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What determines the climatic niche width of species? The role of spatial and temporal climatic variation in three vertebrate clades

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ABSTRACT

Aim Climatic niche breadth (the range of climatic conditions that a species experiences over space and time) is a fundamental topic in ecology, biogeography and evolution. But what determines the climatic niche width of species? In 1967, Janzen suggested that climatic niche widths for temperature were determined by levels of seasonal fluctuation in temperature at each locality, such that niche breadths are narrow in tropical species and broad in temperate species. However, it is unclear whether climatic niche breadths of species are determined more by seasonal variability within sites as opposed to climatic variation between sites across the species' range. We address this question here.

Location Global.

Methods We analysed three vertebrate clades (plethodontid salamanders, hylid frogs and phrynosomatid lizards) for which we had phylogenetic information and climatic data from localities throughout each species' geographic range, collectively including 409 species. We tested how climatic niche breadths of localities (i.e. temporal variation) are related to overall species climatic niche breadths (i.e. temporal and spatial variation) using phylogenetic comparative methods, focusing both on temperature extremes and precipitation.

Results Across the three clades, we find that niche breadths for single localities generally span most of the species' climatic niche breadth, and are strongly correlated with overall species niche breadths. However, species with wider climatic niches also tend to show greater climatic divergence between localities.

Main conclusions The extent to which the climatic niche breadths of species are determined by variation within localities versus spatial variation between localities has been largely unexplored. Our results suggest that within-locality seasonal variation explains most variation in climatic niche breadths among species. However, between-locality variation and local adaptation may also play some role. These results require more general testing, but have several important implications.

Keywords

Amphibians, climate, latitude, niche, niche breadth, phylogeny, reptiles, seasonality.

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INTRODUCTION

Climatic niche breadth is a fundamental topic in ecology, biogeography and evolution. The climatic niche of a species represents the set of climatic conditions (e.g. temperature, precipitation) where the species occurs (realized niche), which may be a subset of those where they can occur (fundamental niche;

sensu Hutchinson, 1957; Soberón, 2007). Species are often confined to a limited set of climatic conditions (i.e. they have narrow climatic niche breadths), and this narrowness may have important implications for many research areas, including species responses to global warming (e.g. Deutsch *et al.*, 2008; Tingley *et al.*, 2009; Sinervo *et al.*, 2010), the spread of invasive species (e.g. Peterson, 2003; Wiens & Graham, 2005; Petitpierre

et al., 2012), allopatric speciation (e.g. Ghalambor *et al.*, 2006; Kozak & Wiens, 2006; Cadena *et al.*, 2011) and large-scale patterns of biogeography and species richness (e.g. Wiens *et al.*, 2006; Rangel *et al.*, 2007; Crisp *et al.*, 2009; Kozak & Wiens, 2010a). Although climatic niche breadth is important for many topics, the factors that determine whether a species will have a narrow or wide climatic niche remain poorly explored.

One of the most important factors in determining the climatic niche breadth of a species may be seasonal variation at each site within the species' range, especially for temperature. In an influential paper, Janzen (1967) suggested that tropical species should have narrow climatic tolerances for temperature (niche breadths) due to limited temperature seasonality in the tropics. In contrast, temperate species should have much broader climatic niche breadths due to seasonal fluctuations in temperature. Janzen suggested that this pattern would lead to tropical species having narrow elevational ranges and temperate species having broad elevational ranges. This hypothesis was based primarily on climatic data from individual sites in temperate and tropical regions, rather than from across species ranges. Many predictions arising from Janzen's hypothesis have been supported (and sometimes refuted) in subsequent studies (e.g. Huey, 1978; Addo-Bediako *et al.*, 2000; Vázquez & Stevens, 2004; Ghalambor *et al.*, 2006; McCain, 2009; Hua & Wiens, 2010; Cadena *et al.*, 2011; Sunday *et al.*, 2011; Olalla-Tárraga *et al.*, 2012; Whitton *et al.*, 2012). These studies have important implications for many topics, such as tropical speciation and species richness (e.g. Kozak & Wiens, 2007; Cadena *et al.*, 2011) and responses to global warming at different latitudes (e.g. Deutsch *et al.*, 2008).

Nevertheless, Janzen's hypothesis makes an important assumption about species climatic niche breadths that has been largely neglected. Specifically, it assumes that within-locality niche breadth drives the overall realized climatic niche breadth of the species (at least for temperature) and that variation in climatic conditions between localities is therefore relatively unimportant (i.e. temporal variation in each locality accounts for the entire species niche breadth, not spatial climatic variation across the species range). An alternative hypothesis is that adaptation to different local climatic conditions across the species range is more influential in determining the overall climatic niche breadth. To our knowledge, no studies have addressed the extent to which a species' climatic niche breadth is determined by climatic variation within localities versus between localities. Although this question could be challenging to address with physiological data (i.e. obtaining data from many individuals from multiple localities across the range of many species), it is actually a question about the distribution of climatic variables within and between localities across the species range. Therefore, this question can be addressed most directly with GIS-based environmental data.

