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Using climate, energy, and spatial-based hypotheses to interpret macroecological patterns of North America chelonians

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Abstract: Our study investigates how factors, such as latitude, productivity, and several environmental variables, influence contemporary patterns of the species richness in North American turtles. In particular, we test several hypotheses explaining broad-scale species richness patterns on several species richness datasets: 1) total turtles, 2) freshwater turtles only, 3) aquatic turtles, 4) terrestrial turtles only, 5) Emydidae, and 6) Kinosternidae. In addition to spatial data, we used a combination of 25 abiotic variables in spatial regression models to predict species richness patterns. Our results provide support for multiple hypotheses related to broad-scale patterns of species richness, and in particular, hypotheses related to climate, productivity, water availability, topography, and latitude. In general, species richness patterns were positively associated with temperature, precipitation, diversity of streams, coefficient of variation of elevation, and net primary productivity. We also found that North America turtles follow the general latitudinal diversity gradient pattern (i.e., increasing species richness towards equator) by exhibiting a negative association with latitude. Because of the incongruent results among our six datasets, our study highlights the importance of considering phylogenetic constraints and guilds when interpreting species richness patterns, especially for taxonomic groups that occupy a myriad of habitats.

Key words biodiversity, biogeography, phylogenetic constraint, latitudinal diversity gradients, turtles, topographical heterogeneity, spatial autocorrelation, water availability

Draft

Introduction

Scientists have long recognized that species are not uniformly distributed over large spatial scales, and understanding these distributional patterns is a central tenet of ecology and biogeography. Over the years, there has been disagreement among ecologists about the underlying processes regulating species assemblages (Ricklefs 2004; 2008), generating numerous hypotheses (see Rohde 1992; Palmer 1994; Willig et al. 2003). In general, species richness of an area is a function of local (i.e., ecological) and regional (e.g., historical) effects, and the strength of their interactions within a region (Ricklefs 2004). This pattern is evident by local species richness being linked not only with contemporary environmental gradients (i.e., climate driven models, Ricklefs 1977; Iverson 1992; Hawkins et al. 2003a; Filipe et al. 2009; Knouft and Page 2011) but also related to regional species richness (Ricklefs 2000, Ricklef 2008) and the historical conditions (Rahbek et al. 2007; Rödder et al. 2013) of the region, such as glacial events and vicariance (Oberdorff et al. 1997; Filipe et al. 2009; Jaquemin and Pyron 2011).

Within many taxonomic groups, a broad pattern emerges – a latitudinal diversity gradient (LDG) where species richness decreases with increasing latitude and more species are found near the equator (see Fischer 1960; Willig 2000; Willig et al. 2003; Hillebrand 2004; Lomolino et al. 2006). There are numerous explanations for this pattern in the literature (for a full list see reviews in Rohde (1992) and Lomolino et al. (2006)) including high productivity (Hutchison 1959; Hawkins et al. 2003a), annual stability (i.e., seasonality; Begon et al. 2006), warm temperatures (Alekseev 1982), glacier flux (Fischer 1960, Pianka 1966), and more precipitation (Begon et al. 2006) for tropical regions. The informative nature of latitudinal gradients in an ecological context has been questioned recently. For example, latitudinal diversity gradients do

not explain and at best only characterize contemporary species richness patterns (Willig et al. 2003; Hawkins and Diniz-Filho 2004; Knouft and Page 2011) because "latitude is a surrogate for a number of primary environmental gradients" (Gaston 2000; Willig et al. 2003), such as temperature, precipitation, elevation, seasonality, and insolation. Although species richness is undoubtedly influenced by the earth's history, these primary or contemporary environmental variables are still valuable in predicting species richness patterns because of niche conservatism. For example, one explanation for LDGs is that most species evolved in the tropics under specific environmental conditions and relatively few species have dispersed and speciated in the extratropical regions (i.e., tropical conservatism hypothesis; Wiens and Donoghue 2004). The relatively limited dispersal and speciation is related to most clades retaining their tropical climate niche; and therefore, the species do not possess the appropriate adaptations to handle climate of extratropical regions. Therefore, to better understand biodiversity patterns, species richness should be investigated via primary environmental variables.

