

**DIVERSITY AND NICHE EVOLUTION ALONG ARIDITY  
GRADIENTS IN NORTH AMERICAN LIZARDS  
(PHRYNOSOMATIDAE)**

John J. Wiens<sup>1,3</sup>, Kenneth H. Kozak<sup>2,4</sup>, and Natalia Silva<sup>1,5</sup>

<sup>1</sup>*Department of Ecology and Evolution, Stony Brook University, Stony Brook, NY 11794-5254*

<sup>2</sup>*Bell Museum of Natural History and Department of Fisheries, Wildlife, and Conservation Biology, University of Minnesota, St. Paul, MN 55108*

<sup>3</sup>*E-mail: wiensj@life.bio.sunysb.edu*

<sup>4</sup>*E-mail: kozak016@umn.edu*

<sup>5</sup>*E-mail: nasilvag@gmail.com*

\*Corresponding author: John J. Wiens, E-mail: wiensj@life.bio.sunysb.edu, Phone: 631-632-1101

**Data deposition:** Data are archived in Supplementary Appendices or on GenBank.

This article has been accepted for publication and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process which may lead to differences between this version and the Version of Record. Please cite this article as doi: 10.1111/evo.12053.

2013 The Author(s). Journal compilation © 2013 The Society for the Study of Evolution

Deserts occupy ~12% of the Earth's land surface, and are thought to have species poor but highly specialized biotas. However, few studies have examined the evolutionary origins of desert biotas and of diversity patterns along aridity gradients. Further, it is unclear if species occurring in more extreme conditions on a given niche axis (i.e., precipitation) are more specialized for those conditions (i.e., have narrower niche breadths). We address these questions here using a time-calibrated phylogeny and climatic data for 117 species of phrynosomatid lizards. Phrynosomatids are the most species-rich family of lizards in North America, and occur from deserts to rainforests. Surprisingly, we find that phrynosomatids have higher richness in more arid environments. This pattern occurs seemingly because they have been present in more arid habitats longer (~55 million years), and lineages in mesic environments are recently derived from more arid-dwelling ancestors. We find little support for the hypothesis that species in more extreme environments are more specialized. Instead, many desert-dwelling species are broadly distributed, and species in the most mesic environments have the broadest niche breadths. In summary, phrynosomatids offer a counterexample to the idea that arid regions are inhabited by a small number of recent and highly specialized lineages.

**KEYWORDS:** aridity, diversification, niche, phylogeny, reptiles, species richness

Desert regions are characterized by low annual precipitation, and encompass a significant portion of Earth's land surface area (~12% by area; Lomolino et al. 2006). Compared to other biomes, deserts are generally thought to have relatively low species richness for many groups (e.g., birds, Orme et al. 2005). Indeed, for warm temperate and tropical regions, precipitation is thought to be the most important environmental correlate of species richness patterns (Hawkins et al. 2003). Yet despite their overall lower richness, deserts may also be inhabited by many seemingly specialized, arid-adapted species and clades (e.g., many cacti and other succulent plants; Arakaki et al. 2011).

Deserts are important for understanding global biodiversity patterns, but few studies have addressed how desert biotas evolve and how diversity patterns arise along aridity gradients. Nevertheless, several important studies have addressed related topics. For example, Byrne et al. (2008) synthesized many phylogenetic and phylogeographic studies on the timing of the origin of Australia's desert biota. Crisp et al. (2009) showed that for plants, deserts tended to be biogeographic sinks, receiving lineages from other biomes, but contributing few or none to more mesic environments (like forests). Edwards and Donoghue (2006) analyzed the evolution of ecophysiological traits and climatic distributions in the basal lineages of Cactaceae. Evans et al. (2009) used a time-calibrated phylogeny and climatic data to demonstrate rapid climatic-niche evolution in a group of desert-dwelling plants. Arakaki et al. (2011) examined the timing of radiation of various succulent plant lineages, including cacti and agaves. Many studies have focused on within-species phylogeographic patterns among different deserts in North America (e.g., Jaeger et al. 2005; Riddle and Hafner 2006), but not on the origins of desert lineages from non-desert lineages.

Similarly, several large-scale studies have documented that there is low richness in arid regions for many groups (but see Powney et al. 2010), but few have attempted to explain why. Specifically, the relationship between aridity and species diversity has not generally been addressed in terms of the processes that directly change species numbers (i.e., speciation, extinction, and dispersal; Ricklefs 1987; Wiens 2011). For example, it is unclear if deserts have lower richness because fewer lineages have invaded them, because the lineages that have invaded them have lower rates of net diversification (speciation - extinction), because they have been invaded only recently (leaving less time for speciation to build up diversity in these habitats), or because of some combination of these factors.

Consideration of the evolution of desert biotas also raises fundamental questions about climatic niches and their evolution. For example, do species occurring in more extreme environments (such as deserts) tend to be more specialized to those environments? More specifically, given a group of organisms that occur along a given environmental niche axis, do species whose distributions extend to the extremes of the gradient on one niche axis (e.g., annual precipitation) also tend to have narrower niche breadths on that same axis relative to species occurring in less extreme environments for that group (Fig. 1A)? This might occur if invading an environment that is very different from the ancestral environment (e.g., more stressful) requires the loss of ability to remain in less extreme environments that are more similar to the ancestral environment (e.g., Lenski and Bennett 1993). Another possibility is that species that can tolerate more extreme environments can tolerate a broader range of environments than other species (Fig. 1B), and thus species in more extreme environments might have broader niches

(e.g., Hoffman and Parsons 1989). Alternately, species within a clade might retain similar niche breadths even as they undergo shifts in their position on that niche axis (Fig. 1C). There might also be different patterns of niche breadths for different extremes of the niche gradient (e.g., narrow at one end, broad at the other; Fig. 1D). For example, tropical species are thought to have generally narrower niche breadths for temperature than species in temperate regions (e.g., Janzen 1967; Ghalambor et al. 2006; Kozak and Wiens 2007; Hua and Wiens 2010). There is considerable interest in documenting trade-offs in traits that are related to the climatic niche (and which might explain limited niche breadths), especially traits such as thermal tolerance (e.g., Huey and Kingsolver 1993; Lenski and Bennett 1993; Bennett and Lenski 2007). There is also considerable interest in the general topics of niche breadth and specialization (e.g., Futuyma and Moreno 1988; Whitlock 1996). However, to our knowledge, the relationship between the position of species on a given climatic niche axis and their niche breadths on that axis has not been explicitly examined.

Here, we address these and related questions using phrynosomatid lizards as a study system. Phrynosomatids are the most species-rich family of lizards in North and Middle America (Uetz 2011), with 138 species and 10 genera (see Methods for references). They collectively occur in almost all terrestrial habitats in these regions, from desert sand dunes to tropical montane forests to temperate woodlands. They include many common and familiar species and genera, such as the spiny lizards (*Sceloporus*), side-blotched lizards (*Uta*), and horned lizards (*Phrynosoma*).

Phrynosomatids offer an excellent system for addressing questions related to diversity and evolution along aridity gradients. First, they occur from highly mesic to

highly arid environments. Second, there is a multi-locus molecular phylogeny for the group that is well resolved and relatively comprehensive in its species sampling (Wiens et al. 2010a). Third, despite some recent changes, the taxonomy and known distributions for most species are relatively stable (e.g., Stebbins 1985 vs. Stebbins 2003). Finally, given that most species are generally common and conspicuous where they occur, there is a wealth of museum specimen localities that can be combined with GIS-based environmental data to document their climatic distributions.

In this study, we combine phylogenetic and climatic data for phrynosomatid lizards to address the following questions: (1) how is diversity distributed along aridity gradients? Are there more species in arid or mesic environments? (2) What causes these patterns of diversity along aridity gradients? For example, are there more species in mesic (or arid) environments because these environments promote more rapid diversification (i.e., more speciation and/or less extinction), or because these environments have been inhabited for longer periods of time? In answering this question, we also address (at least for phrynosomatids) the origin and age of the desert fauna of North America. (3) How does niche breadth contribute to these patterns? For example, are most species that are found in deserts confined to these environments? More generally we ask: do species that occur in more extreme environmental conditions on a given niche axis tend to have narrower niche breadths?

We address these questions by (1) developing a multi-locus, time-calibrated phylogeny that includes most phrynosomatid species, (2) obtaining georeferenced locality data from museum collections and GIS-based climatic data for each locality, and (3) using these data on climate and distribution to characterize patterns of diversity and

distribution along aridity gradients. We then combine the data on climate, distribution, and diversity with the phylogeny to address the questions above using phylogenetic comparative methods.

