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Scott L. Collins; Susan M. Glenn

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EFFECTS OF ORGANISMAL AND DISTANCE SCALING ON ANALYSIS OF SPECIES DISTRIBUTION AND ABUNDANCE

SCOTT L. COLLINS^{1,2} AND SUSAN M. GLENN³

¹Ecological Studies Program, Room 635, National Science Foundation, Arlington, Virginia 22230 USA

²Department of Zoology, University of Maryland, College Park, Maryland 20742 USA

³Center for Applied Conservation Biology, Department of Forest Sciences, University of British Columbia, Vancouver, British Columbia, Canada V6T 1W5

Abstract. As communities and populations become increasingly fragmented, much theoretical and some empirical research has focused on the dynamics of metapopulations. Many metapopulation models describe dynamics among populations in a region, yet the scale of the “region” to which different models apply often is undefined. Because the spatial scale is undefined, testing predictions and assumptions of these models is problematic. Our goal is to present two scaling concepts relevant to these models, distance scaling and organismal scaling, and to apply these scaling notions to patterns of species distribution. To determine distance effects, we analyzed patterns of distribution of four taxonomic groups in tallgrass prairie (grasshoppers, small mammals, vascular plants, and breeding birds) at two spatial scales. To assess organismal effects, we held spatial scale constant and we compared patterns of distribution and abundance among these taxonomic groups.

Using long-term data from Konza Prairie, Kansas, there were significant differences in the pattern of distribution of grasshoppers, small mammals, vascular plants, and breeding birds within a single spatial scale. The number of core species (species occupying >90% of the sites in a region) of plants and birds was less than the number of satellite species (those occupying <10% of the sites in a region). The opposite was true for grasshoppers and small mammals. All four distribution patterns were significantly non-random, but only grasshoppers and small mammals were significantly bimodal at this scale. Plants and birds were unimodal. The patterns of distribution within these taxonomic groups at two spatial scales were significantly different as well. In all cases, the percentage of species in the core group declined, and the percentage of species in the satellite group increased as spatial scale increased. These results demonstrate the difficulty of testing theoretical models with only one taxonomic group at a single spatial scale. One should not accept or reject a model until the spatial domains of organismal and distance scaling have been properly evaluated.

Key words: breeding birds; core-satellite hypothesis; core species vs. satellite species numbers; grasshoppers; Konza Prairie Research Natural Area (Kansas, USA); organismal scaling *cf.* distance scaling; small mammals; species distribution and abundance; tallgrass prairie species; vascular plants.

INTRODUCTION

Fragmentation and isolation of communities have led to theoretical and empirical studies of the dynamics of metapopulations in complex landscapes. In its purest form, a metapopulation describes a collection of geographically isolated populations that are linked by dispersal of new colonists (Hanski and Gilpin 1991, Harrison 1991, Opdam 1991). Although most empirical and theoretical studies of metapopulation dynamics focus on fragmented populations, the assumptions and predictions of metapopulation theory also apply to patches in continuous habitat (De Roos et al. 1991, Hanski 1991, Hanski 1994), just as the theory of island biogeography, developed to explain patterns of species richness on oceanic islands, has been adapted to habitat islands (Brown 1978, Armesto and Contreras 1981,

Reibesell 1982), succession (Gibson and Brown 1991), and vegetation dynamics in continuous habitat (Glenn and Collins 1992). Indeed, populations may be patchily distributed even within continuous habitat (Maurer 1994).

Metapopulation models differ in their fundamental assumptions regarding population size, environmental heterogeneity, and dispersal functions (e.g., Levins 1969, Hanski 1982a, 1991, Isawa and Roughgarden 1986, Maurer 1990, Hastings 1991, Tokeshi 1992). One fundamental assumption of most regional models is that a positive correlation exists between the average abundance of a species in a region and the number of sites occupied by that species (Hengeveld and Haack 1982, Hanski 1982a, 1991, Brown 1984, Kolasa 1989). That is, within a given region, widely distributed species will have higher average abundances than species with limited distributions. There is considerable em-

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pirical support for this notion (Hengeveld and Haack 1982, Bock and Ricklefs 1983, Brown 1984, Bock 1987, Collins and Glenn 1990), although this relationship may not be universal (Wright 1991).

