period.

To gain sufficient power to test and compare the bimodality of species frequency distribution over space at different scales (plot and quadrat) required the use of all 24 plots and 384 quadrats, including those subjected to different experimental treatments. We conducted these analyses knowing that winter annuals responded strongly to experimental treatments whereas summer annuals exhibited minor effects (Brown *et al.* 1986; Samson *et al.* 1992; Guo & Brown 1996). There is no standard statistical test for bimodality. We chose the method proposed by Tokeshi (1992), which has recently been used by Collins & Glenn (1997):

$$P_c = \sum_{i=n_l}^{N-n_r} \sum_{j=n_r}^{N-i} \frac{N! h^{i+j} (1-2h)^{N-i-j}}{i! j! (N-i-j)!} \quad \text{eqn 1}$$

where P_c is the probability under the null hypotheses of the presence of as large or larger numbers of species in the two observed extreme classes, N is the total number of species, i and j are the number of species in the left-most (n_l) and right-most (n_r) fre-

quency classes in the frequency diagram, respectively, and h is the frequency interval. Under the same null hypothesis, the probability of the observed frequency for the left- or right-most class can be calculated separately:

$$P_h = \sum_{i=n_h}^N \binom{N}{i} h^i (1-h)^{N-i} \quad \text{eqn 2}$$

where P_h is the probability of observing n_h or more species in a given frequency class of length h under the null hypotheses of a uniform distribution over frequency classes. If the P value is below 0.05 only for one side, the distribution is unimodal (Collins & Glenn 1997). For the analyses of temporal patterns, the two left- or right-most classes (whichever had the larger number of species) were used to perform the bimodality tests. Although in any description of frequency distributions the choice of a particular value for h could well change the exact frequency distribution of species, this is unlikely to change the general observed pattern unless extreme values for h are selected (e.g. $h=1$ or 2). Additional details about this test can be found in Tokeshi (1992) and Collins & Glenn (1997).

Results

SPATIAL RELATIONSHIPS

Winter and summer annual communities exhibited very similar relationships between abundance and distribution. At both spatial scales (plot and quadrat), we found a highly significant positive relationship between abundance and distribution in both summer 1990 and winter 1992. Log transformed abundances were related approximately linearly to number of plots and quadrats where the species occurred (Fig. 2). Using all sites (including those with zero individuals) to estimate mean density produced tighter relationships (at plot level – summer 1990: $r^2=0.81$, $P < 0.01$; winter 1992: $r^2=0.70$, $P < 0.005$; at quadrat level – summer 1990: $r^2=0.86$, $P < 0.01$; winter 1992: $r^2=0.85$, $P < 0.01$; cf. Fig. 2).

To examine the effects of spatial scale on the distribution of species across sampling units, we examined the frequency distribution of species across both quadrats and plots. All the distributions were significantly different from uniform ($P < 0.01$; using methods of Tokeshi 1992). At the plot scale, for