Here, we analyse three clades of ectothermic vertebrates (plethodontid salamanders, hylid frogs and phrynosomatid lizards) for which extensive climatic and phylogenetic data are available, collectively including 409 species. We use standard GIS-based climatic data from localities throughout the range of

each species (WorldClim; Hijmans *et al.*, 2005). We characterize the niche breadth of each locality in terms of its range of temperature and precipitation values over the course of the year (treating temperature and precipitation separately). We characterize the niche breadth of each species based on the same extremes of temperature and precipitation, but measured across all localities across the species range. We then ask the following questions.

1. On average, how much of the overall niche breadth of a species is spanned by the range of yearly variation within localities?
2. Is the overall climatic niche breadth of species correlated with their mean within-locality niche breadth, such that species with greater seasonal variation within localities have broader overall niche breadths across all localities?
3. Do species in which the within-locality range of climatic conditions makes up a smaller proportion of the overall climatic niche breadth (indicating more subdivision of the overall species' niche range among localities) tend to have broader climatic niches?
4. Similarly, do species in which niche breadths tend to be more variable among localities tend to have broader climatic niches?
5. Do species in which the location of each locality on a given climatic niche axis is more variable (indicating greater differences in climatic conditions among localities) tend to have broader niche breadths on this axis?
6. Finally, we test if these relationships change with latitude, given the hypothesis that climatic niches for temperature should be narrower in tropical species (e.g. Janzen, 1967), whereas the precipitation niche should be broader in tropical species (e.g. Vázquez & Stevens, 2004).

We test these hypotheses here using phylogenetic comparative methods.

In order to test these hypotheses, we introduce three measures of how within-locality climatic variation contributes to the overall climatic niche breadth of each species (Fig. 1). We define the WLS ratio of a species as the ratio of within-locality niche breadth to overall species niche breadth, averaged across the sampled localities for the species (for a given climatic niche axis, such as temperature). We define the niche breadth variance (NBV) of a species as the variance in the width of within-locality niche breadths across the localities sampled for the species (for a given niche axis). We define the niche position variance (NPV) of a species as the variance in niche position (on a given niche axis) among the localities of a species, where niche position is defined here as the midpoint of the niche breadth of that locality on that axis. The WLS ratio and NPV may be related (i.e. species with a large WLS ratio should have a small NPV), but a species could have a small WLS ratio but small NPV if most localities in the species have a narrow niche breadth but similar niche position and a small proportion of localities have highly divergent niche positions that increase the overall niche breadth. In general, we expect that species with a smaller WLS ratio will show broader niche breadths, due to adaptation to different climatic conditions across the species range. We expect that species with greater NBV and greater NPV will also show

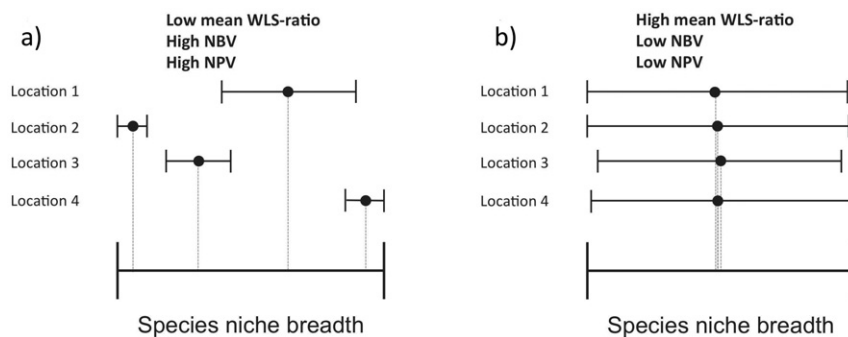


Figure 1 Hypothetical examples illustrating how the overall climatic niche breadth of a species (on a given climatic niche axis, such as temperature) is shaped by spatial climatic variation between localities and temporal climatic variation within localities. The bottom line is the species' overall climatic niche breadth on this axis. Each locality has its own climatic niche breadth (|—|) defined by the range of climatic conditions experienced over the course of a year. Each locality also has a given niche position (black point), defined here as the midpoint of the within-locality niche breadth. The WLS ratio indicates the mean ratio of the within-locality niche breadth relative to the overall species niche breadth. Niche breadth variance (NBV) is the variance in niche breadths across all localities within the species range. Niche position variance (NPV) is the variance in the midpoint of the within-locality niche breadths. In (a) the within-locality niche breadths are small, and make little contribution to the overall species niche breadth. Instead, the species niche breadth (on this axis) is shaped more by differences in climatic conditions across localities, and there is high NBV and NPV. In (b), each locality has a broad niche breadth (caused by seasonal variation) that encompasses all or most of the species niche breadth on that axis, and there is low NBV and NPV.

broader niche breadths, again due to the contribution of climatic variation among localities to the overall species climatic niche breadth.

