Global, regional, and cladistic patterns of variation in climatic niche breadths in terrestrial elapid snakes

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Handling editor: Zhi-Yun Jia

Received on 14 February 2018; accepted on 22 March 2018

Abstract

We obtained geo-referenced occurrence and climatic data from individual localities for 59 species of terrestrial elapid snakes, used phylogenetic generalized least squares regression to investigate spatial and cladistic patterns of variation in climatic niche breadths, and compared patterns within and across regions and clades to see if they parallel or differ from each other. Specifically, we test (1) whether a species’ climatic niche breadth on a given niche axis relates to its position along that axis, and to its climatic niche breadth on another niche axis, and (2) whether variation in niche breadths among species is explained by within-locality variation in climatic conditions or by among-locality variation. We found that: (1) there is an overall global pattern, and patterns in individual regions or clades generally parallel each other and global patterns; (2) species in warmer environments have narrower temperature niche breadths (TNBs); (3) precipitation niche breadth (PNB) and position are positively related; (4) TNB and PNB are not related; and (5) within-locality variation in climatic conditions explains most variation in TNBs, whereas among-locality variation explains most variation in PNBs. Our results are consistent with those reported for lizards of the families Phrynosomatidae and Varanidae, confirm the importance of within-locality niche breadth to species niche breadth, and show a more important role of among-locality niche breadth in affecting species niche breadth in terrestrial elapids than in lizards.

Key words: climate, Elapidae, niche breadth, niche position, niche variance, precipitation, temperature.

Macroecological studies look at global (Francis and Currie 2003; Moles et al. 2007; Olson et al. 2009; Bonetti and Wiens 2014; Lin and Wiens 2017) and regional (Sanders 2001; Supp et al. 2012; Chejanovski and Wiens 2014; Sheth et al. 2014; Velasco et al. 2016) patterns in the diversity and distribution of species, aiming to ask whether and, if so, how macroecological patterns change among species or taxa that occur in different regions (continents), or if in fact all regions have patterns similar to each other and an overall global pattern. Recent studies on spatial variation in climatic niche breadths have revealed several macroecological patterns that are likely to be generalizable to terrestrial vertebrates (Quintero and Wiens 2013; Wiens et al. 2013; Title and Burns 2015; Li et al. 2016). For example, a clade in which species are more successful at diversifying across climatic (temperature and...
precipitation) gradients is better able to buffer from the risk of extinction (Title and Burns 2015), and a species with a broader temperature niche breadth (TNB) can occur over a wider range of latitudes and is less vulnerable to anthropogenic climate change (Li et al. 2016; Velasco et al. 2016). Climatic niche breadth has attracted increasing attention from the scientific community not only because, together with climatic niche position (the actual temperature and precipitation values, rather than the range of values), it may help determine where a species can occur over space and time, but also because of its importance in addressing many lines of inquiry, including species persistence, species diversification, species richness, community structure and dynamics, the colonization and spread of invasive species, and responses of species to anthropogenic climate change (Soberón 2007; Bonetti and Wiens 2014; Title and Burns 2015; Dellinger et al. 2016; Velasco et al. 2016). However, the association between patterns of variation in niche breadths and climatic factors still remains poorly studied, and existing results require more general testing.