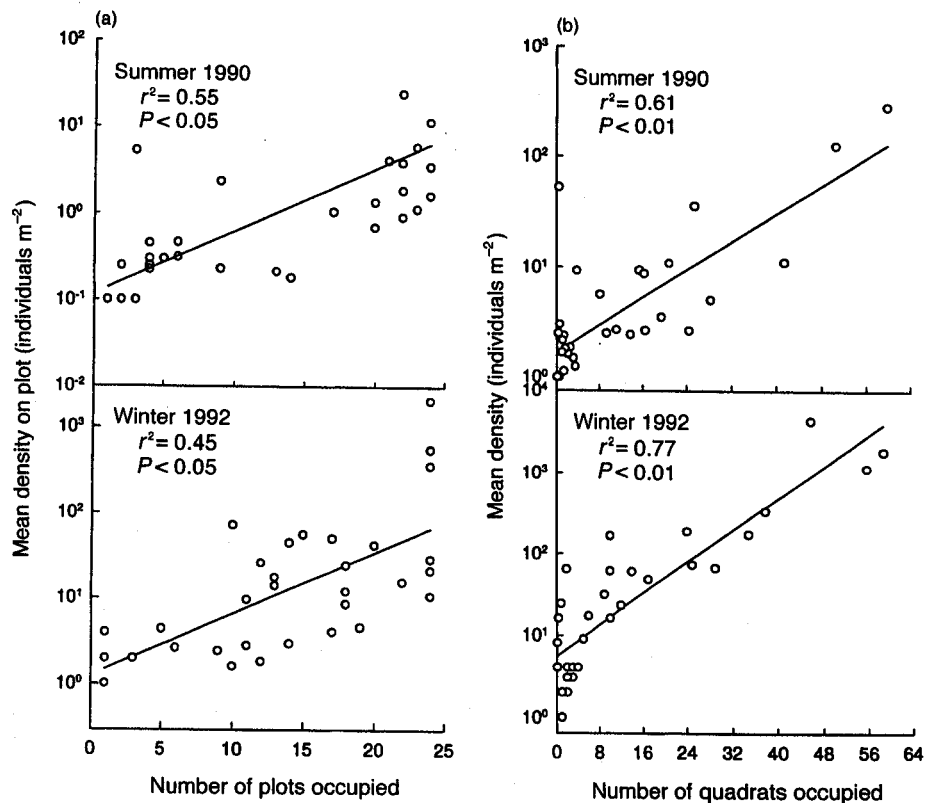


Fig. 2 Relationships between abundance and distribution (number of sites occupied) measured on two spatial scales, (a) 24 plots and (b) 64 quadrats from four control plots, for data from summer 1990 and winter 1992. Mean density values shown were calculated using data only from occupied sites. Each point represents one species.

both summer 1990 and winter 1992, the pattern was significantly bimodal with most species occurring either in very few plots or on most plots. When quadrats were the sampling units, however, patterns for both communities were significantly unimodal with most species having a very limited distribution (Fig. 3).

TEMPORAL RELATIONSHIPS

Both winter and summer annual plants exhibited a positive relationship between abundance and distribution over time (Fig. 4). Frequency distributions of species occurrence over years were significantly different from random or uniform ($P < 0.05$) for both winter and summer annuals; the patterns differed however between winter and summer annuals (Fig. 5). The winter community exhibited a bimodal distribution (the left-most class was marginally significant): most species were either present in 5 or fewer years or they occurred in more than 12 of the 15 years. Summer plants showed a unimodal, right-skewed distribution so that the majority of species occurred in a few years and only a very few species were present nearly every year (Fig. 5).

SPACE-TIME RELATIONSHIPS

In both winter and summer communities, when abundance was analysed as a function of both space and time, we found highly significant positive relationships (Table 1, Fig. 4). Those species that had the highest overall abundance were more widely distributed over sample sites on the study area and were also present in more years during the 15-year duration of the study. Rare species, by contrast, were highly restricted in their distributions in both space and time; they were present in only a small number of sample quadrats and in only a few of the 15 years.

Discussion

Our results indicate that abundance-distribution patterns are scale-dependent, both in space and over time. Several other studies also suggest that the spatial scale of sampling can often affect strongly the resulting patterns (Goodall 1952; McIntosh 1962; Brown 1984; Gotelli & Simberloff 1987; Gaston & Lawton 1989; Collins & Glenn 1991; Nee *et al.* 1991; Brown *et al.* 1995; Scheiner & Rey-Benayas

