

ON THE RELATIONSHIP BETWEEN ABUNDANCE AND  
DISTRIBUTION OF SPECIES

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How environmental conditions and population processes determine the abundance and distribution of species is a central problem of ecology and biogeography. Although it has long been recognized that abundance and distribution are intimately interrelated, the nature of this relationship has not been investigated systematically over the range of spatial scales from local populations to entire geographic ranges of species. On a local scale, i.e., the small habitat patches that constitute most ecologists' study areas, the relationship between population density and spatial distribution of individuals has been studied by many population and community ecologists (e.g., Andrewartha and Birch 1954; Krebs 1978, and numerous references therein). Distribution on a large geographic scale has usually been regarded as the special province of biogeography, whose practitioners often have little experience or interest in population ecology (but see, e.g., Grinnell 1922; MacArthur 1972; Walter 1979; Rapoport 1982; Brown and Gibson 1983). Thus few investigators have systematically studied variation in population density over the geographic range of species. Recently, however, several authors have presented data that suggest a general relationship between local population density and spatial distribution on a geographic scale (e.g., Rabinowitz 1981; Hanski 1982*a*, 1982*b*, 1982*c*; Bock and Ricklefs 1983; J. T. Emlen et al., MS).

Here I reanalyze and synthesize some of the diverse information available on the relationship between abundance and distribution. These data suggest extremely general patterns within and among species that appear to hold for organisms as diverse as vascular plants, intertidal invertebrates, terrestrial arthropods, planktonic crustaceans, and terrestrial vertebrates. I develop a general theory to explain these relationships. This conceptual construct and the empirical observations that motivated it focus attention on problems that span the boundaries between the traditional disciplines of population ecology, community ecology, biogeography, population genetics, and evolution.

Clarification of terminology should facilitate understanding of what follows. The paper is concerned with the relationship between two attributes of populations and species: the density of individuals within a local area and the extent of the distribution of individuals in space. I shall often use the term *abundance* to

refer to local population density, and the terms *rare* and *common* (or *abundant*) to describe extremes of density. Similarly, I shall often use *distribution* or *range* to refer to spatial distribution, and the terms *restricted* (or *local*) and *widespread* to describe the extremes.

#### THE PATTERNS

##### *Spatial Variation in Abundance Within Species*

We are all aware that within their geographic ranges all species are relatively numerous in some habitats and regions, whereas they are scarce or absent in others; the limit of the geographic range occurs where population density over large areas declines to zero. Is there any general pattern of spatial variation in abundance within the area in which a species normally occurs? The answer appears to be yes, density is greatest near the center of the range and declines, usually gradually, toward the boundaries. This pattern holds both within steep, geographically restricted gradients of environmental change, such as on mountainsides and within the intertidal zone, and over the entire geographic ranges of widespread species.

Examples of variation in population density over ecological gradients within local regions are shown in figure 1. These confirm the general pattern noted by Whittaker (1956, 1960, 1965) in his classical papers on patterns of vegetation: although individual species attain different maximum densities in different parts of the gradient, abundances of most species decline relatively gradually and symmetrically with increasing distance in either direction from their peaks. Of course some species attain their highest densities near one end of the measured gradient, so one tail (and sometimes probably the peak as well) of the distribution is missing. The generality of the pattern is demonstrated by the fact that it holds not only for plants in gradients of both moisture and elevation in different geographic regions (e.g., figs. 1*a*, 1*b*, 1*c*, 3, and other data in Whittaker [1956, 1960] and Beals [1969]), but also for invertebrates within the gradient of intertidal exposure, such as on a rocky shore in the northern Gulf of California (fig. 1*d*; see other data in Field and Robb [1970]).

Almost all of these plots of local density as a function of distribution in a gradient resemble normal curves, as indicated by the fact that Whittaker routinely fitted his data on plant distributions with Gaussian curves. Of course, sometimes at least one tail is missing when the distribution of the species extends beyond the measured gradient. Although not all these curves may represent exact normal distributions, they exhibit a strong central tendency and are neither highly skewed nor strongly leptokurtic or platykurtic. These empirical distributions obviously contain sampling error, so it is comforting that the curves appear smoother and more normal as the sample size is increased. The curves plotted in figure 1 are for abundant species, and as expected, distributions of the rarer species exhibit much more sampling error. Many of the distributions for common species do not differ significantly from normal distributions, whereas they are highly significantly different from random distributions (i.e., uniform, but with sampling error) of individuals within the gradients.