MATERIALS AND METHODS

Phylogeny, localities and climatic data

We focused on three clades for which climatic and phylogenetic data were available, and for which species sampling is relatively complete. We only included species for which detailed phylogenetic information was available, to facilitate the use of phylogenetic comparative methods.

We used the phylogeny and associated climatic data for 250 species of plethodontid salamanders from Kozak & Wiens (2010b). The data include several distinct but undescribed species in the genera *Eurycea* and *Desmognathus* (Kozak *et al.*, 2005, 2006). Although there are 419 described plethodontid species (AmphibiaWeb, 2011), the sampling for North American species is relatively complete. The phylogenetic tree is time calibrated, and is based on combining a tree for higher-level relationships and North American species based on nuclear and mitochondrial data (from Kozak *et al.*, 2009) with a tree based on mitochondrial data for 127 tropical species (from Wiens *et al.*, 2007). The combination of these trees is described in Adams *et al.* (2009). The climatic data consist of 16,916 localities for 250 species.

For hylid frogs, we initially used the time-calibrated tree and climatic data from Wiens *et al.* (2011). However, we pruned this tree to only include the members of the tribe Hylini (the clade occurring primarily in North and Middle America), for which the sampling of species and localities is more complete (containing 181 described species; Wiens *et al.*, 2011). The tree is

based on multiple nuclear and mitochondrial genes. The climate data include 2206 localities for 91 species.

For phrynosomatid lizards, we used a time-calibrated tree and climatic data from an unpublished analysis. We describe how these data were generated in detail in Appendix S1 in the Supporting Information (including Table S1). In short, the phrynosomatid phylogeny is based on up to eight nuclear and five mitochondrial genes for each of 123 species by combining data from Leaché (2010) and Wiens *et al.* (2010). The phylogeny is similar to that of Wiens *et al.* (2010) but is time calibrated. The climatic data include 6315 localities for 113 phrynosomatid species. The taxon sampling is relatively comprehensive (138 species recognized, see Appendix S1), but we deliberately excluded four species occurring only on islands (given that the climatic distributions of island species may be determined more by the limited range of climatic conditions that they can access rather than their actual climatic tolerances).

In general, we focused on clades for which our taxon sampling is relatively complete. However, the statistical relationships that we address here should not be overturned by failing to include some species.

Climatic information (averaged from 1950–2000) was obtained from the WorldClim database at c. 1 km resolution (Hijmans *et al.*, 2005). This spatial resolution should be appropriate for these organisms, which generally are not highly mobile over the course of a year or over their life spans (Vitt & Caldwell, 2009). We extracted data from four climatic variables derived from raw monthly precipitation and temperature data (see below for specific variables). We mapped each georeferenced locality and obtained climatic data for it using ArcGIS v.9.3 (ESRI, 2009).

Overall, the climatic data were carefully vetted prior to their inclusion. For example, we confirmed that the mapped

georeferenced localities were consistent with the known, mapped geographic ranges of each species, and that the localities broadly spanned these geographic ranges (rather than representing a small portion of the known range). We preferred to obtain climatic data from actual known localities for each species rather than the predicted geographic distribution from (for example) species distribution modelling. We also addressed the extent to which our climatic data for each species were influenced by species sampling (see below).

Climatic niche breadth of localities and species

We determined the realized climatic niche breadth for each locality and each species, for both temperature and precipitation. We calculated the temperature within-locality niche breadth (T-WL-NB) for each locality by subtracting the minimum temperature of the coldest month (Bio6) from the maximum temperature of the warmest month (Bio5). The overall species temperature niche breadth (T-SNB) was the difference between the minimum value of the minimum temperature of the coldest month (across all localities) and the maximum value of the warmest temperature of the warmest month across all localities (i.e. maximum Bio5 – minimum Bio6). Temperature is measured in $^{\circ}\text{C} \times 10$ for these variables.

The idea that there should be a relationship between within-locality variability over the course of the year within a site and the overall niche breadth of the species is relatively intuitive for temperature, but somewhat less so for precipitation. Nevertheless, precipitation seasonality within localities may also drive overall species niche breadth on this axis (as may adaptation to localities with very different precipitation regimes). We therefore conducted similar analyses using precipitation variables, assessing whether within-locality seasonality drives the overall species niche breadth versus variation between localities. Within-locality niche breadth for precipitation (P-WL-NB) was based on the difference in precipitation between the wettest and driest quarters of the year (i.e. Bio16 and Bio17, respectively). The species precipitation niche breadth (P-SNB) was based on the maximum Bio16 minus the minimum Bio17, taken across all localities. Precipitation is measured in millimetres per unit time.

