

# USING A MACROECOLOGICAL APPROACH TO STUDY GEOGRAPHIC RANGE, ABUNDANCE AND BODY SIZE IN THE FOSSIL RECORD

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**ABSTRACT.**—Macroecology is a rapidly growing sub-discipline within ecology that is concerned with characterizing statistical patterns of species' abundance, distribution and diversity at spatial and temporal scales typically ignored by traditional ecology. Both macroecology and paleoecology are concerned with answering similar questions (e.g., understanding the factors that influence geographic ranges, or the way that species assemble into communities). As such, macroecological methods easily lend themselves to many paleoecological questions. Moreover, it is possible to estimate the variables of interest to macroecologists (e.g., body size, geographic range size, abundance, diversity) using fossil data. Here we describe the measurement and estimation of the variables used in macroecological studies and potential biases introduced by using fossil data. Next we describe the methods used to analyze macroecological patterns and briefly discuss the current understanding of these patterns. This chapter is by no means an exhaustive review of macroecology and its methods. Instead, it is an introduction to macroecology that we hope will spur innovation in the application of macroecology to the study of the fossil record.

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## INTRODUCTION

MACROECOLOGY IS an approach to studying ecological systems that is concerned with characterizing statistical patterns of species' abundance, distribution and diversity (Brown, 1995). Although macroecology attempts to answer the same questions as traditional ecology, it differs in the way macroecologists go about answering those questions. Moreover, macroecology typically operates at relatively large spatial and temporal scales because it is necessary to expand the scale in order to have a sample size that is large enough to characterize the statistical distribution in question. As a result of this expanded focus, macroecology encompasses the overlap between ecology, biogeography, paleobiology and evolution (Smith et al., 2008), making macroecology a promising approach for studying ecology in the fossil record. Indeed, macroecology and macroevolution are scientific siblings and have the potential to greatly enhance one another.

Although macroecology is a relatively young field, it shows great potential for elucidating the linkages between different scales of biological organization (Smith et al., 2008) and has led to the identification of many patterns that are predictable and repeatedly seen across geographic space, taxonomic group, or temporal scale (Brown, 1995; Ernest et al., 2003; Gaston, 2003; Rosenzweig, 1995; Smith et al., 2004) suggesting that they are controlled by predictable and repeatable underlying processes. Some of the most common, repeatable macroecological patterns include the relationship between body size and geographic range size (Blackburn and Gaston, 2001; Brown, 1995; Gaston, 2003; Gaston and Blackburn, 1996b; Madin and Lyons, 2005; Smith et al., 2008; Willig et al., 2009), variation in body size at different spatial scales (Alroy, 1998; Arita and Figueroa, 1999; Bakker and Kelt, 2000; Blackburn and Gaston, 1996a; Brown and Nicoletto, 1991; Lyons et al., 2004; Marquet and Cofre, 1999; Smith et al., 2004), geographic variation

in range size (Arita, 2005; Arita et al., 1997; Lyons and Willig, 1997; Willig et al., 2003; Willig et al., 2009) and the latitudinal gradient in diversity (Colwell and Hurtt, 1994; Colwell et al., 2004; B. A. Hawkins and Agrawal, 2005; Jablonski et al., 2006; Lyons and Willig, 1999; Lyons and Willig, 2002; Rohde, 1992; R. D. Stevens et al., 2003; Willig et al., 2003).

As a field, macroecology is evolving rapidly. Indeed, the number of macroecological publications has increased exponentially over the past two decades (Smith et al. 2008). As a result, new methods for the study of macroecological patterns are constantly being developed. Herein, we consider a variety of macroecological patterns and the methods used to study them. Because this chapter is aimed at using a macroecological approach to the fossil record, we present analyses showing the effect of using fossil data to examine macroecological patterns by degrading modern data using different filters to mimic the effect of the fossil record. We acknowledge that our coverage of macroecological methods is necessarily incomplete. However, we hope that this will provide a basic grounding in macroecology that can be used as a springboard for innovation in the application of macroecology to the fossil record.

## THE BUILDING BLOCKS OF MACROECOLOGY

The most commonly studied macroecological patterns are concerned with variables that are easily measured in the fossil record. They are geographic range size, body size, abundance and diversity. We will start by defining each of these variables and outlining methods used to measure them. We will then discuss how these variables are used to determine many macroecological patterns and the methods used to compare patterns across space, time or taxonomic affinity. At the same time, we will discuss the potential effects of using fossil data to characterize these relationships.

### Geographic range size

At its most broad, ecology is the study of organisms and their relationship to the environment. One facet of this is the drive to understand the factors limiting a species distribution, making a species' geographic range a fundamental unit of study in ecology. In addition, many species traits (e.g., abundance, morphology, body size, life history characteristics, etc.) are

correlated with range size or vary predictably across a species range. Understanding the processes that shape and limit a species geographic range can yield insight into the evolution of these associated traits. Moreover, studying the relationship between species traits and geographic range size at a larger scale (i.e., across taxonomic groups, on different continents, or across time) can provide insight into processes that operate on longer time scales than those typically studied in ecology.

Geographic range size has been estimated using a variety of techniques (Fig. 1). Each method has its own strengths and weaknesses and method choice typically depends upon the type of data available. We discuss several different methods and the type of data needed below.

*Habitat or biome infilling.*—When extant species are under study, it is often possible to get range maps (Fig. 1b). Range maps are created by an expert or a team of experts and often are based on known collection localities that are interpolated using biome or habitat information to infer where the species will occur (e.g., Hall, 1981). The quality of these types of maps is variable and is dependent on how well the underlying localities characterize the habitat of the species in question and the depth of knowledge the expert has about the species and its requirements. In many cases, particularly with older maps of this type, the resulting range map may overestimate the information contained in the data. Unfortunately, this may be the best information available for some groups. If so, it should be used with caution and questionable maps should be checked against other sources such as species accounts and museum collections. If these types of range maps are equal-area projection maps, then the maps can be digitized and geographic area can be measured using GIS programs (e.g., Patterson et al., 2003).

*Minimum convex polygons.*—When the underlying data are collection localities, a more conservative method for measuring geographic range area is to construct minimum convex polygons around the localities to determine the minimum area that encloses all of the localities (e.g., Lyons, 2003; Lyons, 2005; Fig. 1a). It is critical that locality coordinates be projected into an equal area projection before area is calculated. Otherwise the resulting estimate will be incorrect because the

distance between sets of latitude/longitude coordinates varies depending where you are on the globe. Therefore, a grid square that is 1° on a side contains more area in the tropics than it does in the temperate zone. There are many different types of equal area projections (e.g., Albers equal area conic projection, Lambert Azimuthal equal area projection, etc.). Different projections are designed for different purposes and will emphasize and distort different parts of the globe. Therefore, the choice of projection will depend upon your data. For example, the Albers equal area projection is a good choice if your data are concentrated in North America, whereas an equatorial Lambert Azimuthal equal area projection is a better choice for African data.

This method will almost certainly underestimate

true geographic range size particularly in fossil data because it is unlikely that every area where a species occurred will be sampled. However, it is more defensible in that it does not exceed the reach of the data and provides a minimum estimate of the known range size of a species. This method is also problematic because sampling effort is likely to vary among species. Species with more localities will have larger ranges on average than those that have fewer localities. As a result, better-sampled species will have larger inferred ranges than more poorly sampled species. Dealing with this bias is not entirely straightforward. For example, a species with a larger range could have a higher preservation potential. If a species occurs in multiple different habitat types or across more absolute space, it will have more

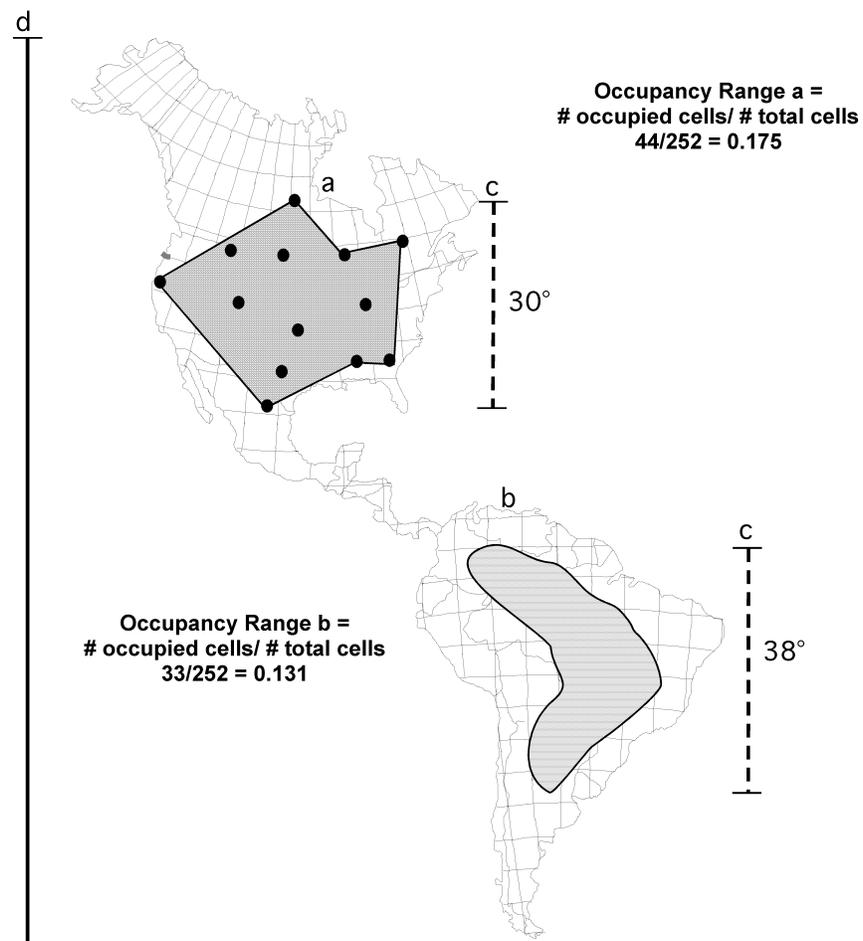


FIGURE 1.—Schematic illustrating the different methods for estimating geographic range size. a) Minimum convex polygon. b) Biome infilling. c) Latitudinal range extents. d) Extent of the domain used to determine the total number of grid cells for measures of occupancy. Modified from Willig et al. (2009) and Lyons and Wagner (2009).

