Including Fossils in Phylogenetic Climate Reconstructions: A Deep Time Perspective on the Climatic Niche Evolution and Diversification of Spiny Lizards (*Sceloporus*)

A. Michelle Lawing,[1,]* **P. David Polly,**[2,3] **Diana K. Hews,**[4] **and Emília P. Martins**[3,†]

1. Department of Ecosystem Science and Management, Texas A&M University, College Station, Texas 77845;   2. Department of Geological Sciences, Indiana University, Bloomington, Indiana 47405;   3. Department of Biology, Indiana University, Bloomington, Indiana 47405; 4. Department of Biology, Indiana State University, Terre Haute, Indiana 47809

abstract: Fossils and other paleontological information can improve phylogenetic comparative method estimates of phenotypic evolution and generate hypotheses related to species diversification. Here, we use fossil information to calibrate ancestral reconstructions of suitable climate for *Sceloporus* lizards in North America. Integrating data from the fossil record, general circulation models of paleoclimate during the Miocene, climate envelope modeling, and phylogenetic comparative methods provides a geographically and temporally explicit species distribution model of *Sceloporus*-suitable habitat through time. We provide evidence to support the historic biogeographic hypothesis of *Sceloporus* diversification in warm North American deserts and suggest a relatively recent *Sceloporus* invasion into Mexico around 6 Ma. We use a physiological model to map extinction risk. We suggest that the number of hours of restriction to a thermal refuge limited *Sceloporus* from inhabiting Mexico until the climate cooled enough to provide suitable habitat at approximately 6 Ma. If the future climate returns to the hotter climates of the past, Mexico, the place of highest modern *Sceloporus* richness, will no longer provide suitable habitats for *Sceloporus* to survive and reproduce.

Keywords: paleobiogeography, climate, evolution, extinction risk, Miocene, *Sceloporus*.

Introduction

Recently, scientists have worked urgently toward a new synthesis of ecological, biogeographic, and phylogenetic tools in an effort to predict the effects of imminent climate change on specific organisms (e.g., see reviews by Salamin et al. 2010; Ronquist and Sanmartín 2011). With new advances in the available data, computation, and theory, one of the most promising approaches has been to combine geographic climate niche modeling with phylogenetic comparative methods (e.g., Dormann et al. 2009; Kozak and Wiens 2010; Schnitzler et al. 2012; Lavergne et al. 2013; Meseguer et al. 2015). The results have been intriguing but heterogeneous, emphasizing that any detailed forecast may depend on the specific climatic variables and phylogenetic methods employed (e.g., Evans et al. 2009). Here, we go one step further toward a comprehensive synthesis by adding paleontological information, mapping the climate tolerances of hypothetical ancestors onto paleoclimatic maps, and using fossils to calibrate our results. We illustrate the approach by analyzing diversification patterns in *Sceloporus* (spiny) lizards related to spatiotemporal climate and geography.

Climate niche modeling uses the massive databases of detailed climatic measures of each geographic site in which a species has been found to create a summary of the climate profile of that species (Franklin 2010; Peterson 2011). By overlaying these climate profiles on phylogenies, we can explore climate niche dynamics through time and compare past geologic or climatic events with hypothesized evolutionary changes along lineages under different evolutionary models (e.g., Graham et al. 2004; Hardy and Linder 2005; Evans et al. 2009). For example, using this type of approach, Lavergne et al. (2013) found that bird species that have evolved little in response to changes in climate are also prone to demographic decline. Others have found evidence that rates of climatic and species diversification are linked in both plants (Evans et al. 2009; Smith and Beaulieu 2009; Schnitzler et al. 2012) and animals (Graham et al. 2004; Knouft et al. 2006; Vieites et al. 2009; Kalkvik et al. 2012). The process of mapping climatic measures onto phylogenies raises some difficult concerns for population geneticists and other evolu-

tionary theoreticians (Meik et al. 2015), but these too are beginning to be addressed (Salamin et al. 2010).

Paleoclimate and fossil evidence offer a potentially powerful way to calibrate and verify any historical reconstruction (Losos 2011; Slater et al. 2012). For example, Yesson and Culham (2006) included paleoclimate evidence in phylogenetic climate niche modeling by projecting the reconstructed climate niche of a putative ancestor at one node of a phylogeny onto a geographic map of paleoclimate available at that time. They found suitable habitat for the ancestor in ancient times but in a different geographic region than extant species are currently found. Here, we use isotopically scaled general circulation models, which are complex mathematical models that infer the climate in ancient times from a combination of geological and other information about Earth's past ocean and atmosphere circulation (e.g., Braconnot et al. 2007). Reconstructed climate niches can be compared to the climates inferred by the general circulation models to identify regions of the world that were available to species living at a particular time and to compare those regions to the locations in which fossils have been found. For example, this approach has been used to show that climate changes over the Late Quaternary were faster than the evolutionary adaptation of reptilian species to the changes (e.g., Lawing and Polly 2011; Rödder et al. 2013).

The relationship between climate and diversification of *Sceloporus* lizards is particularly important because of the dramatic anticipated impact of recent climate change on this genus. Sinervo et al. (2010) estimated that 12% of local populations of *Sceloporus* lizards have gone extinct since 1975 and predicted that 20% of *Sceloporus* species will be extinct by 2080 due to the reduction of suitable habitat resulting from global climate change. *Sceloporus* is a large genus of more than 90 species of lizards (Bell et al. 2003). Although *Sceloporus* spp. are ectothermic homeotherms that maintain stable and high body temperatures during their active periods (Adolph 1990), interspecies variation in active body temperature is high (from 28.8° to 37.5°C; Andrews 1998). Other aspects of *Sceloporus* biology have also shown rapid evolutionary change that may be associated with climate. For example, viviparity has evolved multiple times within the genus (Méndez-de la Cruz et al. 1998), and *Sceloporus* has high variation in genomic arrangements (Hall 2009; Leaché and Sites 2009). Fortunately, *Sceloporus* has been studied extensively, and detailed modern phylogenies are available (Leaché and Sites 2009; Leaché 2010; Wiens et al. 2010).

Here, we combine geographic climate niche modeling with phylogenetic comparative methods to reconstruct the climatic and geographic history of *Sceloporus* lizards. We then calibrate our results using fossil occurrence data and isotopically scaled paleoclimate general circulation models developed for this purpose. Along the way, we identify climate

variables that are important in determining the geographic locations of suitable habitat for *Sceloporus*. We model the geographic location and extant lineage richness of the genus during past climates and compare them with physiologically based models of extinction risk.

To do this, we develop a deep time paleoclimatic model spanning the geological history of the *Sceloporus* genus, with an estimate for origination near 23 Ma (Leaché and Sites 2009). We used isotopically interpolated paleoclimate data to test these hypotheses because it is computationally intensive to run general circulation models with durations of millions of years, so good paleoclimatic models have been developed for only a few specific points in geological time. To estimate climate models at other points in time and to project synchronous climate niche estimates onto time-appropriate climate models, we use the paleophylogeographic approach. This approach was developed initially to analyze species responses to climate change over glacial-interglacial timescales (Lawing and Polly 2011; Rödder et al. 2013).

Methods

Species Occurrences (Living and Fossil)

We downloaded geographic occurrences of all *Sceloporus* species from the Global Biodiversity Information Facility (GBIF 2013) on March 17, 2013, and sorted them according to the operational taxonomic units of Leaché (2010). On the same date, we downloaded expert range maps from the International Union for Conservation of Nature Red List (IUCN 2012) and used these maps to vet occurrence data, deleting any samples from the data set that occurred outside the range maps. We retained occurrences that fell outside the range map of each species if they were accompanied by an accurate location and the taxonomic identity was well established. This vetting process resulted in 18,658 unique and georeferenced occurrences ($n = 53$ *Sceloporus* species).

Models of suitable habitat can be poor when sample sizes are low (Wisz et al. 2008). We supplemented GBIF occurrence data for two occurrence-poor species within their geographic ranges to bring the lowest sample size up to 10. Specifically, we added four points within the range of *Sceloporus grandaevus*, an endemic to Isla Ceravello in the Sea of Cortez, and four points within the range of *Sceloporus macdougalli*, a coastal endemic located in low elevations on the Pacific Slope in the state of Oaxaca. These points were arbitrarily chosen by randomly sampling from within the known geographic range of these species. We obtained 53 *Sceloporus* fossil occurrences in 28 unique spatiotemporal localities from the Paleobiology Database and sorted them into 1-million-year (myr) intervals.

Phylogenetic Ancestral Climate Reconstructions

We used BIOCLIM (Nix 1986; Nix and Busby 1986) to describe the habitats in which each extant *Sceloporus* species is found in terms of the minimum and maximum values of four climate variables including mean annual temperature, temperature seasonality, minimum temperature of the coldest month, and precipitation seasonality. The BIOCLIM model has been used frequently to map climate and geographic space along a phylogeny (e.g., Graham et al. 2004; Hardy and Linder 2005; Yesson and Culham 2006; Vieites et al. 2009) and is consistent with the multivariate climatic niche concept (Hutchinson 1957). We used a maximum entropy approach for species habitat modeling, Maxent (Phillips et al. 2006), to help identify which variables are useful in determining the presence of most *Sceloporus* species. Based on the preliminary analysis, we included temperature seasonality, minimum temperature of the coldest month, and precipitation seasonality, because they are especially relevant for describing *Sceloporus* species' suitable habitat (fig. 1). We also included mean annual temperature, because it is useful to compare that variable with past climate reconstructions of mean annual temperature and to compare our results with other studies on evolution of climatic niches.

