

# Do Turtles Follow the Rules? Latitudinal Gradients in Species Richness, Body Size, and Geographic Range Area of the World's Turtles



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## ABSTRACT

Understanding how and why biodiversity is structured across the globe has been central to ecology, evolution, and biogeography even before those disciplines took their modern forms. Three global-scale patterns in particular have been the focus of research and debate for decades: latitudinal gradients in species richness (richness decreases with increasing latitude), body size (body size increases with increasing latitude in endotherms; Bergmann's rule), and geographic range size (range size increases with increasing latitude; Rapoport's rule). Despite decades of study, the generality and robustness of these trends have been debated, as have their underlying causes. Here we investigate latitudinal gradients in species richness, body size, and range size in the world's turtles (Testudines), and add more evidence that these rules do not seem to apply across all taxa. We show that turtle diversity actually peaks at 25° north, a highly unusual global pattern. Turtles also fail to follow Bergmann's Rule, and may show the converse (larger at lower latitudes), though trends are weak. Turtles also show a complex relationship between latitude and range size that does not directly follow Rapoport's rule. Body size and geographic range size are significantly correlated, and multiple abiotic and biotic variables help explain the relationships between latitude and species diversity, body size, and range size. Although we show that turtles do not strictly follow some classic biogeographical rules, we also call for further in-depth research to investigate potential causal mechanisms for these atypical patterns. *J. Exp. Zool. (Mol. Dev. Evol.)* 324B:270–294, 2015. © 2015 Wiley Periodicals, Inc.

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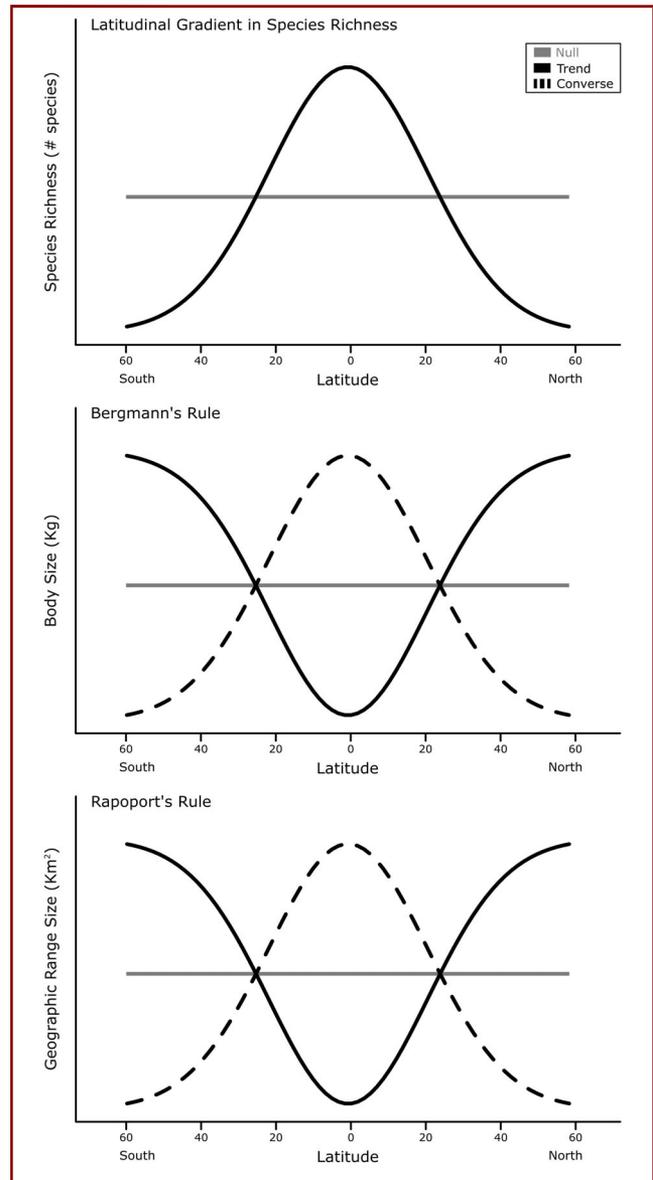
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## INTRODUCTION

A central goal of biogeography, and even much of ecology and evolutionary biology, is to document and understand spatial patterns of biodiversity—how and why does biodiversity vary across the Earth (Gaston, 2000; Gaston and Blackburn, 2008; Lomolino et al., 2010)? Such seemingly simple questions are difficult to answer because life is so diverse, the globe so heterogeneous, and the histories of both complex and often intertwined (Gaston and Blackburn, 2008; Lomolino et al., 2010). Nevertheless, the last two decades have seen a resurgence of macro-scale analyses, as biology has become increasingly integrative, and more powerful computational tools and analyses have become available (Gaston, 2000; Chown et al., 2004; Gaston and Blackburn, 2008; Gaston et al., 2008; Lomolino et al., 2010). At the same time, society has become increasingly concerned over the fate of global biodiversity, creating a heightened sense of urgency to better understand spatial patterns of diversity (Gaston, 2000; Buhlmann et al., 2009).

Three macro-scale patterns that have played a central role in discussions of global patterns of biodiversity are latitudinal gradients in species diversity, body size, and geographic range size (Gaston and Blackburn, 2008; Gaston et al., 2008; Lomolino et al., 2010). The first of these, the latitudinal gradient in species diversity, is one of the most well known global patterns (Forster, 1778; Chown and Gaston, 2000; Gaston, 2000; Hillebrand, 2004); there are more species in the tropics than at temperate regions or the poles, such that species diversity declines away from the equator (Fig. 1). However, the strength and slope of this trend varies across clades, functional groups, and regions, with some taxa actually demonstrating a reverse trend (e.g., Janzen, '81; Hillebrand, 2004; Pyron and Burbrink, 2009; Rivadeneira et al., 2011). Not surprisingly then, the underlying cause (or causes) of the latitudinal gradient in species diversity remains one of the most elusive goals in all of ecology, with more than thirty proposed mechanisms (Chown and Gaston, 2000; Gaston, 2000; Hillebrand, 2004; Jablonski et al., 2006; 2013; Qian and Ricklefs, 2008), ranging from neutral models of packing species into available space (Colwell and Hurtt, '94), to notions of greater productivity, or antiquity, or stability of the tropics (e.g., Hutchison, '59; Fischer, '60; Pianka, '66), to hypotheses of greater species interactions in the tropics (e.g., Pianka, '66; Janzen, '70; Rohde, '99).

The second macro-scale pattern, the latitudinal gradient in body size, was articulated over 160 years ago (Bergmann, 1847) to describe the tendency of endothermic vertebrates to increase in body size with increasing latitude or elevation (Fig. 1) (Mayr, '56; James, '70; Ashton et al., 2000; Ashton, 2002a; Meiri and Dayan 2003; Olson et al., 2009). "Bergmann's rule" has since been examined in ectotherms, which show an array of responses, ranging from robust Bergmann's clines, to the converse, to no



**FIGURE 1.** Predicted responses of turtles to latitudinal gradients under null and alternative hypotheses. (A) Latitudinal gradient in species richness: turtles are expected to show the classic peak in species numbers at the tropics, and richness should decline moving into higher latitudes (black); under the null, numbers of turtle species are not expected to show any relationship with latitude (grey). (B) Bergmann's rule: turtle body sizes are expected to either increase (black) or decrease (dashed) moving into higher latitudes; under the null, turtle body sizes are not expected to show any relationship with latitude (grey). (C) Rapoport's rule: the geographic range sizes of turtles are expected to either increase (black) or decrease (dashed) moving into higher latitudes; under the null, the geographic range sizes of turtles are not expected to show any relationship with latitude (grey).

trend all (e.g., Mousseau, '97; Ashton, 2002b; Ashton and Feldman, 2003; Blanckenhorn and Demont, 2004; Olalla-Tárraga and Rodríguez, 2007; Shelomi, 2012). The diversity of responses in ectotherms has led to substantial debate over the generality of Bergmann's rule, and whether its underlying cause may differ across clades and functional groups (Blackburn et al., '99; Ashton and Feldman, 2003; Watt et al., 2010; Meiri, 2011; Shelomi, 2012).

The third eco-geographic pattern, the latitudinal gradient in range size, or "Rapoport's rule", describes the tendency for the geographic ranges of species to increase in size with increasing latitude (Fig. 1) (Rapoport, '82; Stevens, '89, '92). Although Rapoport's rule seems to hold for a number of taxa, spanning mammals and amphibians to arthropods and even trees (Stevens, '89, '92; Brown et al., '96; Gaston et al., '98; Gaston, 2003), it seems to fail equally often, or hold only in the northern hemisphere (Gaston et al., '98; Gaston, 2003; Ruggiero and Werenkraut, 2007; Whitton et al., 2012), leading to doubts over its validity and questions over its fundamental causes (Gaston et al., '98; Gaston and Chown, '99; Gaston, 2003).

Understanding the generality (and even legitimacy) of these global-scale patterns remains a central goal of biogeography (Gaston et al., 2008; Lomolino et al., 2010), and empirical data from a wide range of systems are needed to fully explore the nature of latitudinal gradients and determine their underlying causes. Here, we examine latitudinal gradients in species diversity, body size, and geographic range size in turtles. Turtles are an ideal group to address global-scale patterns of diversity because they are cosmopolitan (absent only from Antarctica), range tremendously in body size (from <100 g to >900 kg), occupy a wide variety of ecosystems (from pelagic marine forms that traverse ocean basins, to species in some of the world's driest deserts), and display diverse feeding ecologies (from grazers to strict piscivores) (Ernst and Barbour, '89). Turtles also are a "manageable" group with just over 330 species (van Dijk et al., 2012), so there exists literature for almost every taxon related to body size, geographic range, and phylogeny that can be utilized to undertake a fairly complete analysis of global trends. Our goals are to establish whether or not turtles follow the classical latitudinal gradient in species diversity, Bergmann's rule, and Rapoport's rule (Fig. 1). Additionally, we seek to determine whether any of these patterns might covary, as suggested by more synthetic analyses in other lineages (e.g., Stevens, '89; Diniz-Filho et al., 2005; Murray and Hose, 2005; Olson et al., 2009).

It is our hope that by describing global patterns in turtles, we might contribute to broader discussions and analyses of the generality, direction, and robustness of latitudinal patterns, and what their underlying mechanisms might tell us about how biodiversity is structured across the globe. This work might also provide a clearer understanding of the factors that affect modern turtle ranges, and pertain to efforts that model past turtle

distributions (Rödger et al., 2013) or attempt to forecast future distributional shifts in a changing globe (Ilhow et al., 2012).

## METHODS

### Data Collection

We collected several types of data to address our three primary questions: Do turtles follow the latitudinal gradient in species diversity, Bergmann's rule, and Rapoport's rule? To collect data on the distribution and range size of turtles we used the EMYSysWorld Turtle Database (<http://emys.geo.orst.edu/>; downloaded and compiled Jan-Mar. 2013) (Kiestler and Brock, 2007). This global turtle database contains point localities from museum vouchers, and we used these known locality records to estimate the latitudinal ranges for each species using the single most extreme north and south latitudinal records. To avoid potential errors that might result in extraordinarily large ranges due to human introduction, we checked the records for specimens that appeared to be potential outliers from the previously reported ranges of species (e.g., Ernst and Barbour, '89). To combat potential misidentification of species, we checked the cited literature for a random selection of the species records used to build our dataset. No errors were found for the species that were checked, leading to high confidence in taxonomic assignments within EMYSysWorld.

We obtained data on the size of each species' geographic range from Buhlmann et al. (2009). These authors used a similar approach as above, but included all museum records, and used watersheds to delineate ranges (rather than strict polygons around points). This provided a geographic range estimate (in km<sup>2</sup>) for each species based on the sum hydrologic unit compartments (HUCs) each taxon occupied (for further details see Buhlmann et al., 2009).

