

Can latitudinal richness gradients be measured in the terrestrial fossil record?

Danielle Fraser

Abstract.—Studying the deep-time origins of macroecological phenomena can help us to understand their long-term drivers. Given the considerable spatiotemporal bias of the terrestrial fossil record, it behooves us to understand how much biological information is lost. The aim of this study is to establish whether latitudinal diversity gradients are detectable in a biased terrestrial fossil record. I develop a simulated fossilization approach, weighting the probability of terrestrial mammal species appearing in the fossil record based on body size and geographic-range size; larger species with larger range sizes are more likely to enter the fossil record. I create simulated fossil localities from the modern North American mammal record. I vary the percentage of species successfully fossilized and estimate the magnitude of the latitudinal diversity gradient (slope of the richness gradient and degree of species turnover). I find that estimates of the latitudinal diversity gradient are sensitive to the loss of species with small body size and geographic-range sizes. In some cases, simulated fossil-record bias completely obliterates evidence of declining richness with latitude, a phenomenon that is not ameliorated by the application of non-parametric richness estimation. However, if the rate of preservation is medium (50% of species) to high (75% of species), the magnitude of the latitudinal diversity gradient can be reliably estimated. Similarly, changes in the diversity gradient estimates are largely explained by differences in the diversity–climate relationship among iterations, suggesting that these relationships may be measurable in the fossil record.

Danielle Fraser. *Department of Paleobiology, Smithsonian Institution, National Museum of Natural History, 10th and Constitution NW, Washington, D.C. 20013-7012, U.S.A., and Department of Biology, Carleton University, 1125 Colonel By Drive, Ottawa, Ontario, Canada K1S 5B6; E-mail: DFraser@mus-nature.ca. Present address: Palaeobiology, Canadian Museum of Nature, P.O. Box 3443 Station “D,” Ottawa, Ontario, Canada K1P 6P4*

Accepted: 9 January 2017

Published online: 9 March 2017

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.8p0s7>

Introduction

Latitudinal richness gradients (LRGs; i.e., loss of richness from low latitudes to high) are nearly ubiquitous among modern terrestrial organisms, having been observed in many groups, including angiosperms, birds, mammals, insects, and other invertebrates (McCoy and Connor 1980; Stevens 1989; Currie and Fritz 1993; Roy et al. 1998; Currie et al. 1999; Engle and Summers 1999; Condit et al. 2002; Hawkins et al. 2003; Qian et al. 2009; Baselga et al. 2012; Condamine et al. 2012). Terrestrial LRGs have been studied among both extant and extinct organisms (Jablonski et al. 2006, 2013; Fraser et al. 2014; Mannion et al. 2014). The study of LRGs in deep time (millions of years) is motivated by interest in the origins and evolutionary history of marine and terrestrial macroecological phenomena (Roy et al. 1998; Jablonski et al. 2006, 2013; Rose et al. 2011) and the influence of climate, tectonics,

and macroevolution (Rose et al. 2011; Fraser et al. 2014; Mannion et al. 2014). The fossil record is the result of a natural experiment that potentially records the evolutionary history of LRGs. However, the link between biodiversity change and its driving mechanisms is filtered through the processes of fossilization, which introduce considerable bias (Newell 1959; Raup 1972, 1975, 1976, 1979; Kidwell and Flessa 1996; Alroy et al. 2001; Kidwell and Holland 2002; Tomašových and Kidwell 2009, 2010; Alroy 2010b; Benton et al. 2011; Miller et al. 2014). Our understanding of fossil LRGs therefore hinges on the assumption that we can apply methods of sampling correction to reduce the influence of bias, thus interpreting remaining patterns as biologically relevant.

Characteristic terrestrial fossil-record biases include, but are not limited to, bias against species without mineralized skeletons, body and range-size bias, geographic bias in sampling

effort, depositional environmental bias, and rock record–volume bias (Newell 1959; Raup 1972, 1976; Smith 2001; Crampton et al. 2003; Benton et al. 2011; Mannion et al. 2011). At individual fossil localities, biases against species of small body and geographic-range sizes are also well documented (Behrensmeyer et al. 1979, 2000; Donovan and Paul 1998; Kidwell and Flessa 1996; Kidwell and Holland 2002; Cooper et al. 2006). Between 5 and 50% of species in small size classes can go missing from the marine fossil record (Cooper et al. 2006). In terrestrial ecosystems, depending on their trophic group, 30 to 80% of small species are lost from death assemblages (Behrensmeyer and Dechant Boaz 1980; Kidwell and Flessa 1996). Less abundant species (e.g., species higher in the food chain) with small geographic ranges are similarly less likely to enter the fossil record, because they might not occur in appropriate depositional environments or have large enough populations to ensure preservation (Newell 1959; Raup 1972, 1976; Smith 2001; Crampton et al. 2003; Benton et al. 2011; Mannion et al. 2011).

In North America, the numbers and geographic coverage of terrestrial fossil localities increase toward the present (e.g., from the Miocene to the Pleistocene, the number of high-latitude fossil localities increases dramatically), which is problematic given the positive correlation between species diversity and area (the so called species-area effect) (Brown 1995; Rosenzweig 1995; Barnosky et al. 2005; Alroy 2010a). Furthermore, regional sampling changes through time (e.g., the early Cenozoic North American mammal record is mostly limited to the Great Plains and Central Lowlands of North America, while the late Cenozoic record is much more widespread), which is problematic due to likely topographic differences and thus biodiversity differences among regions (Davis 2005; Badgley 2010). Our interpretation of biodiversity time series is made more difficult by rock-record bias; fossil-bearing outcrop areas are often correlated with terrestrial vertebrate taxonomic diversity (Raup 1972; Smith 2001; Crampton et al. 2003; Benton et al. 2011; Mannion et al. 2011). It therefore behooves us to understand how the many biases typical of the terrestrial fossil

record affect our ability to detect changes in macroecological phenomena through time.

In recognition of fossil-record bias, paleoecologists use a variety of compensatory approaches, including rarefaction, subsampling, and model selection (Raup 1975; Colwell and Coddington 1994; Alroy 1996; Miller and Foote 1996; Alroy 2010a; Rose et al. 2011; Benson and Mannion 2012; Valentine et al. 2013; Fraser et al. 2014, 2015; Mannion et al. 2014), the last of which does not attempt to remove bias but allows partitioning of variance among biological and bias-related model terms. Although many compensatory methods reduce sample size differences among localities and time periods, the extent to which true biodiversity patterns are retained after fossilization and whether applying rarefaction or modeling approaches allows apparent diversity patterns to be interpreted as true biological signals remain unknown.

Herein, I divide “latitudinal diversity gradient” into two components: LRGs (i.e., change in the number of species) and latitudinal turnover gradients (LTGs; i.e., change in the species composition of communities). An LTG, as defined here and elsewhere (Bowman 1996; Koleff et al. 2003), refers to the rate of change in community composition or similarity/dissimilarity among sites along a latitudinal axis. The distinction is important, because species composition can turn over entirely with no change in richness and show more rapid change than richness under environmental perturbation (Dornelas et al. 2014). Estimates of community turnover are also more robust to the formation of death assemblages (Tomašových and Kidwell 2009). Although both richness and community composition vary along environmental gradients (Qian and Ricklefs 2007, 2012; Qian et al. 2009; Qian, 2012), for the reasons outlined in the two preceding sentences, they are not necessarily correlated.

For the purposes of this paper, I use extant North American mammals as a test case, because they show a negative LRG (Fig. 1A) that is well explained by latitudinal changes in climate (e.g., mean annual precipitation, temperature, and potential evapotranspiration) (McCoy and Connor 1980; Currie 1991; Kaufman 1995; Badgley and Fox 2000; Hawkins et al. 2003).

North American mammals also show considerable latitudinal change in community composition (Fig. 1B) that is often attributed to environmental filtering (Qian et al. 2009; Kent et al. 2011), a process whereby community composition is partly determined by the environmental tolerances of constituent species (Kraft et al. 2007; Qian et al. 2009; Soininen 2010; Peres-Neto et al. 2012). Furthermore, the North American Cenozoic (65 Ma–present) terrestrial mammal fossil record has been the focus of many paleoecological studies (e.g., Alroy 2000; Figueirido 2012; Raia 2012a,b; Fraser et al. 2014). Although I focus on mammals, the method I develop here allows for the rigorous comparison of modern and fossil communities for any terrestrial group with a fossil and modern record.