A more elusive characteristic of metapopulation models is that they reflect "regional" dynamics of metapopulations, yet the region is spatially undefined in most models (but see Gaston and Lawton 1990, Maurer 1990). Perhaps regional scaling is rarely explicit in metapopulation models in an effort to increase the generality of a given model. However, scaling is likely to vary spatially and temporally, and among taxa. Indeed, analyses at different spatial or temporal scales, or among different organisms, could yield evidence in support of, or counter to, a given metapopulation model (Gaston and Lawton 1990). Thus, the general purpose of our study was to test how two scaling principles, distance scaling and organismal scaling, affect interpretation of empirical evidence used to test model predictions.

In general, we focus on distribution patterns predicted by the core-satellite species model (Hanski 1982a, 1991), although the general implications of these scaling issues apply to empirical tests of any metapopulation model. Unlike most metapopulation models, the core-satellite hypothesis (Hanski 1982a, 1991) has generated controversy because it predicts the occurrence of at least two modes in the pattern of species occurrences among sites in a region. That is, a region will contain very common "core" species that occupy >90% of the habitat patches, and uncommon "satellite" species that occur at $\leq 10\%$ of habitat patches. Despite the controversy surrounding the cause, measurement, and interpretation of bimodality (Gotelli and Simberloff 1987, Nee et al. 1991), there is empirical evidence in support of bimodality from a variety of taxa, such as vascular plants (Hanski 1982b, Collins and Glenn 1990, 1991, Eriksson et al. 1995), bryophytes (Soderstrom 1989), bumblebees (Hanski 1982c), butterflies (Pollard et al. 1986), and intestinal helminths and cynipine gall wasps (Hanski and Gyllenberg 1993). It is unclear, however, how much these patterns are a function of distance or organismal scaling.

Distance and organismal scaling principles: testing the models

Any regional metapopulation model may be scaled along at least two axes, distance and organisms. Distance scaling is simply measured as the aerial extent of the region in question. Given that heterogeneity increases as distance between two habitat patches increases, we predict that as the extent of the area sampled increases, patterns of species regional distribution will shift in such a way that the number of regionally rare species increases and the number of regionally abundant species decreases (Fig. 1: top; Brown 1984, Hanski and Gyllenberg 1993). If dispersal is required

for a species to colonize distant patches, then only species with high dispersal ability and broad ecological tolerances can occur over large geographic areas. To test the effects of distance scaling on the pattern of species distribution among sites, we held taxa constant and varied the size of the area sampled. We used four taxon sets for this analysis: grasshoppers, birds, small mammals, and vascular plants.

Organismal scaling is more hypothetical because organisms may differ in a variety of factors including dispersal ability, mobility, territory size, behavior, body size, etc. It is possible to use incidence functions (Diamond 1975) to assess the effects of differences in relative dispersal ability on patterns of species distribution in a region (Hanski 1992). In this case, mean dispersal ability of a given set of taxa can be mapped onto the incidence function to predict the proportion of sites occupied by poor, intermediate, and good dispersers (Hanski and Gyllenberg 1993). Species with poor dispersal ability will occur at only a few sites in a region. Species with intermediate dispersal ability have intermediate regional distributions, and species with good dispersal ability will be found at most sites (Fig. 1: bottom). The role of organismal scaling can be tested by holding aerial extent constant and assessing the distribution and abundance of different sets of taxa.

To determine the effects of organismal scaling on patterns of distribution and abundance, within a single spatial scale, we again analyzed four sets of taxa: grasshoppers, birds, small mammals, and vascular plants. Our implicit assumption is that these taxon groups differed, in general, in dispersal ability. Using the same logic as Harrison et al. (1992) we assumed that animals that can fly have greater dispersal ability than non-flying animals. Secondly, we assumed that animals have greater dispersal ability than plants. This yielded a dispersal ranking of birds > grasshoppers > small mammals > plants. We placed grasshoppers as better dispersers than small mammals because small mammals have home ranges during the breeding season when our data were collected, whereas many grasshoppers are free-ranging (Evans 1984). Specifically, we tested the hypothesis that the proportion of regionally abundant and regionally rare species differed among taxa following the rank order of dispersal ability.

