

# Comparing macroecological patterns across continents: evolution of climatic niche breadth in varanid lizards

Long-Hui Lin and John J. Wiens

L. H. Lin, Key Laboratory of Hangzhou City for Ecosystem Protection and Restoration, Hangzhou Normal Univ., Hangzhou, China. – J. J. Wiens ([wienj@email.arizona.edu](mailto:wienj@email.arizona.edu)), Dept of Ecology and Evolutionary Biology, Univ. of Arizona, Tucson, AZ, USA.

Macroecological analyses often test hypotheses at the global scale, or among more closely related species in a single region (e.g. continent). Here, we test several hypotheses about climatic niche widths among relatively closely related species that occur across multiple continents, and compare patterns within and across continents to see if they differ. We focus on the lizard genus *Varanus* (monitor lizards), which occurs in diverse environments in Africa, Asia, and Australia. We address three main questions. 1) How do climatic niche breadths of species on a given niche axis change based on the position of species along that niche axis? (E.g. are species that occur in more extreme environments more narrowly specialized for those conditions?) 2) Are there trade-offs in niche breadths on temperature and precipitation axes among species, or are niche widths on different axes positively related? 3) Is variation in niche breadths among species explained primarily by within-locality seasonal variation, or by differences in climatic conditions among localities across the species range? We generate a new time-calibrated phylogeny for *Varanus* and test these hypotheses within and between continents using climatic data and phylogenetic methods. Our results show that patterns on each continent often parallel each other and global patterns. However, in many other cases, the strength of relationships can change dramatically among closely related species on different continents. Overall, we found that: 1) species in warmer environments have narrower temperature niche breadths, but there is no relationship between precipitation niche breadth and niche position; 2) temperature and precipitation niche breadths tend to be positively related among species, rather than showing trade-offs; and 3) within-locality seasonal variation explains most variation in climatic niche breadths. Some of these results are concordant with previous studies (in amphibians and North American lizards), and might represent general macroecological patterns.

Macroecological analysis seeks patterns in the diversity and distribution of species (Brown 1995, Gaston 2000). Many macroecological analyses focus on patterns at the global scale (Francis and Currie 2003, Moles et al. 2007, Olson et al. 2009). Many others focus on specific geographic regions, often comparing relatively closely related species within a continent (Sanders 2001, Supp et al. 2012, Chejanovski and Wiens 2014, Sheth et al. 2014). Here, we ask the general question: do macroecological patterns change among closely related species occurring on different continents, or do all continents show patterns that are similar to each other and to the overall, global pattern?

We address this broader question by focusing specifically on patterns of variation in climatic niche widths. The realized climatic niche width of a species is the size of the range of temperature and precipitation conditions where that species occurs. Along with the climatic niche position (i.e. the actual temperature and precipitation values, rather than the size of the range of values), the climatic niche width may help determine where a species can occur over space and time, either alone or in combination with other abiotic and biotic factors (Soberón 2007), and therefore may be critically

important to many topics. These topics include patterns of species richness (both globally and among habitats within regions), community structure, speciation, the spread of invasive species, and responses of species to anthropogenic climate change (brief review in Bonetti and Wiens 2014). For example, in theory, a species with a very broad climatic niche width for temperature could occur from the tropics to the poles, and might be highly resistant to anthropogenic climate change.

Despite the potential importance of climatic niche widths to many different topics, the factors that are related to variation in niche widths among species remain relatively underexplored. Furthermore, studies that have explored these factors exhibit a strong dichotomy in their taxonomic and geographic scope. For example, Wiens et al. (2013) tested whether species that occur in more arid environments tend to have narrower climatic niche widths, as expected if species that occur in more extreme environments tend to be more specialized for those conditions. They focused on a family of primarily North American lizards (Phrynosomatidae). Bonetti and Wiens (2014) tested this same hypothesis for both temperature and precipitation variables, across 2712

amphibian species (~ 40% of all described species) at the global scale. They also tested whether there were trade-offs in climatic niche widths on different niche axes (e.g. if species with wider temperature niche widths had narrower precipitation niche widths), or whether niche widths tended to be positively related instead. Quintero and Wiens (2013) tested whether climatic niche breadths of species were determined more by within-locality variation (e.g. seasonal temperature extremes) or by variation in climatic conditions across the range of each species. They addressed this question in three clades of predominantly North American taxa (phrynosomatid lizards, hylid frogs, plethodontid salamanders). Thus, these studies have either been global in scale, or else have focused on clades occurring predominantly in a single geographic region.

In this study, we address similar questions about climatic niche widths, but we also evaluate how patterns change within a single genus across different continents. We focus on varanid lizards (genus *Varanus*), a widely distributed genus of 79 species (Uetz and Hošek 2015), with 44 species in Oceania (mostly Australia), 35 in Asia, and 5 in Africa (note that some species occur in multiple regions, so adding numbers across regions yields a higher number than the global total). Importantly, varanids occur in a variety of climatic regimes on each continent, from rainforests to deserts and from tropical to more temperate climates (Supplementary material Appendix 6, Fig. A1). We first obtain climatic data from individual localities for all species of *Varanus* using GIS-based methods. We estimate a new time-calibrated phylogeny for the group that includes ~ 80% of the described species, given that previous phylogenetic studies lacked several species. We then address the following questions using phylogenetic comparative methods: 1) how are climatic niche breadths of species related to the position of species on that niche axis (i.e. temperature vs precipitation)? For example, are species that range into desert conditions narrowly specialized for low precipitation environments? 2) Are there trade-offs in niche breadths on different niche axes among species, or are niche widths on temperature and precipitation axes positively related? 3) Is variation in niche breadths among species explained primarily by within-locality seasonal variation, or by differences in climatic conditions among localities across the species range? We note that these questions have been addressed in previous studies, but to our knowledge, no previous studies have addressed all three in the same group of organisms.

## Methods

### Climatic data

Occurrence data were obtained from museum voucher records from GBIF (<[www.gbif.org/](http://www.gbif.org/)>) and VertNet (<<http://vnet.net.org/>>). For some species with low sample sizes of localities in these databases, we obtained additional localities from papers referenced in species accounts in the Reptile Database (Uetz and Hošek 2015, <[www.reptile-database.org/](http://www.reptile-database.org/)>). Occurrence data were carefully vetted to ensure that sampled localities spanned each species' full geographic range and that no localities were outside that range,

according to distribution maps in the Reptile Database (Uetz and Hošek 2015). Some localities were represented by multiple conspecific museum specimens. However, in our dataset, data were filtered so that each unique locality was represented only once per species.

We obtained occurrence data from varanid lizards across three continents (79 total), with 5 in Africa, 35 in Asia, and 44 in Oceania (mostly Australia; again, note that single species can occur in multiple regions). Among these species, 60 species were included in the phylogeny and in the subsequent comparative analyses (4 in Africa, 25 in Asia, 36 in Oceania). For those 60 species included in the comparative analyses, we obtained climatic data from a mean of 237.8 localities per species, with a range of 1 to 4317 (Supplementary material Appendix 1). We did not exclude species simply because they had few localities. Many species are known from few localities simply because they have small geographic ranges, and excluding species known from few localities might therefore have strongly biased the results against narrowly distributed species. We specifically confirmed that species included in the comparative analyses (i.e. in the tree) that were represented by < 4 localities in our dataset are indeed known from small geographic ranges (specifically, small islands, where greater sampling would have little impact on climatic niche values).