We compiled data on body size from the literature. For turtles, the most commonly used metric of body size is the straight-line carapace length (straight distance across the top shell). For each species we obtained the maximum carapace length (CL) from standard references (e.g., Ernst and Barbour, '89; Bonin et al., 2006; Ernst and Lovich, 2009), but other literature sources were consulted when data were not available for particular species in these references (see Supplementary Material). In cases where species display marked sexual size dimorphism, we used the maximum recorded size for the larger sex.

Because of differences in the data available for each species, our final dataset includes different numbers of species for each kind of data. We have body size (carapace length) data for 336 species, latitudinal ranges for 245 species, and geographic range size for 294 species. Beyond collecting the basic information on the latitudes each species occupies, its range size, and body size, we sought additional abiotic and biotic data for each species with the goal of determining what other ecological or environmental variables might correlate with latitudinal trends.

First, species richness and/or geographic range size might simply reflect the total (or proportional) amount of space available (Connor and McCoy, '79; Rapoport, '82). Thus, we calculated the amount of land available in each continent and across latitudinal bins. Once the geographic range size data were in hand, and we had an estimate of the total latitudinal range spanned by all turtles, we subdivided this range into twenty 5° latitudinal bins. We mapped these bins in ArcGIS v10.2 (ESRI 2013) across an equal area continental projection (Equal Area Sphere). To calculate terrestrial landmass within a continental bin, we made polygons for continental and ocean area for each latitudinal bin, and then calculated the total area under the bin (ArcToolBox; Area Estimation), subtracting ocean area from the estimate. We also estimated areas for individual continents in each bin by subdividing the polygons for each latitudinal bin by continent, and then summing the areas of the individual polygons for a given continent in a given latitudinal bin.

We obtained additional abiotic data for the range of each species using the WorldClim v1.4.3 database in ArcGIS (Hijmans et al., 2005). For each turtle, we generated two point feature shape files containing the northern and southern points respectively, and then joined those two shape files into a single shape file (ArcToolbox; Spatial Join) by computing an average point for latitude and longitude. The subsequent dataset produced midpoints for the ranges of each species. We then used the museum portal HerpNet2 (<http://www.herpnet2.org/>) to locate 10–20 specimens from unique localities nearest the midpoint for each species. Due to biases in collecting for some taxa, less than ten specimen records with locality data may exist. In those cases all specimens with unique locality data were used. In cases where using the nearest ten specimens did not result in 10 unique collection localities, we used the nearest 20 specimens in an attempt to get to 10 unique collection localities. In the few cases this still did not result in ten collection localities, and we used the number of localities available for the 20 specimens. This provided a sample of specimens with known localities for each species that we then plotted back in ArcGIS, and we extracted the 19 bioclimatic variables from WorldClim for each specimen (ArcToolbox; Extract Multi Values to Points). For each species, we used mean values of the bioclimatic variables to represent the abiotic conditions of that taxon. If no vouchers occurred within 100 km of the midpoint, and in cases where specimens with locality data were unavailable, we simply used the midpoint location to extract the 19 bioclimatic variables for that taxon.

We obtained coarse-scale ecological information for each turtle with the World Wildlife Fund's Global 200 database (Olson et al., 2001; Olson and Dinerstein, 2002) in ArcGIS. As above, for each species, we plotted the specimens nearest its midpoint range, and then assigned specimens to their respective biomes and ecoregions with the Global 200 database. We then calculated the modal biome and ecoregion as for each species. As above, if no vouchers occurred within 100 km of the midpoint, we simply used

the midpoint location to extract the biome and ecoregion for that taxon. Note that because biomes are the coarsest groupings of habitat types (14 across the globe), many turtle species occupied the same biome. However, ecoregions are much finer divisions of ecological communities, and in our case most species fell into unique ecoregions. We therefore substituted ecoregion identity for numbers of species occupying that ecoregion, providing an estimate of community diversity for each turtle. We also determined the number of turtles in the same midpoint latitudinal bin for each continent as a measure of turtle richness. Our methods are not ideal because, as above, they compress ranges into a single location (midpoint) even though species often occupy many ecoregions and climates. Nevertheless, the strategy provides an objective measure of ecological communities occupied by turtles and the diversity of those communities. Abiotic and ecological data are presented in the Supplementary Material.

Finally, we scored each species as coarsely occupying one of four functional groups following Jaffe et al. (2011) to explore potential relationships between functional ecology and latitudinal gradients. These groups are: terrestrial species on continents; freshwater; marine; "island" (terrestrial species on oceanic islands). For consistency, we used the same codings as Jaffe et al. (2011) and for species not included in their study, we used occurrence data, reports in the literature of habitat preference and ecology, and anatomical features such as the presence of webbed feet to assign functional groups (Ernst and Barbour, '89; Bonin et al., 2006; Ernst and Lovich, 2009).

To assist with visualizations of the data and to explore any potential regional or clade-specific trends, we also grouped turtles according to their continent occurrences (North America, South America, Asia, Africa, Australia/Oceania, Europe, and marine; turtles whose ranges span multiple continents were included in all applicable bins) and by family (Carettochelyidae, Chelidae, Chelydridae, Cheloniidae, Dermatemydidae, Dermochelyidae, Emydidae, Geoemydidae, Kinosternidae, Pelomedusidae, Platysternidae, Podocnemidae, Testudinidae, Trionychidae). All 336 species have continent, family, and habitat assignments. Note however, that we excluded marine turtles and island tortoises (i.e., Galapagos and Aldabran tortoises) from almost all analyses because the former represent a functionally and phylogenetically distinct group of seven "giant" species that range across ocean basins, and the latter also represent radical evolutionary novelties confined to tiny islands, thus biasing geographic analyses (i.e., both groups represent clear outliers).

#### Phylogenetic Framework

Among the statistical analyses we performed on the data (see below) were phylogenetic comparative methods that require a phylogenetic tree for the included species. However, no single phylogenetic dataset includes all 336 turtle species for which we collected data. Therefore, we used two phylogenetic trees to

provide a framework for the phylogenetic comparative methods. The first tree is a composite phylogeny (Supplemental Fig. 1) we assembled from the literature that includes 240 of the 245 species for which we have latitudinal ranges (Dutton et al., '96; Georges et al., '99; Austin and Arnold, 2001; Caccone et al., 2002; Engstrom et al., 2004; Feldman and Parham, 2004; Spinks et al., 2004; Krenz et al., 2005; Le et al., 2006; Parham et al., 2006a,b; Prashag et al., 2007; Fritz et al., 2008; Naro-Maciel et al., 2008; Spinks et al., 2009; Thomson and Georges, 2009; Barley et al., 2010; Thomson and Shaffer, 2010; Jaffe et al., 2011; Reid et al., 2011; Guillon et al., 2012; Vargas-Ramírez et al., 2012; Angielczyk and Feldman, 2013; Joyce et al., 2013; Spinks et al., 2014a). We did not arbitrarily resolve relationships among taxa for which no phylogenetic hypothesis has been proposed (i.e., polytomies), but we did resolve conflicting relationships reported between works by choosing the arrangement provided by the study (or studies) with the greater amount of data and/or more thorough analyses. Because our composite tree did not include branch lengths, we used four common branch length transformations in our comparative methods: equal branch lengths (all branch lengths = 1); Grafen's (1989) transformation (branch lengths set equal to the number of descendant tips minus 1); Pagel's (1992) transformation (branch lengths set so that a node's depth is equal to the maximum number of bifurcations of the left descendant branch and the right descendant branch plus one); and "Nee's method" (Purvis, '95) (distance between the tips and a given node is equal to  $\log_{10}$  of the number of that node's descendant tips).

The second phylogenetic tree comes from Jaffe et al. (2011) and is based on their analysis of the entire cytochrome *b* mtDNA locus (1140 bp) for 233 extant species and 14 fossil calibration points. This tree has the advantage of including empirical branch lengths, but their list of OTUs includes a number of species that we consider synonyms or that are likely hybrids. After pruning these OTUs, along with marine turtles and island tortoises, the final tree that we used in our analyses included 184 OTUs. The tree was not fully resolved, so we replaced polytomies with zero length branches in our comparative methods analyses.

#### Body Size Distribution

Jaffe et al. (2011) recently examined the body size distribution of 226 turtle species using maximum straight-line CL, and found that there appear to be different optimal body sizes for freshwater turtles, mainland terrestrial turtles, island terrestrial turtles, and marine turtles. Although completely replicating Jaffe et al.'s (2011) results is not the goal of our study, we were interested in whether our larger CL dataset (336 species vs. 226) showed similar general patterns. We generated a histogram for  $\log_{10}$  CL for our 336 species, and kernel density functions for the entire dataset as well as for bins subdivided by habitat preference. We considered *Geoemyda japonica* to be an island species for this analysis, following Jaffe et al. (2011). However, we included it among

mainland terrestrial turtles in subsequent analyses because its size and ecology closely resemble those of mainland terrestrial species and clearly differ from those of the giant island tortoises found in the Galapagos and Seychelles. Both the body size histogram of Jaffe et al. (2011) and our kernel density function for the whole dataset superficially resemble a log-normal distribution, so we tested whether our dataset was log-normally distributed using a Shapiro–Wilk test.

#### Latitudinal Gradient in Species Richness

Our first goal is to determine if there is a latitudinal gradient in global turtle diversity. If turtles follow this classic biogeographic trend, then we expect turtle species richness to be highest near the equator, and to decline in a predictable manner with increasing latitude (Fig. 1). To visually assess this trend, we first assigned each of the 245 species for which we have latitudinal range data to the latitudinal bin or bins in which they occur and then we plotted the resulting totals for each bin versus the latitude of each bin. To test whether the apparent trends differed significantly from our null expectation of a random ordering of increases and decreases in richness (Fig. 1), we used the runs up and down test (e.g., Sokal and Rohlf, '95). In general, the test focuses on two classes of values,  $x \leq 0$  and  $x > 0$ , and compares the number of groups of consecutive values of the same class (runs) to a theoretical value based on the overall size of the dataset. In the case of the runs up and down test, the classes of values are differences between each pair of sequential values (e.g., number of species in one latitudinal bin is lower than in the preceding bin, and so on). Although the runs up and down test can provide insight into whether a sequence of values is randomly ordered, a non-random ordering can result from several potential causes (e.g., trends, autocorrelation), and the test does not provide information to differentiate these causes. We also tested whether species richness was correlated with the absolute value of latitude (using the midpoint of each bin as the values for latitude) with Pearson product-moment correlation test. To fully explore the dataset, we constructed plots and ran the correlation tests for the complete set of 245 species, as well as for subsets of the data based on habitat preference, continent, and family membership. We conducted the statistical tests in PAST 2.17c (Hammer et al., 2001).

#### Bergmann's Rule

Our next goal was to determine if turtles follow Bergmann's rule. If turtles display Bergmann's clines, then we expect the largest turtles to occur near the poles, and the body sizes of various species to decline along with latitude, such that the smallest turtles occur in the tropics (Fig. 1). However, some reptiles, amphibians, and other ectotherms display the reverse trend, or "converse to Bergmann's rule" (Fig. 1) (Mousseau, '97; Ashton, 2002b; Ashton and Feldman, 2003; Blanckenhorn and Demont, 2004; Shelomi, 2012). Our procedure for testing Bergmann's rule

was similar to that used for examining the relationship between species richness and latitude. We assigned each of the 245 species for which we have latitudinal ranges to the bin or bins in which they are found. We then calculated the median  $\log_{10}$  CL for each bin and plotted these values versus the latitude of the bins. We again tested whether the resulting pattern differed significantly from our null expectation of a random ordering of increases and decreases in body size (Fig. 1), with the runs up and down test. We further investigated whether the observed median CL values for each latitudinal bin differed significantly from the expected median CL value for a random draw of the same number of species from the underlying pool of 245 species for which we had latitudinal data. To do this, we generated 5000 replicate assemblages with the same number of species for each bin via bootstrapping in R, and determined whether the observed median value fell outside the 95% confidence interval of the resampled datasets. Finally, we calculated the Pearson product-moment correlation between median  $\log_{10}$  CL and latitudinal midpoint for each bin. As with species richness, we constructed plots and ran the runs and correlation tests (in PAST) for the complete set of 245 species, as well as for subsets of the data based on habitat preference, continent, and family membership. Note that our method examines interspecific variation in body size along latitudes, not intraspecific variation in body size. There has been some debate over whether Bergmann ('47) was discussing interspecific or intraspecific patterns (Mayr, '56; James, '70; Ashton, 2001; Clauss et al., 2013), but a number of authors, including us, consider both approaches useful in understanding clinal variation in morphology and its causes (Ashton, 2001; Olalla-Tárraga, 2011; Shelomi, 2012).

