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Editor's Note

Does the spatial distribution of the abundance of a species reflect any pattern? Do similar patterns occur among different species, or over different spatial scales? If patterns are detected, how might they arise from ecological processes? Brown et al. investigate these questions and arrive at some very interesting conclusions, with implications for ecology, biogeography, and conservation biology. Indeed, patterns exist. For example, most widely distributed species are abundant in only a few "hot spots." This is true not only for breeding passerine birds, which make up the core of their analyses, but for a wide variety of taxa (including annual and perennial plants, ciliate parasites, and fig wasps), and is apparent at spatial scales ranging from a few hectares to over half of North America. To explain these patterns, Brown et al. revive Hutchinson's multidimensional niche concept and utilize it in a simple simulation model of species distributions along multiple independent niche axes. An especially intriguing aspect of the results is that although the model incorporates no spatial structure itself, it leads to patterns that mimic those associated with demonstrably spatially autocorrelated species distributions. This paper should provoke both a search for more large-scale patterns and the generation of new hypotheses to account for them.

John T. Rotenberry

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SPATIAL VARIATION IN ABUNDANCE¹

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Abstract

To quantify the magnitude and pattern of spatial variation in local population density within a single species, we analyzed large numbers of samples, representing a large geographic area or a wide range of ecological conditions. Our analyses focused on, but were not limited to, censuses of birds recorded in the North American Breeding Bird Survey. Birds and other organisms exhibited a common pattern: each species was represented by only a few individuals in most of the sample sites where it occurred, but was orders of magnitude more abundant in a few "hot spots." The highly clumped frequency distributions of intraspecific abundance among sample sites resemble distributions, such as the negative binomial, canonical lognormal, and broken stick, that have been used to characterize the distribution of abundances among species within local ecological communities.

We hypothesize that the spatial variation in abundance largely reflects the extent to which local sites satisfy the niche requirements of a species. Several results are consistent with this hypothesis. First, a computer simulation model in which abundance is determined by the multiplicative combination of several independent environmental variables produces ranked distributions of abundances similar to those observed empirically. Second, geographic patterns of abundance of bird species have been relatively stable over several decades, indicating that different abundances are associated with particular places on the landscape. Third, the abundance of bird species varies in a systematic way over the geographic range, exhibiting positive spatial autocorrelation at small distances and a tendency to increase from the edges toward the center of the range.

The magnitude and pattern of spatial variation in local population density has

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important implications for basic ecology and biogeography, especially for the dynamics and regulation of abundance in both space and time, the limits and internal structure of the geographic range, and the interspecific variation in abundance observed within local communities. Patterns of spatial and temporal variation in abundance should be considered in the design of nature reserves and the conservation of biological diversity.

Key words: abundance; biogeography; community ecology; conservation biology; distribution; niche; population dynamics; spatial variation.

Introduction

The relationships of a species with its environment are reflected in the distribution of its abundance in both time and space. For almost a century, however, when ecologists have studied abundance, they have almost always studied population dynamics: fluctuations in the numbers of a single local population over time. The history of population dynamics extends from the pioneering theoretical contributions of Pearl (1925) and Verhulst (1938) and the classical empirical studies of Elton (1924, 1942) and Varley (1949), to recent attempts to understand the complex fluctuations revealed in long time series (e.g., May 1974, 1987, Schaffer and Kot 1985, 1986*a, b*, Pimm and Redfearn 1988, 1989). When ecologists have studied distribution, they have focused primarily on territoriality, foraging movements, habitat selection, and other processes that influence the spatial dispersion of individual organisms within populations or among habitats (e.g., Skellam 1951, Fretwell 1972). When biogeographers have studied distributions, they have been concerned primarily with the influence of contemporary processes and historical events on the size, location, and limits of the geographic ranges of species as they appear on maps (e.g., Root 1988*b*, Myers and Giller 1989, Hengeveld 1990).

Much less attention has been paid to the patterns and processes of spatial variation in abundance within a species. Ecologists have rarely made comparative geographic studies of abundance, and biogeographers have equally rarely studied the abundance and distribution of individuals or populations within the geographic range. There have been some notable exceptions (e.g., Whittaker 1967, MacArthur 1972, Hengeveld and Haack 1981, 1982, Hanski 1982, Bock and Ricklefs 1983, Bock 1984, Brown 1984, Schoener 1987, 1990, Root 1988*a, b, c*, Maurer 1994).

Still largely missing, however, is any concerted theoretical or empirical research on the magnitude and pattern of intraspecific spatial variation in local pop-

ulation density. Past efforts were often limited by practical difficulties in obtaining adequate data and in performing spatially explicit analyses. Within the last few years, many of these obstacles have been removed. Now the availability of large, computerized data bases, the development of Geographic Information Systems (GIS), geostatistics, and other tools for spatial analysis, and the motivation to address basic and applied ecological questions at regional, continental, and global scales combine to create excellent opportunities to study the spatial distribution of abundance.

In this paper we analyze new data that cause us to reconsider and modify Brown's (1984) previous conclusions about the relationship between the abundance and distribution of species. Our current, ongoing studies are using the North American Breeding Bird Survey (see Bystrak 1979, Robbins et al. 1986, Droege 1990) to analyze the magnitude and spatial pattern of abundance of passerine birds over their entire geographic ranges. To assess the generality of our results we also compile and analyze data sets for other kinds of organisms. In this paper we describe what appears to be a very general pattern of intraspecific spatial variation in local population density, we evaluate mechanistic hypotheses to account for this pattern, and we discuss some of the implications for ecology, biogeography, evolution, and conservation biology.

Pattern

Methods

Most of our results came from analyses of data on abundances of bird species from the North American Breeding Bird Survey (BBS). The BBS consists of standardized censuses conducted annually at >2000 sites across the United States and Canada. At each site, on one morning in June, an experienced observer drives a prescribed 39.4-km (24.5-mile) route, stopping for 3 min every 0.8 km (0.5 miles) and recording the number of birds of each species seen or heard. Some routes in the eastern and central U.S. have been censused annually for >25 yr. The U.S. National Biological Service and the Canadian Wildlife Service supervise the censuses and maintain the data base. The BBS, like any large data set, has problems of replication, bias, and accuracy that must be considered in any analysis and interpretation (e.g., Faanes and Bystrak 1981, Bart and Shoultz 1984, Robbins et al. 1986, Droege 1990, Sauer et al. 1994). Nevertheless, because of its standardized census methods, its quality control by government scientists, and its unprecedented spatial and temporal scale, the BBS is unique in providing quantitative data on the abundance of hundreds of species over several decades and on a continental spatial scale.

Contents

We have now analyzed the spatial distribution of abundance of 90 species of passerine birds whose geographic ranges are largely or entirely within the region of eastern and central North America. Because this region has been well covered by BBS routes for >20 yr, there are many censuses of the bird species. The BBS uses a numerical scale to classify data from individual census routes according to quality; we used only data from routes classified in the 3 highest of the 10 categories of quality. For each species at each sample site (i.e., BBS route) where it was recorded, we calculated the average number of individuals counted during all censuses between 1966 and 1992, using only routes for which there were at least two surveys during that time period. Here we present detailed data on four passerine species (Scissor-tailed Flycatcher, Carolina Chickadee, Carolina Wren, and Red-eyed Vireo). These were the first species that we studied, and they were chosen because they represent a variety of taxonomic groups (four different families), migratory patterns (tropical migrants to permanent residents), habitats (open savanna to deciduous forest), and geographic distributions (Texas to southern Canada). Results for these four species are representative of the larger sample of 90 species, for which we present only summary analyses. More detailed analyses of this larger sample will be presented elsewhere (D. W. Mehlman, *unpublished manuscript*).