We generally followed standard geographic definitions for the three regions considered (Supplementary material Appendix 6, Fig. A1; Grosvenor and Darley 1963), instead of traditional or more recent zoogeographic definitions (Holt et al. 2013). We did this because there are very few varanid species in the traditional Palearctic region, or in the Saharo-Arabian province (Holt et al. 2013). Therefore, we assigned species on continental Africa to Africa, and those in Asia (including the Middle East) to Asia. We considered Oceania to include New Guinea and Australia, and the rest of the Indonesian Archipelago as belonging to Asia (largely following Holt et al. 2013, but placing the Maluku Islands with Asia). The limits of each region and the overall distribution of point localities are shown in Supplementary material Appendix 6, Fig. A1. The number of localities per species per region is shown in Supplementary material Appendix 1. One species (*V. griseus*) occurred in both Asia and Africa. Four species (*V. indicus*, *V. salvadorii*, *V. salvator*, and *V. timorensis*) occurred in both Asia and Oceania. No species occurred across all three continents. When a species occurred in two continents, the analyses of the species from each continent were based only on their localities on that continent, rather than the whole species range.

For each point locality, we extracted relevant climatic variables (see below) at ~ 1-km<sup>2</sup> resolution from the WorldClim database (Hijmans et al. 2005, <[www.worldclim.org/bioclim](http://www.worldclim.org/bioclim)>) using DIVA-GIS ver. 7.5.0 (Scheldeman and van Zonneveld 2010). The WorldClim database consists of 19 climatic variables based on averages of monthly temperature and precipitation data from 1950 to 2000. Data are taken from thousands of weather stations all over the world and are then spatially interpolated to locations between weather stations.

We focused on a limited set of variables to test our hypotheses, following from recent studies on climatic niche breadth (Quintero and Wiens 2013, Wiens et al. 2013,

Bonetti and Wiens 2014). Specifically, we focused on annual mean temperature (Bio1), maximum temperature of the warmest month (Bio5), minimum temperature of the coldest month (Bio6), annual precipitation (Bio12), precipitation of the wettest quarter (Bio16), and precipitation of the driest quarter (Bio17). Bio1 and Bio12 are standard variables for describing the overall climatic distribution of a species, and the temperature extremes (Bio5, Bio6) are essential for describing temperature niche breadth. Bio12 also provides the most intuitive and straightforward way to describe precipitation niche breadth across the species range (Quintero and Wiens 2013).

For these variables, we focused on the mean value of Bio1 across sampled localities in the range of each species (for temperature niche position), and the maximum value of Bio5 (the hottest temperature experienced by the species, both across the year and across the species range) and the minimum value of Bio6 (the lowest temperature across the year and range) for temperature niche breadth (see below for specific hypotheses). We also used mean, maximum and minimum values for Bio12 across the species range for precipitation niche breadth (minimum and maximum) and niche position (mean). We also examined maximum values of Bio16 (wettest quarter) and minimum values of Bio17 (driest quarter) across the range of each species for precipitation niche breadth in some analyses (see below).

We note that our estimates of climatic niches are based on realized climatic niches, and they may reflect a variety of biotic and abiotic factors rather than physiological tolerances alone (including species interactions and non-climatic barriers to dispersal). However, we do not consider physiological tolerances to be the only relevant aspect of climatic niche width, and the standard approach we use allowed us to compare our results to those of other recent studies on realized climatic niche widths.

## Phylogenetic framework

We estimated a time-calibrated phylogeny that included 60 varanid species (76% of the 79 currently described species; Uetz and Hošek 2015), using existing data in the literature and Bayesian estimation of topology and divergence times with BEAST (Bouckaert et al. 2014). We started with the squamate-wide matrix of Pyron et al. (2013), which summarized data from GenBank from 4161 species and data from seven nuclear and five mitochondrial genes. We modified this matrix by first eliminating all non-varanid species, except for two well-established outgroup taxa (the monotypic families Shinisauridae and Lanthanotidae). Numerous recent multi-locus studies show that these two families are the closest relatives of Varanidae (Wiens et al. 2012, Pyron et al. 2013, Reeder et al. 2015, Zheng and Wiens 2016). We then eliminated the PDC gene from the matrix because no varanid species had data for this gene. This left a total of six nuclear genes (BDNF, *c-mos*, NT3, R35, RAG-1, and RAG-2) and five mitochondrial genes (12S, 16S, cytochrome *b*, ND2, and ND4). We then searched GenBank on April 15, 2015 for additional species of varanids that were not included by Pyron et al. (2013) but which had data available for one or more of these genes. We found relevant data from

seven additional *Varanus* species (*V. bangonorum*, *V. cumingi*, *V. nebulosus*, *V. nuchalis*, *V. palawanensis*, *V. sparnus*, and *V. togianus*). When data were available for multiple individuals of the same species, we obtained data from the individual with data for the largest number of the 11 genes used here. GenBank accession numbers are listed in Supplementary material Appendix 2. The data matrix is available on Dryad (Lin and Wiens 2016).

The data matrix contained considerable missing data (70.0% of all data cells). However, detailed analyses suggest that divergence dating and topology estimation in BEAST can both be highly robust to extensive missing data (Zheng and Wiens 2015). This is especially true when at least some genes are present in most of the taxa [such as the genes ND2 (54 taxa) and NT3 (40 taxa) here].

The tree and divergence dates were simultaneously estimated using the Bayesian uncorrelated lognormal approach in BEAST ver. 2.0 (Bouckaert et al. 2014). Prior to conducting the BEAST analyses, we determined the best-fitting combination of partitions among genes and substitution models for partitions, using Partition Finder ver. 1.1.1 (Lanfear et al. 2012). The best-fitting model was determined using the Bayesian Information Criterion. Branch lengths were linked across partitions. The set of models was restricted to those available in BEAST. The greedy search option was used. The partitions and models selected are listed in Supplementary material Appendix 3.

For the time calibration, a secondary calibration point was used. Specifically, we used the estimated age of the split between the outgroup (*Shinisaurus*) and the clade of *Lanthanotus* + *Varanus*. This node was estimated to be 80 Myr old by Zheng and Wiens (2015), based on a BEAST analysis of 20 relatively complete nuclear genes and multiple fossil calibration points. Therefore, we set the prior distribution on the age of this node to be normally distributed with a mean age of 80 Mya, and a standard deviation of 1.

The relaxed lognormal clock model was used. The standard Yule speciation process was specified for the tree prior. Clock models and topologies of individual data partitions were linked, whereas substitution parameters were unlinked across partitions.

