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Geographic patterns of body-mass diversity in Mexican mammals

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At the geographic scale, body mass has been analysed as a correlate of local abundance and area of range, or in terms of latitudinal variations in body mass, both intra- and interspecifically. One productive approach has been the analysis of the frequency distribution of body mass in animal assemblages at different spatial scales. In this paper we use such an approach to describe the geographic patterns of body-mass diversity in the Mexican mammalian fauna. We found contrasting patterns for bats and non-volant species: Non-volant mammals in Mexico followed the already described pattern of a right-skewed distribution of body size at large scales and a more even distribution at smaller scales; bats, in contrast, showed skewed distributions at all scales. Statistical tests based on null models demonstrated that most assemblages of non-volant mammals present higher diversity of body mass than expected by chance, whereas chiropteran assemblages show the variation in body size that would be expected from randomly sampling the whole fauna of the country. Although we found an effect of latitude on body-mass diversity, we also demonstrated that topographic features (peninsulas and mountain ranges) have a strong influence on the patterns of body mass at small scales. Using "SHE" analysis, a method to decompose the elements of diversity, we studied the scaling of body-mass diversity in south-eastern Mexico and documented subtle patterns that had not been observed in comparisons between biomes and local communities. In particular, we found that at intermediate scales the evenness of the distribution of body mass values remains constant, so diversity is determined chiefly by changes in the number of size classes found in the assemblages. In contrast, at the national level, diversity is comparatively low, despite the presence of all size classes, because of the low evenness, reflected in the highly skewed frequency distribution of body-mass values. Our results show that the body-mass structure of mammalian assemblages is determined by a complex interplay of local and regional processes that act at different spatial and temporal scales.

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Size is one of the most apparent traits of animal species. While differences in ecological features and life-history traits are probably the real factors promoting the diversity of life, it is through the variation in size and shape that humans perceive that diversity. Size determines the structure and function of biological entities from cells to individuals to populations through allometric scaling laws that describe the mathematical relation of several biological variables with body size (Schmidt-Nielsen 1984, West et al. 1997).

Body size has received considerable attention in ecological and evolutionary studies because it is the single feature that tells us most about the ecology and life-history traits of animal species (Eisenberg 1981, Peters 1983, Calder 1984, Zeveloff and Boyce 1988, Harvey and Pagel 1991). Among mammals, for example, body mass is correlated with metabolic rate (Schmidt-Nielsen 1984, McNab 1992), physiological and chronological time (Eisenberg 1981) and thermoregulation (Peters 1983). Similarly, birth, growth, and mortality rates, litter size, age at first reproduction, and longevity are

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all related to body size (Eisenberg 1981, Peters 1983, Calder 1984, Blueweiss et al. 1987, LaBarbera 1989).

At the macroecological scale, the study of body size is relevant as it correlates with local abundance and size of distributional range (Gaston 1994, Brown 1995, Gaston and Blackburn 1996a). In general, body size is inversely correlated with local abundance (Damuth 1981, 1987, Peters and Wassenberg 1983, Robinson and Redford 1986, Marquet et al. 1990, Cotgreave 1993, Gaston and Blackburn 1996a), except when comparing taxonomically related species (Nee et al. 1991). In recent studies, it has been suggested that the relationship between size and abundance cannot always be described with simple linear correlations, and polygons of different shapes have been used to analyse the distribution of data points in abundance-body size plots (Brown and Maurer 1987, Silva and Downing 1995, Scharf et al. 1998). In a similar fashion, area of distributional range is negatively correlated with body mass when comparing broad taxonomic groups at large scales, but more complicated patterns, similar to those found for abundance-size plots, have been described as well (Brown 1984, Brown and Maurer 1987, 1989, Arita et al. 1990, Arita 1993, Taylor and Gotelli 1994, Brown et al. 1996a, Gaston and Blackburn 1996b).

If body size is such a good predictor of physiological, ecological, and evolutionary features, then it should be reasonable to describe assemblages of animal species using body-size frequency distributions (Blackburn et al. 1990). Although theoretical models predicting the shape of such distributions are few, empirical studies have produced some broad generalisations. First, within any animal assemblage, smaller species tend to be more frequent than larger ones, producing right-skewed frequency distributions, even on logarithmic scales (Hutchinson and MacArthur 1959, Dial and Marzluff 1988, May 1988, Blackburn and Gaston 1994, Brown 1995). Second, the distribution is distinctly modal: a particular size category, which does not correspond with the smallest size, contains the largest number of species (Brown and Nicoletto 1991, Brown et al. 1993). Third, from the modal category there is a sharp decline in the number of species in categories to the left (smaller sizes) and a gradual decline to the right (larger sizes, Brown 1995). Finally, there is a definitive effect of spatial scale determining the shape of the distribution: local communities of vertebrates tend to follow a more even distribution of sizes than do regional assemblages (Brown and Nicoletto 1991, Brown et al. 1993).