opportunities for preservation. Moreover, some traits that are positively associated with geographic range size can also increase preservation potential. Although the relationship is not linear, in many modern groups larger-bodied species have larger geographic ranges (Brown, 1995; Gaston, 2003; Gaston and Blackburn, 1996b; Madin and Lyons, 2005; Smith et al., 2008). If larger-bodied species have skeletal elements that are more robust, they may be more likely to be preserved and their larger size will make it more likely that they will be recovered. Indeed, examination of the traits of extant taxa that are recorded in the fossil record has indicated that larger body size and larger geographic range favor fossilization in both mammals and marine mollusks (Lyons and Smith, 2006; Valentine et al., 2006; Fig. 2). To help mitigate this problem, a minimum sample size required to accurately represent ranges in your system should be set. Moreover, sensitivity analyses should be performed in which poorly sampled species are excluded from analyses and the effect on the patterns of interest are determined (e.g., Lyons, 2005).

Another important consideration for marine invertebrate taxa is the effect of lithification on sampling. Recent work has shown that there is a size bias in the

skeletal assemblages of lithified, poorly lithified, and unlithified specimens (Hendy, 2009). Overall, smaller-bodied specimens are less likely to be preserved than medium- and large-bodied specimens. However, a much larger proportion of the sample contains small-bodied genera in unlithified sediments than in poorly lithified or lithified sediments (Hendy, 2009). Therefore, the degree of lithification must also be considered when determining any potential effects of variation in preservation potential on sampling and geographic range estimation.

It is important to note that minimum convex polygons will not be the best method to use to estimate geographic range size if a species' distribution is discontinuous or very patchy as is often the case for marine organisms (e.g., organisms such as marine benthic invertebrates or reef fishes live in habitat patches separated by large stretches of uninhabitable land). Minimum convex polygons would greatly overestimate range area. In this case, biome infilling may be more appropriate, particularly if detailed information exists on the biomes in which each part of the species range resides. If habitat or biome information is lacking, then species occupancy (see below) may be appropri-

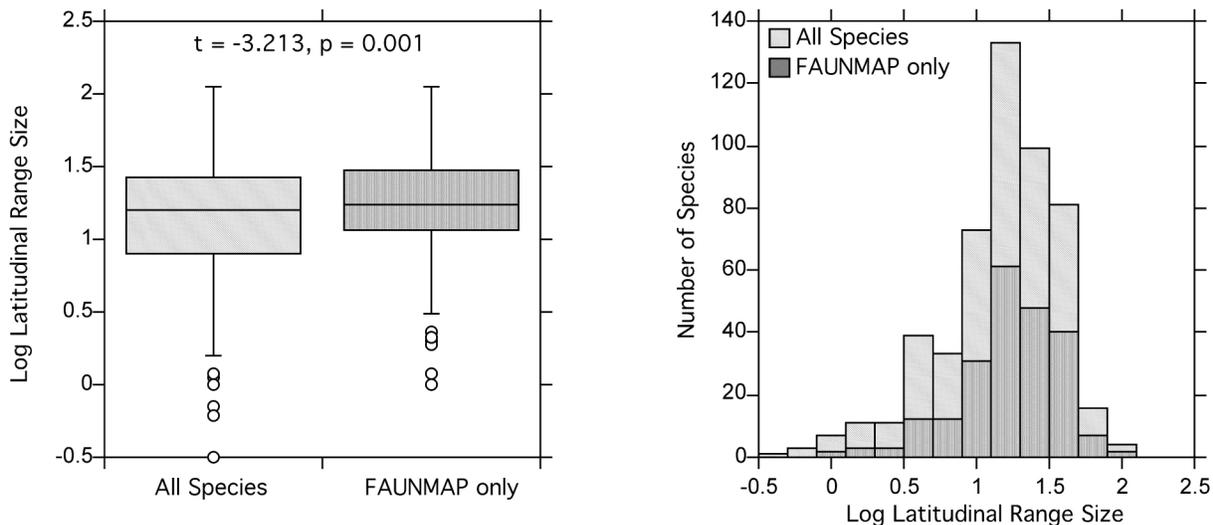


FIGURE 2.—Comparison of the range size distributions for all mammal species north of Mexico and only those species that are recorded in FAUNMAP. Data used to calculate the size of species ranges are for extant species only and are taken from the range maps of Patterson et al. (2003). The comparison asks what is the effect on range size distributions of losing species not recorded in the fossil record? As such, the range size distribution for the FAUNMAP species is also based on modern data. The two distributions are significantly different because species with small-ranges are less likely to be recorded in FAUNMAP.

ate. If the same sampling grid is used for all species, then patchily distributed species will have very low occupancy values relative to species with a more continuous distribution.

*Species occupancy.*—Species occupancy is a method of estimating relative geographic range size that is potentially useful for fossil data (Foote, 2007; Foote et al., 2008; Foote et al., 2007). Occupancy is the ratio of occupied sites to unoccupied sites (Fig. 1) and it is positively correlated with geographic range size (Gaston, 2003). Because occupancy is a relatively new measure, little work has been done on the effects of sampling on occupancy measures and there is no standard protocol for determining the sampling domain of the analysis (Willig et al., 2009). Clearly, as the number of sampled sites increases, the denominator will increase and the estimated value of occupancy will decrease. However, what is not known is the effect of using occupancy to estimate ranges of species whose ranges are not wholly contained within the domain. It will likely depend on how much of each species range falls outside of the domain and is less likely to be a problem if the domain is sufficiently large to capture the majority of a species range. Unfortunately, a rigorous analysis of the effect of sampling on the accuracy of occupancy as a measure of geographic range has not yet been done. Nonetheless, fossil data typically consist of locality data with corresponding species lists, and as such, occupancy lends itself well to this type of data. Assuming that the sampling domain is large enough and similar taphonomic biases are operating on all species under study, occupancy may provide a simple and reliable way to estimate geographic range size for fossil species (Lyons and Wagner, 2009).

*Latitudinal range.*—In some cases, it is not necessary to know the actual geographic areas or reliable data on the longitudinal extents and shape of geographic ranges are not available. In those cases, the latitudinal range can suffice (Harcourt, 2006; Koleff and Gaston, 2001; Krug et al., 2008; Lyons and Willig, 1997; Roy et al., 1995; Ruggiero and Werenkraut, 2007; Willig and Lyons, 1998). Latitudinal range is measured as the distance in degrees of latitude between the northern- and southern-most latitudinal extents of a species range (Fig. 1c). In general, latitudinal range is an excellent proxy for geographic range as they are often highly

correlated (Gaston, 2003; Lyons, 1994; Fig. 3), at least when continents are in their current configuration. For deep time continental configurations, latitudinal range may not be applicable and longitudinal range may be a better proxy. Latitudinal ranges are also preferable when the taxon of interest has geographic ranges that are essentially linear, e.g., marine mollusks or other continental shelf organisms (e.g., Krug et al., 2008; Roy et al., 1994). Finally, latitudinal ranges are preferable when the models being tested require them. For example, mid-domain models posit that when species ranges are randomly placed within a bounded domain, i.e., a land mass or closed ocean basin (Fig. 1d), species ranges will pile up in the middle of the domain and the overlap would result in a diversity gradient with a peak in the middle (Colwell and Hurtt, 1994; Colwell et al., 2004; Willig and Lyons, 1998).

*Species distribution modeling.*—In this method, also known as ecological niche modeling, locality information is combined with information about a species' abiotic environment such as temperature, rainfall, elevation, humidity, etc. and fed into a computer program designed to produce a model of the species' abiotic requirements that best predicts its distributions (e.g.,

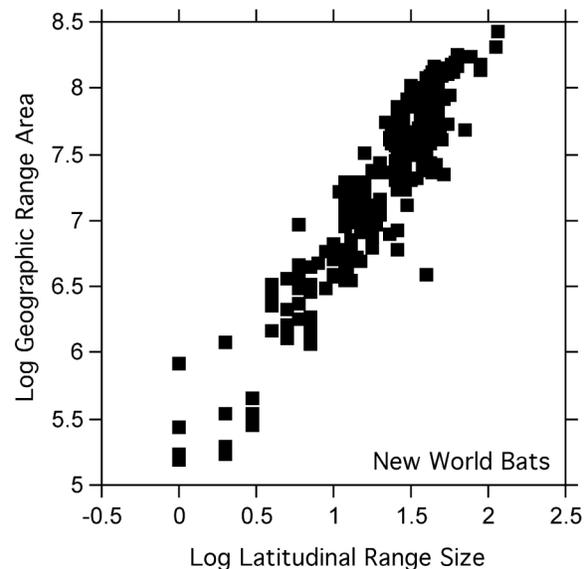


FIGURE 3. Relationship between latitudinal range size (degrees) and geographic range size ( $\text{km}^2$ ) for New World Bats. There is a strong correlation between them ( $R = 0.934$ ,  $p < 0.0001$ ).

