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Dissertation Abstracts

AREOGRAPHY OF NEW WORLD BATS AND MARSUPIALS

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The importance of assessing and preserving the earth's biodiversity is becoming increasingly apparent; however, our knowledge may not be equal to the task, whether it is measuring the diversity of a small community or determining broad scale patterns of species diversity. Although latitudinal gradients in species diversity, species-area relationships, and latitudinal gradients in range size are frequently the focus of areographic studies, most only focus on one topic at a time. In contrast, I examined the association between species-area relationships and latitudinal gradients in diversity as well as latitudinal gradients in range size and its consequences for gradients in diversity.

Latitudinal gradients in species diversity are typically performed by superimposing quadrats on equal-area projection maps and counting the number of species whose range occurs within each quadrat. The quadrats may have lengths and widths equal to fixed distances in miles or equal to fixed degrees latitude and longitude. The former have a constant area; the latter do not. There are several criticisms of previous studies of the latitudinal gradient (Rosenzweig, 1995). First, quadrat size differs among studies. If the effect of area on richnes is unknown, then it is difficult to discern scale-based effects from other biogeographic phenomena. Second, because degree-based quadrats contain more land area in the tropics than in the temperate zone, quadrat size for degree-based studies differs within a study. Morover, latitude and area of degree-based quadrats are not independent; it is not possible to remove variation due to quadrat size without removing variation that correctly should be attributed to latitude. Finally, even studies with quadrats defined by a fixed distance had different quadrat areas within a study, because quadrats at the continent's edge were not full of land.

The mehodological approach of this portion of my thesis was designed to avoid the previously mentioned criticisms. Five quadrat sizes were chosen ranging from 25,000 km^2 to a point defined by the intersection of latitudinal and longitudinal meridia. Nested sets of quadrats were superimposed on equal-area projection maps in a systematic fashion with the constraint that they must be full of land and not overlap adjacent quadrats of the same size. Because the number of quadrats situated at a given latitude differed depending on the width of the continent, only mean number of species found in quadrats at each latitude were used in subsequent analyses. As a consequence, each latitude had equal weight in affecting the form of the diversity gradient. A hierarchical model was then developed to evaluate the degree to which quadrat size (1000 km^2, 10,000 km^2, 15,000 km^2, 20,000 km^2, 25,000 km^2) affects the latitudinal gradient in species richness. The model allows latitude and area to assume non-linear forms and in particular, evaluates the degree to which species richness can be decomposed into three additive components: latitudinal effects, areal effects, and interactive effects (the degree to which the latitude gradient is area-dependent).

For bats, species richness is an additive function of latitude (negative exponential) and area (power function). Patterns of richness for New World marsupials are best explained by area and are latitude-independent. My methodological approach was designed to assess the scale-independence of latitude and consequently should have a wide applicability. In addition, using this method to assess the multiplicative effects of area and latitude on species richness for the New World bats and marsupials are independent of area.

Species diversity gradients have long been of interest to biogeographers, ecologists, and evolutionary biologists. Moreover, the ubiquity of these patterns, the fact that they are found in many taxa, on many continents, has led many researchers to believe that there must be a single factor that can account for these gradients. No less than 22 factors have been proposed to account for latitudinal gradients in species diversity. Half of which are unsubstantiated by data and the other half are circular (Rohde, 1992). One such hypothesis, Rapoport's Rule, states that "when the latitudinal extent of the geographical range of organisms occurring at a given latitude is plotted against latitude, a simple positive correlation is found".

Considerable controversy surrounds the universality of Rapoport's Rule. Although Rapoport's

Rule has been detected in a variety of taxa in North America (Stevens, 1989; Pagel et al., 1991; France, 1992), Rosenzweig (1992) explained the species diversity gradient in the New World based on the assumption that tropical species have larger ranges than do their temperate counterparts. Moreover, other studies have provided evidence against Rapoport's Rule (Rohde et al., 1993; Colwell and Hurtt, 1994; Roy et al., 1994; Smith et al., 1994). As with quadrat based studies of the latitudinal gradient in species richness, studies of the latitudinal gradient in species range size have been plagued with problems. With the exception of Colwell and Hurtt (1994) and Smith et al. (1994), they have not considered a taxon's distribution throughout an entire land mass. However, Colwell and Hurtt (1994) did not test their models with empirical data. If one is trying to predict patterns extending from the temperate zones to the tropics, it is counterproductive to exclude a major portion of the tropics from analyses. Without corroborative evidence for latitudinal trends in South America, caution must be used in extrapolating latitudinal trends in North America to other areas. If similar patterns are not found on both continents, then observed latitudinal trends may be caused by unique attributes of North America (e.g., geography, physiography, evolutionary history; Rapoport, 1982; Willig and Selcer, 1989; Willig and Sandlin, 1991) rather than by latitudinal correlates, per se. A second problem is that assessments of Rapoport's Rule have failed to consider that latitude is not an independent descriptor of range size, regardless of the method used to measure it. Consequently, observed correlations between range size and traditional latitudinal descriptors such as mid-latitude or most-distal point (Stevens, 1989; Pagel et al., 1991; France, 1992; Rohde et al., 1993; Letcher and Harvey, 1994) may be mathematical artifacts rather than a product of biogeographic factors.

Via simulation models, I evaluated the degree to which such patterns are a product of either chance or the geography of the New World for bats and marsupials. Two different kinds of simulations were conducted separately for bats and marsupials. In all cases, 244 ranges were generated fro bats and 82 ranges were generated for marsupials, corresponding to the number of New World species in each taxon. The simulations differed in the kinds of spatial constraints that were incorporated into random algorithms. The first model randomly produced upper and lower latitudinal limits, without any spatial constraint except that species ranges were entirely within the continental New World. The second model incorporated the constraint that the set of randomly generated ranges had a distribution of mid-latitude or most-distal points that corresponded exactly to the distribution of mid-latitudes or most-distal points in each taxon. The correlation between latitudinal range size and latitude was calculated separately for each taxon. Random distributions of correlation coefficients were generated from 1,000 simulations for each taxon. Traditional methods (sensu Stevens, 1989; Rohde et al., 1993) used to evaluate Rapoport's Rule for New World bats and marsupials, show that bats and marsupials do not adhere to Rapoport's Rule in the New World. Nonetheless, simulation analysis showed that, when mid-latitude is used as a descriptor, New World bats and marsupials have ranges that are smaller in the tropics and larger in the temperate zone than would be expected by chance alone. Although more traditional methods of data analysis indicate that Rapoport's Rule is incorrect for New World bats and marsupials, the essence of the idea is in effect. As has been shown with studies of diversity gradients, many environmental factors are correlated with latitude and each may have an effect on diversity gradients. Explanation of patterns in range size will be even more complex because of the variety of factors that can affect ranges at the local, regional, or global levels. These factors could act in concert to produce the observed gradients in range size, reducing the likelihood that a single factor assumes a dominant role.

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