We used three different metrics to characterize how within-locality variation shapes the overall climatic niche breadth for each niche axis (Fig. 1, see Introduction). First, given the within-locality niche breadth (WL-NB) for each locality for each species, we determined how much of the species niche breadth (SNB) it occupies. We then computed the average of these proportions for each species, hereafter referred to as the WLS ratio (Fig 1). 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 refers to localities rather than individuals. Second, to assess how much climatic niche breadths vary among localities within a species, we calculated the NBV. Third, we estimated the variance in the position of each locality on the niche axis for all the localities in each species (the NPV), based on the variance of the temperature midpoints for all localities in

that species (where the midpoint is between the yearly minimum and maximum temperatures, Bio5 and Bio6). A low variance suggests that most localities occupy a similar position on that climatic niche axis.

We addressed the possible impact of limited sampling of localities on these variables in several ways. First, species with only one locality were removed since these species cannot be used to test the contribution of between-locality variation to the overall climatic niche breadth of species. This left 82 species in hylids (9 removed), 218 in plethodontids (32 removed) and 109 in phrynosomatids (4 removed). Values for all the major variables for each of these 409 species are summarized in Table S2 in Appendix S2.

We also tested for the influence of species with five or fewer localities by conducting the main analyses of the study with these species excluded. However, we found little impact on our results when excluding these species (not shown). Therefore, all results are based on including these species.

Moreover, we performed resampling analyses to test if sampling few localities biases estimates of WLS ratios (using R version 2.13.2; R Development Core Team, 2011). First, we excluded species with five localities or fewer. Then, we randomly sampled only five localities per species for each of the remaining species and calculated the average WLS ratio for each species as described above. This was reiterated 1000 times for each species and climatic variable. We then subtracted each simulated WLS ratio from the WLS ratio based on all localities. The mean and variance of these 1000 differences was calculated. If the number of localities sampled had an effect on the WLS ratio, there should be significant differences between the actual species value and the average simulated value, and the magnitude of this difference should be related to sample size (i.e. species with many localities should have a greater difference between the simulated WLS ratios and those using all localities). We first tested for this association with an ordinary linear regression with sample size (localities per species) as the dependent variable and the difference between the simulated and actual WLS ratios as the response variable. Furthermore, if the simulated WLS ratio differed significantly from the value based on all localities, the difference should strongly depart from 0. A one-sample *t*-test was conducted for each species and climatic variable, with a significance threshold based on the sequential Bonferroni correction (Rice, 1989). Since we did not find any biases associated with the number of localities per species (see Fig. S1 and Table S3 in Appendix S1), we used all species with more than one locality.

We also conducted similar analyses using NBV and NPV as response variables to test for possible sampling biases, although these variables should be more dependent on the number of localities. We generally found no evidence of biases due to sample size for these indices (see Figs S1–S3 in Appendix S2). We did find significant but weak ordinary least-squares (OLS) regression relationships between the number of localities and precipitation NPV in hylids (positive) and temperature NBV in plethodontids (negative), and a stronger positive relationship with precipitation NPV in phrynosomatids.

However, as these biases are generally weak and inconsistent, we do not expect them to overturn our results based on these indices.

We did not ‘correct’ for differences in geographic range size among species when estimating species niche widths. Species climatic niche tolerances may determine their geographic extents, so ‘correcting’ estimates of niche width for wider-ranging species would be inappropriate and potentially misleading, even if non-climatic factors also limit ranges in some cases. Furthermore, our results (see below) suggest that climatic niche widths are generally determined by within-locality temporal variation, and so spatial variation in climate across the species range may be of limited importance in determining the niche width (i.e. range size should be irrelevant). Similarly, we did not correct for potential spatial autocorrelation among localities, but our sampling of localities within each species is intended to represent the broad range of conditions found throughout the species range.

Phylogenetic comparative analyses

Given the statistical non-independence of species data due to phylogeny, analyses were conducted primarily using phylogenetic comparative methods, specifically, phylogenetic generalized least-squares regression (PGLS; Martins & Hansen, 1997). We also conducted OLS to test the robustness of these results. All analyses were conducted with R software version 2.13.2 (R Development Core Team, 2011) using the following packages: *ape* version 2.7-3 (Paradis *et al.*, 2004), *geiger* version 1.3-1 (Harmon *et al.*, 2008), *caper* version 0.4 (Orme *et al.*, 2011) and CAIC version 1.0 (R version; Purvis & Rambaut, 1995). Given that the large number of tests could inflate Type I error (i.e. erroneous rejection of a true null hypothesis), we applied a Bonferroni correction to assess significance, but used the sequential correction to retain more statistical power (Rice, 1989).

We used PGLS to test if SNB is related to: (1) mean WL-NB; (2) WLS ratio (ratio of WL-NB to SNB); (3) variance in niche breadth among localities (NBV); (4) variance in niche position (midpoint of niche breadth; NPV); and (5) latitude. We also tested if the WLS ratio is related to latitude.

