USING A MACROECOLOGICAL APPROACH TO THE FOSSIL RECORD TO HELP INFORM CONSERVATION BIOLOGY

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ABSTRACT.—With or without realizing it, macroecology, paleobiology and conservation biology have been addressing similar issues using similar methods and analogous data sets. Much of what we call "paleobiology" overlaps heavily with macroecology, and their shared interest in losses in biodiversity over space and time clearly is of interest to conservation biology. Here we examine how some "classic" macroecological and paleobiological studies and techniques apply to issues that currently are of interest to conservation biology. Our examples are far from exhaustive, but include examining temporal (or possible temporal) shifts in: 1) geographic range sizes; 2) body size distributions; 3) relative abundance distributions; and, 4) morphological diversity. Reframing these issues in terms of how loss of biodiversity and richness affects particular slices of time *including* (but not limited to) the present should do much to communicate the value of macroecological and paleobiological methods and theory to conservation research.

INTRODUCTION

MACROECOLOGY IS a relatively recent subdiscipline within ecology that focuses upon larger scale statistical patterns and explores the area of overlap between multiple disciplines including paleobiology, biogeography, ecology and evolution (Brown, 1995). Although ecological theory successfully explains many different types of ecological interactions, traditional theory often fails to elucidate the interactions between different scales of biological organization (e.g., populations, communities, ecosystems and whole biotas) and has difficulty providing universal causal mechanisms for statistical patterns that are similar across large spatial, temporal or taxonomic scales (Brown and Maurer, 1989; Brown, 1995; Maurer, 1999; Gaston and Blackburn, 2000). Macroecology is increasingly filling this gap.

Macroecological theory offers expected relationships among species-level traits (e.g., body-size, geographic ranges size, abundance distributions) that vary predictably under different scenarios. Paleobiology offers a way to evaluate these expected relationships over greater time scales and under climatic regimes and other scenarios not available to modern macroecologists. Moreover, studying macroecological patterns in the fossil record can help differentiate between patterns that are a result of the anthropological stresses unique to modern ecosystems or are repeatable patterns that are the result of long-term ecological and evolutionary processes. Importantly for conservation theory, paleobiology can give us a baseline with which to evaluate current ecological systems (e.g., Willis and Birks, 2006).

Paleobiology often appears to concern macroevolutionary theory rather than macroecological theory. However, macroevolutionary theory looks to macroecology for possible processes behind large–scale diversification and extinction patterns. Thus, macroecological theory is highly relevant to hypotheses concerning Phanerozoic–level patterns of diversity gains and loses. Macroevolutionary theory and methods pertaining to different levels of extinction might also provide insights for conservation biological theory, as many of the questions asked of modern patterns can be asked of past extinctions. Together, macroecology and paleobiology are crucial for solving the complex problems caused by anthropogenically caused environmental changes such as habitat loss, global climate change and loss of biodiversity (Smith et al., 2008).

In this paper, we review different approaches used by ecologists (both modern and paleontological) for addressing macroecological issues as well as explore how some methods hitherto used largely by paleobiologists might be useful for modern ecological studies. First we will discuss macroecological approaches typically used for modern data and discuss how they can be applied to the fossil record in the emerging field of conservation

paleobiology. Then we will take the opposite tact and discuss traditional macroevolutionary methods and discuss how they can be applied to modern conservation biology to give a fuller picture of a system than would otherwise be available.

MODERN MACROECOLOGICAL METHODS AND THEIR APPLICATION TO CONSERVATION PALEOBIOLOGY

Geographic range size

The study of ecology is fundamentally about understanding the abundance and distribution of species (Begon et al., 1990). As such, a species geographic range is a basic unit of study in ecology. Using a macroecological approach can provide insight into the variation in a species geographic range by calculating correlations between a species' geographic range and other traits such as body size, life history, or abundance. Moreover, such studies of larger scale statistical patterns can provide insight into longer-term processes not typically available to reductionist ecology. For example, macroecological approaches can be used to evaluate the relationship between various species traits including geographic range size and a species extinction risk using a phylogeny and the IUCN redlist of threatened and endangered species for modern groups (e.g., Jones et al., 2003) or the fossil record for older groups (Jablonski, 1986; Jablonski and Raup, 1995), or ideally both for groups that have a substantial fossil record, but extend into the present (e.g., mammals).

Geographic range size can be characterized using a variety of methods, each with its own strengths and weaknesses (Fig. 1). The method used depends upon the type of underlying data available. When incorporating extant species, range maps are sometimes available (Fig. 1.2). Modern range maps are often based upon a few known localities that are interpolated by the creator of the map using biome or habitat information to predict where the species will occur (e.g., Hall, 1981). In many cases, the resulting range map appears to greatly exceed the reach of the locality data available. For some groups, this type of information may be the best that is available. However, it should be used with caution. If the range maps are equal-area projection maps, then geographic range size can be estimated using a planimeter (Willig and Selcer, 1989; Willig and Sandlin, 1991; Willig and Gannon, 1997). These types of range maps can also be digitized and geographic area

can be calculated using GIS programs (e.g., Patterson et al., 2003).

In some cases, the area of a geographic range is not necessary to the study and latitudinal extent can be used instead (Roy et al., 1995; Lyons and Willig, 1997; Willig and Lyons, 1998; Koleff and Gaston, 2001; Madin and Lyons, 2005; Harcourt, 2006; Ruggiero and Werenkraut, 2007; Krug et al., 2008). Latitudinal range size is usually calculated as the number of degrees of latitude between the northern and southern most extents of a species geographic range (Fig. 1.3). Latitudinal extent is positively correlated with geographic range size (Gaston, 2003; Lyons, 1994) and can be used when data allowing a reasonable estimate of geographic range size are not available. Latitudinal extent can also be reliably used when the group in question has geographic ranges that are essentially linear, e.g., marine mollusks (Roy et al., 1994, 1995; Krug et al., 2008). Finally, there are cases where latitudinal range is the unit of interest. For example, mid-domain models argue that if species' latitudinal ranges are randomly placed within a bounded domain (i.e., a land mass or closed ocean basin; Fig. 1.4), the resulting distribution and overlap of species ranges would produce a gradient in diversity with a peak in the middle of the domain (Colwell and Hurtt, 1994; Willig and Lyons, 1998). Obviously, if the mid-domain effect is the subject of a study, then latitudinal ranges are necessary.

When the underlying data are collection localities, more options are available for creating geographic ranges and estimating their area. This is particularly applicable to conservation paleobiology since much of the fossil data available are of this sort. One method involves taking the collection localities and first projecting them into an appropriate equal area projection (Fig. 1.1). Next, calculate the minimum convex hull that encloses the collection localities by identifying the limits of the collection localities and calculating the area within them (e.g., Lyons, 2003, 2005). This is akin to drawing a line around the outermost localities and calculating the area within the resulting shape. There are two potential problems with this method. First, we are unlikely to have a record of a species everywhere it occurred or even in every habitat it occupied. Therefore, this method almost certainly provides an underestimate of a species true range size. The second problem is that sampling and preservation will be uneven across species. Better-sampled species are likely to have larger estimated ranges because the minimum convex polygons
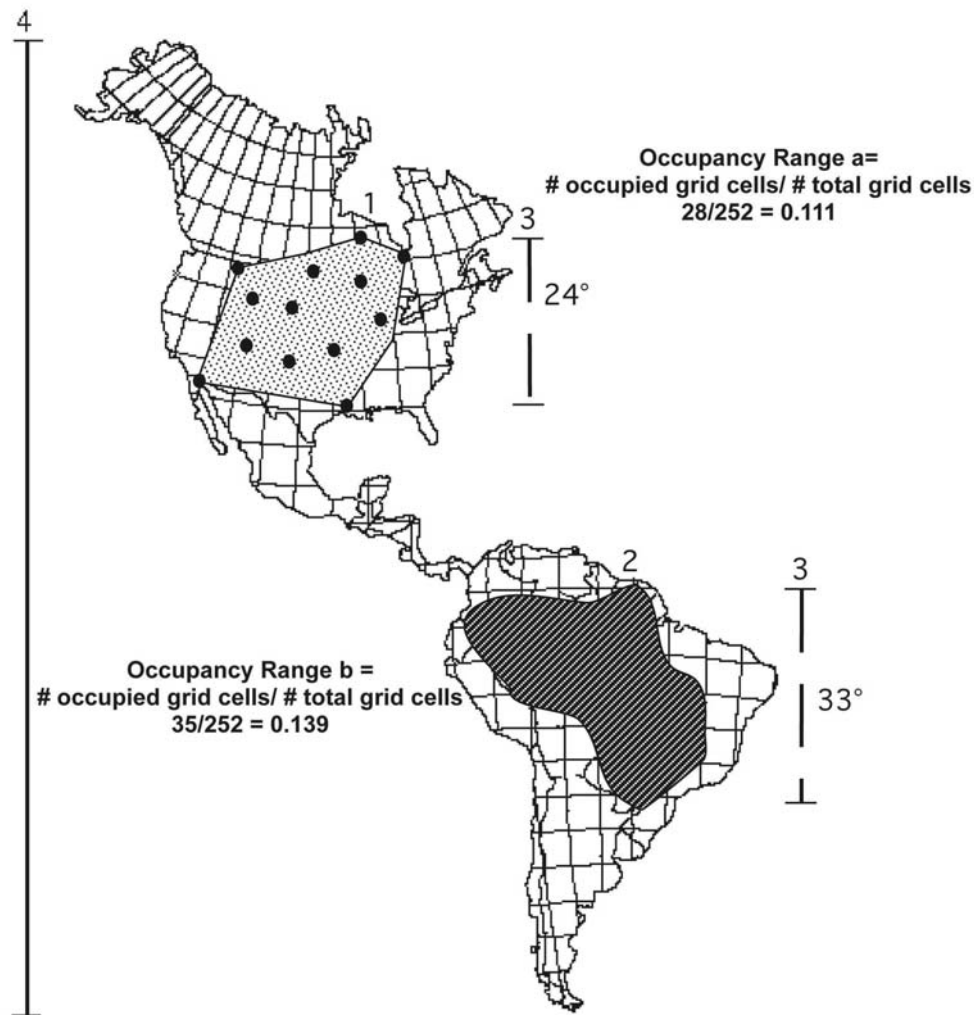
FIGURE *1*.—Schematic of the different methods for estimating geographic range size. *1*, Minimum convex polygon; *2*, Biome infilling; *3*, Latitudinal range extents; *4*, Extent of the domain used to determine the total number of grid cells for occupancy measures. Modified from Willig et al. (2009).

will have more localities spread across a larger space. This can be a difficult bias to solve because there are reasons to expect a species with a larger range to have a higher preservation potential. A species that occurs in multiple habitats or across more space will have more opportunities to be preserved. In some modern groups, there is a relationship between body size and geographic range with larger bodied species having larger geographic ranges (Brown, 1995; Gaston and Blackburn, 1996; Gaston, 2003; Madin and Lyons, 2005; Smith et al., 2008). A similar relationship exists for North American mammals in the late Pleistocene and Holocene (Lyons, unpublished data). Larger-bodied species may be more likely to be preserved and recovered because their skeletal elements are more robust and because they are easier for workers to find. For example, studies of mammals and marine mollusks have shown that extant taxa that are recorded in the fossil record tend to have larger geographic range sizes and larger body sizes (Lyons and Smith, 2006; Valentine et al., 2006). One way to deal with variation in sampling when using minimum convex polygons is to set criteria for the degree of sampling necessary to accurately represent ranges for your system. However, sensitivity analyses should always be performed to determine the effect of the poorly sampled species on the patterns of interest

(Lyons, 2005).

A measure of geographic range size that is being increasingly used is occupancy (Ruggiero and Lawton, 1998; Gaston, 2003; Blackburn et al., 2004; Foote, 2007; Foote et al., 2007, 2008). Occupancy is the ratio of occupied sites to unoccupied sites (Fig. 1). Occupancy is positively correlated with geographic range size (Gaston, 2003). Currently there is no standard protocol for determining the number of sampled sites. As a result, sampling is usually determined by the available data. Unfortunately, there is no rigorous analysis of the effect of sampling on the accuracy of occupancy as a measure of geographic range (Willig et al., in press). However, because of the nature of fossil data, occupancy may prove to be a simple, easy, and reliable way to measure geographic range size in the fossil record. Assuming that similar taphonomic biases are operating on all species within a taxonomic group, then occupancy should give a reasonable estimate of the relative geographic range size of species in that group. In a recent application of occupancy to fossil data, Foote (2007, see also Foote et al., 2007, 2008) evaluated the trajectory of geographic range size through time and found that geographic ranges tend to increase, have a relatively short peak at mid-duration and then decline.

A final method for determining geographic range size is genetic algorithm modeling (Peterson, 2001; Martinez-Meyer et al., 2004; Peterson et al., 2004a). In this method, collection localities are combined with information about the abiotic environment such as temperature, rainfall, elevation, humidity, etc. and fed into a genetic algorithm model called GARP to produce a model of a species' requirements that best predicts its distribution. These models are often produced using part of the locality data and then tested using the rest. These models have been used quite extensively for modern species to predict distribution shifts under different models of climate warming (Peterson et al., 2001, 2002, 2004b; Thomas et al., 2004). These models are likely to be less applicable to deep time systems because of the detailed information on environmental variables that they require. However, for late Pleistocene and Holocene systems where reasonable climate models are available, these models have been used to predict the expected range changes in extinct species (Peterson, 2001; Martinez-Meyer et al., 2004; Peterson et al., 2004a). One drawback to these models is that they rely on species niches to be conservative. That is, they assume that the observed combination of abiotic variables under which a species is currently found represents the full spectrum of possibilities. If it is common for novel combinations of species to occur under novel climatic regimes (e.g., Williams et al., 2001), then predictions of past and future geographic ranges made using genetic algorithm modeling will be inaccurate, particularly for time periods of dramatic climate change.