To explore the generality of results for organisms other than birds, we also analyzed data compiled from the literature, provided by colleagues, and obtained during our own field studies. In selecting data on both the birds and these other organisms for analysis, we applied the following four criteria. First, in order to ensure sampling of independent populations, sample sites must be separated by distances several orders of magnitude larger than the radius of the area utilized by an individual. Second, the samples must be unbiased with respect to ecological conditions, so that, for example, the samples of birds encompass a large proportion of the geographic range, and those of other organisms include a wide range of environmental heterogeneity. Third, the number of sites sampled for any particular species must be sufficiently large to characterize the statistical variation in abundance. Fourth, the sample sites must be sufficiently large to have the potential of containing a large number of individuals. Best resolution is obtained when there are hundreds of sample sites and some samples contain hundreds of individuals. The need for such large samples may explain why the pattern reported below has not generally been appreciated.

Results

Analyses of all data sets revealed similar patterns of variation within all species. Quantitatively, these

can be described by plots of frequency (number of census sites) as a function of abundance (local population density or number of individuals counted at a census site), or by graphs of ranked logarithmically scaled abundances, similar to those used to quantify variation in abundance or importance within communities (Fig. 1). All species that we have examined, and that meet the four criteria for sampling mentioned above, exhibit similar distributions: a hollow curve when plotted on linear axes and a characteristic sigmoidal curve when scaled logarithmically and plotted by rank. Qualitatively, abundance of each species at the sites where it occurs can be characterized as varying from many "cool spots" where it is very rare, to a few "hot spots" where it is orders of magnitude more abundant.

The limited range of variation in the qualitative pattern that is shown in Fig. 1 is typical of all BBS data for common and widespread bird species that we have thus far analyzed. Some indication of the variation among species in the distribution of abundance in the larger sample of passerine birds is given in Fig. 2A. For 77 of the 90 species, >50% of the total individuals were recorded in <25% of the BBS routes where that species occurred.

A similar highly heterogeneous spatial dispersion of individuals among sample sites is observed in many kinds of organisms. It has long been known to characterize the distributions of many kinds of parasites among individual hosts (e.g., Kositzin 1934, Crofton 1971, Anderson and May 1978). Our analyses of data supplied by colleagues provide additional examples. Fig. 3 shows representative examples of similar sigmoidal curves of ranked abundances of parasites among hosts, of arthropods among pitfall traps, and of plants among small census plots.

The statistical distributions of intraspecific abundance among sample sites are similar to a group of mathematical distributions that are familiar to ecologists. These include the negative binomial, broken stick, and canonical lognormal (see May 1975). The negative binomial has been favored by parasitologists because it is discrete, can include the zero category (uninfected hosts), and is a flexible, two-parameter distribution that provides reasonably good fits to many data sets. Broken stick and canonical lognormal distributions have been favored by some ecologists because they may imply that abundance is regulated by particular kinds of mechanistic processes (e.g., MacArthur 1957, Williams 1964, Whittaker 1965, 1975, Sugihara 1980, 1989; but see May 1975).

We do not claim that negative binomial, broken stick, canonical lognormal, or any other mathematical distribution uniquely or best describes the spatial vari-

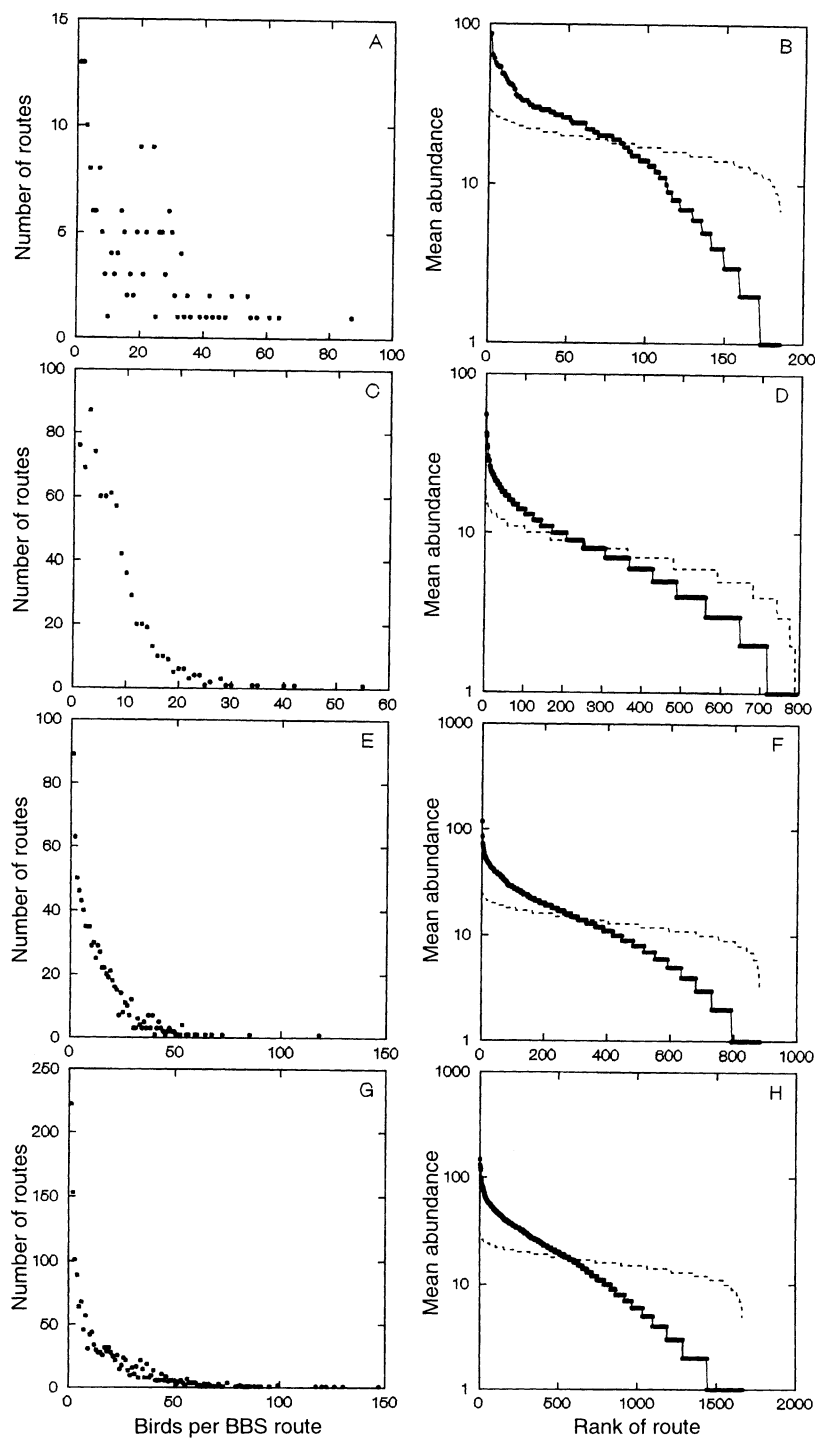


FIG. 1. Frequency distributions of abundance of four species of North American passerine birds among Breeding Bird Survey census routes. The data are plotted as both arithmetic frequency distributions (left) and logarithmically scaled ranked abundances (right, solid lines). The dashed lines (right) represent Poisson distributions fitted using the values for mean abundance. Note that all distributions are much more clumped than expected for a Poisson (all $P \leq 0.05$). Species are: A, B, Scissor-tailed Flycatcher; C, D, Carolina Chickadee; E, F, Carolina Wren; G, H, Red-eyed Vireo.