For the BEAST analyses, we used four replicate searches with 200 million generations each, retaining trees every 10 000 generations. Monophyly of the ingroup was constrained (and note that outgroup taxa had data for all genes). We compared results of independent runs using Tracer ver. 2.2.1 (Rambaut and Drummond 2007) to ensure that the chains were converging and mixing adequately. Then, results from the first 10% of the sampled generations from each run were excluded as burnin. All four runs achieved the recommended adequate effective sample size of 200 for likelihood (Drummond et al. 2006). All four gave effectively identical topologies, ages, and support values. We arbitrarily selected and used the results from one of the four runs (likelihood = -52862.9, ESS = 1191). We chose the maximum clade credibility tree for the target tree using the program TreeAnnotator in BEAST ver. 2.0. We chose mean heights for node heights. This sets the heights (ages) of each node in the tree to the mean height across the entire sample of trees for that clade.

The topology of the phylogenetic tree (Fig. 1) is broadly similar to that of Pyron et al. (2013) except for the addition of seven species, which were not included in phylogenies across varanids in previous studies (Pianka and King 2004, Collar et al. 2011). The tree is provided in nexus format in Supplementary material Appendix 4.

### Testing niche width hypotheses

We used the climatic and phylogenetic data to address three main questions. 1) How are climatic niche breadths of species on a given niche axis change related to the position of

species along that niche axis? 2) Are there trade-offs in niche breadths on different niche axes among species (i.e. negative relationships between temperature and precipitation niche breadths)? 3) Is variation in niche breadths among species explained primarily by within-locality seasonal variation, or by differences in climatic conditions among localities across the species range? We tested these hypotheses on each continent separately, and then globally. We generally followed the methods used in previous studies to test these hypotheses (Quintero and Wiens 2013, Wiens et al. 2013, Bonetti and Wiens 2014).

For all three questions, we first calculated the niche breadth for each species for both temperature and precipitation.

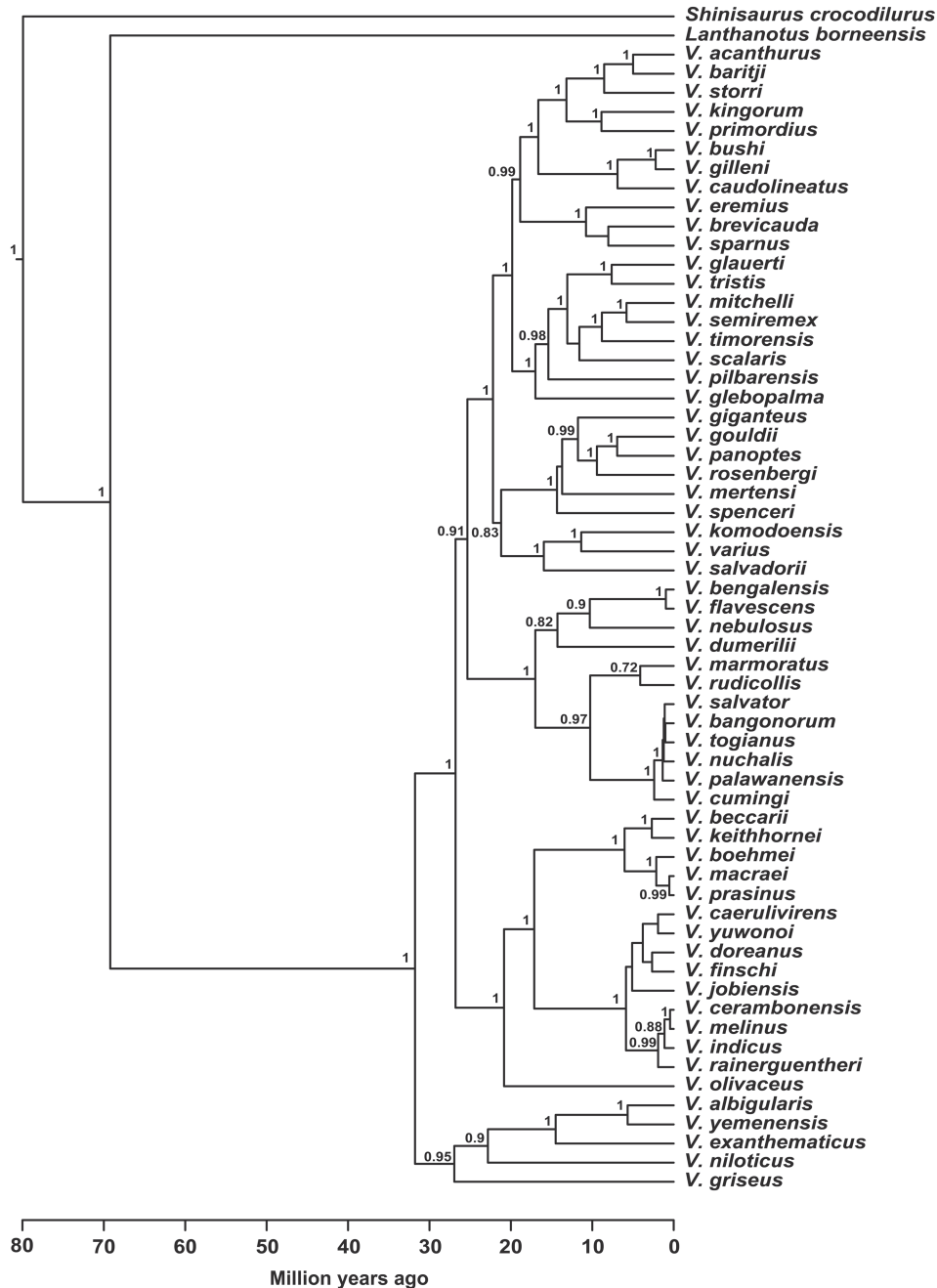


Figure 1. Chronogram for 60 species of varanid lizards and two outgroups estimated in this study using BEAST, based on six nuclear and five mitochondrial genes. Bayesian posterior probabilities greater than 0.7 are shown beside nodes.



For temperature niche breadth (TNB), we subtracted the minimum value of the minimum temperature of the coldest month (Bio6) across all sampled localities of the species from the maximum value of the maximum temperature of the warmest month (Bio5), following Quintero and Wiens (2013). For precipitation niche breadth (PNB), we first used an index based on subtracting the minimum values of Bio12 from the maximum values of Bio12 among all localities for each species. This measure reflects spatial variation in precipitation across the species range, but not seasonal variation. As an alternative index, we used the maximum value of wettest quarter precipitation (Bio16) across all sampled localities minus the minimum value of driest quarter precipitation (Bio17). This alternative measure reflects both seasonal and spatial variation. In general, we think that annual precipitation (Bio12) is the more relevant measure of precipitation niche breadth, rather than those based only on quarterly precipitation (Bio16, Bio17). For example, deserts and rainforests are distinguished by their annual precipitation, not their precipitation during a particular quarter. Therefore, variation in values of Bio12 across the species range was our primary measure of precipitation niche breadth. However, it is not possible to use this index to address the relative contribution of seasonal variation to overall precipitation niche breadth. Therefore, we used the quarterly measures to test our third hypothesis.

To address the first hypothesis, we initially tested the relationship between temperature niche breadth and niche position on the temperature axis, with the niche position of each species based on the mean value of annual mean temperature (Bio1) across localities in the species range. We then tested the relationship between precipitation niche breadth and precipitation niche position, with precipitation niche position based on the mean value of annual precipitation (Bio12) across localities.

