

The evolution of climatic niche breadth in terrestrial vertebrates

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Abstract

Interspecific variation in climatic niche breadth underlies many ecological phenomena, yet only recently have studies focused explicitly on the evolution of climatic niche breadth. Here, we integrate data on geographical distributions, bioclimatic variables, and phylogenetic relationships of 18,404 terrestrial vertebrate species to investigate the evolution of climatic niche breadth. We demonstrate that the evolutionary rates of upper and lower climatic niche boundaries are largely uncoupled. For instance, the rate of evolution of low temperature limits was nearly twice that of high-temperature limits, whereas low- and high-precipitation limits remained relatively constant despite a considerable variation in average precipitation. These results suggest that the evolution of climatic niche breadth is fundamentally different between axes. Finally, we found no relationship between climatic niche breadth and speciation rates. The consistency of these patterns across taxa suggests that they represent general principles governing the evolution of climatic niche breadth.

KEY WORDS

diversification, environmental prevalence, macroecology, speciation, vertebratesResumo

Resumo

A variação interespécifica na amplitude do nicho climático depende de muitos fenômenos ecológicos, embora apenas recentemente estudos tenham focado explicitamente na evolução da amplitude de nicho climático. Aqui, integramos dados de distribuições geográficas, variáveis bioclimáticas e relações filogenéticas de 18,404 espécies de vertebrados terrestres para investigar a evolução da amplitude de nicho climático. Demonstramos que as taxas evolutivas dos limites superiores e inferiores de nicho climático são amplamente desacoplados. Por exemplo, a taxa de evolução dos limites de baixa temperatura foi quase o dobro dos limites de alta temperatura, enquanto os limites de baixa e alta precipitação permaneceram relativamente constantes, apesar de uma variação considerável na precipitação média. Esses resultados sugerem que a evolução da amplitude de nicho climático é fundamentalmente diferente entre os eixos. Por fim, não encontramos nenhuma relação entre a amplitude de nicho climático e as taxas de especiação. A consistência desses padrões entre os táxons sugere que eles representam princípios gerais que guiam a evolução da amplitude de nicho climático.

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1 | INTRODUCTION

The idea of the ecological niche still plays a major role in modern ecological and evolutionary research, despite considerable disagreements over the past 100 years on how to best define it (Chase & Leibold, 2003; Elton, 1927; Grinnell, 1917, 1924; Holt, 2009; Hutchinson, 1957). The troubled history of ecological niche concepts can be understood, at least in part, by the sheer complexity of the phenomenon that one seeks to explain. In particular, Hutchinson's metaphor of an n -dimensional hypervolume resonated with the intuition of ecologists that niches are inherently multidimensional, and that the distribution of species could be best understood by the complex interaction of a multitude of axes (Hutchinson, 1957; Peterson et al., 2011). Of all potential niche dimensions, the climatic niche—climatic conditions that a species experiences over space and time—has been shown to have particularly important implications for a variety of phenomena, such as biogeographical patterns (Verberk et al., 2010), species invasions (Broennimann et al., 2007; Gallagher et al., 2010), and the response of different species to climate change (Hoffmann & Sgro, 2011; Ozgul et al., 2010; Visser, 2008). Therefore, a deeper understanding of the evolutionary processes driving climatic niche evolution might provide valuable insight into the general multidimensional dynamics of ecological niches themselves (Soberón, 2007).