To reconstruct ancestral climates, we mapped the minimum and maximum of each climate variable onto a posterior distribution of 1,000 dated phylogenetic trees (Leaché and Sites 2009). For each phylogeny, we used a phylogenetic generalized least squares regression to infer ancestral states of each climatic measure at each node (Martins and Hansen 1997; Martins and Lamont 1998). When we assume the usual Brownian motion (BM) model of phenotypic evolution (Felsenstein 1985), this phylogenetic generalized least squares approach yields exactly the same ancestral state estimates as do maximum likelihood and least squares parsimony methods (Martins 1999). In addition, we fit regressions using three different assumptions regarding the model of phenotypic evolution (Brownian motion, Ornstein-Uhlenbeck, and early burst) and used the corrected Akaike information criterion (AICc) to choose the model that best fit the data. We then used the parameters from the model with the best fit to transform the phylogenetic distance matrix used to reconstruct ancestral climate niches. Finally, we used linear interpolation between adjacent nodes to estimate the mini-
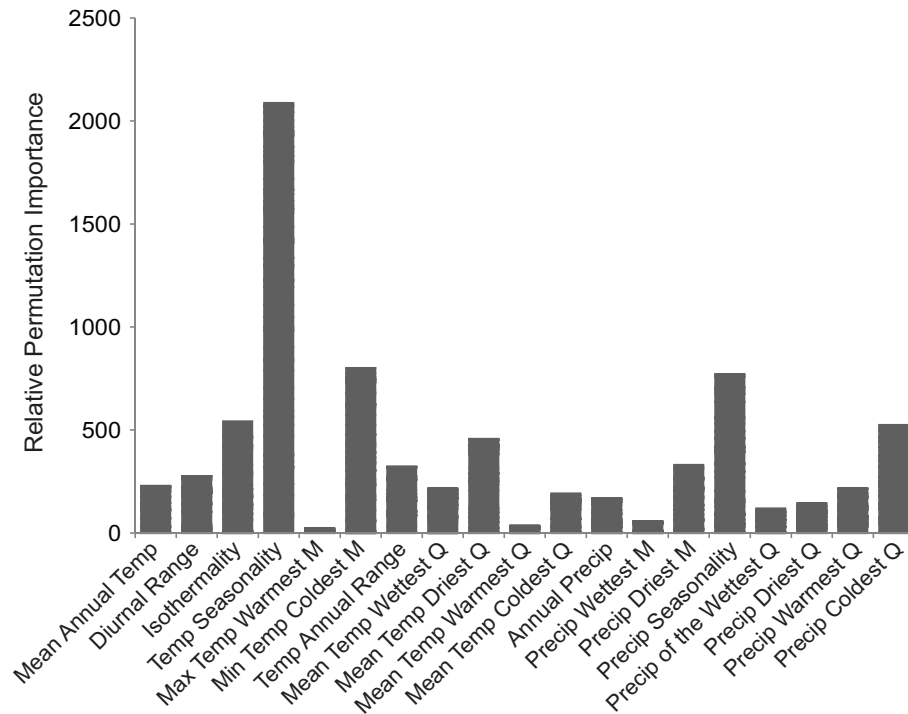

Figure 1: Stacked relative permutation importance for variables used to build a Maxent species distribution model for approximately half the species of the *Sceloporus* genus (*N* = 53). Most models rely heavily on *Sceloporus* response to temperature seasonality, minimum temperature of the coldest month, and temperature seasonality. M = month; max = maximum; min = minimum; precip = precipitation; Q = quarter; temp = temperature.

mum and maximum values of each climatic variable at each 1-myr interval.

We obtained a second set of ancestral climate estimates by incorporating climate information from relevant *Sceloporus* fossils. To get these data, we used paleoclimate map interpolations (see below) to infer the minimum and maximum of each climatic measure for these fossils and then incorporated these into our phylogenetic generalized least squares procedure for estimating ancestral climate variables. Specifically, we used a posterior distribution of 1,000 dated phylogenies and randomly placed fossils along lineages within the 1-myr time interval in which each fossil occurred. This process involved identifying the lineages present during the 1-myr time interval, randomly selecting the lineage to attach the fossil, randomly selecting a branching time within the time interval, and randomly selecting a branch length constrained by the branching time and the time interval. We repeated this analysis 1,000 times to estimate regression parameters. We conducted these phylogenetic analyses using ppgm, an R package available on GitHub specifically developed for this purpose (https://github.com/michellelawing /ppgm; R code is available in a zip file).[1] The ppgm package requires gieger for tree transformation and to estimate the parameters for the evolutionary models (Harmon et al. 2008) and ape for utility functions that allow the user to read, write, and manipulate phylogenetic trees (Paradis et al. 2004). All scripts and data for all analyses are available from the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad .69fc0 (Lawing et al. 2016).

Paleoclimate Interpolations

Paleoclimate interpolation maps were calculated at 1-myr intervals using a stable oxygen isotope curve derived from benthic foraminifera (Ruddiman et al. 1989), changes in which are proportional to global mean annual temperature, as a linear interpolator to generalize what the climate was like between the recent and the geographically explicit general circulation models of the Tortonian, a stage within the Miocene that occurred at 11.6–7.2 Ma (Micheels et al. 2011) and the middle Miocene, at approximately 15 Ma (Krapp and Jungclaus 2011). We sampled geographic space at 50-km equidistant points to reduce spatial redundancy, as the paleoclimate general circulation models have rather low spatial resolution, and also to sample at roughly the same geographic scale as the catchment area of a typical fossil locality. This left 9,699 geographic points for which we interpolated paleoclimate. Continental position and boundaries were adjusted at 5-myr intervals via plate tectonic recon-

structions (Scotese 2001). Paleoclimate-interpolated reconstructions are distributed within the ppgm package.

Multivariate Environmental Similarity Surface

We used multivariate environmental similarity surfaces (MESS) to further investigate the ancestral climate estimates that were calibrated with fossil occurrences. MESS is a measure of the similarity between a set of reference points and each point in geographic space where the analysis takes place. It has been used previously to predict suitable habitat by comparing the climate of the new environments with the climates in which species are already found (e.g., Elith et al. 2006, 2010). Here, we used MESS to compare paleoclimatic maps of North America with our ancestral estimates of the climate suitable for *Sceloporus*. To do so, we amalgamated our ancestral estimates across the genus by determining the range (minimum and maximum) of each climatic variable that was tolerable for at least one *Sceloporus* species existing at each of four points in time (2, 5, 13, and 20 Ma). We chose these four time points because they are somewhat evenly spread from the Miocene to present, thus demonstrating how the models progress over time within our analysis. We then compared these ranges of tolerance with the paleoclimatic maps of North America interpolated for that time period at a resolution of 50 km. Including fossils in the phylogenetic reconstructions of past suitable habitat should improve the estimations, so we used the phylogenetic models that included fossil occurrences for the MESS analysis.

We did this comparison separately on four variables reflecting measures that are likely important to ectotherms: (1) mean annual temperature, (2) temperature seasonality, (3) minimum temperature of the coldest month, and (4) precipitation seasonality. We then used MESS for a combined validation across the four climate variables in our analyses. In addition, we placed the fossils on MESS maps at the locations in which they were found and at the times to which they have been dated.

Hindcasting Unsuitable Habitat

When temperatures are high, lizards restrict even important activities to instead take refuge in cool retreats and thereby potentially risk extinction (Sinervo et al. 2010). Thus, following Sinervo et al. (2010), we calculated and mapped the number of hours of restriction to a thermal refuge (h_r) for lizards across North America throughout the last 20-myr history of *Sceloporus*. The number of hours of restriction to a thermal refuge ($h_r = 6.12 + 0.74 \times [T_{max} - T_b]$) is a function of the maximum environmental temperature (T_{max}) and the preferred body temperature of a particular species (T_b). It serves as a proxy for extinction

risk, since extinction is expected to occur when $h_r > 4$ (Sinervo et al. 2010). We used the mean temperature of the wettest quarter as T_{max} in our calculations because *Sceloporus* usually breed during that quarter (Sinervo et al. 2010) and there is a strong positive relationship between mean and maximum temperatures in the WorldClim database. For preferred body temperature (T_b), we considered four possibilities: 28°, 32°, 35°, and 38°C, using each to calculate h_r, because most *Sceloporus* have body temperatures ranging from 28.6° to 37.5°C (Andrews 1998; Sinervo et al. 2010). We then plotted the resulting values on a map of North America and highlighted regions in which $h_r > 4$.

Results

Species Occurrences

Although most modern *Sceloporus* are found in Mexico, they occur from Panama to the northern United States, with a latitudinal range from 8.7°N (*Sceloporus malachiticus*) to 48.7°N (*Sceloporus graciosus* and *Sceloporus occidentalis*). *Sceloporus* occur in habitats including forest ($n = 59$), savanna ($n = 5$), shrubland ($n = 37$), grassland ($n = 9$), rocky areas (e.g., inland cliffs and mountain peaks; $n = 29$), desert ($n = 11$), coastal intertidal marine ($n = 1$), and coastal supratidal marine ($n = 1$; IUCN 2012). *Sceloporus* range in altitude from sea level to 4,400 m asl, with *Sceloporus bicanthalis* and *Sceloporus palaciosi* occurring at the highest elevations just east of Mexico City in the Sierra Madres Oriental and just south of Mexico City in the Distrito Federal (Flores-Villela and Santos-Barrera 2007*a*, 2007*b*). Many species occur at sea level. Within *Sceloporus*, 10 species are listed as near threatened, vulnerable, endangered, or critically endangered (Hammerson 2007*a*, 2007*b*; Lavin et al. 2007; Mendoza-Quijano 2007*a*–2007*d*; Mendoza-Quijano and Flores-Villela 2007; Vazquez Díaz et al. 2007*a*, 2007*b*). The modern *Sceloporus* genus is the most rich where the tropical rainforest and deciduous forest biomes meet in southern Mexico and is second-most rich where these two biomes meet the desert biome in northeastern Mexico (fig. 2*A*).