Concepts

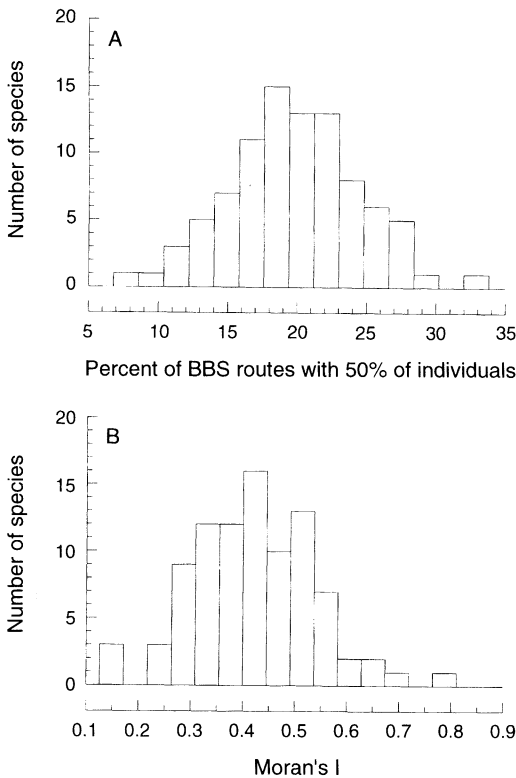


FIG. 2. Frequency histograms for 90 common passerine bird species quantifying two aspects of the spatial distribution of their abundance, based on BBS data. (A) The percentage of BBS census routes where the species was recorded that contained $>50\%$ of the total number of individuals counted at all sites; for reference, for the four species shown in Fig. 1, 50% of the individuals were recorded in 16–26% of the BBS routes. (B) Moran's I , a measure of spatial autocorrelation of abundance among nearby BBS routes. These values correspond to the shortest lag distance (50 km) for each species shown in Fig. 5; for those four species, Moran's I varied from 0.28 to 0.60. For reference, the value of Moran's I for the same lag distance for climatic variables, such as mean temperature or precipitation in July, is about 0.60.

ation in abundance of all species—or any particular species. Such claims seem to have generated more heat than light in ecology. We have presented the data as ranked, logarithmically scaled abundances because such plots are familiar to most ecologists (Tokeshi 1990). They have long been used to characterize another widespread pattern, the highly clumped distribution of abundances among the multiple species that coexist within a local community: most of the species are rare but a few are very common (Preston 1948, 1962a, b, MacArthur 1957, Williams 1964, Whittaker 1965, 1975, May 1975).

A still unanswered question, however, is whether rare species exhibit such clumped distributional pat-

terns as we have documented for common species. Because we have restricted our study to species that have many individuals in at least some samples, we cannot answer this question. Rarer species would by definition have few individuals per sample and thus little absolute variation in abundance among samples, but their occurrences could still be highly aggregated at larger spatial scales.

Process

The null hypothesis of random variation

The occurrence of such an apparently widespread pattern would seem to call for an equally general mechanistic explanation. Here, we evaluate three classes of hypotheses. The first is the null hypothesis of random variation. The concept of randomness is most meaningful when it is specified in terms of both a specific statistical model and a particular mechanistic process. Thus, for example, the Poisson and negative binomial are both random distributions, but the latter includes a clumping parameter that implies some mechanistic process of aggregation. At the present stage of our study, however, it is not clear how to erect and test an appropriate null hypothesis. We can, however, show that the spatial patterns of abundance have several deterministic features that seem to require a mechanistic ecological explanation.

First, the distributions shown in Figs. 1 and 3 are much more clumped than the simplest random distribution, the Poisson. This suggests that some deterministic process causes individuals to aggregate in certain favorable locations.

Second, while there is usually considerable temporal fluctuation in local population density, the spatial pattern of abundance across the landscape tends to remain relatively stable for periods of time longer than the temporal autocorrelations that would be expected from demographic considerations. Thus, analyses of BBS data for abundances at the same census sites 20 yr apart show a substantial degree of consistency (Fig. 4). Two things should be borne in mind when evaluating these patterns. First, the 20-yr temporal separation of these samples is several times longer than the generation times (on the order of 2–5 yr) of small passerine birds. This means that the temporal consistency cannot be explained simply as a consequence of demographic time lags in local population dynamics. In fact, several of the bird species studied so far (e.g., Red-eyed Vireo and Scissor-tailed Flycatcher) are migrants that winter in the tropics and return in spring to breed at temperate latitudes. Second, over the 20-yr time period the environments of some BBS routes have changed substantially, mostly

