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Does Interspecific Competition Limit the Sizes of Ranges of Species?

SYDNEY ANDERSON[1] AND KARL F. KOOPMAN[1]

ABSTRACT

A "competition hypothesis" states that the species in faunas with more species (more diversity) have greater competition, narrower niches, and therefore smaller geographic ranges (less distribution). An alternative "available space hypothesis" states that species occupy suitable available space without regard to the presence or absence of other species. We use American bats and North American rodents as groups to discriminate between the two hypotheses and see that available space is a better predictor of distribution than is diversity. Thus, the competition hypothesis is weakened and the available space hypothesis is strengthened.

INTRODUCTION

In a paper discussing continental steady states and species diversity, Michael Rosenzweig (1975) published a tantalizing graph of data on North American bats and turtles and commented as follows: "average range size declines as diversity increases. Perhaps the decline results from more intense habitat selection in more diverse areas." This was a digression from his main thesis and he did not pursue the matter. Later Rosenzweig (1978) did discuss the "density of a phenotype's competitors" and the depression of fitness and how these may relate to speciation, but he did not return to the relationship between distributional area and diversity.

Calling Rosenzweig's tentative hypothesis above "the competition hypothesis," we develop it in greater detail, then consider an alternative hypothesis, and finally test these hypotheses with data from North and South American Chiroptera and North American Rodentia.

ACKNOWLEDGMENTS

Part of this material was presented (by Anderson) at a symposium on the origin and maintenance of diversity held at the Field Museum in May 1979. Discussion with people there helped in further revision. We are

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grateful to the various sponsors of fieldwork and collectors, especially those of recent years, who have amassed the voluminous raw data on bat distributions (compiled for the first time for South America by Koopman) summarized here. The fruits of the labors of these unnamed colleagues, past and present, will continue to be harvested for decades. The first draft of this paper was written by Anderson. We are grateful to Justine Anderson and Muriel Williams for typing and suggestions and to Russell Robbins for helping tally, compute, and plot data. We are grateful to Dr. François Vuilleumier and Dr. Michael Rosenzweig for helpful and searching comments, and to three persons who reviewed the paper for the journal *Ecology* and also offered helpful comments.

THE COMPETITION HYPOTHESIS

A more detailed consideration of "more intense habitat selection in more diverse areas" and how this might influence the sizes of geographic ranges of species leads to the following amplification:

1. Resources are finite.
2. Species tend to maximize their use of available resources. This occurs on both a short-term ecological scale and a long-term evolutionary scale.
3. Therefore, species compete. Competition operates on both the ecological and the evolutionary scale. The concept of competition is highly varied in the literature. It is not feasible to explore these variations here, but it should be understood that our usage is broad. The nature of the competition and the degree may differ or may vary with time. Competition, at least in theory, can range from negligible to complete. In the latter case, populations of two equally talented (hypothetical) species in the same area would tend to fluctuate stochastically until one becomes extinct. This statement may seem strange in terms of customary competitive exclusion models, which do not consider the logical extremes of the continuum of degrees of competition. The remaining species, incidentally, might also fluctuate stochastically until extinction later. It is not realistic to assume that any two different species are equally talented (i.e., respond in exactly the same way to all environmental conditions). Often, one species will succeed and the other will become extinct because they are not in fact equally talented under the given conditions. This is the focus of most competitive exclusion models. We suggest, however, that populations generally do fluctuate in a stochastic manner, not because different species are equally talented but because the environment will fluctuate independently of the species, and exactly how talented they are may be largely irrelevant. In other words, their maladaption to a changed environment is more important in the outcome than their adaptation to a former environment. The prevalence and significance of the stochastic aspects of such processes deserve more attention by ecologists and evolutionists in our opinion. In reference to speciation, this sort of stochastic aspect has been dubbed Wright's Rule (see Krohn, 1979, and Schopf, 1979, for discussion).
4. One result of competition may be specialization. Specialization by a species for the use of some subset of resources may increase the probability of survival of the specialized species (i.e., the user of narrower subsets of resources) *in* those areas having these resources.
5. Different physical conditions vary geographically and in large part non-congruently.
6. When the tolerable physical conditions for a species are more restricted, fewer places will have these conditions and the geographic range of the species should be smaller.
7. If the presence of more species (i.e., diversity or factor A) is correlated with more restricted conditions on the average (factor B), *then,* given 5 and 6 above, diversity (factor A) will also be correlated (negatively) with geographic extent of range (i.e., distribution or factor C).