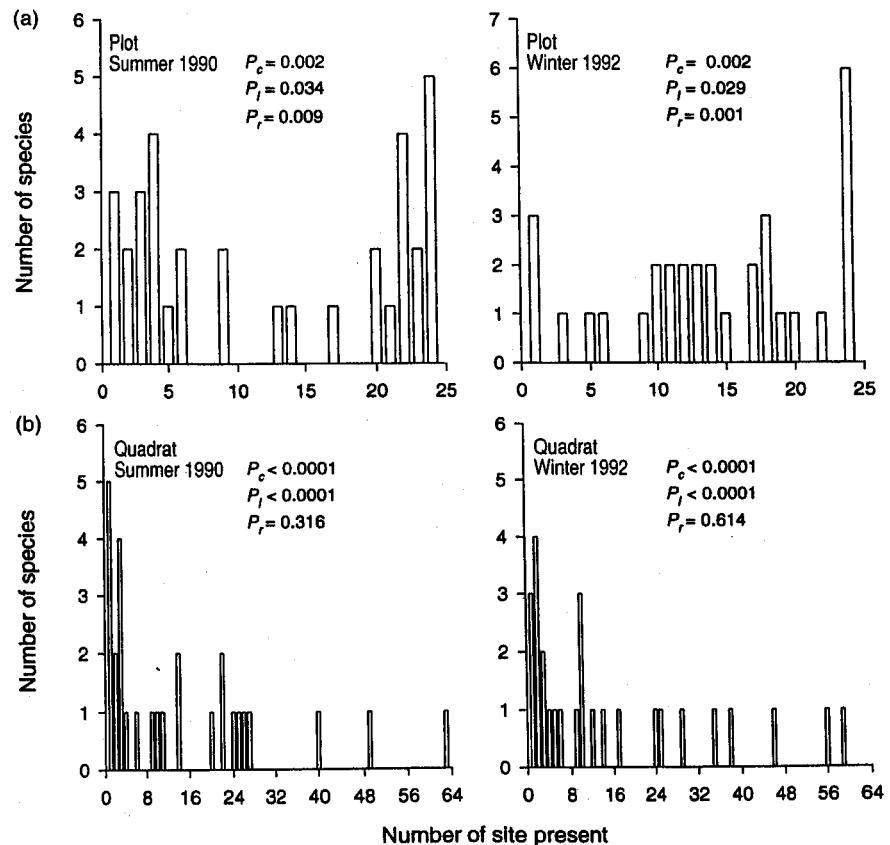


Fig. 3 Number of species vs. number of sites occupied on two spatial scales, (a) all 24 plots and (b) 64 quadrats on the four control plots, for both summer 1990 and winter 1992 annual plant communities. Bimodality tests are based on Tokeshi (1992).

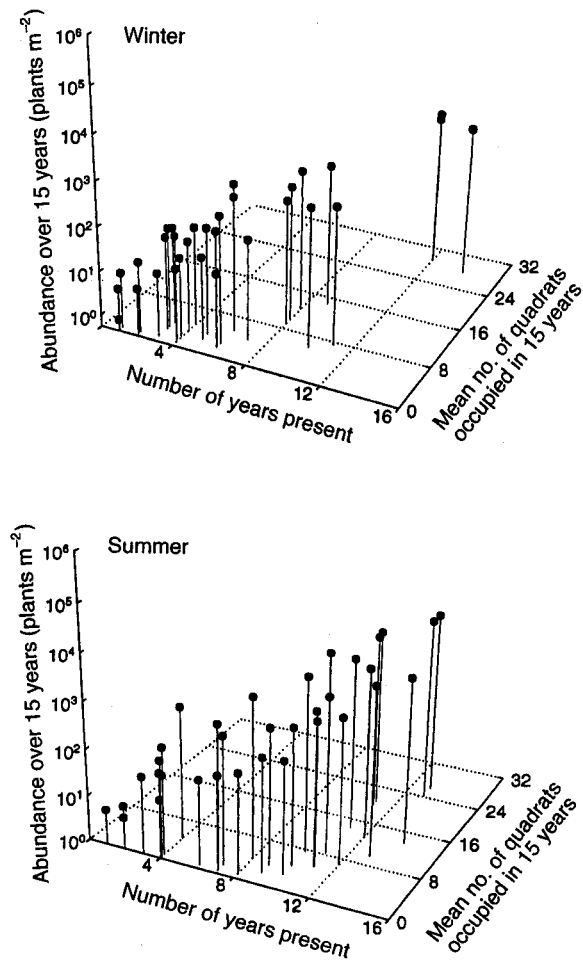


Fig. 4 Three-dimensional graph showing the relationships between spatial distribution (number of quadrats occupied), number of years present and overall abundance for data from 1977 to 1995 for winter and summer annual communities. Data were from the two long-term control plots only. Each point represents one species. See Table 1 for the results of statistical analyses.