To address the second hypothesis, we tested the relationship between temperature niche breadth and precipitation niche breadth. We then evaluated whether the relationship (if present) was negative or positive.

To address the third hypothesis, we first estimated the within-locality niche breadth for temperature and precipitation. For temperature, we subtracted the value of Bio6 (minimum yearly temperature) from Bio5 (maximum yearly temperature) for that locality. For precipitation we used the difference between the wettest and driest quarters of the year (i.e. Bio16 and Bio17, respectively) for that locality. Then, for each locality, we determined how much of the overall species niche breadth is spanned by the within-locality niche breadth. We then computed the average of these proportions across localities for each species, referred to as the WLS ratio (Quintero and Wiens 2013). The WLS ratio is similar to the within-individual component of the niche divided by the total niche width used in other papers (Bolnick et al. 2002, 2003, Araújo et al. 2011), but using localities rather than individuals. We then estimated the mean WLS ratio for each continent and at the global scale. This gives a straightforward quantitative description of the contribution of within-locality niche breadth to overall species niche breadth. Note that for species-level precipitation niche breadth in this analysis, we used the maximum value of Bio16 across the species range minus the minimum value of Bio17. Thus, our measure of

species-level niche breadth here potentially incorporated both spatial and temporal (seasonal) variation in precipitation (instead of merely examining variation in Bio12 across the species range). A detailed simulation study has shown that limited and incomplete sampling of localities within species does not bias estimates of WLS ratios (Quintero and Wiens 2013).

To statistically test the contribution of within-locality niche breadth to overall species niche breadth, we simply tested the relationship between the WLS ratio of each species and species niche breadths. A positive relationship would indicate that within-locality niche breadth drives overall species niche breadth. A significant negative relationship would indicate that between-locality niche breadth makes an important contribution to species niche breadths.

Finally, in a related test, we addressed whether variability in niche position among localities contributed to niche breadth. We calculated the niche position variance (NPV) of each species as the variance in the midpoint of the niche breadths across localities, calculated separately for temperature and precipitation, following Quintero and Wiens (2013). The midpoint for niche breadth for temperature is the midpoint between the yearly minimum (Bio6) and maximum (Bio5) temperatures for each locality. The midpoint for precipitation is the midpoint between the wettest and driest quarters of the year (Bio16 and Bio17) for each locality. We then tested whether the NPV for each species is significantly and positively related to species niche breadths, indicating a contribution of among-locality variation in climatic conditions to overall species niche breadth. Note that NPV also appears to have little consistent bias associated with incomplete sampling of localities across species' ranges.

Species with only one locality were removed from this set of analyses addressing the third question in our study, since these single-locality species cannot be used to test the contribution of between-locality variation to the overall climatic niche breadth of species. This left 70 species (9 removed). Values for each of these 70 species are summarized in Supplementary material Appendix 5. Among these 70 species, 57 species were used in the phylogenetic analyses and 13 species were excluded (*V. bitatawa*, *V. dalubhasa*, *V. hamersleyensis*, *V. kordensis*, *V. mabitang*, *V. nesterovi*, *V. obor*, *V. ornateus*, *V. rasmussenii*, *V. reisingeri*, *V. samarensis*, *V. similes*, and *V. spinulosus*).

We tested our hypotheses in a phylogenetic framework using phylogenetic generalized least squares, PGLS (Martins and Hansen 1997). The lambda model was used for all PGLS analyses (i.e. branch lengths adjusted based on  $\lambda$  values estimated via maximum likelihood), and values of kappa and delta were fixed at 1. The lambda model accounts for the estimated level of phylogenetic signal in the data, and this phylogenetic signal is what PGLS is designed to accommodate (therefore we did not explore other evolutionary models besides the lambda model). PGLS analyses were conducted using the R package *caper*, ver. 0.5 (Orme et al. 2012).

Data available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.h0v84>> (Lin and Wiens 2016).

Table 1. Results of phylogenetic generalized least squares (PGLS) analyses of the relationship between temperature niche breadth (TNB; maximum Bio5 – minimum Bio6) and annual mean temperature (Bio1), precipitation niche breadth (PNB; maximum Bio12 – minimum Bio12) and annual precipitation (Bio12), and between temperature niche breadth (TNB) and precipitation niche breadth (PNB). Results are for each continent separately and all continents combined. *N* is the number of species in each region.  $\lambda$  is the estimated phylogenetic signal in the PGLS analysis.

Variables	Continent	<i>N</i>	$\lambda$	$r^2$	p-value	Coefficient	Intercept
TNB vs Bio1	Africa	4	1	0.663	0.1860	-0.7436	60.4349
	Asia	25	0.738	0.070	0.2120	-1.4113	59.486
	Oceania	36	0.675	0.205	0.0055	-1.2693	57.311
	Global	60	0.672	0.171	0.0011	-1.5444	69.301
PNB vs Bio12	Africa	4	0	0.802	0.1045	8.1522	-5603.449
	Asia	25	0.277	0	0.9236	-0.0284	961.264
	Oceania	36	0	0.190	0.0079	0.5846	739.775
	Global	60	0	0.031	0.1843	0.2294	1042.040
TNB vs PNB	Africa	4	0	0.073	0.7293	0.0004	41.045
	Asia	25	0.992	0.738	<0.0001	0.0066	19.108
	Oceania	36	1	0.577	<0.0001	0.0038	19.323
	Global	60	0.980	0.619	<0.0001	0.0044	25.024

## Results

We used the climatic data and phylogeny to test our three main hypotheses and to address whether patterns varied among continents. First, we tested whether the climatic niche width of species is related to their position on a given niche axis. Overall (globally), species occurring in colder environments (i.e. lower mean values of annual mean temperature; Bio1) tend to have broader thermal niche breadth (maximum – minimum temperatures, or Bio5 – Bio6; PGLS:  $r^2 = 0.171$ ;  $p = 0.0011$ ; Table 1, Fig. 2). However, this pattern differed among continents. In Africa, there was no significant relationship but a positive trend, in contrast to the negative relationship on other continents and globally (Fig. 2). In Asia, the relationship was relatively weak ( $r^2 = 0.070$ ,  $p = 0.2120$ ), despite the large number of species ( $n = 25$ ). Only the pattern in Oceania was similar to the overall pattern across continents in direction and strength.

Performing a parallel test for precipitation also showed very different patterns on different continents (Fig. 2; Table 1). Testing the relationship between mean values of annual precipitation across localities of each species (Bio12) and precipitation niche breadth (maximum – minimum values of annual precipitation, Bio12, across the species range), we found a strong positive relationship in Oceania, and no significant relationships in Africa (but a positive trend), Asia or globally.

Both globally and on separate continents, there is no tradeoff in precipitation and temperature niche breadths among species (Fig. 3; Table 1). Instead, there is a positive relationship between temperature niche breadth and precipitation niche breadths in Asia, Oceania and globally (globally:  $r^2 = 0.619$ ;  $p < 0.0001$ ). The relationship in Asia is stronger than in Oceania ( $r^2 = 0.738$  vs  $0.577$ ). The relationship in Africa is non-significant.