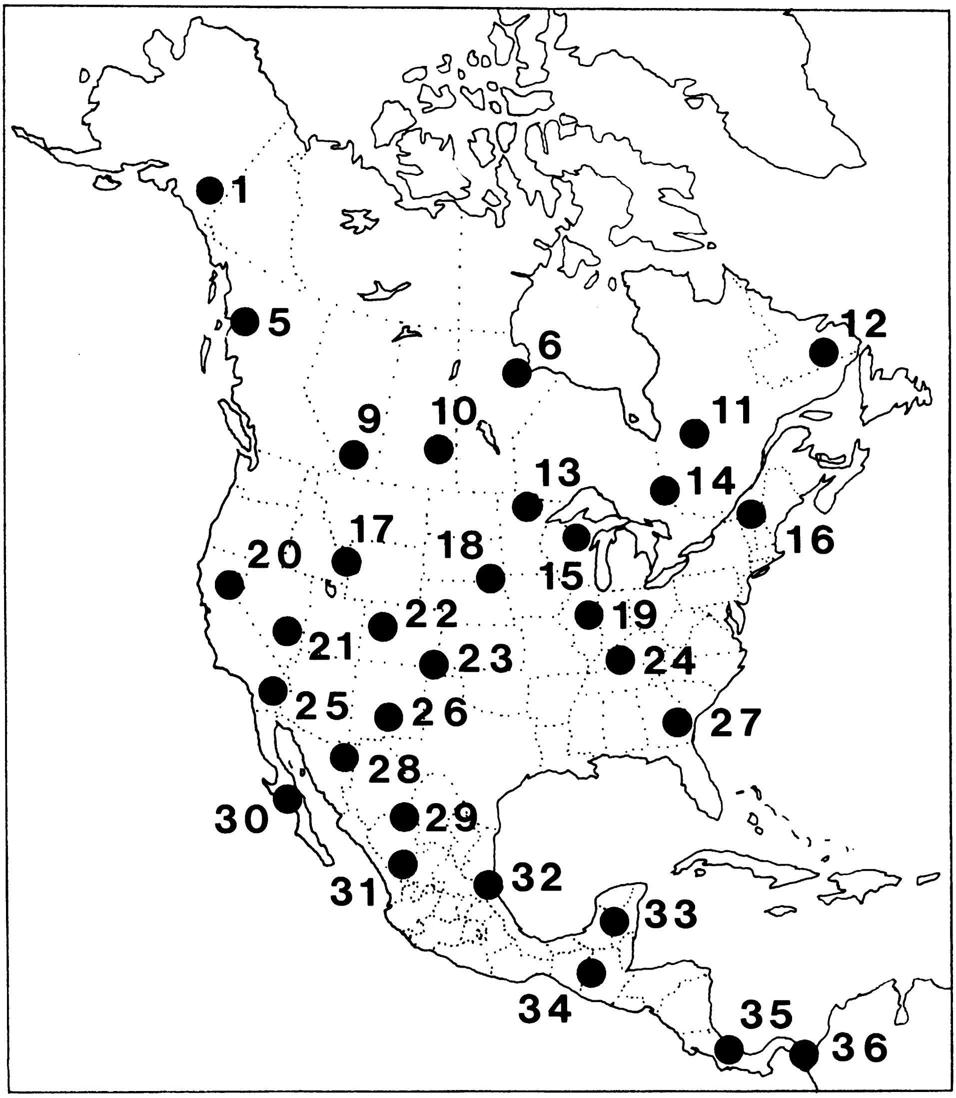

FIG. 1. Map of faunal sample sites in North America.

We can measure A and C; we cannot easily measure B. A given correlation of A and C (diversity and distribution) does not necessarily tell us anything about B because more than one possible model may relate A and B to C. We will outline one alternative hypothesis to the competition hypothesis and proceed to test both models.

If a relevant set of data does not fit a model, then we have grounds for doubting one or more of the conditions of the model or hypothesis.