Evaluating changes in geographic ranges over critical intervals

Predicting changes in species distributions under different scenarios of global climate change is of considerable interest in conservation ecology. Typically, these studies are limited to observing the small shifts in distributions that have already happened, or using the current distributions of species to predict what will happen to their range in the future (Peterson et al., 2002; Walker et al., 2002; Parmesan and Yohe, 2003; Thomas et al., 2004). Both have drawbacks when it comes to understanding and predicting the effects of global climate change. Analyses of current range shifts are limited to species that have extensive museum collections that can be used to define past distributions. Typically, the past is limited to the last hundred years or so. Moreover, the range shifts being observed are relatively small. For example, Parmesan and Yohe (2003) examined 1700 species and found average range shifts of 6.1 km per decade. Although their analysis determined that these were shifts of a significant distance, ecological theory predicts that the edges of species ranges are in marginal habitat and posits that a species geographic range is fluid, particularly at the edges. Therefore, some flux in a distribution is expected over time (Lomolino et al., 2006). Determining how much of a range shift represents a real change versus expected flux is difficult.

Bioclimate envelope modeling attempts to get around this problem by using the current realized niche of a species and climate models to predict what will happen to a species in the future (Foody, 2008; Jeschke and Strayer, 2008; Schweiger et al., 2008). For example, the current temperature range of a species is assumed to be the full range of temperatures under which a species can exist. By modeling what will happen to global temperatures in the future, workers can predict where the habitable area for a species is likely to be and what will happen to a species range. In some cases, the temperature range is expected to disappear and the species is predicted to become extinct (Thomas et al.,

2004). The problem with this method is that it fails to account for the possibility that species ranges are limited by something other than climate or that a species fundamental niche is greater than its realized niche. If some other aspect of its fundamental niche will be available under future climate conditions, the predictions from this type of modeling will be flawed (Willis and Birks, 2006; Willis et al., 2007a, 2007b; Beale et al., 2008; Jeschke and Strayer, 2008).

The incorporation of conservation paleobiology into these types of methods has the potential to greatly enhance our ability to understand and predict the effects of future climate change on species geographic ranges. First we have the ability to measure geographic range in the fossil record using all of the methods described above. With the increasing availability of major online databases like NEOTOMA (the current incarnation of FAUNMAP), the Paleobiology DataBase, NOW (Neogene mammals of the Old World), Miomap (Miocene Mammal Mapping Project) among others, we have the tools and data necessary to do broad scale analyses of changes in geographic ranges through time. These types of analyses have the ability to offer fundamental information that is not available using modern data alone.

Incorporating fossil data can expand our knowledge and understanding of the niches of extant species with a fossil record. For example, Pleistocene plant workers have done extensive work mapping past distributions of plant species to understand how plants shifted their distributions in response to glaciation (Overpeck et al., 1985, 1992; Jackson et al., 1997; Jackson and Overpeck, 2000; Williams et al., 2001, 2002, 2004). This work has focused extensively on identifying and understanding non-analog communities (Overpeck et al., 1992; Williams et al., 2001; Jackson and Williams, 2004). In a paper in which pollen distributions were analyzed in conjunction with climate models, Williams et al. (2001) showed that non-analog plant communities are found in areas of non-analog climate (i.e., novel combinations of temperature and precipitation). Obviously, the aspects of a species niche that are expressed in these no-analog communities are not apparent when only modern distributions are used to define a species niche space.

Our understanding of what happens to species distributions as climate changes is strongly informed by conservation paleobiology. Paleobiological studies quantifying species range shifts during the last glaciation showed that species shift their ranges individualistically and that ecological theory predicting that communities are Clementsian superorganisms are incorrect (Graham, 1986; Graham and Mead, 1987; Webb and Barnosky, 1989; Overpeck et al., 1992; Graham et al., 1996; Davis et al., 1998; Jackson and Overpeck, 2000; Davis and Shaw, 2001; Barnosky et al., 2003; Lyons, 2003; Williams et al., 2004). This work has also shown that species did not shift their ranges in a simple north-south fashion as the glaciers expanded and contracted (Graham et al., 1996, Lyons, 2003), but that individual species are responding to changes in the environment that correspond to their niche requirements and the scale at which they perceive the environment. The widespread dissemination of this work into ecological theory and ecological text books (e.g., Lomolino et al., 2006) likely informed current ecological theory and methods used to evaluate and predict species range shifts as a result of global warming. However, there is room for the expansion of paleobiology in this area. For example, where the data exist, more detailed analyses of species past distributions and their correlation with climate models can provide a better understanding of species fundamental niche. Such information would greatly enhance the accuracy of bioclimatic envelope models in predicting species responses to global warming. As fossil databases grow, there will be more opportunities to shift these types of analyses into deeper time. Analyzing species responses to multiple climate change events can provide a baseline for how species respond under natural scenarios. Similarities and differences with the current climate change can provide insight into possible policy decisions that will mitigate anthropogenic effects.

Evaluating the role of geographic range in extinction events

Analyses of geographic ranges in the fossil record can also provide an understanding of how species geographic ranges change through time in the absence of dramatic climate change. A series of recent papers examines the patterns of geographic range expansion and contraction over a species lifetime using species occupancy as a metric (Foote, 2007; Foote et al., 2007, 2008). In general, occupancy is symmetrical with a rise, a short-lived peak, and then a decrease to extinction. As a result, species geographic ranges are already in decline when they become extinct. Moreover, the authors found no cases of subsequent increase once the decline
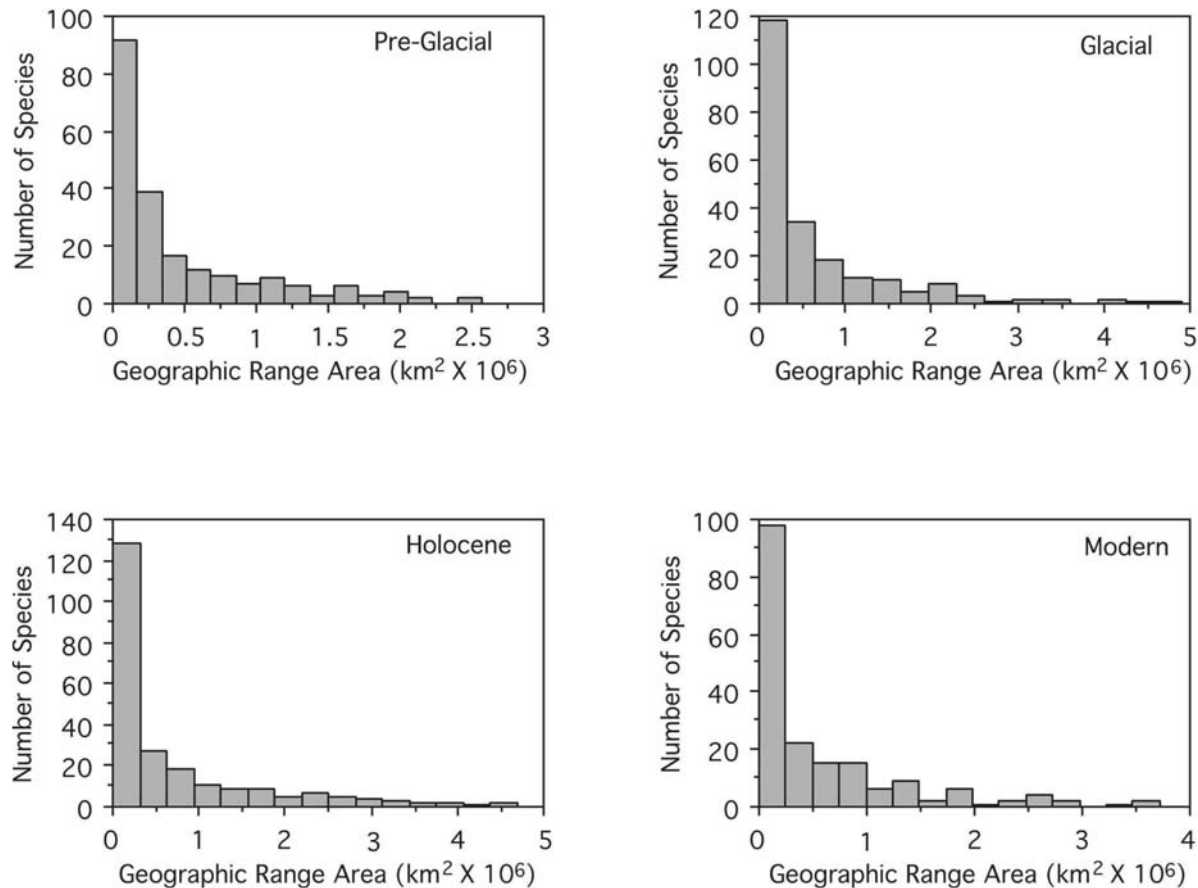
FIGURE 2.—Range size frequency distributions for late Pleistocene mammals in North America. Underlying locality data were taken from FAUNMAP and divided into four time periods. Pre-Glacial (40 kya to 20 kya), Glacial (20 kya to 10 kya), Holocene (10 kya to 500 ya) and Modern (last 500 y). Range sizes were calculated using minimum convex polygons enclosing fossil localities. Modified from Lyons (2005).

started. This implies that, in the absence of mitigating factors, species do not recover once their geographic range begins to decrease. Indeed, the species that were at the greatest risk of extinction were those whose geographic range had been declining for a substantial portion of time (Foote et al., 2007). This type of baseline information on the waxing and waning of geographic ranges is sorely missing from our understanding of species responses to climate change (Willis et al., 2007a). Moreover, it is not possible to obtain it using the modern record.

In addition to providing baseline information on the dynamics of geographic ranges over time, the fossil record allows for analyses of the role of geographic range in different types of extinction events. A classic paper by Jablonski (1986) found that broad geographic ranges enhanced the survivorship of marine mollusks during times of background extinction, but provided little protection during mass extinctions. A similar relationship was found in an analysis of all benthic marine invertebrates across the Phanerozoic (Payne and Finnegan, 2007). Moreover, the extensive analysis of marine invertebrate genera by Foote (2007) confirmed this finding. During times of mass extinction, more of the genera that became extinct did so while their occupancy was holding steady or increasing.

This work has important policy implications for the current biodiversity crisis. It suggests that species whose geographic ranges have already declined substantially, or whose habitat is greatly degraded or destroyed, will take more effort to save. Moreover, if fears that we are in the sixth mass extinction prove true, this work argues that we cannot be complacent and assume that species with broad geographic ranges are safe.

Geographic range size distributions

Another commonly studied macroecological pattern is the frequency distribution of geographic range size. Range size frequency distributions are created by dividing species into range size categories and constructing a histogram of the number of species in each bin. They generally exhibit a characteristic shape when plotted on an arithmetic scale (e.g., Fig. 2; Brown, 1995; Gaston, 2003). Because the majority of species have small ranges and a few species have medium and large ranges, the resulting distributions typically are unimodal and right-skewed. They are typically referred to as "hollow curves" (Willis, 1922). Taking the log does not produce a normal distribution. After log-transformation, range size distributions are typically unimodal and somewhat left-skewed (Willig et al., 2003, in press).

Range size frequency distributions are potentially useful in conservation paleobiology. First, the similarity in the shape of the distribution in modern groups suggests that these patterns are the result of macroecological and evolutionary processes that have predictable effects on geographic ranges despite the multitude of factors that can affect individual ranges. If so, range size frequency distributions of fossil data should show a similar shape and can be used as a way to verify that geographic ranges of fossil taxa are likely reasonable estimates. For example Lyons (2005) used range size frequency distributions of late Pleistocene mammals derived from FAUNMAP to show that the ranges were showing similar patterns to those of modern distributions and therefore were likely to be reasonable estimates. Second, the shapes of these distributions during mass extinctions or climate change events should be evaluated. If these distributions change in predictable ways during critical intervals, then they may prove useful in evaluating the health of modern ecosystems and the impact of the current biodiversity crisis on large spatial scales.

Body size distributions

One of the most common currencies used in macroecological studies is body size. This is in part because it is the most obvious and fundamental characteristic of an organism and in part because many important biological rates and times scale predictably with body size (Calder, 1984; Peters, 1983). Body size is relatively easy to measure in most groups and methods are available for turning body size measures into biovolume so that comparisons may be made across groups with very different underlying morphologies. For example, Payne et al. (2009) used biovolume to compare the maximum size of organisms in all the major phyla since the appearance of life >3.5 billion years ago. Moreover, studies have shown that species body sizes change predictably in response to climate change (Smith et al., 1995, 1998; Hadly et al., 1998). For some species, such as pack rats (i.e., *Neotoma*) body size changes in response to climate change have been documented on the order of decades, centuries and millennial time scales.

Species body size is typically described using a single estimate in most macroecological studies. Ideally, this value should incorporate variation in body size across space, time period of interest, and sex of the species (e.g., Smith et al., 2003). For many groups mean or median body size is used. However, for indeterminate growers, it often makes more sense to use maximum body size (*sensu* Jablonski, 1997). In reality, rare species are often characterized by a single estimate representing a population or individual. Particularly for fossil species, body size *per se* is not available and surrogates must be used. Depending on the group of interest, these include body length, body area, limb measurements, shoulder height, tooth area, etc. Obviously, the best surrogates are those that correlate with body mass. For many mammalian groups, standard regression equations are available to estimate body mass from other morphological measurements such as molar area (Damuth and MacFadden, 1990). Once estimates for body size are available, body size distributions are constructed in the same way as range size distributions. Body sizes are log-transformed and then allocated into categories and the number of species or individuals in each category is tabulated and displayed as a histogram (Fig. 3).