Several hypotheses have been drawn to explain species richness patterns for reptiles and amphibians such as productivity, ambient energy, water, habitat heterogeneity and climatic variability (Hawkins et al. 2003a; Rodriguez et al. 2005). Although climatic variables are strongly tied to latitudinal gradients and consequently species richness, few studies have documented this pattern consistently with turtles. The incongruence among the various studies investigating species richness patterns within turtles is partially due the various geographic scales at which each study was conducted (see Rahbeck 2005). For example, turtle richness, in general, is not related to latitude at the global scale (Iverson 1992; Hecnar 1999; but see Angielczyk et al. 2014). On a smaller scale and using degree squares as a sampling unit, it is inversely related with latitude (i.e., increasing species richness with decreasing latitude) within the Iberian

Peninsula (Schall and Pianka 1977) possibly due to the “peninsular effect” (Busack and Hedges 1984). Although no clear relationship exists between turtle species richness and latitude, there are relationships with abiotic variables at several spatial scales (Rogers 1976; Schall and Pianka, 1977; 1978; Owen and Dixon 1989; Iverson 1992; Rödder et al. 2013; Angielczyk et al. 2014) producing varying results (see Lyons and Willig (2002) and Rahbek (2005) for the effect of scale). In general, a variety of temperature- and precipitation-related variables have been associated with turtle species richness patterns at the various spatial scales (e.g., Texas, Australia, United States, North America, Global) and sampling units (e.g., counties, degree squares, square quadrats, drainage basins, latitudinal bins, and Level 2 watersheds; Rogers 1976; Owen and Dixon 1989; Schall and Pianka 1978, Schall and Pianka 1978; Rödder et al. 2013; Iverson 1992; Angielczyk et al. 2014). However, climatic driven models using contemporary climatic data, similar to past models developed for turtles, are constrained in predicting large-scale species richness patterns because these models are missing critical components related to energy variables (Hawkins et al. 2003a), topography, and large-scale variables characterizing water availability. For example, Hawkins et al. (2003a) found plant productivity was a strong predictor for plant and animal diversity gradients at the global scale, while Knouft and Page (2011) found topography and water availability as strong predictors for fish diversity gradients in North America. These types of variables have not been integrated with spatial data for turtles in North America (e.g., Iverson 1992; Angielczyk et al 2014).

The goal of this study was not only to characterize patterns of turtle richness of North America (a region encompassing 25% of the global turtle fauna represented by seven families and 19 genera, van Dijk et al. 2014), but to also test several leading hypotheses explaining species richness patterns at the continental scale. These hypotheses include productivity, space

(latitude and longitude), coarse habitat (water availability and topography), climatic (combination of temperature, precipitation, and seasonality), and glacier flux hypotheses. We test these hypotheses among several species richness datasets including 1) total turtles (i.e., all North American turtles and tortoises), 2) freshwater only (i.e., excluding terrestrial species and the marsh species, *Malaclemys terrapin* (Schoepff, 1793)), 3) aquatic only (i.e., excluding semi-aquatic and marsh species), 4) terrestrial only (i.e., excluding all semi-aquatic and aquatic species), 5) Emydidae (i.e., semi-aquatic pond and marsh turtles), and 6) Kinosternidae (i.e., mud and musk turtles). The inclusion of the aquatic, freshwater, and terrestrial datasets allow us to test the hypotheses on specific guilds of turtles, while the latter two datasets allow us to test for phylogenetic constraints associated with environmental conditions within the two largest families in North America, Emydidae ($n = 43$) and Kinosternidae ($n = 24$).