Martinez-Meyer et al., 2004; Peterson, 2001; Peterson et al., 2004a). Although these models have great promise, they have not yet been adopted widely. In addition, there is a debate within the community about the best way to test the models produced (R. P. Anderson et al., 2003; Vaughan and Ormerod, 2005). Typically, half of the data are used to create the model and the rest are used to test the model. Another drawback is that the models rely heavily on abiotic information and do not have the ability to integrate information about biotic interactions (Araujo et al., 2005; Austin, 2002). Moreover, their accuracy depends upon the degree to which species niches are conservative. In order to work, these models assume that the combination of abiotic variables that predicts a species distribution represents the fundamental niche of a species. In periods like the late Pleistocene and Holocene where novel combinations of species occurred together with novel climate regimes (Williams et al., 2001), predictions made by species distribution models may be inaccurate or incomplete (Lyons and Wagner, 2009).

Despite the drawbacks, these methods have great potential for predicting range shifts of extant species as climate changes in the future. Indeed, they are commonly used for that purpose (Peterson et al., 2004b; Peterson et al., 2002; Peterson et al., 2003; Peterson et al., 2001; Thomas et al., 2004). Moreover, free programs such as DIVA-GIS (<http://www.diva-gis.org/>) that will easily perform species distribution modeling are now readily available. The applicability of these models to deep time systems is likely to be rare because of the detailed climate information required. However, for more recent systems such as the late Pleistocene and Holocene where reasonable climate models are available, these models have already been used to predict range shifts of extinct species (Martinez-Meyer et al., 2004; Peterson, 2001; Peterson et al., 2004a).

### Body size

*Estimating body size in different groups.*—Living things vary tremendously in their shape and size. The range of mass spans more than 21 orders of magnitude from the smallest known organisms (mycoplasma) at  $\sim 10^{-13}$  g to the largest (blue whale) at  $10^8$  g (180-200 tons). We know now that much of this variation was achieved in two “jumps” of  $\sim 8$  orders of magnitude at 2.1 Ga and 600 Ma that corresponded with the development of major evolutionary innovations (Payne et al., 2009). However, size is of more than just heuristic

interest, it also influences the way animals interact with their environment. For example, the relative importance of forces like the surface tension of water and the influence of gravity and temperature differ greatly depending on the absolute size of organisms. The environment imposes intense selective pressures on organisms over both short and longer time intervals. Moreover, many fundamental life history parameters also scale with body mass (e.g., fecundity, life span, gestation, metabolic rate, etc.; Calder, 1984; R. H. Peters, 1983; Schmidt-Nielsen, 1984). Thus, understanding the factors influencing body mass over both ecological and evolutionary time is essential for a mechanistic understanding of the structure and function of modern and paleocommunities. For these reasons, body mass may be the most important characteristic of organisms in paleoecological studies (Damuth and MacFadden, 1990).

The method used to characterize size is dependent upon the shape of the organism. For fossil mammals, allometric (nonlinear) relationships can be used to estimate mass based on the length and/or width of skulls, long bones or teeth (Damuth and MacFadden 1990 and references therein). These relationships are usually based on known mass and skeletal measurements for extant closely related species for which mass and skeletal measurements are known and tested either with use of the original data, or when available, with new datasets. To evaluate the ‘goodness’ of fit of the regression, percent predicted error (%PE) is computed:

$$\%PE = 100 \left( \frac{\sum_{i=1}^n \left( \frac{\text{predicted} - \text{actual}}{\text{actual}} \right)}{n} \right) \quad (1)$$

where  $n$  represents the number of measurements. %PE represents a comparative index of predictive accuracy. “Reasonable” values range from 18-55% for molar and bone measures (Van Valkenburgh, 1990), although exceeding  $\sim 30\%$  begins to introduce unacceptable error in the estimate. If taxa exhibit high ontogenetic dental variation then information on age or wear stage may be necessary to correctly estimate mass. There is also heterogeneity in the metric that yields the most robust estimator; for some groups (e.g., ungulates) limbs provide a better fit than molars (Scott, 1990). Finally, there is also the issue of extrapolating beyond the range of values the original equation was constructed with

since the implicit assumption is that the scaling of the metric remains constant. It may be more sensible in these instances to use a more general (e.g., order or even class specific) relationship that includes the range of values used to estimate body mass. Although it should be noted that if analyses are conducted with logarithmically transformed data, as is generally the case for macroecological studies, this may introduce only a minor degree of error. A wealth of predictive equations relating molar and limb measures to body mass for both modern and fossil mammals can be found in the appendices of Damuth and MacFadden (1990).

For vertebrates and plants (assuming more or less constant density of tissue), body mass can readily be estimated using overall length. Mass generally scales as the cube of length (Calder, 1984; Niklas, 1994b; R. H. Peters, 1983). While this is useful for measuring skeletons of modern or fossil vertebrates, complete skeletal material is not always available. For example, sauropods are often preserved without their tails, so the margin of error in overall length estimates is particularly high. Other predictive equations have been constructed using specific morphological characters unique to a taxon. For example, using measurements of curvilinear carapace length, researchers have been able to estimate turtle body mass with reasonable accuracy (Georges and Fossette, 2006).

Morphology is also used to estimate “body mass” (biovolume) for terrestrial plants. Stem diameters are often possible to measure in fossil floras and provide a metric that can be converted to mass. Allometric equations for predicting fossil plant height or length from stem diameter are available for a variety of plant types (Niklas, 1994a). These equations are influenced by the anatomy and growth form of the plant; equations for “woody” species differ significantly from those for “nonwoody” species (Niklas, 1994a). With an estimate of overall plant length, biomass can be estimated using the formula for a cylinder ( $Cylinder = \pi r^2 h$ ) or approximated using the cube of length (Niklas, 1994b).

Volumetric measures are often employed to obtain body mass estimates for large sauropods and mammals. This technique employs Archimedes’ principle; that is, the idea that the apparent weight of an object immersed in a liquid decreases by an amount equal to the weight of the volume of the liquid that it displaces. If we assume the dinosaurs had the same density as most land animals today (which seems reasonable given their

physiology), it was approximately equal to that of water ( $1 \text{ g/cm}^3$ ). Thus, one can estimate mass by creating a scale model and measuring water displacement.

To illustrate the difference in mass obtained by these various methods, consider the sauropod, *Brachiosaurus*. Volumetric displacement yielded body mass estimates variously of 78.3, 32, and 46.6 metric tons (Alexander, 1989; Colbert, 1962; Paul, 1988). Using an allometry based on limb bones (and inferring sauropods scale as other reptiles) yielded mass estimates of 15 and 29 metric tons (J. F. Anderson et al., 1985; Russell and Zheng, 1993). Which of these estimates is more accurate is open to debate, but they all lie within the same order of magnitude.

Invertebrate taxa can be more difficult to characterize. Ideally, mass would be directly determined by weighing samples. Of course this option is not available to paleontologists, who must deal with fragmentary remains of hard parts. Often, researchers approximate the body morphology with a geometric formula (Novack-Gottshall, 2008). Depending on the taxon, different shapes may be employed even within the same clade. For example, Arthropoda have variously been considered as blocks, cylinders, cubes or even multiple cylinders (Novack-Gottshall, 2008; Payne et al., 2009). Molluscs have been characterized as cylinders, rectangular prisms, blocks, and cones. For gastropods, the geometric mean of length and height, which is relatively easy to characterize, is often used (e.g., Jablonski, 1996; Jablonski, 1997; Stanley, 1986). This simple technique yields robust results consistent with more complex and difficult to obtain morphometric measurements; the addition of width adds only slightly to the accuracy of the estimate (Kosnik et al., 2006). While use of area (e.g., length and width measures) is appropriate if comparisons are limited to similar clades, to make cross-taxonomic syntheses of organisms with different bauplans it is preferable to use biovolume ( $\text{cm}^3$ ), which is roughly comparable to biomass (g). Similarly, linear dimensions should be converted to biomass or biovolume since they too may conflate cross-taxon interpretations (Loder et al., 1997).