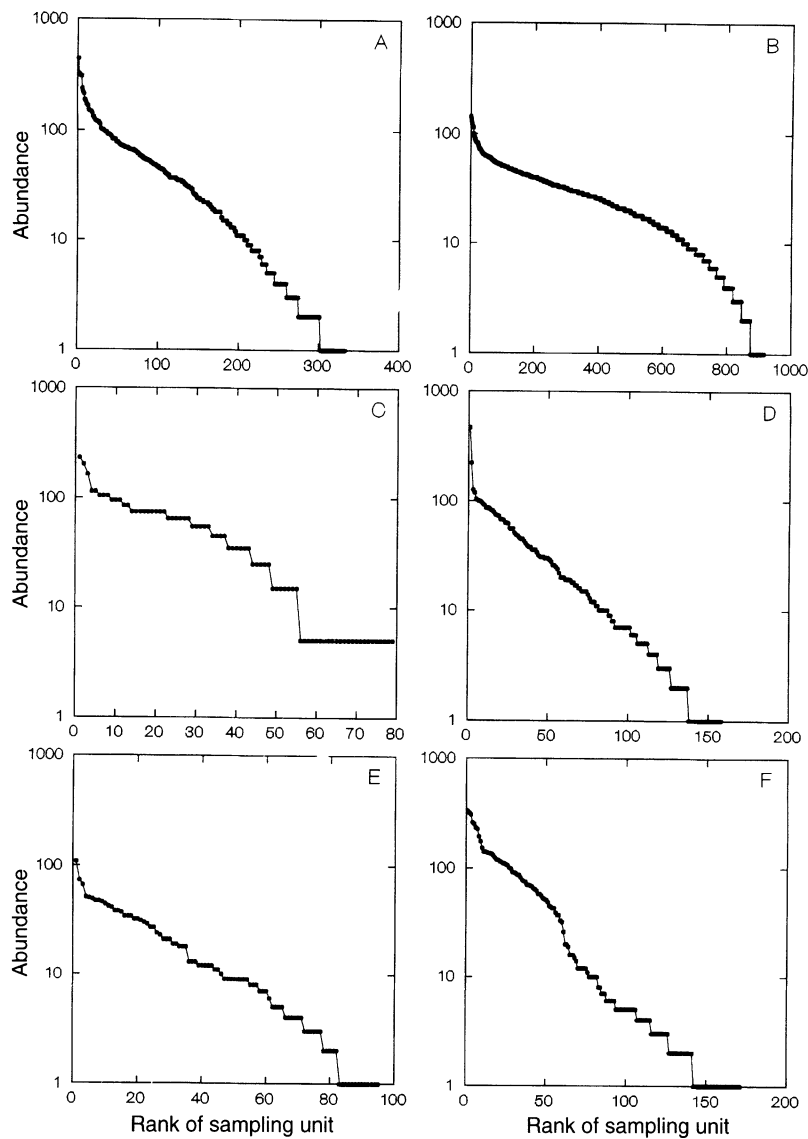


FIG. 3. Logarithmically scaled ranked abundances of six species of animals and plants among spatially dispersed sample sites. (A) An annual plant, *Eriogonum abertianum*, among 333 0.5-m² plots in the Chihuahuan Desert near Portal, Arizona (Q. Guo, *unpublished data*); (B) a tree, *Casearia corymbosa*, among 961 400-m² plots in tropical deciduous forest in Guanacaste Province, Costa Rica (S. P. Hubbell and G. C. Stevens, *unpublished data*); (C) an unidentified agaonid fig wasp species among 79 fruits on one *Ficus* tree near Miami, Florida (J. Bronstein, *unpublished data*); (D) a ciliate parasite, *Trichodina* sp., among 158 hosts of the fish *Fundulus zebrinus* in southern Nebraska (J. Janovy, *unpublished data*); (E) the isopod crustacean, *Porcellio laevis*, among 95 pitfall traps in cottonwood woodland riparian habitat in central New Mexico (C. S. Crawford, *unpublished data*); (F) the beetle *Dyschirius globosus*, among 171 pitfall traps in The Netherlands (data from Hengeveld 1979).

due to ecological succession, changing human land use practices, and other human influences. Thus, ecological processes, not just stochastic variation, probably account for some of the changes in abundances at local sites reflected in Fig. 4.

Finally, abundance exhibits a distinctive pattern of spatial variation within the geographic range of a spe-

cies. This is readily apparent from spatial autocorrelation analyses (Fig. 5). Note that the correlogram shows two peaks of positive values, one at short distances, corresponding to nearby sample sites throughout the geographic range, and another at maximum distances, corresponding to sites at opposite edges of the geographic range. This pattern of autocorrelation

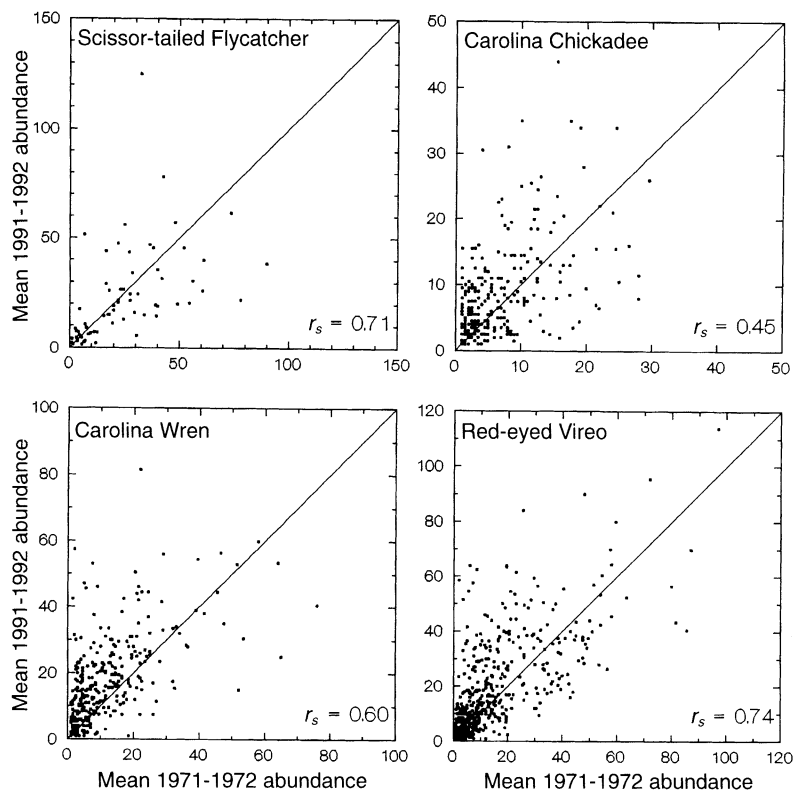


FIG. 4. Temporal consistency in the spatial pattern of abundance of four passerine bird species as indicated by the correlation in the numbers of individuals counted in BBS censuses 20 yr apart. For each BBS route where the species occurred, mean counts for two successive years (1971–1972 or 1991–1992) were calculated and plotted. The line indicates equal values. Note that most species maintained generally similar abundances at the same sites over the 20-yr period.

reflects two underlying patterns of spatial variation. First, the high values of autocorrelation for short lag distances indicate that sites that are close together in space, regardless of their location within the geographic range, tend to support more similar densities of individuals than more widely separated sites. Thus, for example, hot spots tend to be nearer to other hot spots and cool spots tend to be nearer to other sites of low abundance (Fig. 6). Similar spatial autocorrelation at small scales was characteristic of the vast majority of the 90 passerine bird species that we have studied (Fig. 2B). Second, the high values of autocorrelation at maximum lag distances indicate that sites at opposite edges of the range tend to have similar densities. Populations at the periphery of the geographic range tend to have consistently low densities, whereas more centrally located populations on average have higher densities, in part because the hot spots tend to be concentrated toward the center of the range (Fig. 7).

A niche-based hypothesis

If we assume that local abundance reflects the suitability of the local environment, then our data suggest that the environmental variables that limit abundance change slowly over time and vary in predictable ways over the geographic range. We pursued this idea by reviving Hutchinson’s (1957) concept of a multidimensional niche and developing a computer simulation model of how environmental variables might affect local population density. We assumed that the niche of each species consists of multiple, independent factors (dimensions represented by orthogonal axes), each representing a variable (or set of correlated variables) that limits the fitness of individuals and hence abundance and distribution of populations. The effect of variation in each niche factor on abundance was characterized by a mathematical function. In most of our simulations, we have used a simple function with a central maximum: a normal distribution, truncated to zero at one standard deviation unit above and below the mean value (Fig. 8A). The niche was assumed to