## *Materials and Methods*

### **PHYLOGENY AND DIVERGENCE-TIME ESTIMATION**

The phylogeny and divergence times were based on an analysis of 123 phrynosomatid taxa, combining the data set from Wiens et al. (2010a; which incorporated DNA data from most previous studies) with that of Leaché (2010). The combined matrix includes eight nuclear genes (BDNF, ECEL, PNN, PRLR, PTPN, R35, RAG1, TRAF6) and five mitochondrial genes (12S, 16S, ND1, ND2, ND4) and a total of 10,394 characters. GenBank numbers are provided in Appendix S1.

Taxon sampling varied among genes, leading to some missing data for some genes in the combined analysis. However, many simulations and empirical studies suggest that even taxa with extensive missing data can be accurately placed in model-based analyses when many characters are sampled overall (review in Wiens and Morrill 2011). Here, the majority of species were sampled for one or more mitochondrial genes, and five nuclear genes were sampled for most species in a set of ~40 “core” taxa that included at least one species in each genus and in each species group of *Sceloporus* (from Wiens et al. 2010a). Species sampled for each gene are: BDNF = 79, ECEL = 35, PNN = 56, PRLR = 37, PTPN = 36, R35 = 56, RAG1 = 83, TRAF6 = 40, 12S = 113, 16S = 91, ND1 = 77, ND2 = 68, ND4 = 102. Despite missing data, all species are placed in the expected genera with strong support (Figs. S1, S2). Furthermore, an analysis including

much of these data (from Wiens et al. 2010a) showed no relationship between the amount of missing data in a species and the support for its placement (Wiens and Morrill 2011). Finally, missing data may have little impact on estimated branch lengths when data from different genes are partitioned (Wiens and Morrill 2011).

Detailed methods for estimating the phylogeny and divergence times are provided in Appendix S2. In short, the phylogeny (Fig. S1) was estimated using maximum likelihood with RAxML (Stamatakis 2006). Divergence times were estimated primarily using the Bayesian uncorrelated lognormal approach in BEAST (Drummond et al. 2006; Drummond and Rambaut 2007), with three fossil calibration points. All comparative analyses presented below were based on this tree (Fig. S2). We also estimated divergence dates using penalized likelihood (with r8s; Sanderson 2002, 2003), and performed analyses on this phylogeny. The results from these trees are very similar, and together show that our main conclusions are robust to reasonable variation in branch lengths and topology (see Appendix S3 for a description of these methods and results, along with Fig. S3).

## **CLIMATIC DATA**

Climatic data were obtained from the WORLDCLIM database (Hijmans et al. 2004, 2005), which consist of 19 GIS (Geographic Information Systems) “layers” based on monthly temperature and rainfall data, at ~1 km resolution. Data for each species were obtained from georeferenced museum localities. To obtain localities, we first searched the database of the Museum of Vertebrate Zoology (MVZ), Univ. California at Berkeley, which has many carefully georeferenced localities for most phrynosomatid



species. We also searched the HerpNet database ([www.herpnet.org](http://www.herpnet.org)) for additional localities for some species. HerpNet includes locality data for all species represented in dozens of U.S. and foreign collections. We georeferenced additional localities using known georeferenced landmarks. Georeferenced localities were visualized in ArcView 3.2 and compared to published range maps for each species (e.g., Sites et al. 1992; Conant and Collins 1998; Grismer 2002; Stebbins 2003). Localities outside known ranges were deleted. We also confirmed that localities spanned most of the species' range (i.e., localities were not clumped in a small part of the range). Localities per species ranged from 1–1230 (mean = 45.8), and generally appeared to be related to the species' range size. Specifically, species with small ranges had few localities, whereas wide-ranging species had many (e.g., Spearman rank correlation for sample size vs. latitudinal extent for 112 species with >1 localities that are included in the phylogeny yields  $Rho = 0.818$ ,  $P < 0.0001$ ). Climatic data are summarized in Appendix S4. Throughout the paper, we refer to localities with annual precipitation below 501 mm/year as arid and those with 501–1000 mm as being semi-arid, following standard practice.

## **TAXONOMY**

Analyses of climatic distributions and diversity patterns ultimately depend on species-level taxonomy. Our taxonomy generally followed Uetz (2011), and we justify deviations from this standard database in Appendix S5. We obtained climatic data for all 138 putative species. Some of the 123 phrynosomatid taxa treated as distinct units in this and previous phylogenetic analyses do not appear to represent distinct species given present evidence (e.g., subspecies of *Sceloporus dugesii* and *S. torquatus*). These taxa

were pruned from the tree in the analyses described below. The phylogeny used includes 117 putative species.

## **PATTERNS OF DIVERSITY**

We considered diversity patterns along an aridity gradient based on species values for annual precipitation. We divided the overall range of annual precipitation values of the localities where phrynosomatids occur (47–4775 mm/year) into 10 bins of 500 mm (e.g., 0–500, 501–1000). We then determined the distribution of each species on this gradient, based on their minimum and maximum values across localities. A species was considered present in a bin if its range of values for annual precipitation fell within that bin. We then tallied the number of species in each bin, using our climatic data for all 138 putative species.

## **TIME-FOR-SPECIATION EFFECT**

A larger number of species in a given habitat (e.g., desert) might be explained by greater time spent in that habitat or by more rapid diversification in that habitat. We first tested the hypothesis that the number of species in each precipitation bin (habitat type) is related to the amount of time that phrynosomatids have been present and speciating in that bin. We reconstructed precipitation values at each node of the tree, based on the annual precipitation for each species (mean value across localities). Given the reconstructed values and ages of all nodes, we estimated the oldest node for each level of precipitation (i.e., each 500 mm bin). We then tested the relationship between the species richness of each bin and the relative time that phrynosomatids have been present in that

bin. This approach does not estimate exactly when each bin was actually colonized, since it utilizes mean species values. Nevertheless, it provides an approximate index that allows for comparison between bins.

To reconstruct ancestral values, we used phylogenetic generalized least squares (PGLS; Martins and Hansen 1997). We first determined whether the precipitation data best fit a Brownian motion (BM) model or an Ornstein-Uhlenbeck (OU, single optimum) model, by comparing the likelihood of the data under each model using the phylogeny and the *geiger* package in R (Harmon et al. 2008) and Akaike information criterion (AIC). We also used *geiger* to estimate lambda for this variable, and to test whether lambda was significantly different from 0 and from 1, where 0 indicates data with no phylogenetic signal (random noise), and 1 indicates strong fit to the BM model (Pagel 1999). These analyses showed much higher support for an OU model relative to a BM model (OU AIC = 1732.44; BM AIC = 65913.24). The analyses also show the estimated lambda to be 0.215, which differs significantly from a model with no phylogenetic signal (lambda = 0) and perfect fit to the BM model (lambda = 1), using likelihood-ratio tests ( $P < 0.0001$ ). We then used the PGLS-ancestor function in COMPARE version 4.6b (Martins 2004), using the exponential (OU) model and the estimated value of alpha (0.0367; the restraining force). We consider selection of an OU model, combined with rejection of the hypothesis of no signal, to support the hypothesis of niche conservatism (see Kozak and Wiens 2010a; Wiens et al. 2010b). We focused on the single-optimum OU model because evaluating ancestral values at specific nodes for a multi-optimum model is not yet tractable. To evaluate the robustness of our results to an alternative model, we also performed a set of analyses using the BM model.

Accepted Article

We next determined the age of the oldest clade with a reconstructed value falling within a given 500 mm precipitation bin. For the highest-precipitation bins, all nodes had reconstructed mean values that were lower than those bins. In these cases, we used the ages of species whose climatic distributions extended into these bins. More specifically, we used 50% of the ages of these species, assuming that the full climatic distribution was not achieved in the last few years or immediately after splitting (i.e. we used an intermediate value instead). This approach reflects the idea that these bins were colonized relatively recently. We also confirmed that use of the midpoint of the range of Bio12 values for each species gave identical results to those using the mean of Bio12 values among localities (not shown). In addition, to ensure that our results were not an artefact of the particular set of bins used, we performed an analysis using twice as many bins (i.e., intervals of 250 mm). Note that decreasing the number of bins below 10 would have important negative consequences, such as lumping arid and mesic habitats into the same bin.

We then used linear regression to examine the relationship between the time in each precipitation bin and the number of species in that bin. Although previous analyses of the time-for-speciation effect have log-transformed richness (e.g., Wiens et al. 2007; Kozak and Wiens 2010a), this practice assumes that diversity within regions increases exponentially over time (an unnecessary assumption). We therefore used raw richness instead. Log-transforming richness leads to a weaker (but still highly significant) relationship, and this pattern occurs in other data sets as well (Appendix S6).