To address whether latitudinal diversity gradients measured using the fossil record might reflect the true gradients from which they are drawn, I developed a simulated fossilization approach. Using the modern mammal record (i.e., spatially referenced geographic-range data), I created simulated fossil localities based on the geographic distribution of real North American mammal fossil localities from the late Cenozoic and introduce body- and geographic-range size bias as well as variations in sampling effort (0, 25, 50, and 75% species loss). I generated fossil localities iteratively and recalculated the slope of the LRG for each sampling effort and the magnitude of the latitudinal turnover gradient (LTG). It is, however, beyond the scope of this paper to address the causal mechanisms for LRGs.

Methods

I downloaded spatially referenced geographic-range data for modern North American mammals from NatureServe Canada (Patterson et al. 2007). The entire data set for the Western Hemisphere included 1300 species of non-volant Western Hemisphere mammals after the exclusion of a small number of unreadable or corrupted files. Limiting the study to the continental United States and southern Canada (30–50°N) reduced the data set to 370 species.

Measuring the Modern Latitudinal Diversity Gradient.—To quantify the slope of the modern North American mammal LRG prior to the creation of simulated fossil localities, I sampled the ranges of extant mammals using a 1° grid (100 × 100 km at the equator) under a cylindrical equal-area projection. I calculated total richness in each grid cell and regressed richness against latitude to estimate the slope of the modern mammal LRG in the continental United States and southern Canada (30–50°N). I have chosen this latitudinal range due to the high concentration of North American late Cenozoic mammal fossil localities between 30°N and 50°N. When estimating the slope of the LRG, I did not use a method such as generalized least squares regression, which corrects for spatial autocorrelation, because ordinary least squares is an unbiased estimator of regression coefficients (e.g., slope) even if there is a correlation between error terms such as would be introduced by spatial autocorrelation (Dormann et al. 2007). Furthermore, failing to control for spatial autocorrelation does not introduce systematic bias (Diniz-Filho et al. 2003).

As a measure of faunal turnover with latitude (herein termed the latitudinal turnover gradient or LTG) of modern North American mammals, I used detrended correspondence analysis (DCA) (Kent et al. 2011; Oksanen et al. 2012) and nonmetric multidimensional scaling (NMDS), which were applied to the grid cell by species-occurrence matrix.

DCA is a form of indirect gradient analysis that is often used in ecological studies to quantify the degree of community change along environmental gradients (Ejrnæs 2000) but has been infrequently applied to the fossil record (Fraser et al. 2014). DCA is an ordination method; each fossil site with its complement of species occupies a particular position along the first and second axes. Often, the position of each sampled site along the first DCA axis is regressed against the environmental or geographic variable of interest (in this case, latitude) (Bowman 1996). However, I have used the *envfit* function from the 'vegan' R package (Oksanen et al. 2012), which fits environmental vectors to the ordination, effectively testing for a linear

relationship between the position of each site in ordination space and the environmental or geographic variable. For the *envfit* method, the dependent variable is a matrix of ordination scores for sites and the independent variable is the environmental variable measured at each site (e.g., mean annual temperature, latitude, longitude). The *envfit* function then uses a permutation test to assess the significance of environmental variables. The result is a vector or series of vectors that have both direction (the gradient) and length (magnitude of the gradient) that can be plotted in ordination space (e.g., Fig. 1B). The function also calculates how much of the variation among sites is explained by the environmental variable (R^2 ; herein also referred to as the magnitude or strength of the LTG, which are both used as synonyms for effect size). High values of R^2 and long vectors indicate strong LTGs (Tuomisto and Ruokolainen 2006). In this context, R^2 values are precisely correlated with the vector lengths, which are scaled according to the correlation between the environmental vectors and the ordination points (Oksanen et al. 2012). Slopes are not associated with the fitted environmental vectors as they are with a standard linear regression, and so I do not interpret the slope of the LTG as I do with the LRG. I use the DCA approach as opposed to other methods of measuring community turnover (e.g., calculating faunal similarity or dissimilarity among grid cells or latitudinal bands, distance decay of similarity) (Soininen et al. 2007; Qian et al. 2009), because DCA can be applied to species-by-grid cell occurrence matrices (i.e., equally spaced, even coverage) of extant species and species-by-fossil locality occurrence matrices (i.e., unequally spaced, uneven coverage).

NMDS differs from DCA and other ordination methods, such as principle coordinates analysis, in that it uses the rank orders of distances among communities rather than the raw Euclidean distances (Hammer and Harper 2006). Unlike DCA, NMDS requires a matrix of dissimilarities among sites. Here, I use the Bray-Curtis dissimilarity index. NMDS first positions the dissimilar data according to Euclidean distances and transforms the distances into rank distances. NMDS then creates

a new ordination plot and attempts to place the data in a way that preserves the rank distances from the original plot, which is done iteratively. The configuration of the data on the new plot is compared with the original plot based on the rank order of the Euclidean distances in an attempt to reduce the disagreement between them (referred to as stress). As a result, NMDS is often more robust than approaches such as DCA, because it deals more effectively with missing dissimilarities and can accommodate any dissimilarity measure. As with DCA, I employed the *envfit* function to test for latitudinal turnover in the dissimilarity among sites. R^2 values are interpreted the same as above.

I then tested for the effects of typical fossil-record biases by developing a simulated fossilization resampling approach in R (R Development Core Team 2016) as described below.

Creating Simulated Fossil Localities.—To create “fossil localities” from the modern mammal record, I used an iterative, point-sampling approach (R code in Appendix A in the Supplementary Material). I used the latitude and longitude of late Miocene (~7 Ma; early late Hemphillian North American Land Mammal Age) fossil localities as a model. I downloaded the latitudes and longitudes of the 46 early late Hemphillian sites from the MioMAP database (Carrasco et al. 2005). My choice to use the late Miocene is derived from my interest in mammal community changes from the mid- and late Miocene of North America, but my simulated fossilization code allows for input of fossil locality data from any time period. Furthermore, late Miocene mammal fossil localities are fairly well distributed across the continental United States. Due to limits on computing time, it is beyond the scope of this paper to simulate site distributions from other Cenozoic epochs. My approach can be easily modified for any continent and any group for which sufficient extant distribution data exist.

To ensure that I generate “fossil localities” with comparable spatial distributions to the North American fossil record for mammals, I fit frequency distributions (normal, γ , or β) to the latitudes and longitudes of the real fossil localities. The best-fit distributions were

chosen using the Akaike information criterion. For the late Miocene, the best-fit distributions were β and normal for the latitudes and longitudes, respectively. I then generated random sites using the fitted probability density functions for both the latitude and longitude of the late Miocene sites. My approach of generating random sites has the benefit of allowing me to evaluate the effect of small changes in the position of simulated fossil localities and to capture different taxa across iterations (i.e., a species with small range may never show up in the simulated fossil record if a single set of sites is generated based on the exact location of the late Miocene sites as performed by Marcot et al. [2016]). I then created locality-by-species occurrence matrices using the *over* function in the 'sp' R package to return the species present at each "fossil locality." I repeated the procedure 10,000 times (see R code in Appendix A in the Supplementary Material).

Simulating Fossil-Record Bias.—The point-sampling approach I use herein is inherently biased against species with small geographic ranges (i.e., species with small ranges are less likely to overlap with the point sample or simulated fossil locality). Therefore, with the sampling method I employ here, no special correction is needed to ensure that species with small ranges are sampled less frequently than those with large ranges.

I weighted the probability of North American mammal species appearing in the simulated fossil record based on body size and trophic categories. I used body-mass categories rather than body-mass estimates because I did not want to make the assumption that preservation potential varies continuously with body mass. Populations from different trophic levels exist at different relative abundances (e.g., carnivores are typically less abundant than herbivores in terrestrial African ecosystems) and thus differ in their preservation potential (Peters 1983). Herbivores (plus omnivores) and carnivores larger than 15 kg were given a 95% chance of appearing in the "fossil record" (Behrensmeyer and Dechant Boaz 1980; Kidwell and Flessa 1996; Kidwell and Holland 2002). Small herbivores (<15 kg) were assigned a 60% chance of appearing in the fossil record, while small carnivores (<15 kg)

were assigned a 21% chance (Behrensmeyer and Dechant Boaz 1980; Kidwell and Flessa 1996; Kidwell and Holland 2002). Species were placed into body-mass categories based on their estimated species average body mass from PanTHERIA (Jones et al. 2009) and Elton Traits 1.0 (Wilman et al. 2014). The probabilities and body-size categories (Appendix B in the Supplementary Material) I have used here are based on field studies of live-dead assemblages in African savannas (Behrensmeyer and Dechant Boaz 1980).