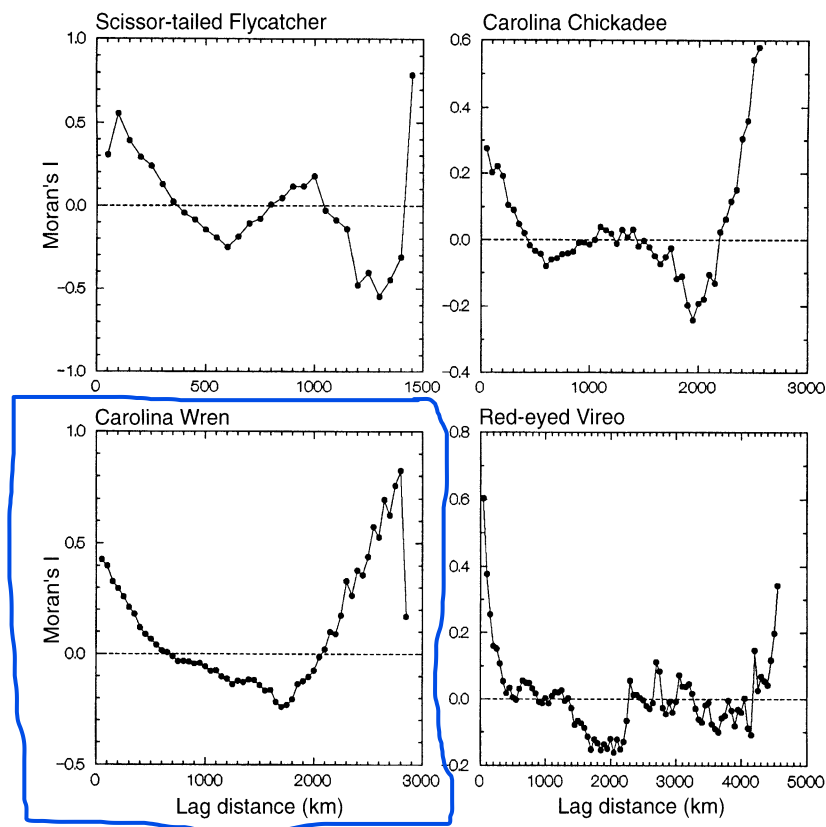


FIG. 5. Spatial autocorrelation of abundance of four passerine bird species over their geographic ranges. The autocorrelation statistic was Moran's I, computed from BBS counts for lag distance increments of 50 km. Note the two peaks of high correlation, one for sites at close proximity from throughout the range, and the other at maximum lag distances corresponding to sites at opposite edges of the range.

comprise some specified number of independent axes, and abundance was determined by the product of the values of the distributions along the different axes. Set up in this way, the model allows abundance to take on values from near zero (if any environmental variable borders on one standard deviation of the modal value), to a maximum that is the product of the modal values for all variables. We then used the model to simulate abundance at a sample site by randomly choosing a value along each niche axis and multiplying the corresponding values of the Gaussian function. This procedure was repeated 594 times to generate a frequency distribution of abundance among many sites.

Results of such simulations are shown in Figs. 8 and 9. Note four things. First, some, but not all, simulations give results that resemble the sigmoidal curves observed empirically. Second, similar results can be obtained when different mathematical functions are used to characterize the effect of an environmental variable on abundance; both highly truncated normal

curves (Fig. 8) and triangles (Fig. 9A), as well as curves assigned different quantitative weight (Fig. 9C), give sigmoidal curves that resemble the empirical ones. Third, the results depend on the number of the niche axes, giving sigmoidal curves when the number of axes is greater than ≈ 4 (Figs. 8D, F). Fourth, while it might be expected that multiplying any number of random values would produce lognormal distributions, only a limited range of parameter values, specifying both niche shape and number of niche axes, produced plots of ranked abundances that were similar to the empirical distributions.

Effects of dispersal and intraspecific interactions

The niche model presented above includes no dynamics. It simply assumes that some combination of reproduction, mortality, and dispersal will maintain the abundance of a species at a local site at a level set by the extent to which the local environment meets the requirements of the individuals. Thus, we assume

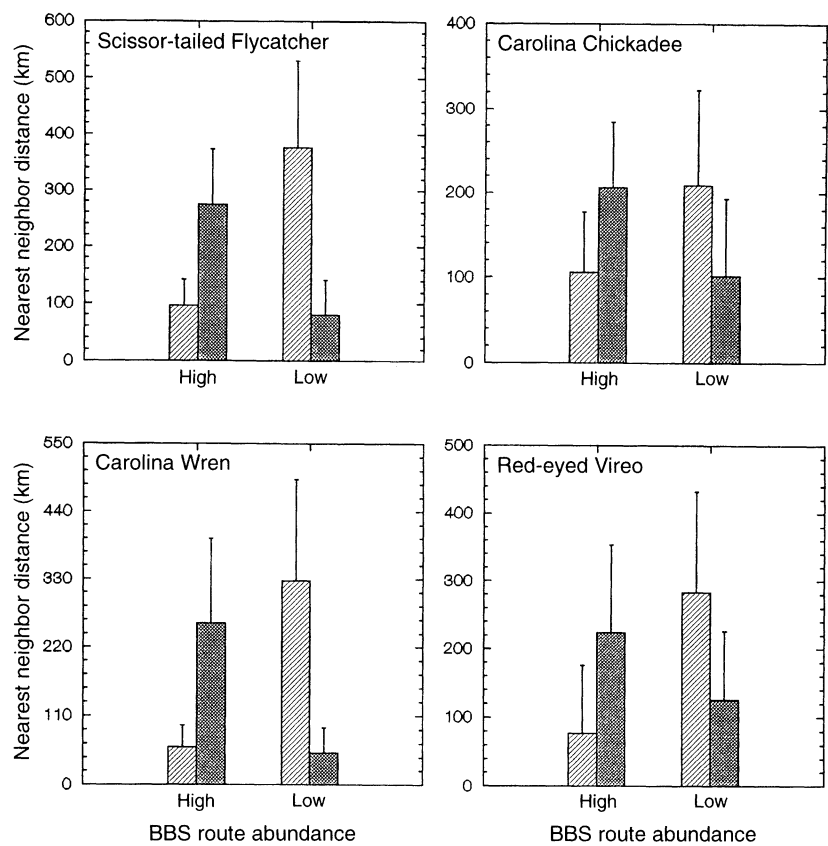


FIG. 6. Mean distance from sites with high and low density (highest and lowest decile of BBS counts, respectively) to the nearest neighbor sites of high □ and low ▨ density for four passerine bird species. Error bars indicate one standard deviation from the mean. Note that “hot spots” tend to be nearer to other sites with high densities and sites with low density tend to be nearer to other low-density sites than expected by chance.

that population density is distributed among sites of varying environmental quality in what Fretwell (1972) called an “ideal free” manner. Some form of resource-based density dependence is implicit in the model, and its form is determined by the shape of the functions used to characterize each niche axis. Beyond this, however, the model contains no birth, death, dispersal, or intraspecific interactions, and no time lags or more complicated consequences of these processes (e.g., nonlinear dynamics). At this stage, we believe that it is appropriate to explore the conceptual insight and empirical explanatory power that can be obtained from such simple models before resorting to more complex ones. The similarity between results of our simulations and our empirical analyses suggests that most of the spatial variation in abundance of many species might be explained by the extent to which local environmental conditions meet a modest number of niche requirements.