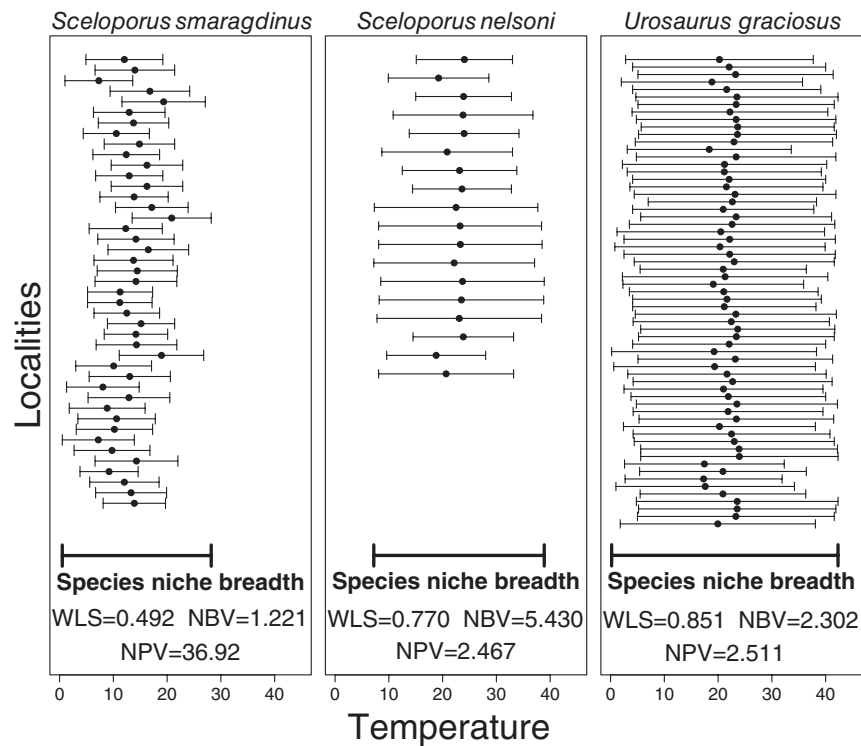
RESULTS

We found that all three clades show surprisingly similar patterns of within-locality niche breadths relative to species niche breadths (Table 1). For temperature, all three clades have mean WLS ratios near 0.75, indicating that for most species, the within-locality range of temperatures is about three-quarters of the overall species niche breadths across all localities (for examples see Fig. 2). Species values range from 0.33 to > 0.95. For precipitation, all three clades show similar mean WLS ratios (near 0.60), with values ranging from a minimum near 0.15 to a maximum near 0.95. Estimates for each species are provided in Table S2 in Appendix S2.

Table 1 Different measures for describing variation in climatic niche breadths among localities within species for three vertebrate clades, where the mean within-locality niche breadth is the proportion of the overall species niche breadth represented by each locality, averaged across all sampled localities for the species (the WLS ratio). The mean, maximum and minimum refer to values for species within the clade (e.g. mean across all species). See Methods for further explanation of variables and units.

Clade	Mean within-locality temperature breadth ratio (T-WLS)	Mean within-locality precipitation breadth ratio (P-WLS)	Within-locality temperature breadth variance (T-NBV)	Within-locality precipitation breadth variance (P-NBV)	Variance in temperature niche position among localities (T-NPV)	Variance in precipitation niche position among localities (P-NPV)
Hylidae	Mean	0.567	29.4	169.0	27.2	182.7
	Max.	0.943	154.5	614.7	143.9	716.1
	Min.	0.208	12.8	6.0	2.9	6.9
Phrynosomatidae	Mean	0.586	24.7	103.9	26.0	111.1
	Max.	0.988	62.3	349.2	88.1	384.6
	Min.	0.125	0.7	1.4	1.4	2.1
Plethodontidae	Mean	0.627	13.3	88.6	20.7	106.8
	Max.	0.998	63.8	539.2	61.4	718.1
	Min.	0.348	0.6	0.6	5.8	0.0

Figure 2 Empirical examples illustrating how within-locality climatic variation contributes to overall climatic niche breadth for temperature (°C) in three species of phrynosomatid lizards (from left to right: *Sceloporus smaragdinus*, with a low WLS ratio, *Sceloporus nelsoni*, with an intermediate WLS ratio, and *Urosaurus graciosus* with a high WLS ratio) – the WLS ratio indicates the mean ratio of the within-locality niche breadth relative to the overall species niche breadth. Niche breadth variance (NBV) is the variance in niche breadths across all localities within the species range. Niche position variance (NPV) is the variance in the midpoint of the within-locality niche breadths.