I then sampled the extant-mammal simulated fossil record, assuming 100, 75, 50, and 25% rates of species preservation. Because the true sampling rate of the fossil record is unknowable, I use sampling rates that fall within the range of preservation rates suggested by Behrensmeyer and Dechant Boaz (1980), Kidwell and Flessa (1996), and Kidwell and Holland (2002). For these analyses, the probability of species being removed or "fossilized" was based on their body-size categories. If a species is not selected for "fossilization," it is removed from the analysis globally (removed from all sites at which it may have occurred). I repeated the procedure 10,000 times each for a total of 40,000 iterations (see R code in Appendix A in the Supplementary Material). Globally removing species from the analyses rather than removing species on a site-by-site basis has no effect on the outcome of the analyses described herein (40,000 iterations; Figs. S1, S2).

I calculated total richness at each simulated fossil locality both before and after application of nonparametric richness estimation, which was only applied when using a species sampling rate of less than 100%. The comparison of raw and estimated richness was made to determine whether the application of methods designed to estimate richness when sampling is incomplete can increase the accuracy with which the slope of the richness gradient is estimated. Due to computational load, I only applied first-order jackknife estimation from the 'fossil' R package (Vavrek 2012) and recalculated the LRG slope. I did not use shareholder quorum subsampling (Alroy 2010a,b), because quorums (combined relative abundances of sampled species) of well below 0.4

were required, which is not recommended for the SQS method (Alroy 2010a). Additionally, I used a latitudinal band method similar to Marcot et al. (2016), in which I divided North America into bands at 2° intervals, calculated richness within each band, both with and without first-order jackknife richness estimation, and calculated the slope of the LRG.

I also applied DCA to the fossil locality by species occurrence matrices to estimate the magnitude of the LTG both with and without simulated fossil-record bias. Rarefaction and richness estimation, which are methods developed to improve the comparability of richness estimates among sites, were not applied in this case, because DCA relies on taxonomic compositions rather than differences in richness. I did not use NMDS, because resulting stress levels were typically above 0.3, which means the ordination is a random representation of the data, thus indicating poor performance of the NMDS (Hammer and Harper 2006).

Because climate is thought to be one of the primary drivers of latitudinal diversity gradients, I also extracted mean annual temperature and mean annual precipitation data from Climate Wizard for the period of 1951–2006 (Mitchell et al. 2005; Girvetz et al. 2009). I calculated the slopes of latitudinal temperature and precipitation gradients (slope of the relationship between climate and richness estimated using ordinary least squares) and variance in faunal turnover explained by precipitation and temperature (R^2 values) for each iteration. That is, temperature and precipitation values were extracted at the latitudinal and longitudinal position of each new simulated fossil locality. The slope of the latitudinal temperature and precipitation richness gradients and the variance explained by these gradients (R^2 values) were then re-estimated for each iteration. As a result, there is variation in the estimated relationship between richness and taxonomic turnover with climate among iterations. The estimated slope and R^2 values were then included as independent variables in the statistical analyses described below. Including the slopes of the climate–richness and climate–turnover gradients allowed me to test whether apparent changes in these relationships explained

apparent changes in the LRG among iterations (i.e., do observed changes in the latitudinal–richness gradient relate to changes in the position of the fossil sites and resultant change in the estimated diversity–climate gradients?).

Statistical Analysis of Results.—I used an information theoretic approach (automated selection of the best-fit generalized linear regression model using *dredge* from the ‘MuMIn’ R package) (Bartoń 2013) to model which combination of factors accounts for changes in LRG slope and LTG magnitude among iterations under simulated fossil-record bias. I included the mean latitude and longitude of all simulated localities, slopes of the latitudinal temperature and precipitation gradients, slopes of the temperature and precipitation richness gradients (or magnitude of the temperature and precipitation turnover gradients), and preservation rate as independent variables in all of the full models. Best-fit linear models were selected using AICc. I also partitioned the explained variance using adjusted R^2 values (Oksanen et al. 2012), calculating model averaged regression coefficients as the average slope values across all candidate models with ΔAICc of less than 10 and variable importance for all model terms as the sum of Akaike weights over all the candidate models with ΔAICc of less than 10 (Burnham and Anderson 2002; Bartoń 2013). I only investigated main effects to reduce computation time.

Results

I estimated the slope of the modern North American mammal LRG to be -0.68 ± 0.10 (standard error) species per degree of latitude ($R^2=0.07$, $p<0.0001$; Fig. 1A) and the longitudinal richness gradient to be -0.96 ± 0.03 species per degree longitude ($R^2=0.54$, $p<0.0001$; Fig. 1B) between 30°N and 50°N. Using DCA, I estimated the magnitude of the LTG in the same region as 0.67 ($p<0.001$) and the longitudinal turnover gradient as 0.86 ($p=0.001$), indicating strong gradients in community change for modern mammals (Fig. 1C). Using NMDS, I estimated the magnitude of the LTG in the same region as 0.45 ($p<0.001$) and the longitudinal turnover gradient as 0.85 ($p<0.001$).

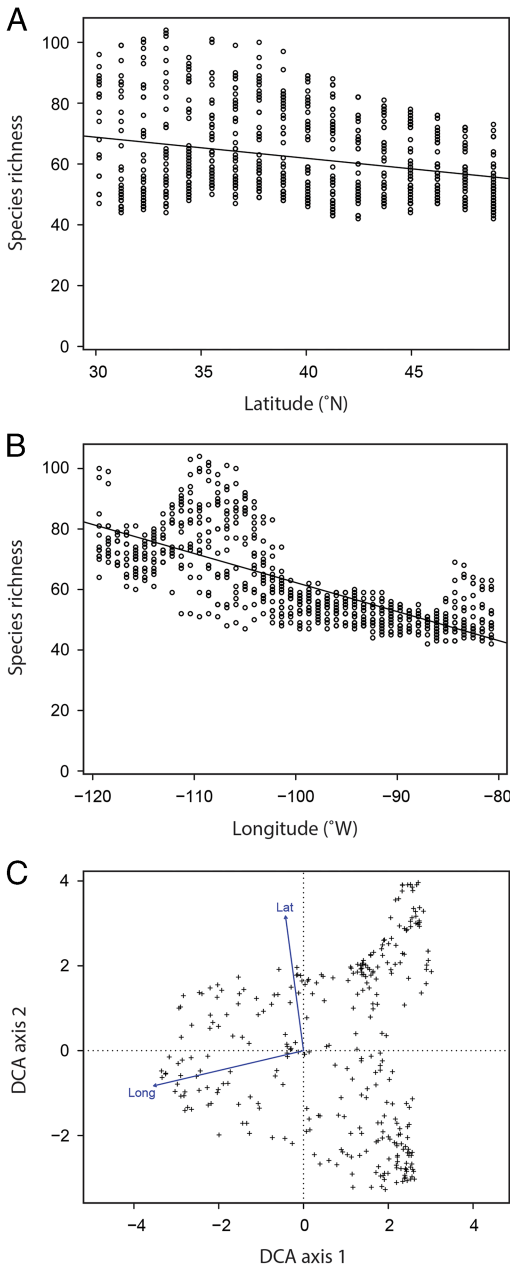


FIGURE 1. Modern North American mammal diversity gradients: A, latitudinal richness gradient; B, longitudinal richness gradient; and C, latitudinal and longitudinal gradients in community turnover.

Among iterations of simulated fossilization, there is considerable variation in estimates of LRG slope and LTG. I also found that the variance in LRG slope estimates decreases at low rates of species sampling, likely due to the loss of all or most of the small-bodied,

narrow-range species. Most of the variation in slope estimates among iterations is explained by change in the correlation between diversity and temperature (Table 1, Fig. 2A–D). In other words, iterations in which climate is strongly associated with richness and species turnover also show steep LDGs and vice versa. Only a small percentage of the variation in the LRG and LTG was explained by changes in the mean latitudes and longitudes of the simulated fossil localities, indicating that iteratively generating new simulated fossil localities did not impact the findings of this study (Table 1). Additional unexplained variation probably reflects both the fact that latitude is not a perfect surrogate for the climate gradient in North America and the fact that the steepness of climate gradients varies longitudinally in North America (i.e., chance variation related to minor changes in the placement of simulated fossil localities).

When applying a bias against species with small body size, reducing the species sampling rate of the simulated mammal fossil record from 100% to 25% increased the estimated slope of the LRG (Fig. 3A) and increased the proportion of positive slope estimates (i.e., richness increasing with latitude). Species sampling rate is therefore one of the top explanatory variables in the fitted models (Table 2A). However, the slopes of the climate–richness gradients remain the top explanatory variables (Table 2A).

Using the method of dividing simulated fossil localities among latitudinal bands produced a very high range of slope estimates for the North American mammal LRG. In fact, the majority of estimates fall on the positive size of a flat gradient (Fig. 3C,D). Application of first-order jackknife richness estimation reduced the explanatory power of species sampling rate (Fig. 2B,D, Table 2B), but not enough to ameliorate the apparent flattening of the LRG slope at the lowest rates of species sampling (Fig. 2B).