For example, if we are willing to postulate as a model that twice as many species will need to divide the habitat so that each one has a narrower niche, and if we assume that this means that the suitable area will be smaller, we would find a negative correlation between diversity and distribution.

Beginning with one of Rosenzweig's sam-

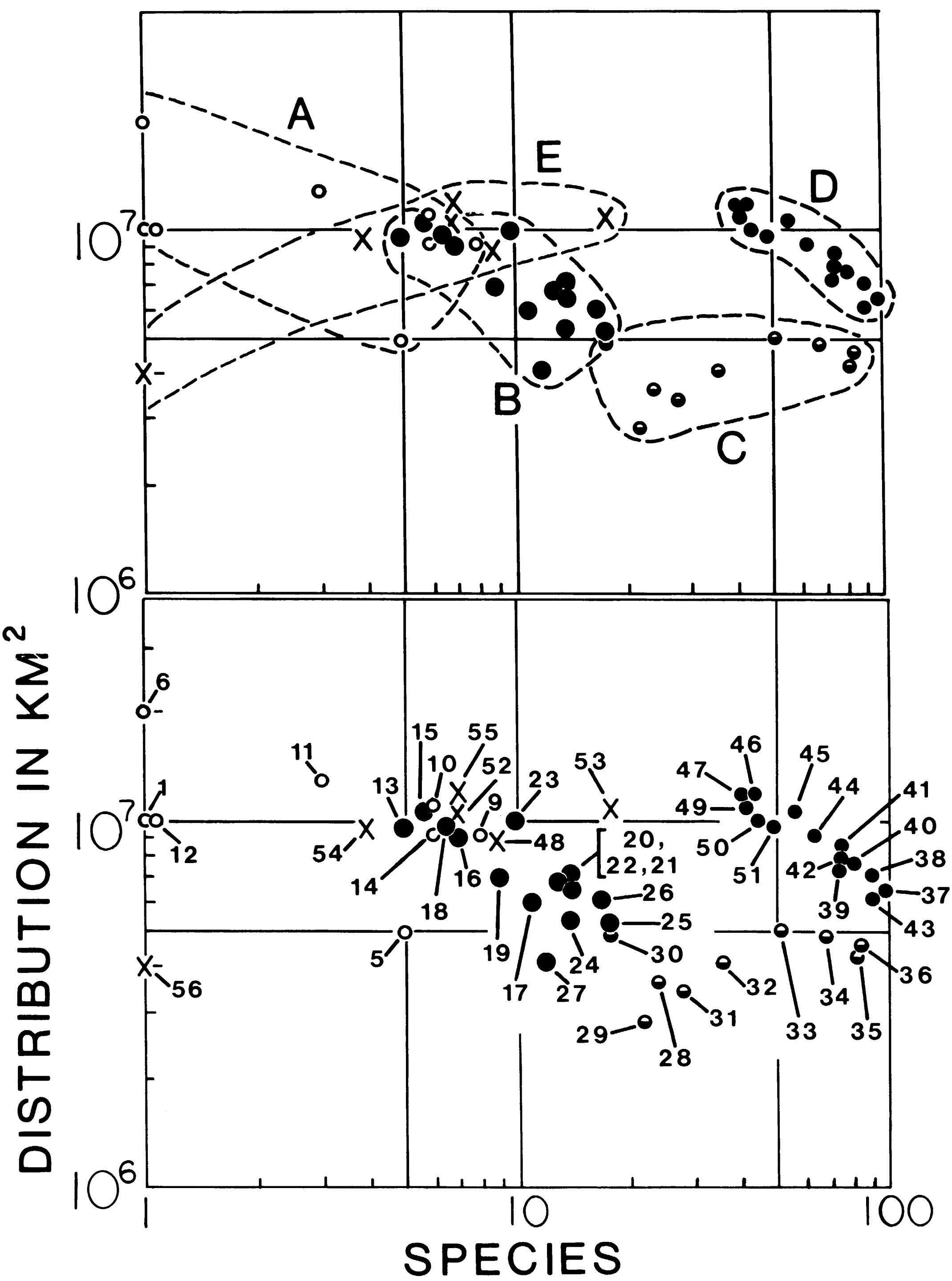

FIG. 2. The relationship of diversity (number of species) and distribution (geometric mean of ranges of each species) in bats present at each of 51 sample sites in North and South America. A. Alaska and Canada, B. United States (48 states only), C. Mexico and Central America, D. tropical South America, E. temperate South America. Same graph at bottom has points numbered to correspond with those in figures 1 and 4. Missing numbers were points with no bats.