Materials and methods

Data collection

We georeferenced all the turtle species distributions ($n = 84$) native to North America using distribution maps generated by Turtle Taxonomy Working Group (van Dijk et al. 2014), and from the species description for *Macrochelys apalachicola* (Thomas et al., 2014) and *M. suwanensis* (Thomas et al., 2014). We excluded all species of sea turtles found in North America, and subspecies were pooled at the species level for our analyses. All distributions were georeferenced using ArcMap v. 10.2.2 (ESRI, Redlands, CA, USA), and overlaid onto a map with 6-digit hydrologic unit code (HUC) from Canada, United States, and Mexico (CEC 2010). We chose HUCs as our sampling units because they are natural and delineated by hydrographic and topographic criteria, both of which are important for biogeographic processes (Matamoros et

al. 2015). Turtle diversity (i.e., species richness or the total number of species) was summed within each HUC ($n = 562$). A species was considered present if any portion of their distribution overlapped with an individual HUC, and therefore, we fully recognize that this will overestimate turtle distribution in some instances. From these data, we created six datasets (i.e., defined groups of species), including total species ($n = 84$), semi-aquatic and aquatic species ($n = 75$; referred to as freshwater turtles, which excluded *Malaclemys terrapin*, an estuarine species), aquatic species ($n = 55$; excluding semi-aquatic species and *M. terrapin*), terrestrial species ($n = 8$), Emydidae species ($n = 43$), and Kinosternidae species ($n = 24$) (Appendix 1).

Following Knouft and Page (2011) and Angielczyk et al. (2015), we collected climate, topography, and stream channel data. Environmental data was collected using WorldClim 30 arc-second resolution data (<http://www.worldclim.org/>; all temperature variables converted to Kelvin, and precipitation variables converted to mm): annual mean temperature, mean diurnal range, isothermality, temperature seasonality (e.g., standard deviation), maximum temperature of the warmest month, minimum temperature of the coldest month, temperature annual range, mean temperature of wettest quarter, mean temperature of driest quarter, mean temperature of warmest quarter, mean temperature of coldest quarter, annual precipitation, precipitation of the driest month, precipitation of the wettest month, precipitation seasonality (e.g., coefficient of variation; Hijmans et al. 2005), precipitation of wettest quarter, precipitation of driest quarter, precipitation of warmest quarter, and precipitation of coldest quarter. We used two topography variables, mean elevation (ELE) and coefficient of variation of elevation (CVE), to characterize each HUC. To calculate these variables, we utilized Global Multi-Resolution Terrain Elevation Data (Danielson and Gesch 2011), a 30 arc-second resolution raster dataset, which produced mean elevation and standard deviation values for each HUC using Zonal Statistics in ArcMap.

Finally, we calculated two stream variables, total stream length (TSL) and stream diversity (H), for each HUC by using the HYDRO1K dataset (USGS 2000), a 30 arc-second resolution polyline shapefile. We obtain total stream length and abundance of Strahler stream order values (Strahler 1957) using Spatial Join in ArcMap. For each HUC, we calculated total stream length (km) and a Shannon diversity index as crude measurements of availability and diversity of aquatic habitats in the landscape. To calculate the Shannon diversity index, we used stream order (e.g., 1-6) and total stream length within each stream order as abundance (see Knouft and Page 2011). We calculated the mean terrestrial net primary productivity (Pg C/yr; abbreviated by NPP) for each HUC using data from Zhao and Running (2010). Finally, we used Pleistocene glaciation data (i.e., glacial maximum of the Wisconsin) from Dyke (2004) to calculate nearest distance (GLD) from the center of each HUC to the Late Wisconsin North American ice sheet complex.

Data analysis

For all quantitative analyses, we included all HUCs with and without turtle species present. Because climate variables can be correlated (i.e., multicollinearity), we used a correlation matrix to remove variables that were correlated (> 0.6), and to improve model stability. To attain normality within the data, all explanatory variables were standardized, and our response variable, total species richness, was log transformed.