Statistical phylogenetic analyses using PGLS show that within-locality niche breadth drives overall species niche breadths, with some contribution from variation between localities (Table 2). First, all three clades show strong positive relationships between within-locality niche breadths and overall species niche breadths, for both temperature and precipitation (Fig. 3). Second, there is a negative relationship between the WLS ratio (i.e. the proportion of within-locality niche breadth to overall species niche breadth) and the species niche breadth. In other words, in species with wide niche breadths, the within-locality niche breadth makes up a smaller proportion of the overall species niche breadth. This suggests that different climatic conditions in different parts of the species range do contribute to overall species niche breadth, despite the very strong influence of within-locality variation on the overall niche breadth. However, this relationship emerges most strongly from PGLS analyses, and some non-phylogenetic analyses using OLS regression do not support the hypothesis that between-locality variation contributes strongly to overall species niche breadths (Table S4 in Appendix S2). In general (Table 2), greater variance in niche breadth among localities within a species, and greater variance in niche position among localities within a species are both correlated with wider species niche breadths (except that the relationship between NPV and niche breadth is non-significant for temperature for hylids). Again, these results suggest that among-locality variation in climate contributes to overall species climatic niche breadths.

The results (Table 2, Fig. S4 in Appendix S2) also show that for all three groups, niche breadth generally increases with

latitude for temperature and decreases with latitude for precipitation (but the latter is not significant for PGLS with plethodontids). The relationships between the WLS ratio and latitude and NPV and latitude for temperature and precipitation are variable between clades and often weak (e.g. plethodontids, temperature in phrynosomatids).

DISCUSSION

Climatic niche breadth is an important topic for ecology, biogeography and evolutionary biology, but the causes of differences in climatic niche breadth among species remain poorly explored. Here we make an initial attempt to understand the causes of variation in niche width among species, focusing on patterns of climatic variation within and between localities across species geographic ranges. Our results from three vertebrate clades show that for the temperature and precipitation variables that we examined, species realized niche breadths are strongly related to WL-NBs (i.e. seasonality). However, our results also suggest that variation in niche width is driven partially by differences in climatic conditions among localities. Thus, our results are consistent with Janzen's (1967) hypothesis, but also suggest that climatic divergence among localities can be important.

Our results also show that species temperature niche breadth increases with latitude, whereas precipitation niche breadth decreases (see also Vázquez & Stevens, 2004). Interestingly, we also find that WLS ratios for temperature consistently show no significant relationship with latitude. Thus, even as temperature niche breadths change across latitudes, the extent to which

Clade	Variables	R ²	P	Relationship	λ
Hylidae	T-WL-NB vs. T-SNB	0.697	< 0.001***	+	0.254
	P-WL-NB vs. P-SNB	0.719	< 0.001***	+	0.045
	T-WLS ratio vs. T-SNB	0.377	< 0.001***	–	0.824
	P-WLS ratio vs. P-SNB	0.272	< 0.001***	–	0.973
	T-NBV vs. T-SNB	0.195	< 0.001***	+	0.550
	P-NBV vs. P-SNB	0.696	< 0.001***	+	0.856
	T-NPV vs. T-SNB	0.089	0.006 ^{n.s.}	+	0.671
	P-NPV vs. P-SNB	0.751	< 0.001***	+	0.851
	T-SNB vs. latitude	0.766	< 0.001***	+	0.000
	P-SNB vs. latitude	0.322	< 0.001***	–	0.189
	T-WLS ratio vs. latitude	0.002	0.680	–	0.284
	P-WLS ratio vs. latitude	0.284	< 0.001***	–	0.112
	T-NPV vs. latitude	0.219	< 0.001***	+	0.987
Phrynosomatidae	P-NPV vs. latitude	0.196	< 0.001***	–	0.000
	T-WL-NB vs. T-SNB	0.704	< 0.001***	+	0.000
	P-WL-NB vs. P-SNB	0.759	< 0.001***	+	0.000
	T-WLS ratio vs. T-SNB	0.398	< 0.001***	–	0.915
	P-WLS ratio vs. P-SNB	0.133	< 0.001***	–	0.855
	T-NBV vs. T-SNB	0.341	< 0.001***	+	0.762
	P-NBV vs. P-SNB	0.760	< 0.001***	+	0.205
	T-NPV vs. T-SNB	0.224	< 0.001***	+	0.790
	P-NPV vs. P-SNB	0.769	< 0.001***	+	0.153
	T-SNB vs. latitude	0.712	< 0.001***	+	0.000
	P-SNB vs. latitude	0.343	< 0.001***	–	0.000
	T-WLS ratio vs. latitude	0.000	0.859	+	0.000
	P-WLS ratio vs. latitude	0.316	< 0.001***	–	0.000
Plethodontidae	T-NPV vs. latitude	0.007	0.381	+	0.048
	P-NPV vs. latitude	0.272	< 0.001***	–	0.000
	T-WL-NB vs. T-SNB	0.336	< 0.001***	+	0.356
	P-WL-NB vs. P-SNB	0.525	< 0.001***	+	0.831
	T-WLS ratio vs. T-SNB	0.622	< 0.001***	–	0.958
	P-WLS ratio vs. P-SNB	0.144	< 0.001***	–	0.896
	T-NBV vs. T-SNB	0.267	< 0.001***	+	0.823
	P-NBV vs. P-SNB	0.528	< 0.001***	+	0.622
	T-NPV vs. T-SNB	0.407	< 0.001***	+	0.827
	P-NPV vs. P-SNB	0.525	< 0.001***	+	0.705
	T-SNB vs. latitude	0.321	< 0.001***	+	0.314
	P-SNB vs. latitude	0.002	0.478	–	0.894
	T-WLS ratio vs. latitude	0.001	0.748	+	0.475
	P-WLS ratio vs. latitude	0.034	0.009**	–	0.223
	T-NPV vs. latitude	0.000	0.197	+	0.293
	P-NPV vs. latitude	0.006	0.244	–	0.475