Because body size is a character that can reasonably be hypothesized to display a phylogenetic signal, we conducted two sets of tests to determine the strength of that signal and its potential effects on apparent latitudinal patterns. First, we computed two common metrics that estimate phylogenetic signal in a dataset, Pagel's  $\lambda$  (Pagel, '99) and Blomberg's K (Blomberg et al., 2003) using the various versions of our composite phylogeny and the pruned phylogeny of Jaffe et al. (2011). However, these methods have been shown to provide misleading information about the necessity of phylogenetic comparative methods in some situations (Revell, 2010). Therefore, we also conducted a series of phylogenetic generalized least squares regressions (PGLS; e.g., Grafen, '89; Martins and Hansen, '97; Garland and Ives, 2000; Rohlf, 2001; Martins et al., 2002) using our composite phylogenies and the pruned phylogeny of Jaffe et al. (2011). Following Revell's (2010) recommendation, we estimated both the regression model and phylogenetic signal in the data (in the form of Pagel's  $\lambda$ ) simultaneously, and used the estimated value of  $\lambda$  as a guide for whether to prefer a non-phylogenetic regression or PGLS results. We also compared the PGLS results to a traditional linear regression using the taxon sample included in the literature trees to determine whether the

inclusion of phylogeny in the analysis greatly increased the amount of variance explained by the regression. Unlike the previous analyses, we did not use latitudinal bins for regressions. Instead, we used the absolute value of the maximum latitudes attained by species and the latitudinal ranges displayed by the species as independent variables in the regressions. We carried out the regressions in R (R Core Team, 2013), and used the packages *caper* (Orme et al., 2013) and *phytools* (Revell, 2013) for the PGLS regressions and tests of phylogenetic signal.

#### Rapoport's Rule

Our final goal was to determine if turtles follow Rapoport's rule. If turtles display patterns consistent with Rapoport's rule, then we expect that turtles with the largest geographic ranges will occur near the poles, and that ranges will decrease in size along with latitude, such that the smallest geographic ranges will occur in the tropics (Fig. 1). However, Hecnar ('99) reported that turtles show the opposite pattern, with larger ranges in the tropics. To test Rapoport's rule, we again assigned each of the 245 species for which we have latitudinal ranges to the bin or bins in which they are found. Then we calculated the  $\log_{10}$  median range area for each bin and plotted these values versus the latitude of the bins. We again tested whether the resulting pattern differed significantly from the null hypothesis of a random ordering of increases and decreases in richness (Fig. 1) with the runs up and down test. As with Bergmann's rule, we also determined whether the observed median range area values for each latitudinal bin differed significantly from the expected median area value for a random draw of the same number of species from underlying pool of species. We generated 5000 replicate assemblages with the same number of species for each bin via bootstrapping in R, and checked if the observed median value fell outside of the 95% CIs for the medians of the resampled sets. Finally, we calculated the Pearson product-moment correlation between  $\log_{10}$  median range and latitudinal midpoint for each bin. As with the previous two cases, we constructed plots and ran the runs and correlation tests (in PAST) for the complete set of 245 species, as well as for subsets of the data based on habitat preference, continent, and family membership.

To test the effects of phylogenetic signal in our geographic range size data, we used the same combination of Pagel's  $\lambda$ , Blomberg's K, PGLS and traditional regressions as we did in our examination of Bergmann's rule. As with those analyses, we used the absolute value of the maximum latitudes attained by species and the latitudinal ranges displayed by the species as independent variables in the regressions and we did not place the species in latitudinal bins. We used the various versions of our composite phylogeny and the pruned phylogeny of Jaffe et al. (2011) as the phylogenetic framework for these tests.

#### Relationships with Available Land Area

As mentioned above, there may be a link between available space and species richness, geographic range size, or both (e.g., Connor

and McCoy, '79; Rapoport, '82), and indeed, the available land area in each of our 20 latitudinal bins is not equal. Therefore, we tested whether  $\log_{10}$  maximum CL, geographic range area, and species richness were correlated with  $\log_{10}$  available land area with the 245 species for which we had latitudinal range data. We also repeated these tests with the species subdivided by the continent(s) on which they occur and using the land area for each continent in the various latitudinal bins. As above, we conducted correlation tests in PAST.

### Relationships Between Latitudinal Gradients

Biogeographers and ecologists have frequently sought common mechanisms to explain the complex and seemingly distinct latitudinal gradients considered here. For example, Stevens ('89) originally proposed Rapoport's rule as a possible explanation for the latitudinal gradient in species richness. The tropics may simply hold more species because the ranges of tropical taxa are smaller, allowing more species with similar resource requirements to pack into a given space, whereas species in higher latitudes possess larger ranges, potentially prohibiting large numbers of species from coexisting in the same space. We might further expect relationships between body size and geographic range size, given that larger species require greater resources, and might move or disperse more easily (Brown, '95; Brown et al., '96).

We explored the potential links between latitudinal gradients (or interactions; Gaston et al., 2008) in two ways. First, we calculated the Pearson product-moment correlation between  $\log_{10}$  maximum carapace length and  $\log_{10}$  geographic range area for our full data set, as well as with the data subdivided by functional group, continent, and family. Second, we conducted a PGLS regression of  $\log_{10}$  range area versus  $\log_{10}$  carapace length using the various versions of our composite phylogeny and the pruned phylogeny of Jaffe et al. (2011). As in our previous analyses we estimated both the regression model and the phylogenetic signal in the data simultaneously.

Because the results of the PGLS regression, and our analyses for Bregmann's rule and Rapoport's rule suggested little to no phylogenetic signal in our data (see below), we further explored the relationships between turtle body size and range size without phylogenetic corrections. Specifically, we used multiple linear regression in R to uncover any relationship between species diversity (response variable) and body size and geographic range size in turtles.

### Relationships Between Abiotic and Biotic Variables and Latitudinal Gradients

Finally, we explored potential correlations between abiotic (available land, continent, latitudinal range, northern and southernmost points, midpoint, 19 bioclimatic variables) and biotic (functional group, family, biome, ecoregion richness) variables with our latitudinal gradients in species richness (here,

number of turtle species occupying the same latitudinal bin as the midpoint bin of a turtle in the same continent), body size, and range size. To identify the most appropriate model for each multiple linear regression and avoid over-parameterization, we performed a model fitting procedure in R using the *glmulti* package v0.6–3 (Calcagno and de Mazancourt, 2010). The method exhaustively tests every combination of explanatory variables in contributing to the response variable under a general linear model, ranking models via AICc. We used this multiple regression approach to examine all three latitudinal gradients, and included each latitudinal gradient in the model fitting exercise because some gradients appear correlated (see below). Note however, that we excluded the latitudinal spread of species when considering variables that contribute to geographic range size because this measure seemed to represent redundant information. We also did not take phylogeny explicitly into account because our previous analyses suggested little, if any, phylogenetic signal.

## RESULTS

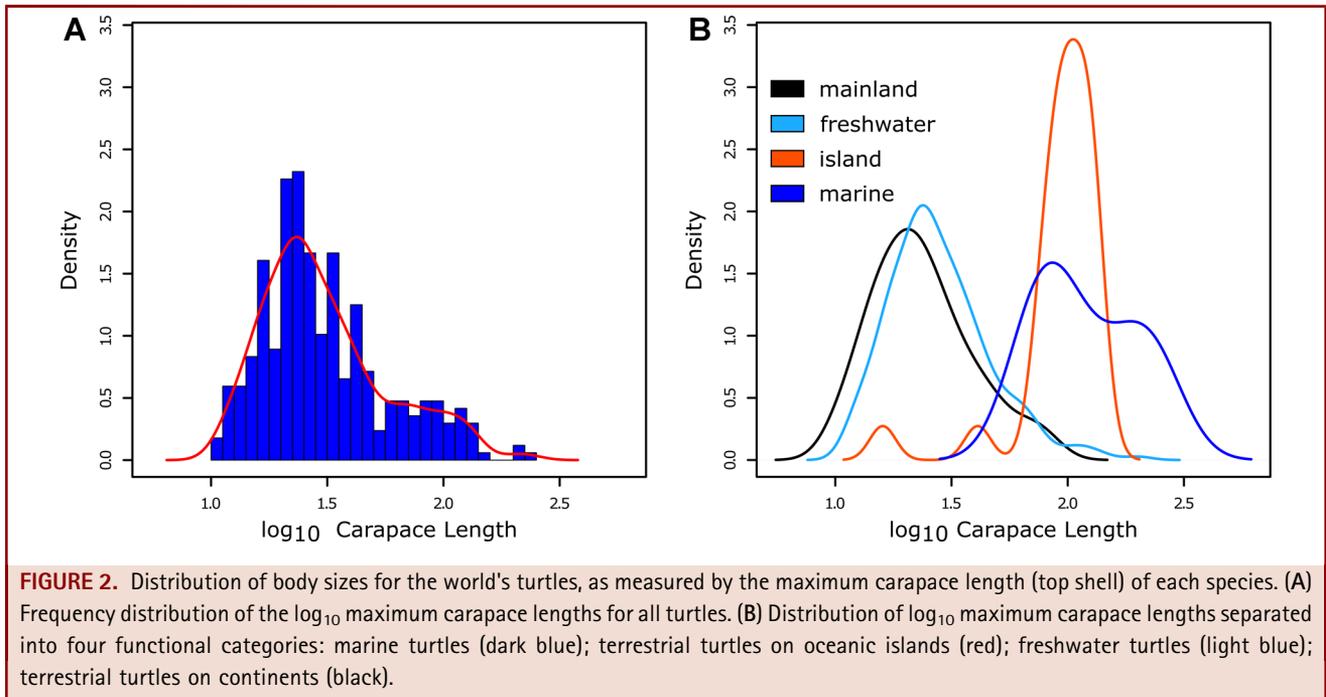
### Body Size Distribution

A histogram and kernel density function showing the distribution of  $\log_{10}$  maximum CL in the 336 turtles species and for those species partitioned into their functional groups is shown in Figure 2. Although the overall distribution superficially resembles a log-normal distribution, the Shapiro-Wilk test demonstrated that the data are not log-normally distributed ( $w=0.9412$ ,  $P \ll 0.001$ ). The distribution shows a close resemblance to that of Jaffe et al. (2011); indicating that their smaller dataset was not unduly affected by sampling artifacts. The size data also appear to be consistent with their modeling results, with each functional group showing a characteristic distribution of body sizes, and island and marine species possessing notably larger average body sizes than mainland terrestrial and freshwater species.

### Latitudinal Gradients in Species Richness

Plots showing overall patterns of species richness versus latitude, as well as data that have been subdivided by habitat preference, continent, and family are shown in Figure 3.