The ultimate cause of these distributions appears to be a combination of ecological and evolutionary processes that act at different temporal and spatial scales. The larger number of small species has been explained in terms of specialisation and a wider array of sites and resources available to smaller animals (Hutchinson and MacArthur 1959, Morse et al. 1985, May 1988). These hypotheses, however, do not fully explain why the smallest species are not the most frequent. A different interpretation of the pattern comes from models based on the use of energy by animal populations (Damuth 1981, 1987, Brown et al. 1993, Brown 1995). Brown et al. (1993) explained the frequency distribution of body sizes by proposing the existence of an optimal size (about 100 g for mammals) that maximises fitness. Species would tend to acquire this optimal size, but competition in local communities would produce species of different sizes. The frequency distribution at the regional or continental scales, resulting from the sum of species in local communities, would be the typical right-skewed distribution with a mode near the optimal body size (Brown et al. 1993). A totally different explanation arises from predictions based on the intraspecific scaling of the rates of assimilation, respiration and mortality (Kozlowski and Weiner 1997). In this model, optimal body size varies among species depending on the values of intraspecific ecological parameters, but the predicted distribution of optimal sizes among species has the typical right-skewed form that has been documented empirically (Kozlowski and Weiner 1997, Purvis and Harvey 1997).

The frequency distribution of body sizes, along with other parameters of animal species assemblages, are determined by different processes at different scales (Wiens et al. 1986, Ricklefs 1987, Wiens 1989, Pimm 1991, Ricklefs and Schluter 1993, May 1994). At the regional and continental scales, historical (macroevolutionary) processes determine the composition and structure of faunas, whereas ecological and microevolutionary processes shape the assemblages at local, relatively homogeneous patches. However, in recent years it has become recognised that processes acting at different scales can be coupled. For example, the organisation of local communities are affected by regional processes simply because local faunas are assembled from regional and continental species pools. Conversely, regional and continental faunas are built in part by the cumulative effect of local phenomena determining the structure of communities (Ricklefs 1987, Cornell and Lawton 1992, Ricklefs and Schluter 1993, Brown 1995).

At the regional and continental scales, the frequency distribution of body sizes is affected by the so-called Bergmann's rule, which establishes a negative correlation between body size and ambient temperature, thus predicting a positive correlation between average body mass and latitude across closely related species (James 1970, Zeveloff and Boyce 1988, Blackburn and Gaston 1996). Because of the right-skewness of the body-size frequency distribution, the presence of large-bodied species in a particular assemblage can increase dramatically the average body size. Thus, if Bergmann's rule applies for interspecific assemblages and larger animals tend to exist at higher latitudes, one would expect to find more even distributions and higher averages for body mass at localities located far from the equator.

In this paper we study the geographic patterns of body mass among the mammals of Mexico. We analyse the frequency distribution of body sizes among volant and non-volant mammals at different spatial scales, and explore the relationships of that distribution with latitude and species richness. Finally, for a particular region of the country, we describe the scaling of body-mass patterns using a novel approach that allows the dissection of the components of diversity.

Methods

The study focused on the body-mass diversity of mammals in mainland Mexico. From current checklists of Mexican mammals (Wilson and Reeder 1993, Ramírez-Pulido et al. 1996, Arita and Ceballos 1997), we excluded introduced and marine species, as well as those restricted to islands, producing a list of 426 terrestrial, non-insular, native species. We drew distributional maps for the 426 species using as starting point the maps of Hall (1981), updating the information with taxonomic and distributional changes published from 1981 to the end of 1995 (Ramírez-Pulido et al. 1996, Arita and Ceballos 1997). We divided the country using a grid of 0.5 by 0.5-degree quadrats, which on average have 2836 km^2 and present comparatively little variation in area despite latitudinal effects (Arita et al. 1997). We constructed a distributional database recording the presence or absence of each species from the 823 quadrats that covered the country (this database is displayed on the internet site of the Mexican Commission on Biodiversity at http://www.conabio.gob.mx).

From the literature, we compiled data on the body mass for all species. When possible, we relied on publications referring to Mexican specimens, but in a few cases data from other countries were used. Averages were calculated when several sources were found or when several specimens were reported; when dealing with published ranges in size (with no access to raw data), we calculated medians instead of mean values. When no information was found in the literature, we obtained data from museum specimens deposited in the mammal collection of the Institute of Biology, National University of Mexico (IBUNAM). For some rare species of bats for which it was impossible to obtain direct information on body mass, we measured forearm lengths of museum specimens and estimated body mass using regression lines (one for each family) built with the data compiled by Arita (1993) for 150 Neotropical bat species. A list of references from which data on body mass was obtained is available upon request from the senior author.