METHODS

Study site

The study was conducted at Konza Prairie Research Natural Area, northeastern Kansas, USA. Konza Prairie is a 36-km² area of native tallgrass prairie vegetation that has been divided into a series of replicated management units, located approximately along watershed boundaries. Management units, which range in size from 12 to 20 ha, are subjected to burning regimes of 1-, 2-, 4-, 10- and 20-yr intervals (Hulbert 1985). For

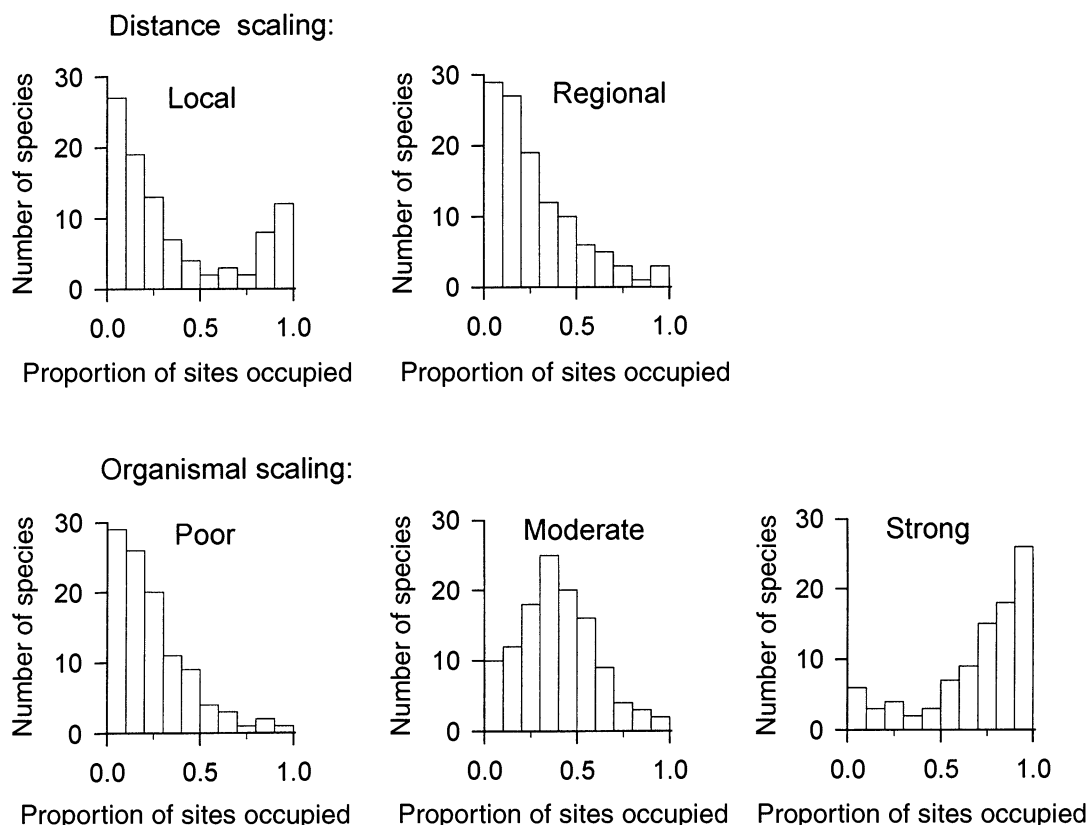


FIG. 1. Hypothesized effects of distance and organismal scaling on patterns of regional distribution of species. *Distance scaling*: when analyzing a single taxon set at different spatial scales, a mode of species is likely in the core group (>90% of sites) at local scales; however, as scale increases, environmental heterogeneity and increased fragmentation create a unimodal distribution of species. *Organismal scaling*: as relative dispersal ability increases among taxa, the likelihood of a distinct mode of core species increases when spatial scale is held constant. Studies of a single taxon set at one scale confound spatial and organismal scaling effects.

a number of management units burning treatments have been in effect since 1972, others were started in 1981. The area is essentially continuous grassland habitat along moderate topographic relief, with scattered gallery forest along the larger streams. Prairie vegetation is dominated by the grasses *Andropogon gerardii*, *A. scoparius*, *Panicum virgatum*, *Poa pratensis*, and *Sorghastrum nutans*. Common forbs include *Ambrosia psilostachya*, *Artemisia ludoviciana*, *Aster ericoides*, and *Solidago* spp. Gallery forests are dominated by *Quercus marilandica*. The surrounding region contains mostly unplowed prairie grazed by cattle.