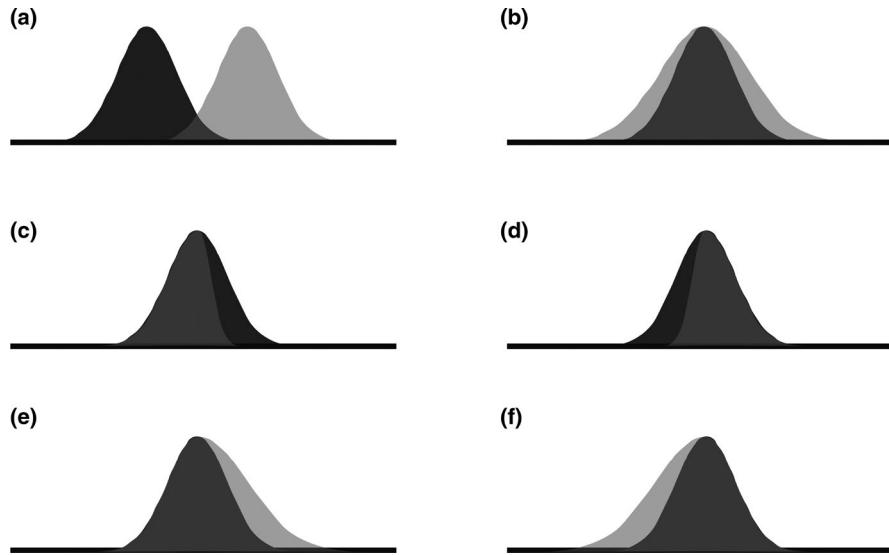
In principle, although there are many ways in which climatic niche evolution can be achieved, to a first approximation they can be understood as changes in the relative position of lower and upper niche limits (Figure 1). In particular, different combinations of shifts in lower and upper limits might lead to alternative routes to changes in niche breadths, depending on their direction and magnitude. However, little is known about the relative importance of mechanisms in governing niche evolution in different organisms. For example, low- and high-latitude geographical limits in the distribution of mammals and squamates experience up to fourfold differences in their rates (Pie & Meyer, 2017). Likewise, physiological adaptation to higher temperatures seems considerably more difficult than to the low temperatures (Araújo et al., 2013; Qu & Wiens, 2020). Evidence from these studies seems to suggest that lower- and upper-climatic niche limits might be uncoupled over evolutionary time, such that patterns of climatic niche breadth might be driven more by changes in one of the climatic niche boundaries, particularly in the case of temperature. However, despite this indirect evidence, few studies have directly assessed variation in evolutionary rates between different climatic range limits (Carscadden et al., 2020). In the largest study to date on this issue, Liu et al. (2020) estimated rates of evolution of upper and lower niche limits for 2087 species of plants and vertebrates and detected substantial differences between these limits. Establishing that this trend is indeed general could represent an important principle regarding the evolution of terrestrial species.

Interspecific differences in geographical distributions, particularly with respect to their range sizes, are largely influenced by climatic niche breadth (Slatyer et al., 2013). For instance, many species show remarkably small geographical ranges due to their

dependence on a peculiar set of climatic conditions (e.g., Essl et al., 2009; Pie et al., 2018). The evolution of climatic niche specialists is intriguing given that, to a first approximation, all species should evolve to become generalists, unless there are trade-offs in organismal performance in different positions along niche axes (Futuyma & Moreno, 1988). Rather, species vary considerably in their niche breadth, with potentially important consequences for their evolution (Fisher-Reid et al., 2012; Janzen, 1967; Quintero & Wiens, 2013). The first study to test such trade-offs in climatic niche axes was carried out by Bonetti and Wiens (2014) using amphibians. They found that climatic niche width decreased with temperature, but increased with precipitation, yet there was no evidence for a trade-off between temperature and precipitation niche widths. Later studies on more taxonomically restricted datasets tended to confirm the relationships between niche position and width for temperature and precipitation, as well as the absence of a trade-off between climatic niche breadths between axes (i.e., lacertid lizards [Fang et al., 2019], varanid lizards [Lin & Wiens, 2017], elapid snakes [Lin et al., 2019]), but the validity of this pattern for more inclusive taxa is still poorly known. However, the fact that Liu et al. (2020) found congruent evidence against this trade-off for vertebrates and plants suggests that it might indeed represent a general principle of climatic niche evolution.