As an alternate approach, we also examined the summed ages of all the inferred colonizations of each precipitation bin. Rather than assuming that only the oldest

Accepted Article

colonization of a bin explains its richness, we included all inferred colonizations, although simulations suggest that this may be unnecessary (Rabosky 2012). We generally only treated a bin as colonized if the mean precipitation value for a clade or species included that bin (ages for colonization events involving single species were again based on 50% of the age of the species). However, for the highest precipitation bins, we again considered the full range of precipitation values for extant species also, rather than just the means.

In theory, these analyses might be biased by one or more factors. One is that the impact of the trait on diversification may influence the reconstruction of its ancestral trait values (e.g., Maddison 2006). However, we find no relationship between precipitation distributions and diversification rates (see Results).

An apparent time-for-speciation effect might also arise as an artifact of reconstruction methods. Specifically, if certain climatic zones have more species, then those climates might be reconstructed at the root, even if they are not ancestral (although this bias is mostly hypothetical at present). If this artifact is present, then the observed correlation between time and richness of climatic bands should be similar to datasets in which species' ranges are randomly placed along the climatic gradient (i.e., datasets with no time-for-speciation effect). To test this possibility, we simulated 1000 datasets in which a "new" precipitation range for each species was randomly drawn from the empirical distribution of precipitation niche breaths (using Mid-Domain Null; McCain 2004). We then tallied the species in each 500 mm precipitation band. Then, we reconstructed the ancestral precipitation midpoint for each node (using PGLS with the R packages *ape* and *geiger*), and used linear regression to quantify the relationship between

Accepted Article

the time that each precipitation band was first colonized and its species richness. Finally, we compared the observed relationships between time and richness to those from the simulated datasets. If fewer than 5% had  $F$ -values greater than the observed data, we rejected the hypothesis that the observed time-for speciation effect was an artifact of ancestral reconstruction. The annotated R code and tree are provided in Appendix S7 (see also Kozak and Wiens 2010).

A third potential factor is that the ancestral reconstructions may be inaccurate because climatic niches (for annual precipitation) are too labile, either between or within species. However, our analyses suggest that this variable exhibits significant conservatism and non-random signal across the phylogeny (see above). In addition, species niche breadths for this variable are relatively narrow on average (mean range of maximum Bio12 - minimum Bio12 = 627 mm/year,  $n = 138$  species), almost equal in size to the climatic bins used (500 mm). Some readers may be concerned with the general idea of mapping climatic traits onto a phylogeny, but these climatic distributions should be tied to genetically-based traits such as physiological tolerances and behavioral habitat preferences, at least at some level.

A fourth potential factor is that the unsampled species in the tree compromise the analysis of diversity patterns. However, the patterns of richness among precipitation bins for the 117 species in the tree are very similar to those for all 138 species (Table 1;  $r^2 = 0.998$ ,  $P < 0.0001$ ).

A fifth potential factor is that the results might be influenced by biased patterns of colonization between different climatic zones. However, we find that the number of inferred increases and decreases in precipitation distribution across the tree are nearly

equal (24 vs. 25) and that the number of transitions between pairs of bins is related to the current mean richness of those bins (Appendix S8), suggesting that richness (or the factors underlying richness) drive the colonization patterns, rather than an asymmetry in colonization patterns driving richness patterns.

Finally, some authors have criticized previous analyses of the time-for-speciation effect for not addressing density-dependent effects on diversification (e.g. Rabosky 2012). However, our goal is to understand what explains patterns of richness, not test for possible signatures of density dependence, and the “process-based” approach advocated by Rabosky (2012) will not distinguish “if time-within-regions is the dominant process influencing species richness” and “if there is no pattern in the data” (p. 229). Most importantly, the time-for-speciation effect and density-dependence are not mutually exclusive (e.g., regions that are inhabited longer may show both greater density-dependence and higher richness; Wiens et al. 2011) and an analysis of hundreds of empirical data sets shows that most clades best fit a model in which diversification slows over time but richness continues to accumulate regardless (Morlon et al. 2010). However, the possibility of density dependence does suggest that species richness should not necessarily be log-transformed (i.e., if richness is not growing exponentially over time).

## **RATES OF DIVERSIFICATION**

High richness in a given habitat may be explained by greater time or more rapid diversification in that habitat. To test the latter hypothesis, we used four approaches. First, we divided phrynosomatids into 27 clades, corresponding either to genera or to

species groups within the species-rich genus *Sceloporus* (following Wiens et al. 2010a). We then estimated the diversification rate for each clade based on the stem-group age and the total number of described species in each clade (not simply the number included in our phylogeny), using the method-of-moments estimator (Magallón and Sanderson 2001). We used three estimates of relative extinction rate (epsilon or  $e$ ), including values that were low (0.00), high (0.90), and intermediate (0.45). We then estimated the average of species mean values for annual precipitation (Bio12) within each clade, and tested for a relationship between the diversification rates of clades and their mean annual precipitation using PGLS (implemented in the R-version of CAIC; Orme et al. 2009). We used stem-group estimates of clade ages (and diversification rates) so that we could include clades with single species or limited taxon sampling. However, preliminary analyses using crown-group ages and excluding the four monotypic clades gave similar results (i.e., no relationship between precipitation and diversification rate). Preliminary (non-phylogenetic) analyses showed a strong relationship between diversification rates and richness of clades, demonstrating that these rates are potentially relevant for explaining richness patterns ( $r^2 = 0.629, 0.682, \text{ and } 0.785$ , for  $e = 0, 0.45, \text{ and } 0.90$ ,  $P < 0.0001$  for all three). The overall advantage of this approach is that it incorporates all described species of phrynosomatids, and not merely those included in the tree. It also allows one to identify particular clades with higher or lower diversification rates.

For the second approach, we used the QuaSSE algorithm (Quantitative Trait Speciation-Extinction model; Fitzjohn 2010), implemented in the R package *diversitree* by R. Fitzjohn. This approach is designed to test how quantitative traits influence rates of speciation and extinction. We utilized data on mean values of annual precipitation across



Accepted Article

the ranges of all 117 species in the time-calibrated tree (and explicitly accounting for the 21 species not in the tree). We used an arbitrary standard deviation of 0.10, but we found that changing this value ten fold (to 1.0) had no impact on any of the estimated values. We tested a model in which there is no relationship between precipitation and diversification (minimal) and models in which there are linear, sigmoidal, and hump-shaped relationships between precipitation and speciation. We held extinction rates constant between models, given the limited ability of QuaSSE to detect different extinction rates (FitzJohn 2010) and because analyses using BiSSE (binary state speciation extinction; Maddison et al. 2007) suggested that extinction rates were very small and that differences in rates between habitats were inconsequential (see below). We also tested models both with a directional diffusion process of character evolution (“drift”) and without. Models were compared using the AIC, with a difference in AIC values  $>4$  considered to be strong support for one model over another (Burnham and Anderson 2002).

To further clarify the relationship between diversification and particular climatic regimes, we also used BiSSE (implemented in *diversitree*) to estimate rates of speciation and extinction in specific sets of climatic regimes. We performed three analyses, one in which all species with mean values of annual precipitation  $>500$  mm were coded as state 1 (all others state 0), a second in which values  $>1000$  were coded as 1, and a third in which values  $>1500$  were coded as 1 (a cut-off of  $>2000$  gives almost identical codings as  $>1500$ , with only 4–5 species with state 1). For each analysis, we first estimated values of speciation and extinction for each state, and then tested model fit when

speciation rates were constrained to be equal between states, and when extinction rates were constrained. Again, models were compared using the AIC.

## **NICHE BREADTH AND NICHE POSITION**

We tested the hypothesis that species that occur in more extreme environments (on a given niche axis) will have a narrower niche breadth (on that same axis). Specifically, we tested whether species that occur in the most arid environments (or the most mesic) will have narrower niche breadths for annual precipitation (where niche breadth is the maximum value of Bio12 among localities for that species, minus the minimum value, or the range of precipitation values where the species occurs). All hypotheses were tested using PGLS with the time-calibrated phylogeny.

We first tested if species with more extreme mean values for Bio12 will have narrower niche breadths for Bio12. To describe extreme niche positions (on either end of the niche axis), we first estimated the midpoint of the observed species means. For each species, we then took the absolute value of the difference between the midpoint and the observed mean. Thus, species with higher values will be those farthest away from the midpoint of species means, in either direction.

We also tested for a relationship between species means and niche breadths, to determine if species in more arid or more mesic environments tend to have narrower niche breadths. We also tested for relationships between niche breadth and minimum values of Bio12 in each species and maximum values of Bio12. For the latter, species that have small maximum values of Bio12 must necessarily have narrow niche breadths. Nevertheless, species with high maximum values for Bio12 could have either narrow or

wide niche breadths. Furthermore, species with low minimum values of Bio12 could have either narrow or wide niches.