The oldest *Sceloporus* fossils (20.6–16.3 Ma) were found in the Marsland Quarry in Nebraska and in the Wood Mountain Formation in Saskatchewan, Canada (fig. 2*B*). These fossils were assigned as *Sceloporus* sp. (fig. 2*C*). The fossil communities include large and small mammals, lizards, snakes, and fish. Fossil evidence from plants and herbivores indicates that precipitation in this region averaged somewhere between 500 and 1,000 mm per year, similar to today, and that mean annual temperatures were about 20.3°C, 10°C warmer on average and less seasonal in its temperature extremes than today (Leopold and Denton 1987; Miller et al. 1987; Janis et al. 2004). Phytoliths and other plant fossils

suggest that the region was covered by riparian deciduous forests mixed with shrub steppe grasslands that differed from today's steppe ecosystems in being dominated by C_3 plants, which gave way to more modern open grasslands dominated by C_4 photosynthesis in the Late Miocene at about 8–5 Ma (Leopold and Denton 1987; Strömberg 2002; Fox and Koch 2004). The lizard assemblage from Marsland Quarry is similar at the generic level to living herpetofaunas from the Sierra Madres and the southern desert and plains of North America (Savage 1960; Yatkola 1976). The morphology of the *Sceloporus* sp. teeth and jawbone segments that were preserved there most closely resemble modern *Sceloporus jarrovii* (Yatkola 1976). *Sceloporus jarrovii* is a montane species and occurs in rocky canyons, cliffs, and hillsides. It occurs mostly in rocky outcrops but also climbs trees. The vegetation associated with living *S. jarrovii* occurrences is oak woodland, thorn scrub, and mixed oak and pine (Stebbins 2003).

The next oldest *Sceloporus* fossils (16–13.6 Ma) are from the Egelhoff Quarry site in Nebraska, which contains a larger mammalian fauna including lagomorphs, rodents, insectivores, proboscideans, rhinos, horses, carnivores, bats, and artiodactyls, as well as lizards, snakes, and amphibians. The site occurred at the time of the Miocene Climatic Optimum and appears to have been frost free in the winter and to have had less continental zonation of rainfall than its modern climate (Holman 1987). The sediments suggest still waters surrounded by marshy grasses, with grasslands and gallery woodland in the region. One of the *Sceloporus* fossils had unicuspid teeth and was possibly ancestral to *Sceloporus merriami*, whereas the other had tricuspid teeth. *Sceloporus merriami* occurs on canyon walls and rocky slopes with sparse vegetation. It shelters in crevices and buries its eggs beneath soil surface (Hammerson et al. 2007).

Fitting Evolutionary Models and the Evolution of Climate Tolerances

The climate tolerances of *Sceloporus* most likely evolved in a manner similar to an Ornstein-Uhlenbeck (OU) process (table 1). Although this model is a simple representation of OU, it was the best fit of the three evolutionary models tested. The AICc is always less than two integers from the next best model, indicating that the OU model is a significantly better fit to the data. This result is robust regardless of the inclusion of fossils in the phylogenetic reconstructions. The strength of α, the OU parameter that represents the strength of the pull toward the optimum, had a few recognizable trends within and between the variables. We report the phylogenetic half-life, which is an intuitively appealing parameter and can be considered the resistance to adaptation (Hansen 1997). Temperature seasonality has by far the greatest phylogenetic half-life of the climate variables
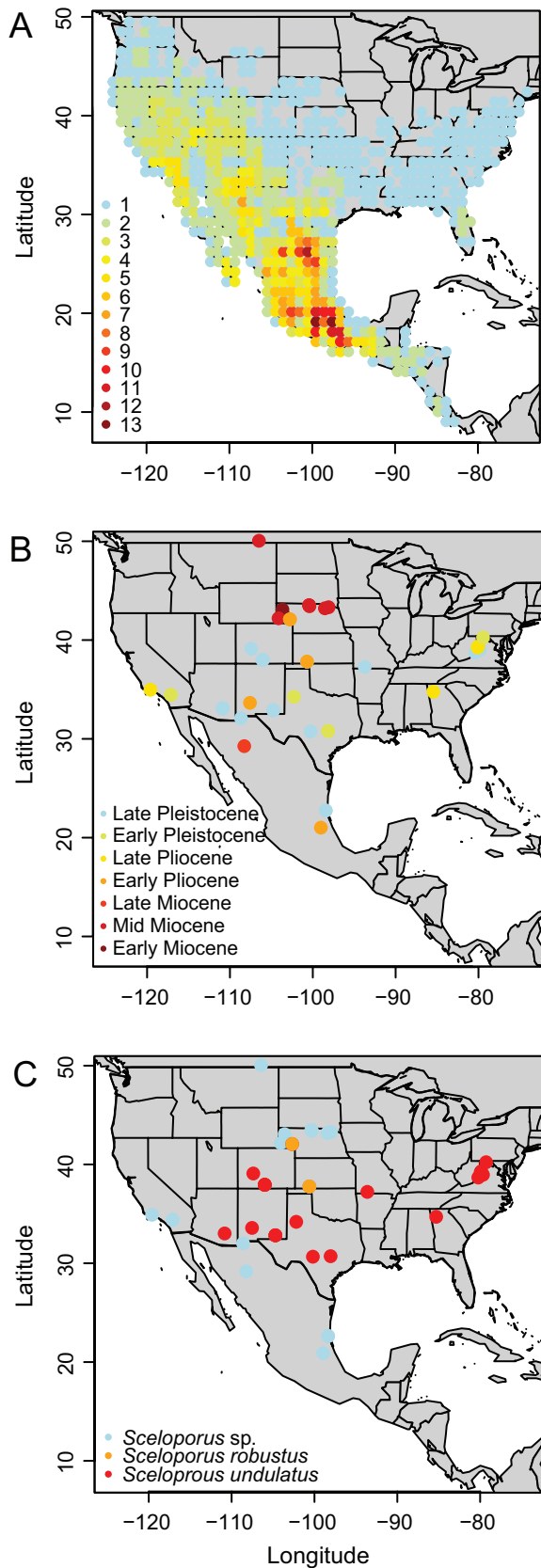
considered in this analysis. The maximum of each variable almost always has a higher phylogenetic half-life than the minimum of each variable, except when fossils are included for the minimum temperature of the coldest month.

Phylogenetic Ancestral Climate Reconstructions

Sceloporus climates during the most recent 10 myr can be reconstructed reasonably well from data based on modern taxa alone. During the most recent 10 myr and for all four climate variables, the ranges of climates reconstructed for ancestral *Sceloporus* were remarkably consistent, whether based on measures of the climates of modern taxa alone or calibrated by the inferred paleoclimates of the *Sceloporus* fossils (fig. 3). Results for some climate variables (e.g., mean annual temperature) were more concordant than others (e.g., temperature seasonality), and there appears to be high discordance between suitability of temperature seasonality and precipitation seasonality near the root of the phylogenies (fig. 3D, 3H). However, the reconstructions were reasonably good for the earliest *Sceloporus* for several of the climate variables (fig. 3B, 3F). For mean annual temperature, mean temperature of the coldest month, and precipitation seasonality, we were able to estimate ancestor climates for minimum measures better than the maximum measures.

Incorporating fossil data was critically important to reconstructing the deep history of the maximum measures of these variables and for both the minimum and maximum of temperature seasonality. For example, according to the paleoclimate maps, the very oldest *Sceloporus* fossils lived in a context of extreme seasonal changes in temperature (fig. 3D, high temperature seasonality), with a relatively low annual minimum temperature (fig. 3G, low mean temperature of the coldest month) and a relatively low seasonal precipitation range (fig. 3I, low precipitation seasonality) than do most extant *Sceloporus*. These sorts of directional changes cannot be detected by phylogenetic reconstructions unless fossil information is included. As a result, there was a discrepancy between ancestral reconstructions based on data from extant taxa and the inferences derived from the paleoclimate of known fossils that could be due to either the inability of phylogenetic comparative methods to detect a consistent long-term trend (e.g., resulting from the global climatic cooling following the Miocene Climatic Optimum)

Figure 2: Modern and fossil *Sceloporus* occurrences. *A*, Modern richness at 50-km equidistant points. The color of the point indicates the number of species; the higher the richness, the hotter the color. *B*, Fossil occurrences of *Sceloporus* binned and colored by the geological time period in which the organisms that produce the fossils lived. *C*, The same fossil occurrences as in *B*, but these are binned and colored by their assigned taxonomy. Data and scripts underlying this figure are deposited in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.69fc0 (Lawing et al. 2016).

Table 1: Best tree transformation model and the phylogenetic half-life

	BM	OU	EB	Parameter
Mean annual temperature:				
No fossils:				
Min	518.63	500.38	520.88	.25
Max	461.46	445.87	463.71	3.01
Fossils:				
Min	980.09	938.38	982.21	.00
Max	972.92	914.16	974.44	1.33
Temperature seasonality:				
No fossils:				
Min	631.11	592.45	633.36	3.65
Max	523.19	513.15	525.44	34.66
Fossils:				
Min	1,172.7	1,120.8	1,174.8	>100
Max	1,087.2	1,047.1	1,089.1	>100
Min temperature of coldest month:				
No fossils:				
Min	640.50	603.80	642.75	.25
Max	581.54	576.26	583.79	3.85
Fossils:				
Min	1,192.6	1,138.0	1,194.7	.69
Max	1,150.1	1,124.3	1,152.3	.23
Precipitation seasonality:				
No fossils:				
Min	919.87	916.48	922.12	1.82
Max	998.33	984.44	1,000.58	1.93
Fossils:				
Min	1,936.0	1,904.0	1,938.1	.69
Max	1,927.6	1,906.7	1,929.7	1.14

Note: BM = Brownian motion; EB = early burst; max = maximum; min = minimum; OU = Ornstein-Uhlenbeck. We used the minimum corrected Akaike information criterion to identify the best model fit of the phylogenetic reconstructions. The OU model is a significantly better fit for all of the variables, regardless of the inclusion of fossils. The parameter column reports the phylogenetic half-life ($\ln(2)/\alpha$) (Hansen 1997), where α is the optimized parameter for the OU model.

or problems with the general circulation models used to reconstruct the paleoclimate maps.