1997). Our spatial analyses conducted within single years revealed that the species in both communities exhibited: (i) positive relationships between distribution and abundance at both plot and quadrat scales,

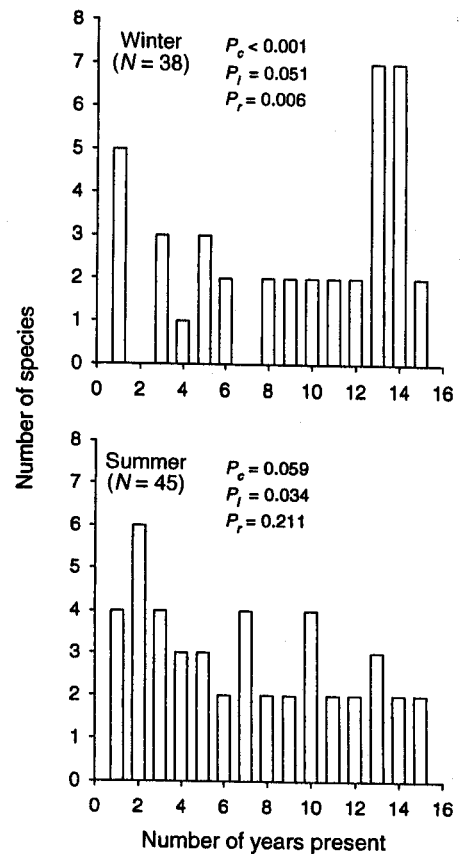


Fig. 5 Number of species vs. the number of the years the species was present for winter and summer annual communities. Only the data from the two long-term control plots were used. Bimodality tests are based on Tokeshi (1992). Note that because of the nature of the species frequency distribution in these two graphs bimodality was tested using the first two and last two frequency classes so as to include the highest values.

but (ii) different-shaped frequency distributions of species across sample units at the different scales: bimodal at the scale of 0.25-ha plots, but unimodal at the scale of 0.25-m² quadrats.

It is possible that the experimental removal of seed-eating animals contributed to the patterns of

Table 1 Regression coefficients for the relationships between abundance and distribution over space (number of quadrats occupied) and time (number of years present) for both winter (above diagonal) and summer annuals (below diagonal). All data were log-transformed prior to analyses

	Regression coefficients (r)		
	Total abundance over 15 years	Number of years present	Quadrats occupied (%)
	Winter		
Total abundance over 15 years	–	0.91**	0.98***
Number of years present	0.84**	–	0.92**
Quadrats occupied (%)	0.98***	0.92**	–
	Summer		

* $0.01 < P < 0.05$, ** $0.001 \leq P \leq 0.01$, *** $P < 0.001$

variation observed at the plot level. It is unlikely, however, that these treatments account for the high degree of bimodality (Fig. 3). The bimodality was at least as pronounced in the summer annuals, where effects of granivores and experimental treatments on abundance and species composition are very small, as in the winter annuals, where experimental manipulation of granivores has a large effect (Samson *et al.* 1992; Guo & Brown 1996). To examine further the potential effects of experimental treatments, we conducted a quadrat-scale analysis on all 384 quadrats across the 24 plots with very similar results (not shown) to those using only the 64 quadrats on the four control plots shown in Fig. 3 (bottom). The treatments can therefore be assumed to have had little effect on the general patterns that we observed. It is also possible that the significance values of the abundance-distribution relationships are inflated by the phylogenetic non-independence of data points (e.g. Harvey & Pagel 1993). For both winter and summer annual communities, we included in the analyses only those species for which we have seed size data and few of these are from the same family or genus. Therefore, such phylogenetic effects, if any, would be minimal and should not affect our general conclusions. Similarly, the fact that all species were living in a common environment may, to a certain extent, impose some interdependency among species due to species interactions. However, we do not believe that such effects are significant enough to alter our main conclusions and such non-interdependency is inherent in studies of distribution and abundance patterns.

Our results support the theoretical predictions of C. B. Williams (1950, 1964) that the frequency distribution of species is determined by both the size of sampling units and the number of samples taken. As the size of sampling unit decreases and as the number of samples increases, one is more likely to observe a unimodal distribution. For one thing, when samples are small (i.e. contain relatively few individuals), stochastic processes become increasingly important in influencing which species are present. In addition, when there are many samples covering a very large area (i.e. a large proportion of the geographical range of the species), the distribution is likely to be unimodal (see Bock & Ricklefs 1983). It is at an intermediate scale, when sampling units are relatively large, few in number and representative of similar habitat types within a small region, that one is most likely to observe a bimodal distribution. There will then be two main categories of species: core species that are able to occur in all or nearly all sample units, and satellite species whose presence or absence depends on subtle differences among the sample units.