In general, turtle diversity is higher at low latitudes (i.e., within  $10^\circ$  of the equator) than at the extreme northern and southern ends of the latitudinal range. However, the peak of turtle diversity is at about  $25^\circ$  north. Subdividing the data by functional groups shows that the latitudinal pattern is almost entirely driven by aquatic taxa; terrestrial turtle diversity is much more even across the latitudinal bins. When the data are partitioned by continent an interesting pattern is apparent; Asia and North America drive the northern hemisphere pattern, as expected given their large land masses, but their latitudinal gradients in species richness also are quite similar. In the southern hemisphere, South America, Africa and Oceania likewise show bimodal latitudinal patterns of



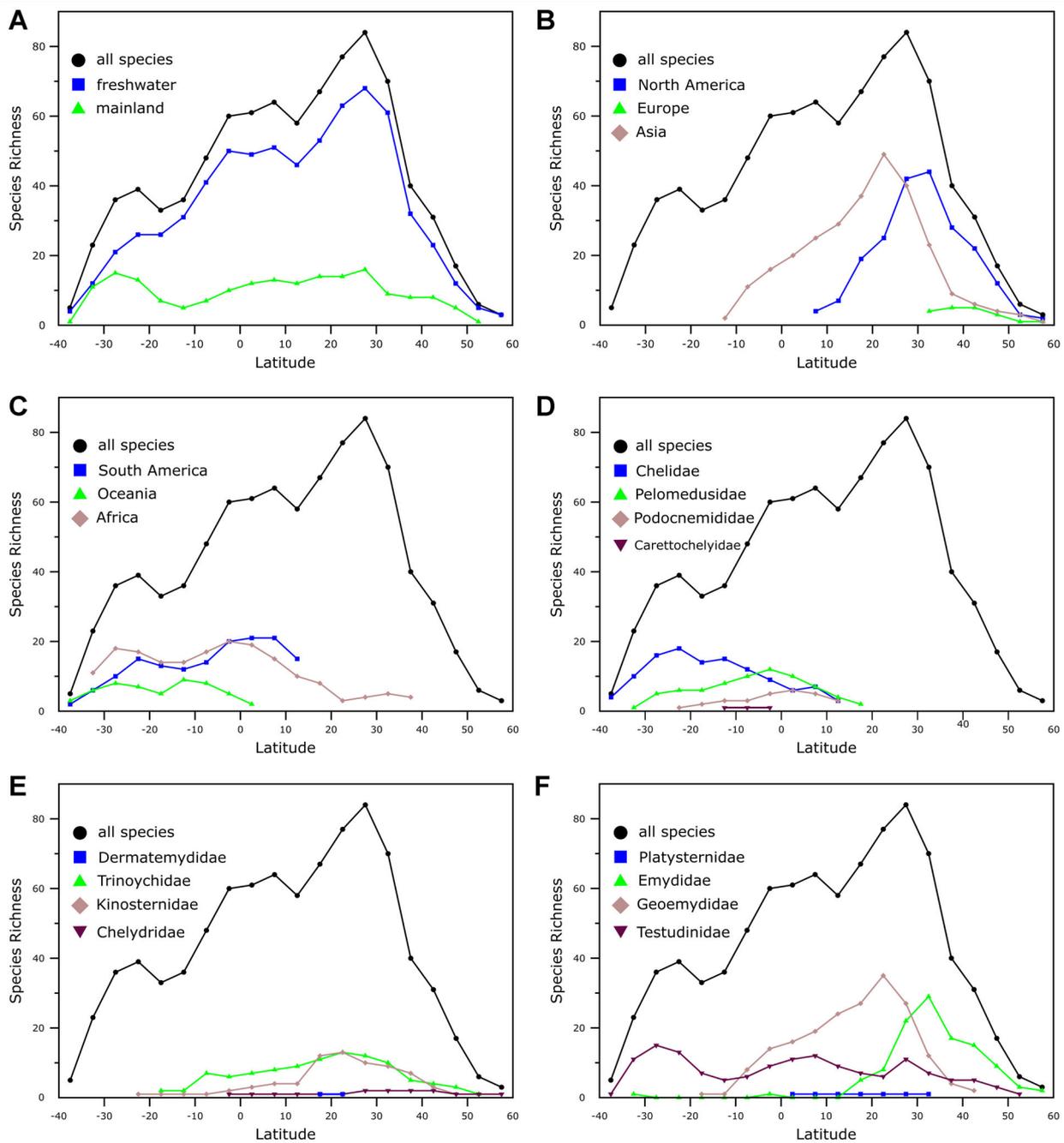
richness that closely approximate each other. When examined by family, Geoemydidae and Emydidae clearly are responsible for the mid-latitude peak in richness in the northern hemisphere. The mid-latitude peak in the southern hemisphere is driven by Chelidae and Testudinidae. The tropical plateau in richness appears to stem from many turtle clades coexisting in this region at moderate levels of richness. Results from the runs up and down test and the correlation tests are shown in Tables 1 and 2. When the entire dataset is considered, the runs up and down test shows that the richness data depart significantly from the null expectation of a random sequence of increases and decreases. The correlation tests show that species richness is negatively correlated with latitude (i.e., richness is higher at low latitudes), and this pattern is consistent if only the northern or southern hemisphere is considered. However, correlations are more variable when the data are subdivided. Only aquatic turtles, South America, Africa, Europe, Pelomedusidae, Podocnemidae, and Testudinidae show significant correlations (all negative) between richness and latitude.

#### Bergmann's Rule

Plots showing overall patterns of body size ( $\log_{10}$  maximum CL) versus latitude, as well as data that have been subdivided by habitat preference, continent, and family are shown in Figure 4.

When the entire dataset is considered, the global pattern of turtle body sizes is not consistent with Bergmann's rule. Instead, there is a significant negative correlation between latitude and

$\log_{10}$  CL (i.e., turtles are larger on average at low latitudes), consistent with the converse to Bergmann's Rule (Table 1, Fig. 4). However, the results of this global correlation should be tempered by the by runs up and down test and randomization tests (Fig. 7, Supplemental Table 1). The former test shows the sequence of body sizes does not depart significantly from a random sequence of increases and decreases, and the latter indicates that the observed medians for each bin fall within the 95% confidence intervals for the randomized data in almost every case. These analyses suggest that turtle body sizes are actually fairly uniform across latitudes, and simply follow the null expectation. The major exception appears to be low latitude turtles; these depart from the null distribution and are somewhat larger than expected, and are larger on average than higher latitude species. In addition, southern hemisphere species are larger on average than their northern hemisphere counterparts. Results from the correlation tests for the subdivided data are shown in Table 1, and as with the species richness data, the latitudinal pattern for body size closely matches that for aquatic turtles (Fig. 4). The pattern for terrestrial turtles is similar to the overall pattern in the northern hemisphere, but shows large deviations in the southern hemisphere. These deviations stem from some of the unusual features of the southern hemisphere tortoise fauna, such as the assemblage of miniaturized tortoises (*Homopus* and *Psammobates* species) found in southern Africa. When the data are subdivided by continent, it is apparent that most continents follow a similar latitudinal pattern, again with some deviations



**FIGURE 3.** Latitudinal gradient in species richness in turtles. (A) Latitudinal trends in richness in functional groups: terrestrial species on continents; freshwater species. (B) Latitudinal trends in richness in the northern hemisphere grouped by continent. (C) Latitudinal trends in richness in the southern hemisphere grouped by continent. (D) Latitudinal trends in richness in the Pleurodira and Carretochelyidae, grouped by family. (E) Latitudinal trends in richness in the Chelydroidea and Trionychoidea (minus Carretochelyidae), grouped by family. (G) Latitudinal trends in richness in the Testudinoidea, grouped by family.

**Table 1.** Results of correlation tests between species richness and latitude,  $\log_{10}$  maximum carapace length (Body Size) and latitude, and  $\log_{10}$  geographic range area (Range Area) and latitude.

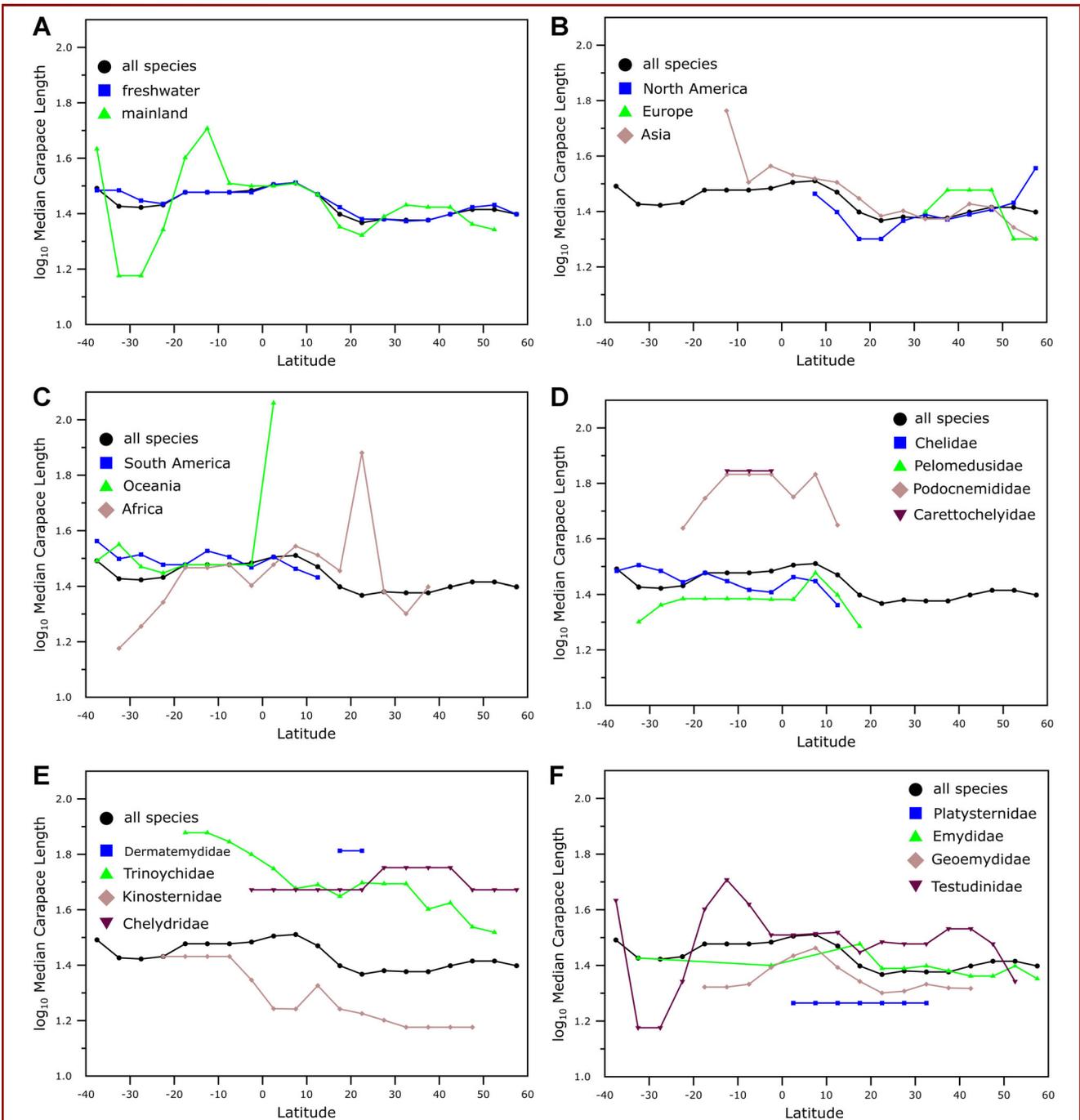
Data Partition	Species Richness		Body Size		Range Area	
	Pearson's r	P	Pearson's r	P	Pearson's r	P
All species	-0.655	0.002	-0.620	0.004	0.408	0.074
Freshwater species	-0.646	0.002	-0.586	0.007	0.458	0.043
Mainland terrestrial species	-0.453	0.052	-0.385	0.103	-0.292	0.225
North American species	-0.135	0.693	0.460	0.154	0.978	<<0.001
South American species	-0.912	<<0.001	0.498	0.119	-0.636	0.036
African species	-0.601	0.023	-0.376	0.167	-0.283	0.308
Asian species	-0.421	0.118	-0.731	0.002	.0748	0.001
European species	-0.845	0.034	-0.627	0.183	0.781	0.067
Oceanian species	0.023	0.954	-0.397	0.290	0.738	0.023
Northern Hemisphere species	-0.785	0.003	-0.605	0.037	0.563	0.057
Southern Hemisphere species	-0.090	0.002	-0.415	0.307	-0.420	0.301
Chelidae	0.130	0.704	0.623	0.041	-0.144	0.672
Emyidae	0.021	0.951	-0.568	0.069	0.974	<<0.001
Geoemydidae	0.012	0.971	-0.660	0.014	0.395	0.182
Kinosternidae	0.188	0.503	-0.593	0.020	-0.204	0.467
Pelomedusidae	-0.807	0.003	-0.543	0.085	0.682	0.021
Podocnemididae	-0.931	0.001	-0.630	0.094	-0.524	0.183
Testudinidae	-0.510	0.026	-0.308	0.120	-0.477	0.039
Trionychidae	-0.311	0.260	-0.767	0.001	0.319	0.247

(e.g., unusually small sizes in southern Africa because of miniaturized tortoises; unusually large sizes in southernmost Asia on account of extremely large members of Trionychidae). Latitudinal patterns for individual families are complex. Most families seem to have a typical body size, with some fluctuation around this central value. A few show more distinctive latitudinal patterns, such as a trend for decreasing body size with increasing northern latitudes among the Trionychidae and Kinosternidae. Correlations are more variable among the subdivided data: aquatic turtles, Asia, Geoemydidae, Kinosternidae, Trionychidae and the northern hemisphere show significant negative correlations between body size and latitude. Most other subsets show non-significant negative correlations. Interestingly, Chelidae shows a significant positive correlation with latitude (i.e., larger sizes at higher latitudes); North and South America also show positive albeit non-significant correlations.