Globally, the average within-locality range of temperatures (Bio5–Bio6) is about 73% of the overall range of temperatures across all localities (maximum Bio5–minimum Bio6), with species values ranging from 0.364 to 1 (Table 2). Values are broadly similar across continents, but substantially

lower in Africa (mean = 0.46). Similarly, for precipitation, the within-locality range is about 57% of the overall species range globally, with values ranging from a minimum near 0.127 to a maximum 0.982 (Table 2). Again, mean values are broadly similar across continents, with somewhat lower values in Africa (0.46) and higher values in Asia (0.64).

Following from these raw values, there is a significant, positive relationship between mean within-locality niche breadths for temperature and species temperature niche breadths for most continents and globally (Table 3; Supplementary material Appendix 6, Fig. A2; but marginally non-significant in Africa). Similarly, for precipitation, there is a significant, positive relationship between within-locality and species-level niche breadths (Table 3; Supplementary material Appendix 6, Fig. A2). However, the strength of this relationship varies considerably among continents, from non-significant (Africa;  $r^2 = 0.411$ ), to significant but weak ( $r^2 = 0.135$ ; Oceania), to relatively strong ( $r^2 = 0.511$ ; Asia).

We also tested whether there was a relationship between the ratio of within-locality to species-level niche breadth (WLS ratio; Quintero and Wiens 2013) and the overall species niche breadth on a given climatic niche axis. A significant negative relationship indicates that species in which the niche breadth is less dominated by within-locality variation have broader niche breadths, potentially indicating a greater role for among-locality variation in determining niche breadth. These relationships were significantly negative globally for both temperature and precipitation (Table 3; Supplementary material Appendix 6, Fig. A3). For temperature, relationships were generally significant and similar in strength across continents (except for Africa, which was non-significant), but with a weaker relationship in Oceania. In contrast, for precipitation, continents differed strikingly, with a very strong relationship in Africa ( $r^2 = 0.966$ ), a weak relationship in Oceania ( $r^2 = 0.137$ ), and intermediate values in Asia ( $r^2 = 0.560$ ) and globally ( $r^2 = 0.271$ ).

Finally, we tested whether species niche breadth is related to the variance in niche position among localities (a positive relationship indicating a greater importance of different

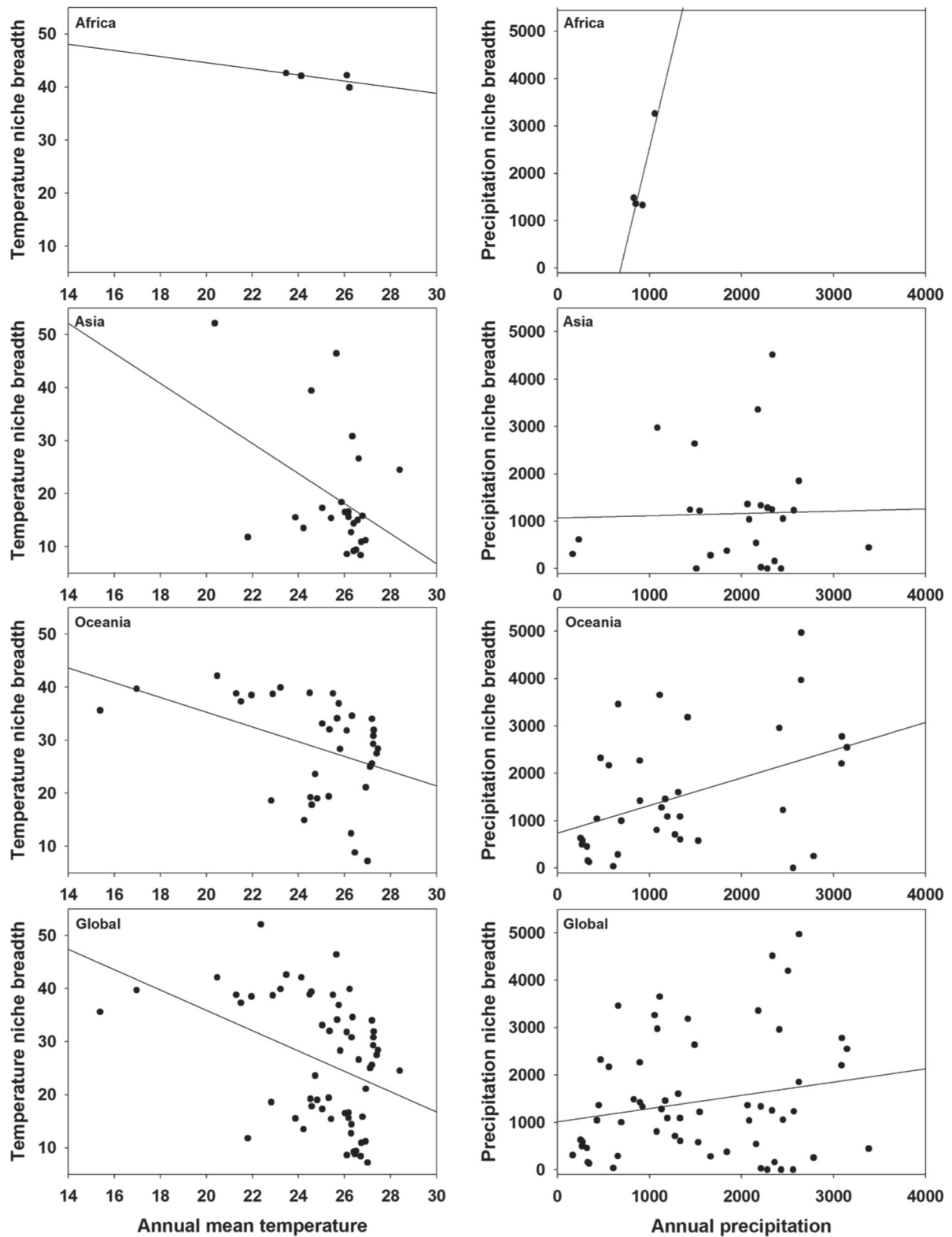


Figure 2. Relationships between temperature niche breadth and annual mean temperature (Bio1), and between precipitation niche breadth and annual precipitation (Bio12) across continents and globally, shown using the raw data for ease of interpretation. PGLS results are shown in Table 1.

climatic conditions among localities in determining overall species niche breadth). Again, these relationships were significant and positive globally, but varied considerably

among continents (Table 3; Supplementary material Appendix 6, Fig. A4). For example, for temperature, the relationship was strong in Asia but non-significant in