To illustrate the effects of sample size (number of quadrats), we plotted species frequency against number of quadrats occupied for each control plot

separately (see Fig. 6 for plot 14). Note that even though the sample unit (quadrat) is the same, the degree of bimodality as indicated by the Tokeshi statistics appears to be higher for 16 quadrats within one plot than for 64 quadrats in four plots (compare Fig. 6 with Fig. 3). The patterns were even less bimodal and were in fact clearly unimodal when data from all 384 quadrats in all 24 plots were analysed (not shown). We suspect therefore that the bimodal pattern seen at the scale of the 24 plots (Fig. 3) reflects, at least in part, the modest number of samples at the plot scale. It is, however, probably more important that the data for each plot actually represents only a small subsample of the total area within the plot (the value for a plot represents the combined samples from the 16 0.25-m² quadrats, i.e. an area of 4 m², or 0.16% of the total area of a plot). Almost certainly, these samples at the plot scale are incomplete, missing many of the rare species whose inclusion would make the distributions much more unimodal. This underscores the importance of sam-

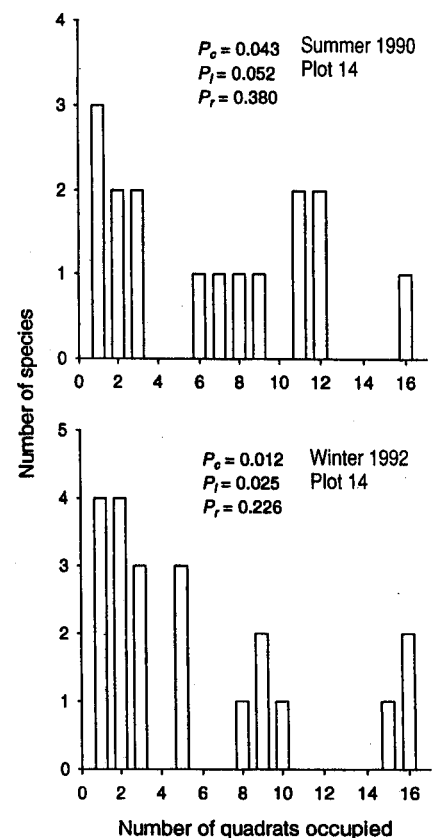


Fig. 6 Number of species vs. the number of quadrats the species occupied for summer 1990 and winter 1992 annual species observed on a single control (i.e. plot 14). The bimodalities of these patterns were different from those in Fig. 3 which were generated from the data on the 24 plots and 64 quadrats on the four control plots. Bimodality tests are based on Tokeshi (1992).

pling methodology and the necessity of distinguishing between complete samples and subsamples in analysing abundance-distribution relationships at different scales.

Similarly, our data suggest that temporal patterns of distribution and abundance relationships will depend on the duration of the study relative to the longevity of the organisms studied (Collins & Glenn 1997). Studies of short duration relative to the longevity of the organisms will tend to observe bimodal core-satellite patterns, because it is more likely that a common set of species (core species) will be present throughout the study (e.g. Holbrook & Schmitt 1996). Studies of longer duration relative to the longevity of the organisms will be less likely to find a common set of species continuously present, and thus are increasingly likely to observe a unimodal frequency distribution (cf. Jablonski 1987; Gaston & Lawton 1989; Brown *et al.* 1995). Furthermore, the time scale over which these different patterns will emerge will depend on the rate of change in community structure. In our 15-year study, the winter annual community exhibited a bimodal frequency distribution over time, while the summer community exhibited a unimodal pattern (Fig. 5). This difference is probably a result of the dramatically different temporal consistencies in rank abundance of species within the two communities (Q. Guo, J.H. Brown & T.J. Valone, unpublished data). The relative abundances of species in the winter community changed very slowly over time, yielding a set of consistently common core species over the duration of the study. In contrast, the rank abundances of species in the summer community shifted rapidly over time, yielding few consistently common species. We can illustrate the effect of time scale by analysing the same data over shorter durations. In Fig. 7, we plot the frequency distributions for summer annual species over two nonoverlapping periods of 8 and 7 years, respectively. These frequency distributions are much more bimodal: nearly bimodal for 1981-88, and significantly bimodal for 1989-95 (compare Fig. 7 with Fig. 5). Thus, these relatively short-term patterns differ from those based on longer-term observations. A relevant statistical point is that temporal and spatial autocorrelations, due to both extrinsic environmental variation and intrinsic biological processes, tend to result in samples being more independent – and therefore more different – when separated by longer times or greater distances (Brown *et al.* 1995).