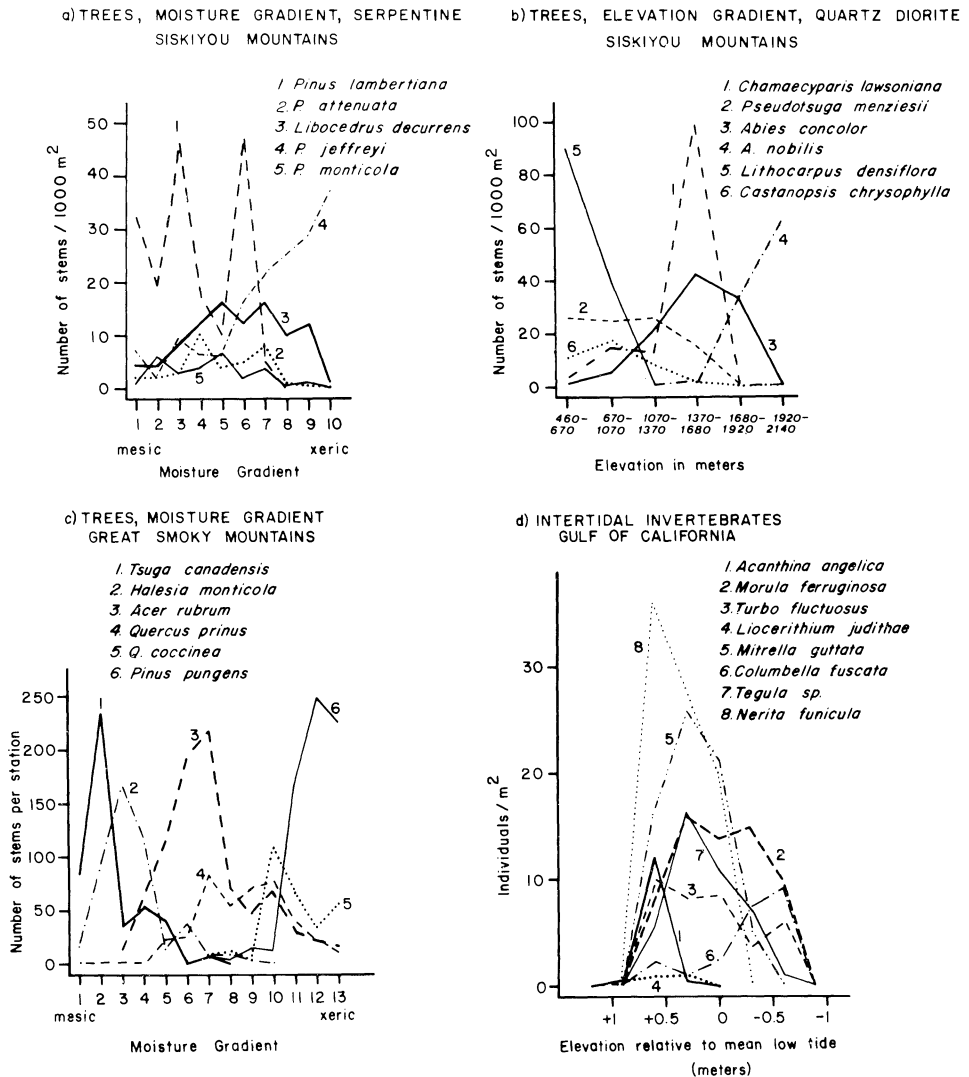


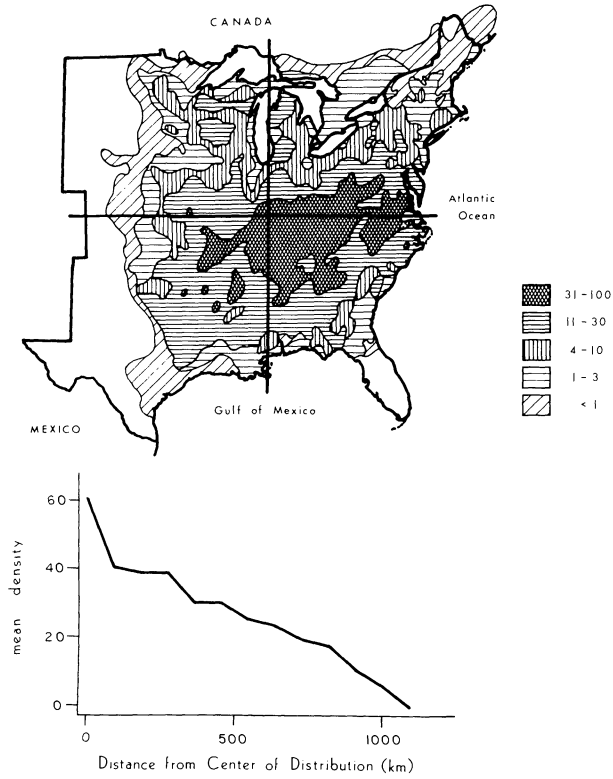
FIG. 1.—Distributions of abundances of terrestrial plant and intertidal mollusk species in local gradients of rapid ecological change: *a* and *b* data replotted from Whittaker (1960); *c* data replotted from Whittaker (1956); and *d* from E. H. Boyer, unpublished data. Note that most of the distributions seem to be surprisingly unimodal and symmetrical, except for those of species that obviously extend well beyond the measured gradient. The most abundant species in each gradient are depicted here; species were not selected on the basis of the pattern of the distribution of density.

The data on local population densities also suggest a gradual decline in abundance from the center to the boundaries of the geographic ranges of widespread species. The best data set available is for birds (but see Delcourt et al. 1981). D. Bystrak of the U. S. Fish and Wildlife Service has prepared maps, based on censuses from the Breeding Bird Survey, showing variation in abundance over the geographic ranges of many North American species. Two of these are shown in figure 2 (see also Bystrak 1979, fig. 5). Note that the greatest abundance of each species occurs near the center of its range, and population density declines gradually toward most boundaries. Even when an abrupt barrier of unsuitable habitat, such as the ocean, limits the distribution, abundance usually declines gradually as this boundary is approached. This general pattern of variation in abundance can be shown graphically by plotting density as a function of distance along four transects through the widest part of the range in four major compass directions and then averaging the values (fig. 2). A similar pattern was reported by J. T. Emlen et al. (MS) who sampled bird populations along a 850-km north-south transect of riparian forest habitat in the Mississippi Valley. They noted that, "The census data revealed convex density profiles for each species, curves that fluctuated considerably from station to station but tended to be level across range centers and slope peripherally to north and south boundaries at rates of up to 30% per degree of latitude." For 7 of the 19 species with northern or southern range boundaries within or close to their survey area, more than 50% of the variation in local density within the transect was related to latitude, with abundance always decreasing toward the northern or southern boundary. In contrast, for only 2 of 22 more widely distributed species that did not reach their northern or southern limits near the survey area was there an equally close correlation between density and latitude.

Although it is difficult to obtain quantitative data for organisms other than birds, the avian distributions exhibit a general pattern long recognized by naturalists (e.g., see Grinnell 1922): along a transect from the center to a boundary of its range a species tends to inhabit a progressively smaller proportion of local sample areas and habitats, and even without local regions where it does occur its average population density declines. Thus Rapoport (1982, fig. 6.3) used aerial photographs to document the decline in both density and frequency of occurrence of the palm tree (*Copernicia alba*) in 1-km<sup>2</sup> sample areas along a 113-km east-west transect through the boundary of its range in Argentina. It is hardly surprising that density within sites and frequency of occurrence among sites are closely inter-related, since both depend on the spatial scale of sampling. This is also true on more local scales, such as within steep ecological gradients. Figure 3a plots some of Whittaker's (1960) data for frequency of occurrence of the commonest herb species in replicated 1-m<sup>2</sup> samples along a moisture gradient in the Siskiyou Mountains of Oregon and California. Note that each species occurs in many sample sites in the center of its range, but becomes much more patchily distributed toward the periphery. Rare species (fig. 3b) show qualitatively similar patterns, but they inhabit only a small proportion of the sites even in the center of their distributions, and of course they exhibit much more sampling error.

That the pattern of abundance is greatest in the center of the distribution and

a) Indigo Bunting



b) Scissor-tailed Flycatcher

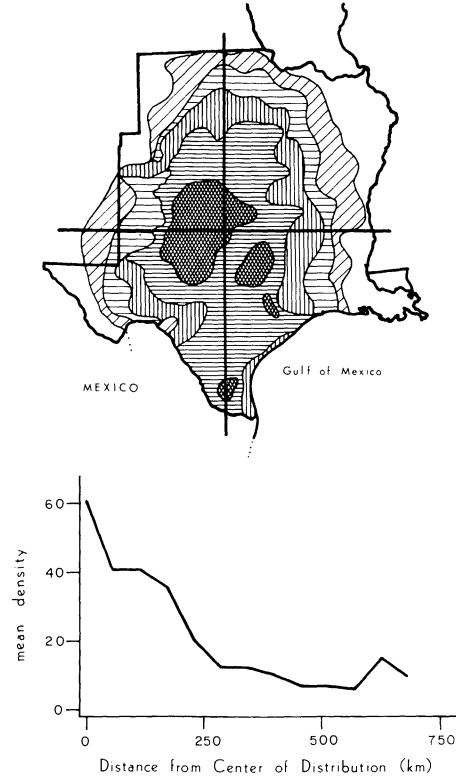
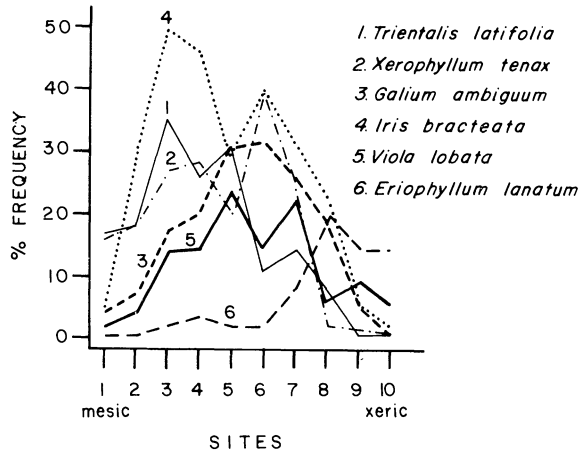


FIG. 2.—Distribution of abundance of two bird species, indigo bunting (*Passerina cyanea*) and scissortailed flycatcher (*Muscivora forficata*) over their geographic ranges. Above, mean population density per standardized census. Below, mean population density along four arbitrary transects running from the center of the range to the periphery as shown above. Compiled from maps drawn by D. Bystrak (see also Bystrak 1979, 1981) and based on the U.S. Fish and Wildlife Service's Breeding Bird Survey.

## a) COMMON HERBS, MOISTURE GRADIENT



## b) RARE HERBS, MOISTURE GRADIENT

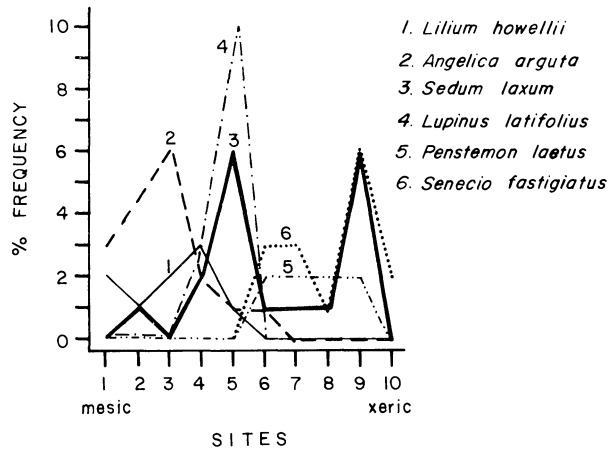


FIG. 3.—Distributions (% frequency in many small replicated samples) of (a) common and (b) rare herbs in the same moisture gradient in the Siskiyou Mountains, plotted from data in Whittaker (1960). Note that the species that occur in a large proportion of samples and presumably also attain high population densities exhibit approximately normal-shaped curves (allowing for missing tails that presumably extend beyond the measured gradient), whereas the rare species show considerable sampling error. The data were not selected except to choose the 6 most abundant species and an arbitrary 6 rare species.