It is also important, however, to recognize that pop-

ulation dynamic processes may account for some of the observed variation in abundance. Three considerations are likely to be especially important. First, time lags in population dynamics will tend to decrease the degree of correspondence between local population densities and local environmental conditions. Second, sufficient levels of nonselective dispersal among sites will tend to have similar effects. Third, density-dependent processes may have complicating effects. On the one hand, territoriality and other forms of “despotic” negative density dependence will tend to cause more even dispersion of individuals across the landscape than expected from the “ideal free” distribution, resulting in lower densities in the most suitable sites and more individuals distributed among relatively low-quality sites. On the other hand, aggregation for group benefits (e.g., flocking and herding) should have the opposite effect, resulting in even more clumped distributions than expected based on environmental suitability alone. At the present stage of our investi-

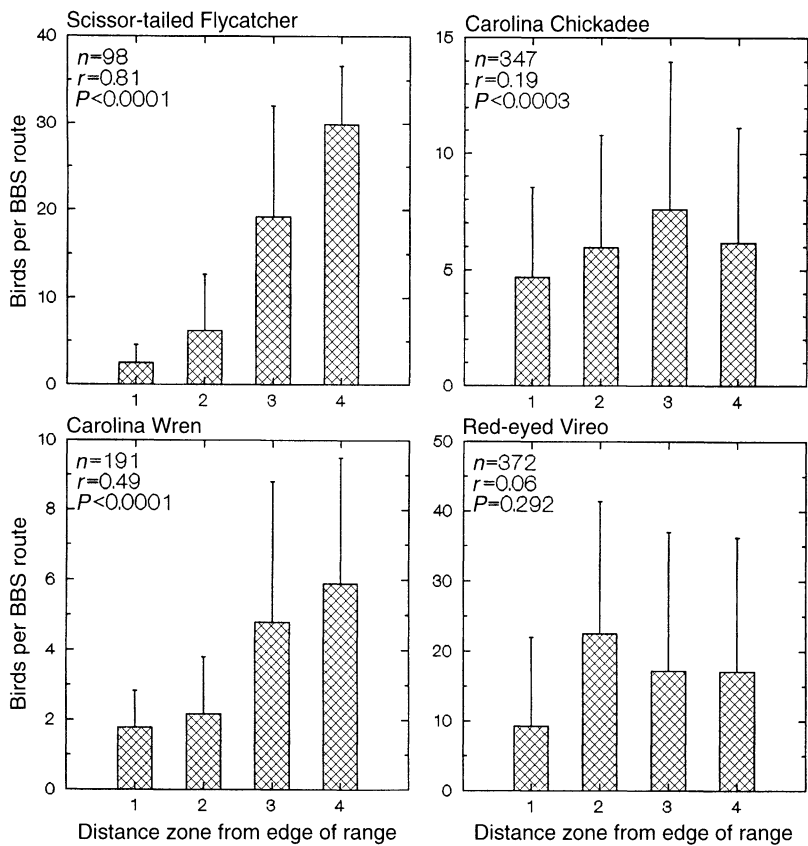


FIG. 7. Mean abundance per BBS route as a function of distance from the edge of the geographic range for four passerine bird species. Data are plotted in quartiles of distance intervals, scaled from the edge to the center of the range. Error bars indicate one standard deviation from the mean. Sites whose closest edge of range was a coastline were not included. Statistics inside each box give Pearson product-moment correlations of log₁₀ abundance as a function of distance from the edge. Note that abundance increases significantly from the edge toward the center in three of the four species.

gations, it is difficult to evaluate the effects of these dynamic population processes.

Implications

Implications for ecology and biogeography

We are very much aware that the correspondence between the output of simulation models of the niche and the observed patterns of variation in abundance does not demonstrate that the models capture the ecological processes that are the most important in determining local population density. Nevertheless, we are encouraged and are continuing to pursue niche-based explanations for the spatial variation in abundance. Two lines of investigation seem especially promising.

First, it should be informative to develop more realistically complex niche-based models. For example, it should be possible to produce spatially explicit models that will simulate patterns of abundance across

heterogeneous landscapes. Brown (1984) suggested that the tendency of abundance to be higher on average at sites near the center of the geographic range than at locations near the range edges could be attributed largely to spatial autocorrelation in the environmental variables that were important dimensions of the niche. It should be possible to use simulations to answer the question: what patterns of spatial variation in environmental variables are required to produce patterns of abundance similar to those observed across the geographic ranges of real species?

Second, these kinds of niche-based models can be applied and evaluated empirically by investigating the environmental correlates of the observed variation in abundance. Thus, it should be possible to begin to characterize the niches of species, using a combination of: (1) census data, such as the BBS, to characterize the distribution of abundance, (2) data on climate, geology, soils, vegetation, etc. that are increasingly becoming available from direct measurements and re-

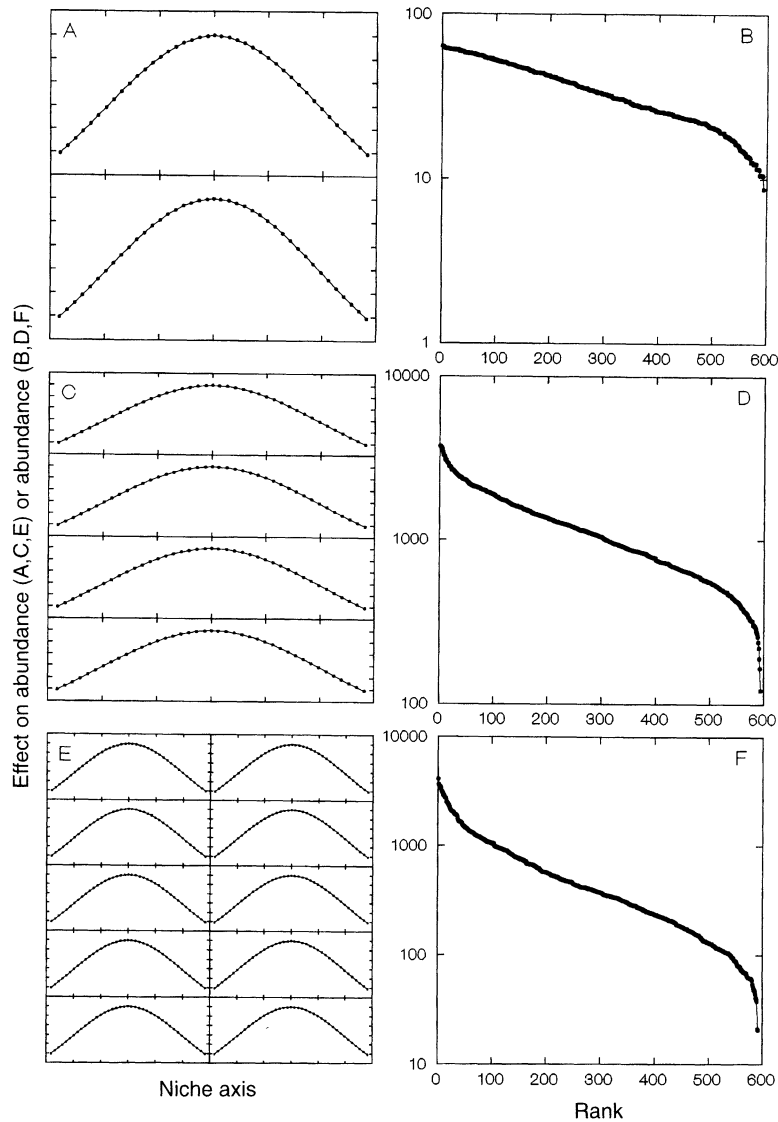


FIG. 8. Results of computer simulation models in which abundance is determined by multiplicative random combinations of normally distributed niche functions. Left (A, C, E): The effects 2, 4, and 10 niche axes have on abundance is modeled by normal curves, truncated to zero at ± 1 standard deviation. Right (B, D, F): The result of multiplying values drawn at random from 2, 4, and 10 such truncated normal functions is plotted as logarithmically scaled ranked abundances. Simulations using a modest number of niche axes (e.g., C, E) produced sigmoidal curves (D, F) similar to the empirical data (Figs. 1 and 2).

remote sensing to characterize variation in the environment, and (3) GIS, geostatistics, and multivariate statistical techniques to perform the analyses. We envision an approach that takes advantage of the orders-of-magnitude variation in local population density to identify the important environmental correlates of niche dimensions, and ultimately to discover the environmental factors and ecological processes that limit abundance and distribution.