Using Program R (R Development Core Team 2015), we examined spatial autocorrelation and directional influences (semivariogram function and nlme package, R, Pinheiro et al. 2013) between measured sample points (i.e., HUCs). To account for spatial autocorrelation within each of the six datasets (i.e., specified groups of turtle species), we ranked five different spatial correlation structures (corSpatial function: spherical, exponential, gaussian, linear and rational),

only including the response variable (species richness) and spatial covariates (latitude and longitude). Generalized least squares (GLS) models fit with the aforementioned spatial correlation structures (Dormann et al. 2007), were ranked using Akaike Information Criterion (AIC; Burnham and Anderson 2004). Subsequently, we determined that a gaussian spatial correlation structure fit the data best for each of the six datasets. Using a GLS model fit with the gaussian spatial correlation structure, we tested the effects of geographic, climate, topography, and stream channel variables on species richness for each dataset. Finally, we determined a group of top models (95% confidence set) that best fit each dataset (package MuMin, Barton and Barton 2014), and model averaged to determine estimates of our most influential variables (Burnham and Anderson 2004).

Results

Species richness patterns

Overall turtle richness within North America was greatest in the southeastern United States. In this region, the highest turtle diversity was located in coastal drainages of the Gulf of Mexico, predominantly the Mobile Bay and Apalachicola River drainages (Fig. 1). Two assemblages of turtle species mirrored this pattern: all freshwater turtles combined and Emydidae species (Fig. 1). Kinosternidae exhibited a different pattern with three geographic centers of high diversity located in Mexico (Fig. 1).

Hypotheses tests

Our spatial regression GLS models predicting total turtle species richness in North America determined that mean annual temperature, mean precipitation of the warmest quarter, stream diversity, mean net primary productivity, and coefficient of variation of elevation were

significant and positive predictors; while latitude was a significant and negative predictor (Table 1). Our aquatic turtle richness model found similar important predictors as the total turtle richness model with the exception of temperature seasonality being a significant and position predictor and the omission of annual mean temperature (Table 1). For freshwater turtle richness, climatic variables were not found significant, and coefficient of variation of elevation, stream diversity, and mean primary productivity were significant and positive predictors. Similar to the previous models, latitude was a significant and negative predictor of freshwater turtle richness. Our GLS models found annual mean temperature, coefficient of variation of elevation, precipitation of the warmest quarter, and temperature seasonality to be significant and positive predictors and latitude to be a significant and negative predictor of species richness for Terrestrial species. For Emydidae species, GLS models found two significant and positive predictors, coefficient of variation of elevation and mean primary productivity, and one significant and negative predictor, latitude. In the Kinosternidae dataset, we found significant and positive predictors to be precipitation of the warmest quarter, stream diversity, and coefficient of variation of elevation. Similar to the all other datasets, latitude was significantly and inversely related to Kinosternidae species richness (Table 1).

Phylogenetic and guild tests

Although all our spatial regression GLS models predicting turtle species richness in our six datasets found a significant inverse relationship with latitude (i.e., increased richness towards the equator), and a significant and positive relationship with the coefficient of variation of elevation (Table 1), our models, in general, found varying results among the six datasets suggesting guild and phylogenetic constraints being important for regulating species richness in North American turtles. For example, GLS models found a significant and positive relationship with mean

primary productivity with the exception of the models using the terrestrial and Kinosternidae datasets (Table 1). The stream diversity variable was a significant and positive predictor in all regression models with the exception of the models using the terrestrial and Emydidae datasets. Additionally, our GLS models found at least one significant and positive climatic predictor with the exception the models using the freshwater and Emydidae datasets.

Discussion

Our results highlight several aspects of contemporary distributions of North America turtles: 1) a latitudinal diversity gradient exists as evident by the inverse relationship of species richness and latitude in all our spatial regression modeling analyses, 2) topographic heterogeneity influences species richness regardless of guild or family, and 3) climatic variables, stream diversity, and mean primary productivity are important predictor for turtles species richness but to a lesser degree than latitude and topographic heterogeneity. Overall, our results provide support for multiple hypotheses explaining broad-scale species richness patterns, but in particular, they mostly provide support for two universal hypotheses, latitudinal and topographical, for North America turtles. It appears that North America turtle species richness patterns are complex and are driven by a combination of latitude, elevation, climatic, productivity, and habitat variables, and their interactions. The incongruence of informative variables among our datasets suggests a phylogenetic and/or guild (i.e., freshwater, aquatic, and terrestrial) constraint on turtle distributions, which is similar to United States fishes (Knouft and Page 2011). Therefore, our research highlights the importance of considering these constraints within groups, especially for studies focusing broad taxonomic groups, when constructing and interpreting models predicting

contemporary species richness patterns but also models predicting range/habitat shifts due to climate change.