There is a long tradition of suggesting a relationship between niche specialization and diversification (Fryer & Iles, 1969; Price, 1980; Vrba, 1980), but the evidence so far has been mixed (e.g., Day et al., 2016; Sexton et al., 2017). In the case of climatic niche breadth, only four studies to date have explicitly tested its relationship with diversification rates. The first explicit test was provided by Gómez-Rodríguez et al. (2015) using a family-level analysis of diversification among frog families. They found a significant positive relationship between family niche width and diversification rate, but a weak relationship between mean species niche width and diversification rate, despite both niche width variables being correlated. Likewise, Castro-Insua et al. (2018) carried out a similar, family-level analyses of terrestrial mammals and also showed a positive relationship between diversification and family-level niche breadth but not for mean species niches. On the other hand, Velasco et al. (2016) found that, for *Anolis* lizards, speciation rates are higher in lineages occupying warmer areas and for lineages with narrow niches. Finally, Rolland and Salamin (2016) carried out a large-scale analysis of the relationship between diversification and temperature niche width in terrestrial vertebrates and found that niche specialists (species with narrow temperature niche breadths) had higher speciation rates and lower extinction rates than generalist species, which directly contradicts the conclusions by Gómez-Rodríguez et al. (2015). However, the results of Rolland and Salamin (2016) should be interpreted with caution for two main reasons. First, they categorized each species as either "generalist" or "specialist" based on whether their niche breadth was above or below the median of the subtending clade, yet niche breadth is a quantitative variable, such that this categorization is inherently arbitrary. Second, they used ClaSSE (Goldberg & Igić, 2012), which is a refinement of the binary-state speciation

FIGURE 1 Diagram representing alternative routes to variation in climatic niche breadths. Horizontal lines indicate a hypothetical niche axis and curves represent ancestral (dark gray) and derived (light gray) changes in niche breadths. For instance, shifts in lower or upper niche limits might cause niche breadth to increase (b, e, f), decrease (c, d) or even to remain constant, with a change in the position of both limits moving in the same direction and magnitude (a)



and extinction (BiSSE) model (Maddison et al., 2007). However, it has been recently shown that heterogeneity in diversification rates of the underlying phylogeny could bias inferences of binary-state-dependent speciation and extinction models when testing associations between traits and diversification regardless of their underlying relationship (Beaulieu & O'Meara, 2016). Therefore, reassessing the relationship between diversification and climatic niche breadth using alternative methods and other niche axes would be important to determine the extent to which their conclusions are robust.

In this study, we explore the causes and consequences of the evolution of realized climatic niche breadth in terrestrial vertebrates with respect to their temperature and precipitation axes. In particular, our goals were to address the following questions: (1) Is there a consistent way in which niche breadth evolves along different niche axes? (2) Do climatic niche minima and maxima evolve at different rates? and (3) Is there a relationship between niche breadth and speciation rate?

2 | MATERIAL AND METHODS

2.1 | Data sources

We obtained data on the phylogenetic relationships of amphibians (Jetz & Pyron, 2018), birds (Jetz et al., 2012; Ericson backbone trees), mammals (Upham et al., 2019; birth-death node-dated trees), and squamates (Tonini et al., 2016) from VertLife.org (<http://vertlife.org/phylosubsets/>). Instead of including all of the species in those clades, we chose to focus on subclades that were more ecologically homogeneous to facilitate the interpretation of the obtained estimates, as well as on the particular species for which there was both phylogenetic and distribution data available. The combined dataset included 18,404 species distributed across mammals (Carnivora [$N = 216$], Cetartiodactyla [$N = 138$], Chiroptera [$N = 1120$], Diprotodontia

[$N = 138$], Primates [$N = 375$]), squamates (Anguimorpha [$N = 147$], Gekkota [$N = 999$], Iguania [$N = 1030$], Lacertoidea [$N = 483$], Scincoidea [$N = 1016$], Serpentes [$N = 1886$]), amphibians (Anura [$N = 4730$], Caudata [$N = 503$], Gymnophiona [$N = 139$]), and birds (Columbiformes [$N = 258$], Passeriformes [$N = 4575$], Piciformes [$N = 331$], Psittaciformes [$N = 320$]). We recognize that the choice of subclades is inherently arbitrary, as one could potentially choose any node across the corresponding trees. We used the following criteria to make our selection of taxon size to be more objective: (1) we included several distinct clades, such that one could assess the extent to which the patterns differ between taxa, as opposed to simply carrying out analyses at the most inclusive taxonomic levels; (2) we established a lower limit of clade size of more than 100 species, so that the corresponding rates could be reliably estimated; and (3) we chose taxa that can be readily understood by the reader as possessing an approximately typical ecology and life history (despite substantial variation that might be found within some clades). For instance, a general reader might be fairly familiar with the main differences between Carnivora and Chiroptera, but the distinction between the Arcoidea and Viverroidea clades might be only obvious to someone with more extensive knowledge on Carnivora. Geographical distributions for each species were obtained from the shapefiles available on The IUCN Red List of Threatened Species database Version 2018-2 (<https://www.iucnredlist.org>, downloaded on 5 January 2019). We omitted all introduced and uncertain ranges based on the specific annotation provided in the IUCN database for the shapefiles of each species. Geographical distributions were adjusted to a cylindrical equal-area projection using QGIS 3.8.3 (QGIS Development Team, 2020). Bioclimatic conditions within each range were obtained from WorldClim version 2.1 (Fick & Hijmans, 2017), at a 2.5' spatial resolution (~278.3 km at the equator), using RASTER 3.0-7 (Hijmans, 2020). Although this is a rather coarse grain, preliminary analyses using finer spatial scales provided nearly identical climatic means for each species, but at considerably higher computation time.