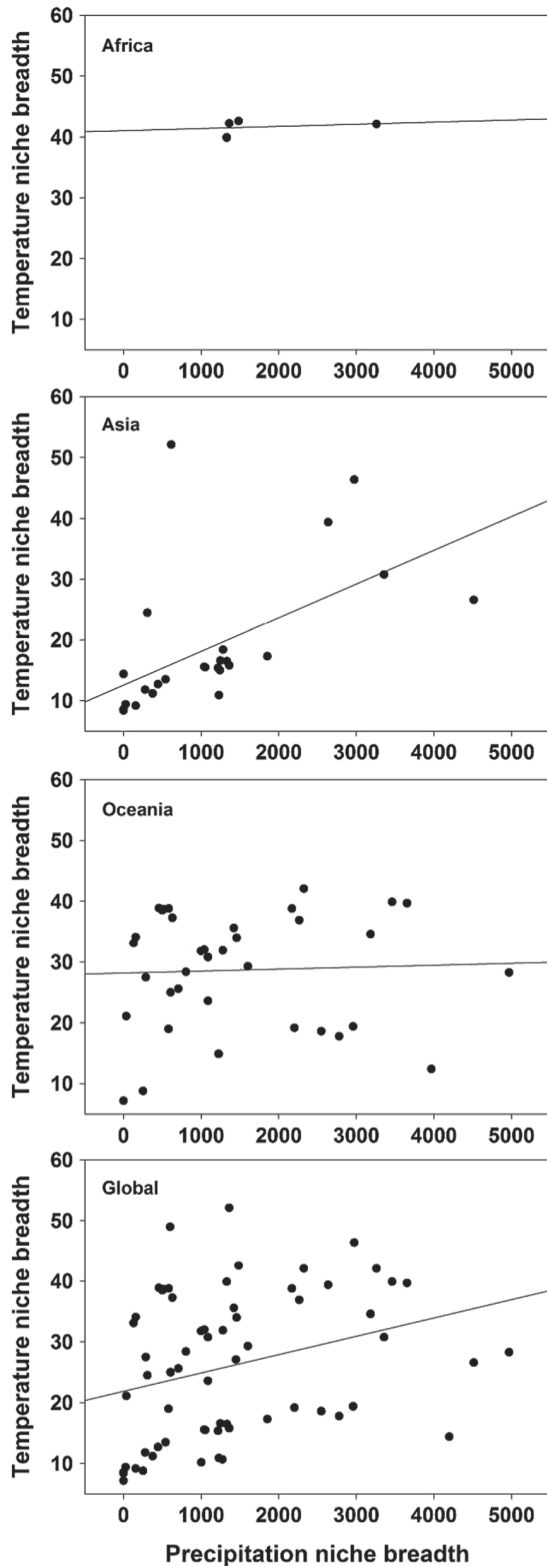


Figure 3. Relationships between temperature niche breadth and precipitation niche breadth across continents and globally, shown using the raw data for ease of interpretation. PGLS results are shown in Table 1.

Africa and Oceania. For precipitation, the relationship was non-significant in Africa, and much stronger in Asia than Oceania ( $r^2 = 0.642$  vs  $0.347$ ).

## Discussion

Our paper had two main goals. First, we used our data from varanid lizards to test general hypotheses about variation in climatic niche width among species. Second, we evaluated how these answers changed across different continents for this group of relatively closely related species (i.e. congeners, with major clades having diverged less than 30 million yr ago; Fig. 1). Even though our global-scale results show many similarities with previous studies on climatic niche widths, we also found many differences in these relationships among continents.

### Differences among continents

Our results show that macroecological patterns can be very different on different continents, even in this group of relatively closely related species. For example, for precipitation niche breadth and niche position, one of the three continents showed a significant, positive relationship, even though there was no significant relationship globally or on other continents (Table 1). For the relationship between within-locality to species niche breadth ratio (WLS) and species niche breadth for precipitation,  $r^2$  values ranged from (0.97) to (0.14) among continents (Table 3). An obvious lesson from this study is that global-scale analyses can mask considerable variation among continents, even in a group of closely related, congeneric species.

What explains these dramatic differences in results among continents? Three explanations seem the most obvious, but are not necessarily true. First, the continents have somewhat different numbers of species. Specifically, Africa has only five varanid species, only four of which could be included in our phylogeny-based analyses. Therefore, some differences between Africa and other continents might be considered trivial, for example, finding non-significant relationships due to limited sample size. However, relationships in Africa could be significant (Table 3), and they sometimes differed strongly in magnitude from those on other continents. More importantly, there were often striking differences in the strength of relationships between continents with relatively large numbers of species (i.e. Asia and Oceania).

Second, it might be seen as trivial that species on different continents have different patterns of climatic niche widths, since different continents are expected to have somewhat different climatic conditions. However, all three continents contain a range of biomes (deserts to rainforests, temperate to tropical), and varanid lizards occur in most of these (although they are absent from the coldest climates).

A third explanation is that all of these patterns are simply sampling artifacts related to different collecting efforts in different regions, leading to fewer localities and species in some regions. However, among the species included in our comparative analyses, the region with the fewest species has many localities per species (Africa, 4 widely distributed species with 171 mean localities per species), whereas Asia has many species but fewer localities per species (25 species, many narrowly distributed on islands, with 22



Table 2. Summary of the ratio of mean within-locality niche breadth to overall species niche breadth (WLS ratio), showing the mean and range (in parentheses) among species in each region and globally. *N* is the number of species included in each region.

Continent	<i>N</i>	Mean within-locality temperature niche breadth ratio	Mean within-locality precipitation niche breadth ratio
Africa	5	0.459 (0.412–0.541)	0.463 (0.204–0.597)
Asia	29	0.755 (0.374–1.000)	0.637 (0.200–0.976)
Oceania	40	0.732 (0.367–0.988)	0.547 (0.127–0.982)
Global	70	0.726 (0.364–1.000)	0.573 (0.127–0.982)

mean localities each). Oceania has many species and many localities per species (36, species, 362 localities per species), although it also has narrowly distributed species known from very few localities.

Overall, we suggest that these different patterns may arise because the varanid lizard faunas on different continents differ in how they respond to climatic variation. For example, African varanids differ substantially from Asian and Australian varanids in having larger mean temperature niche breadths (Fig. 2), with niche breadths that are more dominated by among-locality variation than within-locality temperature variation (Table 2). In short, Africa differs in lacking the narrowly specialized and narrowly distributed species that are predominant in Asia and present in Oceania, and fewer of the intermediate-width species that predominate in Oceania. Although it is tempting to speculate that the results in Africa are simply a phenomenon of having relatively few species (i.e. a sampling artifact), it is important to note that the clade of African varanids is very similar in age to the clade containing all species from Asia and Oceania. Therefore, the differences in

species richness among continents must be caused by differences in rates of diversification (speciation and extinction), rather than colonization time. An intriguing possibility is that the differences in climatic niche width (i.e. Africa consisting mostly of temperature generalists) might be a cause of the differences in species richness between continents, rather than an effect. After all, adaptation to different climatic regimes may be an important mechanism of speciation (Moritz et al. 2000, Kozak and Wiens 2007, Hua and Wiens 2013). However, narrower climatic niche widths at the species level may be only weakly related to higher clade-level diversification rates (Gómez-Rodríguez et al. 2015).

These results raise several questions for future research. First, are differences among continents in climatic niche width patterns common or exceptional? Second, if they are common, do different groups of organisms on the same continent share similar patterns? For example, does Africa contain a large number of species with broad temperature niche breadths in other groups? Third, regardless of their generality, what ecological and/or physiological mechanisms might explain these patterns?