With these data, we assigned species to categories of body mass using a base 2 logarithmic scale (Brown and Nicoletto 1991). We used seven and 18 categories to encompass the whole range of sizes for bats and non-volant species, respectively. We used the parameter g_1, which is derived from the third central moment and measures the asymmetry of a frequency distribution, to assess skewness. A positive value of g_1 indicates that a frequency distribution is skewed to the right (Sokal and Rohlf 1981). Using Smirnov-Kolmogorov goodness-of-fit tests, we compared observed frequency distributions of body mass against hypothetical log-uniform distributions with size intervals equal to those for the whole Mexican fauna (separating volant and non-volant species).

We analysed volant and non-volant mammals separately because the large-scale patterns of species richness and diversity are different for bats and terrestrial mammals (Fleming 1973, Wilson 1974, McCoy and Connor 1980, Kaufman 1995, Arita et al. 1997). Additionally, we expected, and later confirmed, that the body-mass frequency distributions are quite dissimilar, because bats face physiological, ecological, and biomechanical constraints on body size not shared with other mammals (Findley 1993, Arita and Fenton 1997). Our use of different sources for the data on body mass could have biased our allocation of species to body-size categories. However, because we conducted interspecific comparisons and used a very wide spectrum of body sizes to include all Mexican species, our sampling error is not significant at the level of resolution that we employed.

To quantify the diversity of body sizes, we calculated a Shannon diversity index as follows (Fleming 1973):

$$\mathrm{BMDI} = -\sum_{i=1}^{n} p_i \log p_i,$$

where BMDI is the body-mass diversity index, n the number of body-mass categories, and p_i is the proportion of species in body-mass category i. The value of the index depends both on the number of categories represented in a given sample and on the evenness of the distribution of species among these categories.

We compared observed values of the BMDI with expected values generated using a null model. We compiled a BASIC program that generated 1000 random assemblages by sampling from a pool of species that consisted of the whole non-volant or volant mammal fauna of Mexico. The pool of species had the same frequency distribution of body masses as the whole Mexican fauna. A different run of the program was performed for each value of species richness. The program calculated the BMDI for each random assemblage and generated a null frequency distribution that allowed us to estimate the lower and upper 0.05 confidence limits for the distribution of BMDI values for each value of species richness.

We analysed the scaling of body-mass diversity among non-volant mammals in a 4 by 4-degree quadrat located in south-eastern Mexico, including parts of the states of Veracruz, Oaxaca, Tabasco, Campeche and Chiapas (Fig. 1). The structure of the distributional database allowed us to quantify diversity at four scales within the large quadrat: 0.5 by 0.5, 1 by 1, 2 by 2 and 4 by 4 degrees. To complement the analysis, we included a locality found within the sampling quadrat for which the mammalian fauna has been comparatively well surveyed (the Lacandona forest in Chiapas, Medellín 1994). Furthermore, at the other end of the spatial scale, we also included the data for the whole country. We calculated species richness, measured directly as the sum of species in each quadrat, and BMDI, computing averages for each of the spatial scales. In an ideal 4 by 4-degree quadrat there are 64 0.5 by 0.5-degree quadrats, 16 1 by 1-degree quadrats, and four 2 by 2-degree quadrats. However, because some of the smaller quadrats are located outside the continent, actual sample sizes were as follows: 50 0.5 by 0.5-degree quadrats, 15 1 by 1-degree quadrats, four 2 by 2-degree quadrats, and one 4 by 4-degree quadrat.

We used the method of Buzas and Hayek (1996) to dissect the components of biological diversity that are implicit in the information function. These authors used the formula:

$$H' = -\sum_{i=1}^{S} p_i \log p_i,$$

where S is the number of species and p_i is the proportion of individuals of the ith species in samples of ecological communities (Margalef 1957). Buzas and Hayek (1996) proposed the decomposition formula:

$$H' = \log S + \log E,$$

where $E = e^{H'}/S$ is a measure of evenness of the distribution of individuals among species in the sample. When depicted graphically as functions of the number of individuals in the sample, log S, H', and log E show subtle patterns of diversity not detectable with other methods (Buzas and Hayek 1996). Log S and H' are depicted as points in the graph, whereas log E is shown as the distance between log S and H'. Because $E \leq 1$, log $E \leq 0$, so long distances in the graph correspond to low values of E. These "SHE" plots are a new valuable tool for the study of biological diversity, allowing the separation of the complementary but distinct components of diversity.