Latitudinal hypothesis

The inverse relationship between species richness and latitude has been documented in numerous groups, such as trees, mammals, birds, anurans, some orders of invertebrates, and fish (reviewed by Pearson and Boyero 2009), but remains elusive for other groups (e.g., salamanders and caddisflies; Pearson and Boyero 2009) in particular turtles (Iverson 1992; Hecnar 1999; Angielczyk et al. 2015). Our analyses are contrary to the findings of Iverson (1992) and Hecnar (1999) that no latitude-species richness trend exists for turtles, but partially corroborates the findings of Angielczyk et al. (2015) that recovered an inverse relationship with a caveat. Angielczyk et al. (2015) found incongruent results pertaining to latitudinal diversity gradients among their dataset of turtle species. They found inverse relationship between latitude and species richness in aquatic turtles, on several continents (e.g., South America, Africa, and Europe), and within several families (e.g., Pelomedusidae, Podocnemidae, and Testudinidae), but they did not recover latitudinal gradients in other families, guilds, and continents, in particularly North America. Other caveats in comparing our results with other studies are: we included areas without turtles (i.e., HUCs without turtle species), did not include equatorial areas (i.e., Central and South America) needed for us to fully understand how latitudinal gradients affect turtles diversity in the Western Hemisphere, and incorporated all contemporary turtles species except sea turtles.

A central tenet of biogeography is understanding species richness patterns. However, an inverse relationship between species richness and latitude at best only spatially characterizes

species richness patterns within a geographic area and fails to elucidate the underlying local, regional, and historical processes which create and maintain more species near the equator (Willig et al. 2003; Hawkins and Diniz-Filho 2004; Knouft and Page 2011). Many hypotheses have been formulated which recognize that latitude is correlated with abiotic variables (Lamolino et al. 2006). Therefore, we attempt to explain North America turtle species richness in the context of primary abiotic variables and discuss the following hypotheses for which our modelling analyses supported: topography, climatic, seasonality, and productivity.

Topography hypothesis

In general, greater habitat heterogeneity has been hypothesized as an explanation for latitudinal diversity gradients (MacArthur and Connell 1966). For instance, greater topographic heterogeneity is often associated with greater climate variance and hence increased niche space, even at local-spatial scale (see Leutner et al. 2012). For North America turtles, topographic heterogeneity (CV elevation) was informative for predicting contemporary species richness. Our spatial regression GLS models found a positive relationship with topographic heterogeneity, which was similar to other published studies. For example, topographic relief was positively related to species richness of both amphibians and reptile species richness in China (Qian et al. 2007). Owen (1989) found a positive relationship between elevational variance and species richness in turtles and other reptiles of Texas, USA.

Species richness, in general, exhibits an elevational diversity gradient (Sanders and Rahbek 2012), where species richness is greatest in the mid-elevations and decreases toward the extreme high and low elevations. Many taxonomic groups' species richness (fish - Bhatt et al. 2012; Knouft and Page 2011; diatoms - Wang et al. 2010; invertebrates - Wang et al. 2010; frogs

- Goyannes-Araújo et al. 2015; but see Simpson (1964) and Wang et al. (2010) for the contrary) show a strong effect along elevation gradients, sometimes in small geographic areas. However, in our study, mean elevation was not an important variable in predicting turtle species richness in our spatial regression GLS models. The lack of importance of mean elevation in our spatial models could be explained by the inclusion of HUCs without turtles, in particularly northern HUCs in Canada and the arctic, which have low mean elevations or that elevation influences turtle species richness on a local scale.