2.2 | Analyses

We began our analyses by exploring the structure of climatic niches based on variables representing the position of each species along each axis (BIO1, annual mean temperature; BIO12, annual precipitation) and its limits (BIO5, maximum temperature of warmest month; BIO6, minimum temperature of coldest month; BIO16, precipitation of wettest quarter; BIO17, precipitation of driest quarter) (Table S1). We chose these variables, as opposed to minimum and maximum values of BIO1 and BIO12 to avoid potential biases from a few unusually extreme points encompassed by a given shapefile, which in fact might not harbor the corresponding species. It is important to note that this approach is different from that of Bonetti and Wiens (2014), which considered niche breadth as the difference between maximum BIO5 and minimum BIO6 across each species' range (see Quintero & Wiens, 2013). Rather, by using average values in months with the most extreme conditions, we would provide a more typical description of climatic niche boundaries throughout the range of a given species (see Bonetti & Wiens, 2014 for a similar approach). We defined the niche breadth of each species as the difference, between average values of BIO5 and BIO6 for temperature and BIO16 and BIO17 for precipitation across their geographical range, respectively. We began by testing whether niche breadth varies systematically along temperature and precipitation axes, as well as a potential trade-off between temperature and precipitation breadths, using ordinary least squares regressions for each of the studied clades. Significance values for the tested relationships were obtained using phylogenetic independent contrasts (Felsenstein, 1985) using the `pic` function in APE 5.4 (Paradis & Schliep, 2019), as it is largely equivalent to other approaches such as phylogenetic generalized least squares (Blomberg et al., 2012). We also estimated rates of evolution of the boundaries of climatic niches of each taxon as the σ^2 parameter of a Brownian motion model of evolution using the `fitcontinuous` function in GEIGER 2.0.7 (Pennell et al., 2014). In order to account for phylogenetic uncertainty, we repeated independent contrasts and rate estimates for 1000 alternative topologies and provide medians of each estimate, as well as the corresponding 95% quantiles. It is important to note that we recognize the existence of alternative models of evolution that could potentially be fit to our data, such as Pagel's lambda (Pagel, 1999) or the Ornstein-Uhlenbeck model (Martins, 1994) and its variants (e.g., Ingram & Mahler, 2013; Khabbazian et al., 2016). However, our goal was not to find the best model of climatic niche evolution but rather to compare rates between variables and across clades. In this sense, if one niche axis is found to evolve according to a BM model in one clade, whereas a different clade might show a slightly better fit to an OU model, interpreting rate estimates across them would not be straightforward, particularly as one ends up comparing a diversity of models in different taxa and traits. Therefore, we use BM as a first approximation to rates of climatic niche evolution, but we recognize that further work should focus on explicitly modeling climatic niche evolution (Duran et al., 2013; Pie et al., 2017), as well as the timing and position of potential rate shifts within clades (e.g., Duran & Pie, 2015).