declines gradually toward the boundaries has been emphasized by other investigators (e.g., Hengeveld and Haeck 1982), and appears to be very general: it is observed in a wide variety of organisms and over a range of spatial scales. This is not to say that there are no exceptions. If one looks for them, it is easy to find examples of discontinuous variation in abundance and precipitous declines in population density at a range boundary. Often when such examples have been described, they appear to be related to an abrupt change in a single environmental variable: usually either a physical factor or the population density of an intensively interacting species of competitor, predator, or prey. Thus a striking exception to the gradual decline of bird populations toward the boundaries of their ranges in the Mississippi Valley is the abrupt replacement of two chickadee species (southern *Parus carolinensis* by northern *P. atricapillus*) that J. T. Emlen et al. (MS) attribute to competitive exclusion. For other examples of abrupt distributional boundaries apparently caused by competitive or predator-prey interactions, see Krebs (1978) and Brown and Gibson (1983). Equally rapid changes in density are sometimes associated with abrupt discontinuities in the physical environment. For example, terrestrial plant populations often decline precipitously at the edges of bodies of water or in the region of rapid transition between different soil types. When suitable habitat occurs in isolated patches, such as the montane forests inhabited by boreal plants and animals in desert regions, then there are multiple modes in the distribution of abundance over space. On a sufficiently small scale, the environment of most organisms is patchy, so population density should exhibit a multimodal distribution over space. I do not want to minimize the importance of such discontinuous or multimodal spatial variation in abundance, but I note that often these patterns disappear when data from many replicated sites are averaged or when some other technique is used to analyze the distribution over a wider area. At the extreme of fine spatial and temporal scales all distributions are discontinuous, because a single individual is either present or absent, but this does not tell us much of general interest about how species vary in abundance over their ranges.

#### *Correlation Between Abundance and Distribution Among Species*

Several recent studies (e.g., Hanski 1982a, 1982b, 1982c; Bock and Ricklefs 1983) demonstrate a positive relationship between local abundance and geographic distribution among closely related, ecologically similar species. When closely related plants of the same life form or animals of the same guild are compared, those species that have the highest local population densities tend to inhabit a greater proportion of sample sites within a region and to have wider geographic ranges; conversely, species that are always rare, also have restricted spatial distributions. Thus Hanski (1982c) showed that among species in several guilds of terrestrial arthropods, from soil mites in Finland to scarab beetles in Sarawak, there was a highly significant positive correlation between average density within a site (counting only sample sites where the species occurred) and the number of different local sites (within a few kilometers) where the species was found. Bock and Ricklefs (1983) demonstrated the same pattern in birds on a much

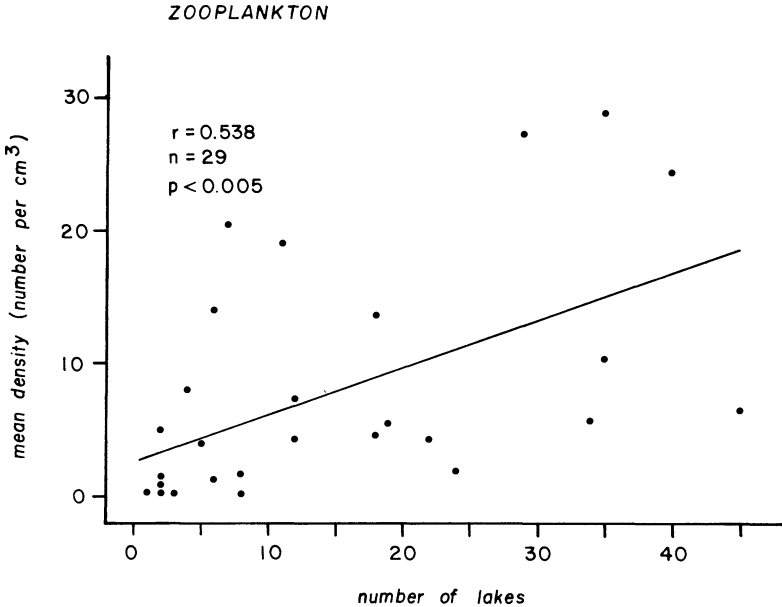


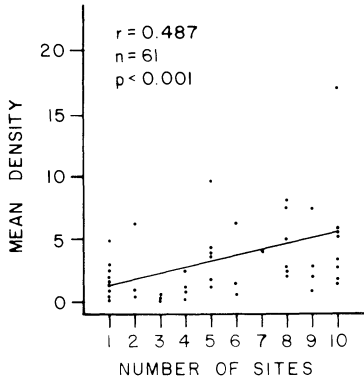
FIG. 4.—Relationship between abundance and distribution of zooplankton species in 45 nearby lakes in northwestern Ontario, plotted from data in Patalas (1971). When mean population density per lake (counting only lakes where the species occurs) is plotted against the number of lakes inhabited, a highly significant positive correlation is obtained.

larger geographic scale. Using Christmas Bird Counts of finch (family *Emberizidae*) species, they found a highly significant positive correlation between average abundance within local censuses (counting only censuses in which the species occurred) and the area of the geographic range.

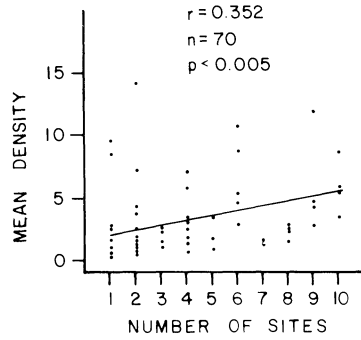
The generality of this pattern can be demonstrated by analysis of other data sets. Plotting Patalas' (1971) data on the abundance and distribution of planktonic crustaceans in 45 lakes in Ontario, Canada, reveals the same relationship described by Hanski: the number of lakes inhabited by a species is positively correlated with its average density in those lakes where it occurs (fig. 4; see also fig. 9a). Reanalysis of Whittaker's (1960) data on plant species distribution in gradients of moisture and elevation in the Siskiyou and Great Smoky Mountains shows highly significant positive correlations between average local density within sites and the range of the species in the gradient (fig. 5). Regardless of plant life form (herb or tree), soil type (diorite, serpentine, or olivine gabbro), or kind of gradient (moisture or elevation), locally abundant species consistently have wide ranges whereas rare species are restricted to a narrow region of the gradient. These correlations are probably considerably more precise than they appear, because Whittaker's data include many species (especially abundant, widely distributed ones) whose distributions apparently extend well beyond the measured gradient. I restricted my analysis to those species that reached a peak



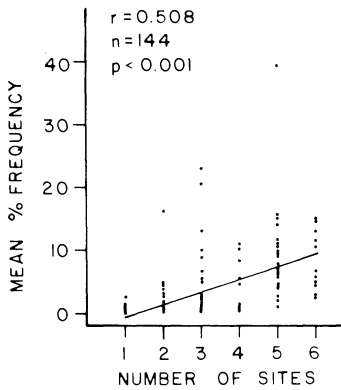
a) HERBS, MOISTURE GRADIENT,  
QUARTZ DIORITE, SISKIYOU MTNS.



b) HERBS, MOISTURE GRADIENT,  
OLIVINE GABBRO, SISKIYOU MTNS.



c) HERBS, ELEVATION GRADIENT,  
QUARTZ DIORITE, SISKIYOU MTNS.



d) TREES, MOISTURE GRADIENT,  
GREAT SMOKY MOUNTAINS

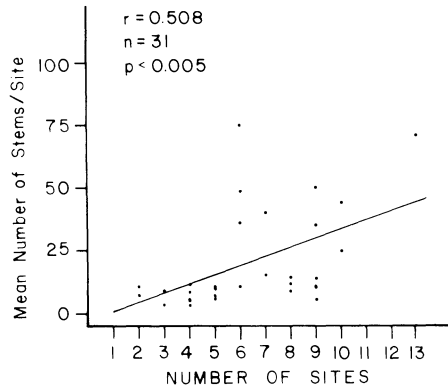


FIG. 5.—Relationship between average local abundance (counting only sites where the species occurred) and number of sites inhabited along a local gradient of rapid ecological change. Data are for terrestrial plants: (a), (b), and (c) replotted from data in Whittaker (1960), and (d) in Whittaker (1956). All species were plotted except those which attained peak abundance at either end of the gradient, because these presumably had distributions that extended well beyond the measured gradient. Note the highly significant positive correlations in all cases.