Hanski (1982a) proposed that core and satellite species should change roles over time. Although this prediction is difficult to address statistically, our data provide some support. While many species were consistently rare, and others remained relatively common, many species varied greatly in abundance over the course of the study. In the winter community, *Haplopappus gracilis* (Nutt.) Gray and

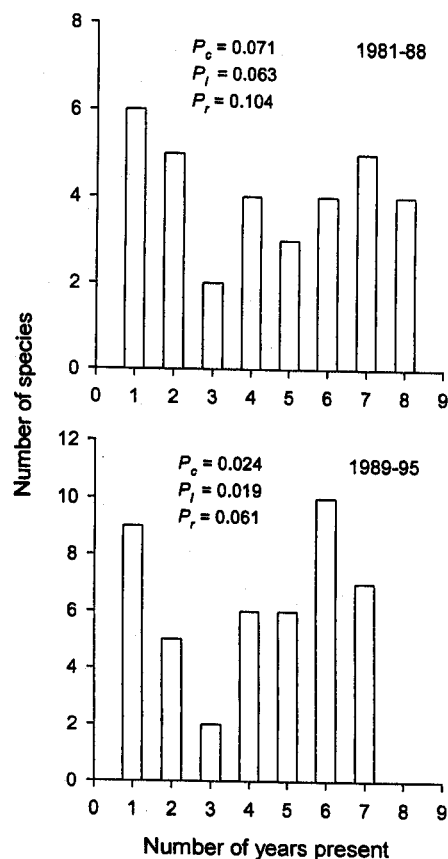


Fig. 7 Number of species vs. the number of years the species was present for summer annual species observed over two relatively short time periods, 1981-88 and 1989-95. These patterns are different from those in Fig. 5 which were generated from 15 years of data. Only the data from the two control plots were used. Bimodality tests are based on Tokeshi (1992). Similar to Fig. 5, the bimodality was tested on the highest values in the first and last two frequency classes.

Vulpia octoflora (Walt.) Rydb. were consistently rare early in the study but became common in later years, while *Erodium cicutarium* (L.) L'Her. and *Cryptantha micrantha* (Torr.) Johnst fluctuated widely in abundance. Among the summer annuals, many species exhibited great year-to-year variation in abundance (Q. Guo, J.H. Brown & T.J. Valone, unpublished results). Such shifts could be due, at least in part, to the stochastic colonization and extinction events hypothesized by Hanski. They could, however, also result from environmental changes, especially in the case of such desert annuals. It is likely that the wide fluctuation in abundance was due primarily to differential germination from the seed bank and differential survival from seedling to adult, rather than to local colonization and extinction. Although we can offer no ready explanation for many of the fluctuations in abundance, the more consistent shifts in abundance of

species such as *H. gracilis* and *V. octoflora* may be a consequence of a climatic change that has occurred in the south-west over the past two decades (Brown *et al.* 1997). Continued monitoring is required to understand more fully how long-term climate change, short-term environmental variation, and stochastic factors influence changes in abundance over time.

In much of the literature concerning distribution and abundance there have been several attempts to distinguish between the alternative hypotheses for the generation of a positive relationship. Workers often propose that hypotheses of niche-based differences in environmental tolerance and resource requirements and metapopulation colonization-extinction dynamics are conflicting or mutually exclusive. The empirical patterns exhibited by desert annuals suggest, however, that several mechanisms are likely to operate simultaneously and may be complementary (Burgman 1989; Gaston *et al.* 1997). Differences among species in environmental tolerances and requirements largely determine the places in the environment that can be inhabited and the length of time that the species can occur there (Guo & Brown 1997). In order to be present in favourable places during favourable periods, species must have some combination of capacity to colonize them during favourable periods and to persist in them (in this case to persist in the seed bank) during unfavourable periods. Of course, all of these characteristics of species (e.g. environmental tolerances, resource requirements, dispersal ability and seed diapause strategy) affect fitness and are subject to evolution by natural selection. Because they affect each other in ways that affect survival and reproduction, abundance and distribution we expect them to co-evolve in complex and interesting ways.