We tested for potential correlates between climatic niche breadth and speciation rates using *ES-sim*, which is a semi-parametric test for trait-dependent diversification analyses (Harvey & Rabosky, 2018). Instead of formally modeling the relationship between traits and diversification, this approach tests for correlations between summary statistics of phylogenetic branching patterns and trait variation at the tips of a phylogenetic tree. *ES-sim* is based on the λ_{DR} statistic, which is computed as:

$$\lambda_{DR_i} = \sum_{j=1}^{N_i} b_j \frac{1}{2^{j-1}}$$

where λ_{DR_i} is the tip rate for species i , N_i is the number of branches between species i and the root, b_j is the length of branch j , starting at the terminal branch ($j = 1$) and ending with the root (Title & Rabosky, 2019). When extinction rates are relatively low, the mean λ_{DR} across tips has been shown to converge on the true speciation rate (Jetz et al., 2012). Although in some conditions other alternatives to estimate diversification rates might outperform λ_{DR} (e.g., Cooney & Thomas, 2021), they are considerably more computationally demanding, such that the exploration of phylogenetic uncertainty at the scale of hundreds of topologies would be unfeasible. The use of tip-specific metrics of speciation rate has been recently suggested as an alternative to parametric state-dependent diversification due to the elevated rates of false-positive results (Beaulieu & O'Meara, 2016). Simulations have demonstrated that the use of *ES-sim* for continuous traits shows equal or superior power than QuaSSE (Harvey & Rabosky, 2018). *ES-sim* was implemented using the code provided by Harvey and Rabosky (2018) (available at <https://github.com/mgharvey/ES-sim>), with 1000 simulations used to build the null distribution of trait-speciation associations for significance testing. However, it is important to note that *ES-sim* is based on the λ_{DR} statistic and, therefore, tends to put more weight on more recent nodes (Jetz et al., 2012). As a consequence, it provides a more reliable index of speciation than net diversification in many scenarios (Belmaker & Jetz, 2015; Title & Rabosky, 2019), so that henceforth, we will treat the results of *ES-sim* analyses as dealing with speciation rates. We modified the original script to use the `fastBM` function in *PHYLTOOLS* 0.7-47 (Revell, 2012) during trait simulations, which resulted in substantially faster computation times (code provided in Script S1). We ran *ES-sim* for BIO1 and BIO12, as well as for the corresponding temperature and precipitation niche breadths indicated above. To account for phylogenetic uncertainty, we repeated each analysis for 1000 alternative topologies. Analyses were carried out separately for each potential correlate. Unless otherwise indicated, all analyses were carried out in R 4.0.2 (R Core Team, 2020).

3 | RESULTS

There is considerable variation in climatic breadths across lineages of each taxon, particularly with respect to temperature (Figure 2). When niche breadths were regressed against their corresponding axes, some consistent patterns were apparent for all taxa (Figure 3).

First, there was a negative relationship between niche breadth and temperature (slopes = -1.19 to -0.36, $R = 0.09$ –0.58, $p << 0.001$) and a positive relationship between niche breadth and precipitation (slopes = 0.03–0.31, $R = 0.02$ –0.59, $p = 0.1$ – $<< 0.001$) (Table S2). In the latter, the only relationship that was not highly significant involved Diprotodontia (Figure 3, Table S2). Finally, a negative relationship between niche breadths in each axis was found in all clades (slopes = -27.55 to -8.39, $R = 0.02$ –0.53, $p << 0.00001$), except for Primates (slope = 9.99, $R = 0.02$, $p = 0.004$), Diprotodontia (slope = -6.86, $R = 0.04$, $p = 0.02$) and Gymnophiona (slope = 24.29, $R = 0.02$, $p = 0.079$). Qualitatively similar results were obtained using Spearman's correlation analyses (Table S2). Nearly all tests based on phylogenetic independent contrasts were significant, except for the relationship between niche breadths in Primates and the relationship between annual precipitation and precipitation breadth in Diprotodontia (Table S3). However, the correlation coefficient of the association between niche breadths in different axes tended to be relatively low (Table S3). These slopes should be interpreted with caution given the strong skew in some of the variables (Figure 3).