## HERBS, QUARTZ DIORITE, SISKIYOU MOUNTAINS

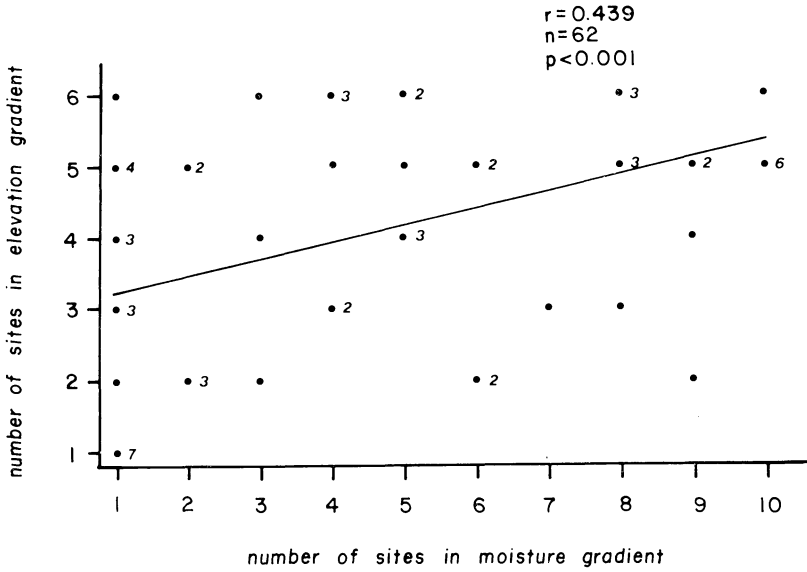


FIG. 6.—Relationship between number of sites inhabited along an elevation gradient and number of sites inhabited along a moisture gradient by herb species in the Siskiyou Mountains. Data are replotted from Whittaker (1960). Numerals beside the points indicate numbers of repeated observations. Note the highly significant positive correlation.

density within the gradient, but nevertheless almost half of the distributions of some species may not have been measured. The effect of this on goodness-of-fit can be seen by comparing the correlation coefficients for the largest data set, herbs in a moisture gradient on serpentine soil, using first the 102 species that occurred most frequently in one of the central 8 of the 10 sites ( $r = 0.26$ ) and then just the 30 species that occurred most frequently in the central 4 of the 10 sites ( $r = 0.49$ ). Because of the overall correlation between abundance and distribution, it is not surprising that species that are widely distributed in a gradient of one environmental variable (moisture) also tend to range more widely in an independent gradient of a second variable (elevation; fig. 6). Finally, compilation of data on another group of North American birds, hawks (families Accipitridae and Falconidae), demonstrates a positive correlation between average local population density and area of the geographic range (fig. 7).

One possible explanation of the correlations presented above is that they are simply the result of statistical sampling processes: the greater the average abundance of a species, the more likely it would be to appear in samples and the greater would be its apparent range. This explanation is inadequate to account for the pattern, however, for at least two reasons. First, although there is a well-documented tendency in statistics for the range of values observed to increase

## NORTH AMERICAN KITES, HAWKS, EAGLES, OSPREYS, FALCONS

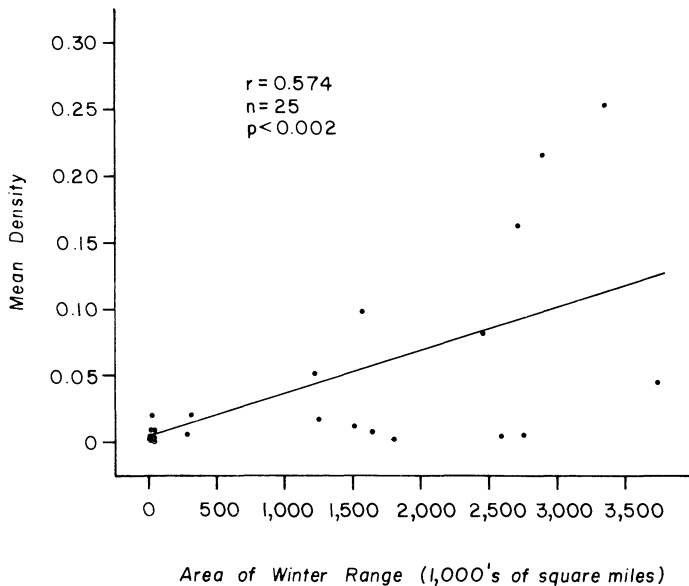


FIG. 7.—Relationship between average local population density (including only sites where the species occurred) and area of the geographic winter range for North American diurnal birds of prey. Densities from Christmas Bird Counts (courtesy of C. E. Bock) and areas from range maps (courtesy of C. S. Robbins). Only species with the majority of their winter ranges in North America were included. Note the highly significant positive correlation.

with the sample size (e.g., for the normal distribution see Tippett [1925]), this effect is much too small to account for the magnitude of change in the geographic range with average population density. Sampling from the same theoretical population, the relative change in the range decreases rapidly with increasing sample size. Thus increasing sample size from 100 to 1,000 increases the expected range by a factor of only 1.30. In contrast, for the data on hawks (all species of which have total population sizes of at least several hundred) shown in figure 7, increasing local densities by a factor of 10 increases the linear dimensions of their geographic ranges (square root of areas) by a factor of approximately 45. The second reason that the pattern cannot be simply a statistical artifact is that in some groups, such as North American land birds, the limits of geographic ranges are known with sufficient accuracy to insure that they are real boundaries. Beyond these range limits local density is not just low; populations simply do not occur.

## THE THEORY

I now propose a single general explanation for both of these patterns: the relatively symmetrical, monotonic decrease in abundance from the center of the

distribution toward all boundaries, and the positive correlation between local population density and extent of spatial distribution among similar species. This theory is based on three major assumptions.

1. This assumption concerns the ecological requirements of species. The abundance and distribution of each species is determined by combinations of many physical and biotic variables that are required for survival and reproduction of its individuals. These requirements define the dimensions of Hutchinson's (1957) multidimensional niche for each species. Variations in population density of a species over space is assumed to reflect the probability density distribution of the required combinations of environmental variables.

2. This assumption concerns the pattern of spatial variation in the environment, which has both stochastic and deterministic components. Some sets of variables (factors) are distributed independently of each other and there is a significant degree of apparently random local variation. Environmental variation also is autocorrelated, so that the probability of sites having similar combinations of environmental variables is an inverse function of the distance between them.

3. This assumption concerns the extent to which species vary in their requirements. I assume that closely related, ecologically similar species differ substantially in only one or a very small number of niche dimensions. This limited differentiation reflects evolutionary constraints on morphology, physiology, and behavior as a result of relatively recent descent from a common ancestor.

#### *Spatial Variation in Abundance Within Species*

From the first two assumptions it follows that population density should be highest near the center of a species range and should decline toward the boundaries. For each species there should be one most favorable site where population density should be greatest because the combination of environmental variables most closely corresponds to the requirements of the species. If spatial variation in the environment is autocorrelated, then with increasing distance from this site the environment will become progressively more different, niche requirements of the species will be met less frequently, and abundance will decline. There will be a decreasing number of local sites where individuals can occur at all, and even within these patches population densities will tend to be lower because resources are scarce and/or conditions approach the limits that can be tolerated.

The exact form of spatial variation in abundance will depend on the number and kind of environmental factors that comprise the niche and on the spatial pattern of variation of these variables. That so many of the empirical distributions resemble normal curves can be explained as follows. The normal probability density function is the limit distribution of a sum of random variables. Therefore it follows that if there are many different niche dimensions which interact additively to determine population density and if these variables are distributed independently of each other in space, then density should approximate a normal distribution along any spatial dimension. This is analogous to the way that many different genes, acting more or less additively and independently tend to produce a normal distribution of a trait in quantitative genetics (Falconer 1960). As in the case of

genetics, it is not necessary that the effect of the environmental variables be exactly additive or random; if there is a sufficiently large number of more or less independent factors that have small effects these variables will tend to result in a normal probability density distribution as a consequence of the central limit theorem.

The additional assumptions required to develop a model that predicts normal distributions of abundance over space are generally consistent with Hutchinson's (1957) formulation of the multidimensional niche. Many different environmental variables, including both physical factors such as temperature, sunlight, water, salinity, pH, and nutrient concentrations, and biotic factors such as competition, availability of prey and mutualists, and ability to avoid predators and pathogens, act in combination to determine local population density and some of these vary independently of each other in space. One feature of the multidimensional niche that at first does not appear consistent with the model is the fact that Hutchinson defined the niche in terms of set theory so that (theoretically) variables interact multiplicatively to determine presence or absence in an all or nothing fashion. "It is supposed that all points in each fundamental niche imply equal probability of persistence of the species, all points outside each niche, zero probability of survival . . . there will however be an optimal part of the niche with markedly suboptimal conditions near the boundaries" (Hutchinson 1957, p. 417). Thus a realistic model of the multidimensional niche and of environmental variation in the niche variables predicts a normal distribution of population density along any transect through the species range. This is consistent with empirical data sets and with the fact that Whittaker (1956, 1960, 1965, and elsewhere) and others have represented such distributions as normal-shaped curves.