Implicit in considering spatial variation in abundance is an investigation of the interface between ecology and biogeography. The geographic range of a species can be viewed as a complex, three-dimensional landscape, where two dimensions represent geographic space and the third dimension represents abundance (e.g., MacArthur 1972, Bystrak 1979, 1981, Hengeveld and Haack 1981, 1982, Brown 1984, Robbins et al. 1986, Root 1988a, Hengeveld 1990). This can then

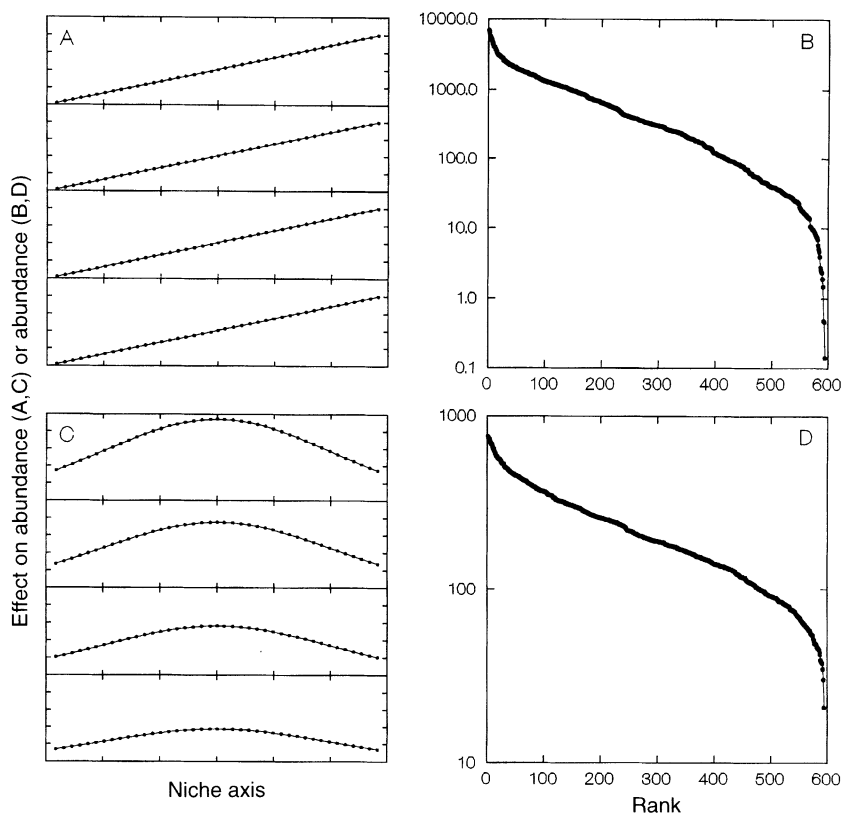


FIG. 9. Results of computer simulation models in which abundance is determined by multiplicative combinations of different niche relationships. Right (B, D): logarithmically scaled ranked abundances generated from simulations drawn from niche axes represented on the left, which represent either four linearly increasing niche functions (A) or four normal-shaped niche functions, each truncated to zero at ± 1 standard deviation, but having different magnitudes of influence on abundance as indicated by the scaling of the Y axis (C).

be extended to view the range as a mosaic of many local sites, each characterized by a set of environmental variables and by a local population density varying over time in response to variation in the environment, intrinsic population dynamics, and exchange of dispersing individuals with other populations. This view helps to clarify the close relationships between the processes that regulate abundance within the geographic range (the traditional province of ecology) and those that determine the limits of the distribution (the traditional province of biogeography).

Most previous treatments of spatial patterns of abundance have failed to recognize, or at least to emphasize, both the true magnitude and the degree of spatial heterogeneity of the variation. Thus, Whittaker (1967, summarizing several earlier studies) fitted smooth, normal-shaped curves to extremely heterogeneous data to characterize the pattern of abundance along transects through the elevational ranges of species. The contour maps of density mentioned above also seriously underestimate the magnitude and spatial

heterogeneity of the variation, because the data have usually been analyzed by computer programs that average and interpolate the data. Furthermore, because the magnitude and spatial heterogeneity of the variation was underestimated empirically, most previous theoretical treatments have assumed a higher degree of spatial autocorrelation extending over larger distances than actually exists—both in abundance itself and in environmental variables that potentially influence local population density (e.g., Hengeveld and Haeck 1981, 1982, Brown 1984, Hengeveld 1989).

One of the most general features of local ecological communities is the qualitative frequency distribution of abundance among the coexisting species: most of the species are very rare and only a few are extremely common (e.g., Fisher et al. 1943, Preston 1948, 1962*a, b*, MacArthur 1957, 1972, Williams 1964, Whittaker 1965, 1975, May 1975). Some investigators have attempted to explain this seemingly universal pattern in terms of interactions and division of resources among the coexisting species (e.g., MacArthur 1957, Sugihara

1980, 1989). The pattern of intraspecific spatial variation in abundance that we have documented suggests a simple alternative explanation: the community-level distribution of abundances among species may just reflect the way that variation in environmental conditions independently affects the local population density of each species. If each species is rare most of the places where it occurs, but orders of magnitude more common in a few sites, then at any given site most of the species will tend to be rare but a few species will be at a hot spot and thus very abundant. Note, that this does not imply that species do not interact and affect each others' abundances; it just implies that it may not be necessary to understand the detailed mechanisms and consequences of such interactions to explain the distinctive, highly skewed distribution of abundances among coexisting species.

The same empirical and theoretical approach that we have applied to spatial variation in abundance could also be applied to temporal variation. Analyses of long time series of data on population density of a single species at one site typically show orders-of-magnitude variation (e.g., see Schaffer 1984, Schaffer and Kot 1986*a, b*, Pimm and Redfearn 1988, 1989, Pimm 1991). We suggest that the pattern of variation over a long period of time is similar to that over geographic space. Thus, for example, the frequency distributions of annual abundance in long-term records of two vertebrate populations produce plots of ranked abundances that are similar to the spatial patterns (compare Fig. 10 with Figs. 1 and 3). Our niche model would suggest that such patterns of long-term dynamics might be explained in terms of responses of a local population to temporal changes in several environmental variables.

Implications for conservation

The magnitude of spatial variation in abundance revealed by our analyses, and the niche-based explanation for this variation that we have proposed, have several important implications for conservation and management. The highly aggregated distribution of individuals across the landscape and within the geographic range of a species should be considered in establishing biological reserves and in managing ecosystems to maintain or restore biological diversity.