Body size distributions are a result of evolutionary processes acting on species body sizes and ecological processes acting to sort species into communities and over longer time scales into biota. There are similarities in the shapes of body size distributions among warm-blooded vertebrates. In modern systems, body size distributions at the continental scale are unimodal and right-skewed. At smaller spatial scales, body size distributions become progressively flatter until they are nearly uniform at the community level (Brown and Nicoletto, 1991). The unimodal, right-skewed pattern seems to be limited to endotherms. Vetebrate ecotherms and invertebrate groups have unimodal, left-skewed

body size distributions (Poulin and Morand, 1997; Roy and Martien, 2001; Boback and Guyer, 2003). Moreover, the pattern of progressive flattening with spatial scale differs on different continents. South American mammal communities show more peaked distributions at the local scale than North American communities (Marquet and Cofre, 1999; Bakker and Kelt, 2000) and African mammal communities are bimodal rather than uniform (Kelt and Meyer, 2009). More specialized groups of mammals such as bats have more peaked distributions at all latitudes (Willig et al., in press).

The methods used to analyze body size distributions depend upon the question being asked. If the question is simply about the shape of the distribution, the moments of the distribution (e.g., mean, median, skew and kurtosis) are often used. In particular, the kurtosis value gives the most information about the overall shape (Alroy, 2000; Lyons, 2007). Oftentimes, the question is whether the distribution in question is significantly different from a model distribution or whether two distributions are significantly different from one another. When both distributions are known, they can be compared using a Mann-Whitney U test or a Kolmorgorov-Smirnov test (Sokal and Rholf, 1981). Randomization techniques are employed to ask whether the distribution is different from a random draw from a larger species pool. For example, Smith et al. (2004) compared continental body size distributions of modern mammals by comparing differences in the real distributions to differences between distributions generated by drawing species randomly from the global pool of species. For each randomly generated distribution, the number of species drawn was equal to the number of species on the continent. These analyses
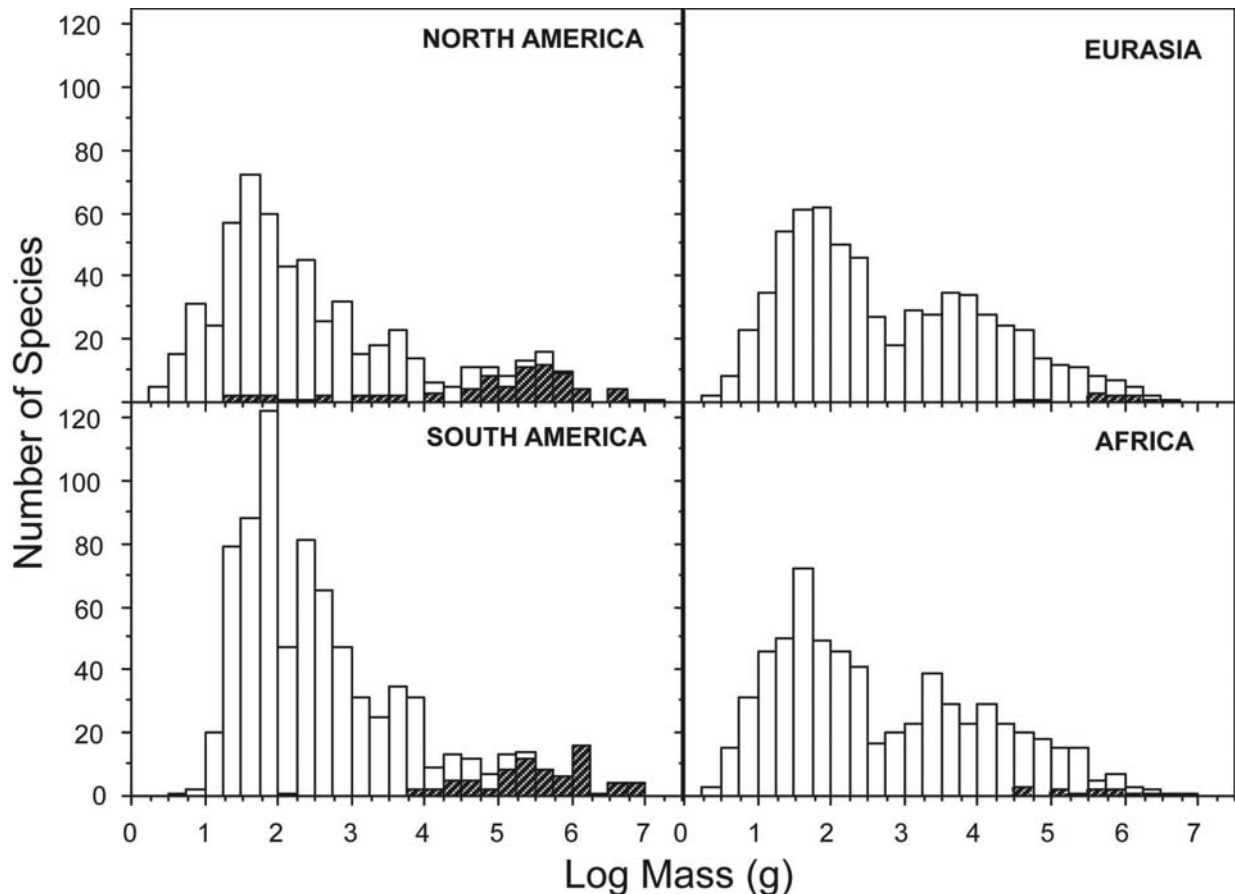

FIGURE *3*.—Body size frequency distributions for late-Pleistocene mammals on four continents. Body size distribution of the surviving species are represented by white bars, those for extinct species are darkly shaded. Body sizes are taken from Smith et al. (2003).

found that continental body size distributions of mammals were significantly different from random distributions (Smith et al., 2004). All of these methods may be applied to body size distributions at any scale.

The similarity in the shapes of body size distributions at different scales suggests evolutionary and ecological factors act in predictable ways in different groups to shape these distributions. If so, then evaluating the shapes of body size distributions may be yet another tool to evaluate the effects of climate change on a biota. However, the modern systems are highly altered systems and we cannot assume that the patterns we see today are not a result of the unique anthropogenic forces acting on modern species. Indeed, analyses of mammalian body size distributions in both deep and near time suggest that modern distributions have been fundamentally altered (Alroy, 1998, 1999; Lyons et al., 2004). Shortly after the K/T extinction mammals expanded their range of body sizes into the full range we see today. Approximately 40 ma medi-
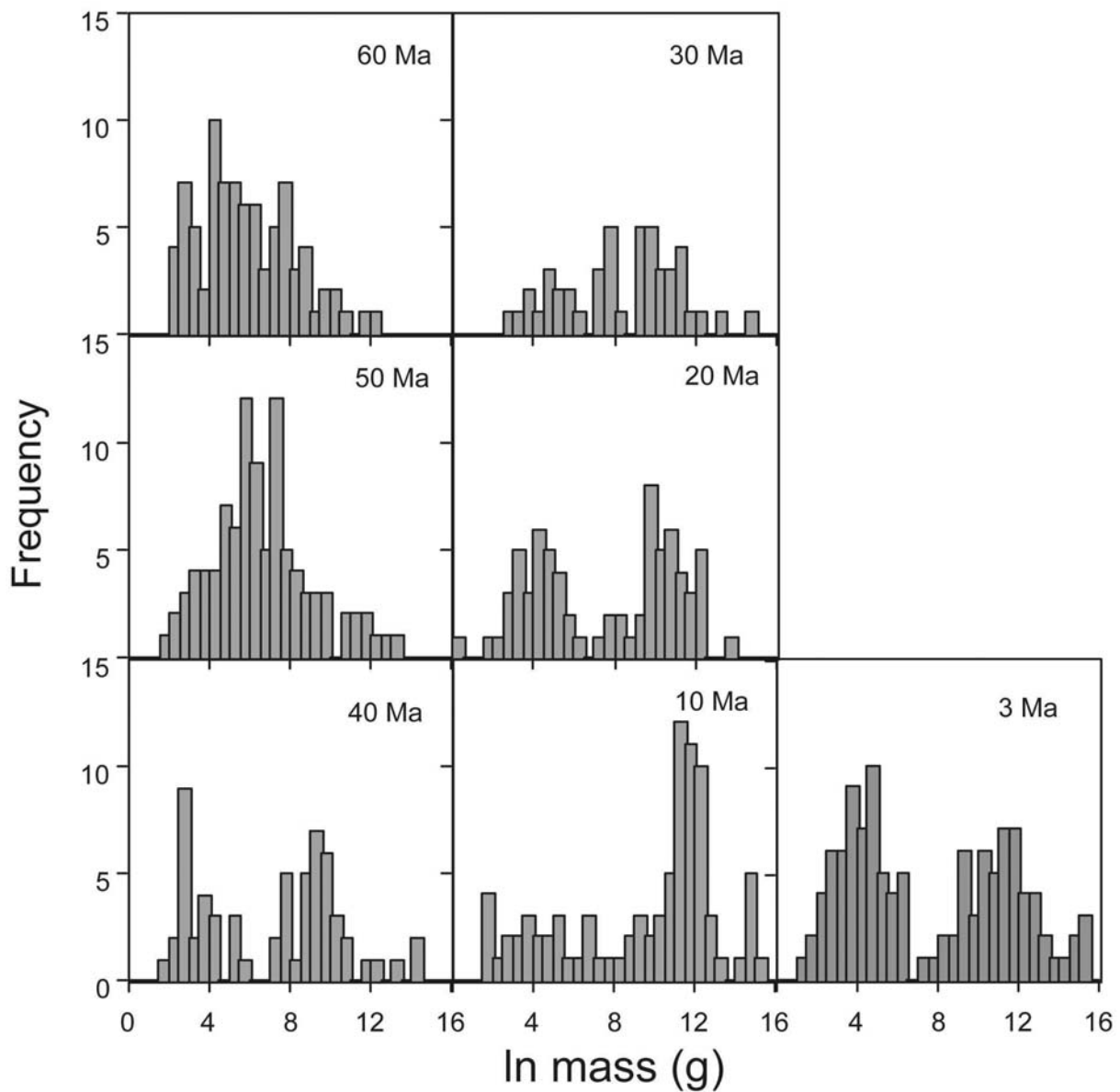

FIGURE 4.—Body size distributions of North American mammals for seven different intervals of 1 ma year each. Species and body sizes are taken from Alroy (1998, 2000).

um-size mammals became rare and a hole opened in the body size space (Alroy, 1998). Macroecological analysis of mammalian body sizes over the Cenozoic suggest that the continental body size distributions were unimodal until 40 ma at which point they became bimodal and remained that way until the extinction of the megafauna at the end of the Pleistocene (Fig. 4). Moreover, the end-Pleistocene extinctions fundamentally altered the shape of the body size distributions on all the continents on which it occurred (Fig. 3; Lyons et al., 2004). These results suggest that the natural state of mammalian body size distributions is not the unimodal, right-skewed distribution we see in the present, but the bimodal, right-skewed distribution we see for the majority of mammalian history.

Conservation paleobiology can provide insight into an additional area of modern conservation ecology, the role of body size in extinction risk. Many modern ecological studies find a strong correlation between extinction risk (as measured by inclusion on the IUCN redlist or by historical extinction) and body size (Gaston and Blackburn, 1995; Cardillo and Bromham, 2001; Jones et al., 2003), however, there is no strong signal of size selectivity in extinction in the fossil record (Jablonski and Raup, 1995; Lockwood, 2004; Jablonski, 2005). Indeed, the only factor that has consistently been associated with extinction in fossil taxa is geographic range size (Jablonski, 1986; Payne and Finnegan, 2007). The obvious difference between modern systems and the majority of history is the impact of humans. Examination of the megafaunal extinction of mammals lends support to the idea that humans are the reason why large-bodied modern species are more vulnerable to extinction, but large-bodied species in the fossil record are not. This extinction event was a highly size selective event on all the continents on which it occurred (Fig. 3, Lyons et al., 2004). Moreover the degree of size selectivity was greater than any other extinction in mammalian history (Elroy, 1999). The common denominator on all the continents that suffered an extinction was the arrival of humans. The extinction in Australia occurred earlier than in North and South America shortly after humans arrived and prior to the climate change associated with the last glaciation (e.g., Lyons et al., 2004). The lack of size selectivity in fossil extinction events combined with the strong size selectivity of the end-Pleistocene event suggests that extinction risk in modern systems is size selective because of the actions of humans and that this is not a natural

characteristic of ecosystems. These insights would not be possible without the contributions of conservation paleobiology.

MACROEVOLUTIONARY METHODS AND THEIR APPLICATIONS TO MODERN CONSERVATION BIOLOGY

Morphological disparity

Morphological disparity is the quantification of morphological diversity (Foote, 1997). Workers have used disparity largely to summarize the results of major radiations, but also to summarize the effects of extinctions (Foote, 1991; Roy, 1996; Wagner, 1997; McGowan, 2004). Roy and Foote (1997) note that it is underutilized as a conservation biology tool. In particular they offer disparity as an alternative to patristic distance or dissimilarity, i.e., summaries of phylogenetic distances among taxa (Faith, 1994, 2002). Simulation (Foote, 1996) and empirical (Wagner, 1997; Cotton, 2001) studies indicate that there is a positive correlation between morphologic disparity and either patristic distance (average numbers of branches separating taxa) or patristic dissimilarity (average sum of inferred changes separating taxa). However, whereas patristic studies require model phylogenies, disparity studies do not. As both studies require the same sort of data, this makes disparity studies a useful way to assess the effects of both past extinctions and *possible* extinctions on existing morphologic diversity.