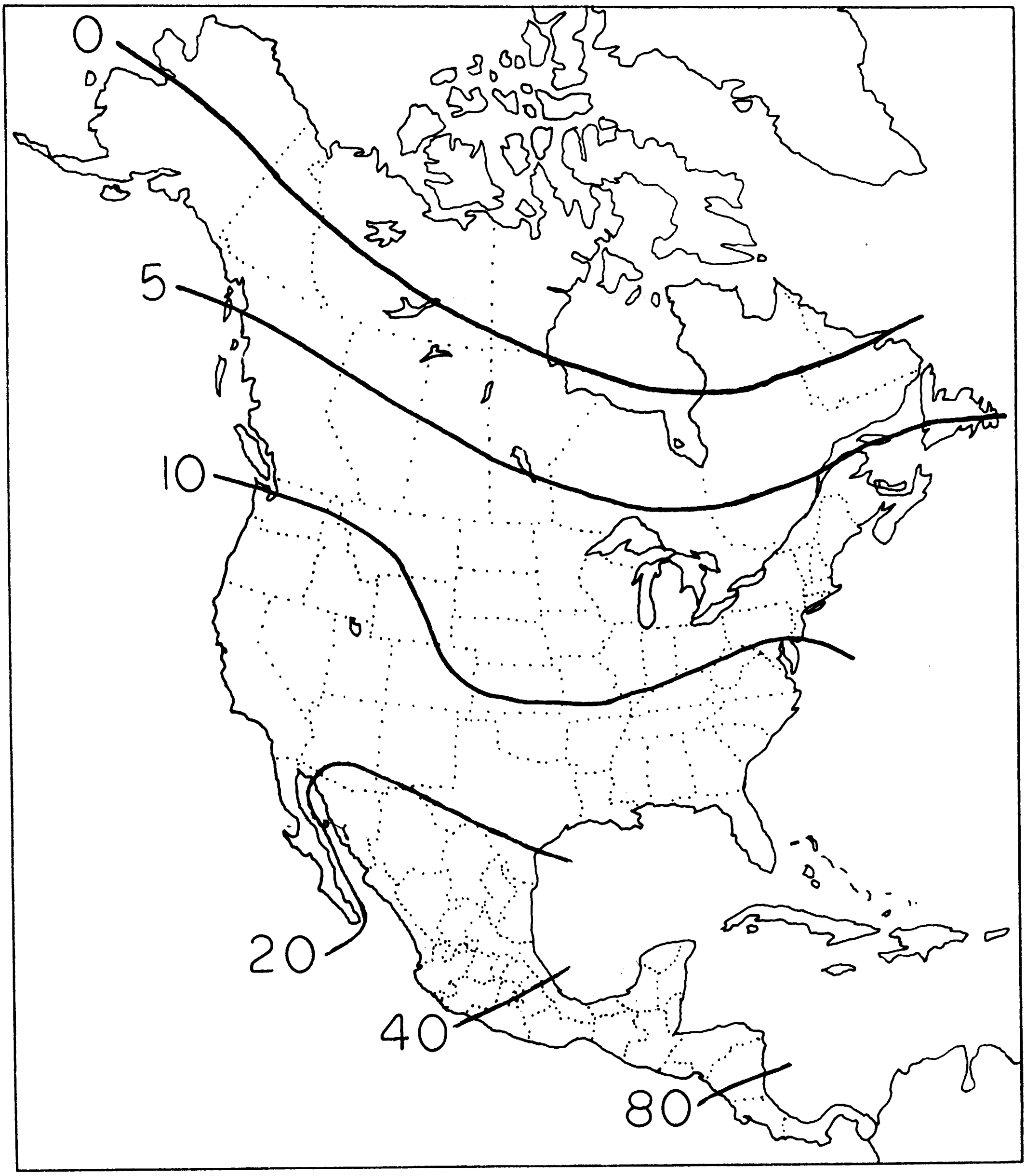

FIG. 3. Map of North America showing species density of bats. Lines (except the zero line) show doublings of density.

ple groups (the other was turtles), we first replicated and extended his analysis for North American bats as described in the next paragraph. His sample points were all north of Mexico; our sample points are distributed also south through Panama. Rosenzweig and the authors have used the entire range of each species. Some species extend into South America.

