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The non-volant mammal fauna of Mexico: species richness in a megadiverse country

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The mammalian fauna of Mexico is one of the world's richest. Mexico can be considered a true country of megadiversity because it has more species of non-volant mammals than any other country in the New World, even after taking account of the effect of size. A comparison with other political units of the New World showed that the country as a whole harbours more non-volant mammals than expected for its size, whereas individual Mexican states have about the number of species that would be expected for their area. Beta, or differentiation diversity and environmental heterogeneity, rather than alpha or within-habitat diversity, are the key factors that determine the unusually high species richness of the country.

Keywords: beta diversity; mammals; megadiversity; Mexico; protected areas.

Introduction

Mexico has one of the richest faunas of the world. It is among the 12 countries that host most (60–70%) of the biological diversity of the world (i.e. it is one of the so-called megadiversity countries; Mittermeier, 1988; Mittermeier and Goettsch, 1992). For example, at the global level, Mexico is the fourth richest country in amphibians and the first in reptiles (Mittermeier and Goettsch, 1992; Flores, 1993).

The mammal fauna of Mexico consists of 500 species, including marine mammals and bats (H. Arita and G. Ceballos, unpublished data). Depending on the database that is used, this fauna is the second or the fourth richest of the world (Ceballos and Navarro, 1991; Fa and Morales, 1993; Sisk *et al.*, 1994). Among countries of the New World, Mexico has a mammal fauna that rivals that of Brazil, despite having less than one-fourth the area of that country. By any standard, the mammal fauna of Mexico seems to be unusually rich.

In apparent contradiction, individual localities in Mexico do not support exceptionally rich communities of mammals. Even the most diverse site, the Lacandona forest in the state of Chiapas, harbours approximately the same number of mammalian species (64 bats, 48 non-volant mammals) as do equivalent humid-forest sites in the Neotropics (Medellín, 1994). Similarly, the dry tropical forest of Chamela, Jalisco, supports fewer mammals (33 bats, 34 non-volant species; Ceballos and Miranda, 1986) than the Guanacaste region in Costa Rica (63 bats, 50 non-volant species; Wilson, 1983).

In this paper I compare Mexico with other New World countries and show that Mexico has indeed an exceptionally rich fauna of non-volant mammals. I suggest that β, or

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'differentiation' diversity, and regional heterogeneity make a more important contribution to total diversity in Mexico than does α, or within-habitat diversity.

Mammal species richness in Mexico

The high species richness of megadiverse countries is probably the result of a combination of several factors. First, megadiverse countries are large: except for Ecuador and Madagascar, all have territories larger than one million km^2 (list of countries from Mittermeier, 1988; areas from Espenshade and Morrison, 1986). Second, and probably related to size, most megadiverse countries support a great variety of environments. Finally, all megadiverse countries, except for the continental United States, have part of their territories in the intertropical region (although the tropical area of China is negligible when compared with the whole country).

To test the idea that area and tropical location are important factors determining diversity, I compared Mexico with other countries of the New World in terms of mammal species richness. The database used in the analyses comes from a previous study on the diversity of Mexican mammals (Arita, 1993) and contains the number of non-volant mammals and the area of countries of Central and South America (12 countries), of political units of the United States (17 units), and of states of Mexico (32 units). Original sources for lists of species include more than 50 papers and books on regional faunas that are fully cited in Arita (1993). Area of the political units was obtained from Goode's World Atlas (Espenshade and Morrison, 1986) and from official data of the Mexican Government (SPP, 1986). Based on the results of previous studies (Wilson, 1974; McCoy and Connor, 1980; Willig and Selcer, 1989; Willig and Sandlin, 1991) and on preliminary analyses (Arita, 1993), bats were excluded from the analyses because the geographic patterns in species richness for chiropterans are different from those for non-volant mammals. An analysis of geographic patterns of β diversity for Mexican mammals, including bats, is in preparation (P. Rodríguez, G. Ceballos, and H. T. Arita, unpublished).