For this set of analyses we excluded four island endemic species (*Uta palmeri*, *Sceloporus angustus*, *S. grandaevus*, and *S. lineatulus*), leaving 113 species. We assume that niche breadths of species are potentially determined by their habitat tolerances and preferences. However, species on islands may have small niche breadths because the islands are too small to contain the full range of climates that the species can tolerate.

## Results

The phylogenies based on likelihood (and Bayesian analyses; Figs. S1–S2) are generally strongly supported and similar to the large-scale phylogeny from Wiens et al. (2010a). Support is particularly strong for monophyly of subfamilies, genera, and species groups of *Sceloporus*, but most relationships within genera are also strongly supported. The Bayesian estimation yields a mean age of ~55 Myr (Million years old) for the most recent common ancestor of phrynosomatids, ~47 Myr for sceloporines, and ~36 for phrynosomatines (Fig. 2). These dates are roughly similar to those from recent analyses with more genes but limited taxon sampling (5 species total, Townsend et al. 2011; ~40 Myr, ~30 Myr, ~35 Myr), but the mean ages estimated here are somewhat older.

Contrary to the general trend in many organisms, phrynosomatids have higher regional species richness in more arid zones than in more mesic ones (Fig. 3; Table 1). Richness is highest in areas with an annual precipitation from 501–1000 mm, and is nearly as high for 0–500 mm. Richness declines in progressively more mesic areas.

Accepted Article

The high richness of relatively arid regions seems to be explained by the time-for-speciation effect. There is a strong positive relationship between the estimated time in each precipitation bin and the species richness of that bin ( $r^2 = 0.970$ ;  $P < 0.0001$ ; Fig. 4). These results are robust to using 20 bins instead of 10 ( $r^2 = 0.857$ ;  $P < 0.0001$ ) and to performing climatic reconstructions using the BM model instead of the OU model ( $r^2 = 0.872$ ,  $P < 0.0001$ ). These relationships are also strong when using the summed ages of colonizations of each band, rather than the age of the oldest colonization alone ( $r^2 = 0.906$ ;  $P < 0.0001$ ). Simulations show that the support for the time-for-speciation effect is not an artifact of bias in reconstruction methods towards more species-rich precipitation zones; the observed  $F$ -value for the empirical data (using 117 species and species midpoints) is 28.04, whereas the highest  $F$ -value among the first 950 of the rank-ordered replicates is 22.65 (with the observed data corresponding to the 31st largest value, or a  $P$ -value of 0.031). Similar results were obtained using the tree from penalized likelihood (Appendix S2), showing their robustness to variation in the phylogeny and branch lengths. The greater time in arid environments may reflect niche conservatism in climatic distributions, as the precipitation data support an OU model, and reject a model with no phylogenetic signal ( $\lambda = 0$  vs. estimated  $\lambda$ ; see Methods).

Reconstructions of species mean values for annual precipitation on the phylogeny (Fig. 2) suggest that phrynosomatids occurred ancestrally in relatively arid habitats (~600 mm) and colonized mesic habitats more recently (even if the precise ancestral values are uncertain). Phrynosomatines occurred ancestrally in drier environments (~410 mm), but some lineages later invaded more mesic environments (e.g., *Holbrookia propinqua*, *Phrynosoma braconieri*, and *P. taurus*). Sceloporines occurred ancestrally in more

mesic environments (~720 mm), with many subsequent invasions of both drier and highly mesic environments. Similar results are found with a BM model (phrynosomatids = 553, phrynosomatines = 475, sceloporines = 586).

We find no evidence that the aridity of habitats where species occur influences their net diversification rates. Using estimated rates for 27 clades (Appendix S9), there is no significant relationship between diversification and the mean precipitation of species in the clade (e0:  $r^2 = 0.106$ ,  $P = 0.098$ ; e45:  $r^2 = 0.106$ ,  $P = 0.098$ ; e90:  $r^2 = 0.108$ ,  $P = 0.094$ ). Although these results approach significance, the relationship between precipitation and diversification is positive, such that clades in more mesic habitats have higher rates. This trend is the opposite of the pattern that would explain high richness in more arid environments. Results using the QuaSSE approach (Table 2; Appendix S10) show that models with no relationship between speciation and precipitation or a negative linear relationship between speciation and precipitation have the best fit (using the AIC), but with no difference in the support for these latter two models. Thus, there is no support from the QuaSSE analyses for a relationship between diversification and precipitation distributions. Results from the BiSSE approach (Table 3) show that differences between models are generally not strongly supported, except when species with mean values of annual precipitation >1000 mm are coded with state 1. In this case, there is strong support (AIC difference > 10) for higher speciation rates in more mesic environments. However, this difference in rates cannot explain why more arid environments have more species (instead, this would explain why mesic environments have more species). Taken together, these analyses of diversification rates strongly

support the idea that higher richness in more arid environments is explained by greater time in these environments and not faster diversification rates.

Our results on patterns of niche breadth do not support the idea that species in more extreme environments tend to be more specialized (i.e., narrower niches). We find a weak, positive relationship between species niche breadths (for precipitation, Bio12) and extreme mean values on the precipitation niche axis ( $r^2 = 0.064$ ,  $P = 0.007$ , based on PGLS; see Fig 5A for raw data), such that species in more extreme environments have somewhat wider niches, in contrast to our initial prediction (Fig. 1A). There is a much stronger, positive relationship between niche breadth and species mean values for annual precipitation (PGLS:  $r^2 = 0.377$ ,  $P < 0.0001$ ; raw data: Fig. 5B). Thus, species that occur predominantly in the most arid environments tend to have narrower niche breadths, whereas species in the most mesic environments have the broadest niche breadths. There is a strong positive relationship between species maximum values for Bio12 and their niche breadths (PGLS:  $r^2 = 0.808$ ,  $P < 0.0001$ ; raw data: Fig. 5C). Species that have very low maximum values for Bio12 must have narrow niche breadths, but species whose ranges extend into more mesic environments often have very broad niches. There is a weak positive relationship between minimum values for Bio12 and niche breadth (PGLS:  $r^2 = 0.0411$ ,  $P = 0.032$ ; raw data: Fig. 5D). Importantly, this weak relationship may reflect the trend for many species that occur in deserts to not occur in deserts exclusively (see Discussion).

## *Discussion*

Gradients in precipitation are considered a major (climatic) driver of diversity in warm temperate and tropical latitudes (e.g., Hawkins et al. 2003). Deserts are generally thought to have low diversity (e.g., Orme et al. 2005) but also many species and clades specialized for these conditions (e.g., cacti; Arakaki et al. 2011). Here, we examine the origin and specialization of desert lineages and the evolution of diversity patterns along aridity gradients. We find that phrynosomatids have higher diversity in relatively arid environments (0–1000 mm/year), and that this pattern is related to longer occupation of these habitats, rather than the impact of aridity on diversification. We also test how occurrence in more extreme environments on a given niche axis is related to niche breadths on that axis. We find that species in deserts do have somewhat narrower niches, but the stronger trend is for species ranging into mesic environments to have broader niches, the opposite of our expectation. We discuss these patterns in more detail below.

Our results show higher diversity in arid and semi-arid environments (Fig. 3), and that these patterns are related to time (Fig. 4), and not diversification rates. This study now adds aridity to the list of environment-richness gradients seemingly explained by niche conservatism (limiting dispersal between habitats; review in Wiens et al. 2010b) and the time-for-speciation effect (more species in habitats and regions occupied longer; reviews in Stephens and Wiens 2003; Wiens 2011). Others include latitudinal diversity in treefrogs (Wiens et al. 2006), elevational diversity in salamanders (Kozak and Wiens 2010a), and large-scale climatic gradients in birds (Rangel et al. 2007) and mammals (Buckley et al. 2010). Nevertheless, some studies do not support the role of time in creating diversity gradients, especially the latitudinal diversity gradient (reviews in

Mittelbach et al. 2007; Wiens 2011). The pattern in phrynosomatids is particularly interesting because precipitation is often positively related to richness (e.g., Hawkins et al. 2003), and deserts are young relative to other biomes (e.g., Lomolino et al. 2006).

Intriguingly, Australian lizards also show higher diversity in arid environments (e.g., Powney et al. 2010). The evolutionary drivers of this pattern (e.g., time, diversification) have not yet been thoroughly explored. However, a study of a major Australian lizard clade (skinks; Rabosky et al. 2007) showed rapid diversification of certain clades in arid environments (but without climatic data). Indeed, Australia's arid zones are relatively recent (~15 Myr; review in Byrne et al. 2008), and very rapid diversification may be the only way for their diversity to exceed that of other habitats.