LTG estimates also appear weaker as species sampling rate is reduced (Fig. 4) but converge on the true value measured for extant mammals before the application of simulated fossilization. Species sampling rate explained a similar amount of model variance for LTGs as LRGs (Table 2A).

TABLE 1. Best-fit generalized linear models relating estimates of the slope of the latitudinal richness gradient (LRG) and magnitude of the latitudinal turnover gradient (LTG) to metrics for the geographic coverage of simulated fossil localities, the magnitude of climate–diversity gradients, and climate changes across the landscape. Note: The terms “temperature–richness gradient” and “precipitation–richness gradient” refer to the slope of the climate–richness relationship. The terms “temperature–turnover gradient” and “precipitation–turnover gradient” refer to the correlation between species turnover and climate.

Dependent variable	Independent variables of best-fit model	Variance explained (%)	Importance	Model averaged coefficients	<i>t</i> -value	<i>p</i> -value
LRG slope	Temperature–richness gradient	54.69	1.00	–0.881	–31.60	<0.0001
	Latitudinal temperature gradient	13.99	1.00	0.639	7.34	<0.0001
	Precipitation–richness gradient	3.15	0.99	0.000	3.61	<0.0001
	Mean sampled latitude	2.39	1.00	0.146	9.58	<0.0001
	Mean sampled longitude	0.71	0.70	0.014	2.15	0.032
LTG magnitude	Temperature–turnover gradient	42.38	1.00	0.509	22.27	<0.0001
	Precipitation–turnover gradient	14.43	1.00	–0.287	–8.43	<0.0001
	Latitudinal precipitation gradient	2.11	0.53	–0.001	1.67	0.091
	Mean sampled latitude	1.49	1.00	–0.032	–3.72	<0.0001
	Latitudinal temperature gradient	0.54	0.29	0.071	1.69	0.095

Discussion

Interest in the origins of macroecological phenomena such as LRGs in deep time is burgeoning (Mannion et al. 2014). However, the fossil record is characterized by considerable taxonomic, temporal, and spatial bias (Newell 1959; Raup 1972, 1976; Smith 2001; Crampton et al. 2003; Benton et al. 2011; Mannion et al. 2011). Herein, I used a simulated fossilization approach to test whether estimates of the LRG and LTG of modern North American mammals are robust to loss of small-bodied, small-range species. In general, I found that LRG estimates are highly impacted by loss of diversity during simulated fossilization, particularly at really low sampling rates. That is, the probability of calculating the true slope of the LRG declines with species sampling rate. In many cases, simulated fossil-record bias completely obliterated evidence of the negative LRG of modern North American mammals, a phenomenon that was not ameliorated by the application of nonparametric richness estimation. The LTG showed a similar loss of signal when species sampling rate fell. However, at medium (50%) to high (75%) rates of species sampling, the magnitude of the latitudinal diversity gradient can be reliably estimated. Furthermore, the relationship of richness and turnover with climate remained strong, even when the species sampling rate was low, suggesting that these relationships might be retained in a fossil

record that is biased against small-bodied and small-range species.

Modern North American mammals show a significant decline in richness between 30°N and 50°N (Fig. 1A). Peaks in mammalian diversity occur in the high-altitude regions of Arizona and New Mexico (~35°N, 110°W) and at the most southern parts of the Appalachian region (~32°N, 85°W; Georgia and Alabama) (Fig. 1B). Modern mammal richness gradients are also associated with significant latitudinal and longitudinal faunal turnover gradients (Fig. 1C). That is, there is considerable change in richness and community composition on both the south–north and west–east axes. The best-supported published models suggest that climate and productivity are the primary drivers of LRGs (Currie et al. 1999; Currie and Fritz 1993; Engle and Summers 1999; Condit et al. 2002; Hawkins et al. 2003; Qian et al. 2009; Baselga et al. 2012; Condamine et al. 2012). The longitudinal gradient in North America reflects the east–west elevation gradient and tendency for topographically complex regions to show steeper richness and β -diversity gradients (Badgley and Fox 2000; Badgley 2010).

On average, simulated fossilization with a species sampling rate of 100% yielded negative estimates of the LRG slope (Fig. 3A,B) and LTG magnitudes indicative of considerable species turnover (Figs. 4, 5). Only small amounts of variation were explained by changes in the mean latitude and longitude of the simulated fossil localities, suggesting that estimation of

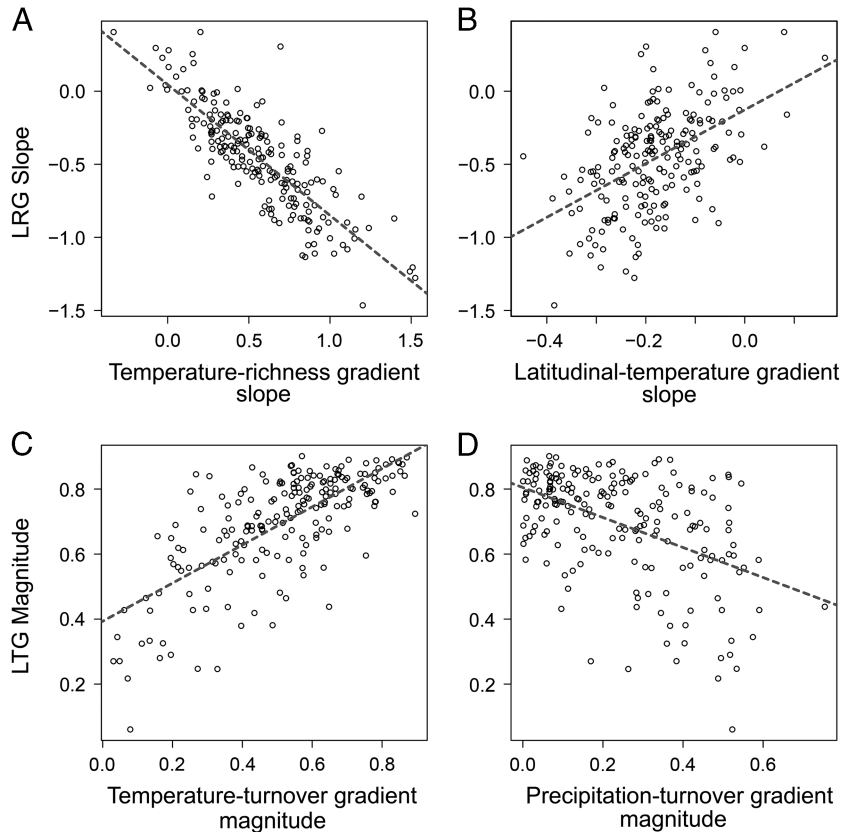


FIGURE 2. Estimated mammal LRG slopes against (A) slope of the temperature–richness gradient and (B) slope of the latitudinal temperature gradient. Correlation of estimated LTGs with estimates of the (C) temperature–turnover gradient and (D) precipitation–turnover gradient for modern North American mammals. A temperature or precipitation–turnover gradient refers to faunal turnover along a spatial gradient in temperature or precipitation, respectively. All estimates are derived from iterations of simulated fossilization with complete species sampling.

the LRG slope is not impacted by small changes in the location of fossil localities (Table 1). The majority of variation in estimated LRG slopes and LTG magnitudes was explained by change in the correlation between diversity and temperature across the landscape (Table 1); within iterations where the relationship between diversity and temperature was tightest, I found steeper LRGs and LTGs.

As I reduced the species sampling rate, I retrieved a higher proportion of positive estimates for the LRG slope (Fig. 3A,B). Positive LRG slopes are particularly interesting, because early Cenozoic North American mammals may have shown flat or positive LRG, which is consistent with contemporaneous climate reconstructions (Rose et al. 2011). Species sampling rate explained a relatively large proportion of the model

variance (Table 2A,B), suggesting that fossil-record bias could be one of the processes leading to apparently positive LRGs. However, the majority of model variance was still explained by the tightness of the relationship between richness and climate (Table 2A,B), also suggesting that the diversity–climate relationship is fairly robust to bias against species with small body and geographic-range sizes. Additionally, at medium (50%) to high (75%) rates of fossilization, the true LRG slope is found well within the upper and lower quartiles of the estimated LRG slopes among iterations (Fig. 3A,B). On average, the “latitudinal band” method produced a very high range of slope estimates for the North American mammal LRG, the majority of which were positive, but modeling results were qualitatively similar (Fig. 3C,D).