Studies conducted so far to explore the role of climatic factors have either been global in scale, or else focused on taxa or clades that occur in a single continent or geographic region. From these studies we know the following. First, species in more arid environments are more specialized for those conditions. For example, amphibians (~38% of all species described globally; Quintero and Wiens 2013; Bonetti and Wiens 2014), lizards of the families Phrynosomatidae (Quintero and Wiens 2013; Wiens et al. 2013) and Varranidae (Lin and Wiens 2017), and a New World plant clade (Ephedra, Loera et al. 2015) that occur in more arid environments have narrower precipitation niche breadths (PNBs). Second, tropical species generally have narrower TNBs but broader PNBs than do species in temperate or cold regions (Wiens et al. 2013; Bonetti and Wiens 2014; Chejanovski and Wiens 2014; Velasco et al. 2016; Lin and Wiens 2017). Third, TNB and PNB are positively interrelated (Bonetti and Wiens 2014; Lin and Wiens 2017), rather than showing trade-offs as expected theoretically (Vázquez and Stevens 2004). Fourth, species with greater within-locality variation in climatic conditions (seasonal temperature and precipitation extremes) tend to have broader niche breadths (Quintero and Wiens 2013; Lin and Wiens 2017). Last, within-locality seasonal variation in climatic conditions explains most of the variation in climatic niche breadths (i.e., the within-locality range of climatic conditions makes up a greater proportion of the overall climatic niche breadth), and between-locality variation across the range of each species may play some role (e.g., the niche position variances for each species is positively related to species niche breadth) (Quintero and Wiens 2013; Lin and Wiens 2017).

Here, we examine climatic niche breadths and evaluate how patterns change within a group of closely related species across regions or clades. We focus on terrestrial elapid snakes of the subfamily Elapinae, a widely distributed (global distribution except Europe) subfamily comprising 162 species (Uetz and Ho 2016). Terrestrial elapid snakes occur in a variety of climates in each region, from rainforests to deserts and from tropical to temperate climates. We first obtained geo-referenced occurrence and climatic data from individual localities for all species included in this study, and then used phylogenetic comparative methods to address 2 main questions: (1) whether a species’ climatic niche breadth on a niche axis relates to its position along the axis (e.g., are species in more extreme environments more narrowly specialized for those conditions?), and to its climatic niche breadth on another niche axis; and (2) whether variation in niche breadths among species is explained by within-locality variation in climatic conditions or by among-locality variation [e.g., do species where the within-locality range of climatic conditions makes up a greater proportion of the overall climatic niche breadth (indicating less subdivision of the overall species’ niche range among localities) have narrower climatic niches?]. Similar questions have been addressed in amphibians, phrynosomatid lizards, and varanid lizards (Quintero and Wiens 2013; Wiens et al. 2013; Bonetti and Wiens 2014; Lin and Wiens 2017) but our study is the first to address these questions in snakes. Our study is also the first to shed light on the cladistic implications in addition to the spatial implications.

Materials and Methods

Four clades of the family Elapidae could be identified in a phylogenetic tree including 4,161 species of lizards and snakes (Janzen 1967). Species with fewer than 6 known localities were excluded from analyses. Occurrence points for 59 species (~36% of all species described globally; Supplementary Tables S1 and S2) of terrestrial elapids included in the phylogeny and phylogenetic comparative analyses were collected from the Global Biodiversity Information Facility (http://www.gbif.org), HerpNet/VertNet (http://www.vernet.org), and literature with information on snake distribution. Occurrence points were carefully checked to verify that the sampled localities were based on the known range of each species (http://www.reptile-database.org; Uetz and Hošek 2016) and that no localities were outside that range. Of the 59 species, 17 occur in Africa, 19 in America, 23 in Asia, 21 in Clad 1 including species of the genera Calliophis, Mackronoides, Symicormus, and Micruroides; 23 in Clad 2 including species of the genera Hemibungarus, Ophiophagus, Dendroaspis, Walterinnesia, Aspidelaps, Hemachatus and Naja; 12 in Clad 3 including species of the genera Elapsoidea and Bungarus, and 1 (Calliophis melanurus, in the root of the phylogenetic tree) in Clad 4 (Supplementary Table S1; Pyron et al. 2013). Clad 4 was not used to test hypotheses within each clade because it only included 1 species. We used DIVA-GIS 7.5.0 to extract climatic variables for each occurrence point at ~1 km² resolution from the WorldClim database (http://www.worldclim.org), using data from 1950 to 2000 as a baseline (Scheideman and van Zonneveld 2010). We obtained climatic data from a mean of 47.7 localities per species, with a range of 6–272 (Supplementary Table S1).