Lambda (λ, phylogenetic signal) values refer to the maximum likelihood λ estimates for each of the PGLS models.

Significance level: *** $P < 0.001$; ** $P < 0.01$; n.s., non-significant after applying a sequential Bonferroni correction.

within versus between locality variation determines the overall species niche breadth remains similar (as implicitly assumed by Janzen, 1967). Precipitation WLS ratios did show significant negative relationships with latitude (Table 2), such that at higher latitudes within-locality variation contributes more to species overall niche breadths.

The generality of these results will need to be tested in other organisms, including plants and endotherms. It should also be

noted that most of the species and localities in our study occur in North and Middle America (although some in South America, Europe and Asia are also included). Given the potential for seasonal variability patterns to vary globally (e.g. Addo-Bediako *et al.*, 2000; Ghalambor *et al.*, 2006), these patterns must be tested in other geographic regions as well. On the other hand, it is striking that we found generally similar results in three different clades that show very different climatic distribu-

Table 2 Results of phylogenetic generalized least squares (PGLS) analyses examining the relationship between species niche breadth (SNB) and the mean ratio of within-locality niche breadth (WL-NB) to overall species niche breadth (WLS ratio), variance in within-locality niche breadth among localities within each species (niche breadth variance, NBV), the variance in the midpoint of within-locality niche breadths for each species (niche position variance, NPV) for each of the three clades studied, for both temperature (T) and precipitation (P).