Applying the SHE analysis to BMDI data, we simply substituted N, the number of body-mass categories for S and calculated the p_i values as proportions of species for each category instead of individuals in each species. Other than that, we followed Buzas and Hayek (1996) in interpreting SHE plots.

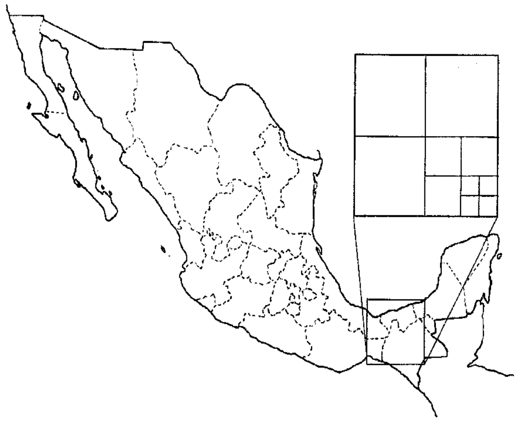

Fig. 1. The location of a study quadrat in south-eastern Mexico. The large quadrat is defined by sides of 4 degrees of latitude and longitude and contains four 2 by 2-degree quadrats, 16 1 by 1-degree quadrats, and 64 0.5 by 0.5-degree quadrats. Because parts of the quadrat fall outside the continent, not all smaller quadrats were included in the analysis.

Results and discussion

Frequency distribution of body mass

Mexican mammals range in average size from about 3 g (Miller's shrew, *Sorex milleri* Jackson, miniature yellow bat, *Rhogeessa mira* LaVal) to about 500 kg (bison, *Bison bison* Linnaeus). The frequency distribution of body masses on a logarithmic scale is unimodal and right-skewed ($g_1 = 0.985$ for non-volant mammals, $g_1 = 0.513$ for bats, Figs 2 and 3), coinciding with the patterns described for continental assemblages of vertebrates (Brown and Nicoletto 1991, Blackburn and Gaston 1994, Brown 1995). The pattern is more pronounced for non-volant mammals than for bats because of the wider range in body sizes among the former, but both distributions departed significantly from log-uniform distributions (Kolmogorov-Smirnoff test, $P < 0.001$ in both cases).

Among Mexican non-volant mammals, 125 species (43.1%) weigh between 16 and 128 g, and the rest are distributed unevenly in smaller and larger sizes (Fig. 2). The median of the distribution corresponds with the category of species between 32 and 64 g, and the geometric mean body size is 169.4 g. Among Mexican bats, size ranges from about 3 g in some vespertilionids to 150 g in the false vampire bat (*Vampyrum spectrum* Linnaeus), but a substantial proportion of species (115, 84.6% of the total) weigh between 4 and 32 g, with a geometric mean of 12.5 g (Fig. 3). Body size in the Microchiroptera, especially the aerial-feeding insectivores, is limited by several physiological and biomechanical constraints related to echolocation and flight (Barclay and Brigham 1991, Jones 1994, Norberg 1994, Arita and Fenton 1997).

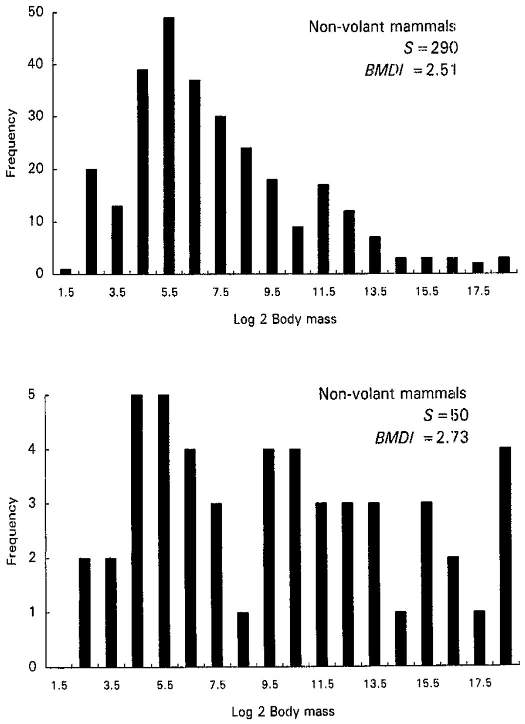

Fig. 2. Frequency distribution of body mass for non-volant mammals in Mexico (290 species, top) and one 0.5 by 0.5-degree quadrat (50 species, bottom). Note the use of base 2 log values to define the body-mass classes. BMDI is body mass diversity index.