Disparity requires a measure of how different two taxa are. When using qualitative character data (such as used in phylogenetic studies), a simple measure is:

$$D_{ij} = \frac{\text{Differences}}{\text{Comparable Characters}}$$

where D_{ij} is the difference between taxa i and j, differences is the number of characters that differ and comparable characters represents the number of characters that can be compared. The latter will be fewer than the total number of characters if there are missing data (e.g., incomplete specimens) or if there are incomparable characters (e.g., feather color characters for non-dinosaurian reptiles.) If there are "ordered" characters (e.g., state 2 is considered two units away from state 0 instead of 1), then the numerator is the sum of the differences (i.e., 1 for differing binary or unordered multistate characters, and the absolute difference between

states for ordered multistate characters). For continuous (e.g., morphometric) characters, one can simply sum the absolute differences between characters. Overall disparity is simply the average among all pairwise comparisons.

We present an example here using extant lepidosaurs. The tuatara (*Sphenodon*) is well known for being the last of the sphenodontians, a formerly diverse clade of lepidosaurs. All other lepidosaur species are squamates (lizards and snakes). It is intuitively obvious that the extinction of the tuatara would eliminate far more evolutionary history than would the loss of the typical lizard or snake species. Here we will show how disparity could demonstrate this even without a complete phylogeny.

We use characters from two data sets. The squamate data are from Conrad's (2008) analysis of 221 extant and fossil lepidosaur taxa. For the purpose of this study, we limit ourselves to 88 extant taxa and 359 characters that vary among them. Conrad uses *Sphenodon* as an outgroup (i.e., an assumed closest relative of a study group thought to share primitive states with the clade of interest). Following standard convention, Conrad coded *Sphenodon* only for those characters that vary among squamates (see Kitching et al., 1998):

thus, the study omits many characters that one would recognize only if trying to discern relationships of sphenodontians, a formerly diverse lepidosaur clade now represented only by *Sphenodon*. The nature of outgroup coding would seem to reinforce this notion of the tuatara as a "living fossil." However, phylogenetic analyses of sphenodontians show that *Sphenodon* is highly derived and differs from outgroup squamates in 37 of 67 characters in one study (Apesteguia and Novas, 2003) and 33 of 49 characters in another series of studies (Reynoso, 1996, 2000). Lacking a study coding both sphenodontians and squamate lepidosaurs, we augment Conrad's matrix with the sphenodontian characters for which *Sphenodon* and lepidosaurs differ, using Apesteguia and Novas's character data. As the latter study codes squamates as polymorphic if some squamates shared states with some sphenodontians, this should not introduce redundant characters.

We calculated disparity as described above assuming unordered character states. We wish to address what the effect on lepidosaur morphological disparity would be if we lost *Sphenodon*. Foote (1993) contrasted disparity with and without whole clades to assess a similar question. Here, a whole clade is reduced to a single taxon. Therefore, we assess the effect of removing sin-
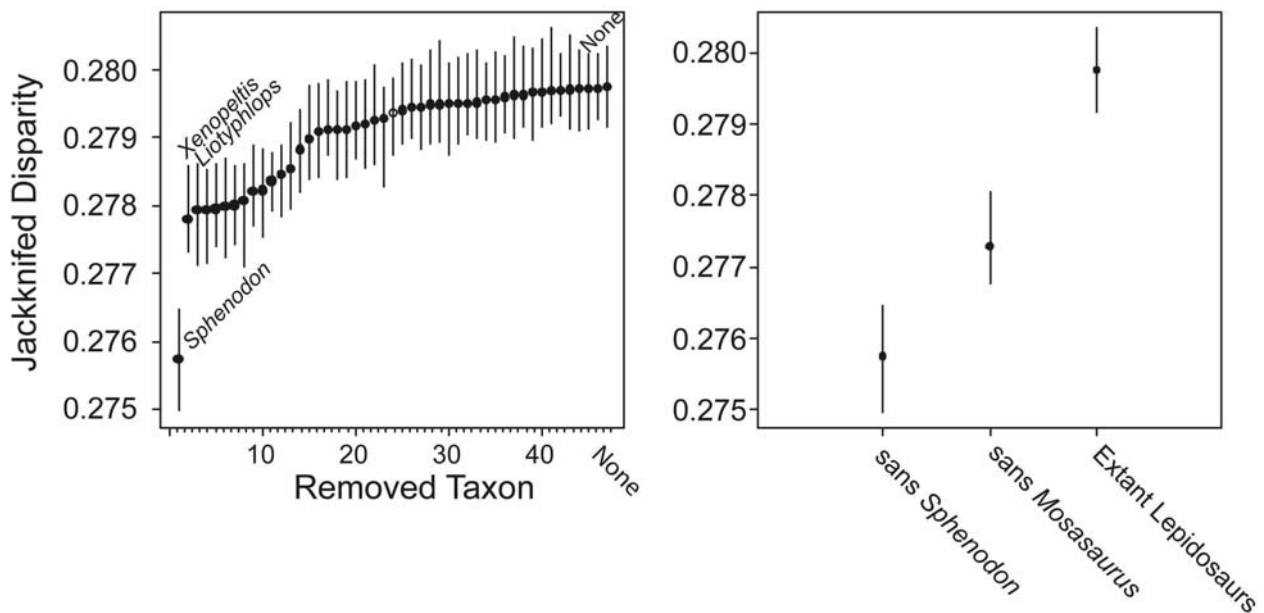

FIGURE 5.—*1*, Lepidosaur disparity following the removal of single taxa, with "none" giving disparity of all extant lepidosaurs. Error bars reflect 500 bootstrap replications; *2*-Lepidosaur disparity without *Sphenodon* vs. lepidosaur disparity without *Mosasaurus*. Data from Conrad (2008) and Apesteguia and Novas (2003).

gle taxa by jackknifing the dataset, i.e., calculating the morphospace for 89 times: once with all 88 taxa, and 88 times with one taxon removed (see Foote, 1991). Phylogenetic autocorrelation (e.g., Felsenstein, 1985) makes formal tests of differences in disparity problematic. However, bootstrapping of pairwise dissimilarities (e.g., Foote, 1992) provides an idea of how easily one could recover similar changes in disparity.

Finally, it is instructive to examine how losing another "living fossil" might affect morphological disparity. Pretend that the Maastrichtian *Mosasaurus hoffmannii* survived until the present. This presents an interesting contrast with *Sphenodon* because although mosasaurs are long extinct, they are nested high in squamate phylogeny being closely related to modern varaniforme lizards (Conrad, 2008). Thus, we have similar patristic distances between either *M. hoffmannii* or *Varanus komodoensis* (the Komodo dragon) and iguanids or gekkos. The highly derived nature of mosasaurs would elevate the patristic dissimilarity between *M. hoffmannii* and other lizards, but the majority of differences between *M. hoffmannii* and other lizards would be synapomorphies shared between mosasaurs and varaniformes.

Unsurprisingly, removing tuataras has a far greater effect on lepidosaur disparity than does removing any squamate taxon (Fig. 5.1). Removing tuataras has a far greater effect than removing the more obviously derived mosasaurs (Fig. 5.2), although losing a relic mosasaur species would reduce lepidosaur disparity greater than would losing any other lepidosaur.

There are three critical points to this analysis. One, we can easily recognize just how much morphological disparity a relict taxon such as tuatara creates only by refering to extinct taxa: without extint sphenodontians, we would have no frame of reference for describing the 30+ unique tuataran features. Second, disparity quickly recognizes that highly derived taxa closely related to other taxa (e.g., *Mosasaurus*) still represent considerable evolutionary novelty: although *Mosasaurus* and *Varanus* are equally distant from most other lizards, we lost much more morphological diversity with the loss of *M. hoffmanni* than we would with *V. komodoensis*. Finally, these disparity analyses point to other potential loses. *Sphenodon* represents an example that many non-scientists can appreciate; however, although it probably would not surprise herpetologists that losing taxa such as *Xenopeltis* and *Liotyphlops* would greatly reduce lepidosaur diversity, these taxa are nowhere as well known to non-specialists. Disparity presents an easily repeatable and easily communicated summary of just how much diversity these few taxa actually represent.

Relative abundance distributions

Traditionally, paleontologists and conservation biologists both have equated diversity with richness (i.e., numbers of taxa; e.g., Sepkoski, 1978; Gaston and Blackburn, 2003). However, ecologists typically consider richness to be only one aspect of diversity, with the relative abundance being the other component (e.g., Hurlbert, 1971). Diversity is just as important as richness because ecological theory allows predictions about how species should allocate resources under different circumstances. This, in turn, allows predictions about different *relative abundance distributions* (RADs) describing expected proportions of species in a community. Workers have adopted two basic approaches to summarizing diversity. One is to summarize the entire RAD in a single metric, such as evenness. Another is to parameterize the RAD, usually using one of several models with theoretical implications.

Evenness metrics

Workers have devised numerous metrics to describe evenness (e.g., Smith and Wilson, 1996). In general, these metrics summarize how abundances deviate from uniform (i.e., all S taxa having abundance $1/S$). A more detailed description of several different evenness metrics is presented in Appendix 1. Studies contrasting "live" and "dead" assemblages suggest that preservational factors elevate evenness but still should permit us to discern relative evenness in assemblages (Olszewski and Kidwell, 2007). Thus, trends in evenness should be discernible in the fossil record.

Kempton (1979) suggested that there should be a positive correlation between evenness and the "health" of a community. If taxa divide resources fairly equally or when numerous taxa find "new" ways to utilize resources, then evenness should be high. Conversely, if a few taxa monopolize resources or if few taxa can find "new" ways to access resources, then evenness should be low. Most paleobiological studies have used the first proposition to assess diversification over long periods of time. For example, Cenozoic marine assemblages show significantly higher evenness than do Ordovician marine assemblages (Powell and Kowałewski, 2002). Similarly, assemblage evenness increases over the

course of major radiations in both the Cambrian and the Ordovician (Peters, 2004). Conversely, evenness decreases in assemblages following rebounds from regional Ordovician extinctions (Layou, 2009).

McElwain et al. (2007) and McElwain et al. (2009) document decreasing evenness in plant communities leading up to the end-Triassic extinction. However, evenness has been under utilized as a metric for summarizing ecosystems leading up to extinctions.

Empirical examples

Here we present two empirical examples of evenness under suspected declining ecological systems. One re-examines Rhaetian (Late Triassic) plant diversity from Greenland leading up to the end-Triassic extinction (McElwain et al., 2007). The other re-examines the response of grassland diversity from 19th-20th century Sweden in response to nitrogen fertilizer (Brenchley and Warrington, 1958).

McElwain et al. (2007) use only E to note that evenness generally decreases in younger beds leading to the end-Triassic extinction, with the younger three beds showing much lower evenness than the older three beds (Fig. 6.1). All other evenness metrics repeat this, although the difference is less marked with J, F and PIE. However, Swedish grasses present an interesting contrast: all metrics show evenness decreasing from the 19th century to the 20th century, but two metrics (E and

D) suggest that the final evenness increases whereas the other three suggest that evenness plummets (Fig. 6.2). The apparent increase is an artifact of the very low sampled richness, $S_o=3$. S_o is the sole determinant of D_{min} and the primary determinant of E_{min}. Here, the observed value ($E_o=0.343$ and $D_o=0.337$) are only marginally greater than the minimum possible given S_o and $N=1245$ ($E_{min}=0.338$ and $D_o=0.335$). Rescaling E and D relative to the minimum possible results in evenness plummeting for the final grassland sample.

Evenness limitations

The example above illustrates additional limitations with evenness metrics. Assessing the significance of diversity change is ineloquent. Evenness metrics do not offer exact predictions about abundances. Thus, one usually must resort to bootstrapping or subsampling to contrast individual assemblages. Testing hypotheses of trends in evenness requires copious sampling, as individual assemblages are the sole data point rather than numbers of specimens. Finally, two beds might have the same evenness yet have different model RADs with very different ecological implications. Evenness clearly represents a useful exploratory tool, as it suggests patterns in examples such as the two illustrated above. However, actually examining RADs should provide far greater power for a variety of other tests.
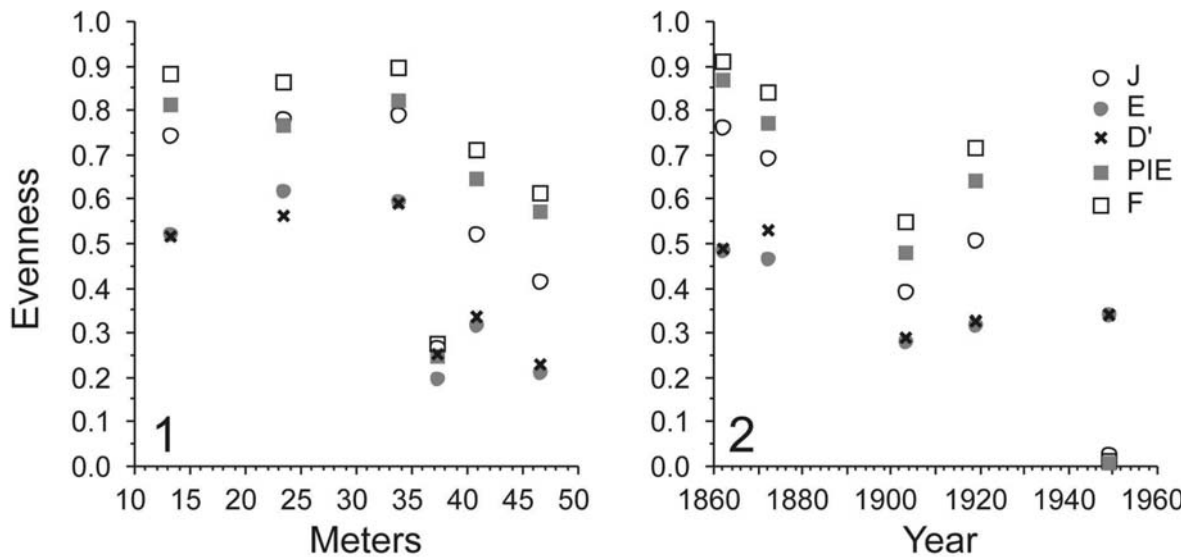

Figure 6.—1, Evenness over meters of sediment for Rhaetian plants, with the final bed marking the Triassic-Jurassic boundary; 2, Evenness over years in Swedish grasslands.