*Body size and allometry* - Many physiological and ecological traits vary in predictable ways with the body mass of organisms. Thus, changes in size over time or space may lead to differences in energy use, life history and even rates of evolution. If a trait scales

linearly with mass (e.g., the slope = ~1), the scaling is termed isometric (iso = same, metric = measure). The gut capacity of vertebrate animals is an example of an isometric trait (Parra, 1978). However, most important life history characteristics (e.g., metabolic rate, fecundity) vary non-linearly with body mass (e.g., slopes not equal to 1); these are known as allometries (allos = different, metron = measure). An allometric relationship is thus a power function of the form:

$$Y=aM^b \quad (2)$$

where  $Y$  is the variable of interest,  $M$  is body size,  $b$  is the slope, and  $a$  represents a taxon-specific constant, sometimes referred to as the normalization or proportionality constant (the intercept at unity body mass when  $M=1$ ). In practical use, power laws are often logarithmically transformed such that

$$\log y = \log a + b \log M \quad (3)$$

because the exponent becomes the slope of a straight line, facilitating computations and cross taxa comparisons. The intercept generally varies in a regular way among clades. For example, marsupials have a metabolic rate 30% lower than placental mammals, which is reflected in the value of their normalization constant. Such allometric relationships facilitate comparisons within and among species at different taxonomic levels and also allow reasonably accurate predictions of many biological rates and times. Often what appear to be significant differences among organisms are actually consequences of scaling effects, but true deviations from predicted values can provide important insights into evolutionary history and adaptation. Over the past few decades, there has been a resurgence of interest in formulating and comparing allometric relationships (Calder, 1984; Damuth, 1987; Damuth, 2007; Enquist et al., 1998; Enquist et al., 1999; Ernest et al., 2003; Gillooly et al., 2001; Hendriks and Mulder, 2008; Jun et al., 2003; Kerkhoff and Enquist, 2006; Kerkhoff et al., 2005; Kodric-Brown et al., 2006; Marquet et al., 1995; R. H. Peters, 1983; Polishchuk and Tseitlin, 2001; Schmidt-Nielsen, 1984; Sibly and Brown, 2007; West and Brown, 2004; West et al., 1999; West et al., 2002).

*Diversity and abundance.*—There are numerous methods for estimating species diversity and abun-

dance, many more than we can cover here (Magurran, 1988; Magurran, 2004; Magurran, 2005). In general, the metric you use will depend upon your needs and the available data.

*Richness, diversity and evenness measures.*—Although ecologists and paleontologists often use richness and diversity as interchangeable terms (Gaston and Blackburn, 2003; Sepkoski Jr, 1978), they do mean very different things. Richness is simply the number of taxa in your sample. Diversity measures combine richness with a measure of relative abundance into a single metric. Evenness measures are used to characterize a species' relative abundance and are a measure of how similar the proportions of different species in a sample are. There are many different diversity metrics to choose from, but two of the most popular are the Shannon index and the Simpson index.

The Shannon index is based on information theory and is a measure of the order in a system:

$$H' = -\sum_i^S p_i \ln p_i \quad (4)$$

where  $S$  is the observed richness, and  $p_i$  is the proportion of the  $i$ th species in the sample or the observed relative abundance. This index is maximized when a sample has high evenness, that is, all species occur in equal proportions (i.e.,  $p_i = 1/S$ ). In that case  $H' = \ln(S)$ .  $H'$  typically varies between 1.5 and 3.5 for ecological data. However, it has been criticized because it is difficult to interpret when values are in the middle range.

The Simpson index measures the probability that any two individuals drawn at random from an infinitely large sample will be the same species:

$$D = \sum p_i^2 \quad (5)$$

where  $p_i^2$  is the square of the proportion of the  $i$ th species in the sample. The Simpson index is usually expressed as  $1-D$  or  $1/D$  so that the value of  $D$  increases as diversity increases.

As with diversity metrics, there are a large number of possible evenness metrics. We outline only a few here. It is possible to calculate a measure of evenness using the Shannon index and species richness,  $S$ . These include Pielou's  $J$  (Pielou, 1966) and  $E$  (Buzas and Gibson, 1969). Pielou's  $J$  is:

$$J = \frac{H'}{\ln S} \quad (6)$$

In this case, if a sample is perfectly even, then  $J = 1$ . However, if abundances are very dissimilar as is usually the case for ecologic data, then  $J$  is greater than 1 (Magurran, 1988). Buzas and Gibson's  $E$  is given as:

$$E = \frac{e^{-H'}}{S} \quad (7)$$

where  $H'$  is the Shannon index and  $S$  is species richness. As with equation 3, these evenness metrics will equal 1 when abundances are equal.

Other evenness metrics use the sums of squared frequencies. Two commonly used metric are Hurlbert's Probability of Intraspecific Encounter (*PIE*; Hurlbert, 1972) and Peter's  $F$  (S. E. Peters, 2004). *PIE* measures the probability of sampling the same taxon twice in a row and is given as:

$$PIE = \left( \frac{N}{N-1} \right) \left( 1 - \sum_{i=1}^s p_i^2 \right) \quad (8)$$

where  $N$  is the total number of individuals in the sample,  $S$  is the species richness, and  $p_i$  is the proportion of the  $i$ th species in the sample. Peter's  $F$  uses the sum of squared differences between the observed and expected abundances, where the expected distribution of abundances is perfectly uniform (i.e.,  $p_i = 1/S$ ) and is given as:

$$F = 1 - \frac{S \sum_i (p_i - \frac{1}{S})^2}{S-1} \quad (9)$$

When abundances are equal,  $F = 1$ . However, *PIE* increases as richness increases and can never reach 1.

It is very important to consider sample size when choosing an evenness metric. Some, like *PIE*, have maximum values that depend on richness of the sample. However, for all evenness metrics, the minimum value depends upon richness (i.e., the number of taxa) and sample size (i.e., the number of specimens in the sample). Because the common taxa make the greatest contributions to the values of *PIE* and  $F$ , small samples yield accurate estimates (Gotelli and Graves,

1996; S. E. Peters, 2004). Rare taxa have little effect on the sum of squared proportions. In contrast, rare taxa have a large effect on the Shannon index and the Simpson index.

### Abundance

Typically, in macroecological studies, the pattern of interest is the relationship between abundance and something else such as body size or geographic range size. In that case, the metric of interest is simply the average observed population size of a species. In some cases, density is used which is the average number of individuals per unit area. Obviously, these measures are going to be affected by the sample size. In practice, abundance data are rare and macroecologists will simply use any data that are available. However, the assumption is that effect of sample size should be different for different species and should add noise to the relationship under study and not a systematic bias.

Because there is a strong, positive relationship between occupancy and abundance (Gaston et al., 2000; He and Gaston, 2000; Holt et al., 2002; Murphy et al., 2006; Selmi and Boulinier, 2004), occupancy is sometimes used as a proxy for abundance (e.g., Raia et al., 2006). This is particularly useful when using fossil data as it is relatively simple to calculate the ratio of the number of localities in which a species is found to the total number of localities sampled. However, it should be noted that occupancy is more commonly used a measure of geographic range size. Although the effects of sampling on measures of occupancy have not been systematically investigated, a recent study comparing occupancy for one neotropical primate species with field estimates found that occupancy was a good predictor of abundance (Figueiredo and Grelle, 2009). Nonetheless, until more such studies are done, results from the use of occupancy as a proxy for abundance should be interpreted with caution.

## MACROECOLOGICAL PATTERNS

### Macroecological patterns of geographic range size

Understanding the factors that determine the limits of species ranges is a central question in ecology and is made difficult by the fact that these factors are multifaceted, complex, and unique to particular species. Nonetheless, macroecology offers some insights because many ecological and physical traits

are correlated with a species range. Two of the most common and consistent patterns are the relationship between geographic range size and body size (Brown, 1995; Diniz et al., 2005; Gaston, 2003; Gaston and Blackburn, 1996c; Pyron, 1999; Reed, 2003; Willig et al., 2009) or abundance (Beck et al., 2006; Blackburn et al., 1997; Brown, 1995; Gaston, 2003; Pyron, 1999; Raia et al., 2006).

*Range size frequency distributions.*—Range size frequency distributions (RSFD) are constructed by allocating species into range size categories and counting the number of species within each one (Fig. 2). This is one of the most consistent and robust macroecological patterns that has been identified. Regardless of taxon, the majority of species have small ranges and a few species have large ranges (Brown, 1995; Gaston, 2003). The resulting distributions are often called “hollow curves” and are typically right-skewed and unimodal (Willis, 1922). In this case, logging geographic range size does not produce a normal curve. Instead, frequency distributions of log range size are typically unimodal and somewhat left-skewed (Fig. 2).

RSFDs are usually plotted and used for visual inspection only. However, they have several possible uses in fossil systems. Because they have such a characteristic distribution, RSFDs of fossil taxa could be constructed and compared to a RSFD for a closely related modern taxon. Several methods are available for comparing distributions. A simple method is to use a Student’s t-test (e.g., Fig. 2). However, non-parametric methods such as the Kolmogorov-Smirnov or Mann-Whitney U-tests are preferred because of the non-normality of the data. To determine if there was a systematic bias in preservation potential for mammal species of differing range sizes, we compared the RSFD of modern mammals that occur north of Mexico to the RSFD of a degraded data set that used modern range size information, but included only species that were found in FAUNMAP. Using a Student’s t-test, we found that the two distributions were significantly different because narrow-ranging species were less likely to be recorded in FAUNMAP, suggesting a lower preservation potential.

Another potential application of RSFDs to fossil data is to determine if the range sizes estimated using fossil taxa are reasonable estimates. If the resulting distribution follows a hollow curve similar to that

of extant taxa, it suggests that the estimates of range sizes are likely to be a reasonable representation of the fauna even if species are missing. For example, Lyons (2005) used the similarity between RSFDs for modern North American mammals and RSFDs calculated using FAUNMAP data to argue that for the species pool available, the estimated range sizes were reasonable.