Climatic hypotheses

There are several hypotheses proposed as explanations for species richness patterns that are predicated on one or a combination of climatic variables, such as precipitation (aridity; Rohde 1992; Lomolino et al. 2006) and temperature. One such hypothesis is the physiological tolerance hypothesis (Currie et al. 2004), which posits species richness is related to species' tolerance to local environmental conditions. Therefore, more tolerable environmental conditions, such as warm and wet conditions of the tropics (see Kleidon and Mooney 2000; Hawkins et al. 2003a), would favor greater species richness. Similar to the physiological tolerance hypothesis, Wiens and Donoghue (2004) proposed the tropical conservatism hypothesis, which posits that the tropical environment is the ancestral state of the planet. Many clades, therefore, have not evolved adaptations for the environmental conditions (cold and dry) of extratropics regions.

Our results suggest that precipitation and temperature influences contemporary turtle distributions in North America. Mean precipitation of the warmest quarter had a positive relationship on turtle species richness in most of our modeled datasets. Similarly, mean precipitation of the wettest month was positively related to global turtle species richness (Iverson

1992); however, this relationship was largely driven by turtle species within the family Trionychidae. Additionally, both Angielczyk et al. (2015) and Rödder et al. (2013) found precipitation important in predicting turtle species richness and niches, respectively.

Temperature, in general, is an important abiotic variable in determining species distributions in several vertebrate groups (e.g., fish – Knouft and Page 2011; Griffiths et al. 2013; mammals – Owen 1990) including turtles (Schall and Pianka 1977; 1978; Iverson 1992, Rödder et al. 2013; Angielczyk et al. 2015). This is particularly true for ectothermic animals, including turtles that are restricted to climatic regions (both latitudinally and elevationally) causing them to regulate body temperatures within a tolerable range, largely through behavioral responses including basking, shade seeking, and brumation. Temperature extremes ultimately may limit the distribution of turtles by exposure to lethal critical thermal maxima or minima of adults, eggs, or neonates, or by exceeding a physiological limit (Huey and Stevenson 1979) perhaps during brumation. It is also possible that seasonal climates do not allow adequate time for development of eggs and embryos (St. Clair and Gregory 1990). Additionally, regions with warmer temperatures can "promote higher metabolic rates and shorter generation times" thereby increasing the rate of speciation (Lamolino et al. 2006). Despite the importance of temperature to ectotherms, those variables were only informative for three data sets within our analysis: total, aquatic, and terrestrial turtle species richness.

Water availability

Stream diversity was an important predictor of species richness in all our data sets except the Emydidae and terrestrial species. Many terrestrial turtle species, especially the five *Gopherus* species, are not intrinsically linked to aquatic habitats relative to other groups, which explains the

lack of importance of stream diversity in these models. Although the majority of Emydidae species are either aquatic or semiaquatic, there are several terrestrial species, *Terrapene*, that do not rely solely on aquatic habitats and might have influenced the model results and exclusion of stream diversity. For example, in our freshwater dataset, which excluded terrestrial species (e.g., *Terrapene* and others) but includes all other species of Emydidae species along with the other aquatic and semiaquatic species, stream diversity was an important predictor of species richness.

The finding that turtle diversity is related to water availability, in general, is perhaps not surprising due to the aquatic proclivity of most turtle species. For example, 88% of turtle species in North America are fully aquatic or have at least a portion of their annual cycle dependent on aquatic habitats (van Dijk et al. 2014). Turtles rely on water availability to varying degrees both spatially and temporally. For example, *Graptemys* species (family Emydidae) are highly aquatic only leaving water to bask and nest, while many species within Kinosternidae inhabit ephemeral water sources and have the availability to aestivate on land during droughts. Even among those species best adapted to aridity (e.g., tortoises), none are found in the driest deserts (e.g., Arabian Peninsula, Choco, Atacama, Gobi, Baja Peninsula, interior Sahara) as noted by Morafka and Berry (2002). Less clear is the lack of a relationship between turtle richness and annual precipitation, which has been associated with turtle species richness in other regions (Rogers 1976; Schall and Pianka 1978; Owen and Dixon 1989) and globally (Iverson 1992).