RAD models: theoretical expectations

Ecological models for the evolution of communities and the division of resources therein often predict relative abundance distributions (see, e.g., May, 1975; Gray, 1987; Hubbell, 2001). These models divide into two general classes. One class assumes that individuals from different species compete with each other in similar ways for resources. Examples include the geometric distribution (Motomura, 1932), the log-series distribution (Fischer et al., 1943) and the zero sum multinomial (Hubbell, 1997, 2001). These models assume that the primary controls on relative abundance are: 1) the rates at which species enter communities; 2) rates of population growth; and; 3) population size, with the different models making somewhat different assumptions about these parameters. The second class assumes that some or all species create ecological opportunities, either for themselves or for other species. Examples include the Zipf and Zipf-Mandelbrot distributions (Frontier, 1985) and the log-normal distribution (Preston, 1948). Here again, RADs reflect the order in which species colonize communities, but RADs now also reflect other biological factors such as "new" ecospace created by taxa and/or hierarchical partitioning of general niches into more specific niches. Although workers typically describe processes behind RADs in terms of the development of communities, these principles should also let us make predictions about how RADs should change as ecosystems deteriorate. In particular, we might expect changes in RAD models if ecosystems lose complexity, or we might expect changes in parameters if diversity is lost within the same RAD model. A detailed discussion of the mathematics of 4 common RAD models is provided in Appendix 1.

Unlike evenness metrics, RADs make explicit predictions about numbers of specimens and thus allow conventional tests of hypotheses predicting changes in those numbers over time. Paleontological studies have used RADs to contrast communities over space (Buzas et al., 1977) and over time (Olszewski and Erwin, 2004; Wagner et al., 2006; Harnik, 2009; McEwlain et al., 2009). The Olszewski and Erwin and McElwain et al. studies are particularly germane here as both examine RAD shifts in response to long-term environmental change. Moreover, the likelihood framework that they employ sets up the way in which we think RAD patterns leading to extinctions (or possible extinctions) should be examined.

Testing shifts in RADs over time

Kempton (1979) noted that evenness decreased in Rothamsted grasslands over time, likely as a response to intense nitrogen-rich fertilizers. Despite the drastic decrease in the final year, there is no satisfactory test of whether the decrease is significant. Following convention (e.g., Burnham and Anderson, 2004), we accept the model with the lowest Akaike's Modified Information Criterion score as the best model (Table 1). (More exact tests can be performed using Akaike's weights; e.g., Wagner et al., 2006.) These indicate that the zero sum multinomial is the best model for the first 60+ years. However, the geometric is the best model for the final survey.

Within the first four assemblages, there is a significant decrease in θ between 1872 and 1903 (Fig. 7.1). One interpretation of this is that the realistic pool of

TABLE *1*.—Log-likelihoods and Akaike's Modified Information Criterion (AICc) scores for Rothamsted grasslands over 80 years for geometric, zero sum multinomial, Zipf and lognormal models. S_S gives sampled richness. N gives numbers of specimens, in units of biomass. $AICc = 2*\ln L + 2k + (\frac{N}{N-k-1})$ where k=the number of varying parameters. Data from Brenchley and Warrington (1958).

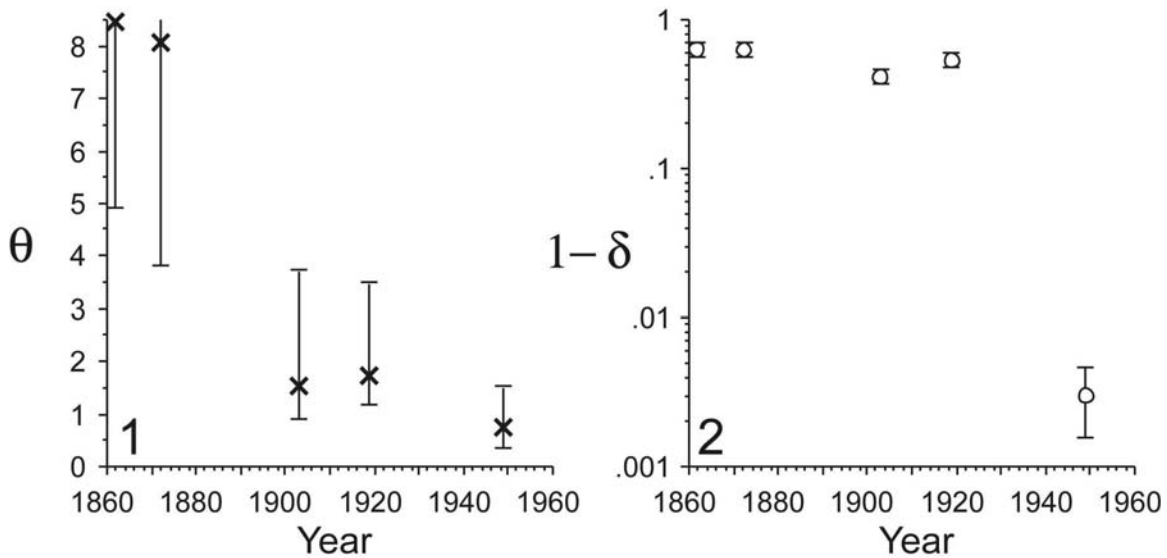|			Log-Likelihood				AICc			
Year	S_S	N	Geo	Zero	Zipf	LogN	Geo	Zero	Zipf	LogN
1862	21	3249	-128.0	-121.4	-241.4	-122.0	258.1	246.8	486.8	247.9
1872	12	2319	-72.2	-68.9	-87.7	-77.2	146.4	141.9	179.5	158.4
1903	8	1977	-76.9	-41.8	-194.2	-124.3	155.9	87.5	392.5	252.6
1919	10	4899	-72.1	-58.3	-330.8	-138.1	146.2	120.6	665.6	280.2
1949	3	1245	-7.9	-15.0	-7.3	-7.7	17.8	18.5	19.4	34.0

Figure 7.—Support bars giving diversity parameters with log-likelihoods within 1.0 of the most likely (given by x or ○). *1*, Zero sum multinomial (the best model for the first four assemblages). Each θ uses the m maximizing the θ's likelihood; *2*, Geometric (the best model for the final assemblage). If support bars do not overlap, then the log-likelihood of 2 differing parameters is significantly greater than the log-likelihood of only 1-parameter.

species that could immigrate into the Rothamsted community decreased. The local increase in nitrogen due to intense fertilizer treatments would not have affected the larger metacommunity, but it could have eliminated some species in Rothamsted and reduced the number of species within the metacommunity that could have immigrated there. Notably, the most likely *m*'s (migration rates) increase drastically, suggesting much more exchange between the local community and the larger metacommunity among those species that could migrate back and forth.

The final assemblage not only shows a shift from the zero sum to the geometric, but also to a geometric that is drastically steeper (and thus less even) than the best geometrics from prior years (Fig. 7.2). There are two issues here. One, the geometric can be thought of as a conceptual special case of the zero sum in which migration no longer is important. This would be consistent with the idea that only a few (possibly only three) species from the larger metacommunity could tolerate the heavily fertilized environment. Second, it indicates that success is very different among those few species that could tolerate the new environment.

CONCLUSIONS

Both macroecology and paleobiology concern themselves with changes in biodiversity over longer periods of time and larger spatial scales than do traditional ecological studies. Their shared concern in loss in biodiversity (over any time scale) is shared with conservation biology. As such, pertinent methods that both fields use, whether derived independently or in tandem, should be of interest to conservation biologists. We have provided examples here from a variety of temporal and spatial scales, as well as from a variety of data types. There are, of course, several other research avenues (e.g., confidence intervals on temporal ranges or relationships between macroecological parameters) that we have not covered in this paper that clearly apply to macroecology, paleobiology and conservation biology, and which have (to varying degrees) evolved in parallel or in tandem in these different fields. Our primary point might seem obvious, but it clearly has not been properly appreciated: all three fields are dealing in similar issues and all three fields have much to offer one another.

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REFERENCES

ALROY, J. 1998. Cope's rule and the dynamics of body mass evolution in North American fossil mammals. Science, 280(5364):731-734.

ALROY, J. 1999. Putting North America's end-Pleistocene megafaunal extinction in context: Large scale analyses of spatial patterns, extinction rates, and size distributions, p. 105-143. *In* R. D. E. MacPhee (ed.), Extinctions in near Time: Causes, Contexts, and Consequences. Kluwer Academic/Plenum, New York.

ALROY, J. 2000. New methods for quantifying macroevolutionary patterns and processes. Paleobiology, 26(4):707-733.

APESTEGUIA, S., AND F. E. NOVAS. 2003. Large Cretaceous sphenodontian from Patagonia provides insight into lepidosaur evolution in Gondwana. Nature, 425(6958):609-612.

BAKKER, V. J., AND D. A. KELT. 2000. Scale-dependent patterns in body size distributions of neotropical mammals. Ecology, 81(12):3530-3547.

BARNOSKY, A. D., E. A. HADLY, AND C. J. BELL. 2003. Mammalian response to global warming on varied temporal scales. Journal of Mammalogy, 84(2):354-368.

BEALE, C. M., J. J. LENNON, AND A. GIMONA. 2008. Opening the climate envelope reveals no macroscale associations with climate in European birds. Proceedings of The National Academy of Sciences of the United States of America, 105(39):14908-14912.

BEGON, M. J., L. HARPER, AND C. R. TOWNSEND. 1990. Ecology: Individuals, Populations and Communities. Blackwell Scientific Publications, London, 960 p.

BLACKBURN, T. M., K. E. JONES, P. CASSEY, AND N. LOSIN. 2004. The influence of spatial resolution on macroecological patterns of range size variation: A case study using parrots (Aves: Psittaciformes) of the world. Journal of Biogeography, 31(2):285-293.

BOBACK, S. M., AND C. GUYER. 2003. Empirical evidence for an optimal body size in snakes. Evolution, 57(2):345-351.

BRENCHLEY, W. E., AND K. WARRINGTON. 1958. The Park Grass Plots at Rothamsted. Rothamsted Experimental Station, Harpenden, 144 p.

BROWN, J. H. 1995. Macroecology. University of Chicago Press, Chicago, Illinois, 269 p.

BROWN, J. H., AND B. A. MAURER. 1989. Macroecology: The division of food and space among species on continents.

Science, 243(4895):1145-1150.

BROWN, J. H., AND P. F. NICOLETTO. 1991. Spatial scaling of species composition: Body masses of North-American land mammals. American Naturalist, 138(6):1478-1512.

BURNHAM, K. P., AND D. R. ANDERSON. 2004. Multimodel inference: Understanding AIC and BIC in model selection. Sociological Methods and Research, 33(2):261-304.

BUZAS, M. A., AND T. G. GIBSON. 1969. Species diversity: Benthonic foraminifera in western North Atlantic. Science, 163:72-75.

BUZAS, M. A., R. K. SMITH, AND K. A. BEEM. 1977. Ecology and systematics of Foraminifera in two *Thalassia* habitats, Jamaica, West Indies. Smithsonian Contributions to Paleobiology, 31:1-139.

CALDER, W. A., III. 1984. Size, Function, and Life History. Harvard University Press, Cambridge, Massachusetts, 448 p.

CARDILLO, M., AND L. BROMHAM. 2001. Body size and risk of extinction in Australian mammals. Conservation Biology, 15(5):1435-1440.

COLWELL, R. K., AND G. C. HURTT. 1994. Nonbiological gradients in species richness and a spurious Rapoport effect. The American Naturalist, 144:570-595.

CONRAD, J. L. 2008. Phylogeny and systematics of Squamata (Reptilia) based on morphology. Bulletin of the American Museum of Natural History:1-182.

COTTON, T. J. 2001. The phylogeny and systematics of blind Cambrian ptychoparoid trilobites. Palaeontology, 44(1):167-207.

DAMUTH, J., AND B. J. MACFADDEN. 1990. Body Size in Mammalian Paleobiology: Estimation and Biological Implications. Cambridge University Press, New York, 442 p

DAVIS, A. J., J. H. LAWTON, B. SHORROCKS, AND L. S. JENKINSON. 1998. Individualistic species responses invalidate simple physiological models of community dynamics under global environmental change. Journal of Animal Ecology, 67:600-612.

DAVIS, M. B., AND R. G. SHAW. 2001. Range shifts and adaptive responses to Quaternary climate change. Science, 292(5517):673-679.

DEWDNEY, A. K. 1998. A general theory of the sampling process with applications to the "Veil Line." Theoretical Population Biology, 54(2):294-302.