*Relationship between body size and range size.*— This relationship is typically evaluated by plotting log geographic or latitudinal range size as a function of log body size (Fig. 4). In general the relationship is triangular with small-bodied species having a large amount of variation in geographic range size, whereas large-bodied species tend to have large ranges. This relationship has been found for many different taxonomic groups (Brown, 1995; Gaston, 2003; Pyron, 1999; Reed, 2003; Smith et al., 2008; Willig et al., 2009) and in fossil data (Lyons, unpublished data). Because of the complex nature of the relationship, statistical methods for evaluating it are lacking. In general, one of three approaches has been used: avoid applying statistical methods and simply verbally describe the shape of the relationship, calculate the parametric or non-parametric correlation between range size and body size, or focus on the upper and lower bounds of the data and evaluate the constraint envelope that encompasses the data. Constraint envelopes are determined by splitting the data into the upper quartile of species with the largest geographic range sizes per body size bin and the lower quartile of species with the smallest geographic range sizes per body size bin. For each quartile, a regression is calculated for the relationship between body size and range size. This method is also used to identify species at risk of extinction because the lower constraint line is predicted to be the minimum geographic range size necessary to minimize extinction over geologic time (Diniz et al., 2005; Gaston and Blackburn, 1996a; Pyron, 1999).

Characterizing the relationship between body size and range size is complicated because the scale of the analysis affects the resulting relationship. If the domain of the study encompasses a significant portion of the geographic range sizes of the taxa in question then a positive relationship is typically found, whereas if the domain is smaller than the geographic range sizes of the taxa in question then the result is unpredictable (Gaston and Blackburn, 1996c; Madin and Lyons, 2005).

Modeling efforts have shown that this unpredictability is because incomplete sampling tends to underestimate the size of the largest geographic ranges and completely miss many of the smaller geographic ranges (Madin and Lyons, 2005). Interestingly, the potential use of fossil data does not seem to affect the resulting relationship. We compared the body size – range size relationship for all extant mammals that occur north of Mexico to the relationship for those same mammals as recorded by the FAUNMAP database (FAUNMAP Working group, 1994). That is, we asked what relationship would we expect if we had detailed knowledge of a species range, but the pool of species evaluated was affected by taphonomic biases in preservation potential (Fig. 4). Although small-ranged species are less likely to be recorded in FAUNMAP (Fig. 2), the relationships between body size and range size had similar somewhat triangular shapes and similar correlation coefficients (Fig. 4).

*Relationship between abundance and range size.*—The relationship between abundance and geographic range size, also known as the abundance – occupancy relationship, is similar to the relationship between body size and range size. It is triangular, with wide-ranging species having a great deal of variation in abundance and narrow ranging species having low abundances (Brown, 1995; Brown et al., 1996; Gaston, 2003). Local population abundance, density and population size have all been used as proxies for abundance. However, regardless of metric, the log of geographic range size and abundance should be used. As with the body size – range size relationship, the complicated nature of the pattern makes statistical evaluation difficult. Constraint envelopes, correlation coefficients and pattern inspection have been used.

*Range size as a function of latitude.*—The shape and causes of the latitudinal gradient in geographic range size are hotly debated in macroecology (Black-

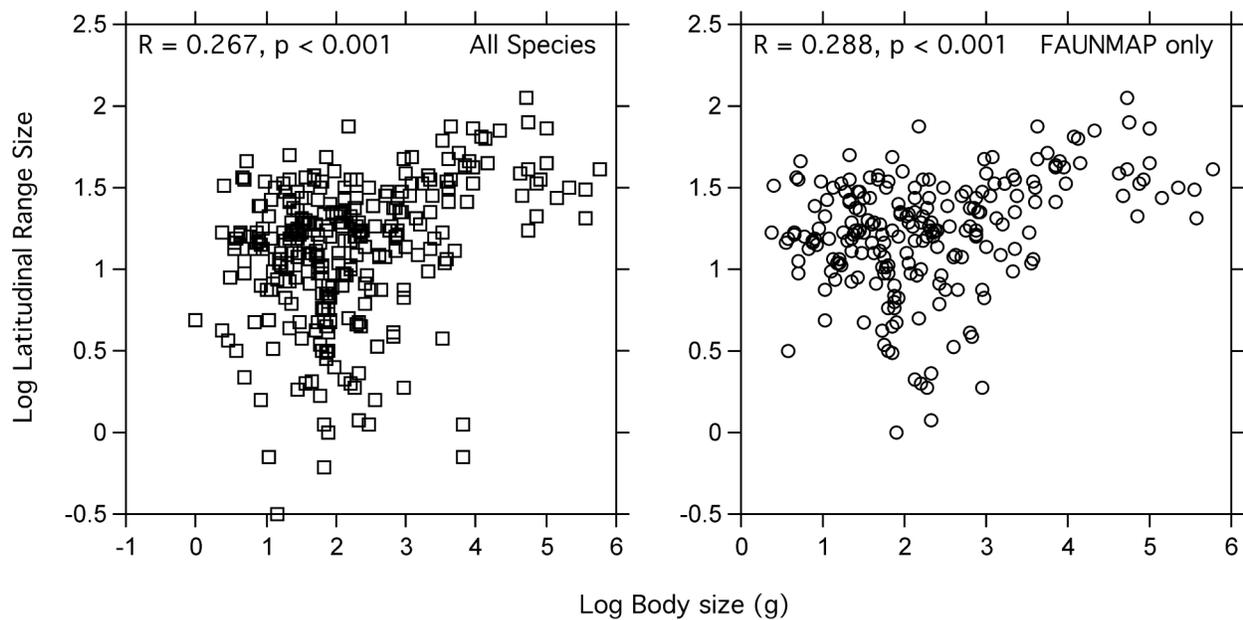


Figure 4.—Comparison of the relationship between body size and range size for all mammal species north of Mexico and only those species that are recorded in FAUNMAP. The comparison asks what is the effect on body size - range size patterns of losing species not recorded in the fossil record? As such, the range size and body size data used are data for extant species. The difference is the removal of species not recorded in FAUNMAP. The two patterns have very similar shapes and correlation coefficients. In general, using fossil data does not bias the resulting pattern.

burn and Gaston, 1996b; Gaston et al., 1998; Gaston and Chown, 1999; Lyons and Willig, 1997; Rohde et al., 1993; Roy et al., 1994; G. C. Stevens, 1989; Taylor and Gaines, 1999). Stevens (1989) identified a pattern he called Rapoport's Rule. The average range size of a species decreases as you move toward the tropics. He calculated the pattern by taking the average range size of all species whose ranges overlapped a 5° latitudinal band (e.g., Fig. 5). This method was later termed the Stevens Method (Lyons and Willig, 1997; Rohde et al., 1993; Roy et al., 1994). It was criticized because each species is counted multiple times and therefore the data are not independent (Rohde et al., 1993; Roy et al., 1994). These authors suggested instead that range size be plotted as a function of the mid-latitude of a species range (e.g., Fig. 6). However, this method is biased toward finding large ranges at the center of the domain of interest. Because a species range is symmetrical around its mid-latitude, a range with a mid-latitude at the center of a domain has the potential to expand throughout the entire domain, whereas a species with a mid-latitude at the edges of a domain can only extend the range to the domain boundary and will, on average, have a smaller range (Lyons and Willig, 1997). This method is biased toward finding a peak in range size at low latitudes and that is indeed what has typically been reported (Hecnar,

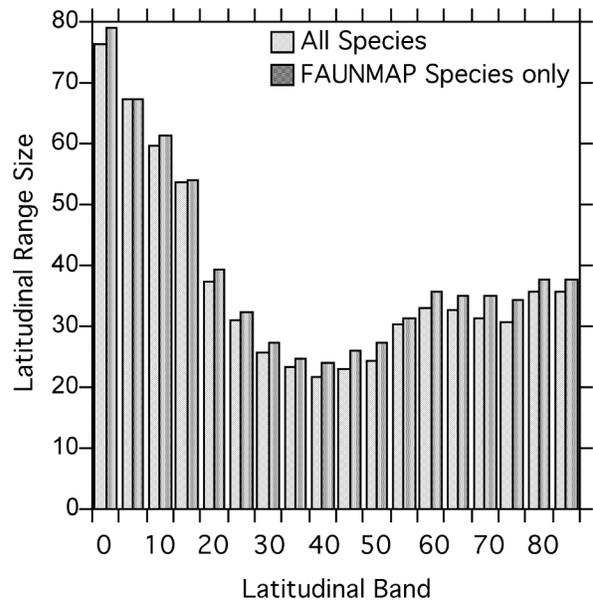


Figure 5.—Latitudinal gradient in species range size calculated using the Stevens Method for all mammal species north of Mexico (light gray bars) and only those mammals recorded in FAUNMAP (dark gray bars). Range data used to create the graph are modern range data.