I classified political units (excluding Mexican states) in two categories: tropical (eight countries) and temperate (20 political units). To control the effect of area I calculated, for each category, a regression of species richness versus area using log-transformed data. I compared the regression parameters for the two categories using two-tailed t-tests, and found no significant difference in slope ($t = 0.08$, d.f. $= 24$, $p > 0.1$) or y-intercept ($t = 1.89$, d.f. $= 24$; $p > 0.05$). This result indicates that New World political units of equivalent size maintain similar numbers of non-volant mammal species, regardless of their geographic position. Therefore, the idea that megadiverse countries are so diverse because they have a portion of their territory in tropical areas is rejected, at least for countries in the New World.

Because no difference could be found between tropical and temperate areas, I calculated a single regression of species richness versus area for the 28 political units ($R^2 = 0.48$, $p < 0.001$):

$$\log S = 0.26 \log A + 1.15$$

Where S is the species richness and A is the area of the political units. This regression will be called 'reference regression' henceforth.

The relatively high proportion of variance in species richness that is explained simply by area (48%) suggests that megadiversity countries in the New World support more species of non-volant mammals simply because they are larger than other political units. More than half of the variance, however, remains unexplained by the regression so other factors should be considered in the analysis of megadiversity.

When compared with the reference regression, Mexico had a significantly higher number of non-volant mammal species (302) than expected for a political unit of its area (expected value: 137 species, one-tailed t-test, $t = 2.14$, d.f. $= 27$, $p < 0.05$). In contrast, a previous study (Arita, 1993) has shown that the chiropteran fauna of Mexico is not unusually diverse, and that bat species richness is close to the value that would be expected for a country its size.

Results so far indicate that: (1) Mexico has an unusually high richness in non-volant mammalian species, even when compared with other megadiverse countries of the New World, and (2) the effect of area can explain the high mammal species richness of other megadiverse countries of the New World, such as Brazil, Colombia, Peru, and the United States, but not that of Mexico.

Patterns of alpha and beta diversity

Diversity, measured in terms of species richness, can be quantified either as an inventory of species at a given spatial scale or as a rate of species turnover between sites. Several nomenclatures have been proposed to describe the patterns of diversity at different scales (Whittaker, 1960, 1977; Cody, 1975; Shmida and Wilson, 1985). For simplicity, in this paper I use the term α-diversity to refer to the species richness of a locality or geographic area (including α or within-locality diversity and γ or within-habitat diversities in Whittaker's, 1977, nomenclature), and the terms 'differentiation' or β-diversity to refer to the rate of species turnover regardless of the spatial scale (β and δ diversities according to Whittaker, 1977). This convention has been used in other recent papers dealing with species diversity at geographic scales (Willig and Sandlin, 1991; Harrison *et al.,* 1992).

The unusually high species richness of Mexico can be the result of one of the following patterns: a high α-diversity, a high β-diversity, or a combination of both. If within-locality and within-habitat diversities are high, then all localities and habitats of Mexico should exhibit an unusually high species richness. In contrast, if between-locality and between-habitat diversities are high, then at smaller scales (single localities and small political units) Mexico should show no unusual species richness.

These possible patterns can be tested by comparing the regression lines of species versus area for the states of Mexico ('Mexico regression' henceforth) with the reference regression. Four outcomes are possible for such comparison (Fig. 1). Because an unusually high species richness has already been shown for the country as a whole, an equality of slopes and intercepts for both lines (Fig. 1*a*) would suggest a high among-locality diversity for Mexico. Such a case would indicate that species richness for the individual states is close to the expected value. A similar case (Fig. 1*b*) would result in smaller states having lower species richness than expected but larger states supporting higher diversity. A similar slope but a higher intercept for the Mexican line (Fig. 1*c*) would indicate that every state has an unusually high diversity, thus indicating a high within-locality diversity. Finally, a higher value for both the slope and the intercept would indicate that each state is very rich and that larger states are even richer than expected. This would suggest that both within- and among-locality diversities are high for Mexico.