Paleoclimates and Multivariate Environmental Similarity Surfaces

Global warming was the dominant trend during the first 5 myr of *Sceloporus* diversification, with the warmest conditions occurring during the Miocene Climatic Optimum, ~16–14.8 Ma (Flower and Kennett 1994; Barnosky et al. 2003). Global cooling ensued with the increased production of cold Antarctic waters and the expansion of the East Antarctic ice sheet, which occurred at approximately 14.8–14.5 Ma. On the long-term average, global temperatures have been cooling ever since (Zachos et al. 2001).

The MESS maps (fig. 4) confirmed that suitable climates for *Sceloporus* were widely available in geographic space through time. The variables mean annual temperature and mean temperature of the coldest month were probably more restricting to *Sceloporus* distributions than temperature sea-

sonality and precipitation seasonality (fig. 4). In addition, these MESS maps indicate that southern North America probably did not provide suitable climates for *Sceloporus* during the early evolutionary history of this genus (fig. 4*S*, 4*T*). The multivariate MESS maps show that the fossil occurrences are in the areas of highest similarity (red areas in fig. 4*Q*–4*T*), with their MESS scores showing >90% similarity between paleoclimate and the fossil-informed phylogenetic reconstructions. There is less available suitable habitat for *Sceloporus* regarding the mean temperature of the coldest quarter at 5 and 13 Ma (fig. 4*J*, 4*K*). Nevertheless, the MESS maps confirm that the ancestral climate reconstructions are useful indicators of potentially suitable habitat for *Sceloporus* species lineages through time.

Hindcasting Unsuitable Habitat and Extinction Risk

Twenty million years ago, suitable habitat for *Sceloporus* appears to have been concentrated in central North America (fig. 4*T*). While no *Sceloporus* fossils are known from
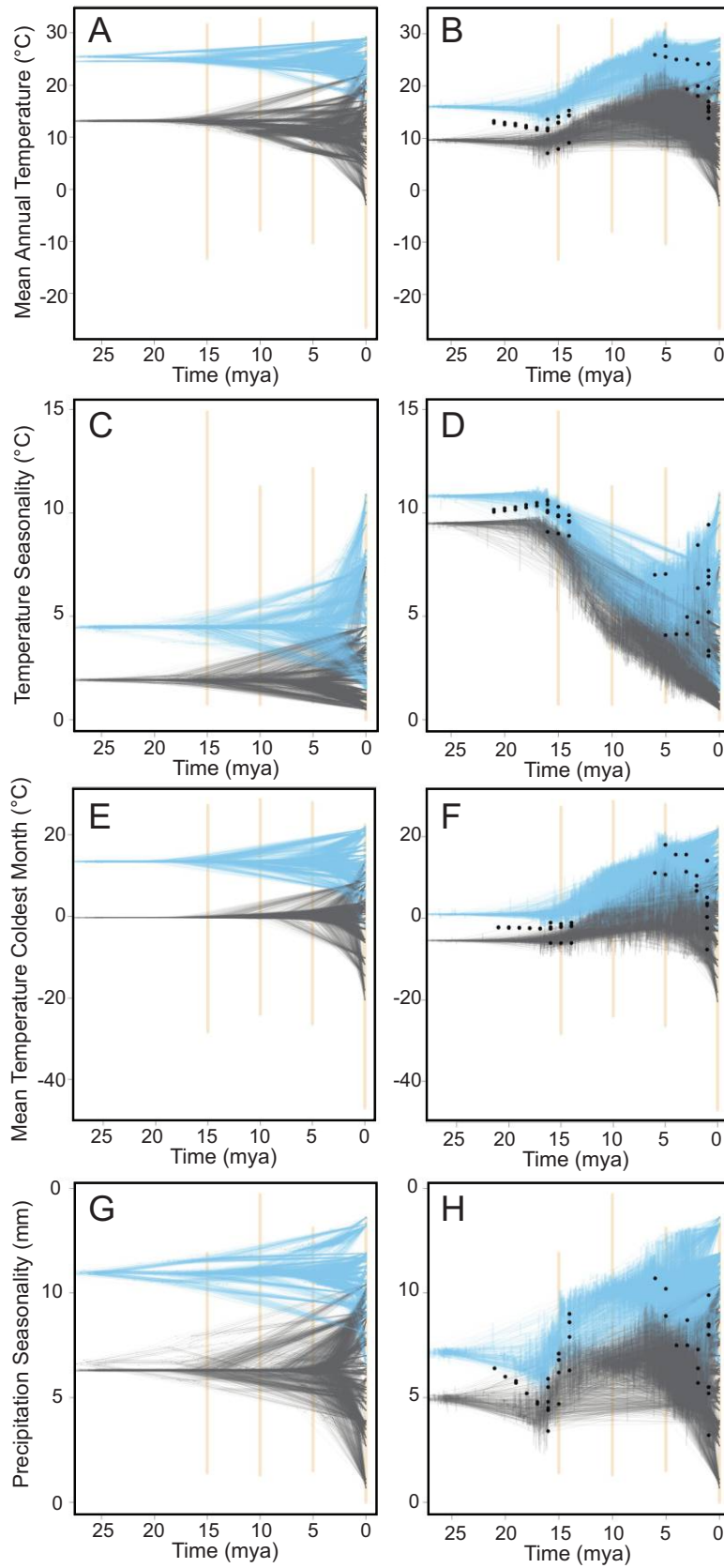
south of this area, three fossil sites provide glimpses of the environment. A rich site dated around 22 Ma from Newton County, Texas, preserves a tropical coastal forest fauna with an amphiumid salamander, soft-shelled turtles, an erycine boid snake, an anguid lizard, tapirs, rhinos, rodents, extinct carnivores, and other mammals (Albright 1994, 1999). Farther inland, a fauna of about the same age from Big Bend, Texas, suggests a drier subtropical savanna that includes an extinct helodermatid lizard, a didelphid marsupial, small to medium-sized rodents, carnivores, camels, and a small rhino (Stevens 1977). During the onset of global cooling at approximately 14.8–14.5 Ma, all of our estimates (regardless of variable set and phylogenetic hypothesis) show a slow southward geographic expansion during this period, producing a highly suitable habitat across the center of North America.

On the long-term average, global temperatures have been cooling ever since (Zachos et al. 2001), with a break in global cooling occurring at approximately 9–7 Ma (Prothero 1998), before beginning again. If the age of the crown clade is approximately 23 Ma, as we assume in our analysis and as calculated by Leaché and Sites (2009), *Sceloporus* species richness appears to have been relatively stable after the initial bout of diversification and continuing through the lag in cooling (from 14 to 7 Ma). *Sceloporus* underwent a second burst of speciation at the end of the break, when global cooling began again at the time that grasslands expanded across the Great Plains of North America (~7 Ma). *Sceloporus* reached current levels of species richness at about 6 Ma. Many species with modern geographic distributions in Mexico had greatly reduced or no suitable habitat in Mexico before ~6 Ma.

Mapping extinction risk through time, we found that most of Mexico was inhospitably hot before 5 Ma for species with body temperatures 32°C or lower (fig. 5*B*–5*D*, 5*F*–5*H*). It would have been difficult for species with such low body temperatures to maintain enough activity to find mates and eat, because they would have been restricted to thermal retreats for long daily periods. The fossils indicate that early *Sceloporus* were found at higher latitudes, and these species would have had little pressure to spend long hours in thermal refuge, regardless of their body temperature. However, the MESS maps indicate that there is moderately suitable habitat for early *Sceloporus* in the northern regions of Mexico. If *Sceloporus* actually inhabited this region, the species would have had to maintain body temperatures >35°C. Thus, the fossil locality at 5 Ma likely represents a species that had a very high body temperature