EDWARDS, A. W. F. 1992. Likelihood - Expanded edition. Johns Hopkins University Press, Baltimore, 275 p.

FAITH, D. P. 1994. Phylogenetic pattern and the quantification of organismal biodiversity. Philosophical Transactions of the Royal Society of London, B, 345:45-58.

FAITH, D. P. 2002. Quantifying biodiversity: A phylogenetic perspective. Conservation Biology, 16:248-252.

FELSENSTEIN, J. 1985. Phylogenies and the comparative method. The American Naturalist, 125(1):1-15.

FISHER, R. A., A. S. CORBET, AND C. B. WILLIAMS. 1943. The relation between the number of species and the number

of individuals in a random sample of an animal population. Journal of Animal Ecology, 12(1):42-48.

FOODY, G. M. 2008. Refining predictions of climate change impacts on plant species distribution through the use of local statistics. Ecological Informatics, 3(3):228-236.

FOOTE, M. 1991. Morphologic patterns of diversification: Examples from trilobites. Palaeontology, 34(2):461-485.

FOOTE, M. 1992. Early morphologic diversity in blastozoan echinoderms. Fifth North American Paleontological Convention, Field Museum of Natural History, Special Publication No. l6:102.

FOOTE, M. 1993. Contributions of individual taxa to overall morphological disparity. Paleobiology, 19(4):403-419.

FOOTE, M. 1996. Models of morphologic diversification, p. 62 - 86. In D. Jablonski, D. H. Erwin, and J. H. Lipps (eds.), Evolutionary Paleobiology: Essays in honor of James W. Valentine. University of Chicago Press, Chicago.

FOOTE, M. 1997. The evolution of morphologic diversity. Annual Review of Ecology and Evolution, 28:129-152.

FOOTE, M. 2007. Symmetric waxing and waning of marine invertebrate genera. Paleobiology, 33(4):517-529.

FOOTE, M., J. S. CRAMPTON, A. G. BEU, AND R. A. COOPER. 2008. On the bidirectional relationship between geographic range and taxonomic duration. Paleobiology, 34(4):421-433.

FOOTE, M., J. S. CRAMPTON, A. G. BEU, B. A. MARSHALL, R. A. COOPER, P. A. MAXWELL, AND I. MATCHAM. 2007. Rise and fall of species occupancy in Cenozoic fossil mollusks. Science, 318(5853):1131-1134.

FRONTIER, S. 1985. Diversity and structure in aquatic ecosystems, p. 253-312. In M. Barnes (ed.), Oceanography and Marine Biology: An Annual Review. Aberdeen University Press, Aberdeen.

GASTON, K. J. 2003. The Structure and Dynamics of Geographic Ranges. Oxford University Press, Oxford, 280 p.

GASTON, K. J., AND T. M. BLACKBURN. 1995. Birds, body-size and the threat of extinction. Philosophical Transactions of the Royal Society of London, B, 347(1320):205-212.

GASTON, K. J., AND T. M. BLACKBURN. 1996. Global scale macroecology: Interactions between population size, geographic range size and body size in the Anseriformes. Journal of Animal Ecology, 65(6):701-714.

GASTON, K. J., AND T. M. BLACKBURN. 2000. Pattern and Process in Macroecology. Blackwell Science, Oxford, 377p.

GASTON, K. J., AND T. M. BLACKBURN. 2003. Macroecology and Conservation Biology, p. 345-367. In T. M. Blackburn and K. J. Gaston (eds.), Macroecology: Concepts and Consequences. Blackwell Science, Oxford.

GOSSELIN, F. 2006. An assessment of the dependence of evenness indices on species richness. Journal of Theoretical Biology, 242(3):591-597.

GOTELLI, N. J., AND G. R. GRAVES. 1996. Null Models in Ecology. Smithsonian Press, Washington, D.C., 368 p.

GRAHAM, R. W. 1986. Response of mammalian communities to environmental changes during the late Quaternary, p. 300-313. In J. Diamond and T. J. Case (eds.), Community Ecology. Harper and Row, New York.

GRAHAM, R. W., E. L. LUNDELIUS, M. A. GRAHAM, E. K. SCHROEDER, R. S. TOOMEY, E. ANDERSON, A. D. BARNOSKY, J. A. BURNS, C. S. CHURCHER, D. K. GRAYSON, R. D. GUTHRIE, C. R. HARINGTON, G. T. JEFFERSON, L. D. MARTIN, H. G. MCDONALD, R. E. MORLAN, H. A. SEMKEN, S. D. WEBB, L. WERDELIN, AND M. C. WILSON. 1996. Spatial response of mammals to late Quaternary environmental fluctuations. Science, 272(5268):1601-1606.

GRAHAM, R. W., AND J. I. MEAD. 1987. Environmental fluctuations and evolution of mammalian faunas during the last deglaciation in North America, p. 372-402. In W. F. Ruddiman and H. E. Wright Jr. (eds.), North American and Adjacent Oceans during the Last Deglaciation. The Geological Society of America, Boulder, Colorado.

GRAY, J. S. 1987. Species-abundance patterns, p. 53 - 67. In J. H. R. Gee and P. S. Gillier (eds.), Organization of Communities Past and Present. Blackwell, Oxford.

HADLY, E. A., M. H. KOHN, J. A. LEONARD, AND R. K. WAYNE. 1998. A genetic record of population isolation in pocket gophers during Holocene climate change. Proceedings of the National Academy of Sciences of the United States of America, 95(12):6893-6896.

HALL, E. R. 1981. The Mammals of North America. Wiley, New York.

HARCOURT, A. H. 2006. Rarity in the tropics: Biogeography and macroecology of the primates. Journal of Biogeography, 33(12):2077-2087.

HARNIK, P. G. 2009. Unveiling rare diversity by integrating museum, literature and field data. Paleobiology, 35(2):190 - 208.

HAYEK, L.-A. C., AND M. A. BUZAS. 1997. Surveying Natural Populations. Columbia University Press, New York, 563 p.

HUBBELL, S. P. 1997. A unified theory of biogeography and relative species abundance and its application to tropical rain forests and coral reefs. Coral Reefs, 16 Supplemental:S9-S21.

HUBBELL, S. P. 2001. The Unified Neutral Theory of Biodiversity and Biogeography. Princeton University Press, Princeton, New Jersey, 375 p.

HURLBERT, S. H. 1971. The nonconcept of species diversity: A critique and alternative parameters. Ecology, 52:577-586.

JABLONSKI, D. 1986. Background and mass extinctions: The alteration of macroevolutionary regimes. Science, 231:129-133.

JABLONSKI, D. 1997. Body-size evolution in Cretaceous molluscs and the status of Cope's Rule. Nature, 385:250-

252.

JABLONSKI, D. 2005. Mass extinctions and macroevolution. Paleobiology, 31(2):192-210.

JABLONSKI, D., AND D. M. RAUP. 1995. Selectivity of end-Cretaceous marine bivalve extinctions. Science, 268:389-391.

JACKSON, S. T., AND J. T. OVERPECK. 2000. Responses of plant populations and communities to environmental changes of the late Quaternary. Paleobiology, 26(4):194-220.

JACKSON, S. T., J. T. OVERPECK, T. WEBB, S. E. KEATTCH, AND K. H. ANDERSON. 1997. Mapped plant-macrofossil and pollen records of late Quaternary vegetation change in eastern North America. Quaternary Science Reviews, 16(1):1-70.

JACKSON, S. T., AND J. W. WILLIAMS. 2004. Modern analogs in Quaternary paleoecology: Here today, gone yesterday, gone tomorrow? Annual Review of Earth and Planetary Sciences, 32:495-537.

JESCHKE, J. M., AND D. L. STRAYER. 2008. Usefulness of bioclimatic models for studying climate change and invasive species, p. 1-24, In R. S. Ostfeld, and N. H. Schlesinger, Year in Ecology and Conservation Biology 2008.Wiley-Blackwell Publishing, Oxford.

JONES, K. E., A. PURVIS, AND J. L. GITTLEMAN. 2003. Biological correlates of extinction risk in bats. American Naturalist, 161(4):601-614.

KELT, D. A., AND M. D. MEYER. 2009. Body size frequency distributions in African mammals are bimodal at all spatial scales. Global Ecology and Biogeography, 18(1):19-29.

KEMPTON, R. A. 1979. Structure of species abundance and measurement of diversity. Biometrics, 35:307–322.

KITCHING, I. J., P. L. FOREY, C. HUMPHRIES, AND D. M. WILLIAMS. 1998. Cladistics. 2nd. Edition. The Theory and Practice of Parsimony Analysis. Oxford University Press, Oxford, 228 p.

KOCH, C. F. 1980. Bivalve species duration, areal extent and population size in a Cretaceous sea. Paleobiology, 6(2):184-192.

KOLEFF, P., AND K. J. GASTON. 2001. Latitudinal gradients in diversity: Real patterns and random models. Ecography, 24(3):341-351.

KRUG, A. Z., D. JABLONSKI, AND J. W. VALENTINE. 2008. Species–genus ratios reflect a global history of diversification and range expansion in marine bivalves. Proceedings of the Royal Society, B, 275(1639):1117-1123.

LAYOU, K. M. 2009. Ecological restructuring after extinction: the Late Ordovician (Mohawkian) of the Eastern United States. Palaios, 24(2):118-130.

LOCKWOOD, R. 2004. The K/T event and infaunality: Morphological and ecological patterns of extinction and recovery in veneroid bivalves. Paleobiology, 30(4):507-521.

LOMOLINO, M. V., B. R. RIDDLE, AND J. H. BROWN. 2006. Biogeography. Sinauer Associates, Inc., Sunderland, Massachusetts, 846 p.

LYONS, S. K. 1994. Areography of New World bats and marsupials. Unpublished Masters Thesis, Texas Tech University, Lubbock.

LYONS, S. K. 2003. A quantitative assessment of the range shifts of Pleistocene mammals. Journal of Mammalogy, 84(2):385-402.

LYONS, S. K. 2005. A quantitative model for assessing community dynamics of pleistocene mammals. American Naturalist, 165(6):E168-E185.

LYONS, S. K. 2007. The relationship between environmental variables and mammalian body size distributions over space and time. Annual meeting of the Ecological Society of America. Ecological Society of America, San Jose.

LYONS, S. K., AND F. A. SMITH. 2006. Assessing biases in the mammalian fossil record using late Pleistocene mammals from North America. Abstracts with Programs, Geological Society of America, 38.

LYONS, S. K., F. A. SMITH, AND J. H. BROWN. 2004. Of mice, mastodons and men: Human-mediated extinctions on four continents. Evolutionary Ecology Research, 6(3):339-358.

LYONS, S. K., AND M. R. WILLIG. 1997. Latitudinal patterns of range size: Methodological concerns and empirical evaluations for New World bats and marsupials. Oikos, 79(3):568-580.

MADIN, J. S., AND S. K. LYONS. 2005. Incomplete sampling of geographic ranges weakens or reverses the positive relationship between an animal species' geographic range size and its body size. Evolutionary Ecology Research, 7:607-617.

MARQUET, P. A., AND H. COFRE. 1999. Large temporal and spatial scales in the structure of mammalian assemblages in South America: A macroecological approach. Oikos, 85(2):299-309.

MARTINEZ-MEYER, E., A. T. PETERSON, AND W. W. HARGROVE. 2004. Ecological niches as stable distributional constraints on mammal species, with implications for Pleistocene extinctions and climate change projections for biodiversity. Global Ecology and Biogeography, 13(4):305-314.

MAURER, B. A. 1999. Untangling Ecological Complexity: The Macroscopic Perspective. University of Chicago Press, Chicago, Illinois, 262 p.

MAY, R. M. 1975. Patterns of species abundance and diversity, p. 87-120. In M. L. Cody and J. M. Diamond (eds.), Ecology and Evolution of Communities. The Belknap Press of Harvard University Press, Cambridge.

McELWAIN, J. C., M. E. POPA, S. P. HESSELBO, M. HAWORTH, AND F. SURLYK. 2007. Macroecological responses of terrestrial vegetation to climatic and atmospheric change across the Triassic/Jurassic boundary in East Greenland. Paleobiology, 33(4):547-573.

McGill, B. J. 2003. Does Mother Nature really prefer rare species or are log-left-skewed SADs a sampling artefact? Ecology Letters, 6(8):766-773.

McGowan, A. J. 2004. The effect of the Permo-Triassic bottleneck on Triassic ammonoid morphological evolution. Paleobiology, 30(3):369-395.

Motomura, I. 1932. A statistical treatment of associations. Zoological Magazine, Tokyo, 44:379-383.

Olszewski, T. D. 2004. A unified mathematical framework for the measurement of richness and evenness within and among multiple communities. Oikos, 104(2):377-387.

Olszewski, T. D., and D. H. Erwin. 2004. Dynamic response of Permian brachiopod communities to long-term environmental change. Nature, 428(6984):738-741.

Olszewski, T. D., and S. M. Kidwell. 2007. The preservational fidelity of evenness in molluscan death assemblages. Paleobiology, 33(1):1-23.

Overpeck, J. T., R. S. Webb, and T. Webb. 1992. Mapping Eastern North-American vegetation change of the past 18 ka: No-analogs and the future. Geology, 20(12):1071-1074.

Overpeck, J. T., T. Webb, and I. C. Prentice. 1985. Quantitative Interpretation of Fossil Pollen Spectra: Dissimilarity Coefficients and the Method of Modern Analogs. Quaternary Research, 23(1):87-108.

Parmesan, C., and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature, 421(6918):37-42.