We used 6 climatic variables to address our questions: Bio1 (annual mean temperature), Bio5 (maximum temperature of the warmest month), Bio6 (minimum temperature of the coldest month), Bio12 (annual precipitation), Bio16 (precipitation of the wettest quarter), and Bio17 (precipitation of the driest quarter) (Supplementary Table S2). We used these 6 variables because (1) Bio1 and Bio12, respectively, reflect the availability of energy and water and are of importance in determining the distribution of a species, (2) mean values for Bio1 and Bio12 across a species’ range, respectively, represent their temperature and precipitation niche positions, (3) the extreme values for Bio5 and Bio6 are used to calculate TNB, and (4) the extreme values for Bio12, Bio16, and Bio17 are used to calculate 2 indices of PNB (Collevatti et al. 2013; Quintero and Wiens 2013; Bonetti and Wiens 2014; Chejanovski and Wiens 2014; Lin and Wiens 2017).

We calculated TNB and PNB for each species. For TNB, we simply subtracted the minimum value of Bio6 across all sampled localities of a species from the maximum value of Bio5. For PNB, we first calculated an index by subtracting the minimum value of Bio12...
from the maximum value of Bio12 across a species’ range. This index reflects spatial but not season variation in precipitation across a species’ range. We then calculated an alternative index of PNB by subtracting the minimum value of Bio17 from the maximum value of Bio16 across a species’ range. We used this alternative index to address our second question about the relative contribution of seasonal variation to PNB, as it reflects both spatial and seasonal variation in precipitation. Each index had pros and cons (Lin and Wiens 2017).

We calculated within-locality temperature niche breadth (TNBWL), within-locality precipitation niche breadth (PNBWL), overall mean value for the mean ratio of within-locality niche breadth to species niche breadth for temperature (TNBRWL-S), overall mean value for the mean ratio of within-locality niche breadth to species niche breadth for precipitation (PNBRWL-S), niche position variance for temperature (NPVT), and niche position variance for precipitation (NPVP) for each species with multiple localities (Supplementary Table S3). For TNBWL, we subtracted Bio6 from Bio5 for each locality, and for PNBWL, we subtracted Bio17 from Bio16 for each locality. For TNBRWL-S and PNBRWL-S we determined the ratio of species niche breadth accounted by within-locality niche breadth for each locality, and then calculated the mean ratios for each species. A higher value of TNBRWL-S or PNBRWL-S implies that the within-locality range of climatic conditions makes up a bigger proportion of the overall climatic niche breadth (indicating less subdivision of the overall species’ niche range among localities). We calculated the mean values and ranges of TNBRWL-S and PNBRWL-S for each region and globally and described the contribution of within-locality niche breadth to species niche breadth by testing the relationship between these 2 ratios and species niche breadth. A significant positive relationship indicates that within-locality niche breadth drives overall species niche breadth, and a significant negative relationship indicates that among-locality niche breadth makes an important contribution to species niche breadth. We calculated the niche position variance using the midpoint of the niche breadths across localities to test whether variability in niche position among localities contributed to niche breadth. For each locality, the temperature midpoint is the midpoint between Bio6 and Bio5, and the precipitation midpoint is the midpoint between Bio16 and Bio17. We tested whether niche position variance for each species is positively related to species niche breadth and, if so, the relationship would indicate a contribution of among-locality variation in climatic conditions to species niche breadth.