(fig. 5*J*). Species with body temperatures ≥38°C did not have any locations or times in our analyses in which they were restricted to <4 h of daily activity.
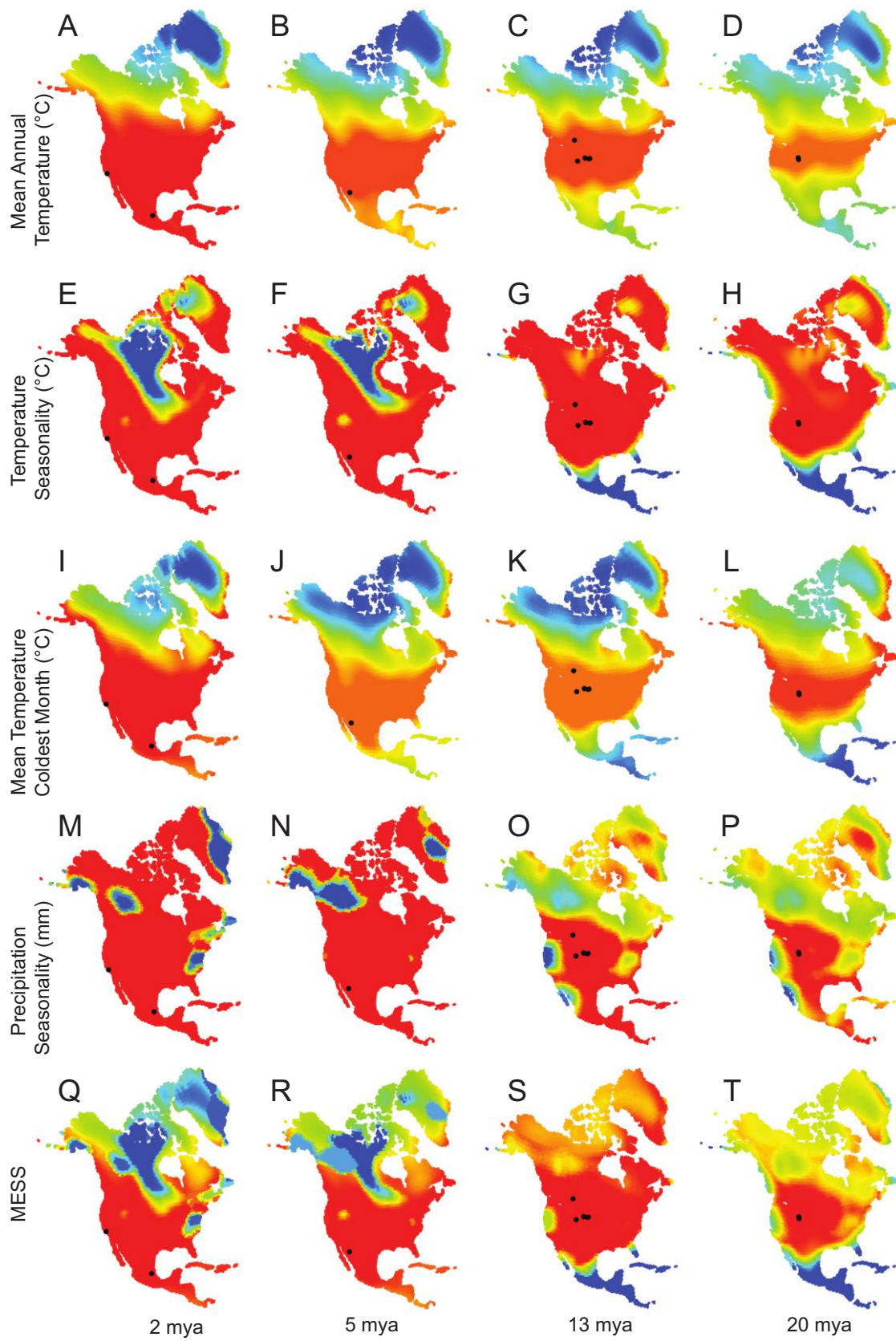
All of our analyses greatly overestimated where *Sceloporus* actually occurs today, finding moderately suitable *Sceloporus* habitat in Greenland, Alaska, and the Caribbean islands (fig. 4). Our hindcast ranges can thus be considered conservative in regard to where *Sceloporus* could not have lived in the past. Most likely *Sceloporus* had a smaller range than our hindcasts suggest because of dispersal limitations and biotic interactions that likely further restricted its geographic range. The geographic results for models with fossil calibrations were similar to those for models without fossil calibrations in more recent times. Deeper in the phylogeny, fossil calibrations had a more important effect, leading to projections that were always geographically north of those without fossil calibration.

Discussion

Our results emphasize the importance of incorporating fossil data and paleontological approaches into the reconstruction of historical climates and biogeographies, particularly over very long periods of time. Although phylogenetic comparative methods did a good job back to 10 Ma, older models of paleoclimate and geographic range benefited from including the associated paleoclimate data from the 53 fossil localities. Fossil information was especially important for inferring variables relevant to temperature, seasonality, and fluctuation. The mapping of extinction risk suggests that *Sceloporus* is particularly vulnerable to rapid global warming because the current center of diversification will become completely inhospitable.

There are two sources of uncertainty that we did not account for in this analysis: uncertainty in the interpolated paleoclimates and uncertainty in the age of the crown clade of *Sceloporus*. The interpolated paleoclimates were derived from two general circulation models that are known to underestimate temperature increases over northern latitudes, especially during the mid-Miocene (Micheels et al. 2007, 2011; You et al. 2009; Herold et al. 2011). That bias might account for the slight trend in the mean annual temperature and the mean temperature of the coldest month (fig. 3*B*, 3*F*). It might also account for the trend in temperature seasonality (fig. 3*D*). However, the difference in the temperature seasonality during the Miocene and recent is greater than the variation within the Miocene general circulation

Figure 3: Ancestral reconstructions for the minimum (gray lineages) and maximum (blue lineages) of four climate variables for the posterior distribution of phylogenies. The *X*-axis represents time in millions of years before present (Ma [mya]). *A, C, E,* and *G* do not include fossils in the ancestral climate envelope estimations. *B, D, F,* and *H* include fossils in the estimations. Black points represent estimates of the climate in which the fossils occurred, and the beige bars represent the available climate at four points in the geological past. Data and scripts underlying this figure are deposited in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.69fc0 (Lawing et al. 2016).

Mean Annual Temperature (°C)

Temperature Seasonality (°C)

Mean Temperature Coldest Month (°C)

Precipitation Seasonality (mm)

MESS

A	B	C	D
E	F	G	H
I	J	K	L
M	N	O	P
Q	R	S	T

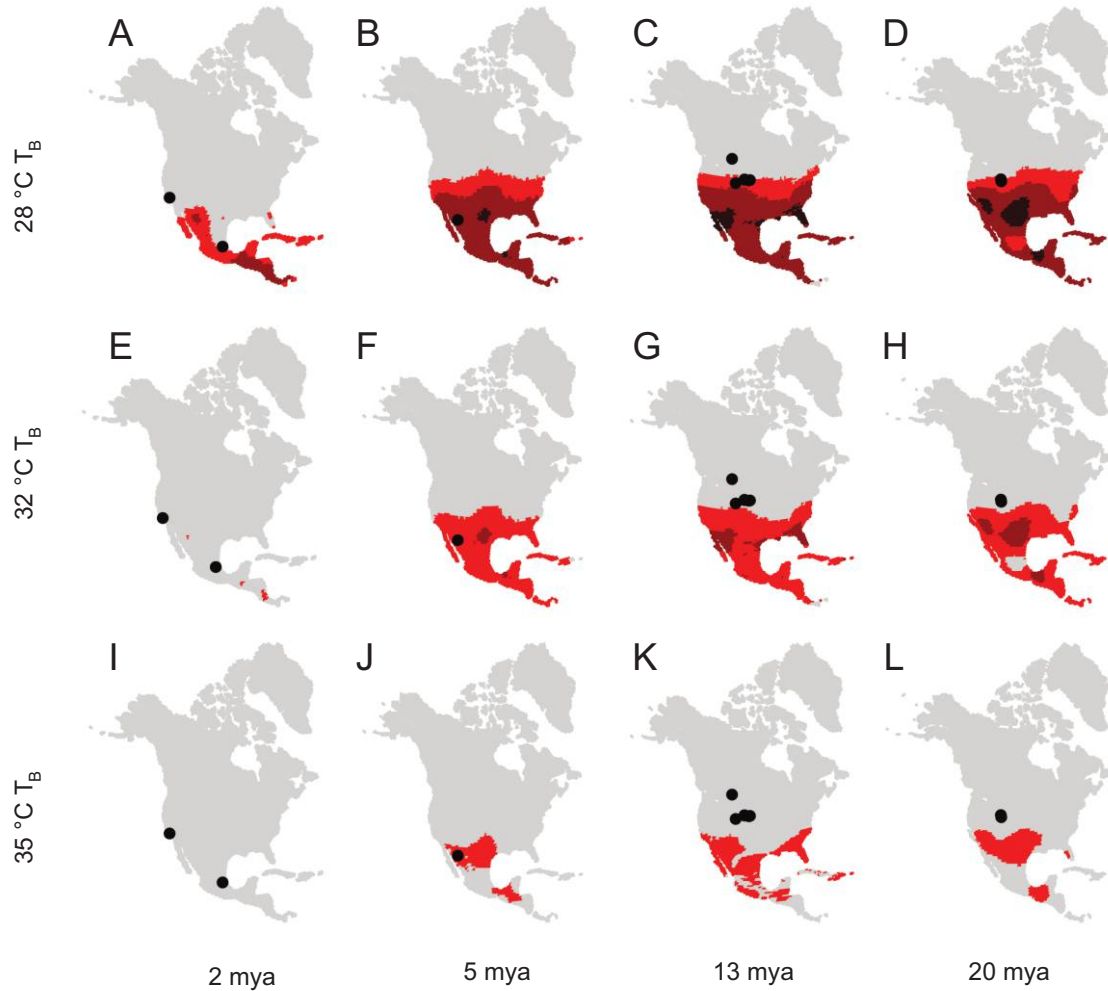2 mya   5 mya   13 mya   20 mya

Figure 5: Hours of restriction to a thermal refuge for species with various body temperatures. *A–D*, Hours of restriction for species with a body temperature of 28°C or lower. *E–H*, Hours of restriction for species with a body temperature from 28° to 32°C. *I–L*, Hours of restriction for species with a body temperature from 32° to 35°C. *A, E, I*, Models of restriction plotted at 2 Ma (mya). *B, F, J*, Models of restriction plotted at 5 mya. *C, G, K*, Models of restriction plotted at 13 mya. *D, H, L*, Models of restriction plotted at 20 mya. Shades of red indicate ≥4 h of restriction, and the darker the shade, the higher the number of hours of restriction. Gray shading indicates <4 h of restriction. Black points indicate fossil occurrences. Data and scripts underlying this figure are deposited in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.69fc0 (Lawing et al. 2016).

models or between Miocene general circulation models built with different algorithms but for the same time (Tong et al. 2009).