Instead of a biased view that would favour one of several alternative hypotheses, what appears to be emerging is a very general phenomenology of abundance, distribution, and related ecological and evolutionary attributes of species. Our study of desert annuals suggests that the positive relationship between abundance and distribution holds not only for distribution over space but also for distribution over time (Table 1, Fig. 4). E. Hadly and B. Maurer (personal communication) have observed a similar relationship, but at much larger scales of both space and time (see also Blackburn *et al.* 1998; Gaston *et al.* 1998). They found that the abundance of mammal species was positively correlated with their geographical distributions among isolated mountain ranges in western North America and with their temporal distributions among stratigraphic sequences of fossils that span several thousand years. While caution should be exercised in generalizing on the basis of only two studies, abundance-distribution relationships may represent another case where similar phenomena occur in both space

and time. The scaling behaviours, temporal and spatial relationships, and other features of these phenomena are becoming increasingly well documented empirically. A general theory of evolutionary ecology to place these empirical patterns in a synthetic conceptual framework is, however, still largely missing.

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References

- Blackburn, T.M., Gaston, K.J., Greenwood, J.J.D. & Gregory, R.D. (1998) The anatomy of the interspecific abundance-range size relationship for the British avifauna. II. Temporal dynamics. *Ecology Letters*, **1**, 46–55.
- Bock, C.E. (1987) Distribution-abundance relationships of some Arizona landbirds: a matter of scale. *Ecology*, **68**, 124–129.
- Bock, C.E. & Ricklefs, R.E. (1983) Range size and local abundance of some North American songbirds: a positive correlation. *American Naturalist*, **122**, 295–299.
- Brown, J.H. (1984) On the relationship between abundance and distribution of species. *American Naturalist*, **124**, 255–279.
- Brown, J.H., Mehlman, D.W. & Stevens, G.C. (1995) Spatial variation in abundance. *Ecology*, **76**, 2028–2043.
- Brown, J.H. & Munger, J.C. (1985) Experimental manipulation of a desert rodent community: food addition and species removal. *Ecology*, **66**, 1545–1563.
- Brown, J.H., Davidson, D.W., Munger, J.C. & Inouye, R.S. (1986) Experimental community ecology: the desert granivore system. *Community Ecology* (eds J.M. Diamond & T.D. Case), pp. 41–61. Harper & Row, New York.
- Brown, J.H., Valone, T.J. & Curtain, C.G. (1997) Reorganization of an arid ecosystem in response to recent climate change. *Proceedings of the National Academy of Sciences of the USA*, **94**, 9729–9733.
- Burgman, M.A. (1989) The habitat volumes of scarce and ubiquitous plants: a test of the model of environmental control. *American Naturalist*, **133**, 228–239.
- Collins, S.T. & Glenn, S.M. (1990) A hierarchical analysis of species abundance patterns in grassland vegetation. *American Naturalist*, **135**, 633–648.
- Collins, S.T. & Glenn, S.M. (1991) Importance of spatial and temporal dynamics in species regional abundance and distribution. *Ecology*, **72**, 654–664.
- Collins, S.T. & Glenn, S.M. (1997) Effects of organismal and distance scaling on analysis of species distribution and abundance. *Ecological Applications*, **7**, 543–551.
- Davidson, D.W., Samson, D.A. & Inouye, R.S. (1985) Granivory in the Chihuahuan Desert: interactions