Our results suggest that relatively arid environments can be a source of lineages for mesic environments, rather than merely a sink. We find that phrynosomatid species in the most mesic environments (e.g., *Sceloporus* in temperate deciduous forests, cloud forests, and tropical rainforests) are derived from ancestors that occurred predominantly in relatively arid environments (e.g., mean ~600 mm/year, as in dry tropical forest). We also find some species in dry tropical forests are seemingly derived from more arid-dwelling ancestors (e.g., *Phrynosoma braconnieri* and *P. taurus*). However, we find no cases where highly mesic species (mean >1500 mm) are derived from highly arid ancestors (mean <500 mm). Nevertheless, our results provide an interesting counter-example to the overall "desert sink" pattern documented for plants (Crisp et al. 2009).

Other evidence is consistent with our results showing phrynosomatids that have occurred in semi-arid habitats (501–1000 mm/year) for ~55 Myr. Based on paleobotanical evidence (Axelrod 1979), relatively arid tropical forest and scrub



dominated the southwestern U.S. and northern Mexico in the Eocene (~760–635 and 635–380 mm/year, respectively), and semi-desert (<380 mm) plant communities in the southwest date back to 17 Myr ago and expanded during the Miocene and more recently. Similarly, using molecular dating methods, a Mexican plant clade (*Bursera*) largely confined to dry tropical forests is ~60 Myr old (Becerra 2005) whereas the modern desert-adapted flora is more recent (i.e., ~10 Myr; Arakaki et al. 2011). Interestingly, we find no clades of desert specialists (maximum annual precipitation <500 mm) that are >17 Myr old.

Arid and semi-arid environments presently occupy a much larger geographic area than do more mesic environments within the range of phrynosomatid lizards (from the U.S. to Panama; Appendix S9). Thus, there is a strong relationship between phrynosomatid richness in these precipitation zones and the geographic area of these zones ( $r^2 = 0.848$ ;  $P = 0.0002$ ; from data in Table 1 and Appendix S10). Although it may be tempting to suggest that area therefore explains their richness patterns rather than time or diversification rates, a relationship between area and richness must still be explained by the processes that directly change species numbers (i.e., speciation, extinction, dispersal). Our results do not support the idea that the larger area of more arid zones drives richness patterns through their influence on diversification rates (i.e., more speciation or less extinction), given the lack of relationship between aridity and diversification rates. Furthermore, the presently large extent of the most arid zones is relatively recent (e.g., <5 Myr, Axelrod 1979) and so seems unlikely to explain the origin of phrynosomatids in semi-arid environments >50 Myr ago. Thus, the present area of these zones alone does not seem to explain these richness patterns.

Accepted Article

In this study, we also test the relationship between the position of species on a niche axis and their niche breadth. Our results do not support the hypothesis that species that occur in increasingly extreme environments on a given niche axis tend to have narrower niche breadths. Species with low mean values for precipitation do have narrower niche breadths on this axis, as predicted. However, at the wetter end, the pattern is the opposite: species in more mesic environments have broader distributions. This is particularly interesting given that these highly mesic environments are derived within the group. This pattern might be explained if mesic environments are less stressful (i.e., if niche breadths become attenuated in more stressful environments). Alternately, invasion of mesic environments may require adaptations that then permit these lineages to colonize a diversity of mesic environments. For example, mesic environments are generally forested and phrynosomatids are heliophilic, and they may need to cope with shade and cloud cover to maintain adequate body temperatures (e.g., Adolph 1990). Much work is needed to understand the mechanisms underlying these patterns, and these mechanisms may be somewhat group-specific. Nevertheless, this study represents an initial attempt to explore the relationships between niche breadth and niche position on a given climatic niche axis.

Our results also suggest that deserts are not necessarily dominated by species that are desert specialists. There are 78 phrynosomatid species occurring partially or exclusively in arid environments (i.e., localities with  $\leq 500$  mm; Appendix S4). Ten are island endemics, and so their niche breadths are not necessarily explained by climatic conditions. Of the remaining 68, only 21 (30.9%) are truly confined to deserts (i.e., maximum Bio12  $\leq 500$  mm). Some of the most extreme desert dwellers are sand-dune

Accepted Article

specialists (Stebbins 2003), including all five *Uma*, some *Phrynosoma* (*P. goodei*, *P. mcallii*) and some *Sceloporus* (*S. arenicolous*). Thus, their ranges may be determined more by microhabitat preferences than climate alone. Others have very small ranges within a larger desert region (e.g., *S. cyanostictus*, *S. maculosus*, and *S. merriami* in the Chihuahuan desert), again suggesting that climatic tolerances alone do not drive their distributions. Some phrynosomatid species also occur over a broad range of precipitation regimes from desert to >2000 mm/year (e.g., *S. grammicus*, *S. occidentalis*, *S. torquatus*), although future studies may show some of these wide-ranging species to be polytypic. In summary, our results show that most species that occur in arid environments are not desert specialists, but rather are more broadly distributed. The generality of these patterns should be tested in other groups, especially those in which distributions may be more closely tied to precipitation (e.g., plants).

We issue several caveats about these analyses. First, some of our conclusions are dependent on ancestral reconstructions and their accuracy. However, precipitation distributions exhibit conservatism and significant non-random signal across the phylogeny (suggesting limited lability between species), with relatively narrow mean species niche breadths (suggesting limited lability within species). Further, despite dramatic changes in climate in the region in the past 60 Myr (e.g. Axelrod 1979), our analyses do not depend on species remaining stationary over time (e.g., species may track climatic niches over space as climate changes). Our reconstructions are also broadly concordant with estimated past climates in the region based on paleontological evidence (see above).

Accepted Article

Second, data on species' climatic distributions may not reflect their full range of climatic tolerances. Nevertheless, these data represent a minimum estimate of their climatic tolerances. We find that some species are broadly distributed, including those in deserts and in high precipitation areas. Showing that other species could also be more broadly distributed will not overturn this. In fact, species ranges may not be set directly by precipitation or climatic tolerances at all. For example, precipitation might be important as an ultimate driver of distributions, but the mechanisms setting range limits may be more indirect and complex (e.g., precipitation influences vegetation patterns, which then influence food availability and microclimate). A diversity of biotic and abiotic factors may set range limits, and different factors may limit different parts of a single species' range (e.g., latitudinal and elevational warm edges vs. cool edges). It is also possible that other traits influence species distributions on precipitation gradients, such as body size, but previous analyses (Oufiero et al. 2011) show that precipitation and body size are unrelated across most phrynosomatids (i.e., *Sceloporus*).

Similarly, patterns of richness along aridity gradients may be related to environmental factors not directly related to precipitation. One obvious candidate is temperature. However, we find no relationship between the mean annual temperature of species ranges and their mean annual precipitations for phrynosomatids ( $r^2 = 0.016$ ,  $P = 0.142$ ,  $n = 138$  species).

In summary, our analyses of phrynosomatid lizards reveal that their diversity in arid and semi-arid regions is surprisingly high and ancient. In contrast, phrynosomatids in mesic environments are derived from relatively recent invasions from more arid environments. We also find that most species occurring in deserts are surprisingly

Accepted Article

unspecialized, and that there is little tendency for species at more extreme ends of the precipitation gradient to be more specialized. Instead we find that species in more mesic environments have the largest niche breadths. Other groups may show very different patterns. Nevertheless, phrynosomatids offer an important counterexample to the conventional wisdom that arid and semi-arid regions are inhabited by a small number of recent and highly specialized species and clades.

#### **ACKNOWLEDGMENTS**

We thank A. Nieto Montes de Oca for advice on *Sceloporus* taxonomy. We are grateful to J. Bronstein, K. Gaston, A. Phillimore, E. Svennsson, and anonymous reviewers for helpful comments on the manuscript. This research was partially supported by a grant from the U.S. National Science Foundation (EF 0334966) to J.J.W.