Seasonality hypothesis

The seasonality hypothesis is predicated on the fact that species can become specialized in less variable and more predictable environments (Stevens 1989; Lomolino et al. 2006). Therefore, allowing for higher levels of species diversity. In general, species richness patterns should have

an inverse relationship with seasonality (Brown and Gibson 1983), especially globally where more species occur in the tropics (Stevens 1989). In some instances, temperature variability was inversely related to species richness patterns in both the Southern and Northern Hemispheres (Dunn et al. 2009). However, in other studies, only weak or non-significant relationships have been recovered (Currie and Paquin 1987; Currie 1991; Kerr 1999). In the case of North America turtles, our results, in general, were incongruent with the seasonality hypothesis as well as the findings of Angielczyk et al. (2015), who found an inverse relationship between turtle species richness and precipitation seasonality. Our models found the seasonality-species richness relationship was positive for the aquatic and terrestrial species richness datasets, and was driven by temperature seasonality and not precipitation. Our incongruence with the seasonality hypothesis (i.e., inverse relationship), where most studies have focused on terrestrial taxa, might be explained by water availability mitigating the extreme temperature variability, or the fact that our variable was based on terrestrial temperatures and not aquatic temperature. Many turtle species have the ability to aestivate or hibernate during periods of extreme weather (e.g., temperature and precipitation), which might explain our incongruence with the seasonality hypothesis (Ernst and Lovich 2009).

Productivity hypothesis

Scientists have long debated the exact nature of the relationship between species diversity and productivity (Šímová et al. 2013). While it might seem intuitive that the relationship would be positive across the spectrum, evidence largely supported a “hump-shaped” relationship, increasing from low to moderate values and decreasing at high levels of productivity (Gaston 2000). This relationship seems to generally hold true at small spatial scales, but not in all cases

or all organisms (Adler et al. 2011). However, in general, a positive relationship between productivity and species richness occurs at larger spatial scales (e.g., continental; Hawkins et al. 2003a,b; Šímová et al. 2013). Many explanations have been proposed to elucidate the mechanism behind the positive relationship between species richness and productivity (see Lomolino et al. 2006). However, it is generally thought that higher net primary productivity within a community will support more consumers within a community (Lomolino et al. 2006).

In the case of turtles, we found a positive relationship between total turtle richness and primary productivity, which appears to be driven by high species diversity (mostly driven by freshwater and aquatic species richness) and net primary productivity of the southeastern United States. This region is a biodiversity hotspot for numerous vertebrate groups (e.g., bivalves, amphibians, reptiles, and freshwater fish) and also primary producers (Lydeard and Mayden 1995; Jenkins et al. 2015), which may provide or support a diversity of prey items for turtle species. However, net primary productivity was not important in the terrestrial and Kinosternidae species richness datasets suggesting phylogenetic constraint within more terrestrial species (e.g., *Gopherus* and *Kinosternon*). Many of these terrestrial and Kinosternidae species occupy desert or arid habitats that are relatively unproductive (i.e., lower net primary productivity) in comparison to other habitats (e.g., swamps, rivers, lakes, and temperate forest). Therefore, precipitation is more important predictor of species richness for terrestrial and Kinosternidae species than net primary productivity because precipitation is related to the phenology, quantity, and quality germination of plants in these habitats.