Although I suggest the normal probability density distribution as a useful general model of spatial variation in abundance, I admit that there are many exceptions. One of the chief values of the model, however, is its ability to account for even these exceptions. There are two main classes of exceptions (fig. 8), and each corresponds to a case in which a different one of the assumptions of the model is conspicuously violated. Multimodal patterns of abundance occur when the assumption that environmental similarity is a continuously decreasing function of the distance between sites is violated. This happens whenever environmental conditions are patchily distributed, which is almost always true when abundance is analyzed on a sufficiently small spatial scale. The second kind of exceptions, abrupt changes in abundance over a short distance, occurs when, instead of density being limited by the combined effects of many variables, a rapid environmental change causes one factor (or several covarying factors) to assume overwhelming importance. Examples include changes in both the physical environment, such as abrupt interfaces between terrestrial and aquatic habitats, and the biotic environment, such as may be caused by the presence or absence of severe competitors or predators.

Many empirical studies of the influence of specific environmental factors on the abundance and distribution of species have naturally focused on situations in which one particular variable changes abruptly and discontinuously while all others vary so gradually so as to remain essentially constant (e.g., see Krebs 1978;

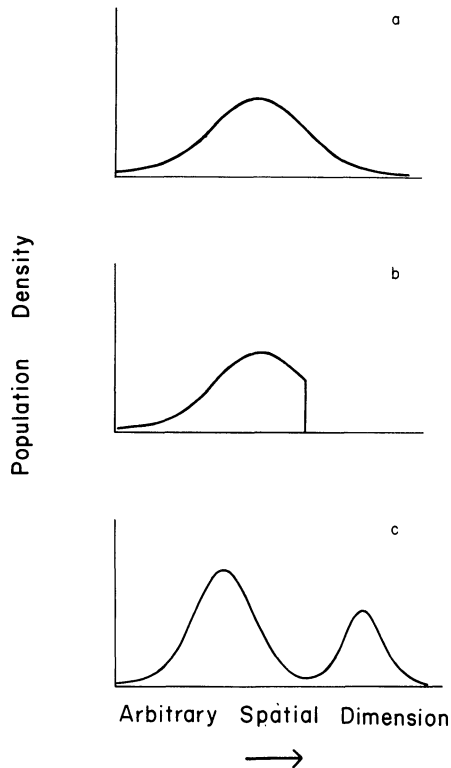


FIG. 8.—Hypothetical distributions of population density along transects through the species range when: *a*, all assumptions of the simple model are met and the distribution approaches a normal curve; *b*, a single limiting variable changes abruptly and the distribution is truncated; and *c*, spatially separated sites have similar combinations of variables and the distribution is multimodal, combined from more than one approximately normal curve.

Brown and Gibson 1983). Although such studies are useful for identifying important dimensions of the niche, in retrospect, I believe they have diverted attention from the multidimensional nature of the niche and importance of this concept for understanding the fundamental relationship between abundance and distribution. Although a single variable can exert a threshold effect to determine whether or not a species occurs on a site, if a population is present its abundance will depend on the contributions of several relatively independent factors. As a consequence of their multiple niche requirements, almost all species have highly restricted distributions; they are confined to only a part of a continent or ocean and they are found in only one or a small number of habitat types. Furthermore, they tend to be limited by different factors at different boundaries of their geographic ranges. For example, different environmental variables and biological processes must cause the death and reproductive failure at opposite extremes of the highly symmetrical distributions of species in environmental gradients on mountainsides or in the intertidal (fig. 1).

*Correlation Between Abundance and Distribution Among Species*

If niches are multidimensional and if spatial variation in the environment tends to be autocorrelated, then there should be a positive correlation between abundance and distribution for those species that differ in only a very few niche dimensions. Changes in requirements for one or a small number of variables that increase local abundance within the range should also enable the species to colonize new areas at the periphery of its distribution where those factors were previously limiting. Stated more generally, those species that can tolerate conditions and acquire sufficient resources so as to attain high densities in some places, should also be able to occur (albeit often at lower densities) in many other sites over a relatively large area. On the other hand, species that are otherwise similar, but have such narrow requirements that they cannot attain high abundances anywhere, will necessarily be restricted to the few sites within the limited geographic region where they can satisfy their needs. Thus there are positive correlations between maximum density, average density over the area where the species occurs, the number of sites inhabited within a local region, and the area of the geographic range, but only for closely related, ecologically similar species.

These correlations break down when distantly related, ecologically dissimilar species are compared, because such organisms have evolved niches of entirely different configuration. Even among such species, however, there appear to be some predictable relationships between abundance and distribution that can be explained in terms of their niche requirements. For example, the laws of thermodynamics dictate that populations of predators be less dense than prey of comparable body size and reproductive rate. If predators and prey are constrained by the dynamics of speciation and extinction processes (see MacArthur and Wilson 1967; Rosenzweig 1975; Brown 1981) to have similar distributions of population sizes (or at least similar minimum population sizes) among species, then it follows that, on average, individual consumers should use the environment on a larger spatial scale and their populations should exhibit lower densities and wider distributions than producers. Similarly, organisms of large body size interact with the environment on a larger scale than smaller species that can better exploit the spatial heterogeneity that Hutchinson (1959, p. 155) termed the "mosaic nature of the environment." Thus larger organisms tend to have less dense, more widely distributed populations, whereas smaller ones attain higher densities and exhibit more local and patchy distributions (see Brown 1981).

The empirical relationship between abundance and distribution was called to my attention by the papers of Hanski (1982*a*, 1982*c*) and Bock and Ricklefs (1983). The latter presents no detailed explanation for the pattern, and I disagree with Hanski's interpretation, which he calls the core and satellite species hypothesis. From data primarily on the distribution of terrestrial arthropods among local regions of superficially similar habitat, Hanski noted not only that frequency of occurrence among sites is positively correlated with average abundance (fig. 9*a*), but also that the distribution among species of number of sites inhabited is bimodal (fig. 9*b*). He assumed that all sites are equally suitable for all species and that species distributions among those sites vary randomly over time. He then