## LITERATURE CITED

- Adolph, S. C. 1990. Influence of behavioral thermoregulation on microhabitat use by two *Sceloporus* lizards. *Ecology* 71:315–327.
- Arakaki, M., P.-A. Christina, R. Nyffeler, A. Lendel, U. Eggli, R. M. Ogburn, E. Spriggs, M. J. Moore, and E. J. Edwards. 2011. Contemporaneous and recent radiations of the world's major succulent plant lineages. *Proc. Natl. Acad. Sci., U.S.A.* 108: 8379-8384.
- Axelrod, D. I. 1979. Age and origin of Sonoran desert vegetation. *Occ. Pap. Cal. Acad. Sci.* 132:1–74.
- Bennett, A. F., and R. E. Lenski. 2007. An experimental test of evolutionary trade-offs during temperature adaptation. *Proc. Natl. Acad. Sci., U.S.A.* 104:8649–8654.
- Buckley, L. B., T. J. Davies, D. D. Ackerly, N. J. B. Kraft, S. P. Harrison, B. L. Anacker, H. V. Cornell, E. I. Damschen, J. A. Grytnes, B. A. Hawkins, C. M. McCain, P. R. Stephens, and J. J. Wiens. 2010. Phylogeny, niche conservatism, and the latitudinal diversity gradient in mammals. *Proc. R. Soc. Lond. B* 277:2131–2138.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multi-model inference: a practical information-theoretic approach. Springer-Verlag, New York.
- Byrne M., D. K. Yeates, L. Joseph, M. Kearney, J. Bowler, M. A. Williams, S. Cooper, S. C. Donnellan, J. S. Keogh, R. Leys, J. Melville, D. J. Murphy, N. Porch, and K.-H. Wyrwoll. 2008. Birth of a biome: insights into the assembly and maintenance of the Australian arid zone biota. *Mol. Ecol.* 17:4398–4417.
- Conant, R., and J. T. Collins. 1998. Reptiles and amphibians of eastern and central North America. Third edition. Houghton-Mifflin, Boston, MA.

- Crisp, M. D., M. T. K. Arroyo, L. G. Cook, M. A. Gandolfo, G. J. Jordan, M. S. McGlone, P. H. Weston, M. Westoby, and H. P. Linder. 2009. Phylogenetic biome conservatism on a global scale. *Nature* 458:754–756.
- Drummond, A. J., and A. Rambaut. 2007. BEAST: Bayesian evolutionary analysis by sampling trees. *BMC Evol. Biol.* 7:214.
- Drummond, A. J., S. Y. W. Ho, M. J. Phillips, and A. Rambaut. 2006. Relaxed phylogenetics and dating with confidence. *PLoS Biol.* 4:e88.
- Edwards, E. J., and M. J. Donoghue. 2006. *Pereskia* and the origin of the cactus life form. *Am. Nat.* 167:777–793.
- 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*). *Am. Nat.* 173:225–240.
- FitzJohn, R. G. 2010. Quantitative traits and diversification. *Syst. Biol.* 59:619–633.
- Futuyma, D. J., and G. Moreno. 1988. The evolution of ecological specialization. *Ann. Rev. Ecol. Syst.* 19:207–233.
- Ghalambor, C. K., R. B. Huey, P. R. Martin, and G. Wang. 2006. Are mountain passes higher in the tropics? Janzen’s hypothesis revisited. *Integr. Comp. Biol.* 46:5–17.
- Grismer, L. L. 2002. *Amphibians and Reptiles of Baja California, including its Pacific Islands and the islands of the Sea of Cortes*. Univ. California Press, Berkeley, CA.
- Harmon, L. J., J. Weir, C. Brock, R. E. Glor, and W. Challenger. 2008. GEIGER: a statistical package for investigating evolutionary radiation in a comparative context. *Bioinformatics* 24:129–131.

- Hawkins, B. A., R. Field, H. V. Cornell, D. J. Currie, J.-F. Guégan, D. M. Kaufman, J. T. Kerr, G. G. Mittelbach, T. Oberdorff, E. M. O'Brien, E. E. Porter and J. R. G. Turner. 2003. Energy, water, and broad-scale geographic patterns of species richness. *Ecology* 84:3105–3117.
- Hijmans, R. J., S. E. Cameron, J. L. Parra, P. G. Jones, and A. Jarvis. 2004. The WorldClim interpolated global terrestrial climate surfaces. Version 1.3. Available at <http://biogeو.berkeley.edu/>
- Hijmans, R. J., S. E. Cameron, J. L. Parra, P. G. Jones, and A. Jarvis. 2005. Very high resolution interpolated climate surfaces for global land areas. *Int. J. Climatol.* 25:1965–1978.
- Hoffmann, A. A., and P. A. Parsons. 1989. An integrated approach to environmental stress tolerance and life-history variation: desiccation tolerance in *Drosophila*. *Biol. J. Linn. Soc.* 37:117–136.
- Hua, X., and J. J. Wiens. 2010. Latitudinal variation in speciation mechanisms in frogs. *Evolution* 64:429–443.
- Huey, R. B., and J. G. Kingsolver. 1993. Evolutionary responses to extreme temperatures in ectotherms. *Am. Nat.* 141:S31–S46.
- Jaeger, J. R., B. R. Riddle, and D. F. Bradford. 2005. Cryptic Neogene vicariance and Quaternary dispersal of the red-spotted toad (*Bufo punctatus*): insights on the evolution of North American warm desert biotas. *Mol. Ecol.* 14:3033–3048.
- Janzen, D. H. 1967. Why mountain passes are higher in the tropics. *Am. Nat.* 101:233–249.



- Kozak, K. H., and J. J. Wiens. 2007. Climatic zonation drives latitudinal variation in speciation mechanisms. *Proc. R. Soc. Lond.* 274:2995–3003.
- Kozak, K. H., and J. J. Wiens. 2010a. Niche conservatism drives elevational diversity patterns in Appalachian salamanders. *Am. Nat.* 176:40–54.
- Kozak, K. H., and J. J. Wiens. 2010b. Accelerated rates of climatic-niche evolution underlie rapid species diversification. *Ecol. Lett.* 13:1378–1389.
- Leaché, A. D. 2010. Species trees for spiny lizards (genus *Sceloporus*): identifying points of concordance and conflict between nuclear and mitochondrial data. *Mol. Phylogenet. Evol.* 54:162–171.
- Lenski, R. E., and A. F. Bennett. 1993. Evolutionary response of *Escherichia coli* to thermal stress. *Am. Nat.* 142:S47–S64.
- Lomolino, M. V., B. R. Riddle, and J. H. Brown 2006. *Biogeography*. 3rd edition. Sinauer, Sunderland, MA.
- Maddison, W. P. 2006. Confounding asymmetries in evolutionary diversification and character change. *Evolution* 60:1743–1746.
- Maddison, W. P., P. E. Midford, and S. P. Otto. 2007. Estimating a binary character's effect on speciation and extinction. *Syst. Biol.* 56:701–710.
- Magallón, S., and M. J. Sanderson. 2001. Absolute diversification rates in angiosperm clades. *Evolution* 55:1762–1780.
- Martins, E. P. 2004. COMPARE, ver. 4.6b: computer programs for the statistical analysis of comparative data. Distributed by the author. Department of Biology, Indiana University, Bloomington. <http://compare.bio.indiana.edu/>.
- 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. *Am. Nat.* 149:646–667.

McCain, C. M. 2004. The mid-domain effect applied to elevational gradients: species richness of small mammals in Costa Rica. *J. Biogeogr.* 31:19–31.

Mittelbach G. G., D. W. Schemske, H. V. Cornell, A. P. Allen, J. M. Brown, M. B. Bush, S. P. Harrison, A. H. Hurlbert, N. Knowlton, H. A. Lessios, C. M. McCain, A. R. McCune, L. A. McDade, M. A. McPeck, T. J. Near, T. D. Price, R. E. Ricklefs, K. Roy, D. F. Sax, D. Schluter, J. M. Sobel, and M. Turelli. 2007. Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. *Ecol. Lett.* 10:315–331.

Morlon, H., M. Potts, and Plotkin, J. 2010. Inferring the dynamics of diversification: a coalescent approach. *PLoS Biol.* 8:e1000493.

Orme, D., R. Freckleton, G. Thomas, T. Petzoldt, and S. Fritz. 2009. CAIC: comparative analysis using independent contrasts. URL: <http://R-Forge.R-project.org/projects/caic/>.

Orme, C. D. L., R. G. Davies, M. Burgess, F. Eigenbrod, N. Pickup, V. A. Olson, A. J. Webster, T. S. Ding, P. C. Rasmussen, R. S. Ridgely, A. J. Stattersfield, P. M. Bennett, T. M. Blackburn, K. J. Gaston, and I. P. F. Owens. 2005. Global hotspots of species richness are not congruent with endemism or threat. *Nature* 436:1016–1019.

Oufiero, C. E., S. C. Adolph, G. E. A. Gartner, and T. Garland, Jr. 2011. Latitudinal and climatic variation in body size and dorsal scale rows in *Sceloporus* lizards: a phylogenetic perspective. *Evolution* 65:3590-3607.