Information on hot spots is desirable for several reasons. First, a large fraction of the individuals of a species occur in a few hot spots. Our analyses of BBS data suggest that >50% of all individuals of nearly all common passerine species were concentrated in a small proportion of the sites where the species occurred (Fig. 2A; and note that we have not even con-

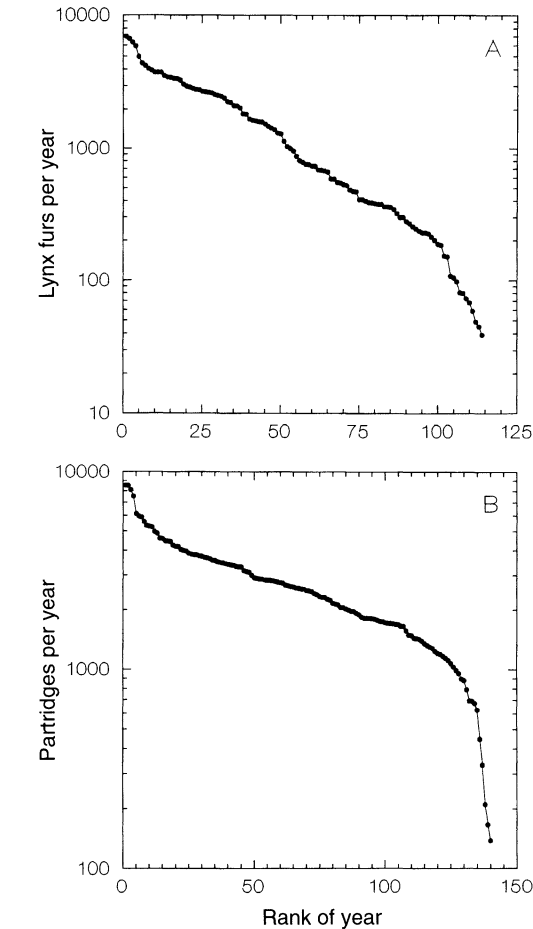


FIG. 10. Data from long time series of numbers of (A) lynx pelts harvested in Canada (data from Elton and Nicholson 1942), and (B) partridges killed on an estate in Britain (data from Middleton 1934) plotted as logarithmically scaled ranked abundance graphs. Note that these have a sigmoidal shape similar to the spatial graphs of spatial variation in abundance shown in Figs. 1 and 3.

sidered the many sites within and outside the geographic mapped range where the species was not recorded and is presumed to be absent). It is clearly important to identify the “hot spots” where species are most abundant and to design reserves that protect such hot spots (Schoener 1987).

Second, it is also important to discover the niche variables and other possible factors that cause the variation in abundance. Only if this is done can management plans be designed that will preserve and improve the environmental conditions required by the species of concern. We have suggested how the wide variation in abundance might be used to begin to characterize quantitatively the environmental variables that comprise the niches of species. Here we suggest that this

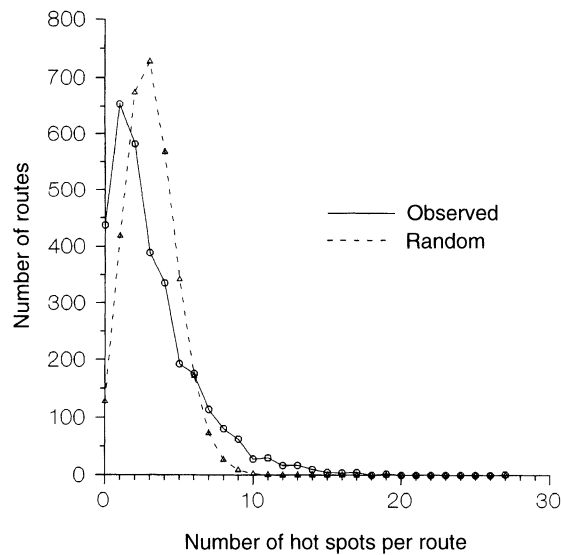


FIG. 11. Frequency distribution of hot spots among BBS routes. Circles connected by solid line: the observed number of BBS routes that were hot spots for 0, 1, 2, . . . , n species of the 90 passerine birds studied. Triangles connected by dashed line: the expected number of BBS routes that would be hot spots for 0, 1, 2, . . . , n species if hot spots were distributed randomly among routes. Expected values are the means of 20 simulations in which hot spots for each species were randomly drawn from the 3144 BBS routes. Species hot spots were clumped: i.e., there were more routes than expected by chance that were hot spots for more than seven species and also for zero or one species.

approach can be applied and modified to search for previously undetected sites where poorly known endangered species are likely to survive and for hot spots where they are likely to be especially abundant. It might also be used to search for changing environmental variables that cause declines in abundance—either widespread decreases throughout the geographic range or contractions of geographic range boundaries owing to more localized declines. Similar applications could be used to seek means to control exotic or pest species that are increasing in abundance and/or expanding their geographic ranges.

Third, our data and analyses raise important questions about how the abundances of different species covary over the landscape: do pairs of species exhibit independent, positive, or negative patterns of variation? The answers, especially for rare and endangered species, are of obvious importance in designing nature reserves. We analyzed the number of BBS census routes that are hot spots for one species, two species, and so on. Results suggest that rather than being distributed independently of each other, the hot spots of different species are significantly positively associated (Fig. 11). There are consistently more routes than ex-

pected by chance that are hot spots for seven or more species. It should be important to identify the characteristics of such sites that support abundant populations of many species. Such sites should be given high priority for protection as nature preserves.

Finally, our analyses underscore the importance of using information on abundance, not just presence or absence, in making conservation management and policy decisions. Several U.S. government agencies and non-governmental conservation organizations are promoting GAP analysis (Scott et al. 1993) as a practical, efficient, and relatively inexpensive method for organizing distributional data and applying them to develop conservation priorities. GAP analysis, as it has been developed and applied to date, however, is based on presence-absence data; it is often based on the potential presence of a species, as indicated by a site occurring within the geographic, elevational, and habitat ranges of the species, rather than on its confirmed presence at a site. GAP analysis often combines presence-absence data for multiple species to identify sites of high actual or potential species richness for consideration for protection.

The effectiveness of GAP analysis in correctly identifying areas that are good candidates for reserves to preserve populations of multiple species is crucially dependent on the abundance of the individual species in the sites of high diversity. It is easy to imagine that often local abundance of species of conservation concern might be uncorrelated or even negatively correlated with overall species richness. For example, sample areas that represent ecotones among habitat types or mosaics of small patches of different habitats, might have many species present but few if any of them in sufficiently high densities to sustain these species if the surrounding habitats are degraded.

We do not mean to imply that all methods of assigning conservation priorities based only on presence-absence data are without merit. When a geographic area or a group of organisms has received little study, there may be no practical alternative to using species lists as a basis for making policy and management decisions. When doing so, however, it is essential to evaluate carefully any implicit or explicit assumptions of methods that are based on presence-absence data or overall species diversity. The order-of-magnitude spatial variation in abundance that appears to be characteristic of nearly all species must be borne in mind when designing conservation programs to preserve endangered species.

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