## DESERT RODENTS

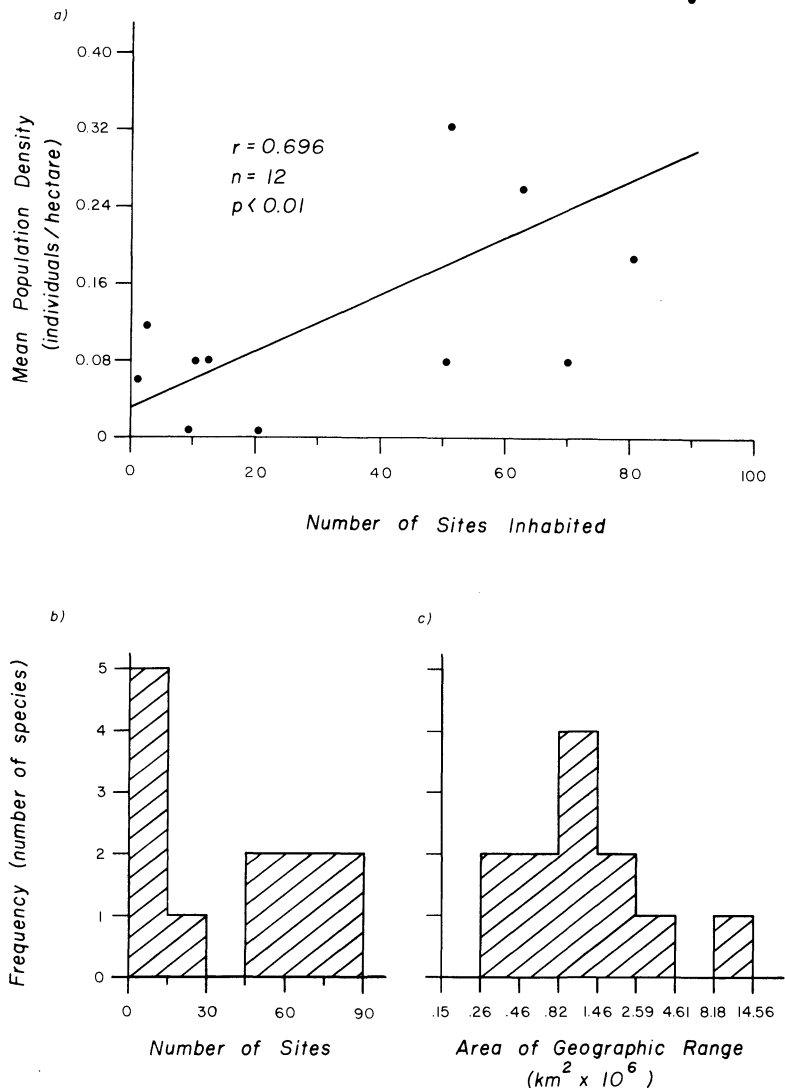


FIG. 9.—Distributions and abundance of 12 desert rodent species that occur together in southern Nevada (plotted from data of Jorgensen and Hayward [1965]). *a*, Relationship between mean population density per site (counting only sites where the species occurred) and the number of sites (out of a total of 115) inhabited. Note the significant positive correlation. *b*, Frequency distribution of the 12 species with respect to the number of sites inhabited. Such a bimodal distribution is the basis of Hanski's (1982*a*, 1982*b*, 1982*c*) division of a community into core and satellite species (right and left modes, respectively). *c*, Frequency distribution of the 12 species with respect to the areas of their geographic ranges (plotted on a logarithmic scale from measurements of range maps in Hall [1981]). Note the unimodal, approximately lognormal distribution.



developed a simple model which suggests that communities are comprised of two kinds of species: core species, which are locally abundant and inhabit virtually all suitable sites, and satellite species, which are rare and distributed essentially at random among a few sites. I have three criticisms of Hanski's model. First, it is highly unlikely that all sites are equally favorable for all species. It is much more realistic to assume that the differences in local distribution and abundance of closely related, ecologically similar species, although they may have a stochastic component, are primarily the result of different requirements and tolerances. Otherwise, what determines the population densities and spatial distributions? Second, Hanski's model is based on a stochastic process analogous to genetic drift affecting allele frequency, which assumes that the distributions of species vary randomly in time between two stable boundary conditions: ubiquitous (inhabiting all local sites) and extinct throughout the region. Therefore, Hanski must invoke colonization from outside the local area to account for the high frequency of species that are found in only a very few sites instead of none at all as the random walk model would predict. This seems contrived and unrealistic, because a large scale perspective would show that many of these rare species are unlikely to produce such colonists because they are just as uncommon in surrounding regions; they are species of limited geographic distribution and low average abundance. A final and related point is that the bimodal distribution of frequency of occurrence is almost certainly an artifact of sampling a small number of sites with a local region. Other evidence suggests that both local population densities and areas of entire geographic ranges exhibit unimodal, approximately lognormal distributions among species (e.g., Preston 1962; Williams 1964; Rapoport 1982). Since these two variables are positively correlated with each other, this means that there are many rare, restricted species and few abundant, widespread ones. Now if one samples a limited number of sites within a local region, one finds a frequency distribution with two modes, one, a result of the rare species that are restricted to a few sites, and the other, a result of the common species that inhabit many or all of the sites (fig. 9*b*; see also Hanski 1982*c*, figs. 8, 9, 10). If the spatial frame of reference were expanded to include the entire geographic ranges of all the species, however, the second mode would disappear because the frequency distributions of areas of geographic ranges are unimodal and approximately lognormal (e.g., fig. 9*c*).

#### GENERAL DISCUSSION

The ideas developed in this paper constitute a very general, qualitative kind of theory. The empirical patterns of variation in abundance over space within species and correlation between local density and geographic distribution among species can be explained with simple arguments that follow logically from assumptions that seem to be robust empirical generalizations. I have shown that the theory can be derived more formally by redefining the concept of the multidimensional niche so that the distribution of population density over space should approach a normal probability density distribution. If these ideas have merit, eventually it should be possible to develop more precise mathematical models that

will generate specific testable predictions about niche relationships within and among species. Such models would differ from those currently in vogue (but see MacArthur and Wilson 1967), because they would focus on variation in abundance over space rather than over time and because they would be based explicitly on the concept of multidimensional niches.

My synthesis builds on themes developed by Hutchinson (1957, 1959; see also Whittaker 1965; McNaughton and Wolf 1970) in his classical papers on the multidimensional niche and diversity of species. I find it interesting that these papers of Hutchinson have so often been cited, yet the ideas I have resurrected here seem to have had little direct impact on the development of ecological and biogeographic theory. Clearly we have much to learn before we can answer Hutchinson's question, Why are there so many kinds of organisms? I believe the statistical approach I have begun to develop here focuses attention on some of the important questions, but it does not yet provide many satisfying answers. The species in different taxonomic groups, life forms, and guilds exhibit different relationships between abundances and distribution. Aside from a few general comments on the consequences of trophic status and body size (see Hutchinson 1959; Brown 1981), I have not explored these relationships, although the central questions of population and community ecology can be phrased in these terms: How many different factors constitute major dimensions of the niche of a species and how do these vary in space and time so as to limit abundance and distribution? How do the multidimensional niches of coexisting species relate to each other? How does this organization vary as the identity and diversity of species changes over the surface of the earth? Elsewhere (Brown 1981) I have advocated what I now call a statistical approach to ecology that focuses on the distributions of variables among many discrete units, either individuals within species or species within local communities and larger geographic regions. The present paper provides an example of this approach, which is focused here on the spatial distribution of individuals within and between closely related populations.

Some critics may object that the perspective that I have adopted ignores the really interesting and important problem: what environmental variables and population attributes determine the abundance and limit the distribution of particular local populations? Indeed, we need a better understanding of these mechanisms in order to pursue the approach that I advocate. On the other hand, there are over two million species in the world, each has its own unique geographic range, and its local abundance is determined by different combinations of environmental variables in different parts of its range. Obviously, to describe and explain all this diversity in detail is an impossible task. Sometimes in such cases scientific progress can be made by finding a frame of reference in which the apparently idiosyncratic features of small systems are revealed as general statistical patterns of larger systems that then suggest common explanations. There appears to be such a general relationship between abundance and distribution for most species and closely related groups of species that has important implications for many areas of ecology and evolutionary biology.

First consider the number of and degree of independence among the environmental variables that importantly affect the abundance and distribution of each

species. Preliminary investigations suggest that the number of independent niche dimensions is modest, perhaps between five and 10 for most species. This would be large enough to produce the fairly regular spatial patterns described above, and small enough to produce the kinds of exceptions often observed (fig. 8). On the one hand, ecological constraints appear to limit the number of dimensions. Computer simulations (performed in collaboration with M. Sanderson and A. Harvey) show that as the number of independent limiting factors increases, it becomes increasingly difficult for the species to exist anywhere, because favorable combinations of all variables become increasingly unlikely to occur for purely statistical reasons. On the other hand, when only one or two factors limit distribution and abundance, populations should be subject to strong directional selection to adapt to these conditions, thereby diminishing their negative effects until other factors become limiting and the intensity of selection resulting from any one factor is reduced. Such evolution of the niche should reinforce the tendency of independent limiting factors to result in symmetrical, normal-shaped curves of abundance over the range of species. The ecological and evolutionary consequences of the dimensionality of niches seem to offer opportunities for both empirical and theoretical research.

A related problem also concerns the dimensionality of the niche and its consequences for the abundance and distribution of species. Many of the ideas of current evolutionary ecology are based on widespread acceptance of the trade-off principle. The data and ideas presented in this paper (see also Hanski 1982c) appear to challenge currently held notions about the ecological consequences of the purported trade-off between specialization and generalization implied by the saying "jack-of-all-trades-master-of-none." This dictum would predict that specialists with narrow tolerances should be more efficient in exploiting a more limited range of resources, and hence should have more restricted distributions but higher local abundances than generalists. I can find no evidence of such a trade-off, at least among closely related, ecologically similar species. There is a very general tendency for species that have restricted distributions (presumably because they are specialized and able to tolerate only a narrow range of conditions) to be rare, whereas more widespread species attain higher local population densities. At least some data (e.g., fig. 6) also suggest a lack of trade-offs among different niche dimensions; species that can tolerate wide variation in one factor also tend to be tolerant of other factors, and hence to be both locally abundant and spatially widespread. There are apparent exceptions—species that attain high densities within particular habitat types but are restricted to small areas (e.g., see Rabinowitz 1981)—but I believe that these species usually violate an assumption of my model. They differ from their nearest wide-ranging relatives along many niche dimensions, and this is indicated by the fact that they are often members of well-differentiated endemic taxa. For example, a suite of special adaptations to several niche variables must be required to exploit highly localized, physically harsh environments such as salt marshes, hypersaline lakes, and hot springs, and the few species that can inhabit these are often both locally abundant and well differentiated from their relatives in more benign habitats (Terborgh 1973; Brown 1981; Brown and Gibson 1983). Thus my model makes predictions about the

ecological and evolutionary consequences of niche dimensionality that can be tested by evaluating further the relationships among environmental limiting factors, patterns of abundance and distribution, and degree of evolutionary differentiation in taxa for which adequate data are available.