We found 35 points at which to sample the fauna in North America (excluding Greenland, fig. 1) by randomly selecting 40 points and then eliminating five that were either where there are no bats or that were within 200 km. of other points selected. We prepared lists of the species of bats occurring at each point. The size (areal surface in km^2) of the range for each of these species was measured on distribution maps (revised from those of Hall and Kelson, 1959). The geometric mean of the ranges of all species at each locality was calculated. A geometric mean was used because the ranges vary over nearly three orders of magnitude and arithmetic means tend to be biased by extreme values, in this case by the extremely large values. The numbers of species at each locality were plotted against the geometric means in figure 2.

The direction of the slope for the faunal samples north of Mexico (groups A and B) in this graph is the same as that observed by Rosenzweig, the same pronounced negative correlation is evident. But, are there alternative models that fit these data as well?

THE AVAILABLE SPACE HYPOTHESIS

Suppose that each species has certain environmental requirements and that each species occupies all accessible geographic areas that meet these requirements *regardless of the presence or absence of other species*.

For example, in North America (fig. 3) bat faunas are more diverse farther south. Whatever the conditions that cause this increase in diversity, it is clear that there is simply less space available farther south in North America for the ranges of bats that do live there. This assumes roughly comparable latitudinal ranges of species. The ranges could not be as large as those of species farther north.

The set of data for bats in North America north of Mexico fits both the "competition hypothesis" and the "available space hypothesis." It is not enough to adduce data that fit a hypothesis, one should adduce data that do not fit alternative hypotheses and thus help in choosing between hypotheses (or among them if there are more than two).

One way to test these alternative hypotheses would be to examine other groups of organisms in North America. We chose the rodents (370 species) for such a comparison, presented below. Another test would be to examine the correlation of distribution and diversity in the bat fauna of some other continent. An ideal continent for this test should have large tropical areas, since bats are largely tropical. If diversity restricts distribution (the competition hypothesis), the correlation would be strongly negative as in northern North America. If diversity does not restrict distribution (the available space hypothesis), the correlation might be positive or weakly negative. If this ideal continent were also narrower in the less tropical areas, the contrast would be even greater and a positive rather than negative correlation would be expected, under the available space hypothesis.

Fortunately, South America, a real continent, meets these ideal specifications and exists in a most convenient place.

Unfortunately, there were no published distribution maps for most species in South America, so Koopman prepared the maps for bats using information in the literature and unpublished data (for example specimens in the American Museum of Natural History).

We mapped the ranges of 182 species of bats in South America, selected 20 faunal sample points (arbitrarily using a grid, fig. 4), made lists of the species whose ranges encompassed each point, measured the sizes of their ranges, calculated geometric means, and plotted these against diversity (number of species) at each point as done for North America. These 20 values are also plotted in figure 2.

The data on the relationship of distribution and diversity of North American rodents are shown in figure 5. There is no noteworthy correlation (diagonal slope in clustering of points) of distribution and diversity, either positive or negative. This tends to falsify the competition hypothesis, at least as a principle generally applicable to different groups