Table 3. Results of phylogenetic generalized least squares (PGLS) analyses of the relationship between species niche breadths (NB) and a) mean within-locality niche breadths (WL–NB), b) the mean ratio of within-locality niche breadth to species niche breadth (WLS ratio), and c) the variance in the midpoint of within-locality niche breadths for each species (niche position variance, NPV) for varanid lizards, for both temperature (T) and precipitation (P). Results are for each continent separately and all continents combined. *N* is the number of species in each region.  $\lambda$  is the estimated phylogenetic signal in the PGLS analysis. For the first row (asterisk), PGLS optimization failed for the four species in Africa, and we present the results from ordinary-least squares regression instead.

Variables	Continent	<i>N</i>	$\lambda$	<i>r</i> <sup>2</sup>	p-value	Coefficient	Intercept
T–WL–NB vs TNB	Africa*	4	0	0.855	0.0783	0.3270	–28.566
	Asia	22	0	0.800	0.0001	0.4457	4.399
	Oceania	35	1	0.601	0.0001	0.4822	5.527
	Global	57	0.936	0.425	<0.0001	0.2918	9.435
P–WL–NB vs PNB	Africa	4	0	0.411	0.3589	0.0274	395.247
	Asia	22	0	0.511	0.0003	0.3330	257.233
	Oceania	35	0.300	0.135	0.0302	0.1726	306.451
	Global	57	0.260	0.220	0.0003	0.2071	277.298
T–WLS ratio vs TNB	Africa	4	0	0.706	0.1559	0.0168	–0.260
	Asia	22	0	0.402	0.0011	–0.0089	0.906
	Oceania	35	0.882	0.288	0.0009	–0.0091	0.939
	Global	57	0.611	0.433	<0.0001	–0.0118	1.016
P–WLS ratio vs PNB	Africa	4	0	0.966	0.0169	–0.0002	0.729
	Asia	22	0.852	0.560	<0.0001	–0.0002	0.791
	Oceania	35	0	0.137	0.0288	–0.0002	0.686
	Global	57	0.414	0.271	<0.0001	–0.0002	0.739
T–NPV vs TNB	Africa	4	1	0.606	0.2217	5.0273	–196.699
	Asia	22	0.142	0.438	0.0011	0.1357	–0.024
	Oceania	35	0.492	0.032	0.3008	0.0695	1.792
	Global	57	0.624	0.295	<0.0001	0.2389	–0.929
P–NPV vs PNB	Africa	4	1	0.628	0.2079	7.2833	5913.234
	Asia	22	0.806	0.642	<0.0001	21.9086	–7063.104
	Oceania	35	0.173	0.347	0.0002	29.2710	–10259.675
	Global	57	0	0.417	<0.0001	26.2149	–10584.363

## General patterns in climatic niche width

Despite the variation that we find among continents, our results also show many parallels with previous analyses of climatic niche breadths in vertebrates. Here and throughout, all of the patterns described for varanid lizards are at the global scale, including species from all three continents. First, our results confirm previous studies on the relationship between climatic niche breadth and climatic niche position. We found a strong negative relationship between temperature niche breadth and annual mean temperature, as found globally in amphibians (Bonetti and Wiens 2014). This pattern has an intuitive explanation: at higher latitudes, temperature seasonality increases, such that species have broader temperature niche breadths, even if they occur at only a single locality (Janzen 1967, Vázquez and Stevens 2004, Quintero and Wiens 2013). Thus, we suggest that this pattern might be relatively general.

In contrast, we failed to find a positive global relationship between precipitation niche breadth and precipitation niche position (based on annual precipitation), as found in North American lizards (Phrynosomatidae; Wiens et al. 2013) and amphibians globally (Bonetti and Wiens 2014). In varanids, there is a significant positive relationship between these variables in Oceania and a positive trend in Africa (together encompassing 65% of sampled varanid species), but the relationship is not significant in Asia or globally (Table 1). The positive relationship makes intuitive sense in that species in more arid climates may be more specialized for those conditions, whereas those that occur in more mesic environments may not be. Bonetti and Wiens (2014) noted that the very wettest environments ( $> 4000$  mm yr<sup>-1</sup> annual precipitation) were typically restricted to mesic tropical regions, and that little adaptation and specialization may be needed to colonize a very wet rainforest relative to a rainforest with more typical precipitation.

Second, our results provide further refutation of the idea that there is a trade-off in niche widths on the precipitation and temperature niche axes. Instead, we found a positive relationship between niche widths on these axes, as found globally in amphibians (Bonetti and Wiens 2014). This result is still somewhat surprising, given that a trade-off might be expected given that temperature niche widths and precipitation niche widths are expected to show contrasting latitudinal patterns (i.e. at any given locality, a temperate species should have a broad temperature niche breadth and a narrow precipitation niche breadth, whereas a tropical species should have a narrow temperature niche breadth and a wide precipitation niche breadth: Vázquez and Stevens 2004, Quintero and Wiens 2013, Bonetti and Wiens 2014). However, as suggested for amphibians (Bonetti and Wiens 2014), species might use similar mechanisms to cope with stress from extremes of both temperature and low precipitation (e.g. seasonal inactivity), potentially leading to wide niche breadths for species on both axes. Alternately, species that are confined to a small geographic range because of their tolerance to a limited range of conditions on one axis (e.g. precipitation) might consequently be exposed to a limited range of conditions on the other (e.g. temperature).

Third, our results confirm those from three predominantly North American reptile and amphibian clades in showing

that species' climatic niche breadths seem to be determined largely by within-locality niche breadths, with a smaller contribution from among-locality variation in climatic conditions across species ranges (Quintero and Wiens 2013). In fact, the numbers are strikingly similar across clades. Across three reptile and amphibian clades, Quintero and Wiens (2013) found that within-locality niche breadth explained ~ 75% of the variation in species-level temperature niche breadths (means of 73, 76, and 80% per clade), and ~ 60% for precipitation (means of 57, 59, 63%). Here, we find that for varanid lizards, within-locality niche breadth explains ~ 73% of species niche breadths for temperature, and ~ 57% for precipitation. Interestingly, African varanid species are somewhat different, showing a greater importance of between-locality variation, with within-locality variation explaining only 46% of species-level niche breadths, for both temperature and precipitation (Table 2). Also in parallel to the results of Quintero and Wiens (2013) we still found a significant contribution of among-locality variation to overall species niche breadths, using both WLS ratios and niche-position variance.

## Conclusions

In summary, our results show striking differences in patterns of climatic niche widths on different continents in a group of relatively closely related species. These results suggest that global-scale analyses can mask surprisingly different patterns on different continents. Nevertheless, our global-scale analyses found several patterns that are in agreement with previous studies in vertebrates (that mostly focused on amphibians or North American lizards). These include the negative relationships between climatic niche breadth and niche position (at least for temperature), the positive relationships between niche breadths on different niche axes, and the overall importance of within-locality niche breadth to overall species niche breadths (along with among-locality climatic variation). Our results provide further evidence that these patterns may be very widespread.

*Acknowledgements* – Financial support was provided by grants from Natural Science Foundation of China (31270571), China Scholarship Council (201408330038), and the 131 Talent Project of Hangzhou City. We are grateful to E. C. Miller, S. M. Lambert, Y. F. Qu, Y. T. Yao, L. Zhang, Y. C. Zheng, and X. X. Zheng for help during research.