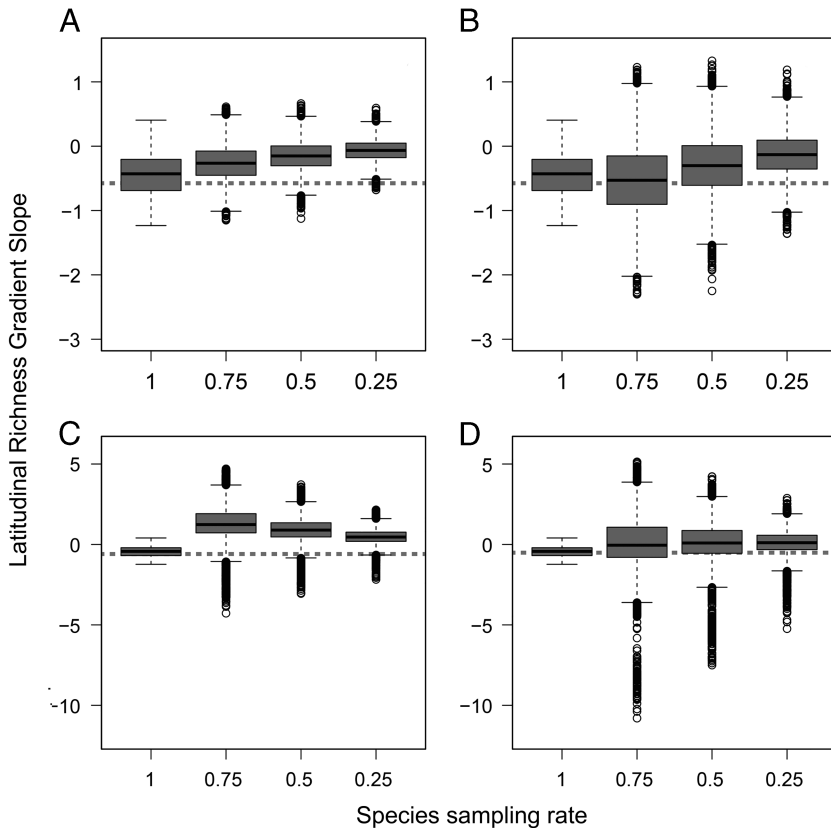


FIGURE 3. Box plots of estimated North American mammal LRG slope when species sampling is reduced from 100% to 25% with and without the application of first-order jackknife richness estimation. LRG slope estimates (A) without and (B) with first-order jackknife richness estimation. LRG slope estimates when richness is estimated within latitudinal bands (C) without and (D) with first-order jackknife richness estimation. The dashed line represents the true value of the modern North American mammal LRG between 30°N and 50°N.

Flattening of the LRG as species sampling rate falls is likely explained by both Bergmann's rule, that is, the increase in mean body size with latitude (McNab 1979; Blackburn et al. 1999; Freckleton et al. 2003), and Rapoport's rule, that is, the increase in mean geographic-range size with latitude (Stevens 1989; Kaufman 1995; Whittaker et al. 2001). Between 30°N and 50°N, there is an apparent increase in the mean and variation of mammal geographic-range sizes (measured here as species occupancy or the number of grid cells occupied by a species; Fig. 5), which is most often attributed to loss of productivity toward the poles (Blackburn et al. 1999; Stevens 1989). Selective removal of small-bodied, narrow-range species from the simulated fossil record therefore means disproportionate loss of low latitude species and a flattening of the estimated LRG slope.

To what extent might the loss of power to detect the true LRG slope of mammals at low rates of preservation be a product of modern mammal distributions? Modern and Quaternary mammal communities may show steeper gradients in body size (Carotenuto et al. 2015) and range size (Veter et al. 2013) than communities in the past; there were likely times in the past when gradients in body and range size were shallower, such as during the early and mid-Cenozoic (except perhaps when sampling is restricted to a particularly small region of North America, as during Paleocene and early Eocene). Thus, estimates of the richness and turnover gradients for terrestrial mammals may have been less biased. That is, if richness gradients were less correlated with body and range size, flattening of the richness and turnover gradients may not have occurred

TABLE 2. Best-fit generalized linear models relating estimates of the slope of the latitudinal richness gradient (LRG) and magnitude of the latitudinal turnover gradient (LTG) (A) without nonparametric richness estimation and (B) with nonparametric richness estimation to metrics for the species sampling rate of the simulated fossil record, geographic coverage of simulated fossil localities, the magnitude of climate–diversity gradients, and climate changes across the landscape. Note: The terms “temperature–richness gradient” and “precipitation–richness gradient” refer to the slope of the climate–richness relationship. The terms “temperature–turnover gradient” and “precipitation–turnover gradient” refer to the correlation between species turnover and climate.

Dependent variable	Independent variables of best fit model	Variance explained (%)	Importance	Model averaged coefficients	<i>t</i> -value	<i>p</i> -value	
A							
LRG slope	Temperature–richness gradient	56.01	1.00	–0.966	–222.18	<0.0001	
	Latitudinal temperature gradient	4.67	1.00	0.274	29.94	<0.0001	
	25% species loss	4.62	1.00	n/a	–6.50	<0.0001	
	50% species loss				–4.41	<0.0001	
	75% species loss				–2.43	0.025	
	Precipitation–richness gradient	2.95	1.00	3.820	17.27	<0.0001	
	Mean sampled latitude	1.41	1.00	0.080	54.55	<0.0001	
	Mean sampled longitude	0.60	0.98	0.003	3.27	0.001	
	Latitudinal precipitation gradient	0.45	1.00	0.003	15.01	<0.0001	
	LRG slope (bands)	Temperature–richness gradient	35.70	1.00	–0.402	–146.20	<0.0001
		25% species loss	12.05	1.00	n/a	10.45	<0.0001
		50% species loss				16.23	<0.0001
		75% species loss				21.50	<0.0001
		Mean sampled latitude	8.15	1.00	0.404	65.17	<0.0001
Latitudinal precipitation gradient		1.24	1.00	–0.009	–15.38	<0.0001	
Mean sampled longitude		0.36	1.00	0.013	3.62	<0.001	
Precipitation–richness gradient		0.19	1.00	–1.230	–14.67	<0.0001	
Latitudinal temperature gradient		0.16	0.97	0.114	2.99	0.003	
LTG magnitude		Temperature–turnover gradient	34.15	1.00	0.562	127.83	<0.0001
		25% species loss	9.79	1.00	n/a	–10.63	<0.0001
		50% species loss				–4.95	<0.0001
		75% species loss				–2.21	0.027
		Precipitation–turnover gradient	3.31	1.00	–0.09141	–17.84	<0.0001
	Latitudinal temperature gradient	0.70	1.00	0.189	18.76	<0.0001	
	Mean sampled latitude	0.62	1.00	–0.026	–16.73	<0.0001	
	Mean sampled longitude	0.40	1.00	–0.012	–12.66	<0.0001	
	Latitudinal precipitation gradient	0.17	1.00	–0.001	–6.07	<0.0001	
	B						
	LRG slope	Temperature–richness gradient	55.99	1.00	–0.966	–222.07	<0.0001
		Latitudinal temperature gradient	4.68	1.00	0.546	29.90	<0.0001
		25% species loss	4.54	1.00	n/a	–1.96	0.051
		50% species loss				0.22	0.829
75% species loss					2.42	0.015	
Precipitation–richness gradient		2.89	1.00	3.828	17.29	<0.0001	
Mean sampled latitude		1.41	1.00	0.160	54.47	<0.0001	
Mean sampled longitude		0.60	0.99	0.006	3.28	0.001	
Latitudinal precipitation gradient		0.45	1.00	3.828	15.02	<0.0001	
LRG slope (bands)		Precipitation–richness gradient	22.25	1.00	–0.257	–93.84	<0.0001
		Temperature–richness gradient	4.79	1.00	–0.141	–38.35	<0.0001
		Mean sampled latitude	1.45	1.00	0.348	29.23	<0.0001
		Latitudinal precipitation gradient	1.38	1.00	–0.016	–14.42	<0.0001
		Latitudinal temperature gradient	0.27	1.00	0.962	12.98	<0.0001
	25% species loss	0.10	1.00	n/a	4.46	<0.0001	
	50% species loss				4.85	<0.0001	
	75% species loss				4.92	<0.0001	

to the same degree as I record herein for modern mammals.