Patterson, B. D., G. Geballos, W. Sechrest, M. Toghelli, G. T. Brooks, L. Luna, P. Ortega, I. Salazar, and B. E. Young. 2003. Digital Distribution Maps of the Mammals of the Western Hemisphere. Version 1.0. Nature Serve, Arlington, Virginia.

Payne, J. L., A. G. Boyer, J. H. Brown, S. Finnegan, M. Kowalewski, R. A. Krause, S. K. Lyons, C. R. McClain, D. W. McShea, P. M. Novack-Gottshall, F. A. Smith, J. A. Stempien, and S. C. Wang. 2009. Two-phase increase in the maximum size of life over 3.5 billion years reflects biological innovation and environmental opportunity. Proceedings of the National Academy of Sciences of the United States of America, 106(1):24-27.

Payne, J. L., and S. Finnegan. 2007. The effect of geographic range on extinction risk during background and mass extinction. Proceedings of the National Academy of Sciences of the United States of America, 104(25):10506-10511.

Peters, R. H. 1983. The Ecological Implications of Body Size. Cambridge University Press, Cambridge.

Peters, S. E. 2004. Evenness of Cambrian-Ordovician benthic marine communities in North America. Paleobiology, 30(3):325-346.

Peterson, A. T. 2001. Predicting species' geographic distributions based on ecological niche modeling. Condor, 103(3):599-605.

Peterson, A. T., E. Martinez-Meyer, and C. Gonzalez-Salazar. 2004a. Reconstructing the Pleistocene geography of the *Aphelocoma* jays (Corvidae). Diversity and Distributions, 10(4):237-246.

Peterson, A. T., E. Martinez-Meyer, C. Gonzalez-Salazar, and P. W. Hall. 2004b. Modeled climate change effects on distributions of Canadian butterfly species. Canadian Journal of Zoology-Revue Canadienne de Zoologie, 82(6):851-858.

Peterson, A. T., M. A. Ortega-Huerta, J. Bartley, V. Sanchez-Cordero, J. Soberon, R. H. Buddemeier, and D. R. B. Stockwell. 2002. Future projections for Mexican faunas under global climate change scenarios. Nature, 416(6881):626-629.

Peterson, A. T., V. Sanchez-Cordero, J. Soberon, J. Bartley, R. W. Buddemeier, and A. G. Navarro-Siguenza. 2001. Effects of global climate change on geographic distributions of Mexican Cracidae. Ecological Modelling, 144(1):21-30.

Pielou, E. C. 1966. Species diversity and pattern diversity in the study of ecological succession. Journal of Theoretical Biology, 10:370-383.

Poulin, R., and S. Morand. 1997. Parasite body size distributions: Interpreting patterns of skewness. International Journal for Parasitology, 27(8):959-964.

Powell, M. G., and M. Kowalewski. 2002. Increase in evenness and sampled alpha diversity through the Phanerozoic: Comparison of early Paleozoic and Cenozoic marine fossil assemblages. Geology, 30(4):331-334.

Preston, W. H. 1948. The commonness and rarity of species. Ecology, 29(3):254-283.

Reynoso, V.-H. 1996. A Middle Jurassic Sphenodon-Like Sphenodontian (Diapsida: Lepidosauria) from Huizachal Canyon, Tamaulipas, Mexico. Journal of Vertebrate Paleontology, 16(2):210-221.

Reynoso, V.-H. 2000. An unusual aquatic sphondontian (Reptilia: Diapsida) from the Tlayua Formation (Albian), Central Mexico. Journal of Paleontology, 74(1):133-148.

Roy, K. 1996. The roles of mass extinction and biotic interaction in large-scale replacements: A reexamination using the fossil record of stromboidean gastropods. Paleobiology, 22(3):436-452.

Roy, K., and M. Foote. 1997. Morphological approaches to measuring biodiversity. Trends in Ecology and Evolution, 12(7):277-281.

Roy, K., D. Jablonski, and J. W. Valentine. 1994. Eastern Pacific Molluscan provinces and latitudinal diversity gradient - no evidence for "Rapoport's rule". Proceedings of the National Academy of Sciences of the United States of America, 91(19):8871-8874.

Roy, K., D. Jablonski, and J. W. Valentine. 1995. Thermally anomalous assemblages revisited: Patterns in the extraprovincial latitudinal range shifts of Pleistocene ma-

rine mollusks. Geology, 23(12):1071-1074.

ROY, K., AND K. K. MARTIEN. 2001. Latitudinal distribution of body size in north-eastern Pacific marine bivalves. Journal of Biogeography, 28(4):485-493.

RUGGIERO, A., AND J. H. LAWTON. 1998. Are there latitudinal and altidudinal Rapoport effects in the geographic ranges of Andean passerine birds? Biological Journal of the Linnean Society, 63(2):283-304.

RUGGIERO, A., AND V. WERENKRAUT. 2007. One-dimensional analyses of Rapoport's rule reviewed through meta-analysis. Global Ecology And Biogeography, 16(4):401-414.

SCHWEIGER, O., J. SETTELE, O. KUDRNA, S. KLOTZ, AND I. KUHN. 2008. Climate Change Can Cause Spatial Mismatch of Trophically Interacting Species. Ecology, 89(12):3472-3479.

SEPKOSKI, J. J., JR. 1978. A kinetic model of Phanerozoic taxonomic diversity: I. Analysis of marine orders. Paleobiology, 4(2):223-251.

SHANNON, C. E. 1948. A mathematical theory of communication. Bell Systems Technology Journal, 27:379-423.

SMITH, B., AND J. B. WILSON. 1996. A consumer's guide to evenness indices. Oikos, 76(1):70-82.

SMITH, F. A., J. L. BETANCOURT, AND J. H. BROWN. 1995. Evolution of body-size in the woodrat over the past 25,000 years of climate-change. Science, 270(5244):2012-2014.

SMITH, F. A., J. H. BROWN, J. P. HASKELL, S. K. LYONS, J. ALROY, E. L. CHARNOV, T. DAYAN, B. J. ENQUIST, S. K. M. ERNEST, E. A. HADLY, K. E. JONES, D. M. KAUFMAN, P. A. MARQUET, B. A. MAURER, K. J. NIKLAS, W. P. PORTER, B. TIFFNEY, AND M. R. WILLIG. 2004. Similarity of mammalian body size across the taxonomic hierarchy and across space and time. American Naturalist, 163(5):672-691.

SMITH, F. A., H. BROWNING, AND U. L. SHEPHERD. 1998. The influence of climate change on the body mass of woodrats *Neotoma* in an arid region of New Mexico, USA. Ecography, 21(2):140 - 148.

SMITH, F. A., S. K. LYONS, S. K. M. ERNEST, AND J. H. BROWN. 2008. Macroecology: More than just the division of food and space among species on continents. Progress in Physical Geography, 32(2):115-138.

SMITH, F. A., S. K. LYONS, S. K. M. ERNEST, K. E. JONES, D. M. KAUFMAN, T. DAYAN, P. A. MARQUET, J. H. BROWN, AND J. P. HASKELL. 2003. Body mass of late quaternary mammals. Ecology, 84(12):3403-3403.

SOKAL, R. R., AND F. J. RHOLF. 1981. Biometry: The Principles and Practice of Statistics in Biological Research. W. H. Freeman and Company, New York, NY.

SUGIHARA, G. 1980. Minimal community structure: An explanation of species abundance patterns. The American Naturalist, 116:770-787.

THOMAS, C. D., A. CAMERON, R. E. GREEN, M. BAKKENES, L. J. BEAUMONT, Y. C. COLLINGHAM, B. F. N. ERASMUS, M. F. DE SIQUEIRA, A. GRAINGER, L. HANNAH, L. HUGHES, B. HUNTLEY, A. S. VAN JAARSVELD, G. F. MIDGLEY, L. MILES, M. A.

ORTEGA-HUERTA, A. T. PETERSON, O. L. PHILLIPS, AND S. E. WILLIAMS. 2004. Extinction risk from climate change. Nature, 427(6970):145-148.

VALENTINE, J. W., D. JABLONSKI, S. KIDWELL, AND K. ROY. 2006. Assessing the fidelity of the fossil record by using marine bivalves. Proceedings of the National Academy of Sciences of the United States of America, 103(17):6599-6604.

VOLKOV, I., J. R. BANAVAR, S. P. HUBBELL, AND A. MARITAN. 2003. Neutral theory and relative species abundance in ecology. Nature, 424:1035-1037.

WAGNER, P. J. 1997. Patterns of morphologic diversification among the Rostroconchia. Paleobiology, 23(1):115-150.

WAGNER, P. J., M. A. KOSNIK, AND S. LIDGARD. 2006. Abundance distributions imply elevated complexity of post-Paleozoic marine ecosystems. Science, 314:1289-1292.

WALKER, K. V., M. B. DAVIS, AND S. SUGITA. 2002. Climate change and shifts in potential tree species range limits in the Great Lakes region. Journal of Great Lakes Research, 28(4):555-567.

WEBB, S. D., AND A. D. BARNOSKY. 1989. Faunal dynamics of Pleistocene mammals. Annual Review of Earth and Planetary Sciences, 17:413-438.

WILLIAMS, J. W., D. M. POST, L. C. CWYNAR, A. F. LOTTER, AND A. J. LEVESQUE. 2002. Rapid and widespread vegetation responses to past climate change in the North Atlantic region. Geology, 30(11):971-974.

WILLIAMS, J. W., B. N. SHUMAN, AND T. WEBB. 2001. Dissimilarity analyses of late-uaternary vegetation and climate in eastern North America. Ecology, 82(12):3346-3362.

WILLIAMS, J. W., B. N. SHUMAN, T. WEBB, P. J. BARTLEIN, AND P. L. LEDUC. 2004. Late-Quaternary vegetation dynamics in North America: Scaling from taxa to biomes. Ecological Monographs, 74(2):309-334.

WILLIG, M. R., AND M. R. GANNON. 1997. Gradients of species density and turnover in marsupials: A hemispheric perspective. Journal of Mammalogy, 78(3):756-765.

WILLIG, M. R., AND S. K. LYONS. 1998. An analytical model of latitudinal gradients of species richness with an empirical test for marsupials and bats in the New World. Oikos, 81(1):93-98.

WILLIG, M. R., S. K. LYONS, AND R. D. STEVENS. In press. Spatial methods for the macroecological study of bats. *In* T. H. Kunz and S. Parsons (eds.), Ecological and Behavioral Methods for the Study of Bats. Johns Hopkins University Press, Baltimore, Maryland.

WILLIG, M. R., B. D. PATTERSON, AND R. D. STEVENS. 2003. Patterns of range size, richness, and body sizes in Chiroptera., p. 580-621. *In* T. H. Kunz and M. B. Fenton (eds.), Bat Ecology. University of Chicago Press, Chicago, Illinois.

WILLIG, M. R., AND E. A. SANDLIN. 1991. Gradients of species density and turnover in New World bats: a comparison of quadrat and band methodologies, p. 81-96. *In*

M. A. Mares and D. J. Schmidly (eds.), Latin American Mammals: Their Conservation, Ecology and Evolution. University of Oklahoma Press, Norman, Oklahoma.

WILLIG, M. R., AND K. W. SELCER. 1989. Bat species density gradients in the New World: A statistical assessment. Journal of Biogeography, 16(2):189-195.

WILLIS, J. C. 1922. Age and Area: A Study in Geographical Distribution and Origin of Species. Cambridge University Press, Cambridge, 259 p.

WILLIS, K. J., M. B. ARAUJO, K. D. BENNET, B. FIGUEROA-RANGEL, C. A. FROYD, AND N. MYERS. 2007a. How can a knowledge of the past help to conserve the future? Biodiversity conservation and the relevance of long-term ecological studies. Philosophical Transactions of the Royal Society of London, B, 362(1478):175-186.

WILLIS, K. J., A. KLECZKOWSKI, M. N. A., AND R. J. WHITTAKER. 2007b. Testing the impact of climate variability on European plant diversity: 320, 000 years of water-energy dynamics and its long-term influence on plant taxonomic richness. Ecology Letters, 10(8):673-679.

WILLIS, K. J., AND H. J. B. BIRKS. 2006. What is natural? The need for long-term perspective in biodiveristy conservation. Science, 314(5803):1261-1265.

APPENDIX 1

Evenness metrics

Although the basic concept of evenness, i.e., typical deviation from uniform abundance, is simple, many evenness metrics exist. When examining the logarithms of distributions, the Shannon-Wiener index, H, (Shannon, 1948) is intuitively informative. H is:

$$H = \sum_i^{S_o} f_i \ln(f_i)$$

where S_o is the observed richness, and f_i is the observed relative abundance (frequency) of taxon i. The maximum value for H occurs when f_i is uniform for all taxa (i.e., $f_i = \frac{1}{S_o}$) and yields $H = -\ln(S_o)$.

Two evenness metrics use this relationship: J (Pielou, 1966) and E (Buzas and Gibson, 1969). These are given as:

$$J = \frac{-H}{\ln(S_o)}$$

and:

$$E = \frac{e^{-H}}{S_o}$$

In both cases, the numerator will equal the denominator when

$$f_1 = f_2 = \ldots = f_{So} = \frac{1}{S_o}$$

and thus the evenness will equal 1.0 when sampled abundances are uniform.

Other ways of estimating evenness examines sums of squared frequencies. Hurlbert's Probability of Intraspecific Encounter (PIE) is given as:

$$PIE = 1 - \sum_i^{S_o} f_i^2$$

Here, the second term is simply the probability of sampling the same taxon (an interspecific encounter) twice in a row. Peters (2004) sum of squared evenness relies on the sum squared differences between observed and expected ($f = \frac{1}{S_o}$) abundances:

$$F = 1 - \frac{S_o \sum_i^{S_o} (f_i - \frac{1}{S_o})^2}{S_o - 1}$$

In both cases, the minimum sum of squares occurs when $f_1 = f_2 = \ldots = f_{So} = \frac{1}{S_o}$.