- Powney, G. D., R. Grenyer, C. D. L. Orme, I. P. F. Owens, and S. Meiri. 2010. Hot, dry and different: Australian lizard richness is unlike that of mammals, amphibians and birds. *Glob. Ecol. Biogeogr.* 19:386–396.
- Rabosky, D. L. 2012. Testing the time-for-speciation effect in the assembly of regional biotas. *Methods Ecol. Evol.* 3:224–233.
- Rabosky, D. L., S. C. Donnellan, A. L. Talaba, and I. J. Lovette. 2007. Exceptional among-lineage variation in diversification rates during the radiation of Australia's most diverse vertebrate clade. *Proc. R. Soc. Lond.* 274:2915–2923.
- Rangel, T. F. L. V. B., J. A. F. Diniz-Filho, and R. K. Colwell. 2007. Species richness and evolutionary niche dynamics: a spatial pattern-oriented simulation experiment. *Am. Nat.* 170:602–616.
- Riddle, B. A., and D. J. Hafner. 2006. A step-wise approach to integrating phylogeographic and phylogenetic biogeographic perspectives on the history of a core North American warm deserts biota. *J. Arid Env.* 66:435–461.
- Sanderson, M. J. 2002. Estimating absolute rates of molecular evolution and divergence times: a penalized likelihood approach. *Mol. Biol. Evol.* 19:101–109.
- Sanderson, M. J. 2003. r8s: inferring absolute rates of molecular evolution and divergence times in the absence of a molecular clock. *Bioinformatics* 19:301–302.
- Sites, J. W., Jr., 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. *Bull. Am. Mus. Nat. Hist.* 213:1–110.

- Stamatakis, A. 2006. RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics* 22:2688–2690.
- Stebbins, R. C. 1985. *A field guide to western reptiles and amphibians*. Second edition. Houghton Mifflin, Boston, MA.
- Stebbins, R. C. 2003. *A field guide to western reptiles and amphibians*. Third edition. Houghton-Mifflin Company, New York, NY.
- Stephens, P. R., and J. J. Wiens. 2003. Explaining species richness from continents to communities: the time-for-speciation effect in emydid turtles. *Am. Nat.* 161:112–128.
- Uetz, P. 2011. The TIGR reptile database. <http://www.reptile-database.org>. Accessed 25 June 2011.
- Townsend, T. M., D. G. Mulcahy, J. W. Sites, C. A. Kuczynski, J. J. Wiens, and T. W. Reeder. 2011. Phylogeny of iguanian lizards inferred from 29 nuclear loci, and a comparison of concatenated and species-tree approaches for an ancient, rapid radiation. *Mol. Phylogenet. Evol.* 61:363–380.
- Whitlock, M. C. 1996. The Red Queen versus the Jack-of-All-Trades: Evolutionary rates and the evolution of specialization. *Am. Nat.* 148:S65–S77.
- Wiens, J. J. 2011. The causes of species richness patterns across space, time, and clades and the role of "ecological limits." *Quart. Rev. Biol.* 86:75–96.
- Wiens, J. J., and M. C. Morrill. 2011. Missing data in phylogenetic analysis: reconciling results from simulations and empirical data. *Syst. Biol.* 60:719–731.

- Accepted Article
- Wiens, J. J., C. H. Graham, D. S. Moen, S. A. Smith, and T. W. Reeder. 2006. Evolutionary and ecological causes of the latitudinal diversity gradient in hylid frogs: treefrog trees unearth the roots of high tropical diversity. *Am. Nat.* 168:579–596.
- Wiens, J. J., G. Parra-Olea, M. Garcia-Paris, and D. B. Wake. 2007. Phylogenetic history underlies elevational patterns of biodiversity in tropical salamanders. *Proc. R. Soc. Lond.* 274:919–928.
- Wiens, J. J., C. A. Kuczynski, S. Arif, and T. W. Reeder. 2010a. Phylogenetic relationships of phrynosomatid lizards based on nuclear and mitochondrial data, and a revised phylogeny for *Sceloporus*. *Mol. Phylogenet. Evol.* 54:150–161
- Wiens, J. J., D. D. Ackerly, A. P. Allen, B. L. Anacker, L. B. Buckley, H. V. Cornell, E. I. Damschen, T. J. Davies, J. A. Grytnes, S. P. Harrison, B. A. Hawkins, R. D. Holt, C. M. McCain, and P. R. Stephens. 2010b. Niche conservatism as an emerging principle in ecology and conservation biology. *Ecol. Lett.* 13:1310–1324.
- Wiens, J. J., R. A. Pyron, and D. C. Moen. 2011. Phylogenetic origins of local-scale diversity patterns and causes of Amazonian megadiversity. *Ecol. Lett.* 14:643–652.

## *Supporting Information*

The following supporting information is available for this article:

**Appendix S1.** GenBank numbers for sequences used in the phylogenetic analyses.

**Appendix S2.** Detailed methods for estimation of phylogeny and divergence times.

**Appendix S3.** Estimation of divergence dates using penalized likelihood and results of comparative analyses using the alternate topology and branch lengths.

**Appendix S4.** Climatic distributions of 138 phrynosomatid lizard species for annual precipitation.

**Appendix S5.** Taxonomic decisions.

**Appendix S6.** Relationships between age and richness.

**Appendix S7.** R commands for simulations used to test the time-for-speciation effect.

**Appendix S8.** Inferred numbers of transitions between pairs of precipitation zones.

**Appendix S9.** Data for 27 phrynosomatid clades used to examine relationship between precipitation and net diversification rates.

**Appendix S10.** Parameter estimates from the quantitative state speciation and extinction analysis (QuaSSE).

**Appendix S10.** The geographic area of each bin of annual precipitation.

**Figure S1.** Maximum likelihood phylogeny of phrynosomatid lizards based on a combined, partitioned analysis of eight nuclear genes and five mitochondrial genes.

**Figure S2.** Bayesian time-calibrated phylogeny of phrynosomatid lizards based on a combined, partitioned analysis of eight nuclear genes and five mitochondrial genes.

**Figure S3.** Time-calibrated phylogeny of 117 species of phrynosomatid lizards based on penalized likelihood analysis showing ancestral reconstructions for mean values of annual precipitation within species.

**Table 1.** Number of species and relative time of colonization for each bin of annual precipitation (in Millions of years, Myr), using two measures of relative time, and contrasting richness patterns for all 138 species and for those 117 species included in the phylogeny.

Precipitation (mm)	Number of species (in tree)	Minimum age (Myr)	Summed ages (Myr)
0—500	78 (68)	35.82	156.18
501—1000	92 (86)	54.74	119.28
1001—1500	66 (59)	31.14	139.64
1501—2000	32 (29)	17.59	28.67
2001—2500	14 (11)	8.04	16.84
2501—3000	11 (8)	8.80	13.92
3001—3500	7 (5)	4.02	5.12
3501—4000	4 (2)	4.02	5.12
4001—4500	2 (1)	1.10	1.10
4501—5000	1 (1)	1.10	1.10



**Table 2.** Results of QuaSSE analyses of the relationship between speciation and climatic distribution (annual precipitation values). Best-fitting AIC values are boldfaced. See Appendix S8 for parameter estimates and other details.

Model	Parameters	Ln-likelihood	AIC
Minimal	3	-6080.2	<b>12166</b>
Linear	4	-6079.4	12167
Sigmoidal	6	-6080.1	12172
Hump	6	-6080.1	12172
Linear (with drift)	5	-6078.1	<b>12166</b>
Sigmoidal (with drift)	7	-6080.1	12174
Hump (with drift)	7	-6080.0	12174

**Table 3.** Results of BiSSE analyses on the relationship between speciation, extinction, and climate. Each column shows results using a different cut-off value for coding species as state 1 or state 0, based on species values of annual precipitation (mean among localities for each species). Lambda 0 is the speciation rate among species having state 0, and Lambda 1 is the speciation rate for state 1. Mu 0 is the estimated extinction rate among species with state 0 (Mu 1 is for state 1). q01 is the estimated rate of transition from state 0 to state 1, whereas q10 is the reverse rate. Each column first shows the estimated parameters under the model when all parameters are estimated, followed by the overall ln-likelihood and AIC, followed by the overall likelihood and AIC for constrained models in which speciation rates are set to be equal between states, and extinction rates are set to be equal. Note that AIC values should be compared within columns, but not between them. The results show strong support for higher speciation rates in more mesic environments when state 1 represents species with mean values > 1000 mm.