Mean estimates of the LTG magnitude also decrease as preservation rates decreases (Fig. 5A,B). For medium (50%) to high (75–100%) rates of fossilization the true LTG

magnitude is found well within the upper and lower quartiles of the estimated LTG magnitudes among iterations (Fig. 4). Some estimates of the LTG, excepting a fossilization rate of 25% of species, were slightly higher than estimated for modern mammals prior to the application

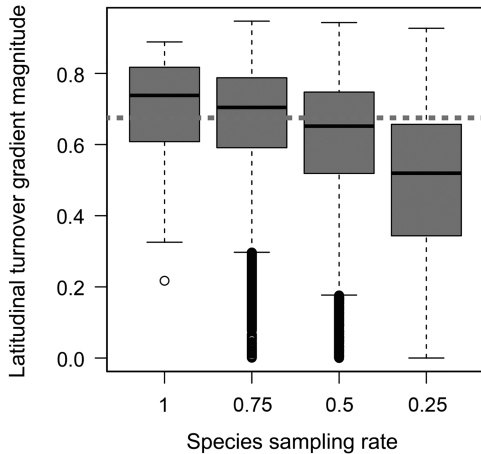


FIGURE 4. Box plots of estimated North American mammal LTG magnitude when species sampling is reduced from 100% to 25%. The dashed line represents the true magnitude of the modern North American mammal LTG between 30°N and 50°N.

of simulated fossilization. Slight overestimation of LTG magnitude results from the discontinuity introduced by the creation of simulated fossil localities. As with the LRG, only a small amount of variation in LTG estimates was explained by the mean latitude and longitude of the simulated fossil localities (Table 2A,B). As for the LRG, the majority of model variance was explained by the tightness of the relationship between species turnover and climate (Table 2A,B), suggesting that measuring the LTG in the fossil record might reflect the underlying diversity–climate relationship even when bias against small-bodied, small-range species is fairly high.

I restricted my study to the region of North America between 30°N and 50°N, as have studies of ancient latitudinal diversity gradients (e.g., Fraser et al. 2014; Marcot et al. 2016). I chose this latitudinal range because: (1) it is one of the best-sampled regions for Cenozoic fossil mammals, (2) very few mammal fossil localities occur above 50°N in North America due to Quaternary glaciation, and (3) far fewer well-sampled localities occur below 30°N due to differences in preservation potential among the tropical and temperate zones. Restricting my analysis of modern mammals to the same latitudinal range as the fossil record therefore increases the comparability of the modern and fossil richness gradients. It is likely that

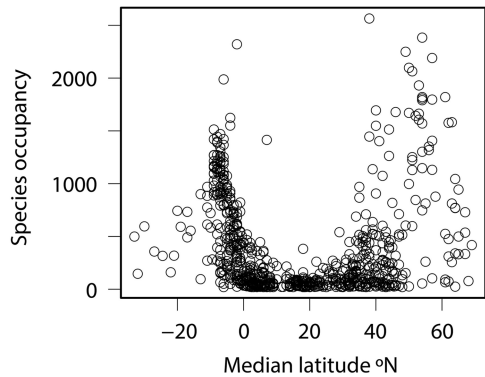


FIGURE 5. Relationship of species geographic-range size measured as species occupancy or the number of grid cells occupied with the median latitude of each species' geographic range.

sampling such a narrow range of latitudes, between which the mammalian LRG is comparatively shallow, has reduced the power to detect a negative LRG. However, I show that, regardless of restricting the latitudinal range of the study, on average, I am able to detect a negative LRG for terrestrial mammals, particularly if species sampling is somewhere between 50% and 100% (Fig. 3A,B). I predict, however, that performing the same analyses across a much wider range of latitudes (e.g., 0°N to 70°N) would increase the power to detect the true richness gradient of terrestrial mammals even at low rates of species preservation (e.g., 25%).

There have been several recent attempts to characterize the stability or change in latitudinal diversity gradients through time using the fossil record of Cenozoic North American mammals (e.g., Rose et al. 2011; Fraser et al. 2014; Marcot et al. 2016). Using different methods for characterizing the latitudinal diversity gradient of extinct Cenozoic mammals of North America, Fraser et al. (2014) and Marcot et al. (2016) both concluded that shallow and steep latitudinal diversity gradients characterize the early and late Cenozoic, respectively. Both also suggest that that global cooling and drying as well as increased polar glaciation are likely drivers of the observed changes in gradient steepness. Given my finding that the true latitudinal diversity gradient for modern North American mammals is detectable even when the preservation rate is fairly low (50% of the fauna), the

conclusions Fraser et al. (2014) and Marcot et al. (2016) are not in conflict with my current study. Furthermore, Marcot et al. (2016) replicate the findings of Fraser et al. (2014), thus suggesting that steep latitudinal diversity gradients are characteristic of late Cenozoic and modern mammalian assemblages and not their early Cenozoic counterparts.

Conclusions

Studying the deep-time origins of macroecological phenomena can help us understand their long-term climatic and macroevolutionary drivers. Given the considerable taxonomic and spatiotemporal bias of the fossil record, we must understand how the inference of macroecological patterns from the fossil record are impacted by typical biases. I used a simulated fossilization approach to show that estimates of the LRG slope and magnitude of the LTG of modern North American mammals are sensitive to the loss of small-bodied, narrow-range species from the fossil record. However, changes in the slope and magnitude estimates were largely explained by differences in the diversity–climate relationship among iterations, suggesting that these relationships may be measurable in the fossil record using the LRG and LTG as surrogates, with the caveat that at least some of the change among time periods might relate to changes in fossil-record quality. Although I have focused solely on North American mammals, I am confident that the effects reported herein are generalizable to other groups of terrestrial vertebrates that show a decline in richness from low latitudes to high as well as numerical abundance of small-bodied, narrow-range species at low latitudes.

The simulated fossilization approach presented herein allows for the direct comparison of modern diversity gradients with gradients measured in the past. My approach allows users to estimate the modern North American mammal diversity gradient using a similar distribution of localities to the fossil record, when removing different percentages of species in the community, and when adjusting the weighted probabilities of different species entering the simulated fossil record. My

approach therefore allows users to directly estimate whether a measured fossil diversity gradient might be reflective of biological reality versus fossil-record bias. Direct comparisons between modern and fossil mammal diversity gradients can be made by “fossilizing” modern mammals using the exact distribution of fossil localities or by fitting frequency distributions as done here and by Fraser et al. (2014) from each time period of interest (removing varying percentages of species from the simulated fossil record) and comparing the simulation results to the estimated fossil gradient using methods such as the single sample *t*-test. Although the simulated fossil approach presented herein does not account for all possible sources of bias in the fossil record, it is a significant step toward increasing the rigor with which diversity of fossil taxa is being studied.

Acknowledgments

I thank David Polly, John Alroy, Catherine Badgley, and an anonymous reviewer for insightful review of this article. I also thank Christopher Hassall for considerable help with R coding for this project. I thank S. Kathleen Lyons and the Evolution of Terrestrial Ecosystems working group at the Smithsonian National Museum of Natural History for suggestions that led to the improvement of this paper. I would also like to thank Natalia Rybczynski and Root Gorelick for reading and copyediting earlier iterations of this paper. I thank David Currie and Lenore Fahrig for feedback related to this project and for reading an earlier version of this paper. The work was supported by a Natural Science and Engineering Research Council of Canada (NSERC) postgraduate fellowship, an Ontario Graduate Scholarship, and Sir James Lougheed Award of Distinction from the Government of Alberta.

Literature Cited

- Alroy, J. 1996. Constant extinction, constrained diversification, and uncoordinated stasis in North American mammals. *Palaeogeography, Palaeoclimatology, Palaeoecology* 127:285–311.
- . 2010a. Fair sampling of taxonomic richness and unbiased estimation of origination and extinction rates. *In* J. Alroy and G. Hunt, eds. *Quantitative methods in paleobiology*. *Paleontological Society Papers* 16:55–80.