However, whereas F (like J and E above) is 1.0 at uniform abundance, the maximum possible PIE increases as richness (S) increases, and never can reach 1.0. PIE has a direct relationship to rarefaction curves, as the expected subsampled richness at 2 specimens is 1+PIE (Olszewski, 2004).

Finally, Powell and Kowałewski (2002) use the Kolmogorov-Smirnov D statistic, which is simply one minus the sum of the differences between f_i and $\frac{1}{S_o}$ for all $f_i > \frac{1}{S_o}$. Again, this is 1.0 when frequencies are uniform.

We note above that the maximum value of PIE depends on the sampled richness. For all evenness metrics, the minimum possible value depends on both sampled richness and sample size (e.g., Gosselin, 2006). For N specimens and S_o observed taxa, this would be when $f_1 = N+1-S_o$ and $f_2 = f_3 = \ldots = f_{So} = 1$. As we shall show below, this can be very important when examining trends

in evenness when S_o changes.

Sample size is also important for the accuracy of evenness metrics. Small sample sizes yield accurate estimates of PIE and F (Gotelli and Graves, 1996; Peters, 2004). This is because the taxa that make the greatest contributions to PIE and F are the most common taxa. Rare taxa typically alter the sum of squared (or squared difference from expectations) only slightly whereas they alter H appreciably. Sampling standardization overcomes this problem (Layou, 2009), but then leaves all evenness metrics reflecting the most common taxa.

RAD models: theoretical expectations

Workers have proposed many more RAD models than we can review here. Therefore, we will focus on four that workers commonly use (Fig. A1). The simplest is the geometric distribution (Motomura, 1932), which relies on one parameter,

$$\delta = \frac{f_{i+1}}{f_i}$$

which reflects the rate of species entry relative to the rate of population expansion. The frequency of species rank i is approximately:

$$f_i \simeq (1-\delta)\delta^{(i-1)}$$

Although f_1 only approaches $(1-\delta)$ asymptotically, in practice only a few taxa are necessary for f_1 to approach $(1-\delta)$ to the third decimal place, especially as δ decreases. This allows us to approximate RADs using a single parameter.

The geometric is very similar to the more commonly used log series (Fisher et al., 1943), which differs in assuming that species arrival is stochastic rather than regular. However, the log series requires an iterative solution that does not lend itself so easily to calculating f_i's as the geometric does (e.g., Hayek and Buzas, 1997).

The geometric makes simplifying assumptions about both true population size and migration/origination rates. The zero-sum multinomial (Hubbell, 1997, 2001) explicitly accommodates these. The calculation is too complex to repeat here (see Volkov et al., 2003: box 1), but relies on three parameters: the local community size (N_T), the probability of immigration (m) from the larger "metacommunity" (i.e., collection of adjacent communities), and a compound parameter (θ) that is the product of the origination rate and "metacommu-

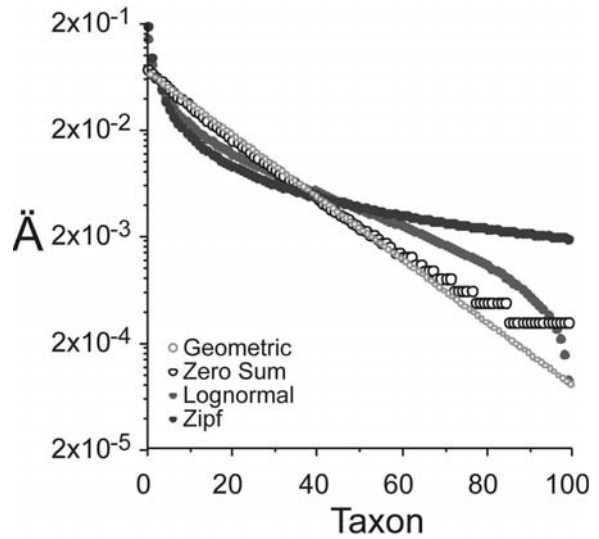FIGURE *A1*.—Model relative abundance distributions reviewed here. Each has true richness $S_T=100$ and true $J = 0.80$.

nity" population size (usually given as J_M). Volkov et al.'s (2003) formula allows one to estimate the exact number of species with n specimens, and thus an exact RAD. As θ increases, the probability of interspecific encounter increases, meaning a richer and more even community.

Other RAD models assume that species utilize resources differently, either by entering fundamentally different niches or by making new resources available either for themselves or for other species. The Zip-Mandelbrot (e.g., Frontier, 1985) relies on three parameters:

$$f_i = \frac{(i + \beta)^{-\gamma}}{\sum_{j=1}^{S_T}(j + \beta)^{-\gamma}}$$

Like δ for the geometric, γ reflects ecosystem stability and the regularity of immigration. However, the assumption is that new species expand the total ecospace slightly, resulting in the difference in f_i decreasing. β reflects the diversity of basic niches. The Zipf distribution is the special 2-parameter case where $\beta=0$ and yields a RAD that is linear on a log-log plot. Although f_i is proportional to the numerator regardless of true richness (S_T), it always is 1.0 for the first species. Moreover, the denominator (i.e., the sum of relative proportions) changes markedly with the addition
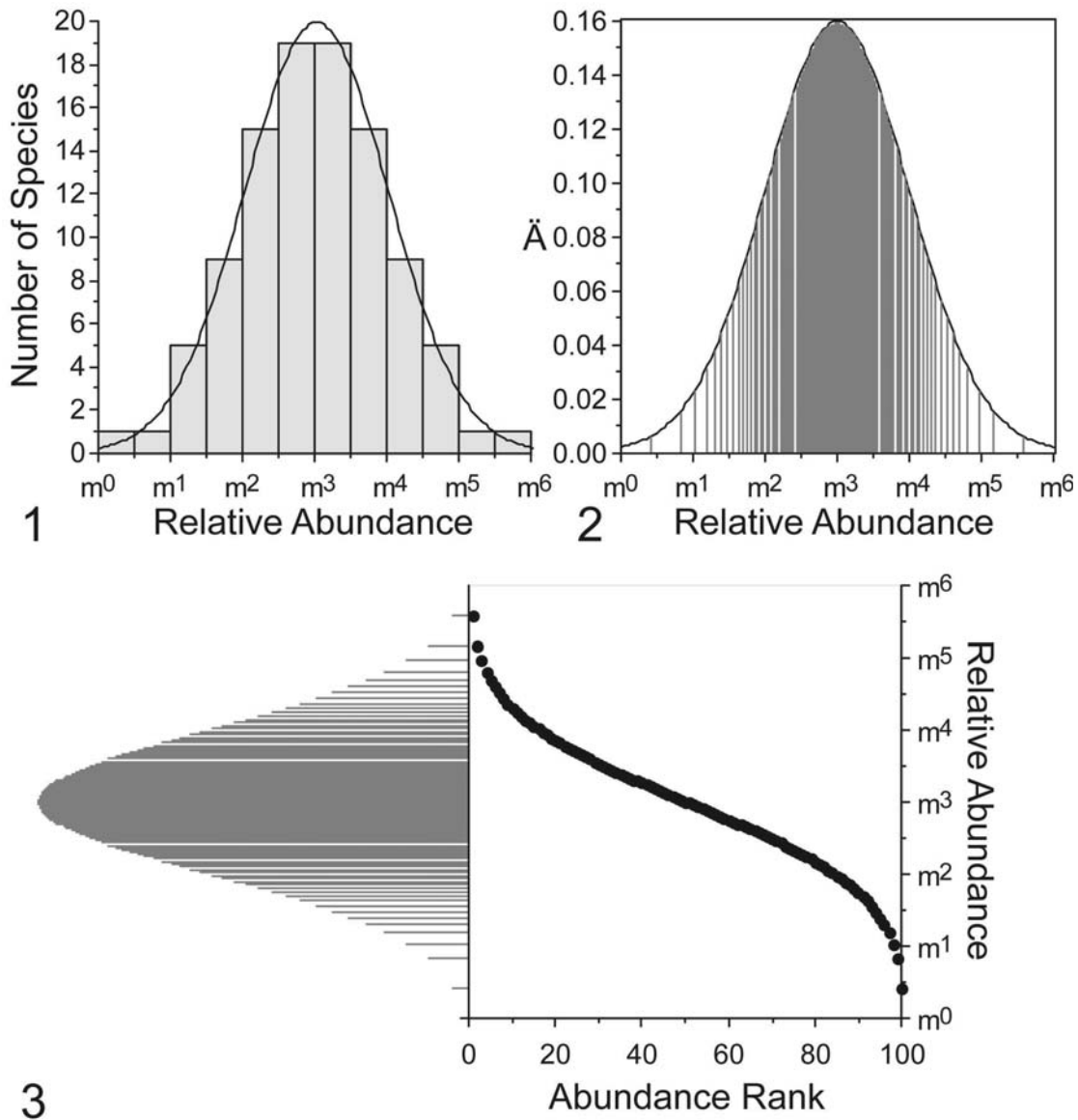
Figure *A2*.—Deriving lognormal RAD. *1*, Typical depiction of a lognormal distribution for 100 species. Species in each octave are m times more abundant than are species in the prior octave; *2*,The same normal curve divided by 100 partitions into 101 units of equal area, *3*, The position of each partition I on the X-axis gives the relative abundance of the ith species and becomes the Y-axis of a standard log-linear RAD plot. Modified from Wagner et al. (2006).

of new taxa even at high values of S_T. Thus, we cannot predict abundances given β and γ without specifying S_T.

RADs frequently fit lognormal distributions (Preston, 1948). This might be a simple artifact of mixing exponential distributions (May, 1975); however, it also can reflect hierarchical division of niches by incoming taxa (Sugihara, 1980). Lognormal RADs depend on two parameters (Figure A2.1): true richness (S_T) and the magnitude difference in abundance between species separated by X standard deviations under the normal curve (m). This provides only a very general RAD: although it specifies the number of taxa in any one octave, it does not specify their relative abundances. This can be done by a simple iterative procedure where the normal curve is divided into (S_T+1) partitions of equal
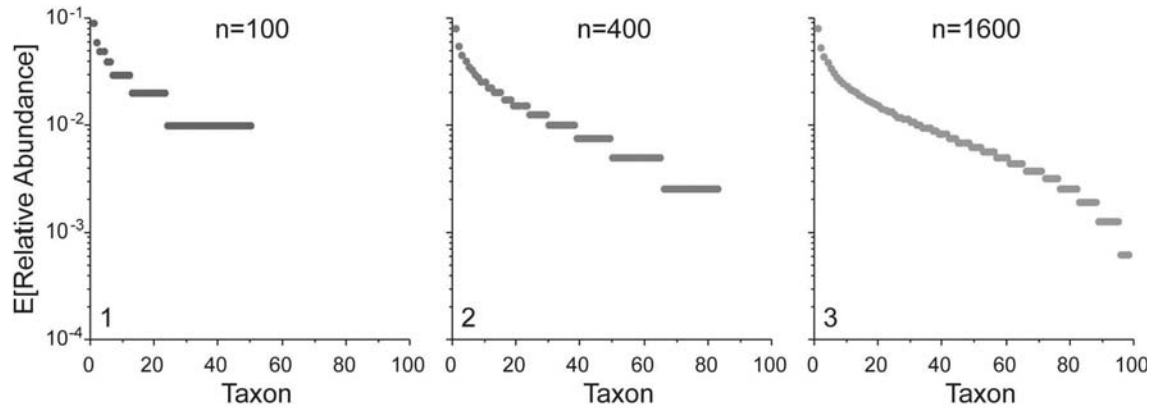
FIGURE *A3*.—Expected sampled RADs from the same model RAD (= lognormal from Fig. 7). As sample size (n) increases, the expectations become increasingly sharply delimited. This reflects both tightening of binomial error bars on expected numbers of finds given a true proportion and decreasing probabilities of sampled abundance ranks differing from true abundance ranks.

area (Fig. A2.2). The position of partition i is directly proportional to the relative abundance taxon i (Fig. A2.3).

Expected observed RADs given sampling

When comparing RADs, it is tempting to examine the goodness of fit to observed rank abundance to hypothesized curves such as shown in Figure A1. Another relevant concern is sample size (Koch, 1980; Gotelli and Graves, 1996; Dewdney, 1998; McGill, 2003). Consider the lognormal example in Figure A1. At 100 and even 400 specimens (Fig. 9.1-2), the *sampled* RADs look more like Zipf or even log series RADs than like the original model (Fig. A1). We need over 1000 specimens to recognize the characteristic lognormal sigmoidal RADs (Fig. 9.3).

Figure A3 emphasizes what we do have: predictions of expected frequencies of taxa with 1, 2, 3, etc. finds. For models predicting exact abundance frequencies given rank abundance, the expected sampled richness with abundance n given total sample N is:

$$E[S_{\mathbf{n}}|N] = \sum_{i=1}^{S} \binom{N}{n} \left[(1 - f_i)^{N-n} \times f_i^n \right]$$

where f_i is the frequency of species i implicit to the hypothesized RAD. Simple multinomial probability now gives us the likelihood of RADs that assumes that sampled RADs will differ from the original model RAD (Olszewski and Erwin, 2004). Equally important, we can use log-likelihood tests to test for changes within particular RAD models over time (e.g., Edwards, 1992); Alternatively, we can use information theory tests to test for changes in basic models over time (Burnham and Anderson, 2004).

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