Field methods

Birds.—Bird species were sampled while walking along ≈ 1 -km permanently located transects in 12 management units during June of each year from 1981 until 1990 (11 units in 1981). At 15–20 m intervals along each transect, all individuals seen or heard were counted during a 3–5 min sampling period. Abundance of each species is the total number of individuals counted along a transect. Wide-ranging species such as the Red-tailed hawk (*Buteo jamaicensis*) were not included in

the analyses because the entire region was potentially encompassed within the territory of a single pair. See Zimmerman (1992, 1993) for further details of the bird community dynamics at Konza Prairie.

Grasshoppers.—Grasshopper populations were sampled each year from 1982 to 1990 on 8–15 management units across Konza Prairie. Samples were taken by sweeping with standard 38-cm canvas nets during the midsummer of each year. In 1982, 200 sweeps (10 sets of 20 sweeps) were taken at each site; 400 sweeps were used in subsequent years (20 sets of 20 sweeps). Sweeps were taken along parallel 10-m transects. A sweep was taken at each step by traversing an arc of 180° with the net through the top layer of vegetation. After 20 sweeps, the contents of the net were emptied into a bag and returned to the laboratory for identification. Abundance of each species is the total number of individuals counted at each site. Further details of this sampling technique, its biases, and grasshopper community dynamics at Konza Prairie are given in Evans (1984, 1988).

Plants.—Plant species composition has been monitored at 19 sites in 12 management units across Konza

Prairie. Permanent vegetation plots were established in 1981, 1983, and 1984. Plots have been sampled in May, July, and September of each year from the time each site was established. Vegetation of each site is sampled in five permanently marked 10-m² circular quadrats located along each of four 50-m transects. Cover of each species was visually estimated using the Daubenmire cover scale: 1 = <1% cover (e.g., present), 2 = 2–5%, 3 = 6–25%, 4 = 26–50%, 5 = 51–75%, 6 = 76–95%, and 7 = >95%. Abundance of each species at each site was determined by converting the Daubenmire scale value to the midpoint of the cover range and averaging across the 20 quadrats at a site. See Collins and Glenn (1991) for further details of sampling and plant community dynamics on Konza Prairie.

Small mammals.—Small mammals were sampled from 1982 to 1990 along permanently located trap lines in 10–14 management units on Konza Prairie. Each trap line contained 20 stations; stations were located at 15-m intervals and consisted of two large Sherman live traps (7.6 × 8.9 × 22.9 cm). Traps were baited with peanut butter and oatmeal on four consecutive nights in spring and fall of each year. Captured animals were identified, toe-clipped, and released at the site of capture. Abundance is measured as the average of the spring and fall counts of total number of individuals of each species at each site. Further details of small-mammal community dynamics on Konza Prairie are given in Finke et al. 1986 and Kaufman et al. (1990).

Data analyses

Linear regression was used to determine if a positive relationship existed between number of sites occupied and average abundance (calculated for occupied sites only) in the region. Regressions were calculated for each taxonomic set for each year sampled. Patterns in the regional distribution of species were assessed by plotting the number of species occurring in 1, 2, 3, . . . , n sites for each taxon set for each year. In all cases where the number of sites sampled was ≥ 10 , distribution was expressed as proportion of sites occupied. This permits a uniform scaling of axes among taxa sampled at different numbers of sites. If the number of sites sampled was < 10 , the actual number of sites occupied was used because proportional scaling would bias distribution patterns by creating classes with no occurrences.

We focused our analyses on the core and satellite modes because they can be defined objectively, and these modes differentiate the predicted regional distribution patterns among metapopulation models (Hanski 1991). Core species were defined as those occupying $> 90\%$ and satellite species occupied $\leq 10\%$ of the sites sampled in a region. Most metapopulation models predict a unimodal distribution of species among sites, with the mode often occurring in the left-most frequency interval (e.g., Fig. 1: top: Regional), implying that most species are regionally rare. The core–satellite

model predicts bimodality, with modes in both the left-most and right-most frequency intervals. Thus, most species are either regionally rare or regionally common.

Because we were interested in organismal scaling, we wanted to determine if differences existed among taxa in the proportion of species in the core and satellite modes within a fixed region. To test for differences in organismal scaling, we calculated the average pattern (averaged over time) of distribution of each taxon group on Konza Prairie using only samples from years in which ≥ 10 sites were sampled. We then compared these average distribution patterns among all possible pairs of species using a Kolmogorov-Smirnov two-sample test (Siegel 1956). Statistical differences in frequency distributions would indicate different patterns of organismal scaling among taxa within a fixed spatial framework.