Our analysis was based on an estimated age of ~23 Ma for the origin of the crown clade of *Sceloporus* (Leaché and

Sites 2009), but the origin of the crown clade has also been estimated at 40–38 Ma (Zheng and Wiens 2015), ~45 Ma (Wiens et al. 2013), ~70 Ma (Pyron and Burbrink 2014), and 80–75 Ma (Schulte and Moreno-Roark 2010). The older divergence dates do not affect the climate niches at-

Figure 4: Univariate and multivariate environmental similarity surface (MESS) for reconstructed climate envelopes at 2, 5, 13, and 20 Ma (mya). MESS is the similarity of a set of reference points to the modeled paleoclimate at each geographic location. Hotter colors indicate higher similarity between the reference set and the modeled paleoclimate. The set of reference points includes all the lineages present for each modeled interval and consists of the reconstructed ancestral climate envelopes estimated by incorporating fossil occurrences. *A–D*, Mean annual temperature. *E–H*, Temperature seasonality. *I–L*, Minimum temperature of the coldest month. *M–P*, Precipitation seasonality. *Q–T*, The combined MESS maps. *A, E, I, M*, and *Q* show the models at 2 mya. *B, F, J, N*, and *R* show the models at 5 mya. *C, G, K, O*, and *S* show the models at 13 mya. *D, H, L, P*, and *T* show the models at 20 mya. Black points indicate fossil occurrences on the maps. Data and scripts underlying this figure are deposited in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.69fc0 (Lawing et al. 2016).

tributed to the fossils given the paleoclimate maps, but if true, would have resulted in a more drastic increase in the rate of change of the climate variables that show strong trends, because the suite of possible lineages a fossil might attach to is larger and younger. We repeated our analysis, pushing back the crown age of *Sceloporus* to 70 Ma, and found that our main conclusions still hold. The OU model was always the best fit to the data (both with and without including fossils in the phylogenetic reconstructions), younger node estimates were more reliable than the older node estimates, and there was no suitable habitat in the southern part of North America for this genus before the Early Pliocene, approximately 5 Ma and earlier.

Fossil data are especially useful for reconstructing evolutionary history of measures that show directional trends and that act on all lineages simultaneously, such as global warming or cooling, or as in our study, seasonal temperature fluctuations. Currently, phylogenetic comparative methods using data only from modern taxa are not able to detect directional trends and so are unlikely to estimate very old (>10 Ma) climates accurately unless fossil data are incorporated. Fossil records, though sparse, provide indisputable lines of evidence for where organisms occurred in the past and can be critical for inferring geographic history and relationship to paleoclimate (Svenning et al. 2011). Other researchers have also begun to use fossil data to corroborate the results of phylogenetic comparative analyses (Polly 2001; Finarelli and Flynn 2006) and to develop techniques for incorporating fossil evidence into phylogenetic comparative analyses (e.g., Slater et al. 2012; Bapst 2014). More will be needed as we work toward a new evolutionary synthesis that includes paleobiology (Fritz et al. 2013; Pennell and Harmon 2013).

Our estimates of the place of origin of *Sceloporus* are in sharp contrast to previous studies that suggested an origin in the southwestern United States (Hall 1973) or western Mexico (Sites et al. 1992). The earliest fossil *Sceloporus* are from Nebraska and Canada, our MESS analysis of paleoclimate maps finds very little suitable *Sceloporus* habitat in Mexico before 13 Ma, and our geographic reconstructions of extinction risk based on physiological models and activity periods conclude that Mexico was inhospitable to *Sceloporus* with normal ranges of body temperature before 6 Ma. Thus, several lines of evidence suggest that the genus *Sceloporus* originated in what is currently the central United States.

Other early fossils that have been inconclusively identified as *Sceloporus* are from Saskatchewan (16.3–13.6 Ma) and South Dakota (30.8–20.6 Ma; Holman 1970; Macdonald 1972), and other closely related lizard fossils from the same time period (Miocene) are also found in Nebraska: *Holbrookia* (Yatkola 1976) and *Phrynosoma* (Estes and Tihen 1964). Although more work is needed on fossil rep-

tiles in Miocene sites, especially in Mexico, no *Sceloporus* fossils have been reported from any of the Miocene sites that document squamate reptiles in the southwestern United States (eight sites) and Mexico (four sites; http://pbdb.org). Our results agree with earlier hypotheses that *Sceloporus* originated in a thorn scrub environment similar to that in the modern Sonoran Desert (Sites et al. 1992). In northwest Nebraska during the Miocene, the vegetation shifted from predominantly forest to shrubland at the time of *Sceloporus'* origin and to grassland by ∼8–6 Ma (Strömberg 2002). In contrast, the Sonoran Desert is a geologically recent biotic community (assembling at ∼8 Ma as the shrub of the earlier Miocene shifted southward) that was a tropical forest (not thorn scrub) during the Early Miocene (Martínez-Cabrera et al. 2006). Note also that Mexico was much hotter and drier at 20 Ma, so any future discoveries of Miocene *Sceloporus* fossils from there would only add support to our conclusion regarding the deep historical shifts in seasonal temperature fluctuation and the importance of including fossils in phylogenetic comparative reconstructions.

In *Sceloporus*, the evolution of viviparity may account, in part, for the pattern of diversification. Viviparity has arisen independently several times within the *Sceloporus* genus (Guillette et al. 1980; Shine 1985; Sites et al. 1992) and has been linked to cooling (Lambert and Wiens 2013). Pronounced global cooling during the evolution of *Sceloporus* provided environmental cues acting on all lineages at the same time that may have induced similar responses of egg retention and increased vascularity, potentially resulting in the parallel evolution of viviparity (Shine and Guillette 1988). The evolution of viviparity may also promote both prezygotic speciation through links to evolutionary shifts in communicative signals (Ossip-Klein et al. 2013) and postzygotic speciation because of subsequent maladaptation to warmer climates (Pincheira-Donoso et al. 2013). Further studies are needed to determine whether viviparity is also linked to the unusually high variation in chromosome number and sex chromosome heteromorphisms (Hall 2009), which has been linked to rapid diversification within *Sceloporus* (Leaché and Sites 2009).

The predicted effects of climate change on lizard diversity are alarming. Sinervo et al. (2010) found that in as few as 70 years, 39% of local populations and 20% of species are projected to become extinct. Our results confirm the urgency of this concern. Conservative climate models (Houghton et al. 2001) predict that the mean annual surface temperature in North America will increase by approximately 3.2° and 4.4°C by the years 2050 and 2080, respectively. Not since the Late Miocene, 9–5 Ma, has North America had mean annual temperatures that high (Barnosky et al. 2003). It was only after North America cooled to that temperature (∼6 Ma) that *Sceloporus* reached modern levels of species richness and expanded. Our models also suggest

that any *Sceloporus* with body temperatures lower than 38°C occurring in Mexico at 5 Ma would have been subject to very high levels of extinction risk. Most *Sceloporus* have body temperatures ranging from 28.6° to 37.5°C (Andrews 1998; Sinervo et al. 2010). Thus, if the future climate returns to the hotter climates of the past, Mexico, the place of highest modern *Sceloporus* richness, will no longer provide suitable habitats for *Sceloporus* to survive and reproduce.

Acknowledgments

Literature Cited

Adolph, S. C. 1990. Influence of behavioral thermoregulation on microhabitat use by two *Sceloporus* lizards. Ecology 71:315–327.

Albright, L. B. 1994. Lower vertebrates from an Arikareean (earliest Miocene) fauna near the Toledo Bend dam, Newton County, Texas. Journal of Paleontology 68:1131–1145.

———. 1999. Ungulates of the Toledo Bend local fauna (Late Arikareean, Early Miocene), Texas Coastal Plain. Florida Museum of Natural History Bulletin 42:1–80.

Andrews, R. M. 1998. Geographic variation in field body temperature of *Sceloporus* lizards. Journal of Thermal Biology 23:329–334.

Bapst, D. W. 2014. Assessing the effect of time-scaling methods on phylogeny-based analyses in the fossil record. Paleobiology 40:331–351.

Barnosky, A. D., E. A. Hadly, and C. J. Bell. 2003. Mammalian response to global warming on varied temporal scales. Journal of Mammalogy 84:354–368.

Bell, E. L., H. M. Smith, and D. Chiszar. 2003. An annotated list of the species-group names applied to the lizard genus *Sceloporus*. Acta Zoologica Mexicana 90:103–174.

Braconnot, P., B. Otto-Bliesner, S. Harrison, S. Joussaume, J. Y. Peterchmitt, A. Abe-Ouchi, M. Crucifix, et al. 2007. Results of PMIP2 coupled simulations of the mid-Holocene and Last Glacial Maximum. I. Experiments and large-scale features. Climates of the Past 3:261–277.

Dormann, C. F., B. Gruber, M. Winter, and D. Herrmann. 2009. Evolution of climate niches in European mammals? Biology Letters 6:229–232.

Elith, J., C. H. Graham, R. P. Anderson, M. Dudik, S. Ferrier, A. Guisan, R. J. Hijmans, et al. 2006. Novel methods improve prediction of species' distributions from occurrence data. Ecography 29:129–151.

Elith, J., M. Kearney, and S. Phillips. 2010. The art of modelling range-shifting species. Methods in Ecology and Evolution 1:330–342.

Estes, R., and J. A. Tihen. 1964. Lower vertebrates from the Valentine Formation of Nebraska. American Midland Naturalist 72:453–472.

Evans, M. E. K., S. A. Smith, R. S. Flynn, and M. J. Donoghue. 2009. Climate, niche evolution, and diversification of the "Bird-Cage" evening primroses (*Oenothera*, sections *Anogra* and *Kleinia*). American Naturalist 173:225–240.