We performed phylogenetic generalized least squares (PGLS) regressions in R 3.3.0 (R Development Core Team 2015) with the package Caper (Orme et al. 2013) to account for the non-independence of data due to the shared evolutionary history of species. To do that, we reconstructed a phylogeny for the 59 species using Mesquite 3.04 ( Maddison and Maddison 2015) based on the species-level phylogenetic relationships (Pyron et al. 2013). We downloaded the Supplementary Material of the paper by Pyron et al. (2013) and revised the Newick file by deleting the irrelevant species. The λ model was used for all PGLS analyses with branch lengths adjusted based on λ values estimated via maximum likelihood and values of kappa and delta fixed at 1. The λ model accounts for the estimated level of phylogenetic signal in the data, and this phylogenetic signal is what PGLS is designed to accommodate. We applied a Bonferroni correction to avoid inflating type I error when multiple (n) independent hypotheses were performed on a set of data. Therefore, the statistical significance level that should be used for n hypotheses separately was 1−(1−0.05)1/6 if we adopted a significance level of 0.05 when only 1 hypothesis was tested (Bland and Altman 1995). We adopted n = 5, with a significance level of 0.01. We performed spatial autocorrelation analysis in DPS 14.10 ( Tang and Zhang 2013) to calculate Moran statistic I for all 6 climatic variables, finding that none of Moran’s I values deviated significantly from 0 (all P > 0.139, Supplementary Table S4). A Moran’s I value near 0 indicates a lack of spatial autocorrelation (values at 1 location do not depend on values at neighboring locations).

**Results**

Globally, species in colder climates with lower mean Bio1 values generally have a broader TNB (r² = 0.217, P < 0.0001), and species in drier climates with low mean Bio12 values generally have a narrower PNB (r² = 0.210, P < 0.001, Table 1 and Figure 1). Regionally, the negative relationship between TNB and Bio1 is significant in America (r² = 0.451, P < 0.01) but not in Africa or Asia, and no significant relationship between PNB and Bio12 is found in each region (Table 1 and Figure 1). Neither globally nor regionally is there a trade-off between TNB and PNB among species (Table 1 and Figure 2).

Globally, the TNBRWL-S is 0.635, with species mean values ranging from 0.333 to 0.872 (Table 2). Regional mean values for TNBRWL-S are very similar and range from 0.660 to 0.651, with species mean values ranging from 0.409 to 0.747 in Africa, 0.333 to 0.868 in America, and 0.455 to 0.872 in Asia (Table 2). Globally, the PNBWL-S is 0.433, with species mean values ranging from 0.153 to 0.784 (Table 2). Regional mean values for PNBWL-S are broadly similar, but comparatively lower in America (0.387) and higher in Asia (0.471); species mean values ranging from 0.170 to 0.653 in Africa, 0.153 to 0.598 in America, and 0.209 to 0.784 in Asia (Table 2).

**Table 1. PGLS results of the relationship between TNB and annual mean temperature (Bio1), between PNB and annual precipitation (Bio12), and between TNB and PNB**

|                          | N  | λ  | r²     | P-value | Slope | Intercept |
|--------------------------|----|----|--------|---------|-------|-----------|
| TNB vs. Bio1             |    |    |        |         |       |           |
| Africa                   | 17 | 0  | 0.071  | −0.538  | 45.06 |           |
| America                  | 19 | 0  | 0.451  | <0.01   | 2.415 | 82.22     |
| Asia                     | 23 | 0  | 0.214  | 0.026   | 1.515 | 65.44     |
| Clade 1                  | 23 | 0  | 0.439  | <0.001  | 2.461 | 83.20     |
| Clade 2                  | 23 | 0  | 0.277  | <0.01   | 1.473 | 66.04     |
| Clade 3                  | 12 | 0  | 0.010  | 0.760   | −0.233| 35.75     |
| Global                   | 59 | 0  | 0.217  | <0.0001 | −1.387| 62.05     |
| PNBRWL vs. Bio12         |    |    |        |         |       |           |
| Africa                   | 17 | 0  | 0.255  | 0.039   | 1.559 | 120.05    |
| America                  | 19 | 0  | 0.138  | 0.092   | 0.949 | 645.36    |
| Asia                     | 23 | 0.534| 0.204 | 0.031   | 0.652 | 819.20    |
| Clade 1                  | 23 | 0  | 0.096  | 0.151   | 0.720 | 798.73    |
| Clade 2                  | 23 | 0  | 0.413  | <0.001  | 1.096 | 511.83    |
| Clade 3                  | 12 | 0.367| 0.254 | 0.095   | 0.577 | 879.77    |
| Global                   | 59 | 0  | 0.210  | <0.001  | 0.780 | 737.01    |
| TNB vs. PNB              |    |    |        |         |       |           |
| Africa                   | 17 | 0  | 0.122  | 0.170   | 0.0022| 29.69     |
| America                  | 19 | 0  | 0.033  | 0.456   | 0.0010| 26.35     |
| Asia                     | 23 | 0  | 0.000  | 0.978   | −0.0001| 29.62    |
| Clade 1                  | 23 | 0  | 0.027  | 0.455   | 0.0009| 26.83     |
| Clade 2                  | 23 | 0  | 0.004  | 0.785   | 0.0004| 31.05     |
| Clade 3                  | 12 | 0  | 0.005  | 0.819   | −0.0006| 31.61     |
| Global                   | 59 | 0  | 0.007  | 0.519   | 0.0001| 29.24     |