Although there are no statistical tests to determine bimodality, Tokeshi (1992) developed a method to determine the exact probability of obtaining an observed frequency value (P_c) for the left- and right-most classes under the null hypothesis of random occurrence of species in a region:

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

where N = the total number species, i and j are the number of species in the left-most (n_l) and right-most (n_r) frequency classes, respectively, and h is the frequency interval. In addition, the probability of obtaining the observed frequency for the left- or right-most class can be calculated separately under the same null hypothesis:

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

where P_h = the probability in h^{th} frequency class, and n_h = the number of species in the h^{th} frequency class. If $P < 0.05$ for the left- and right-most frequency classes, then the distribution is bimodal. If $P < 0.05$ for only one of these classes, the distribution is unimodal. These indices are designed to recognize modality patterns rather than as “foolproof” statistical test procedures (see Tokeshi 1992), yet these methods provide the first and only quantitative mechanisms to assess bimodality. These indices were applied to the average distribution patterns for each taxon set sampled at Konza Prairie.

RESULTS

For all taxa in all years, there was a highly significant and positive relationship between distribution and abundance (Table 1). For the animal data sets, no regression had an $r^2 < 0.49$, and the r^2 's for the more species-rich plant data set ranged from 0.40 to 0.50. Thus, our results supported the fundamental assumption of many metapopulation models that a positive

TABLE 1. Relationship between number of sites occupied and average abundance for each species group in each year based on linear regression. Average abundance was calculated based on the number of occupied sites rather than the total number of sites.

Species group	Year	No. species	No. sites	r^2	P
Grasshoppers	1982	15	12	0.49	0.001
	1983	21	12	0.52	0.0002
	1984	21	15	0.71	<0.0001
	1985	18	10	0.71	<0.0001
	1986	26	8	0.81	<0.0001
	1987	20	11	0.77	<0.0001
	1988	18	7	0.74	0.0003
	1989	21	7	0.64	0.001
Small mammals	1990	20	8	0.78	0.0002
	1982	13	11	0.71	0.0003
	1983	11	10	0.88	<0.0001
	1984	8	10	0.62	0.02
	1985	11	12	0.76	0.0005
	1986	13	14	0.76	0.0001
	1987	13	14	0.53	0.005
	1988	7	14	0.80	0.0002
Plants	1989	9	7	0.78	0.001
	1990	8	7	0.72	0.007
	1981	123	8	0.50	<0.0001
	1983	137	14	0.49	<0.0001
	1984	144	19	0.50	<0.0001
	1985	127	19	0.48	<0.0001
	1986	152	19	0.45	<0.0001
	1987	148	19	0.44	<0.0001
Birds	1988	137	19	0.45	<0.0001
	1989	153	19	0.46	<0.0001
	1990	162	19	0.40	<0.0001
	1981	30	11	0.81	<0.0001
	1982	39	12	0.61	<0.0001
	1983	43	12	0.56	<0.0001
	1984	36	12	0.59	<0.0001
	1985	38	12	0.67	<0.0001
	1986	39	12	0.59	<0.0001
	1987	43	12	0.74	<0.0001
	1988	34	12	0.52	<0.0001
	1989	38	12	0.53	<0.0001
	1990	42	12	0.56	<0.0001

relationship exists between the number of sites occupied by a species and its average abundance in a region.

The frequency distributions for all taxa exhibited a mode in both the core and satellite frequency intervals (Fig. 2). However, only the grasshopper and small mammal data sets were significantly bimodal (Table 2). The plant and bird frequency distributions differed from random, but this occurred because of significant modes in the satellite frequency interval. The core modes were not statistically significant. In addition, the frequency distributions for the animal data sets, in particular, exhibited additional smaller modes at intermediate intervals, but these modes were not significantly different from random expectation. Within a taxon there was considerable variation between the frequency distributions from one year to the next (Fig 2). These patterns reflected year-to-year changes in the number of sites occupied by some species, as would be predicted by several models of metapopulation dynamics.

The overall patterns of frequency distributions differed among the four taxa (Fig. 2). For plants and birds, the proportion of species in the core mode was always smaller than the proportion of species in the satellite mode. The opposite was true for grasshoppers and small mammals. The regional frequency distributions of plants and birds were significantly different from grasshoppers, and the frequency distributions of birds and small mammals were nearly distinguishable statistically (Table 3). These differences reflect the proportional differences in core vs. satellite modes among these species. Overall, of the four groups studied, grasshoppers were the most widely distributed on Konza Prairie, followed by small mammals, plants, and birds. This pattern differs from the hypothesized pattern based on inferred dispersal ability. These results clearly demonstrate differences in organismal scaling within a fixed spatial scale at Konza Prairie.