## References

- Araújo, M. B. et al. 2011. The ecological causes of individual specialization. – *Ecol. Lett.* 14: 948–958.
- Bolnick, D. I. et al. 2002. Measuring individual-level resource specialization. – *Ecology* 83: 2936–2941.
- Bolnick, D. I. et al. 2003. The ecology of individuals: incidence and implications of individual specialization. – *Am. Nat.* 161: 1–28.
- Bonetti, M. F. and Wiens, J. J. 2014. Evolution of climatic niche specialization: a phylogenetic analysis in amphibians. – *Proc. R. Soc. B* 281: 20133229.

- Bouckaert, R. et al. 2014. BEAST 2: a software platform for Bayesian evolutionary analysis. – *PLoS Comput. Biol.* 10: e1003537.
- Brown, J. H. 1995. *Macroecology*. – Univ. of Chicago Press.
- Chejanovski, Z. A. and Wiens, J. J. 2014. Climatic niche breadth and species richness in temperate treefrogs. – *J. Biogeogr.* 41: 1936–1946.
- Collar, D. C. et al. 2011. Evolution of extreme body size disparity in monitor lizards (*Varanus*). – *Evolution* 65: 2664–2680.
- Drummond, A. J. et al. 2006. Relaxed phylogenetics and dating with confidence. – *PLoS Biol.* 4: e88.
- Francis, A. P. and Currie, D. J. 2003. A globally consistent richness–climate relationship for angiosperms. – *Am. Nat.* 161: 523–536.
- Gaston, K. J. 2000. *Pattern and process in macroecology*. – Blackwell Science.
- Gómez-Rodríguez, C. et al. 2015. Is climatic niche width related to diversification rate? – *Global Ecol. Biogeogr.* 24: 383–395.
- Grosvenor, M. B. and Darley, J. M. 1963. *National Geographic atlas of the world*. – National Geographic Society, Washington, DC.
- Hijmans, R. J. et al. 2005. Very high resolution interpolated climate surfaces for global land areas. – *Int. J. Climatol.* 25: 1965–1978.
- Holt, B. G. et al. 2013. An update of Wallace’s zoogeographic regions of the world. – *Science* 339: 74–78.
- Hua, X. and Wiens, J. J. 2013. How does climate influence speciation? – *Am. Nat.* 182: 1–12.
- Janzen, D. H. 1967. Why mountain passes are higher in the tropics. – *Am. Nat.* 101: 233–249.
- Kozak, K. H. and Wiens, J. J. 2007. Climatic zonation drives latitudinal variation in speciation mechanisms. – *Proc. R. Soc. B* 274: 2995–3003.
- Lanfear, R. et al. 2012. PartitionFinder: combined selection of partitioning schemes and substitution models for phylogenetic analyses. – *Mol. Biol. Evol.* 29: 1695–1701.
- Lin, L.-H. and Wiens, J. J. 2016. Data from: Comparing macroecological patterns across continents: evolution of climatic niche breadth in varanid lizards. – Dryad Digital Repository, <<http://dx.doi.org/10.5061/dryad.h0v84>>.
- Martins, E. P. and Hansen, T. F. 1997. Phylogenies and the comparative method: a general approach to incorporating phylogenetic information into the analysis of interspecific data. – *Am. Nat.* 149: 646–667.
- Moles, A. T. et al. 2007. Global patterns in seed size. – *Global Ecol. Biogeogr.* 16: 109–116.
- Moritz, C. et al. 2000. Diversification of rainforest faunas: an integrated molecular approach. – *Annu. Rev. Ecol. Syst.* 31: 533–563.
- Olson, V. A. et al. 2009. Global biogeography and ecology of body size in birds. – *Ecol. Lett.* 12: 249–259.
- Orme, D. et al. 2012. caper: comparative analyses of phylogenetics and evolution in R. – R package ver. 0.5, <<http://CRAN.R-project.org/package=caper>>.
- Pianka, E. R. and King, D. R. (eds) 2004. *Varanoid lizards of the world*. – Indiana Univ. Press.
- Pyron, R. A. et al. 2013. A phylogeny and revised classification of Squamata, including 4161 species of lizards and snakes. – *BMC Evol. Biol.* 13: 93.
- Quintero, I. and Wiens, J. J. 2013. What determines the climatic niche width of species? The role of spatial and temporal climatic variation in three vertebrate clades. – *Global Ecol. Biogeogr.* 22: 422–432.
- Rambaut, A. and Drummond, A. J. 2007. Tracer v1.4. – Inst. of Evolutionary Biology, Univ. of Edinburgh, Edinburgh (UK), <<http://beast.bio.ed.ac.uk/software/tracer>>.
- Reeder, T. W. et al. 2015. Integrated analyses resolve conflicts over squamate reptile phylogeny and reveal unexpected placements for fossil taxa. – *PLoS One* 10: e0118199.
- Sanders, N. J. 2001. Elevational gradients in ant species richness: area, geometry, and Rapoport’s rule. – *Ecography* 25: 25–32.
- Scheldeman, X. and van Zonneveld, M. 2010. *Training manual on spatial analysis of plant diversity and distribution*. – Bioversity International, Rome, Italy.
- Sheth, S. N. et al. 2014. Identifying the paths leading to variation in geographical range size in western North American monkeyflowers. – *J. Biogeogr.* 41: 2344–2356.
- Soberón, J. 2007. Grinnellian and Eltonian niches and geographic distributions of species. – *Ecol. Lett.* 10: 1115–1123.
- Supp, S. R. et al. 2012. An experimental test of the response of macroecological patterns to altered species interactions. – *Ecology* 93: 2505–2511.
- Uetz, P. and Hošek, J. (eds) 2015. *The Reptile Database*. – <[www.reptile-database.org](http://www.reptile-database.org)>, accessed 13 August, 2015.
- Vázquez, D. P. and Stevens, R. D. 2004. The latitudinal gradient in niche breadth: concepts and evidence. – *Am. Nat.* 164: E1–E19.
- Wiens, J. J. et al. 2012. Resolving the phylogeny of lizards and snakes (Squamata) with extensive sampling of genes and species. – *Biol. Lett.* 8: 1043–1046.
- Wiens, J. J. et al. 2013. Diversity and niche evolution along aridity gradients in North American lizards (Phrynosomatidae). – *Evolution* 67: 1715–1728.
- Zheng, Y. and Wiens, J. J. 2015. Do missing data influence the accuracy of divergence-time estimation with BEAST? – *Mol. Phylogenet. Evol.* 85: 41–49.
- Zheng, Y. and Wiens, J. J. 2016. Combining phylogenomic and supermatrix approaches, and a time-calibrated phylogeny for squamate reptiles (lizards and snakes) based on 52 genes and 4,162 species. – *Mol. Phylogenet. Evol.* 94: 537–547.

Supplementary material (Appendix ECOG-02343 at <[www.ecography.org/appendix/ecog-02343](http://www.ecography.org/appendix/ecog-02343)>). Appendix 1–6.