Note: N is the number of species.
The positive relationship between TNBWL and TNB is significant globally ($r^2 = 0.533$, $P < 0.0001$) and for America ($r^2 = 0.595$, $P < 0.001$) and Asia ($r^2 = 0.600$, $P < 0.0001$) but not for Africa (Table 3 and Figure 3). The positive relationship between PNBWL and PNB is significant globally ($r^2 = 0.517$, $P < 0.0001$) and for America ($r^2 = 0.387$, $P < 0.01$) and Asia ($r^2 = 0.544$, $P < 0.0001$) but not for Africa (Table 3 and Figure 3). The negative relationship between TNBRWL-S and TNB is significant globally ($r^2 = 0.157$, $P < 0.01$) and for America ($r^2 = 0.378$, $P < 0.01$) but not for Africa or Asia, and the negative relationship between PNBRWL-S and PNB is significant for globally ($r^2 = 0.134$, $P < 0.01$) and for Africa ($r^2 = 0.394$, $P < 0.01$) but not for America or Asia (Table 3 and Figure 4). The positive relationship between NPVT and TNB is significant globally ($r^2 = 0.306$, $P < 0.0001$) and for America ($r^2 = 0.496$, $P < 0.001$) but not for Africa or Asia (Table 3 and Figure 5). The positive relationship between NPVF and PNB is significant for globally ($r^2 = 0.597$, $P < 0.0001$) and for America ($r^2 = 0.899$, $P < 0.0001$) and Asia ($r^2 = 0.572$, $P < 0.0001$) but not for Africa (Table 3 and Figure 5). These relationships highlight the importance of local climatic conditions in determining species niche breadth.

Data analyzed on the basis of cladistic grouping showed that climatic niche breadth patterns were similar across different clades, and that cladistic patterns paralleled overall patterns (Tables 1–3).

Testing whether similar macroecological patterns arise because terrestrial elapids in different regions do not differ in how they
respond to climatic variation, we found that terrestrial elapids did not differ among regions in mean TNB after accounting for Bio1 with ANCOVA ($F_{2,55} = 2.085, P = 0.134$; Figure 1). TNB was more likely to be dominated by within-locality variation in thermal conditions (Table 2).