In order to account completely for the general relationships between abundance and distribution, it is necessary to understand not only the multidimensional nature of the niche but also the spatial variation in the dynamics of population growth and regulation. Other investigators have noted and proposed explanations for the gradual decline in population density toward the edge of the range. For example, Grinnell (1922) and Wiens and Rotenberry (1981) suggested that the geographic distributions of bird populations may represent a dynamic equilibrium between the exportation of emigrants from source areas (usually regions near the center of the geographic range where birth rates exceed death rates) and the importation of these individuals into sink areas (usually regions at the periphery of the range where this continual immigration sustains local populations whose death rates exceed birth rates). Although such centrifugal dispersal might account, at least in part, for spatial variation in population density in organisms as vagile as birds (but see J. T. Emlen et al. [MS] for alternative hypotheses), it probably cannot explain similar patterns in less mobile organisms, such as plants with limited seed dispersal. Nevertheless, it should be possible to develop and test mathematical models that account for spatial variation in population dynamics by considering the effects of both population density and extrinsic environmental variables on the rates of birth, death, immigration, and emigration (Hanski 1982*c*, Holt 1983; B. A. Maurer and J. H. Brown, MS).

The fact that local abundance may depend to some extent on the pattern of distribution on a larger spatial scale has important implications for community ecology. It has long been recognized that the frequency distribution of population densities among species within a local region exhibits a regular pattern in which there are many relatively rare species and only a few common ones (e.g., MacArthur 1957; Preston 1962; Williams 1964; Whittaker 1965), but this has long defied a satisfying biological explanation (but see May 1975; Sugihara 1980). The present paper focuses attention on the fact that many of the locally rare species represent the tails of the spatial distributions of species that are more common in other regions. This appears to support Gleason's (1926) classical "individualistic" concept of species distribution and community organization: assuming dispersal is not limiting, species tend to occur relatively independently of most other species wherever environmental conditions are suitable, and local population densities are determined by the extent to which the local environment meets the requirements of individuals. Over their geographic ranges most species coexist with many different combinations of other species, and even those that are sufficiently abundant to dominate their guilds and communities in some regions are rare and relatively unimportant in others. The limited study areas of most community ecologists are too small to be representative of the variety of conditions that have shaped the evolution of the niches of most of the species. Note that this Gleasonian view does not necessarily imply, as some authors have suggested, that interspecific interactions are unimportant in determining the abundance and distri-

bution of species and the organization of communities. It simply implies that communities are not highly integrated units comprised of many species that have coevolved to interact specifically with each other. The general approach that I apply here to analyze the statistical distribution of individuals within species and among closely related species, might also be used in an analogous way to investigate the density and distribution of species within and among communities.

So far in this paper I have treated species and their niches as if they were constant over space, even though I am aware of substantial geographic variation in some species. This simplifying assumption seems justified so long as the ecological variation within species is small relative to the differences between species. This must be true generally, because it is the basis of classifying closely related populations into species.

Consideration of this problem, however, raises important questions about the evolutionary dynamics of speciation and extinction that underlie the general relationship between abundance and distribution of species. The apparent absence of a trade-off between generalists and specialists suggests a wide distribution of evolutionary success among species. If I define success of species as the analogue of fitness of individuals, the probability of leaving descendants over evolutionary time, then in general the abundant, widespread species must be more successful than the rare, restricted ones. If the latter have substantially higher extinction rates, however, whence come the new species that replace them? Do the abundant, widely distributed species continually bud off small, isolated differentiating populations around the margins of their geographic ranges? This mechanism of allopatric speciation seems consistent not only with much evolutionary theory (e.g., see Mayr 1963; Futuyma and Mayer 1980; Wiley 1981), but also with the ecological patterns and processes developed here.

In particular the ecological relationships appear to support some but not all of Brown's (1957, 1959) ideas about general adaptation and centrifugal speciation. Central populations of widespread, abundant species would seem relatively resistant to rapid, directional evolutionary change. Not only do these populations so dominate their guilds and communities that relatively little improvement in ecological performance is likely, they are also distributed relatively continuously over a variety of local environments so that there is little opportunity for spatial isolation to facilitate genetic differentiation of locally adapted populations. Thus most of the selection will be stabilizing selection that tends to maintain the generalized adaptations. In contrast, peripheral populations of the same widespread species will tend to be not only rare, but also restricted to isolated patches of suitable habitat. If this spatial isolation reduces gene flow sufficiently, these peripheral populations can respond to directional selection, adapt to local conditions, and eventually differentiate into new species. Over evolutionary time such newly formed species could increase substantially in abundance and distribution in two situations: if the environment changes so as to favor forms with their special adaptations, or if they are able to evolve to increase their share of limited resources, perhaps in part by increasing their ability to compete with ancestral and other closely related species.

This evolutionary scenario, based on ecological and genetic processes operating

at the population level, would seem to go a long way toward explaining many macroevolutionary phenomena.

1. The apparent stasis observed in many fossil species over long periods of evolutionary time (Eldredge and Gould 1972; Stanley 1979) can be attributed to stabilizing selection acting on the central populations of widespread, abundant species. Representatives of these populations should dominate the fossil record because of the statistics of sampling, so that rate of evolution within most species should appear to be very slow.

2. The association between substantial evolutionary change and speciation events (Eldredge and Gould 1972; Stanley 1979) can be explained in terms of strong directional selection resulting in the local adaptation and genetic differentiation of isolated peripheral populations. In order to become sufficiently abundant and widespread to appear in the fossil record, newly formed species would usually have to benefit from environmental change or undergo enough ecological (and usually also morphological) differentiation to compete successfully with ancestral and other closely related species. This would also account for the commonly observed pattern (Hennig 1979) that after a speciation event one of the resulting sister species is usually extremely similar to the ancestral species whereas the other is highly differentiated.

3. Many macroevolutionary trends that appear to be the result of different speciation or extinction rates within different phyletic lines might be explained in terms of the positive correlation between abundance and distribution among closely related species. Compared to their rare, restricted relatives, abundant widespread species should have lower extinction rates. Whether they should also exhibit higher speciation rates is not so clear, especially since most speciation should occur in small, peripheral, isolated populations, so it may be difficult to detect in the fossil record. Despite these kinds of difficulties it should be possible to develop and test macroevolutionary hypotheses based on the ecological relationships between abundance and distribution. For example, Hansen (1980) and Jablonski and Lutz (1983) describe relationships between speciation and extinction rates, area of geographic range, and mode of larval dispersal in fossil mollusks: species with planktonic larvae have lower rates of both speciation and extinction, and larger geographic ranges than species that brood their young. If this partly results from the fact that these species are distributed along a spectrum from rare and restricted to abundant and widespread, then the planktonic forms should on average have maintained higher local population densities than their nonplanktonic relatives. This could be tested if the fossil record can be used to estimate relative population densities.

4. Finally, I would expect major evolutionary innovations to evolve initially as special adaptations of rare, restricted populations (usually at the periphery of the geographic or ecological ranges of their more abundant and widespread relatives) in response to directional selection caused by unusual local environmental conditions. This seems to fit well with recent empirical findings of Jablonski et al. (1983) that new phyletic lines appear to have evolved primarily in marginal habitats.

Because of all these implications, I encourage further investigation of macroscopic, statistical patterns in the spatial and temporal distributions of individuals

within species and among closely related species. In trying to characterize these patterns and understand the mechanistic processes that are responsible for them, it should be possible to make progress in integrating the disciplines of ecology, biogeography, population genetics, and evolution.

#### SUMMARY

There appears to be a general relationship between abundance and distribution that has two parts. First, within species, population density tends to be greatest in the center of the range and to decline gradually toward the boundaries. This pattern holds over a range of spatial scales from steep environmental gradients within local regions to the entire geographic range. Exceptions include: (1) abrupt changes in abundance that usually correspond to sharp, discontinuous changes in single environmental variables; and (2) multimodal patterns of abundance that are caused by environmental patchiness. The second general relationship is that among closely related, ecologically similar species spatial distribution is positively correlated with average abundance. Again this pattern holds over a variety of spatial scales from local regions to entire geographic ranges. These empirical patterns have already been reported in the literature, but their generality is demonstrated by analysis of additional data for diverse kinds of organisms.