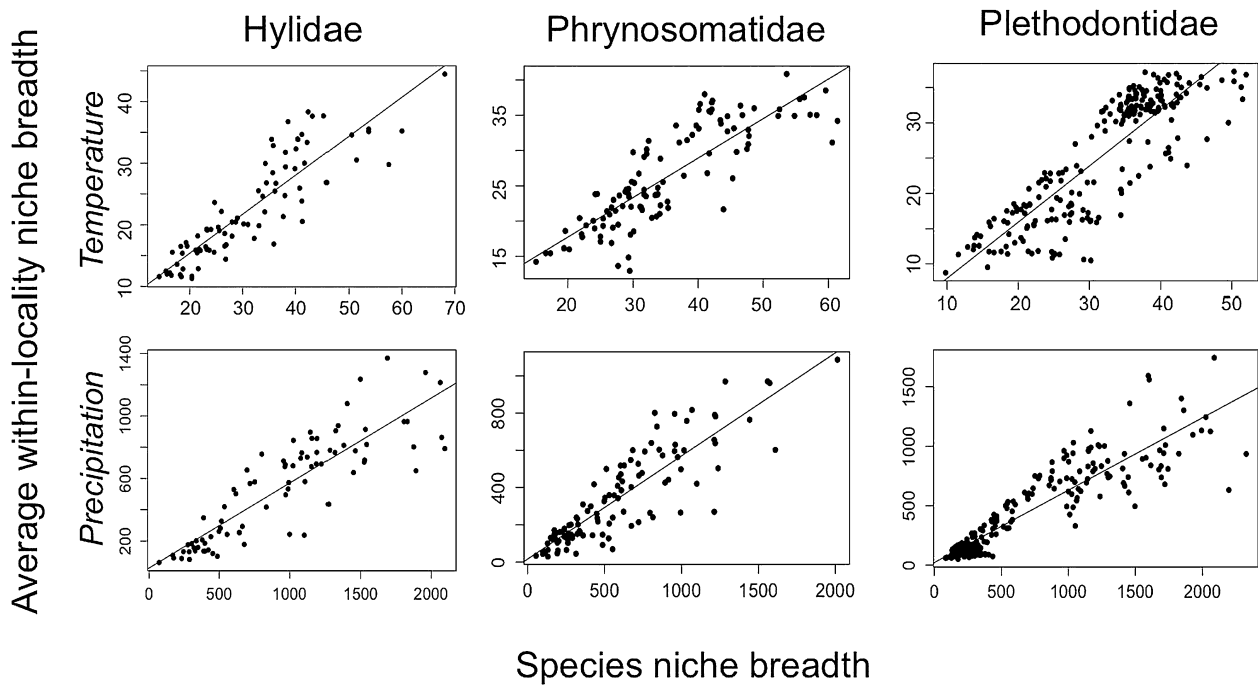


Figure 3 Within-locality niche breadth is strongly correlated with the overall species niche breadth for all three vertebrate clades studied here (plethodontid salamanders, hylid frogs and phrynosomatid lizards) for both temperature ($^{\circ}\text{C}$) and precipitation (mm year^{-1}) niche axes, showing results from ordinary least squares regressions for illustrative purposes (see Table 2 for phylogenetic generalized least squares results): Hylidae (temperature, $r^2 = 0.778$, $P < 0.0001$; precipitation, $r^2 = 0.752$, $P < 0.0001$); Phrynosomatidae (temperature, $r^2 = 0.704$, $P < 0.0001$; precipitation, $r^2 = 0.759$, $P < 0.0001$); Plethodontidae (temperature, $r^2 = 0.728$, $P < 0.0001$; precipitation, $r^2 = 0.810$, $P < 0.0001$).

tions. For example, phrynosomatids are most diverse in relatively arid environments (J.J.W., unpublished), hylids are most diverse in mesic tropical forests (Wiens *et al.*, 2011) and plethodontids are most species-rich in temperate and tropical montane regions (Wiens *et al.*, 2007; Kozak & Wiens, 2010b). These groups also differ fundamentally in physiology, life history and other attributes (e.g. phrynosomatid lizards are active and diurnal with high body temperatures; plethodontid salamanders are lungless, nocturnal and typically have low metabolism and low body temperatures; hylid frogs are nocturnal, have intermediate temperatures and have aquatic larvae; Vitt & Caldwell, 2009). Thus, we speculate that similar patterns may occur in other groups, even groups that differ in climatic distributions, physiologies and life-history patterns.

The most important caveat regarding our results is that they are based on patterns of climatic variation, and not directly on physiological tolerances. However, our focus here is on analysing these patterns of climatic distribution, and not estimating physiological parameters from large-scale climatic data (e.g. we want to know the coldest and warmest temperatures where species occur, not their active body temperatures). In general, there must be some relationship between climatic distributions and climatic tolerances, since species cannot occur under macroclimatic conditions that they cannot tolerate. Some analyses suggest that there can be strong relationships between climatic distributions and physiological measurements, such as body temperatures (e.g. for plethodontids; Kozak & Wiens, 2007).

However, this relationship may be weakened if there is behavioural thermoregulation (e.g. Kearney *et al.*, 2009), and some species may be able to tolerate climatic conditions beyond those where they currently occur (i.e. the fundamental climatic niche may be greater than the realized climatic niche, particularly if species ranges are set by non-climatic factors; e.g. Barve *et al.*, 2011). Again, we can only directly address climatic distributions here, not physiological tolerances. Fully understanding the causes of these patterns of climatic distribution will require more mechanistic analyses, incorporating physiology, biotic interactions and other factors. The causes of the patterns for precipitation are particularly unclear (e.g. for many species it seems unlikely that they will suffer from overly high precipitation, and a lack of rain during the driest quarter may have little biological impact). It should also be noted that we focused on yearly extremes in temperature and precipitation to describe the climatic niche, but other aspects of temperature and precipitation might set their range limits and determine their geographic and climatic distributions instead (including their climatic distributions for the variables we examined).

The extent to which species are (or are not) variable in their climatic niche distributions in different populations across the species range may have important implications for many topics, including parapatric speciation (Coyne & Orr, 2004), predicting the spread of invasive species (e.g. Schulte *et al.*, 2011) and responses to global warming in different parts of a species' range (e.g. Rehfeldt *et al.*, 1999). Our results suggest the possi-

bility that many species in these clades may be surprisingly homogeneous in their climatic distributions across their geographic ranges (even though divergence among localities may still contribute to species niche breadth). Future studies will be needed to understand the causes of this homogeneity. For example, is it caused by gene flow, with individuals with different tolerances dispersing across the range of the species? Or by shared physiological tolerances to similar conditions among localities? Are species with a lower contribution of within-locality niche breadth to overall species niche breadth those that have more limited gene flow among localities?

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Appendix S1. Detailed methods for generating the climatic and phylogenetic information for phrynosomatid lizards. Includes Table S1.

Appendix S2. Results of the analyses addressing the possible impacts of sampling bias on estimates of species WLS ratios (ratio of a species as the ratio of within-locality niche breadth to overall species niche breadth, averaged across the sampled localities for the species). Includes Tables S2–S4, and Figs S1–S4.

BIOSKETCHES

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