### Discussion

Our study has 2 main goals, of which 1 is to examine global and regional patterns of variation in TNB and PNB among species, and the other is to compare patterns within and across regions to see if they parallel or differ from each other. Macroecological patterns in different regions are similar and parallel global patterns. Our results

### Table 2. Summary of the species mean ratios of within-locality niche breadth to species niche breadth for temperature (TNBR$_{WL-S}$) and precipitation (PNBR$_{WL-S}$), showing the mean and range (in parentheses) among species in each region and globally

| Region | N | TNBR$_{WL-S}$ | PNBR$_{WL-S}$ |
|--------|---|---------------|---------------|
| Africa | 17 | 0.606 (0.409–0.747) | 0.432 (0.170–0.653) |
| America | 19 | 0.640 (0.333–0.868) | 0.387 (0.153–0.598) |
| Asia | 23 | 0.651 (0.455–0.872) | 0.471 (0.209–0.784) |
| Clade 1 | 23 | 0.644 (0.333–0.872) | 0.425 (0.153–0.784) |
| Clade 2 | 23 | 0.633 (0.409–0.860) | 0.415 (0.170–0.653) |
| Clade 3 | 12 | 0.618 (0.433–0.841) | 0.473 (0.345–0.621) |
| Global | 59 | 0.635 (0.333–0.872) | 0.433 (0.153–0.784) |

Note: $N$ is the number of species.

### Table 3. PGLS results of the relationships between species niche breadth (TNB and PNB) and mean within-locality niche breadths for temperature (TNB$_{WL}$) and precipitation (PNB$_{WL}$), species mean ratios of within-locality niche breadth to species niche breadth for temperature (TNBR$_{WL-S}$) and precipitation (PNBR$_{WL-S}$), and niche position variances for temperature (NPVT) and precipitation (NPVP)

| Relationship | Region | N | $\lambda$ | $r^2$ | P-value | Slope | Intercept |
|--------------|--------|---|-----------|--------|---------|-------|-----------|
| TNB$_{WL}$ vs. TNB | Africa | 17 | 0 | 0.241 | 0.045 | 0.337 | 8.47 |
| America | 19 | 0.830 | 0.595 | <0.001 | 0.447 | 6.83 |
| Asia | 23 | 0 | 0.600 | <0.0001 | 0.492 | 4.11 |
| Global | 59 | 0 | 0.533 | <0.0001 | 0.480 | 4.16 |
| PNB$_{WL}$ vs. PNB | Africa | 17 | 0 | 0.346 | 0.013 | 0.114 | 260.72 |
| America | 19 | 0 | 0.387 | <0.01 | 0.151 | 247.37 |
| Asia | 23 | 0 | 0.544 | <0.0001 | 0.279 | 290.19 |
| Global | 59 | 0.591 | 0.517 | <0.0001 | 0.250 | 259.36 |
| TNBR$_{WL-S}$ vs. TNB | Africa | 17 | 0 | 0.232 | 0.050 | –0.0092 | 0.91 |
| America | 19 | 0.923 | 0.378 | <0.01 | –0.0082 | 0.93 |
| Asia | 23 | 0 | 0.148 | 0.070 | –0.0056 | 0.81 |
| Global | 59 | 0 | 0.157 | <0.01 | –0.0060 | 0.82 |
| PNB$_{WL-S}$ vs. PNB | Africa | 17 | 0 | 0.394 | <0.01 | –0.0001 | 0.57 |
| America | 19 | 0 | 0.249 | 0.030 | –0.0001 | 0.50 |
| Asia | 23 | 0 | 0.148 | 0.070 | –0.0056 | 0.81 |
| Global | 59 | 0 | 0.157 | <0.01 | –0.0060 | 0.82 |
| NPVT vs. TNB | Africa | 17 | 0 | 0.265 | 0.034 | 8.214 | 1657.20 |
| America | 19 | 0 | 0.899 | <0.0001 | 39.990 | 23258.59 |
| Asia | 23 | 0 | 0.572 | <0.0001 | 38.062 | 6589.89 |
| Global | 59 | 0.654 | 0.597 | <0.0001 | 34.085 | 2508.67 |
| NPVP vs. PNB | Africa | 17 | 0 | 0.572 | 0.031 | 38.318 | 26492.06 |
| America | 19 | 0 | 0.899 | <0.0001 | 39.990 | 23258.59 |
| Asia | 23 | 0 | 0.572 | <0.0001 | 38.062 | 6589.89 |
| Global | 59 | 0.654 | 0.597 | <0.0001 | 34.085 | 2508.67 |