As noted above, we used two phylogenies to test for a phylogenetic signal in our body size data. The first is a composite phylogeny compiled from literature sources with four sets of estimated branch lengths, whereas the second is a smaller tree with empirical branch lengths based on the results of Jaffe et al.'s (2011) phylogenetic analysis. We conducted our analyses only for the entire sample of species (i.e., we did not subdivide the data by habitat preference, continent, etc.). Results for the initial tests of phylogenetic signal (Pagel's  $\lambda$  and Blomberg's K) are presented in Table 3. The  $\lambda$  values for  $\log_{10}$  maximum CL imply that the data generally fit any of our phylogeny/branch length combinations better than a star phylogeny, but the relatively low to moderate values of K indicate a poor fit between the data and the assumption of a Brownian motion model of evolution across the trees/branch lengths. These results are not surprising given that Jaffe et al. (2011) found that their body size data fit a multi-optimum

**Table 2.** Results of runs up and down tests for species richness,  $\log_{10}$  maximum carapace length (Body Size), and  $\log_{10}$  geographic range area (Range Area).

	$N_1 (<0)$	$N_2 (>0)$	Runs	Expected Runs	Z	P
Species Richness	11	8	6	10.26	-2.067	0.039
Body Size	12	7	7	9.842	-1.448	0.1476
Range Area	10	9	12	10.47	0.7227	0.4698



**FIGURE 4.** Latitudinal gradient in body size in turtles (Bergmann's rule). (A) Latitudinal trends in  $\log_{10}$  maximum carapace lengths (Body Size) in functional groups: terrestrial species on continents; freshwater species. (B) Latitudinal trends in Body Size in the northern hemisphere grouped by continent. (C) Latitudinal trends in Body Size in the southern hemisphere grouped by continent. (D) Latitudinal trends in Body Size in the Pleurodira and Carretochelyidae, grouped by family. (E) Latitudinal trends in Body Size in the Chelydroidea and Trionyochoidea (minus Carretochelyidae), grouped by family. (G) Latitudinal trends in Body Size in the Testudinoidea, grouped by family.

**Table 3.** Results of tests of phylogenetic signal (measured with Pagel's  $\lambda$  and Blomberg's K) for  $\log_{10}$  maximum carapace length (Body Size) and  $\log_{10}$  geographic range area (Range Area).

	Literature (equal)		Literature (Grafen)		Literature (Nee)		Literature (Pagel)		Jaffe et al. (mtDNA)	
	$\lambda$	K	$\lambda$	K	$\lambda$	K	$\lambda$	K	$\lambda$	K
Body Size	0.960	0.661	0.947	0.045	0.872	0.727	0.826	0.377	0.948	0.137
Range Area	0.318	0.237	0.253	0.018	0.272	0.337	0.254	0.160	0.164	0.030

Results are presented for the topology and four sets of estimated branch lengths for the literature tree and the empirical branch lengths from the mtDNA tree of Jaffe et al. (2011). For the literature the four sets of branch lengths used were: equal branch lengths; branch lengths transformed using the methods of Grafen (1989); Nee (Purvis 1995); Pagel (1992). See text for details.

Ornstein-Uhlenbeck model better than a Brownian motion model. Results for the PGLS and traditional regressions are shown in Table 4. In general, there was not a significant relationship between  $\log_{10}$  maximum carapace length and the absolute value of maximum latitude, regardless of whether phylogeny was taken into account, and the regressions consistently explained very small amounts of variance in the dataset. A significant relationship did exist between  $\log_{10}$  maximum carapace length and latitudinal range, although these regressions also accounted for little variance in the dataset. The values of Pagel's  $\lambda$  estimated during PGLS fitting process were very similar to those estimated independently, indicating that there is some phylogenetic signal in the body size data (i.e., they fit our topology/branch length combinations better than a star phylogeny).

#### Rapoport's Rule

Plots showing overall patterns of geographic range size ( $\log_{10}$  geographic range area) versus latitude, as well as data that have been subdivided by habitat preference, continent, and family, are shown in Figure 5.

When the entire dataset is considered, geographic range size shows a complex relationship with latitude, with a low latitude plateau, decreases at mid-latitudes in the northern and southern hemisphere, and peaks at high northern and southern latitudes (more extreme in the northern hemisphere). The runs up and down test shows that the sequence of data points does not differ significantly from a random sequence of increases and decreases (Table 2). However, a majority of bins (13 of 20) had observed median areas that fell outside of the 95% confidence interval for our randomized data (Fig. 7, Supplemental Table 1). All of these deviations were cases where the observed median was larger than expected, and the cases where the observed medians fell within the confidence intervals for the randomized data were concentrated at mid-latitudes in the northern and southern hemisphere. The aquatic turtles follow the overall pattern more closely than terrestrial species, although the main deviations for the terrestrial turtles occur in the tropics and southern hemisphere (unusually large ranges in the tropics and mid southern latitudes, and unusually small ranges in the high southern latitudes). When the

data are subdivided by continent, it is apparent that turtles on each continent display more or less unique patterns that often have little resemblance to the overall pattern. For example, North America and Oceania show almost linear trends for increasing range sizes with latitude, whereas Africa shows a tendency for range area to decrease with increasing latitude and South America has a strong peak in range area near 10° south. Each family also displays its own distinctive pattern. Particularly striking among these is the nearly linear trend for geographic range size to increase with latitude among the Emydidae. Results from the correlation tests are shown in Table 1. When the entire dataset is considered, we see no significant relationship between geographic range area and latitude; the same is true if only the northern hemisphere or southern hemisphere is considered. Geographic range area shows a significant positive correlation (high latitude turtles have larger geographic ranges) for aquatic turtles, North America, Asia, Oceania, Emydidae and Pelomedusidae. A significant negative correlation is found between geographic range area and latitude for South America, and Testudinidae.

Results for the initial tests of phylogenetic signal (Pagel's  $\lambda$  and Blomberg's K) are presented in Table 3. The  $\lambda$  values for  $\log_{10}$  geographic range area indicate a poor fit to the phylogeny/branch length combinations; instead the data better fit a star phylogeny. The low values of K corroborate the apparent lack of phylogenetic signal, and show that the geographic range data poorly fit the phylogenies/branch lengths and a Brownian motion model of evolution. The results from the PGLS and traditional regressions are shown in Table 5.  $\log_{10}$  geographic range area was significantly correlated with maximum latitude and latitudinal range regardless of whether phylogeny was taken into account. The regressions using maximum latitude as an independent variable typically explained only low to moderate levels of variance, whereas those using latitudinal range as the independent variable explained large amounts of variance in the data. The latter result is not surprising because one would expect larger geographic ranges to include a broader spread of latitudes. The values of Pagel's  $\lambda$  estimated during PGLS fitting process are somewhat higher than those estimated independently, but they

**Table 4.** Results of the traditional (non-phylogenetic) regression and the PGLS regressions of  $\log_{10}$  maximum carapace length (Body Size) versus absolute value of maximum latitude or latitudinal range.

	Coefficient	P	F	d.f.	P	Adjusted $r^2$	$\lambda$	$\lambda$ 95% CI
Traditional regression Maximum Latitude			3.52	1, 229	0.062	0.011	–	–
Intercept	1.489	<<0.001						
Maximum Latitude	–0.002	0.062						
Traditional regression Latitudinal Range			13.21	1, 229	<0.001	0.050	–	–
Intercept	1.370	<<0.001						
Latitudinal Range	0.005	<0.001						
Literature (equal) Maximum Latitude			0.40	1, 201	0.529	–0.003	0.938	0.816, NA
Intercept	1.617	<<0.001						
Maximum Latitude	–0.001	0.5289						
Literature (equal) Latitudinal Range			4.64	1, 201	0.0325	0.018	0.949	0.830, NA
Intercept	1.563	<<0.001						
Latitudinal Range	0.002	0.0325						
Literature (Grafen) Maximum Latitude			0.30	1, 201	0.059	–0.004	0.934	0.860, 0.968
Intercept	1.519	<<0.001						
Maximum Latitude	–0.001	0.588						
Literature (Grafen) Latitudinal Range			9.18	1, 201	0.003	0.039	0.927	0.842, 0.965
Intercept	1.455	<<0.001						
Latitudinal Range	0.003	0.003						
Literature (Nee) Maximum Latitude			0.18	1, 201	0.673	–0.004	0.843	0.689, 0.950
Intercept	1.488	<<0.001						
Maximum Latitude	–0.001	0.673						
Literature (Nee) Latitudinal Range			7.95	1, 201	0.005	0.033	0.826	0.663, 0.940
Intercept	1.432	<<0.001						
Latitudinal Range	0.003	0.005						
Literature (Pagel) Maximum Latitude			0.43	1, 201	0.509	–0.003	0.806	0.662, 0.900
Intercept	1.508	<<0.001						
Maximum Latitude	–0.001	0.509						
Literature (Pagel) Latitudinal Range			7.69	1, 201	0.006	0.032	0.790	0.636, 0.892
Intercept	1.441	<<0.001						
Latitudinal Range	0.003	0.006						
Jaffe et al. Maximum Latitude			0.19	1, 163	0.662	–0.005	0.940	0.871, 0.972
Intercept	1.583	<<0.001						
Maximum Latitude	–0.001	0.662						
Jaffe et al. Latitudinal Range			8.57	1, 163	0.004	0.004	0.952	0.896, 0.977
Intercept	1.513	<<0.001						
Latitudinal Range	0.003	0.004						