Felsenstein, J. 1985. Phylogenies and the comparative method. American Naturalist 125:1–15.

Finarelli, J. A., and J. J. Flynn. 2006. Ancestral state reconstruction of body size in the Caniformia (Carnivora, Mammalia): the effects of incorporating data from the fossil record. Systematic Biology 55:301–313.

Flores-Villela, O., and G. Santos-Barrera. 2007a. *Sceloporus bicanthalis*. IUCN Red List of Threatened Species. Ver. 2012.1. http://www.iucnredlist.org.

———. 2007b. *Sceloporus palaciosi*. IUCN Red List of Threatened Species. Ver. 2012.1. http://www.iucnredlist.org.

Flower, B. P., and J. P. Kennett. 1994. The Middle Miocene climatic transition: East Antarctic ice sheet development, deep ocean circulation and global carbon cycling. Palaeogeography, Palaeoclimatology, Palaeoecology 108:537–555.

Fox, D. L., and P. L. Koch. 2004. Carbon and oxygen isotope variability in Neogene paleosol carbonates: constraints on the evolution of the C₄-grasslands of the Great Plains, USA. Palaeogeography, Palaeoclimatology, Palaeoecology 207:305–329.

Franklin, J. 2010. Mapping species distributions: spatial inference and prediction. Cambridge University Press, Cambridge.

Fritz, S. A., J. Schnitzler, J. T. Eronen, C. Hof, K. Böhning-Gaese, and C. H. Graham. 2013. Diversity in time and space: wanted dead and alive. Trends in Ecology and Evolution 28:509–516.

GBIF (Global Biodiversity Information Facility). 2013. *Sceloporus* occurrence records. Global Biodiversity Information Facility. http://www.gbif.org.

Graham, C. H., S. R. Ron, J. C. Santos, C. J. Schneider, and C. Moritz. 2004. Integrating phylogenetics and environmental niche models to explore speciation mechanisms in dendrobatid frogs. Evolution 58:1781–1793.

Guillette, L. J. J., R. E. Jones, K. T. Fitzgerald, and H. M. Smith. 1980. Evolution of viviparity in the lizard genus *Sceloporus*. Herpetologica 36:201–215.

Hall, W. P. 1973. Comparative population cytogenetics, speciation, and evolution of the crevice-using species of *Sceloporus* (Sauria, Iguanidae). PhD diss. Harvard University, Cambridge, MA.

———. 2009. Chromosome variation, genomics, speciation and evolution in *Sceloporus* lizards. Cytogenetic and Genome Research 127:143–165.

Hammerson, G. A. 2007a. *Sceloporus arenicolus*. IUCN Red List of Threatened Species. Ver. 2014.3. http://www.iucnredlist.org.

———. 2007b. *Sceloporus woodi*. IUCN Red List of Threatened Species. Ver. 2014.3. http://www.iucnredlist.org.

Hammerson, G.A., J. Vazquez Díaz, H. Gadsden, G. E. Quintero Díaz, P. Ponce-Campos, and P. Lavin. 2007. *Sceloporus merriami*.

IUCN Red List of Threatened Species. Ver. 2014.3. http://www .iucnredlist.org.

Hansen, T. F. 1997. Stabilizing selection and the comparative analysis of adaptation. Evolution 51:1341–1351.

Hardy, C. R., and H. P. Linder. 2005. Intraspecific variability and timing in ancestral ecology reconstruction: a test case from the Cape flora. Systematic Biology 54:299–316.

Harmon, L. J., J. T. Weir, C. D. Brock, R. E. Glor, and W. Challenger. GEIGER: investigating evolutionary radiations. Bioinformatics 21: 129–131.

Herold, N., M. Huber, and R. D. Müller. 2011. Modeling the Miocene Climatic Optimum. I. Land and atmosphere. Journal of Climate 24:6353–6372.

Holman, J. A. 1970. Herpetofauna of the Wood Mountain Formation (Upper Miocene) of Saskatchewan. Canadian Journal of Earth Sciences 7:1317–1325.

———. 1987. Herpetofauna of the Egelhoff site (Miocene: Barstovian) of north-central Nebraska. Journal of Vertebrate Paleontology 7:109–120.

Houghton, J. T., Y. Ding, D. J. Griggs, M. Noguer, P. J. van der Linden, X. Dai, K. Maskell, et al. 2001. Climate change 2001: the scientific basis. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge.

Hutchinson, G. E. 1957. Concluding remarks. Cold Spring Harbor Symposium on Quantitative Biology 22:415–457.

IUCN (International Union for Conservation of Nature). 2012. The IUCN Red List of Threatened Species. Ver. 2012.1. http://www .iucnredlist.org.

Janis, C. M., J. Damuth, and J. M. Theodor. 2004. The species richness of Miocene browsers, and implications for habitat type and primary productivity in the North American grassland biome. Palaeogeography, Palaeoclimatology, Palaeoecology 207:371–398.

Kalkvik, H. M., I. J. Stout, T. J. Doonan, and C. L. Parkinson. 2012. Investigating niche and lineage diversification in widely distributed taxa: phylogeography and ecological niche modeling of the *Peromyscus maniculatus* species group. Ecography 35:54–64.

Knouft, J. H., J. B. Losos, R. E. Glor, and J. J. Kolbe. 2006. Phylogenetic analysis of the evolution of the niche in lizards of the *Anolis sagrei* group. Ecology 87:29–38.

Kozak, K. H., and J. J. Wiens. 2010. Accelerated rates of climatic-niche evolution underlie rapid species diversification. Ecology Letters 13: 1378–1389.

Krapp, M., and J. H. Jungclaus. 2011. The Middle Miocene climate as modelled in an atmosphere-ocean-biosphere model. Climate of the Past 7:1169–1188.

Lambert, S. M., and J. J. Wiens. 2013. Evolution of viviparity: a phylogenetic test of the cold-climate hypothesis in phrynosomatid lizards. Evolution 67:2614–2630.

Lavergne, S., M. E. K. Evans, I. J. Burfield, F. Jiguet, and W. Thuiller. 2013. Are species' responses to global change predicted by past niche evolution? Philosophical Transactions of the Royal Society B: Biological Sciences 368:20120091.

Lavin, P., G. E. Quintero Díaz, G. A. Hammerson, H. Gadsden, and J. Vazquez Díaz. 2007. *Sceloporus maculosus*. IUCN Red List of Threatened Species. http://www.iucnredlist.org.

Lawing, A. M., and P. D. Polly. 2011. Pleistocene climate, phylogeny, and climate envelope models: an integrative approach to better understand species' response to climate change. PLoS ONE 6: e28554.

Lawing, A. M., P. D. Polly, D. K. Hews, and E. P. Martins. 2016. Data from: Including fossils in phylogenetic climate reconstructions: a deep time perspective on the climatic niche evolution and diversification of spiny lizards (*Sceloporus*). American Naturalist, Dryad Digital Repository, http://dx.doi.org/10.5061/dryad.69fc0.

Leaché, A. D. 2010. Species trees for spiny lizards (genus *Sceloporus*): identifying points of concordance and conflict between nuclear and mitochondrial data. Molecular Phylogenetics and Evolution 54: 162–171.

Leaché, A. D., and J. W. Sites. 2009. Chromosome evolution and diversification in North American spiny lizards (genus *Sceloporus*). Cytogenetic and Genome Research 127:166–181.

Leopold, E. B., and M. F. Denton. 1987. Comparative age of grassland and steppe east and west of the northern Rocky Mountains. Annals of the Missouri Botanical Garden 74:841–867.

Losos, J. B. 2011. Seeing the forest for the trees: the limitations of phylogenies in comparative biology. American Naturalist 177:709–727.

Macdonald, L. J. 1972. Monroe Creek (Early Miocene) microfossils from the Wounded Knee area, South Dakota. Science Center, University of South Dakota, Vermillion.

Martínez-Cabrera, H. I., S. R. S. Cevallos-Ferriz, and I. Poole. 2006. Fossil woods from Early Miocene sediments of the El Cien Formation, Baja California Sur, Mexico. Review of Paleobotany and Palynology 138:141–163.

Martins, E. P. 1999. Estimation of ancestral states of continuous characters: a computer simulation study. Systematic Biology 48:642–650.

Martins, E. P., and T. F. Hansen. 1997. Phylogenies and the comparative method: a general approach to incorporating phylogenetic information into the analysis of interspecific data. American Naturalist 149:646–667.

Martins, E. P., and J. Lamont. 1998. Estimating ancestral states of a communicative display: a comparative study of *Cyclura* rock iguanas. Animal Behaviour 55:1685–1706.

Meik, J. M., J. W. Streicher, A. M. Lawing, O. Flores-Villela, and M. F. Fujita. 2015. Limitations of climatic data for inferring species boundaries: insights from speckled rattlesnakes. PLoS ONE 10:e0131435.

Méndez-de la Cruz, F. R., M. Villagrán-Santa Cruz, and R. M. Andrews. 1998. Evolution of viviparity in the lizard genus *Sceloporus*. Herpetologica 54:521–532.

Mendoza-Quijano, F. 2007a. *Sceloporus chaneyi*. IUCN Red List of Threatened Species. http://www.iucnredlist.org.

———. 2007b. *Sceloporus exsul*. IUCN Red List of Threatened Species. http://www.iucnredlist.org.

———. 2007c. *Sceloporus goldmani*. IUCN Red List of Threatened Species. http://www.iucnredlist.org.

———. 2007d. *Sceloporus oberon*. IUCN Red List of Threatened Species. http://www.iucnredlist.org.

Mendoza-Quijano, F., and O. Flores-Villela. 2007. *Sceloporus megalepidurus*. IUCN Red List of Threatened Species. http://www .iucnredlist.org.