Note: $N$ is the number of species.
are generally consistent with those reported for amphibians and lizards (Quintero and Wiens 2013; Wiens et al. 2013; Bonetti and Wiens 2014; Lin and Wiens 2017) and show few differences in relationships (patterns) among regions. It is worth noting that the differences detected here and in previous studies make no change or, if any, a little change in the pattern itself except some variation in the strength or significance of relationships between these variables. In terrestrial elapids, for example, TNB and position are negatively interrelated globally (Figure 1), but the relationship is not significant in Africa or Asia (Table 1). Another example is that at the global scale the positive relationship between PNB and position is significant in terrestrial elapids (Table 1) and amphibian (Bonetti and Wiens, 2014) but not in varanid lizards (Lin and Wiens 2017).

All 3 regions have a wide range of biomes (from deserts to rainforests, and from tropical to temperate climates) (Figure 6) and, although terrestrial elapids are absent from extremely cold climates, they occur in most of these environments. We suggest that similar macroecological patterns arise presumably because terrestrial elapids in different regions do not differ in how they respond to climatic variation. Our results are consistent with previous studies on amphibians and lizards (Quintero and Wiens 2013; Bonetti and Wiens 2014; Lin and Wiens 2017), allowing us to conclude that: (1) there is an overall global pattern on niche breaths for temperature and precipitation, (2) patterns in each region or clade are generally parallel with each other and global patterns, and (3) ectothermic vertebrates of different groups or clades share similar patterns of TNB and PNB.

We found a significant negative relationship between TNB and Bio1 in America and globally (Figure 1 and Table 1), as found globally in amphibians (Bonetti and Wiens 2014) and varanid lizards (Lin and Wiens 2017). Our explanation for this negative relationship is that at higher latitudes with lower mean Bio1 values, temperature seasonality increases such that species have broader TNB
an index based on Bio12) and position (Figure 1 and Table 1), as this pattern is generalizable to terrestrial ectothermic vertebrates.

Similarly, we found a positive relationship between PNB (using an index based on Bio12) and position (Figure 1 and Table 1), as found regionally (North America) in phrynosomatid lizards (Wiens et al. 2013) and globally in amphibians (Bonetti and Wiens 2014) and varanid lizards (Lin and Wiens 2017). This result is a bit surprising given that a trade-off might be expected as TNB and PNB show contrasting latitudinal trends (Vázquez and Stevens 2004; Bonetti and Wiens 2014); that is, at any given locality, a temperate species should have a broad TNB and a narrow PNB, whereas a tropical species should have a narrow TNB and a wide PNB (Vázquez and Stevens 2004; Bonetti and Wiens 2014; Lin and Wiens 2017). However, as suggested for terrestrial ectotherms in more extreme environments, species might use similar mechanisms to cope with stress from both temperature and precipitation extremes, potentially leading to wide or narrow niche breadths for species on both axes (Wiens et al. 2013; Bonetti and Wiens 2014). Alternately, species that are confined to a small geographic range (e.g., island or mountain species) because of their tolerance to a limited range of conditions on 1 niche axis (e.g., precipitation) might consequently be exposed to a limited range of conditions on the other axis (e.g., temperature). However, it is worth noting that we cannot rule out the possibility that the measured niche characteristics and their correlations are driven by factors partly or completely extrinsic to the species, such as the spatial distribution of climatic conditions. Since these niche measurements are all taken directly from species distributions that are not independent, and as such, the null expectation is not necessarily symmetric or centered on zero.