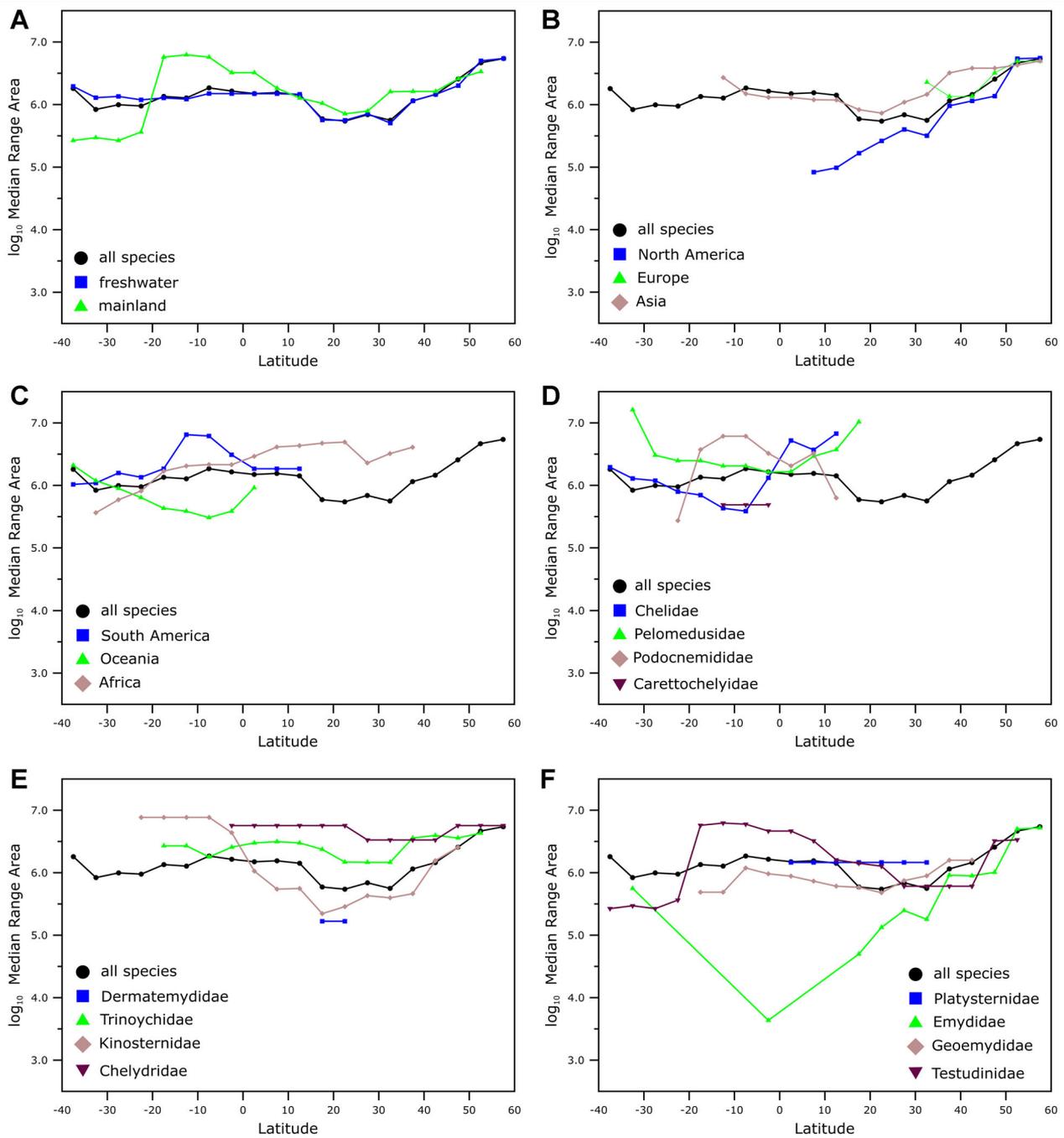
Summary statistics are presented for the topology and four sets of estimated branch lengths for the literature tree and the empirical branch lengths from the mtDNA tree of Jaffe et al. (2011). For the literature tree the four sets of branch lengths used were: equal branch lengths; branch lengths transformed using the methods of Grafen (1989); Nee (Purvis 1995); Pagel (1992). NA is listed as the lower confidence interval value for  $\lambda$  when the confidence interval included zero. NA is listed for the upper confidence interval value when the confidence interval included 1. See text for details.

still imply a relatively poor fit between the geographic range areas and our phylogenies.

#### Relationships with Available Land Area

Results of the correlation tests with available land area in each latitudinal bin are shown in Table 6. Species richness does not

show a significant correlation with available land area for the dataset as a whole or when the data are subdivided by continent, although the correlations for the entire dataset and for Oceania are close to significant. Body size was significantly negatively correlated with available land area for the entire dataset (i.e., turtles are smaller on average in the larger latitudinal bins);



**FIGURE 5.** Latitudinal gradient in geographic range size in turtles (Rapoport's rule). (A) Latitudinal trends in  $\log_{10}$  median geographic range area (Range Area) in functional groups: terrestrial species on continents; freshwater species. (B) Latitudinal trends in Range Area in the northern hemisphere grouped by continent. (C) Latitudinal trends in Range Area in the southern hemisphere grouped by continent. (D) Latitudinal trends in Range Area in the Pleurodira and Carretochelyidae, grouped by family. (E) Latitudinal trends in Range Area in the Chelydroidea and Trionyochoidea (minus Carretochelyidae), grouped by family. (G) Latitudinal trends in Range Area in the Testudinoidea, grouped by family.

**Table 5.** Results of the traditional (non-phylogenetic) regression and the PGLS regressions of  $\log_{10}$  geographic range area (Range Area) versus absolute value of maximum latitude or latitudinal range.

	Coefficient	P	F	d.f.	P	Adjusted $r^2$	$\lambda$	$\lambda$ 95% CI
Traditional regression Maximum Latitude			15.01	1, 229	<<0.001	0.057	–	–
Intercept	5.111	<<0.001						
Maximum Latitude	0.017	<0.001						
Traditional regression Latitudinal Range			245.50	1, 229	<<0.001	0.515	–	–
Intercept	4.907	<<0.001						
Latitudinal Range	0.053	<<0.001						
Literature (equal) Maximum Latitude			38.48	1, 201	<<0.001	0.157	0.433	0.209, 0.664
Intercept	5.181	<<0.001						
Maximum Latitude	0.023	<<0.001						
Literature (equal) Latitudinal Range			194.00	1, 201	<<0.001	0.489	0.138	0.009, 0.379
Intercept	5.145	<<0.001						
Latitudinal Range	0.044	<<0.001						
Literature (Grafen) Maximum Latitude			36.64	1, 201	<<0.001	0.150	0.569	0.181, 0.804
Intercept	4.927	<<0.001						
Maximum Latitude	0.031	<<0.001						
Literature (Nee) Maximum Latitude			36.36	1, 201	<<0.001	0.149	0.436	0.215, 0.667
Intercept	4.877	<<0.001						
Maximum Latitude	0.031	<<0.001						
Literature (Nee) Latitudinal Range			209.20	1, 201	<<0.001	0.508	0.090	NA, 0.326
Intercept	4.983	<<0.001						
Latitudinal Range	0.050	<<0.001						
Literature (Pagel) Maximum Latitude			32.56	1, 201	<<0.001	0.135	0.385	0.172, 0.606
Intercept	4.892	<<0.001						
Maximum Latitude	0.029	<<0.001						
Literature (Pagel) Latitudinal Range			209.10	1, 201	<<0.001	0.508	0.061	NA, 0.272
Intercept	4.974	<<0.001						
Latitudinal Range	0.050	<<0.001						
Jaffe et al. Maximum Latitude			21.91	1, 163	<<0.001	0.113	0.356	0.137, 0.641
Intercept	5.449	<<0.001						
Maximum Latitude	0.234	<<0.001						
Jaffe et al. Latitudinal Range			180.8	1, 163	<<0.001	0.523	0.186	0.039, 0.480
Intercept	5.244	<<0.001						
Latitudinal Range	0.451	<<0.001						

Summary statistics are presented for the topology and four sets of estimated branch lengths for the literature tree and the empirical branch lengths from the mtDNA tree of Jaffe et al. (2011). For the literature tree the four sets of branch lengths used were: equal branch lengths; branch lengths transformed using the methods of Grafen (1989); Nee (Purvis 1995); Pagel (1992). NA is listed as the lower confidence interval value for  $\lambda$  when the confidence interval included zero. Results are not shown for the regression of  $\log_{10}$  geographic range area versus latitudinal range for the literature tree with Grafen branch lengths because R was unable to optimize  $\lambda$  for this analysis. See text for details.

significant negative correlations also exist for Asia and Oceania, whereas a significant positive correlation exists for Africa. Geographic range area was not significantly correlated with available land area for the complete dataset. Significant positive correlations were apparent for North America and South America. (i.e., turtles with larger geographic ranges tend to occur in bins with larger available land areas).

#### Relationships Between Latitudinal Gradients

To fully explore the relationship of body size and geographic range area in our dataset, we carried out correlation tests as well as PGLS regressions that explicitly take phylogeny into account. Results from the correlation tests are presented in Table 7. When the entire dataset of 293 species for which we have size and geographic range area data is considered, there is a significant

**Table 6.** Results of correlation tests between species richness and  $\log_{10}$  available land area,  $\log_{10}$  maximum carapace length (Body Size) and  $\log_{10}$  available land area, and  $\log_{10}$  geographic range area (Range Area) and  $\log_{10}$  available land area.

Data Partition	Species Richness		Body Size		Range Area	
	Pearson's r	P	Pearson's r	P	Pearson's r	P
All species	0.414	0.070	-0.555	0.011	-0.084	0.724
North American species	0.004	0.991	0.603	0.065	0.713	0.021
South American species	0.307	0.359	0.228	0.500	0.745	0.009
African species	0.137	0.628	0.507	0.054	0.415	0.124
Asian species	0.260	0.349	-0.912	<<0.001	0.043	0.880
European species	-0.506	0.384	-0.768	0.130	0.392	0.514
Oceanian species	0.597	0.089	-0.800	0.010	-0.047	0.905

positive correlation between  $\log_{10}$  maximum CL (body size) and  $\log_{10}$  geographic range area (i.e., larger turtles tend to have larger geographic ranges). This pattern is consistent for terrestrial and aquatic turtles, and also is apparent in the data for South America, Asia, Africa, and Oceania. However, the relationship is not as apparent when data for individual families are considered; only Chelidae, Geoemydidae, and Testudinidae show significant relationships between body size and geographic range area.

The results of the PGLS analyses are shown in Table 8 and Figure 6. Regardless of the phylogeny/branch length combina-

tion considered, the estimated  $\lambda$  values are low with a 95% confidence interval that includes zero in almost all cases. This indicates that there is little need to explicitly take phylogeny into account in the regression analyses, and this is further confirmed by the very small difference in the non-phylogenetic and PGLS regressions (Fig. 6). If the PGLS results are taken at face value, there is a significant relationship between body size and geographic range area. However, only a small proportion of the variance in the geographic range data is explained by the regression, implying that other factors are likely equally or more important in determining range size.

We also used multiple linear regression procedures to explore the relationships between all three latitudinal gradients. We found that turtle species richness does not show a significant relationship with range size + body size ( $F = 2.51$ ,  $P = 0.08342$ ,  $r^2 = 0.01243$ ; Table 9). The lack of correspondence between species richness and range size is evident in Figure 7. On the other hand, geographic range size is correlated with turtle body size, as seen above, though adding turtle species richness to this model does not improve the relationship ( $F = 11.93$ ,  $P < 0.0001$ ,  $r^2 = 0.0835$ ; Table 9). The close relationship between geographic range size and body size is shown in Figure 7.

#### Relationships Between Abiotic and Biotic Variables and Latitudinal Gradients

Our model fitting approach suggests that turtle species richness is best explained by the following variables: biome, southernmost latitude,  $\log_{10}$  available area, family, continent, mean diurnal temperature range (bioclim 2), isothermality (bioclim 3), maximum temperature of the warmest month (bioclim 5), mean temperature of the driest quarter (bioclim 9), mean temperature of the warmest quarter (bioclim 10), and precipitation seasonality (bioclim 15) (Table 9). Together these account for 58.8% of the total variance in turtle richness ( $F = 28.30$ ,  $P < < 0.0001$ ).