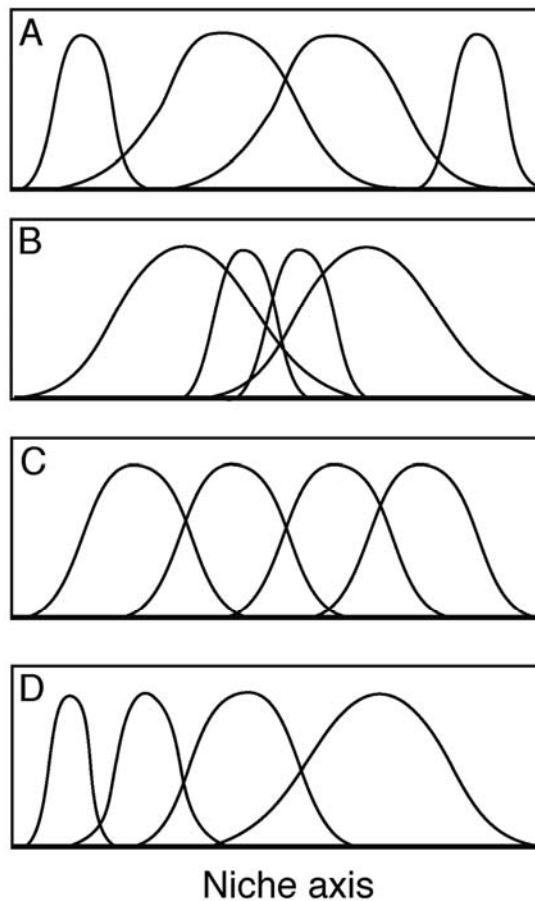
	State 1 > 500 mm	State 1 > 1000 mm	State 1 > 1500 mm
Lambda 0	5.065424e-02	4.955017e-02	7.568899e-02
Lambda 1	8.655018e-02	1.172413e-01	6.689644e-02
Mu 0	3.177927e-06	1.392337e-07	1.165721e-07
Mu 1	1.111800e-06	9.484211e-06	1.939391e-06
q01	6.957467e-03	7.552921e-06	1.653141e-03
q10	2.220351e-02	6.952872e-02	2.324335e-02
<u>All estimated</u>			
Ln likelihood	-479.90	-476.99	-436.45

---

AIC	971.8	965.98	884.90
<u>Lambda equal</u>			
Ln likelihood	-481.95	-484.04	-436.48
AIC	973.9	978.08	882.96
<u>Mu equal</u>			
Ln-likelihood	-479.90	-476.99	-436.45
AIC	969.8	963.98	882.90

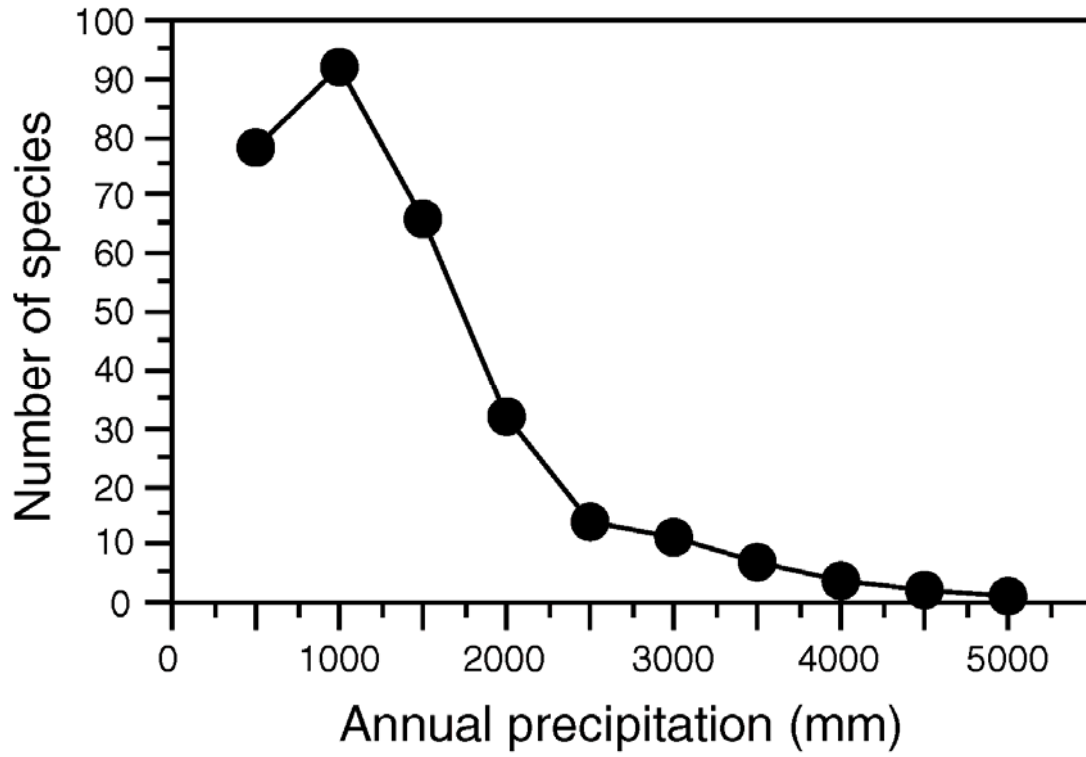
---

**Figure 1.** Diagrammatic illustration of possible distributions of niche breadths and niche positions along a given niche axis (e.g., precipitation). Each graph shows the frequency distribution of individuals of four species along the environmental gradient. (A) Species occurring in both of the more extreme conditions along the niche axis are more narrowly adapted to these conditions and have narrower niche breadths. (B) Species whose ranges extend into more extreme conditions are able to tolerate a broader range of conditions than others, and have broader niche breadths. (C) All species have similar niche breadths, regardless of their position along the niche axis. (D) Species at one extreme of the niche axis have broader niche breadths, and species at the other extreme have narrower niche breadths.

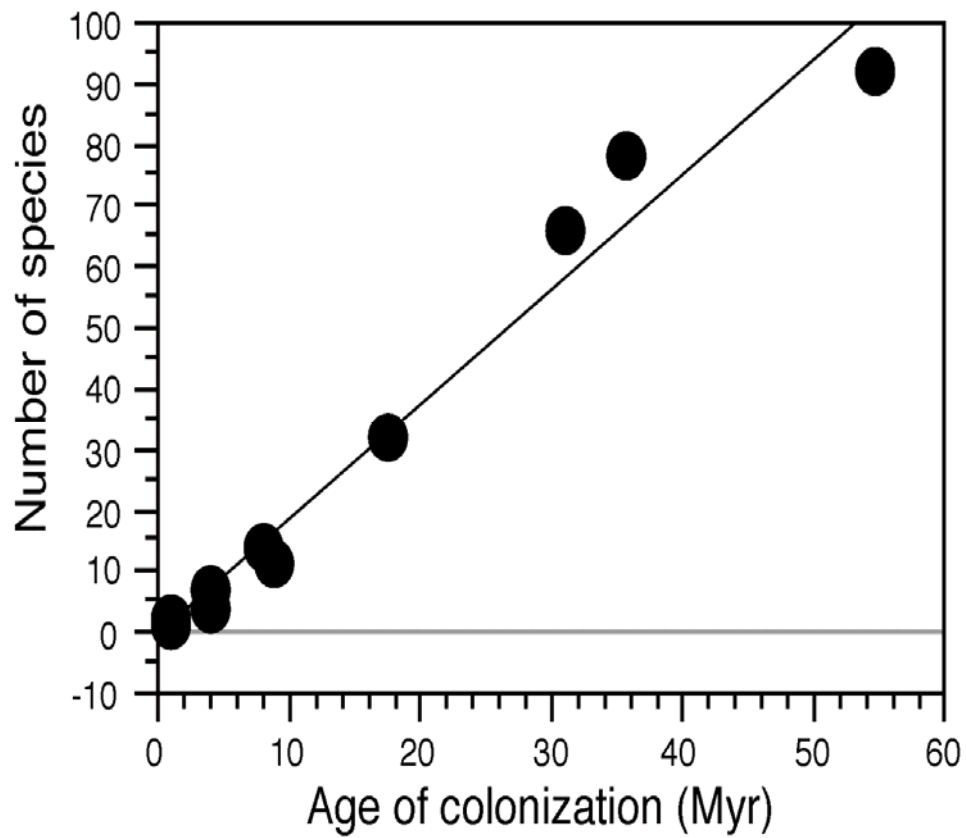




**Figure 3.** Patterns of species richness along an aridity gradient for 138 species of phrynosomatid lizards based on species values for annual precipitation.



**Figure 4.** Relationship between the number of species in each 500 mm/year bin of annual precipitation regime (as in Fig. 3, from 0–500, 501–1000, etc.) and the estimated amount of time that the precipitation regime has been occupied by phrynosomatid lizards, based on the oldest inferred colonization of phrynosomatids in each precipitation bin (Table 1).



**Figure 5.** Relationships between niche breadths and positions of species along a niche axis (annual precipitation), using different ways of characterizing the position of species on this axis, including (A) absolute value of the difference between species mean values and the midpoint of mean values, (B) species mean values, (C) maximum values of annual precipitation across the species range, and (D) minimum values of annual precipitation across the species range.