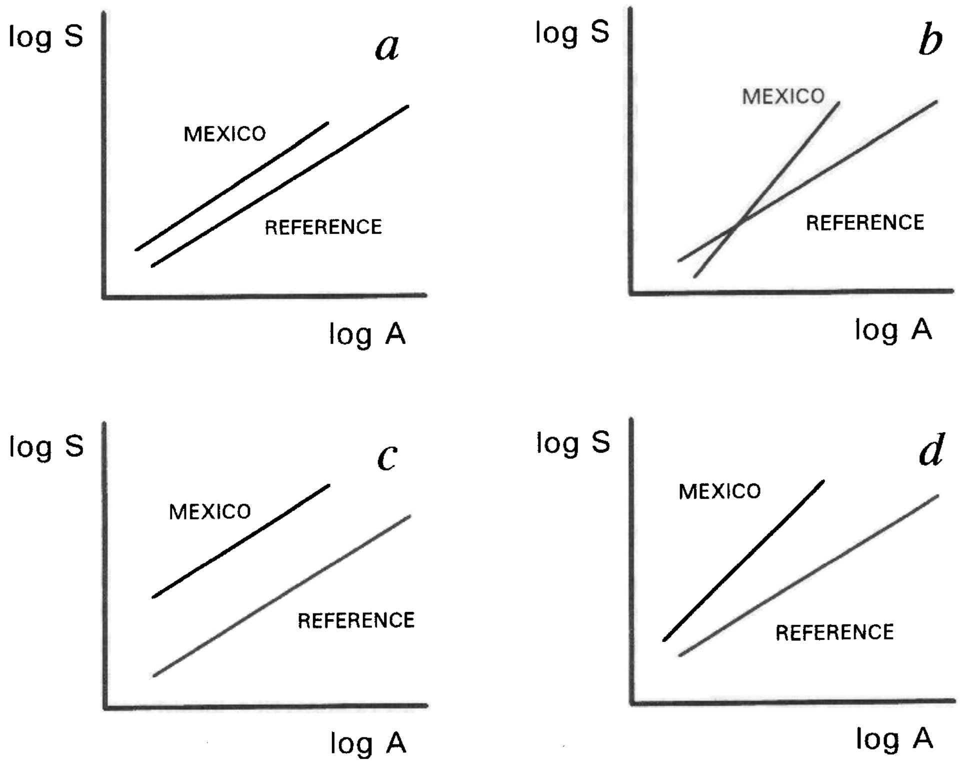

Figure 1. Four possible outcomes of a comparison of the Mexico regression and the reference regression. (*a*) Slopes and *y*-intercepts not significantly different. (*b*) Different slopes and *y*-intercepts, lines cross. (*c*) Slopes not different, *y*-intercepts different. (*d*) Slopes and *y*-intercept different, lines do not cross.

The species–area relationship for Mexican states can be described with the formula:

$$\log S = 0.24 \log A + 1.52$$

Neither the slope nor the *y*-intercept was different for the two regression lines (for the comparison of slopes $t = 0.04$, d.f. = 57, $p > 0.1$; for the subsequent comparison of *y*-intercepts, $t = 1.62$, d.f. = 57, $p > 0.05$; two-tailed tests; Fig. 2). Thus, the comparison of lines showed a result similar to the one in Fig. 1*a*. Mexican states in general have the species richnesses that would be expected for units of their respective sizes. This, coupled with the fact that the whole country is unusually rich, shows that the unusual species richness of non-volant mammals in Mexico is better explained by the degree of differentiation (β diversity) than by the pattern of α diversity.

The effect of regional heterogeneity

High β diversity is normally associated with a high degree of environmental heterogeneity that allows different sets of species to exist in different environments. To test the idea that this is the case with the Mexican mammal fauna, I analysed the effect of environmental variables on species richness among states.