The best-fit model explaining global variation in turtle body size (Bergmann's rule) include the following variables:  $\log_{10}$  median range size, family, continent, and functional group

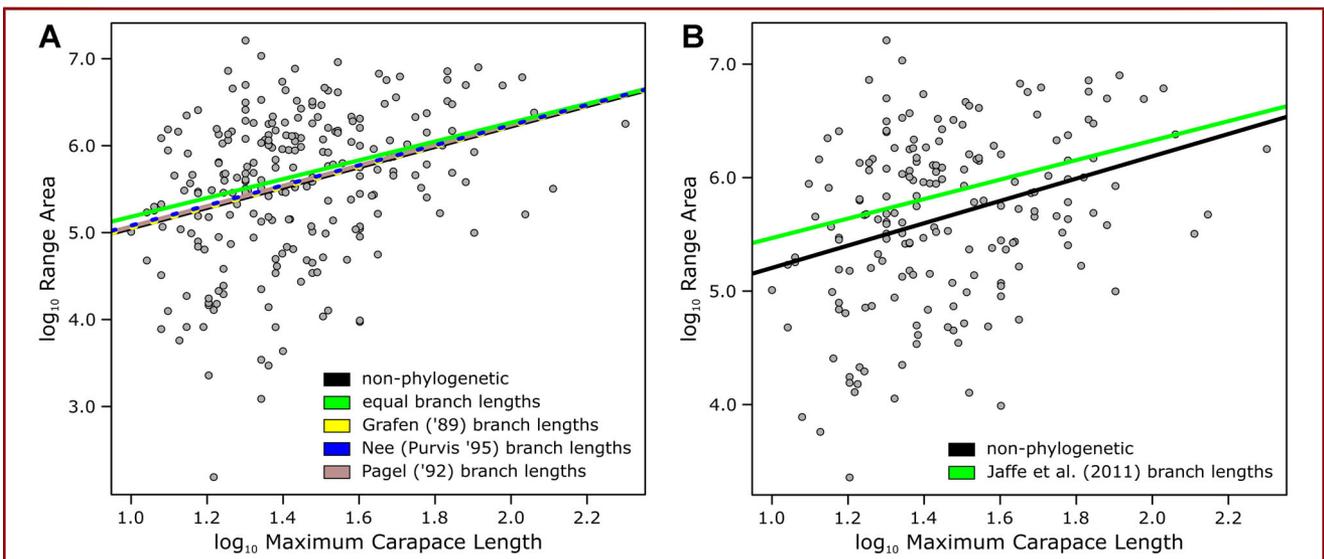
**Table 7.** Results of correlation tests between non-phylogenetically transformed  $\log_{10}$  maximum carapace length (Body Size) and non-phylogenetically transformed  $\log_{10}$  geographic range area (Range Area).

Data Partition	Pearson's r	P
All species	0.310	<<0.001
Freshwater species	0.320	<<0.001
Mainland terrestrial species	0.308	0.020
North American species	0.130	0.248
South American species	0.413	0.004
African species	0.353	0.011
Asian species	0.375	0.001
European species	0.084	0.857
Oceanian species	0.430	0.011
Chelidae	0.301	0.030
Chelydridae	0.436	0.564
Emydidae	-0.034	0.817
Geoemydidae	0.391	0.001
Kinosternidae	0.225	0.279
Pelomedusidae	0.339	0.156
Podocnemididae	0.579	0.133
Testudinidae	0.345	0.025
Trionychidae	-0.028	0.888

**Table 8.** Results of the PGLS regressions of  $\log_{10}$  geographic range area (Range Area) versus  $\log_{10}$  maximum carapace length (Body Size).

	Coefficient	P	F	d.f.	P	Adjusted $r^2$	$\lambda$	$\lambda$ 95% CI
Literature (equal)			17.02	1, 238	<<0.001	0.063	0.247	NA, 0.541
Intercept	4.100	0.052						
Body Size	1.083	<<0.001						
Literature (Grafen)			27.01	1, 238	<<0.001	0.098	0	NA, 0.248
Intercept	3.880	<<0.001						
Body Size	1.171	<<0.001						
Literature (Nee)			19.25	1, 238	<<0.001	0.071	0.217	NA, 0.482
Intercept	3.926	<<0.001						
Body Size	1.155	<<0.001						
Literature (Pagel)			19.93	1, 238	<<0.001	0.073	0.190	NA, 0.454
Intercept	3.900	<<0.001						
Body Size	1.170	<<0.001						
Jaffe et al.			12.73	2, 182	<<0.001	0.060	0.117	0.003, 0.390
Intercept	4.609	<<0.001						
Body size	0.858	0.001						

Summary statistics are presented for the topology and four sets of estimated branch lengths for the literature tree and the empirical branch lengths from the mtDNA tree of Jaffe et al. (2011). For the literature tree the four sets of branch lengths used were: equal branch lengths; branch lengths transformed using the methods of Grafen (1989); Nee (Purvis 1995); Pagel (1992). NA is listed as the lower confidence interval value for  $\lambda$  when the confidence interval included zero. See text for details.



**FIGURE 6.** Relationship between body size and geographic range size. (A) Regressions of  $\log_{10}$  maximum carapace length (Body Size) against  $\log_{10}$  median geographic range area (Range Area) with linear model not accounting for phylogenetic non-independence ( $r^2 = 0.102$ ;  $P < 0.01$ ), and using PGLS regressions with four sets of estimated branch lengths for the literature tree. (B) Regressions of Body Size against Range Area again with a standard linear model and with PGLS regression PGLS regressions with empirical branch lengths from the molecular phylogeny of Jaffe et al. (2011).

**Table 9.** Summary statistics of multiple linear regressions considering only the correlation between the three latitudinal gradients (first two models) as well as more complex models that include multiple abiotic and biotic variables.

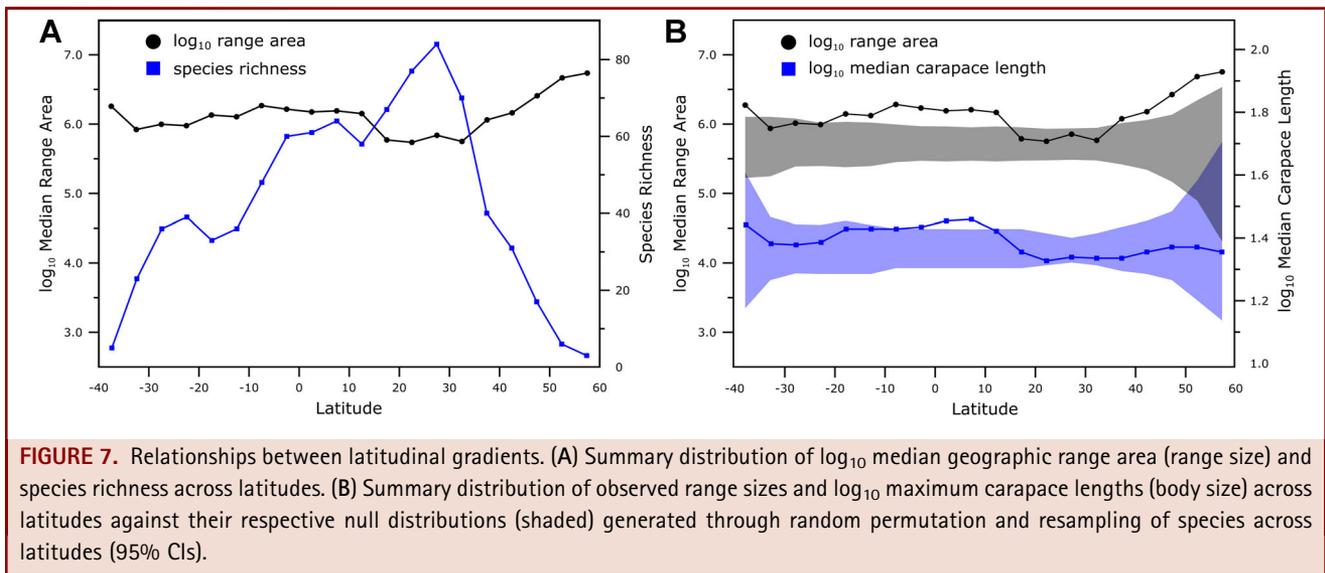
Response explanatory	t-value	P	F-stat	d.f.	P	Adjusted $r^2$
Species Richness			11.49	2, 238	<<0.001	0.0804
Intercept	4.692	<<0.001				
Body Size ( $\log_{10}$ maxCL)	-1.179	0.240				
Range Size ( $\log_{10}$ area)	-1.486	0.139				
Range Size			11.93	2, 238	<<0.001	0.0835
Intercept	12.222	<<0.001				
Body Size ( $\log_{10}$ maxCL)	4.467	<<0.001				
Species Richness	-1.486	0.139				
Species Richness			28.30	11, 199	<<0.001	0.5884
Intercept	-1.376	0.170				
Biome	-3.061	0.003				
Southernmost latitude	3.102	0.002				
Available land ( $\log_{10}$ area)	3.514	<0.001				
Family	1.556	0.1217				
Continent	-2.491	0.0136				
Mean Diurnal Temp Range (bioclim 2)	7.545	<<0.001				
Isothermality (bioclim 3)	-6.720	<<0.001				
Max Temp Warmest Month (bioclim 5)	-5.849	<<0.001				
Mean Temp Driest Quarter (bioclim 9)	4.665	<<0.001				
Mean Temp Warmest Quarter (bioclim 10)	6.155	<<0.001				
Precipitation Seasonality (bioclim 15)	-3.637	<0.001				
Body Size			15.38	4, 283	<<0.001	0.1669
Intercept	10.825	<<0.001				
Range Size ( $\log_{10}$ area)	4.678	<0.001				
Family	3.900	0.00012				
Continent	2.693	0.0075				
Functional Group	-4.693	<0.001				
Range Size			40.12	7, 203	<<0.001	0.5660
Intercept	6.702	<<0.001				
Ecoregion Richness	3.252	0.001				
Biome	1.607	0.110				
Body Size ( $\log_{10}$ maxCL)	3.336	0.001				
Northernmost latitude	14.420	<<0.001				
Midpoint latitude	-13.775	<<0.001				
Max Temp Warmest Month (bioclim 5)	2.148	0.033				
Min Temp Coldest Month (bioclim 6)	-2.553	0.011				

Best-fit models were selected by AICc ranks after exhaustively testing every combination of explanatory variables in contributing to the response variable under a general linear model. See text for details.

(Table 9). These variables account for 16.7% of the total variance in turtle body size ( $F = 15.38, P << 0.001$ ). It is interesting to note that no climatic variables are included in this model.

The multiple regression of our best-fit model examining latitudinal gradients in geographic range size (Rapoport's rule) suggests that geographic range size in turtles is best explained by:

ecoregion richness, biome,  $\log_{10}$  maximum carapace length, northernmost latitude, midpoint latitude, maximum temperature of the warmest month (bioclim 5), and minimum temperature of the coldest month (bioclim 6) ( $F = 40.12, P << 0.001$ ; Table 9). Variation in these features explains 56.6% of the variance in geographic range size.



## DISCUSSION

Documenting and understanding how biodiversity varies across the globe is a central aim of biogeography and ecology (Gaston et al., 2008; Lomolino et al., 2010). Here, we examine three of the most celebrated and oft debated rules in biogeography: latitudinal gradients in species diversity, body size, and geographic range size. We explore these patterns in turtles, an ideal group because of their antiquity, worldwide distribution, and diversity of body sizes, forms, and ecologies. Our goals are to determine whether turtles follow the latitudinal gradient in species diversity, Bergmann's rule, and Rapoport's rule, and whether any of these patterns correlate to each other or additional abiotic or biotic attributes. Although a full consideration of the mechanisms underlying latitudinal gradients is beyond the scope of any one study, our aim is to provide a foundation for more comprehensive analyses and discussions of latitudinal patterns and their significance.