To test for distance scaling with these taxa, we increased the spatial scale of analysis by plotting frequency distributions of (1) prairie plants among cemeteries in Illinois and Indiana (Betz and Lamp 1989), (2) birds among the Apostle Islands of Wisconsin (Beals 1960), (3) grasshoppers in desert grasslands in Texas (Joern 1979), and (4) small mammals on mountains in the southwestern United States (Brown 1978). The distinct mode of core species decreased in these data sets (Fig. 3), and now the frequency distributions are somewhat unimodal except for grasshoppers, which have a second mode in the 0.41–0.50 frequency class. In all cases, however, the frequency distribution of each taxon group at the larger spatial scale is significantly different (Kolmogorov-Smirnov two-sample test, $P < 0.05$) from the average frequency distribution at the smaller spatial scale. Although the large-scale data sets cover wide, but variable, geographic ranges, it is interesting to note that for all taxa there is still a group of core species occurring at >90% of the sites in each region.

DISCUSSION

We can draw three general conclusions from our comparative analyses of distribution and abundance of grasshoppers, small mammals, vascular plants, and birds. First, all four groups of species generally conformed to patterns predicted by the core-satellite species hypothesis (Hanski 1991, Tokeshi 1992). All data sets exhibited core and satellite modes, but only two groups, grasshoppers and small mammals, were significantly bimodal. These results lend support to the notion that core and satellite species occur for some taxa at local spatial scales, but the model does not apply to all taxa within a single spatial scale. In addition, for all data sets in all years we found a positive correlation between number of sites occupied and average abundance in a region. These patterns of modality occurred in each data set despite year-to-year variation in patterns of distribution among the species within each

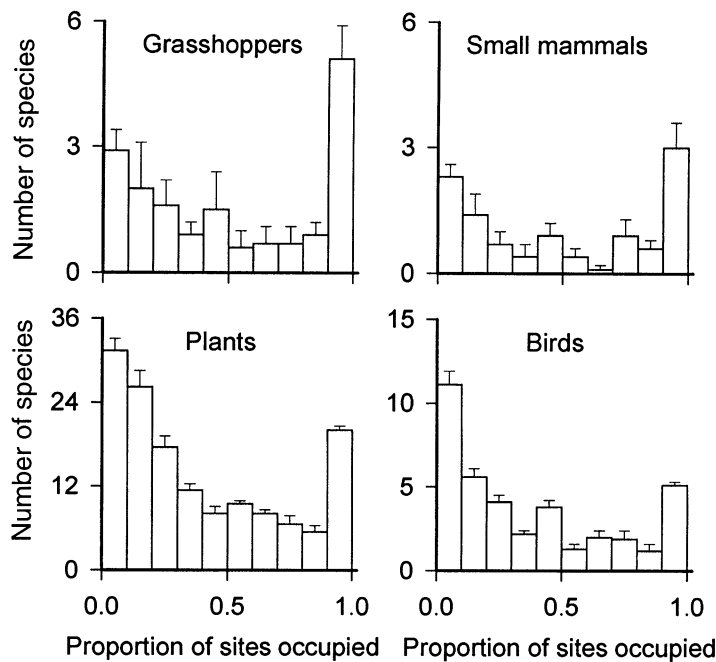


FIG. 2. Patterns of distribution and abundance of grasshoppers, small mammals, plants, and birds among sample sites at Konza Prairie Research Natural Area (Kansas, USA). Data are means (and 1 SE) across years in which the number of sites sampled was ≥ 10 : $N = 5$ yr of data for grasshoppers, $N = 7$ yr for small mammals, $N = 8$ yr for plants, and $N = 10$ yr for birds.

taxon set. This stochasticity results from annual variation in climate and the regional patterns of large-scale disturbances including fire and grazing (e.g., Kaufman et al. 1990, Collins and Glenn 1991, Zimmerman 1993).