- . 2010b. The shifting balance of diversity among major marine animal groups. *Science* 329:1191–1194.
- Alroy, J., P. L. Koch, and J. C. Zachos. 2000. Global climate change and North American mammalian evolution. *Paleobiology* 26:259–288.
- Alroy, J., C. R. Marshall, R. K. Bambach, K. Bezusko, M. Foote, F. T. Fürsich, T. A. Hansen, S. M. Holland, L. C. Ivany, D. Jablonski, D. K. Jacobs, D. C. Jones, M. A. Kosnik, S. Lidgard, S. Low, A. I. Miller, P. M. Novack-Gottshall, T. D. Olszewski, M. E. Patzkowsky, D. M. Raup, K. Roy, J. J. Sepkoski, M. G. Sommers, P. J. Wagner, and A. Webber. 2001. Effects of sampling standardization on estimates of Phanerozoic marine diversification. *Proceedings of the National Academy of Sciences USA* 98:6261–6266.
- Badgley, C. 2010. Tectonics, topography, and mammalian diversity. *Ecography* 33:220–231.
- Badgley, C., and D. L. Fox. 2000. Ecological biogeography of North American mammals: species density and ecological structure in relation to environmental gradients. *Journal of Biogeography* 27:1437–1467.
- Barnosky, A. D., M. A. Carrasco, and E. B. Davis. 2005. The impact of the species–area relationship on estimates of paleodiversity. *PLoS Biol* 3:1356–1361.
- Bartolo, K. 2013. Model selection and model averaging based on information criteria (AICc and alike). <http://cran.r-project.org/web/packages/MuMIn/index.html>.
- Baselga, A., J. M. Lobo, J.-C. Svenning, P. Aragón, and M. B. Araújo. 2012. Dispersal ability modulates the strength of the latitudinal richness gradient in European beetles. *Global Ecology and Biogeography* 21:1106–1113.
- Behrensmeyer, A. K., and D. E. Dechant Boaz. 1980. The Recent bones of Amboseli Park, Kenya, in relation to East African paleoecology. Pp. 72–92. *in* A. K. Behrensmeyer, ed. *Fossils in the making*. University of Chicago Press, Chicago.
- Behrensmeyer, A. K., S. M. Kidwell, and R. A. Gastaldo. 2000. Taphonomy and paleobiology. *Paleobiology* 26:103–147.
- Behrensmeyer, A. K., D. Western, and D. E. D. Boaz. 1979. New perspectives in vertebrate paleoecology from a recent bone assemblage. *Paleobiology* 5:12–21.
- Benson, R. B. J., and P. D. Mannion. 2012. Multi-variate models are essential for understanding vertebrate diversification in deep time. *Biology Letters* 8:127–130.
- Benton, M. J., A. M. Dunhill, G. T. Lloyd, and F. G. Marx. 2011. Assessing the quality of the fossil record: insights from vertebrates. Pp. 63–94. *in* A. J. McGowan, and A. B. Smith, eds. *Comparing the geological and fossil records: implications for biodiversity studies*. Geological Society of London, London.
- Blackburn, T. M., K. J. Gaston, and N. Loder. 1999. Geographic gradients in body size: a clarification of Bergmann's rule. *Diversity and Distributions* 5:165–174.
- Bowman, D. M. J. S. 1996. Diversity patterns of woody species on a latitudinal transect from the monsoon tropics to desert in the Northern Territory, Australia. *Australian Journal of Botany* 44:571–580.
- Brown, J. H. 1995. *Macroecology*. University of Chicago Press, Chicago.
- Burnham, K. P., and D. R. Anderson. 2002. *Model selection and multimodel inference: a practical information-theoretic approach*, 2nd ed. Springer, New York, New York.
- Carotenuto, F., J. A. F. Diniz-Filho, and P. Raia. 2015. Space and time: the two dimensions of Artiodactyla body mass evolution. *Palaeogeography, Palaeoclimatology, Palaeoecology* 437: 18–25.
- Carrasco, M. A., B. P. Kraatz, E. B. Davis, and A. D. Barnosky. 2005. Miocene mammal mapping project (MIOMAP). University of California Museum of Paleontology, Berkeley. <http://www.ucmp.berkeley.edu/miomap>.
- Colwell, R. K., and J. A. Coddington. 1994. Estimating terrestrial biodiversity through extrapolation. *Philosophical Transactions of the Royal Society of London B* 345:101–118.
- Condamine, F. L., F. A. H. Sperling, N. Wahlberg, J.-Y. Rasplus, and G. J. Kergoat. 2012. What causes latitudinal gradients in species diversity? Evolutionary processes and ecological constraints on swallowtail biodiversity. *Ecology Letters* 15:267–277.
- Condit, R., N. Pitman, E. G. L., Jr., J. Chave, J. Terborgh, R. B. Foster, P. N. V., S. Aguilar, R. Valencia, G. Villa, H. C. Muller-Landau, E. Losos, and S. P. Hubbell. 2002. Beta-diversity in tropical forest trees. *Science* 295:666–669.
- Cooper, R. A., P. A. Maxwell, J. S. Crampton, A. G. Beu, C. M. Jones, and B. A. Marshall. 2006. Completeness of the fossil record: estimating losses due to small body size. *Geology* 34:241–244.
- Crampton, J. S., A. G. Beu, R. A. Cooper, C. M. Jones, B. Marshall, and P. A. Maxwell. 2003. Estimating the Rock Volume Bias in Paleobiodiversity Studies. *Science* 301:358–360.
- Currie, D. J. 1991. Energy and large-scale patterns of animal- and plant-species richness. *American Naturalist* 137:27–49.
- Currie, D. J., and J. T. Fritz. 1993. Global patterns of animal abundance and species energy use. *Oikos* 67:56–68.
- Currie, D. J., A. P. Francis, and J. T. Kerr. 1999. Some general propositions about the study of spatial patterns of species richness. *Ecoscience* 6:392–399.
- Davis, E. B. 2005. Mammalian beta diversity in the Great Basin, western USA: palaeontological data suggest deep origin of modern macroecological structure. *Global Ecology and Biogeography* 14:479–490.
- Diniz-Filho, J. A. F., L. M. Bini, and B. A. Hawkins. 2003. Spatial autocorrelation and red herrings in geographical ecology. *Global Ecology and Biogeography* 12:53–64.
- Donovan, S. K., and C. R. C. Paul. 1998. *The adequacy of the fossil record*. Wiley, New York.
- Dormann, C. F., J. M. McPherson, M. B. Araújo, R. Bivand, J. Bolliger, G. Carl, R. G. Davies, A. Hinz, W. Jetz, W. Daniel Kissling, I. Kühn, R. Ohlemüller, P. R. Peres-Neto, B. Reineking, B. Schröder, F. M. Schurr, and R. Wilson. 2007. Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. *Ecography* 30:609–628.
- Dornelas, M., N. J. Gotelli, B. McGill, H. Shimadzu, F. Moyes, C. Sievers, and A. E. Magurran. 2014. Assemblage time series reveal biodiversity change but not systematic loss. *Science* 344:296–299.
- Ejrnæs, R. 2000. Can we trust gradients extracted by detrended correspondence analysis? *Journal of Vegetation Science* 11: 565–572.
- Engle, V. D., and J. K. Summers. 1999. Latitudinal gradients in benthic community composition in Western Atlantic estuaries. *Journal of Biogeography* 26:1007–1023.
- Figueirido, B., C. M. Janis, J. A. Pérez-Claros, M. D. Renzi, and P. Palmqvist. 2012. Cenozoic climate change influences mammalian evolutionary dynamics. *Proceedings of the National Academy of Sciences USA* 109: 722–727.
- Fraser, D., R. Gorelick, and N. Rybczynski. 2015. Macroevolution and climate change influence phylogenetic community assembly of North American hoofed mammals. *Biological Journal of the Linnean Society* 114:485–494.
- Fraser, D., C. Hassall, R. Gorelick, and N. Rybczynski. 2014. Mean annual precipitation explains spatiotemporal patterns of Cenozoic mammal beta diversity and latitudinal diversity gradients in North America. *PLoS ONE* 9:e106499.
- Freckleton, R. P., P. H. Harvey, and M. Pagel. 2003. Bergmann's rule and body size in mammals. *American Naturalist* 161: 821–825.
- Girvetz, E. H., C. Zganjar, G. T. Raber, E. P. Maurer, P. Kareiva, and J. J. Lawler. 2009. Applied climate-change analysis: the climate wizard tool. *PLoS ONE* 4:e8320.