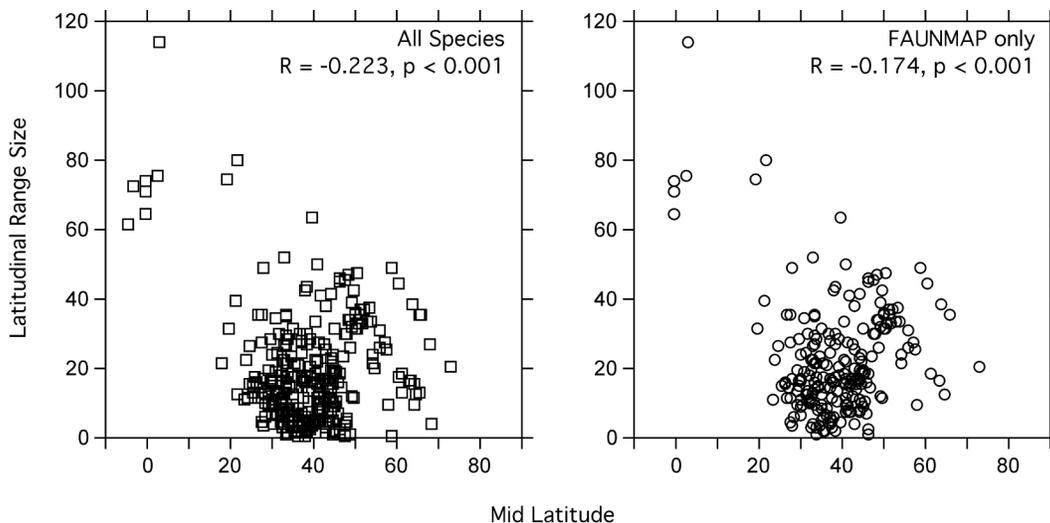


Figure 6.—Relationship between mid latitude and range size for all mammal species north of Mexico (squares) and only those species that are recorded in FAUNMAP (circles). Only data on extant species are used and species not recorded in FAUNMAP are eliminated from the right-hand graph. The two patterns have very similar shapes and very similar correlation coefficients. In general, using fossil data does not bias the resulting pattern.

1999; Husak and Husak, 2003; Rohde et al., 1993; Roy et al., 1994; Ruggiero and Lawton, 1998).

Using the same data as in previous analyses in this paper, we analyzed the latitudinal variation in range size for modern mammals north of Mexico and a degraded data set that contained only those species recorded in FAUNMAP using both the Stevens Method (Fig. 5) and the Midpoint Method (Fig. 6). Using the Stevens Method, average latitudinal range size decreased toward the middle of the domain and increased toward both edges (Fig. 5), a pattern inconsistent with Rapoport's Rule which requires range size to decrease to the tropics. Using the Midpoint Method, we found the predicted bias with the largest range sizes at the equator, and range size decreased toward the northern hemisphere (Fig. 6), again a pattern inconsistent with Rapoport's Rule. However, we did not find a difference in the pattern when using the full dataset or the degraded "fossil" dataset. This suggests that although species with smaller ranges are more likely to be missed (Fig. 2), there is no systematic bias with respect to latitude.

In one of the few studies to use both methods with the same data, Lyons and Willig (1997) found that the Steven's method produced a pattern consistent with Rapoport's Rule, whereas the Midpoint method did not. This is in contrast to the pattern found here (Figs.

5 and 6) where both methods were inconsistent with Rapoport's Rule. Because both methods were flawed, Lyons and Willig (1997) advocated using null models and simulation methods to determine whether the latitudinal distribution of range sizes was significantly different from that expected by chance. Simulations were performed in three ways, first by choosing both range endpoints at random, second by using the distribution of midpoints and randomly choosing a range endpoint, and third by using the distribution of most-distal points (MDPs) or range endpoints farthest from the equator and randomly choosing the other end point (Lyons and Willig 1997). In every iteration of the simulation, the correlation coefficient between midpoint and range size was calculated and recorded. This process was repeated 1000 times and the actual correlation coefficient for the raw data was compared to the simulated distribution of correlation coefficients. If the actual value fell in the tails of the distribution, the relationship between midpoint and geographic range size was significant. Using this method, Lyons and Willig (1997) found that range sizes were larger than expected in the temperate zones and smaller than expected in the tropics, a pattern they termed a Rapoport effect. Range sizes were absolutely larger in the tropics, a pattern inconsistent with Rapoport's Rule, but they were smaller than predicted

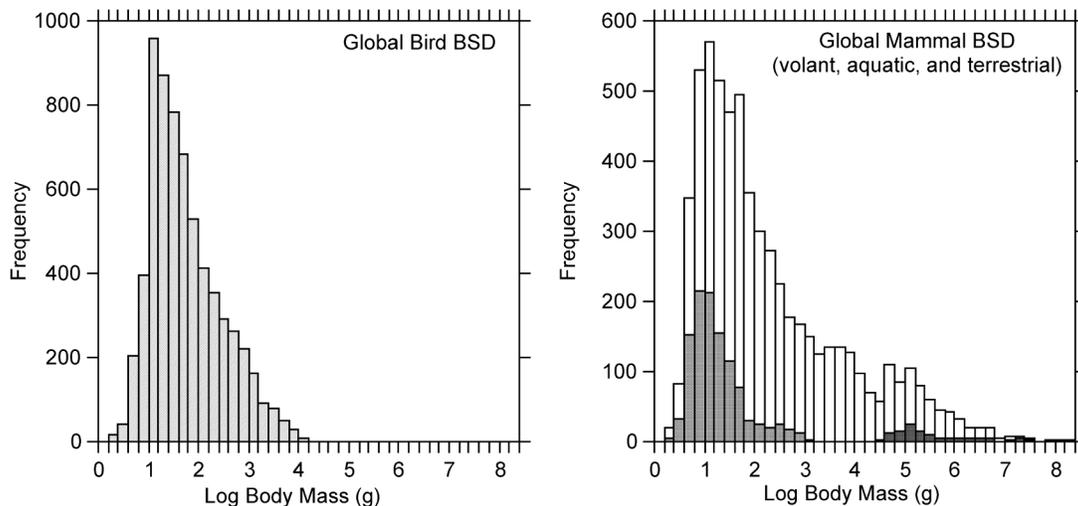


Figure 7.—Global body size distributions of birds (left-hand graph) and mammals (right-hand graph). Note that volant, aquatic and terrestrial mammals are shaded differently. All mammals are shown in white, bats are the light gray bars and aquatic mammals are the dark gray bars. All distributions display a strong right skew; that for mammals is bimodal. Modified from Smith et al. 2008.

by the simulations. In an analysis of multiple data sets, Ribas and Schoereder (2006) performed similar simulations and found no support for Rapoport's Rule. The simulations described here are identical to simulations for the mid-domain effect (MDE)(Colwell and Hurtt, 1994; Colwell et al., 2004; Willig and Lyons, 1998) except that in MDE models, the interest is in the number of species per latitudinal band rather than latitudinal variation in range size.

### Macroecological patterns of body size

*Body size frequency distributions.*—Body size frequency distributions (BSD) are a common way to illustrate patterns of taxa over spatial scales ranging from populations and local communities to global assemblages. Typically, the number of species in each size class is tabulated on the y-axis and the size class is plotted on the x-axis (Fig. 7). Investigators employ either natural or base 10 logarithms so that the proportional change in mass is similar among different size classes. The body size distribution of many taxonomic groups illustrates a strikingly log skewed (right skewed on logarithmic axes) pattern with many more species of small than large size; this holds for many taxa at large spatial scales (e.g., Blackburn and Gaston, 1994; Brown and Nicoletto, 1991; Hutchinson and MacArthur, 1959;

May, 1978; McClain, 2004). However, this may not be universal - some ectothermic vertebrates and invertebrate groups demonstrate unimodal, left-skewed body size distributions (Boback and Guyer, 2003; Poulin and Morand, 1997; Roy and Martien, 2001). The mechanistic underpinnings of these relationships are unclear. For example, a recent study attributed body size patterns in benthic marine invertebrates to tradeoffs between mechanical and energetic constraints (Sebens, 2002). What drives differences in body size frequency distributions and whether mechanisms are universally applicable is still actively debated (e.g., Loder 1997; Smith et al. 2008).

Studies that have directly compared the body size distributions of fossil and modern communities have generally found good congruence as long as sampling is adequate (Lyons et al., 2003). Although the absolute number of species recovered may be less in fossil localities, the overall shape appears to be robust if the sampling and spatial scale is sufficient (Fig. 8). It must be noted that our comparison in Fig. 8 uses the late Quaternary North American record, an exceptionally good record. In deeper time records, particularly terrestrial records, the consistent undersampling of small-bodied species (e.g., Lyons and Smith, 2006; Valentine et al., 2006) is likely to have a greater effect.