Our results are in agreement with patterns found in plethodontid salamanders, hylid frogs, phrynosomatid lizards, and varanid lizards (Quintero and Wiens 2013; Lin and Wiens 2017) where species-level TNB is more likely to be determined by within-locality niche breadths, with a smaller contribution from among-locality variation in thermal conditions across species ranges. In fact, the values are strikingly similar across clades. Across the aforementioned 4 clades, within-locality variation in niche breadths explained ~75% of the variation in species-level TNB [species mean values for plethodonitids, hylids, phrynosomatids, and varanids are 80%, 73%, 76%, and 73%, respectively (Quintero and Wiens 2013; Lin and Wiens 2017)]. For elapids, within-locality niche breadth explains ~64% of species-level TNB. Interestingly, in elapids, among-locality variation is of greater importance to PNB, as revealed by the fact that within-locality variation explains only 43% of species-level PNB (Table 2), a proportion noticeably lower than those reported for plethodonitids (63%), hylids (57%), phrynosomatids (59%), and varanids (57%) where within-locality variation in hydric conditions plays a more important role in affecting species-level PNB (Quintero and Wiens 2013; Lin and Wiens 2017). Similar to the studies on plethodonitids, hylids, phrynosomatids, and varanids (Quintero and Wiens 2013; Lin and Wiens 2017), our analyses show a significant contribution of among-locality variation to overall species niche breadths using both WLS ratios and niche position variance. Also, it is worth noting that within-locality variation in niche breadths is consistent across regions and clades. This could potentially indicate that the ratio is constrained by variables extrinsic to species.

It should be noted that our results are based on patterns of climatic variation not directly on physiological tolerances, but here we focus on analyzing these patterns of climatic distribution not estimating physiological parameters from large-scale climatic data (Quintero and Wiens 2013). Another important caveat regarding our results is that our focus is on estimating the climatic niche using yearly extremes in temperature and precipitation, but other aspects

Figure 5. Relationship between niche position variances for temperature (NPV_T) and precipitation (NPV_P) and species niche breadths across regions and globally. The regression lines are shown using dotted lines instead of solid lines when the linear models are not significant. PGLS results are given in Table 3.
of temperature and precipitation might set their range limits and determine their geographic and climatic distributions instead (Quintero and Wiens 2013).

In summary, our results show that patterns of climatic niche breadth are similar across different regions for terrestrial elapids, and that regional patterns parallel global patterns. Patterns observed in terrestrial elapids are in agreement with those reported for amphibians and lizards of the families Phrynosomatidae and Varanidae. These include a negative relationship between TNB and position, a positive relationship between PNB and position, and a positive relationship between mean within-locality niche breadth and overall (species-level) climatic niche breadth. Our results provide further evidence that these patterns may be widespread among ectothermic vertebrates. Our results confirm the overall importance of within-locality niche breadth to overall species niche breadth and show that among-locality niche breadth has a comparatively more important role in affecting species-level niche breadth in terrestrial elapids than in lizards mentioned above. Results reported here for elapids and in previous studies for amphibians and lizards raise 2 questions for future research: (1) Are the patterns observed generalizable to animals including endothermic vertebrates (birds and mammals)? (2) What are the underlying ecological and/or physiological mechanisms of these patterns?

**Author Contributions**

L.-H.L. and X.J. conceived the ideas. X.J. supervised the study. L.-H.L. and X.J. wrote the paper. All authors reviewed and contributed to editing of the manuscript and approved its final publication.

**Acknowledgments**

This work was supported by grants from the Natural Science Foundation of Zhejiang Province to L.-H.L. (LY17C030003) and National Natural Science Foundation of China to X.J. (31272294 and 30770378). We are grateful to Lin Zhang and Xiao-Xiao Zheng for help during this research.

**Supplementary Material**

Supplementary material can be found at https://academic.oup.com/cz.

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**Figure 6.** Point localities of terrestrial elapid snakes involved in this study, showing the distribution range globally. L.-H.L. used DIVA-GIS 7.5.0 (http://www.diva-gis.org/download) to create the figure. Bold solid lines indicate boundaries between regions. Different colors indicate different clades: Clade 1 in blue, Clade 2 in green, Clade 3 in red, and Clade 4 in black.
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