- Hammer, Ø., and D. A. T. Harper. 2006. Paleontological data analysis. Blackwell, Malden, Mass.
- Hawkins, B. A., R. Field, H. V. Cornell, D. J. Currie, J.-F. Guegan, D. M. Kaufman, J. T. Kerr, G. G. Mittelbach, T. Oberdorff, E. M. O'Brien, E. E. Porter, and J. R. G. Turner. 2003. Energy, water, and broad-scale geographic patterns of species richness. *Ecology* 84:3105–3117.
- Jablonski, D., C. L. Belanger, S. K. Berke, S. Huang, A. Z. Krug, K. Roy, A. Tomašových, and J. W. Valentine. 2013. Out of the tropics, but how? Fossils, bridge species, and thermal ranges in the dynamics of the marine latitudinal diversity gradient. *Proceedings of the National Academy of Sciences USA* 110:10487–10494.
- Jablonski, D., K. Roy, and J. W. Valentine. 2006. Out of the tropics: evolutionary dynamics of the latitudinal diversity gradient. *Science* 314:102–106.
- Jones, K. E., J. Bielby, M. Cardillo, S. A. Fritz, J. O'Dell, C. D. L. Orme, K. Safi, W. Sechrest, E. H. Boakes, C. Carbone, C. Connolly, M. J. Cutts, J. K. Foster, R. Grenyer, M. Habib, C. A. Plaster, S. A. Price, E. A. Rigby, J. Rist, A. Teacher, O. R. P. Bininda-Emonds, J. L. Gittleman, G. M. Mace, and A. Purvis. 2009. PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals. *Ecology* 90:2648.
- Kaufman, D. M. 1995. Diversity of New World mammals: universality of the latitudinal gradients of species and bauplans. *Journal of Mammalogy* 76:322–334.
- Kent, R., A. Bar-Massada, and Y. Carmel. 2011. Multiscale analyses of mammal species composition-environment relationship in the contiguous USA. *PLoS ONE* 6:e25440.
- Kidwell, S. M., and K. W. Flessa. 1996. The quality of the fossil record: populations, species, and communities. *Annual Review in Earth and Planetary Science* 24:433–464.
- Kidwell, S. M., and S. M. Holland. 2002. The quality of the fossil record: implications for evolutionary analyses. *Annual Review of Ecology and Systematics* 33:561–588.
- Koleff, P., J. J. Lennon, and K. J. Gaston. 2003. Are there latitudinal gradients in species turnover? *Global Ecology and Biogeography* 12:483–498.
- Kraft, N. J. B., W. K. Cornwell, C. O. Webb, and D. D. Ackerly. 2007. Trait evolution, community assembly, and phylogenetic structure of ecological communities. *American Naturalist* 170: 271–283.
- Mannion, P. D., P. Upchurch, R. B. J. Benson, and A. Goswami. 2014. The latitudinal biodiversity gradient through deep time. *Trends in Ecology and Evolution* 29:42–50.
- Mannion, P. D., P. Upchurch, M. T. Carrano, and P. M. Barrett. 2011. Testing the effect of the rock record on diversity: a multi-disciplinary approach to elucidating the generic richness of sauropodomorph dinosaurs through time. *Biological Reviews* 86:157–181.
- Marcot, J. D., D. L. Fox, and S. R. Niebuhr. 2016. Late Cenozoic onset of the latitudinal diversity gradient of North American mammals. *Proceedings of the National Academy of Sciences USA* 113:7189–7194.
- McCoy, E. D., and E. F. Connor. 1980. Latitudinal gradients in the species diversity of North American mammals. *Evolution* 34:193–203.
- McNab, B. K. 1979. The influence of body size on the energetics and distribution of fossorial and burrowing mammals. *Ecology* 60:1010–1021.
- Miller, A. I., and M. Foote. 1996. Calibrating the Ordovician radiation of marine life: implications for Phanerozoic diversity trends. *Paleobiology* 22:304–309.
- Miller, J. H., A. K. Behrensmeyer, A. Du, S. K. Lyons, D. Patterson, A. Tóth, A. Villaseñor, E. Kanga, and D. Reed. 2014. Ecological fidelity of functional traits based on species presence-absence in a modern mammalian bone assemblage (Amboseli, Kenya). *Paleobiology* 40:560–583.
- Mitchell, T. D., and P. D. Jones. 2005. An improved method of constructing a database of monthly climate observations and associated high-resolution grids. *International Journal of Climatology* 25:693–712.
- Newell, N. D. 1959. Adequacy of the fossil record. *Journal of Paleontology* 33:488–499.
- Oksanen, J., F. G. Blanchet, P. L. Roeland Kindt, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, and H. Wagner. 2012. Vegan package, Version 2.0-7. <https://cran.r-project.org/web/packages/vegan/index.html>.
- Patterson, B. D., G. Ceballos, W. Sechrest, M. F. Tognelli, T. Brooks, L. Luna, P. Ortega, I. Salazar, and B. E. Young. 2007. Digital distribution maps of the mammals of the Western Hemisphere, version 3.0. NatureServe, Arlington, VA.
- Peres-Neto, P. R., M. A. Leibold, and S. Dray. 2012. Assessing the effects of spatial contingency and environmental filtering on metacommunity phylogenetics. *Ecology* 93:S14–S30.
- Peters, R. H. 1983. The ecological implications of body size. Cambridge University Press, New York.
- Qian, H., and R. E. Ricklefs. 2007. A latitudinal gradient in large-scale beta diversity for vascular plants in North America. *Ecology Letters* 10:737–744.
- Qian, H. 2012. Disentangling the effects of geographic distance and environmental dissimilarity on global patterns of species turnover. *Global Ecology and Biogeography* 21:341–351.
- Qian, H., C. Badgley, and D. L. Fox. 2009. The latitudinal gradient of beta diversity in relation to climate and topography for mammals in North America. *Global Ecology and Biogeography* 18:111–122. Raup, D. M. 1972. Taxonomic diversity across the Phanerozoic. *Science* 177:1065–1071.
- Raia, P., F. Carotenuto, F. Passaro, P. Piras, D. Fulgione, L. Werdelin, J. Saarinen, and M. Fortelius. 2012a). Rapid action in the Palaeogene, the relationship between phenotypic and taxonomic diversification in Cenozoic mammals. *Proceedings of the Royal Society, Series B* 280: 20122244.
- Raia, P., F. Passaro, D. Fulgione, and F. Carotenuto. 2012b. Habitat tracking, stasis and survival in Neogene large mammals. *Biology Letters* 8:64–66.
- R Development Core Team 2016. R: A language and environment for statistical computing. Vienna, Austria: Foundation for Statistical Computing.
- Raup, D. M. 1975. Diversity estimation using rarefaction. *Paleobiology* 4:333–342.
- . 1976. Species diversity in the Phanerozoic: an interpretation. *Paleobiology* 2:289–297.
- . 1979. Biases in the fossil record of species and genera. *Bulletin of the Carnegie Museum of Natural History* 13: 85–91.
- Rose, P. J., D. L. Fox, J. Marcot, and C. Badgley. 2011. Flat latitudinal gradient in Paleocene mammal richness suggests decoupling of climate and biodiversity. *Geology* 39:163–166.
- Rosenzweig, M. L. 1995. Species diversity in space and time. Cambridge University Press, Cambridge.
- Roy, K., D. Jablonski, J. W. Valentine, and G. Rosenberg. 1998. Marine latitudinal diversity gradients: tests of causal hypotheses. *Proceedings of the National Academy of Sciences USA* 95: 3699–3702.
- Smith, A. B. 2001. Large-scale heterogeneity of the fossil record: implications for Phanerozoic biodiversity studies. *Philosophical Transactions of the Royal Society of London B* 356:351–367.
- Soininen, J. 2010. Species turnover along abiotic and biotic gradients: patterns in space equal patterns in time? *BioScience* 60:433–439.
- Soininen, J., R. McDonald, and H. Hillebrand. 2007. The distance decay of similarity in ecological communities. *Ecography* 30:3–12.

- Stevens, G. C. 1989. The latitudinal gradient in geographical range: how so many species coexist in the tropics. *American Naturalist* 133:240–256.
- Tomašových, A., and S. M. Kidwell. 2009. Preservation of spatial and environmental gradients by death assemblages. *Paleobiology* 35:119–145.
- . 2010. Predicting the effects of increasing temporal scale on species composition, diversity, and rank-abundance distributions. *Paleobiology* 36:672–695.
- Tuomisto, H., and K. Ruokolainen. 2006. Analyzing and explaining beta diversity: understanding the targets of different methods of analysis. *Ecology* 87:2697–2708.
- Valentine, J. W., D. Jablonski, A. Z. Krug, and S. K. Berke. 2013. The sampling and estimation of marine paleodiversity patterns: implications of a Pliocene model. *Paleobiology* 39:1–20.
- Vavrek, M. J. 2012. Fossil: palaeoecological and palaeogeographical analysis tools. <https://cran.rstudio.com/web/packages/fossil/index.html>.
- Veter, N. M., L. R. G. DeSantis, L. T. Yann, S. L. Donohue, R. J. Haupt, S. E. Corapi, S. L. Fathel, E. K. Gootee, L. F. Loffredo, J. L. Romer, and S. M. Velkovsky. 2013. Is Rapoport's rule a recent phenomenon? A deep time perspective on potential causal mechanisms. *Biology Letters* 9:20130398.
- Whittaker, R. J., K. J. Willis, and R. Field. 2001. Scale and species richness: towards a general, hierarchical theory of species diversity. *Journal of Biogeography* 28:453–470.
- Wilman, H., J. Belmaker, J. Simpson, C. de la Rosa, M. M. Rivadeneira, and W. Jetz. 2014. EltonTraits 1.0: Species-level foraging attributes of the world's birds and mammals. *Ecology* 95:2027.