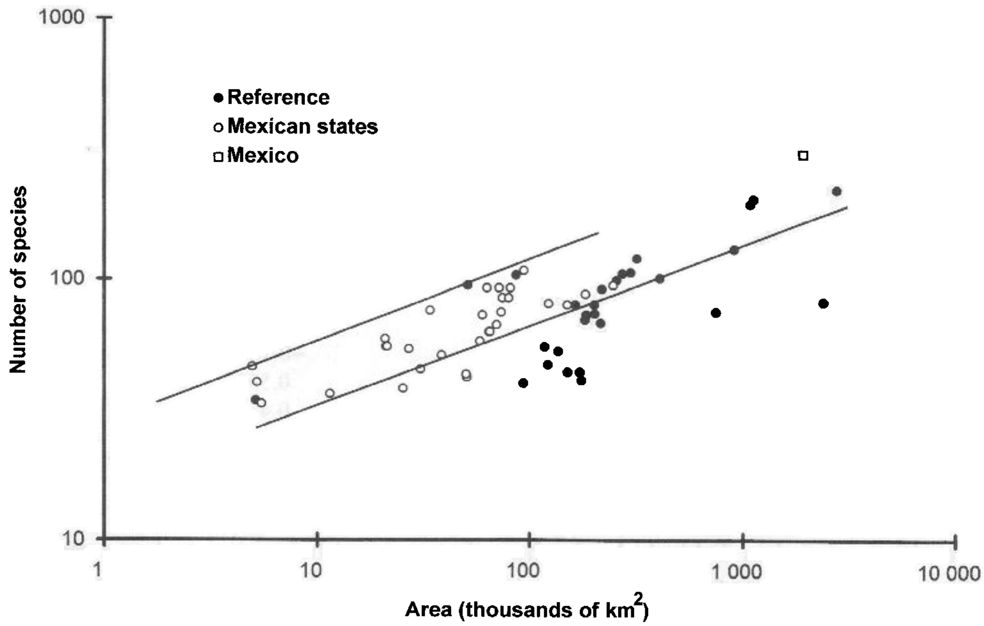

Figure 2. Species–area relationship for 29 South and Central American countries and political units of the United States ('Reference'), 32 political units of México ('Mexican States'), and México as a whole.

I gathered climatological data from García (1988). Data on latitude, altitude, mean annual temperature and mean annual rainfall were compiled for 793 meteorological stations in Mexico. Each Mexican state is represented by at least 15 stations with full data for at least 15 years of observations. Data were grouped by state, and the mean and standard deviation of each variable were calculated. Means were used as rough measures of local conditions, whereas standard deviations were conceived as measures of regional heterogeneity within states.

From the Mexican regression, I extracted the residuals for the 32 political units. These residuals indicate whether a particular state is richer (positive values) or poorer (negative values) in species than expected, and their magnitude is a measure of species richness that is independent of the area of the states, thus allowing a valid comparison among political units.

The residuals for the 32 political units were correlated with the climatological data by calculating Pearson's correlation coefficients. A significant correlation of these residuals with any of the means would indicate that local conditions have an effect on diversity. For example, a correlation with the average of the mean annual precipitation of a state would suggest that rainfall regime is an important factor determining richness. A significant correlation with one of the standard deviations would indicate, on the other hand, an effect of heterogeneity. A correlation with the standard deviation of the mean annual precipitation within states would suggest that differences in rainfall within states (a reflection of that state's heterogeneity) are a key factor in determining diversity.

Table 1. Pearson's product–moment correlation coefficients of climatological variables with the residuals of the 32 political units of Mexico from the species-area regression for non-volant mammals. Latitude, altitude, temperature, and precipitation are mean values by state. The standard deviations of these variables were also calculated by state to reflect variation within political units

Variable	*r*	*p*
Mean latitude	−0.154	0.400
Mean altitude	0.255	0.159
Average of mean annual temperatures	−0.177	0.333
Average of mean annual rainfall	0.152	0.407
Standard deviation of latitude	−0.164	0.369
Standard deviation of altitude	0.550	0.001[a]
Standard deviation of mean annual temperatures	0.412	0.019[a]
Standard deviation of mean annual rainfall	0.560	0.001[a]

[a] $P < 0.050$.

Results presented in Table 1 clearly show that regional heterogeneity has a more definitive effect on species richness than do local conditions. The three significant correlations are with the standard deviations of altitude, mean annual temperature and mean annual precipitation. In the case of the non-volant mammals of Mexico, variation of environmental conditions is clearly the key factor that promotes high species richness.