According to a hypothesis put forward by Brown et al. (1993), the thermodynamics of acquiring and transforming energy into offspring would determine an optimal size of about 100 g for mammals. Because of the combined effects of local ecological interactions and regional patterns of distribution, a "log-skewed" pattern similar to the one observed for Mexican mammals should be expected, but with a mode closer to 100 g (Blackburn and Gaston 1994). The hypothesis of Brown et al. (1993) has been criticised on the basis of its usage of a particular energetic definition of fitness (Kozlowski 1996, Brown et al. 1996b), and has been questioned by data on life-history parameters of bats that do not show the scaling with body size predicted by the model (Jones and Purvis 1997).

The recent hypothesis of Kozlowski and Weiner (1997), which also predicts a frequency distribution of sizes similar to the one observed for Mexican mammals, cannot be tested directly with our data because it does not predict a specific value for the median of the distribution. That value would be determined, according to Kozlowski and Weiner (1997), by the particular values of the regression parameters of the intraspecific scaling of respiration, assimilation, and mortality. Our results are in accord with the predictions of the two current competing hypotheses explaining the frequency distribution of body size (Brown et al. 1993, Kozlowski and Weiner 1997).

Body-mass diversity at lower spatial scales

At the scale of the 0.5 by 0.5 degree quadrats, the patterns for volant and non-volant mammals are totally different. In the case of non-volant mammals, the distribution of species among size categories is more even than in the case of the whole Mexican fauna, as shown by a quadrat of the state of Chiapas, in southern Mexico, for which the geometric mean body mass of 50 non-volant mammals is 867.1 g (Fig. 2). Among 1000 null 50-species assemblages built by randomly sampling from the pool, none showed a BMDI equal or larger than the observed value of 2.73. Therefore, the probability of obtaining a frequency distribution as even as the one shown in Fig. 2 is < 0.001. The frequency distribution of this quadrat is only slightly skewed to the right ($g_1 = 0.307$) and does not differ from a log-uniform distribution (Kolmogorov-Smirnoff test, $P = 0.657$).

Similar patterns are shown by many 0.5 by 0.5-degree quadrats (Fig. 4, top). Several quadrats, especially at intermediate values of species richness (30 to 70 spe-

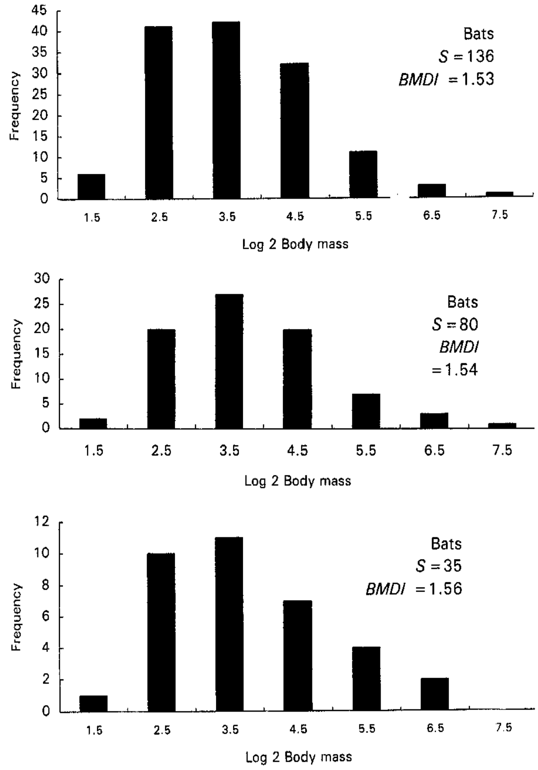

Fig. 3. Frequency distribution of body mass for bats in Mexico (136 species, top) and two 0.5 by 0.5-degree quadrats (80 and 35 species, middle and bottom). Note the use of base 2 log values to define the body-mass classes. BMDI is body mass diversity index.