A single general theory accounts for these observations and follows logically from three assumptions. First, the abundance and distribution of each species are limited by the combination of physical and biotic environmental variables that determines the multidimensional niche. Second, spatial variation in these environmental variables is somewhat stochastic but autocorrelated, so that nearby sites tend to have more similar environmental conditions than more distant ones. Third, closely related, ecologically similar species differ in no more than a very few niche dimensions. A more formal model can be developed that predicts that under these assumptions the distribution of population density over space should approximate a normal probability density distribution. Most exceptions to this predicted pattern can be explained as cases in which assumptions of the model are clearly violated.

This paper represents an example of a statistical approach that should be useful for investigating complex ecological systems comprised of many components, such as species of many individuals or communities of many species. The general relationships between abundance and distribution developed here eventually should contribute to our understanding of the biogeography, population genetics, and evolution of species as well as the ecological attributes of populations and communities.

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## LITERATURE CITED

- Andrewartha, H. G., and L. C. Birch. 1954. *The distribution and abundance of animals*. University of Chicago Press, Chicago.
- Beals, E. W. 1969. Vegetational change along altitudinal gradients. *Science* 165:981–985.
- Bock, C. E., and R. E. Ricklefs. 1983. Range size and local abundance of some North American songbirds: a positive correlation. *Am. Nat.* 122:295–299.
- Brown, J. H. 1981. Two decades of homage to Santa Rosalia: toward a general theory of diversity. *Am. Zool.* 21:877–888.
- Brown, J. H., and A. C. Gibson. 1983. *Biogeography*. Mosby, St. Louis, Mo.
- Brown, W. L. 1957. Centrifugal speciation. *Q. Rev. Biol.* 32:247–277.
- . 1959. General adaptation and evolution. *Syst. Zool.* 7:157–168.
- Bystrak, D. 1979. The breeding bird survey. *Sialia* 1:74–79.
- . 1981. The North American Breeding Bird Survey. *Stud. Avian Biol.* 6:34–41.
- Delcourt, H. R., D. C. West, and P. A. Delcourt. 1981. Forests of the southeastern United States: quantitative maps for aboveground woody biomass, carbon, and dominance of major tree taxa. *Ecology* 62:879–887.
- Eldredge, N., and S. J. Gould. 1972. Punctuated equilibria: an alternative to phylogenetic gradualism. Pages 82–115 in T. J. M. Schopf, ed. *Models in paleobiology*. Freeman Cooper, San Francisco.
- Falconer, D. S. 1960. *Introduction to quantitative genetics*. Oliver & Boyd, Edinburgh.
- Field, J. G., and F. T. Robb. 1970. Numerical methods in marine ecology: gradient analysis of rocky shore samples from False Bay. *Zool. Afr.* 5:191–210.
- Futuyma, D. J., and G. C. Mayer. 1980. Non-allopatric speciation in animals. *Syst. Zool.* 29:254–271.
- Gleason, H. A. 1926. The individualistic concept of plant associations. *Bull. Torrey Bot. Club* 53:7–26.
- Grinnell, J. 1922. The role of the “accidental.” *Auk* 39:373–380.
- Hall, E. R. 1981. *The mammals of North America*. Wiley, New York.
- Hansen, T. A. 1980. Influence of larval dispersal and geographic distribution on species longevity in neogastropods. *Paleobiology* 6:193–207.
- Hanski, I. 1982a. Communities of bumblebees: testing the core-satellite species hypothesis. *Ann. Zool. Fenn.* 19:65–73.
- . 1982b. Distributional ecology of anthropochorus plants in villages surrounded by forest. *Ann. Bot. Fenn.* 19:1–15.
- . 1982c. Dynamics of regional distribution: the core and satellite species hypothesis. *Oikos* 38:210–221.
- Hengeveld, R., and J. Haeck. 1982. The distribution of abundance. I. Measurements. *J. Biogeogr.* 9:303–316.
- Hennig, W. 1979. *Phylogenetic systematics*. 3d ed. Transl. by D. D. Davis and R. Zanderl. University of Illinois Press, Urbana.
- Holt, R. 1983. Immigration and the dynamics of peripheral populations. Pages 680–694 in A. Rhodin and K. Miyata, eds. *Advances in herpetology and evolutionary biology*. Museum of Comparative Zoology, Harvard University, Cambridge, Mass.
- Hutchinson, G. E. 1957. Concluding remarks. *Cold Spring Harbor Symp. Q. Biol.* 22:415–427.
- . 1959. Homage to Santa Rosalia, or why are there so many kinds of animals? *Am. Nat.* 93:145–159.
- Jablonski, D., and R. A. Lutz. 1983. Larval ecology of marine benthic invertebrates: paleobiological implications. *Biol. Rev.* 58:21–89.
- Jablonski, D., J. J. Sepkoski, D. J. Bottjer, and P. M. Sheehan. 1983. Onshore-offshore patterns in the evolution of Phanerozoic shelf communities. *Science* 222:1123–1125.
- Jorgensen, C. D., and C. L. Hayward. 1965. *Mammals of the Nevada test site*. Brigham Young Univ. Sci. Bull. Biol. Ser. 6(3):1–81.



- Krebs, C. J. 1978. *Ecology: the experimental analysis of distribution and abundance*. Harper & Row, New York.
- MacArthur, R. H. 1957. On the relative abundance of bird species. *Proc. Natl. Acad. Sci. USA* 43:293–295.
- . 1972. *Geographical ecology*. Harper & Row, New York.
- MacArthur, R. H., and E. O. Wilson. 1967. *The theory of island biogeography*. Princeton University Press, Princeton, N.J.
- McNaughton, S. J., and L. L. Wolf. 1970. Dominance and the niche in ecological systems. *Science* 167:131–139.
- May, R. M. 1975. Patterns of species abundance and diversity. Pages 81–120 *in* M. L. Cody and J. M. Diamond, eds. *Ecology and evolution of communities*. Harvard University Press, Cambridge, Mass.
- Mayr, E. 1963. *Animal species and evolution*. Harvard University Press, Cambridge, Mass.
- Patalas, K. 1971. Crustacean plankton in forty-five lakes in the Experimental Lakes Area, northwestern Ontario. *J. Fish. Res. Board Can.* 28:231–244.
- Preston, F. W. 1962. The canonical distribution of commonness and rarity. *Ecology* 43:185–215, 410–432.
- Rabinowitz, D. 1981. Seven forms of rarity. Pages 205–215 *in* H. Synge, ed. *The biological aspects of rare plant conservation*. Wiley, New York.
- Rapoport, E. H. 1982. *Areography: geographical strategies of species*. Pergamon, Oxford.
- Rosenzweig, M. L. 1975. On continental steady states of species diversity. Pages 121–141 *in* M. L. Cody and J. M. Diamond, eds. *Ecology and evolution of communities*. Harvard University Press, Cambridge, Mass.
- Stanley, S. M. 1979. *Macroevolution*. Freeman, San Francisco.
- Sugihara, G. 1980. Minimal community structure: an explanation of species abundance patterns. *Am. Nat.* 116:770–787.
- Terborgh, J. 1973. On the notion of favorableness in plant ecology. *Am. Nat.* 107:481–501.
- Tippett, L. H. C. 1925. On the extreme individuals and the range of samples taken from a normal population. *Biometrika* 17:364–387.
- Walter, H. 1979. *Vegetation of the earth and ecological systems of the geo-biosphere*. Springer-Verlag, Berlin.
- Whittaker, R. H. 1956. Vegetation of the Great Smoky Mountains. *Ecol. Monogr.* 22:1–44.
- . 1960. Vegetation of the Siskiyou Mountains, Oregon and California. *Ecol. Monogr.* 30:279–338.
- . 1965. Dominance and diversity in land plant communities. *Science* 147:250–259.
- Wiens, J. A., and J. T. Rotenberry. 1981. Censusing and evaluation of avian habitat occupancy. *Stud. Avian Biol.* 6:522–532.
- Wiley, E. O. 1981. *Phylogenetics, the theory and practice of phylogenetic systematics*. Wiley, New York.
- Williams, C. E. 1964. *Patterns in the balance of nature and related problems in quantitative ecology*. Academic Press, New York.