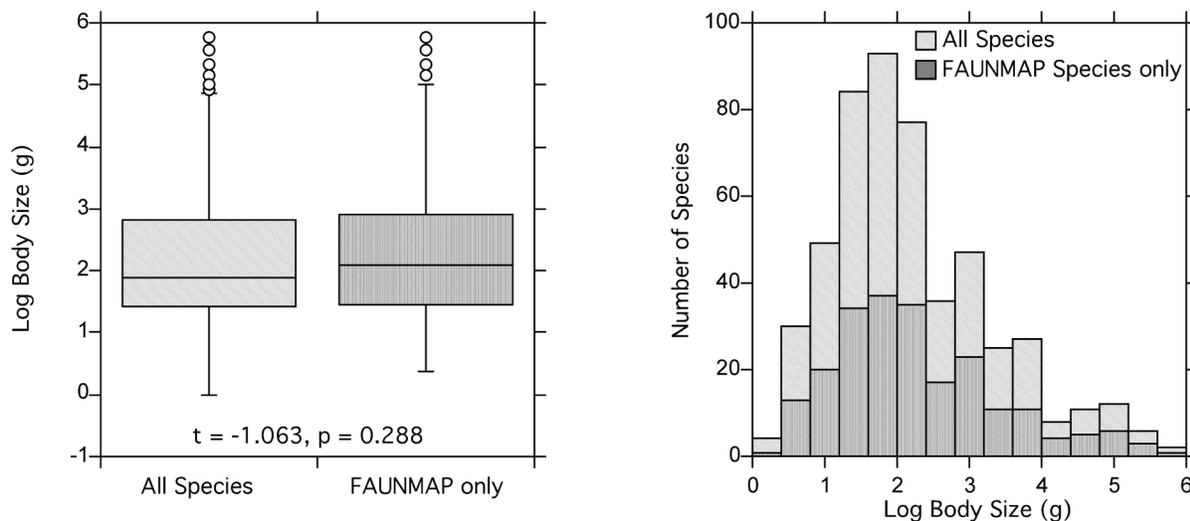


Figure 8.—Comparison of the body size distributions for all mammal species north of Mexico and only those species that are recorded in FAUNMAP. Only data on extant species are used and species not recorded in FAUNMAP are eliminated from that body size distribution. The two distributions are not significantly different. Although fewer species are recorded in FAUNMAP, they are not a biased sample of the body size distribution.

*Cenogram analyses.*—Cenogram analysis is a method for reconstructing paleoenvironments using mammalian body sizes. It was described by Valverde (1964; 1967) and then modified and extended by Legendre (1986; 1989). In this kind of analysis, the natural logarithm of body size for each species is plotted on the y-axis as a function of the rank order of body size from the largest to the smallest (Fig. 9). Carnivores and bats are excluded. The shape of the overall body size distribution as well as the placement of gaps is used to indicate the general climate. If the overall rank order distribution of body sizes is continuous with no gaps (Fig. 9, top panels), the environment is characterized as closed. However, if there are very few or no medium-bodied species, defined here as species that are >500 g but less than 8 kg, the environment is characterized as open (Fig. 9, bottom panels). Medium-bodied species are often arboreal and are more likely to be found in a forested or closed habitat. The number of large-bodied species, defined here as species that are >8 kg, is indicative of how wet the environment is. A habitat rich in large-bodied species is associated with more mesic conditions, and is characterized as a humid habitat (Fig.

9, left-hand panels). If a community is depauperate in large-bodied species, it is associated with more xeric conditions, and is characterized as an arid habitat (Fig. 9, right-hand panels).

An alternative method to cenogram analyses was developed by Alroy (2000). In this method, the BSFD is constructed as described above and the moments of the distribution (mean, median, skew, and kurtosis) are calculated. Using a dataset of modern mammalian communities with good global coverage, Alroy (2004) showed that the higher order moments correlated with climate. In particular, kurtosis showed a strong linear relationship with rainfall with higher kurtosis values found in communities with high rainfall. He tested this method using fossil mammal faunas with independent proxies for habitat and found that kurtosis was an accurate predictor of habitat type.

*Body size distributions at different spatial scales.*—Since the abundance of species is related to their body size, it should come as no surprise that body size influences community structure and dynamics. Although still debated, there appear to be regular patterns in the shape of body size distributions with respect to spatial scale. A seminal study was that of Brown and Nicoletto (1991), who observed that body size distributions of modern mammals change with spatial scale in North America. At the continental level, the overall distribution is multi-modal and right skewed (Lyons et al., 2004; Smith et al., 2004); this bimodality has been the norm for the past ~40 million years (Alroy, 1998; Alroy, 2003). However, as the spatial scale decreases the body size distribution become progressively flatter until it is nearly uniform for local communities (Brown and Nicoletto 1991). The proximate cause of these differences is likely to be turnover of species in the modal body size class of ~100g across communities. Because large species tend to have large geographic ranges (Brown 1995), there are fewer turnovers in these size classes. Whether these patterns are universal across taxa remains unclear. While some other vertebrate groups demonstrate similar relationships (Blackburn and Gaston, 1994; Brown, 1995; Maurer et al., 2004), such regular patterns are not found in other vertebrates (e.g. snakes, Boback and Guyer, 2003) or in many invertebrate groups (Poulin and Morand, 1997; Roy and Martien, 2001).

If the shape of body size distributions is indeed

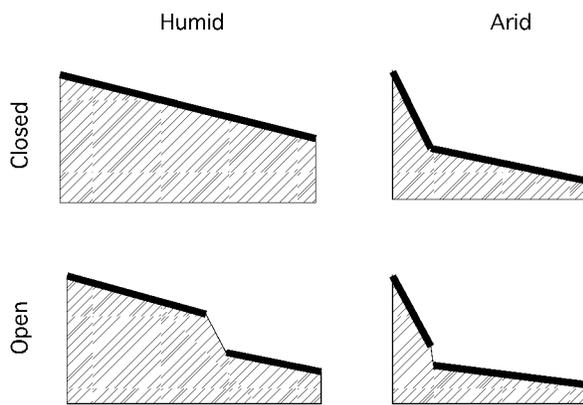


Figure 9.—Graphical illustration of the different shapes of a cenogram and their interpretation. In closed habitats, the rank order body size distribution is continuous (top row). In open environments, medium sized species (e.g., 500 g < mass < 8000 g) are rare or absent (bottom row). In humid environments (left-hand column), the right hand tail is extended because there are numerous large-bodied species (e.g., Mass > 8000 g), whereas in arid environments, large bodied species are rare (right-hand column).

regular across spatial scales, this must reflect common underlying ecological and evolutionary processes. One might expect then to observe consistent patterns in body size distributions across temporal scales. To date, little research has explored this idea because of the difficulty in reconstructing body size assemblages of fossil communities. Lyons *et al.* (2003) reconstructed 328 mammal communities over the late Quaternary and evaluated the statistical moments of the resulting body size distributions. Following Alroy's (2000) method of moments describe above in the section on cenogram analyses, the mean and median body mass as well as skew and kurtosis for the fossil assemblages were compared to those for modern assemblages ranging across different habitat types. The descriptive statistics of the shapes of most fossil assemblages (>60%) fell within the range of values for the modern assemblages, suggesting that body size was an inherent component of communities. Because of the limits of the fossil record, some of the variation was likely due to errors in body size estimation of fossil species and/or taphonomic biases. However, the markedly different shapes of forest versus open habitats body size distributions in South America (Bakker and Kelt, 2000), and the bimodality in body size distributions at all spatial scales in Africa (Kelt and Meyer, 2009), suggest that some of the variation was due to climatic differences (Lyons *et al.* 2003). Others have also linked turnover in the body size structure of fossil mammal communities to paleoenvironmental changes (Croft, 2001; Legendre, 1989; Montuire, 1999). Future work will undoubtedly explore these ideas further; the development of large publically accessible community level databases over the past decade or so (e.g., Neogene mammals of the world [NOW; <http://www.helsinki.fi/science/now/>], Paleobiology Database [PaleoDB; [www.pbdb.org](http://www.pbdb.org)], a database of Recent mammal and their ecological traits [PanTHERIA; <http://esapubs.org/archive/ecol/E090/184/default.htm>]), some of which include body size estimates for fossil species (PBDB), make these comparisons feasible.

*Latitudinal or temperature gradients in body size.*—Regular patterns of morphological variation with temperature have been observed repeatedly over time and space. These “ecogeographic” gradients often involve body size, although coloration or dimensions can be influenced as well (Mayr, 1956; Rensch, 1938).

The best supported is Bergmann's rule: the principle that within a broadly distributed genus, species of larger size are found in colder environments and species of smaller size are found in warmer areas (Mayr, 1956; Rensch, 1938). Although originally formulated in terms of species within a genus, it is often recast in terms of populations within a species. Typically Bergmann's rule is evaluated by plotted log mean body size of populations as a function of temperature (Freckleton *et al.*, 2003; Hunt and Roy, 2006; Smith *et al.*, 1995). The strength of the relationship is usually determined using regression analyses or correlation coefficients. When Bergmann's rule is evaluated at the species level rather than the population level, mean body size of all species within a latitudinal band is plotted as a function of latitude (Blackburn *et al.*, 1999; Blackburn and Ruggiero, 2001; Hausdorf, 2003). This method is similar to and suffers from the same issues as the Stevens Method discussed in the section on latitudinal gradients in range size. An alternative method used to evaluate Bergmann's rule at the species level is to determine the mean body size of all species whose ranges fall within a grid cell and plot that as a function of latitude of temperature (Olalla-Tarraga *et al.*, 2006; Rodriguez *et al.*, 2008).