Southeastern United States

Our observation of high aquatic turtle species diversity and endemism in the southeastern United States is not surprising because many other freshwater taxa achieve exceptionally high biodiversity in this region, including fish, snails, crayfish, and mussels (Lydeard and Mayden 1995; Taylor et al. 2007). North America is inhabited by approximately 25% of the known turtle species in the world (van Dijk et al. 2014), and the southeastern United States is already a known turtle hotspot (Iverson 1992; Buhlmann et al. 2009; Mittermeier et al. 2015). Besides contemporary climatic and productivity factors, another possible explanation for this high diversity is historical factors that are not taken into account in our models. There are multiple factors that may contribute to Southeastern United States turtle diversity. For example, the region 1) has been geologically stable (e.g., no volcanic activity or direct glacial impact) for millions of years limiting the number of extinctions and provided glacial refugia for northern species (see Rödder et al. 2013 for turtles), 2) has high geologic and physiographic diversity that promotes more habitats, and thus more speciation, 3) has had extended periods with tropical-like conditions (i.e., warm and wet) dating back to the Middle Eocene in the region promoting high metabolic rates and generation times for ectotherms, and 4) possess a large number of coastal rivers draining into the Gulf of Mexico that have repeatedly been inundated and exposed by glacial and interglacial sea level fluctuations causing a sequence of vicariant and dispersal events allowed for periods of species separation and mixing, fostering the diversity observed today (Thornbury 1965; Swift et al. 1986; Lamb et al. 1994; Lydeard and Mayden 1995; Bentley and Knight 1998; Rödder et al. 2013). These historical factors-species richness relationships undoubtedly exist on other continents (i.e., Southeast Asia; Sodhi et al. 2004), and future research on chelonians may be warranted to help understand global species richness patterns.

Conclusions

Species richness patterns of North American chelonians follow a latitudinal diversity gradient that is driven by a combination of climatic, productivity, topography, and stream diversity. However, the incongruence among our datasets highlights the importance of considering phylogenetic constraints and species guilds when interpreting species richness patterns. Additionally, the slight incongruence among our species richness models and others (Iverson 1992; Rödder et al. 2013; Angielczyk et al. 2015) likely stems from but not limited to differences in geographic scale (e.g., global vs. North America), sampling unit scale (e.g., HUC vs. latitudinal bins vs. point data), including areas without turtles, and independent variables used in the models. For example, Angielczyk et al. (2015) and Iverson (1992) conducted global analyses of turtle species richness, while our study was restricted to North America. The sampling unit for Angielczyk et al. (2015) was twenty 5° latitudinal bins, which is a larger scale sampling unit than HUC6. Also, Rödder et al. (2013) used Maxent software (Phillips et al. 2004, 2006), which uses maximum entropy models and point data. Further efforts in modeling patterns of species richness will benefit from inclusion of scale-specification and adjusting ecological inference. Finally, our findings highlight the use of environmental variables within species distribution modeling, and potentially the broader implications of using contemporary climate variables as species distribution predictors.

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Table 1 Summary of significant/suggestive coefficients after model averaging for each tested group (Total: All Species, A: Aquatic Species, F: Freshwater Species, T: Terrestrial Species, E: Emydidae species, K: Kinosternidae species. For Table 1, + and – denote positive and negative coefficients with 95% confidence intervals that do not overlap 0. NS, not statistically significant.

Variable	Abbreviation	Total	A	F	T	E	K
Coefficient of Variation of Elevation	CVE	+	+	+	+	+	+
Stream Diversity	H	+	+	+	NS	NS	+
Latitude	LAT	–	–	–	–	–	–
Net Primary Productivity	NPP	+	+	+	NS	+	NS
Annual Mean Temperature	AMT	+	NS	NS	+	NS	NS
Precipitation of Wettest Quarter	PWAQ	+	+	NS	+	NS	+

Fig. 1 Species richness of A) all North American turtles ($n = 84$), B) freshwater turtles ($n = 75$), C) Emydid turtles ($n = 43$), D) Kinosternid turtles ($n = 24$), E) terrestrial turtles ($n = 8$), and F) aquatic turtles ($n = 56$) per 6-digit hydrological unit code (HUCs). HUCs with no color contain zero turtle species. In all other HUCs, species richness is represented by a color gradient, blue to red (1 to 19 turtle species).
279x361mm (300 x 300 DPI)