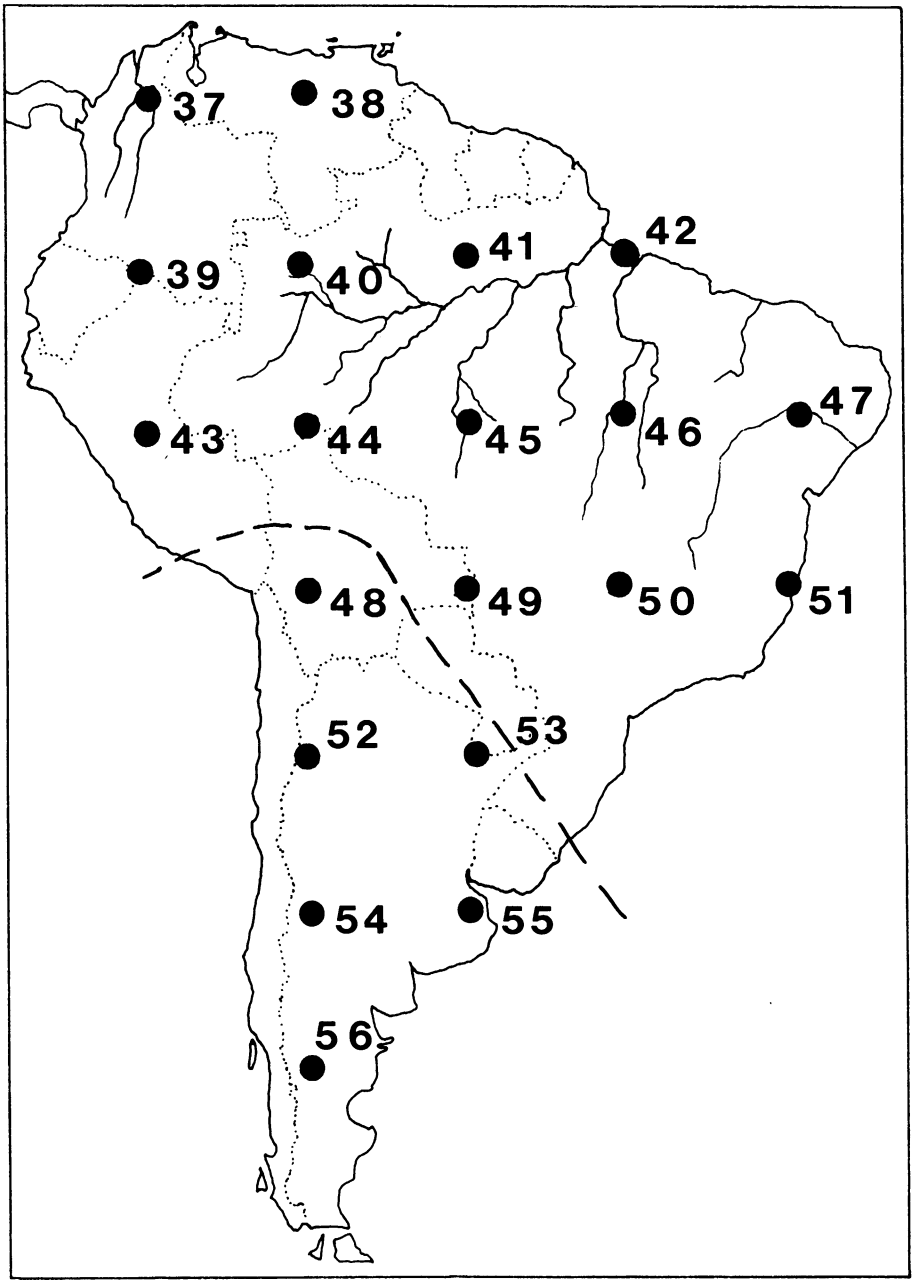

FIG. 4. Map of faunal sample sites in South America. The broken line shows the division of temperate and tropical sites mentioned in legend for figure 2.

of organisms. As shown in figure 6, the density of rodent species reaches a peak at about latitude 35 to 40, rather than continuing to increase southward. This difference in lati-