Secondly, when the size of the region is held constant, different taxonomic groups were distributed differently. That is, patterns of distribution and abundance differed among grasshoppers, small mammals, plants, and birds within a fixed spatial scale at Konza Prairie. However, observed differences did not conform with our predictions, which were based on our assumptions about organismal scaling. The proportion of core species for birds was less than predicted, and for grasshoppers was greater than predicted based on general assumptions of dispersability. Interactions among factors including population density, scaling issues, mobility, body size, etc., most likely contributed to these differences. Indeed, animals appear to perceive environments as either heterogeneous or homogeneous based on the relationship of body size to habitat heterogeneity (Wiens et al. 1995). This factor has not been effectively incorporated into metapopulation models (With and Crist 1995).

Our third conclusion, noted previously with plant species data (Collins and Glenn 1991), is that within a taxon the pattern of frequency distribution changed as the spatial scale of the region was increased. As spatial scale increased, the size of the core mode decreased, and the frequency distributions of each taxon set conformed to the patterns predicted by Brown's (1984) niche-based model and Tokeshi's (1992) model in which immigration is, on average, less than extinction. Such models lead to a unimodal pattern of distribution with a peak in the satellite mode. This seems reasonable because the effectiveness of dispersal will decrease with increasing spatial scale. In addition, environmental heterogeneity increases at larger scales, increasing the degree of variation among sites and the likelihood of sampling sites in which species are rare or absent (Brown 1984, 1995).

Differences between taxa in patterns of distribution result, in part, from several biological factors characteristic of a given taxon set, and from sampling errors. Species-rich taxonomic groups are likely to have a large satellite mode because rarity tends to increase as richness increases (MacArthur and Wilson 1967). This was true for our data in which the two most species-

TABLE 2. Classification of distribution patterns of grasshoppers, small mammals, plants, and birds based on Tokeshi (1992). P_c = overall distribution, P_l = left-most mode (satellite species), P_r = right-most mode (core species); NS = not significant. See *Methods: Data analyses* for further explanation.

Species	P_c	P_l	P_r	Diagnosis
Grasshoppers	<0.0001	0.02	<0.0001	Weakly bimodal
Small mammals	<0.0001	0.0004	<0.0001	Bimodal
Plants	<0.0001	0.0004	NS	Unimodal
Birds	<0.0001	<0.0001	NS	Unimodal

TABLE 3. Differences in patterns of regional distribution among species (four taxa) at Konza Prairie. Values in the table are statistical probabilities based on pairwise Kolmogorov-Smirnov two-sample tests.

Species	Species		
	Grasshoppers	Small mammals	Plants
Small mammals	0.999		
Plants	0.037	0.111	
Birds	0.016	0.054	0.999

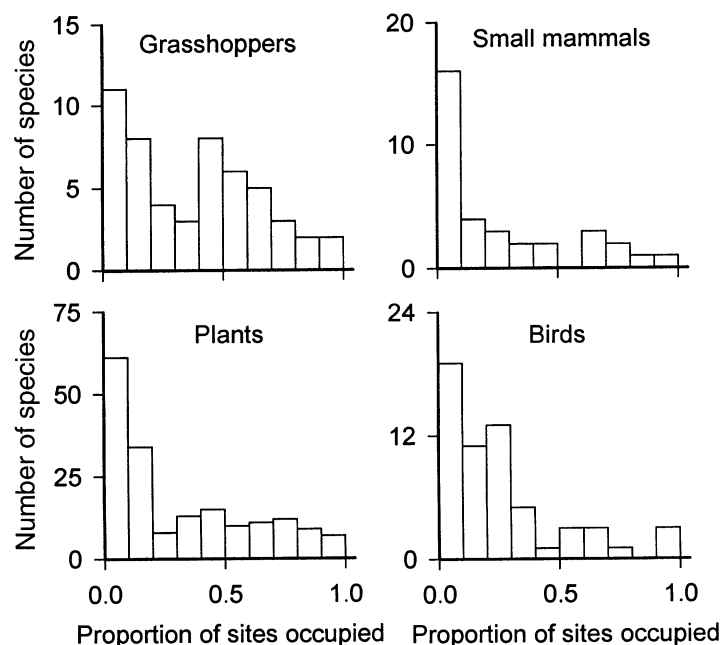
rich groups had statistically significant modes in the satellite frequency interval. Also, the effectiveness of sampling techniques may vary among taxa. Thus, sweep samples of grasshoppers may be most effective for capturing common species and relatively ineffective at sampling rare species. Use of permanent plots for measurement of plant species composition allows for a careful survey of species presence and absence over time, thus enhancing the component of rare species in the data set. Nevertheless, the differences among taxon groups may also reflect biological differences in dispersal ability. During the breeding season birds are territorial, plants are rooted in place, and small mammals have burrows and home ranges. Grasshoppers are more likely to be wider ranging during the breeding season as food source abundance and quality changes seasonally (Evans 1992, Kemp et al. 1990). Therefore, the differences in patterns of distribution among organisms reflect biological and statistical differences so that no one group can provide a complete test of any metapopulation model.