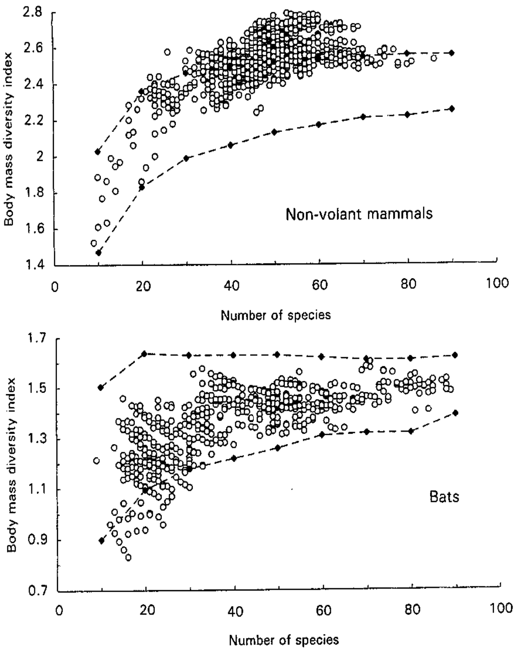

Fig. 4. Relationship between the body mass diversity index and species richness for 823 0.5 by 0.5-degree quadrats in Mexico for non-volant and volant mammals. Lines mark the lower and upper 0.05 confidence limits for samples taken randomly from the pool of species (the whole Mexican fauna).

cies), show values of the body-mass diversity index that are higher than expected from a random draw of species from the pool ($P < 0.05$, null test described in Methods). A single statistical test using the 823 quadrats simultaneously would be invalid because of the spatial autocorrelation effect produced by the non-independence of the sampling quadrats. However, the comparison of individual quadrats against the null distribution, as shown in Fig. 4, is a valid statistical test that shows that the general trend is for the quadrats to have higher values of the BMDI of non-volant mammals than expected by chance. This result indicates that most quadrats contain assemblages of species that show more even distributions of body sizes than expected by chance, in patterns similar to that depicted in Fig. 2, bottom. This result coincides with the observation that at smaller scales the frequency distributions of body masses are nearly log-uniform, contrasting with the log-skewed pattern observed at continental scales (Brown and Nicoletto 1991, Blackburn and Gaston 1994).

In a contrasting pattern, the frequency distribution of bat species among size classes remains right-skewed even at smaller scales (Fig. 3). For the quadrats shown in Fig. 3, with 80 and 35 species, the geometric mean body mass was 13.8 and 13.9 g, respectively. The probabilities of obtaining BMDI values equal or higher than the observed values (1.54 and 1.56) are not significant ($P = 0.195$ and 0.168, respectively, as calculated from the null models). Both distributions differ significantly from log-uniform distributions (Kolmogorov-Smirnoff test, $P < 0.001$ and $P = 0.005$, respectively). Most quadrats have BMDI values within the range that would be expected from a random draw of species ($P > 0.05$, one-tailed null tests described in Methods, Fig. 4, bottom). There is a larger variation in BMDI values at lower species richness ($S < 40$ species), but this pattern would be expected even from a random draw of species from the pool (Fig. 4). Because no claim can be done on the contrary, we conclude that local assemblages of bats are not more evenly distributed than the national fauna.

Brown and Nicoletto (1991) explained the more even distribution of the body sizes of non-volant North American mammals at localities as opposed to at regional or continental scales as an effect of local competitive exclusion, higher extinction rates for larger species, and higher levels of specialisation of modal-sized species. Although our data do not directly test the validity of this hypothesis, our results with the Mexican non-volant mammal fauna are consistent with the predictions of Brown and Nicoletto (1991). In contrast, our results with bats suggest that other mechanisms besides those proposed by Brown and Nicoletto (1991) should be determining the composition and structure of chiropteran faunas. This suggestion is in accord with studies that have shown that regional processes have a greater influence on structuring Neotropical bat communities than do local interactions (Willig and Moulton 1989, Findley 1993, Heller and Volleth 1995, Arita 1997).

Geographic trends

There is a distinct relationship between the value of the body-mass diversity index and the number of species (Fig. 4). At lower values of species richness (< 45 species for non-volant mammals and < 30 species for bats), there is a positive correlation between the two variables. At higher values of species richness, however, the value of the body-mass diversity index does not increase proportionally. This pattern implies that sites with high body-mass diversity are not necessarily very rich in species. In fact, for non-volant mammals, the highest values of the body-mass diversity index correspond to quadrats of intermediate species richness, with approximately 45 to 65 species, whereas quadrats with the highest species richness (up to 85 species) have lower values of the BMDI (Fig. 4, top).

The value of the index of body-mass diversity is determined by the number of body-size categories and the evenness of the distribution of species among these categories. Given the log-skewed distribution of body masses for non-volant mammals for the whole country, to attain high values of the index, a particular assemblage of species must include a proportionally higher number of large species. In Fig. 2, bottom, for example, 24 out of 50 species (48.0%) are distributed among the last nine body-size categories (body mass > 1024 g), whereas for the whole country (Fig. 2, top), only 59 of 290 species (20.3%) are so large. In North America, tropical communities of non-volant mammals tend to be more diverse in small forms than temperate assemblages, because they contain a larger proportion of arboreal and scansorial mammals, which tend to be of small or intermediate body size (Fleming 1973). Furthermore, a positive correlation between latitude and average body mass, across species, has been shown for several vertebrate groups (Zeveloff and Boyce 1988, Taylor and Gotelli 1994, Blackburn and Gaston 1996), conforming with Bergmann's rule. Therefore, one would expect higher values of body-mass diversity for temperate areas than for tropical zones.