- within and between trophic levels. *Ecology*, **66**, 486–502.
- Gaston, K.J. (1996) The multiple forms of the interspecific abundance–distribution relationship. *Oikos*, **76**, 211–220.
- Gaston, K.J. & Lawton, J.H. (1989) Insect herbivores on bracken do not support the core-satellite hypothesis. *American Naturalist*, **134**, 761–777.
- Gaston, K.J. & Lawton, J.H. (1990) Effects of scale and habitat on the relationship between regional distribution and local abundance. *Oikos*, **58**, 329–335.
- Gaston, K.J., Blackburn, T.M. & Lawton, J.H. (1997) Interspecific abundance–range size relationships: an appraisal of mechanisms. *Journal of Animal Ecology*, **66**, 579–601.
- Gaston, K.J., Blackburn, T.M., Gregory, R.D. & Greenwood, J.J.D. (1998) The anatomy of the interspecific abundance–range size relationship for the British avifauna. I. spatial patterns. *Ecology Letters*, **1**, 38–46.
- Goodall, D.W. (1952) Quantitative aspects of plant distribution. *Biological Review*, **27**, 194–245.
- Gotelli, N.J. & Simberloff, D. (1987) The distribution and abundance of tallgrass prairie plants: a test of the core-satellite hypothesis. *American Naturalist*, **130**, 18–35.
- Guo, Q. (1994) *Dynamic desert plant community ecology: changes in space and time*. PhD Thesis, University of New Mexico, Albuquerque.
- Guo, Q. & Brown, J.H. (1996) Temporal fluctuations and experimental effects in desert plant communities. *Oecologia*, **107**, 568–577.
- Guo, Q. & Brown, J.H. (1997) Interactions between winter and summer annuals in the Chihuahuan desert. *Oecologia*, **111**, 123–128.
- Guo, Q., Brown, J.H., Valone, T.J. & Kachman, S.D. (2000) Constraints of seed size on plant abundance and distribution. *Ecology* (in press).
- Hanski, I. (1982a) Dynamics of regional distribution: the core and satellite species hypothesis. *Oikos*, **38**, 210–221.
- Hanski, I. (1982b) Distribution ecology of anthropochorous plants in villages surrounded by forest. *Annales Botanica Fennici*, **19**, 1–15.
- Hanski, I. & Gyllenberg, M. (1993) Two general metapopulation models and the core-satellite species hypothesis. *American Naturalist*, **142**, 17–41.
- Hanski, I. & Gyllenberg, M. (1997) Uniting two general patterns in the distribution of species. *Science*, **275**, 397–400.
- Hanski, I., Kouki, J. & Halkka, A. (1993) Three explanations for the positive relationship between distribution and abundance of species. *Species Diversity in Ecological Communities* (eds R.E. Ricklefs & D. Schluter), pp. 108–16. University of Chicago Press, Chicago, USA.
- Harvey, P.H. & Pagel, M.D. (1993) *The Comparative Method in Evolutionary Biology*. Oxford University Press, Oxford.
- Heske, E.J., Brown, J.H. & Guo, Q. (1993) The effects of kangaroo rat exclusion on vegetation structure and plant species diversity in the Chihuahuan Desert. *Oecologia*, **95**, 520–524.
- Holbrook, S.J. & Schmitt, R.J. (1996) On the structure and dynamics of temperate reef fish assemblages. *Long-term Studies of Vertebrate Communities* (eds M.L. Cody & J.A. Smallwood), pp. 19–48. Academic Press, San Diego, USA.
- Jablonski, D. (1987) Heritability at the species level: analysis of geographic ranges of Cretaceous molluscs. *Science*, **238**, 360–363.
- Levin, S.A. (1976) Population dynamic models in heterogeneous environment. *Annual Review of Ecology and Systematics*, **7**, 287–310.
- Maurer, B.A. (1990) The relationship between distribution and abundance in a patchy environment. *Oikos*, **58**, 181–189.
- McIntosh, R.P. (1962) Raunkiaer's 'law of frequency'. *Ecology*, **43**, 533–535.
- Nee, S., Gregory, R.D. & May, R.M. (1991) Core and satellite species: theory and artifacts. *Oikos*, **62**, 83–87.
- Rees, M. (1995) Community structure in sand dune annuals: is seed weight a key quantity? *Journal of Ecology*, **83**, 857–863.
- Samson, D.A., Philippi, T.E. & Davidson, D.W. (1992) Granivory and competition as determinants of annual plant diversity in the Chihuahuan Desert. *Oikos*, **65**, 61–80.
- Scheiner, S.M. & Rey-Benayas, J.M. (1997) Placing empirical limits on metapopulation models for terrestrial plants. *Evolutionary Ecology*, **11**, 275–288.
- Tokeshi, M. (1992) Dynamics of distribution in animal communities: theory and analysis. *Research in Population Ecology*, **34**, 249–273.
- Williams, C.B. (1950) The application of the logarithmic series to the frequency of occurrence of plant species in quadrats. *Journal of Ecology*, **38**, 107–138.
- Williams, C.B. (1964). *Patterns in the Balance of Nature*. Academic Press, New York.
- Williams, M.R. (1996) Species–area curves: the need to include zeroes. *Global Ecology and Biogeography Letters*, **5**, 91–93.
- Wright, D.H. (1991) Correlation between incidence and abundance are expected by chance. *Journal of Biogeography*, **18**, 463–466.

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