### Latitudinal Gradients in Turtle Diversity

Based on prior studies on the distribution of squamate reptiles (snakes and lizards), turtles, and birds (e.g., Schall and Pianka, '78, Hawkins et al., 2003; Araújo et al., 2007, Mittlebach et al., 2007), as well as the pioneering biogeographical works that established biodiversity "hotspots" (e.g., Forster, '78; von Humboldt, 1807), our expectation was that turtle species richness primarily would be concentrated at low latitudes. Although a considerable amount of the diversity in our dataset is concentrated at these lower latitudes, the peak of turtle richness is not. Instead, our peak richness occurs at approximately 25° north, close to the northern edge of the tropics. This pattern is surprising and is seen in only a few groups, often with unusual

life histories (such as parasitoids, Janzen, '81; reviewed in Willig et al., 2003; Hillebrand, 2004). Hecnar ('99) reported a similar result, and briefly posited that it might reflect a Laurasian center of origin for most major extant clades, with a subsequent dispersal into the southern continents, especially the Neotropics. This notion, that global regions containing the greatest diversity are also those regions in which that diversity has arisen, and thus serve as "cradles" of biodiversity (Rohde, 1992; Chown and Gaston, 2000; Hillebrand, 2004), is a simple mechanism explaining species richness that might be tested with fossil evidence and through phylogenetic analyses. Indeed, Stephens and Wiens, (2003) showed that species richness in Emydidae is positively correlated with the amount of time lineages have occupied regions, allowing more time for speciation to occur and thus generate diversity. Similar patterns have been reported in lampropeltine snakes (Pyron and Burbrink, 2009).

In our dataset, the richness peak at 25° north is driven by the speciose clades Emydidae and Geoemydidae. Nearly all of the species in both clades have ranges in the northern hemisphere, and together they represent more than a third of total extant turtle diversity (van Dijk et al., 2012). However, these two lineages are not more ancient than other turtle clades (Joyce et al., 2013), so why these two groups should be so diverse and drive global patterns of turtle richness remains an open question. One possibility is that the history of glaciation in the northern hemisphere is responsible for these patterns. Based on a combination of fossil occurrence data and ecological modeling, Rödder et al. (2013) hypothesized that turtle ranges contracted during the Last Glacial Maximum (LGM) as species tracked their preferred climatic and environmental parameters. It is possible that these glacial cycles were "speciation pumps" (Willis and

Whittaker, 2000) that fragmented and isolated many formerly connected populations, leading to the extensive diversity we see today in temperate turtles (e.g., Arbogast and Slowinski, '98; Weir and Schluter, 2004).

An alternative interpretation of this pattern of mid-latitude turtle richness, however, is that it does not reflect a genuine biological signal but is simply an artifact of “sampling”. The Emydidae and Geoemydidae are among the most well studied turtle clades, and species richness in both clades is well understood compared to many other turtle groups. The last few decades have seen a number of wide ranging species split (multiple subspecies have been elevated to species), following the widespread use of molecular genetic tools to refine our ability to identify and demarcate genetic variation in turtles (McGaugh et al., 2007). These methods have been widely applied to the North American Emydidae (Seidel, '81; Seidel and Miranda, '84; Spinks et al., 2013, 2014b). On the other hand, diversity in some clades may actually be overestimated. A number of new geoemydid species have been described from very limited material, often with a great deal of uncertainty surrounding their geographic ranges, habitat preferences, and ecology (Yasukawa et al., 2001; Spinks et al., 2012). In an attempt to compensate for this sampling issue, we did not include the most contentious *Pseudemys* and *Trachemys* taxa within our analysis. Nevertheless, the pattern is still evident. Perhaps focused work on the remaining turtle clades will uncover similar diversity, and demonstrate that the mid-latitude peak in diversity we see is simply an artifact of scientific attention on the clades in the northern hemisphere.

We found that turtle species richness is correlated to a number of biotic and abiotic variables, such as ecoregion richness, latitude, available area, continent, family, and three climatic variables related to temperature. Examining some of these relationships in more detail by sub-dividing the data by continent, functional ecology, or family helps illustrate the degree to which pattern is driven by diversity and ecology. A negative correlation between richness and range was found for aquatic turtles, and specifically for Podocnemidae, Pelomedusidae, and Testudinidae. This potentially reflects the centralization of the diversity of Podocnemidae and Pelomedusidae in aquatic marshes and rivers in the Amazon basin and central-African rainforest respectively. Members of Testudinidae are primarily found in semi-arid environments that are concentrated at mid-latitudes such as the periphery of the Sahara desert today and in the recent past (Ernst and Barbour, '89; Sereno et al., 2008). Further work exploring the unusual distribution of turtle diversity and its causes is surely warranted.

#### Bergmann's Rule in Turtles

Few studies have examined body size trends in turtles, and Ashton and Feldman, (2003) summarized these and conducted a meta-analysis suggesting that turtles follow Bergmann's rule. However, they cautioned that too few species have been

examined and the trend appears weak. Although that study took an intraspecific approach (variation within species across latitudes), we summarize interspecific patterns across latitudes and also find only weak trends in a few lineages. Here, Bergmann's clines appear to be largely driven by a few regions that contain high species diversity with low morphological disparity (e.g., southern African miniaturized tortoises). The significant negative correlation between body-size and latitude, while opposite of that reported by Ashton and Feldman (2003) does follow anticipated patterns for some poikilotherms. Specifically, both proximate (neutral) and selective (adaptive) mechanisms might be expected to produce larger turtles at lower latitudes and smaller turtles at higher latitudes. At lower latitudes, climates are warmer and less seasonal, allowing for long, possibly uninterrupted, growth throughout the year in reptiles, which display indeterminate growth, leading to larger species (Lindsey, '66; Adolph and Porter, '96; Ashton and Feldman, 2003; Head et al., 2009; Head, 2010). Larger individuals will also possess greater thermal inertia, and may be less susceptible to small temperature fluctuations. This mechanism has been proposed to explain fossil and extant Trionychidae, which are largest in the tropics and reached massive proportions during some of the warmest periods in the past (Vitek, 2012). Conversely, at higher latitudes climates are less stable, fluctuating daily and seasonally, and therefore might constrain activity and growth, leading to smaller individuals (Lindsey, '66; Adolph and Porter, '96; Ashton and Feldman, 2003). Such climates might even select for smaller body sizes, because smaller individuals will have lower thermal inertia, and should be able to more easily exploit small amounts of thermal energy in the environment for activity and growth (Lindsey, '66; Ashton and Feldman, 2003). Contrasting these trends is the positive correlation between body size and latitude found in Chelidae. The diversity of chelids in both Australia and South America is nearly equal (18 and 19 species, respectively), and body size distributions among those taxa are also nearly equal, suggesting that the trends are not artifacts. Nevertheless, the potential reason behind this Bergmann's cline remains unknown. Furthermore, the variables that correlate with body size in turtles (geographic range size, family, continent, and functional group) may simply reflect correlations with other trends (Rapoport's rule) or the regional and clade specific patterns discussed, and might not hint at direct causality. Bergmann's clines, if they do exist in turtles, may be rare and reflect the unique aspects of certain groups or ecosystems, or a complex interplay of environmental and other factors (e.g., Rose et al., 2011; Orcutt and Hopkins, 2013).

#### Rapoport's Rule in Turtles

Interpreting Rapoport's rule in turtles is more difficult. The only other study to test Rapoport's rule in turtles (Hecnar, '99) found that they display the converse of Rapoport's Rule (i.e., larger ranges at low latitudes). Here, however, we see that North

American taxa do appear to follow Rapoport's Rule, with increased range area (size) at higher latitudes. This pattern has been noted in a number of taxa in the northern hemisphere but not the southern, leading some to question why the rule would hold only in the north (Gaston, 2003; Ruggiero and Wrenkraud, 2007; Whitton et al., 2012). In our study, this trend is well supported by the robust sampling of North American taxa relative to the rest of the globe. The correlation between range area and latitude within Emydidae also appears to be well supported by robust sampling and it is this clade that is likely driving the pattern found in North America, because emydid taxa form the majority of North American turtles. Likewise the patterns found in Oceania, which also appear to follow Rapoport's Rule, are likely reflective of robust sampling within the region. The remaining patterns, particularly those found in Africa (range size decreasing with increased latitude) and South America (range area greatest near 10° south latitude), could be due to less complete sampling. Regions of Africa, South America, and southeast Asia (where the diversity of Geoemydidae is highest) remain poorly sampled due to inaccessibility stemming from issues of political instability or logistical difficulty in accessing those regions. Therefore, even though our observed patterns, such as the concentration of South American turtle diversity at roughly 10° south latitude are likely reflective of the known diversity of turtles (Buhlmann et al., 2009), more detailed sampling in other regions will be needed to confirm whether these patterns are reflective of biological reality.

Using vouchered specimens to construct range area estimates is a well-known problem of herpetological studies (LaDuc and Bell, 2010; Ihlow et al., 2012). With respect to turtles, collections of turtles are typically centered in urban areas or rural areas with considerable economic value and therefore high levels of survey and exploration (e.g., areas with intense agriculture) (Buhlmann et al., 2009; Ihlow et al., 2012). Our sampling includes these potential biases because it is based on vouchered specimens. However, our range estimates are limited solely to the range contained within simple polygons that are constrained at the latitudinal maxima and minima by known specimens. As a result our range area estimates are likely undersized and not completely reflective of the true total range of species. At the same time the total area estimated may not be entirely occupied in species with broad geographic distributions because preferred habitats likely do not span the entire area. For example, aquatic turtles will tend to occupy bodies of water within their ranges and spend relatively little time in more terrestrial habitats. Nevertheless, our results are largely consistent with those of previous works estimating or evaluating turtle ranges and distributions (e.g., Hecnar, '99; Buhlmann et al., 2009; Ihlow et al., 2012; Rödder et al., 2013). Our view is that increased sampling will only serve to improve our knowledge of the system and that collection of vouchers is still essential for addressing spatial and other biodiversity questions (e.g., LaDuc and Bell, 2010; Bell and Mead, 2014). In particular,

vouchers from conservation regions proposed by Buhlmann et al. (2009) would greatly improve our understanding the distributional limits of species and fully establish the extant diversity of turtles.

Hecnar ('99) suggested that functional group, diet, body size, and available land area all influenced range size. These results approximate our more comprehensive analysis that included more species and more abiotic and biotic variables. We also found a relationship between range size and body size, which fits with our expectations that larger species should hold larger geographic ranges due to increased resources requirements and roaming abilities. This pattern is fairly well established in endotherms (birds and mammals), and may be a universal feature of Rapoport's rule, linking physiology with macroecology (Brown, '95; Brown et al., '96). We also found that ecoregion richness, biome, northernmost latitude, midpoint latitude, maximum temperature of the warmest month (bioclim 5) are all correlated to range size. These suggest regional patterns partly driven by ecological or abiotic conditions.

#### Concluding Remarks

Broadly speaking, turtles do not always follow the rules. Turtles display an unusual distribution of richness across latitudes, with a peak of diversity in the northern hemisphere, and they fail to conform to Bergmann's Rule or Rapoport's Rule. Further study is needed to understand the uncommon latitudinal gradient in species richness in turtles, and why Bergmann's and Rapoport's trends are not seen in turtles. We suggest focusing on those rare cases where lineages or even regions display expected body size and range size trends, and contrasting those cases to sister clades or regions where such trends are absent. The inclusion of fossil data also is rarely attempted in macro-scale analyses but may provide critical perspective on the historical causes of contemporary patterns. For example, Rödder et al.'s (2013) investigation of fossil and extant turtle distributions in North America provides insight into how fluctuating climates have likely contributed to small range sizes at lower latitudes. Additionally, an examination of other clades (e.g., certain snakes, crustaceans, macroalgae; Pyron and Burbrink, 2009; Rivandeniara et al., 2011, and Keith et al., 2014) that do not follow traditional biogeographic patterns, and the underlying processes structuring those patterns, may provide testable hypotheses that can be investigated for turtles. These cases offer some hope that causal mechanisms behind macroecological patterns can be uncovered, as well as explanations for why turtles seem to break the rules.

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