This seems to be the case for Mexican assemblages of non-volant mammals, although the pattern is complicated by the complex topography of the country. With few exceptions, such as the jaguar *Panthera onca* (Linnaeus) and the tapir *Tapirus bairdii* (Gill), diversity in Mexican tropical areas is determined chiefly by the presence of small and medium-sized mammals. In contrast, in temperate zones large species are proportionally better represented in terms of number of species. Besides species shared with tropical areas, such as the jaguar and the cougar *Puma concolor* (Linnaeus), temperate zones feature a high diversity of large mammals, such as the grey wolf *Canis lupus* Linnaeus, the black bear *Ursus americanus* Pallas, the grizzly bear *Ursus arctos* Linnaeus, the mule deer *Odocoileus hemionus* (Rafinesque), the pronghorn *Antilocapra americana* (Ord), the bighorn sheep *Ovis canadensis* Shaw, and the bison (*B. bison*). As a consequence, temperate areas in general show higher values of the BMDI of non-volant mammals despite having lower species richness than tropical zones.

The relationship between BMDI and latitude is shown in Fig. 5. At first glance there seems to be no regular pattern, but a closer examination reveals a general trend obliterated by two major topographic features of Mexico: the Yucatan peninsula and the Transmexican Volcanic Belt. The Yucatan peninsula is a flat, tropical lowland area in eastern Mexico that extends approximately from 17.5 to 21.5 degrees North latitude. The peninsula harbours most of the large tropical mammals characteristic of the tropical areas of Mexico, but its diversity of small and medium-sized mammals is comparatively low. This combination of elements, perhaps related to the "peninsula effect" identified by Simpson (1964), produces mammalian assemblages with high values of mean body mass and of BMDI. These high values stand out in Fig. 5 as the points on the left side of the graph with the highest values for the BMDI. Points at the same latitude with lower values for the BMDI correspond to other tropical parts of Mexico with a full complement of small and medium-sized mammals. A contrasting pattern is shown by the Mexican Volcanic Belt, a mountainous chain in central Mexico (approximately between 19 and 20 degrees latitude) that harbours a diverse array of small and medium-sized mammals, including several endemic mice and rats (Sigmodontinae), and pocket gophers (Rodentia: Geomyidae, Fa and Morales 1991). The low values of the BMDI corresponding to the quadrats in the Volcanic Belt are highlighted in Fig. 5. The particular structure of the mammalian faunas found in the Yucatan peninsula and the Mexican Volcanic Belt is in great part determined by historical (macrogeographic) patterns and processes such as the peninsula effect and, in the case of the Volcanic Belt, the topographic heterogeneity and the confluence of two biogeographic regions: the Nearctic and the Neotropical realms (Fa and Morales 1991).

Ignoring the values corresponding to the Yucatan peninsula, there seems to be a trend of low mean body mass at intermediate latitudes (between 18 and 23 degrees) and a wider range of values at lower and higher latitudes. This pattern is probably caused by the combination of tropical lowland and temperate highland faunas in lower and higher latitudes, while mountainous areas in Central Mexico are dominated by temperate assemblages. Because of the comparatively narrow latitudinal range in Mexico, Bergmann's rule, stated as a positive correlation between body size and latitude, cannot be tested adequately. However, the pattern in Fig. 5, including the effects of the Yucatan peninsula and the Volcanic Belt, suggests that Bergmann's rule is a more complex phenomenon than a simple relationship between body mass and latitude. The Yucatan peninsula is an example of a tropical area harbouring a mammalian fauna with a comparatively high percentage of large mammals. In contrast, the highlands of the Volcanic Belt are a temperate zone

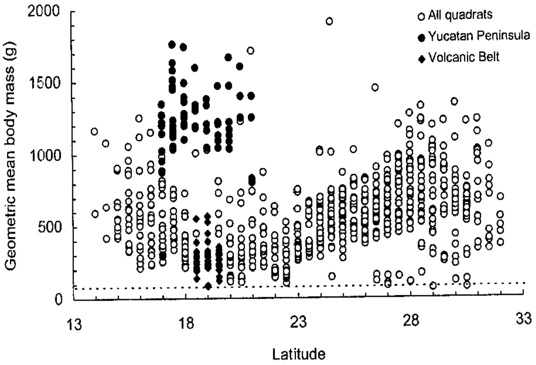

Fig. 5. Relationship between the geometric mean body mass of 0.5 by 0.5-degree quadrats and midpoint latitude. Points corresponding to the Yucatan peninsula and the Mexican Volcanic Belt are highlighted. Dashed line shows the geometric mean body mass for the whole Mexian fauna.

with an unusual diversity of small and medium-sized mammals. Clearly, Bergmann's rule, if at all real, needs to be explained in the context of the macroevolutionary, geological history of the areas.