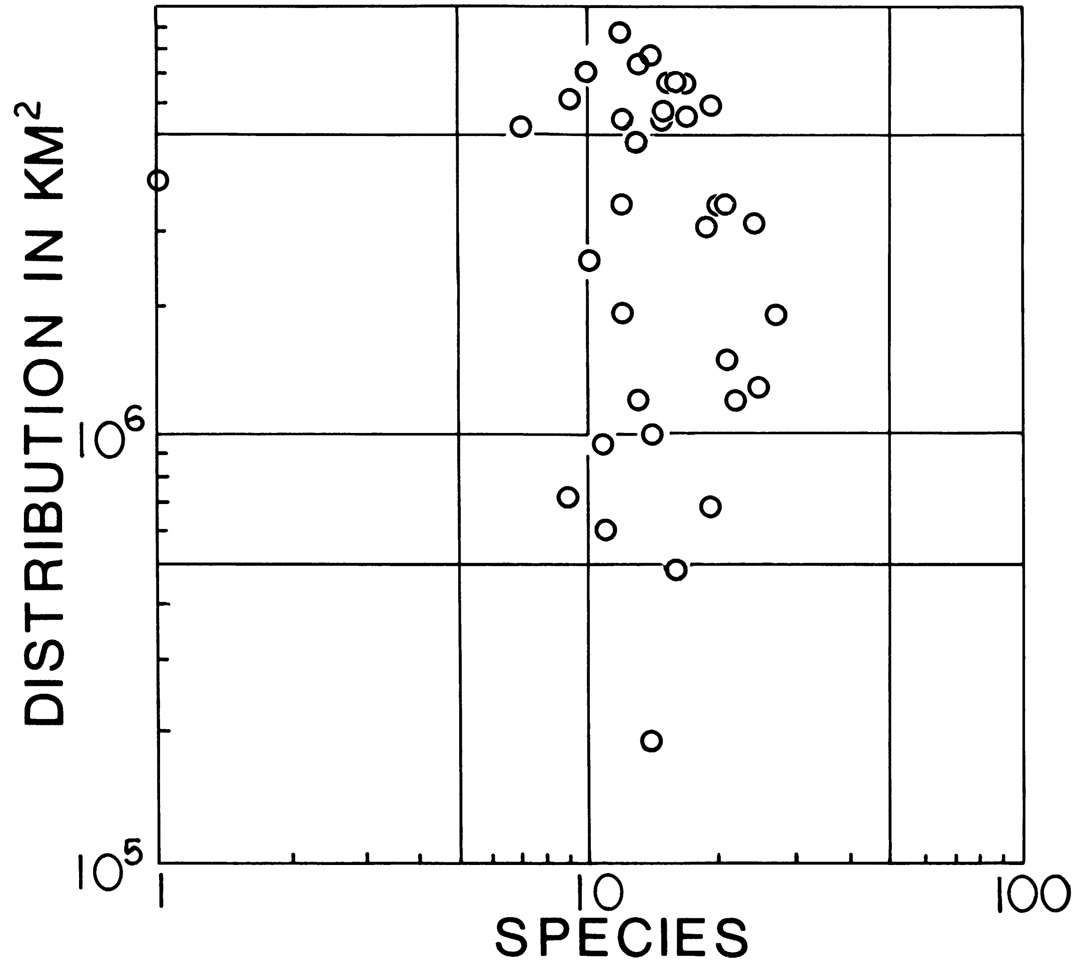

FIG. 5. The relationship of diversity and distribution in rodents at each of 35 sample sites in North America. There are more sample sites for rodents than for bats (in fig. 2) because some sites that have rodents do not have bats and are hence not graphed.

tudinal density gradients between bats and rodents has been noted frequently (Wilson, 1974; Anderson, 1977; McCoy and Connor, 1980).

The composite North and South American data for bats in figure 2 do not show a conspicuous overall negative correlation between distribution and diversity, which would support the competition hypothesis and falsify the available area hypothesis. Successive points on the graph as one proceeds from north temperate through tropical and into south temperate areas tend to follow a loop (from A to B to C etc., and even within these arbitrary groups as a close examination of numbers and maps will reveal).

Within groups A and B, as noted previously, there is a distinct negative correlation. Among tropical South American localities, group D, there is also a distinct negative correlation. In comparing B and D, it is clear that the species density of bats for a given average geographic range size is about an order of magnitude greater in tropical South