The degree of variation in patterns of distribution over time within taxa reflect temporal heterogeneity in

environmental conditions. One characteristic of prairie ecosystems is the highly stochastic annual variation in precipitation and temperature (Risser et al. 1981). This, coupled with a fire regime that varies spatially and temporally (Collins 1987, 1992, Collins et al. 1995), and grazing by large ungulates produces the stochastic environmental variation necessary to drive metapopulation dynamics (Collins and Glenn 1991). In addition, Konza Prairie is not a highly fragmented environment as assumed in most metapopulation models. At Konza the prairie vegetation is relatively continuous, with small discontinuities formed by woody vegetation in low-lying drainage areas. Thus, there is less environmental discontinuity in this system to inhibit dispersal among sites. However, this expanse of mostly continuous vegetation does not preclude the use of this system for testing patterns predicted from these metapopulation models (Hanski and Gyllenberg 1993).

Understanding patterns of distribution and abundance of species represents a fundamental question in ecological research. As habitat fragmentation continues, the ability of species to disperse among sites becomes increasingly important. In fragmented systems we predict that the proportion of core species within a taxon will be lower than in a similar-sized area of continuous habitat (Collins and Glenn 1995). This implies that core species are highly susceptible to fragmentation (Tilman et al. 1994) and could be viewed as indicator species of the effects of fragmentation, particularly those species that are short-lived but widely distributed. Currently, metapopulation models represent one of the fundamental principles guiding reserve selection and design, and the conservation of species and biodiversity (Hanski 1989).

FIG. 3. Effects of increasing spatial scale on patterns of distribution of vascular plants, breeding birds, small mammals, and grasshoppers. As spatial scale increases, the proportion of species in the core mode (found at >90% of sites) decreases, and the proportion of species in the satellite mode (at ≤10% of sites) increases. Plant data are from Betz and Lamp (1989), bird data from Beals (1960), grasshopper data from Joern (1979), and small mammal data from Brown (1978). These distributions are significantly different ($P < 0.05$) from the distributions for each taxon group in Fig. 2 based on a Kolmogorov-Smirnov two-sample test.



As noted above, the patterns of species distribution that we observed at Konza Prairie conformed to the predictions of the core-satellite hypothesis (Hanski 1991). The core-satellite metapopulation model applies to a suite of species where dispersal ability between sub-populations is high enough for all individuals to be capable of reaching all sites in a region (Hanski 1982a). Therefore, the larger the region being considered, the greater the dispersal ability of the organisms required to conform to the core-satellite predictions. With fragmentation there should be a shift in species in the core mode from those that require undisturbed habitat for dispersal to those that can use human-dominated habitats for dispersal (Glenn and Nudds 1989). Because of "memory" in the system, or the storage effect (Chesson and Huntly 1989), longer-lived organisms are more likely to conform to the core-satellite predictions than short-lived organisms with the same dispersal abilities. This occurs because chance dispersal events in a long-lived species can be compounded over time (C. C. Vaughn, *unpublished data*).

Our study demonstrated that results of tests of models, regardless of their nature, will vary with spatial scale and types of organisms involved. In cases where data do not fit the distribution patterns predicted by a particular model (e.g., Gaston and Lawton 1989, Kemp et al. 1990, Tokeshi 1992) one possible contributing factor might be scaling. Although this general conclusion may not be surprising, comparative empirical tests of patterns predicted by metapopulation models with different species and at different spatial scales have not been conducted. Specifically, the validity and utility of metapopulation models like the core-satellite hypothesis, the niche-based model (Brown 1984), or other models of distribution and abundance, must be evaluated at different spatial scales and with different sets of taxa. All such models may apply within a range of spatial scales, and that range of scales will differ among different sets of taxa. Thus, rather than accepting or rejecting a given model, a primary goal of linking empirical data to model predictions is to define the spatial and temporal domains within which a model applies (Pickett et al. 1994). If such domains are highly restrictive, then the general validity and utility of a given model may be limited. Such decisions cannot be based on a single set of taxa nor within a single spatial scale.

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