Several recent studies have documented that Bergmann's rule applies to temporal responses over the Pleistocene (Dayan *et al.*, 1991; Smith *et al.*, 1995). Size changes in Quaternary mammal species have often been attributed to the climate change occurring during this period. Animals became smaller during the warmer conditions of the middle and late Holocene, and were larger during the cooler conditions of the full glacial, the Little Ice Age and the Younger Dryas (Smith and Betancourt, 1998; Smith and Betancourt, 2003; Smith and Betancourt, 2006; Smith *et al.*, 1995). For some of these species, physiological constraints may be important: both maximum and minimum environmental temperatures have also been demonstrated to scale inversely with body mass as does lethal temperature (Smith *et al.*, 1995). In deeper time, Bergmann's rule may drive the size increase observed in deep-sea ostracods over the past 40 million years (Hunt and Roy, 2006). These authors found that size increases over the Cenozoic were consistent with temperature-size relationships found geographically in modern populations. It has also been proposed that Bergmann's rule and Cope's rule (the tendency for organisms in evol-

ing lineages of size increase over geological time) are related patterns, which reflect the strong selective force of environmental temperature changes (Hunt and Roy, 2006).

Given the robust pattern of Bergmann's rule for most mammal species across modern spatial gradients, it is possible to use fossil body sizes as a proxy for paleotemperatures (Dayan et al. 1991, Smith and Betancourt, 2003, 2006). To do this, a modern relationship between mass and temperature must first be established (Smith and Betancourt, 1998, 2003); ideally, size must also be heritable so that observed patterns are genetically determined (Smith and Betancourt, 2006). Given the paucity of local paleoreconstructions that extend further than a few thousand years, this approach may be of great use in evaluating the magnitude and rapidity of climatic fluctuations over the late Quaternary.

### Macroecological patterns of diversity

Documenting and understanding geographic variation in biodiversity across large spatial scales, ranging from regional to global, is one of the oldest pursuits in macroecology and predates the establishment of the field by a couple of centuries (see papers in Lomolino et al., 2004). Indeed, some of these very early papers considered and rejected explanations such as the great flood and other theological arguments to explain the geographic distribution of organisms. However, the basic patterns were recognized very early on and have remained remarkably similar despite our increased sophistication in data collection and analyses.

*Latitudinal gradient in species diversity.*—The increase in the numbers of species from the poles to the tropics is one of the most well-known and well-

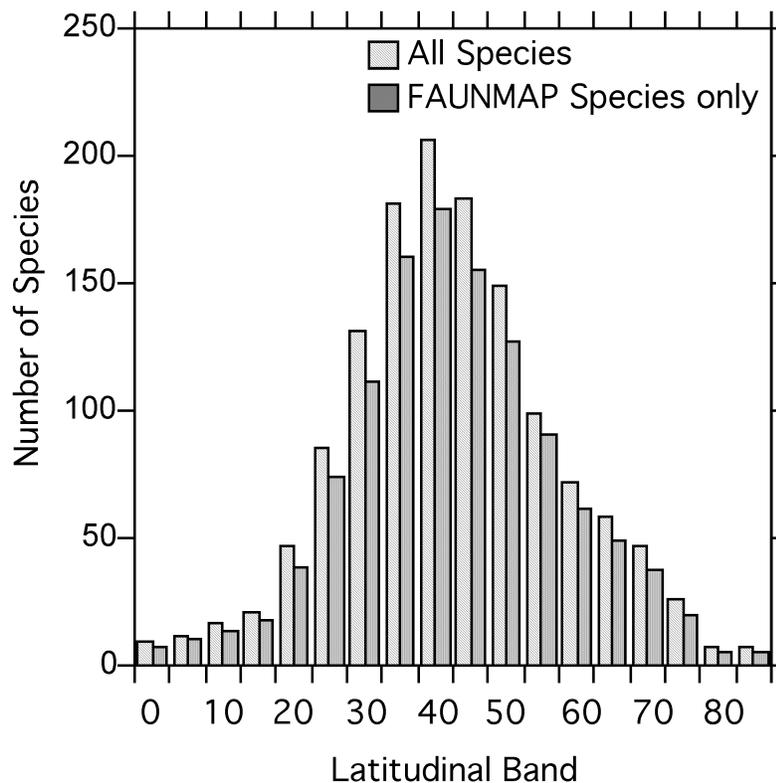


Figure 10.—Latitudinal gradient in species diversity calculated for all mammal species north of Mexico (light gray bars) and only those species recorded in FAUNMAP (dark gray bars). Range data used to create the graph are modern range data.

studied patterns in macroecology (Hillebrand, 2004; Rohde, 1992; Rosenzweig, 1995; Willig et al., 2003). Typically, the pattern is calculated by counting the number of species whose geographic or latitudinal range falls within a latitudinal band of predetermined width and plotting the number of species as a function of latitude (e.g., Fig. 10). Note that the modern data and the FAUNMAP data show almost identical patterns indicating that the bias in range sizes is not biased with respect to latitude and fossil data can, in theory, be used to understand latitudinal gradients in species diversity.

In some cases, a grid system is superimposed upon a map and all species whose geographic range falls within a particular grid square are counted and then plotted as a function of the latitudinal position of the grid square (e.g., Lyons and Willig, 1999; Lyons and Willig, 2002). In this case, the multiple grid squares at the same latitude but different longitudes constitute replicate samples. If the areas contained within the latitudinal bands or the grid squares are equal (i.e., an equal area projection map was used to determine geographic ranges), then ordinary least squares regression (OLS) can be used to characterize the relationship between latitude and number of species (Willig et al., 2009). However, studies conducted in this manner suffer from the problem of spatial autocorrelation. Essentially, the number of species estimated for bands or quadrats that are adjacent in space and not independent estimates. As a result, the degrees of freedom for OLS models are overestimated and test statistics are unrealistic (Willig et al., 2009). Fortunately, there is now a greater awareness of this problem and a variety of approaches that can be used with OLS models to account for the inflation of richness estimates associated with spatial autocorrelation (Dormann, 2007; B. Hawkins et al., 2007; Kissling and Carl, 2008; Rangel et al., 2006; Tognelli and Kelt, 2004). Bootstrapping and randomization methods can also be used to account for spatial autocorrelation.

Understanding the mechanisms behind the latitudinal gradient in species richness has been much more difficult, in part because so many of the proposed hypotheses are circular or untestable (Gaston and Blackburn, 2000; Rohde, 1992; Willig et al., 2003). Nonetheless, the majority of the hypotheses assume that the underlying variation is environmental or climate. As a consequence, a majority of tests of hypotheses gather information on climatic and environmental variation

and use multiple regression models to determine the factors that account for the greatest amount of variation in the pattern of species richness (Currie, 1991; Kerr and Packer, 1997; Kerr and Packer, 1999; Rahbek et al., 2007; Rahbek and Graves, 2001).

A second class of mechanisms emphasizes the role of evolutionary time and variation in evolutionary rates (see Rodhe, 1992; Willig et al., 2003 for a review). Essentially, the argument is that the tropics are a source of evolutionary novelty because of higher speciation rates. These papers have engendered arguments about whether the tropics are a cradle of species or a museum that maintains and houses biodiversity (Chown and Gaston, 2000; Jablonski, 1993; Jablonski et al., 2006). In a recent paper, Jablonski et al. (2006) argued that for marine mollusks, the tropics are both a cradle and a museum. They showed that extant tropical mollusk genera have younger first appearances in the fossil record. This implies that the tropical genera have higher origination rates. After origination species expand their distributions from the tropics to the temperate zones without losing their tropical presence. Thus, they argued that an "out of the tropics" model is the best explanation for the latitudinal gradient in diversity.

A final class of models emphasizes the geometry of bounded domains and argues that peaks in diversity are expected in the middle of bounded domains if species ranges are wholly contained within those domains (Colwell and Hurtt, 1994; Colwell et al., 2004; Colwell et al., 2005; Connolly, 2005; Willig and Lyons, 1998). The latitudinal gradient in species richness represented in Fig. 10 exemplifies this pattern. Because the data are the complete geographic ranges for only those species that are found north of Mexico, it is essentially a dataset of ranges within a bounded domain. Although the true latitudinal diversity gradient continues to increase in richness toward the equator, the data represented here show a mid-domain effect or a peak in the middle of the distribution. This is a result of the bounded nature of the dataset. These mid-domain models (MDE) include both simulation and analytical approaches in which species ranges are randomly placed within a bounded domain and the resulting species richness distributions are compared to the actual distribution. Simulations are typically conducted in one of three ways: randomly placing species ranges within a bounded domain, randomly choosing from a species range size distribution and randomizing the position

within the bounded domain or randomly choosing from the distribution of midpoints and randomizing range endpoints around them (e.g., Colwell and Hurtt, 1994). Proponents of MDE models argue that the deviations from the distribution produced by the raw data and the distributions produced by the model can provide valuable information about the underlying causes of the latitudinal gradient in species diversity (Colwell et al., 2004; Colwell et al., 2005).

### CONCLUSIONS

As an approach to solving problems and answering scientific questions, macroecology should feel familiar to paleoecologists. Indeed, many paleoecologists, upon learning about macroecology, point out that they have been doing macroecology all along. Although there is some communication between the subdisciplines, a robust exchange of information and ideas between the two is lacking. Here we have attempted to discuss the variables of interest to both fields, the methods used to estimate those variables, and the potential biases when estimating them using fossil data. We have also highlighted the most commonly studied patterns in macroecology and the methods used to study them. This review is not meant to be exhaustive as there many aspects of macroecology not discussed herein (e.g., metabolic scaling; Brown et al., 2004; Enquist et al., 1998; Gillooly et al., 2001; West et al., 1997). We hope that it will provide the basic information necessary to apply macroecological ideas and methods to paleoecological data and will spur a greater level of communication between the two areas of study.

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