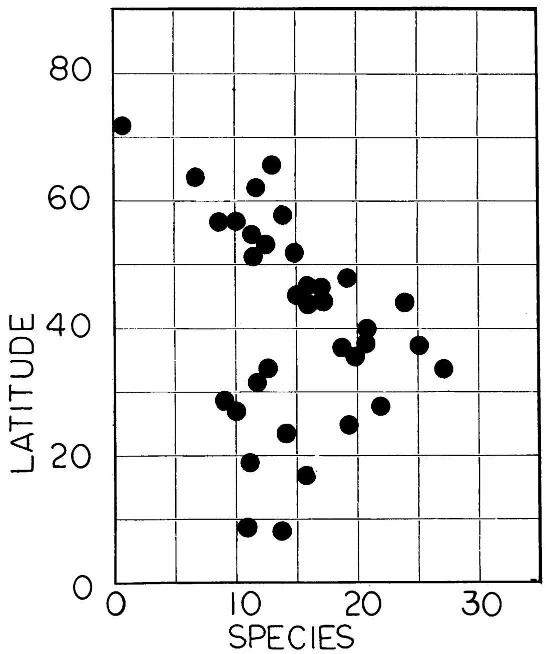

FIG. 6. The relationship of rodent diversity and latitude in North America.

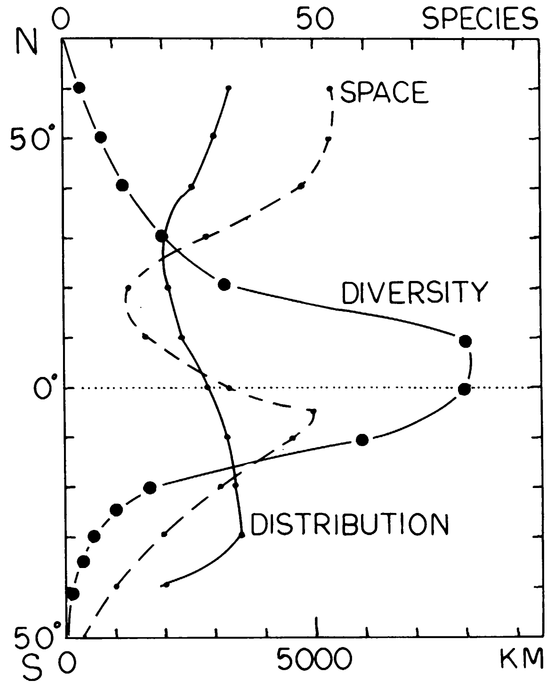

FIG. 7. Graph relating available space (width across the continent), diversity (number of species), and distribution (the square root of the geographic range in km²) for bats through North and South America. Data points are shown. Lines were drawn by eye.

America than in temperate North America. In tropical group C and in temperate group E the correlations are positive.

Figure 7 allows simultaneous visualization of distribution, diversity, and space available. Available geographic space is a better predictor of distribution than is diversity.

DISCUSSION

Using the values plotted in figure 7, we find that the correlation coefficient of available space and distribution is 0.559. The correlation coefficient of diversity and distribution is −0.166. In order to remove the effect of available space on distribution, the residual differences between the actual values for distribution and the values based on the regression ($y = 4.5 \times 10^6 + .946 \times 10^3X$) of distribution ($y$ = mean of ranges in km²) on available space (X = width of continent in km) were compared with the values for diversity (species density) at each latitude (the use of residuals in this way to detect second order effects was described by Mosteller and Tukey, 1977). These residual values for distribution had a weak and non-significant positive correlation with diversity. Our data examined in this way do not detect any significant effect of diversity on distribution.

It is axiomatic that animals compete and we know of specific studies in which one species does tend to restrict the distribution of another species both ecologically and geographically. We are not trying to disprove an axiom or deny that which has been clearly demonstrated. We are considering two variables, diversity and available space, and their relative importance in affecting (and predicting) distributions (sizes of geographic ranges) in general. We have not dismissed the competition hypothesis but we suggest that the role of competition is a relatively subtle one not detectable at this level of generality. More and better data will be needed to test hypotheses about the effects of competition in more refined ways, with other groups, and in other situations. The available space hypothesis has been strengthened and now needs further critical testing with more data, other groups, and in other areas.

This paper was submitted to the journal *Ecology* and then withdrawn after the editor indicated that he would require us to extract differences in food habits from the data and treat them separately. For example, seed-eating rodents must be separated from grass-eating rodents, or insectivorous bats from fruit-eating bats. We have suggested that more refined testing of hypotheses would be interesting, but we did not agree that this consideration renders the analysis we have done any less interesting. We would be glad to provide the data that we have to anyone who would like to use it in other analyses. We do not have an adequate set of data on food habits or any of the other specific means by which these mammals may compete or avoid competition.

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