Meseguer, A. S., J. M. Lobo, R. Ree, D. J. Beerling, and I. Sanmartin. 2015. Integrating fossils, phylogenies, and niche models into biogeography to reveal ancient evolutionary history: the case of *Hypericum* (Hypericaceae). Systematic Biology 64:215–232.

Micheels, A., A. Bruch, J. Eronen, M. Fortelius, M. Harzhauser, T. Utescher, and V. Mosbrugger. 2011. Analysis of heat transport mechanisms from a Late Miocene model experiment with a fully-coupled atmosphere–ocean general circulation model. Palaeogeography, Palaeoclimatology, Palaeoecology 304:337–350.

Micheels, A., A. A. Bruch, D. Uhl, T. Utescher, and V. Mosbrugger. 2007. A Late Miocene climate model simulation with ECHAM4/ML and its quantitative validation with terrestrial proxy data. Palaeogeography, Palaeoclimatology, Palaeoecology 253:251–270.

Miller, K. G., R. G. Fairbanks, and G. S. Mountain. 1987. Tertiary oxygen isotope synthesis, sea level history, and continental margin erosion. Paleoceanography 2:1–19.

Nix, H. 1986. A biogeographic analysis of Australian elapid snakes. Atlas of Elapid Snakes of Australia 7:4–15.

Nix, H., and J. Busby. 1986. BIOCLIM, a bioclimatic analysis and prediction system. CSIRO annual report. CSIRO Division of Water and Land Resources, Canberra.

Ossip-Klein, A. G., J. A. Fuentes, D. K. Hews, and E. P. Martins. 2013. Information content is more important than sensory system or physical distance in guiding the long-term evolutionary relationships between signaling modalities in *Sceloporus* lizards. Behavioral Ecology and Sociobiology 63:1513–1522.

Paradis, E., J. Claude, and K. Strimmer. 2004. APE: analysis of phylogenetics and evolution in R language. Bioinformatics 20:289–290.

Pennell, M. W., and L. J. Harmon. 2013. An integrative view of phylogenetic comparative methods: connections to population genetics, community ecology, and paleobiology. Annals of the New York Academy of Sciences 1289:90–105.

Peterson, A. T. 2011. Ecological niches and geographic distributions (MPB-49). Princeton University Press, Princeton, NJ.

Phillips, S. J., R. P. Anderson, and R. E. Schapire. 2006. Maximum entropy modeling of species geographic distributions. Ecological Modeling 190:231–259.

Pincheira-Donoso, D., T. Tregenza, M. J. Witt, and D. J. Hodgson. 2013. The evolution of viviparity opens opportunities for lizard radiation but drives it into a climatic cul-de-sac. Global Ecology and Biogeography 22:857–867.

Polly, P. D. 2001. Paleontology and the comparative method: ancestral node reconstructions versus observed node values. American Naturalist 157:596–609.

Prothero, D. R. 1998. The chronological, climatic, and paleogeographic background to North American mammalian evolution. Pages 9–36 *in* C. M. Janis, K. M. Scott, and L. L. Jacobs, eds. Evolution of Tertiary mammals of North America. Vol. 1. Terrestrial carnivores, ungulates, and ungulatelike mammals. Cambridge University Press, Cambridge.

Pyron, R. A., and F. T. Burbrink. 2014. Early evolution of viviparity and multiple reversions to oviparity in squamate reptiles. Ecology Letters 17:13–21.

Rödder, D., A. M. Lawing, M. Flecks, F. Ahmadzadeh, J. Dambach, J. Engler, J. Habel, et al. 2013. Evaluating the significance of paleophylogeographic species distribution models in reconstructing quaternary rangeshifts of Nearctic Chelonians. PLoS ONE 8:e72855.

Ronquist, F., and I. Sanmartín. 2011. Phylogenetic methods in biogeography. Annual Review of Ecology, Evolution, and Systematics 42:441–464.

Ruddiman, W. F., M. E. Raymo, D. G. Martinson, B. M. Clement, and J. Backman. 1989. Pleistocene evolution of Northern Hemisphere ice sheets and North Atlantic Ocean. Paleoceanography 4:353–412.

Salamin, N., R. O. Wüest, S. Lavergne, W. Thuiller, and P. B. Pearman. 2010. Assessing rapid evolution in a changing environment. Trends in Ecology and Evolution 25:692–698.

Savage, J. M. 1960. Evolution of a peninsular herpetofauna. Systematic Zoology 9:184–212.

Schnitzler, J., C. H. Graham, C. F. Dormann, K. Schiffers, and H. P. Linder. 2012. Climatic niche evolution and species diversification in the Cape flora, South Africa. Journal of Biogeography 39:2201–2211.

Schulte, J. A., and F. Moreno-Roark. 2010. Live birth among Iguanian lizards predates Pliocene-Pleistocene glaciations. Biology Letters 6:216–218.

Scotese, C. R. 2001. Digital paleogeographic map archive on CD-ROM. PALEOMAP Project, Arlington, TX.

Shine, R. 1985. The evolution of viviparity in reptiles: an ecological analysis. Pages 605–694 *in* C. Gans and F. Billet, eds. Biology of the Reptilia. Academic Press, New York.

Shine, R., and L. J. J. Guillette. 1988. The evolution of viviparity in reptiles: a physiological model and its ecological consequences. Journal of Theoretical Biology 132:43–50.

Sinervo, B., F. R. Méndez-de la Cruz, D. B. Miles, B. Heulin, E. Bastiaans, M. Villagrán-Santa Cruz, R. Lara-Resendiz, et al. 2010. Erosion of lizard diversity by climate change and altered thermal niches. Science 328:894–899.

Sites, J. W., J. W. Archie, C. J. Cole, and O. Flores-Villela. 1992. A review of phylogenetic hypotheses for lizards of the genus *Sceloporus* (Phrynosomatidae): implications for ecological and evolutionary studies. Bulletin of the American Museum of Natural History 213:1–110.

Slater, G. J., L. J. Harmon, and M. E. Alfaro. 2012. Integrating fossils with molecular phylogenies improves inference of trait evolution. Evolution 66:3931–3944.

Smith, S. A., and J. M. Beaulieu. 2009. Life history influences rates of climatic niche evolution in flowering plants. Proceedings of the Royal Society B: Biological Sciences 276:4345–4352.

Stebbins, R. C. 2003. A field guide to Western reptiles and amphibians. 3rd ed. Peterson Field Guide Series. Houghton Mifflin, Boston.

Stevens, M. S. 1977. Further study of the Castolon local fauna (Early Miocene), Big Bend National Park, Texas. Texas Memorial Museum, Austin.

Strömberg, C. A. E. 2002. The origin and spread of grass-dominated ecosystems in the Late Tertiary of North America: preliminary results concerning the evolution of hypsodonty. Palaeogeography, Palaeoclimatology, Palaeoecology 177:59–75.

Svenning, J.-C., C. Fløjgaard, K. A. Marske, D. Nógues-Bravo, and S. Normand. 2011. Applications of species distribution modeling to paleobiology. Quaternary Science Reviews 30:2930–2947.

Tong, J. A., Y. You, R. D. Müller, and M. Seton. 2009. Climate model sensitivity to atmospheric CO_2 concentrations for the Middle Miocene. Global and Planetary Change 67:129–140.

Vazquez Díaz, J., H. Gadsden, G. E. Quintero Díaz, P. Ponce-Campos, and P. Lavin. 2007a. *Sceloporus cyanostictus*. IUCN Red List of Threatened Species. http://www.iucnredlist.org.

———. 2007b. *Sceloporus ornatus*. IUCN Red List of Threatened Species. http://www.iucnredlist.org.

Vieites, D. R., S. Nieto-Roman, and D. B. Wake. 2009. Reconstruction of the climate envelopes of salamanders and their evolution through time. Proceedings of the National Academy of Sciences of the USA 106:19715–19722.

Wiens, J. J., K. H. Kozak, and N. Silva. 2013. Diversity and niche evolution along aridity gradients in North American lizards (Phrynosomatidae). Evolution 67:1715–1728.

Wiens, J. J., C. A. Kuczynski, S. Arif, and T. W. Reeder. 2010. Phylogenetic relationships of phrynosomatid lizards based on nuclear and mitochondrial data, and a revised phylogeny for *Sceloporus*. Molecular Phylogenetics and Evolution 54:150–161.

Wisz, M. S., R. J. Hijmans, J. Li, A. T. Peterson, C. H. Graham, A. Guisan, and NCEAS Predicting Species Distributions Working Group. 2008. Effects of sample size on the performance of species distribution models. Diversity and Distributions 14:763–773.

Yatkola, D. A. 1976. Mid-Miocene lizards from western Nebraska. Copeia 1976:645–654.

Yesson, C., and A. Culham. 2006. Phyloclimatic modeling: combining phylogenetics and bioclimatic modeling. Systematic Biology 55:785–802.

You, Y., M. Huber, R. D. Müller, C. J. Poulsen, and J. Ribbe. 2009. Simulation of the Middle Miocene Climate Optimum. Geophysical Research Letters 36:L04702.

Zachos, J., M. Pagani, L. Sloan, E. Thomas, and K. Billups. 2001. Trends, rhythms, and aberrations in global climate 65 Ma to present. Science 292:686–693.

Zheng, Y., and J. Wiens. 2015. Combining phylogenomic and super-matrix approaches, and a time-calibrated phylogeny for squamate reptiles (lizards and snakes) based on 52 genes and 4142 species. Molecular Phylogenetics and Evolution 94:537–547.

Associate Editor: David C. Collar
Editor: Judith L. Bronstein

A desert spiny lizard (*Sceloporus magister*) chows down on a moth in Washington County, Utah. Photo: Jay K. Goldberg, http://www.kechephoto.portfoliobox.me.