Discussion

Mexico is indeed a country of megadiversity in Mittermeier's (1989; Mittermeier & Goettsch, 1992) sense. The country has the richest mammal fauna of the New World and one of the richest of the world. Results reported here and in a previous study (Arita, 1993) show several patterns for this richness. First, Mexico is unusually rich in non-volant mammal species when compared to other political units of the New World, even after considering their area. In contrast, the bat fauna of the country is not especially rich and is comparable to what would be expected for a tropical country the size of Mexico. Finally, it is the differentiation, or β-diversity, coupled with regional heterogeneity, that contributes the most to the high richness of non-volant species.

Although complete lists of species for individual localities in Mexico are scarce, it seems safe to extrapolate to other Mexican localities the finding of Medellín (1994) that even the richest local fauna of Mexico is not particularly diverse when compared with similar sites in other countries. Alpha-diversity cannot explain the unusually high species richness of Mexico. As shown in this paper, the explanation for that richness has to be related with the patterns of β-diversity and the high heterogeneity of the country.

Two regional features of Mexico seem to be responsible for such heterogeneity. First, the complicated topography of the country produces a mosaic of environments that determine a high degree of environmental differentiation among localities, thus promoting high levels of β-diversity. Second, Mexico is the only country of the world that contains the totality of a continental border between two zoogeographical regions, in this case the Nearctic and the Neotropical. The existence of other Neotropical countries with equally complicated topographies that are less diverse than Mexico shows that heterogeneity alone cannot explain the unusual species richness in Mexico. Therefore, both the influence of two different faunas and environmental heterogeneity seem to be necessary conditions for the development of a truly megadiverse fauna, such as the one in Mexico.

It is interesting to note that this pattern of unusual diversity of non-volant mammals is paralleled by the Mexican herpetofauna, but not by the fauna of bats or by the avifauna. In effect, while Mexico is among the four richest countries in amphibians and reptiles, it is not among the first ten in the list of countries with the highest richness of birds (Mittermeier and Goettsch, 1992). Similarly, the fauna of Mexican bats is comparable in number of species with areas of South America of the same size as Mexico (Arita, 1993). The physiographic barriers that produce regional heterogeneity for amphibians, reptiles, and non-volant mammals seem to be less effective for vagile species such as birds and bats.

All these patterns have important implications for the conservation of the Mexican mammal fauna. One of the basic objectives of conservation biology is the preservation of biodiversity. Because resources are scarce and social pressures are high, the conservation of biodiversity is by necessity a process of choosing priorities. Thus, an important task for conservation biologists is the identification of sets of priority areas for the conservation of the diversity of a given group. Two recent approaches, 'critical faunas analysis' (Vane-Wright *et al.,* 1991) and the network procedure of Margules *et al.* (1988), rely heavily on the concept of complementarity (Pressey *et al.,* 1993, 1994).

From early approaches to reserve design (Simberloff and Abele, 1976, 1982; Higgs and Usher, 1980) it is known that similarity, or the number of species shared by sites, should be an important criterion to establish the number and location of priority areas for conservation. In the more recent approaches, the related concept of complementarity is the basis for the choices. The basic idea is that the importance of a given area is proportional to the number of species that cannot be found in the other protected areas of a network.

Each of the sites of a country with high α-diversity would contain the majority of the species of the country. Protection of any one of these sites would be sufficient to preserve the biodiversity of the whole country. Conversely, in a country with high β-diversity, protection of one site would guarantee the conservation of only a small fraction of the total species richness of the country.

The diversity of non-volant mammals in Mexico is the result of low similarity, and high complementarity, of sites within the country. This pattern implies that the conservation of Mexican mammals cannot be based on the establishment of a few protected areas. A large system of diverse reserves would be required to guarantee the presence of the majority of species in protected areas. For example, the 48 species of non-volant mammals that the rich Lacandona forest supports represent only 15% of the total fauna of the country. In contrast, the area of La Selva contains more than 50% of the mammal fauna of Costa Rica. Clearly, proportionally many more reserves would be required for the conservation of Mexico's mammal fauna than for Costa Rica's, even after compensating for the difference in size between the countries.

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