The geographic patterns of body mass for bats differ from that of non-volant mammals. Tropical and subtropical bat assemblages present higher species richness and body-mass diversity than do temperate communities. This is a consequence of the greater variety of diets, foraging strategies, and roosting habits that characterise tropical bat communities (Fleming 1973). Contrasting with the case of non-volant mammals, the largest chiropteran species are tropical carnivorous bats, such as the false vampires, *V. spectrum* and *Chrotopterus auritus* (Peters). While harbouring some large species, such as the mastiff bats, *Eumops perotis* (Schinz) and *Eumops underwoodi* Goodwin, temperate assemblages are characterised by small, aerial-feeding insectivorous bats (mostly Vespertilionidae). As a group, chiropterans do not show the geographic trends of non-volant mammals. In particular, Bergmann's rule does not hold when applied to a comparison among species, and tropical assemblages are the most diverse both in terms of number of species and in terms of body-mass diversity.

The scaling of BMDI

A total of 102 non-volant mammals have potential distribution in the 4 by 4-degree quadrat in south-eastern Mexico. Of these, an average of 58.7 species are contained in the 0.5 by 0.5-degree quadrats (range 35 to 75), 63.5 species are included in each 1 by 1-degree quadrat (range 37 to 80), and 74.8 species occur in each 2 by 2-degree quadrat (range 61–91). The BMDI value shows a distinct pattern when performing the SHE analysis, which allowed us to dissect the relative contribution of the number of body-mass categories and evenness in determining the body-mass diversity index (Fig. 6). Along the spatial gradient from 0.5 by 0.5-degree to 4 by 4-degree quadrats, the value of BMDI shows a slight increase, especially from 1 by 1-degree to 2 by 2-degree quadrats. This increase in BMDI is due basically to a slight increase in the number of body-size categories, as the value of evenness remains almost constant as evidenced by the four vertical lines of almost equal length in the SHE plots (Fig. 6). The local assemblage shows a much lower value of BMDI caused by both a decrease in the number of categories represented and a decrease in evenness, shown by the longer vertical arrow in the SHE plot. The fauna of the whole country also shows a decrease in BMDI, but in this case the trend is caused by a sharp decrease in evenness, as the number of represented categories increases to the total of 18 categories present in Mexico (Fig. 6).

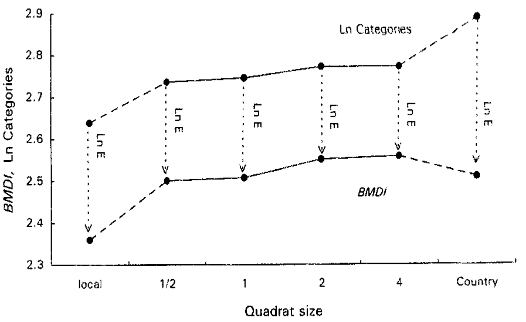

Fig. 6. SHE plots of body-mass diversity of non-volant mammals corresponding to a local community (the Lacandona Forest), 0.5 by 0.5, 1 by 1, 2 by 2, and 4 by 4-degree quadrats in south-eastern Mexico, and the whole country. Points represent the values of log number of body-size categories and of body-mass diversity index; vertical arrows represent the value of evenness. Because evenness values are always ≤ 1.0, log values are always negative, so the larger the arrow, the less even is the distribution of body sizes.

Brown and Nicoletto (1991) demonstrated that local communities in North America (including some localities in Mexico) show more even distributions of body sizes than biomes or the whole continent. Our results show that subtler patterns can be detected when examining intermediate spatial scales. We agree with Brown and Nicoletto's (1991) suggestion that the shape and extent of the frequency distribution of body mass at local and regional scales are determined by the complex interplay of local ecological interactions (perhaps principally interspecific competition among similarly sized species) and regional macroevolutionary processes, such as speciation, extinction, and colonisation. The patterns and processes of ecological communities and species assemblages at the "mesoscale" (Ricklefs and Schluter 1993) remain largely undescribed. The complete understanding of the patterns of body-mass diversity will come only through a comprehensive analysis of the coupling of phenomena that occur at different spatial and temporal scales.

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