Several congruent patterns were found when comparing evolutionary rates for each climatic niche boundary among taxa. First, the rate of evolution of BIO6 (minimum temperature of coldest month) was considerably higher than BIO5 (maximum temperature of warmest month) (Figure 4). The magnitude of this difference varied among taxa, varying from 42% in Caudata to being 5.8 times higher in Columbiformes (Table S4). The only exception was Iguania, in which BIO5 evolved 5% faster than BIO6. These results indicate that variation in climatic niche breadth related to temperature is mostly driven by changes in the lower (colder) niche limits (Figure 2, Table S3). A clear discrepancy is also found between the rates of evolution of BIO16 (precipitation of wettest quarter) and BIO17 (precipitation of driest month), with BIO16 evolving 87% faster in Diprotodontia to 10.5 times faster in Iguania (Table S3), suggesting that climatic niche breadth related to precipitation is predominantly driven by changes in the "wet" boundaries of this niche axis (Figure 2). However, the evolution of BIO12 (annual precipitation) was 3.8–9.5 times faster than even BIO16 (Figure 4, Table S3). This suggests that lineages tend to adapt to different conditions of average precipitation, while their climatic niche limits remain relatively unaltered. In other words, species evolve along a precipitation axis by changing the skewness of their distribution in climatic space as opposed to their boundaries. Conclusions based on square-root transformed precipitation values, which show less skew than the original precipitation data, were qualitatively identical (Figure S1, Table S3). Finally, tests of trait-dependent diversification using tip rate correlations failed to uncover any significant relationship across all of the tested traits and topologies (Figure S2, Table S5).

4 | DISCUSSION

Our results uncovered several clear principles governing the evolution of realized climatic niche breadth and its consequences.

First there was a significant relationship between climatic niche breadth and the position along a given niche axis, with this relationship being negative for temperature and positive for precipitation. In other words, there were narrower niches at high temperatures, but broader niches at higher precipitation. Second, for most clades, there was a negative relationship between niche breadth among axes, although the magnitude of this association was relatively low. Our results corroborate and extend previous studies with more limited taxonomic coverage in land vertebrates, although the relationship of climatic breadths between axes was at times slightly positive (e.g., Bonetti & Wiens, 2014; Liu et al., 2020; Qu & Wiens, 2020). The general congruence between patterns in organisms of such a variety of evolutionary histories, ecologies and geographical distributions would imply that they are generated by common underlying evolutionary mechanisms. There are at least two broad classes of explanation for the observed variation in climatic niche breadths. First, there could be inherent differences in the ability of organisms to evolve their physiological tolerances in different ends of niche axes. This was first argued explicitly by Araújo et al. (2013) in a comparison of temperature tolerances for ectotherms, endotherms, and plants, which found that tolerance to heat is largely conserved across lineages, whereas tolerance to cold varies between and within species. These patterns were later confirmed using explicit estimation of rates of physiological limits (Bennett et al., 2021; Qu & Wiens, 2020). Araújo et al. (2013) argued that the most likely explanation for this discrepancy was that variation in lower thermal limits is a consequence of differences in thermodynamic effects of temperature on reaction rates, and most likely those responsible for maintaining ion homeostasis (Hosler et al., 2000; MacMillan et al., 2012), whereas, changes in heat tolerance would result from a limited variation in the ability of organisms to counter the destabilizing effects of high temperature on membranes and proteins (Angilletta, 2009). We believe that this hypothesis is unlikely to explain the observed asymmetry in climatic niche breadth across axes for three main reasons. First, any fundamental physiological constraint would result in an upper boundary (in the case of temperature) that would be congruent within and across taxa, which does not seem to be the case in our data (Figure 2). Second, this limit should differentially affect species that are relatively close to it (e.g., warm-adapted species), yet the asymmetry in evolutionary rates seems widespread across lineages, regardless of how close they are to the limits in their subtending taxa. Finally, there was a similar asymmetry with respect to precipitation—with opposite sign—despite no obvious physiological constraints that would work in an analogous way with respect to temperature.

The second class of explanation for the observed variation in climatic niche breadths has to do with the geographical availability of different climatic regimes, a phenomenon recently dubbed environmental prevalence (Meyer & Pie, 2018). The basic idea of environmental prevalence is the observation that climatic conditions are not isotropic, that is, not all environmental conditions are equally available. Rather, given that some conditions are more prevalent, different lineages have adapted their environmental niches in

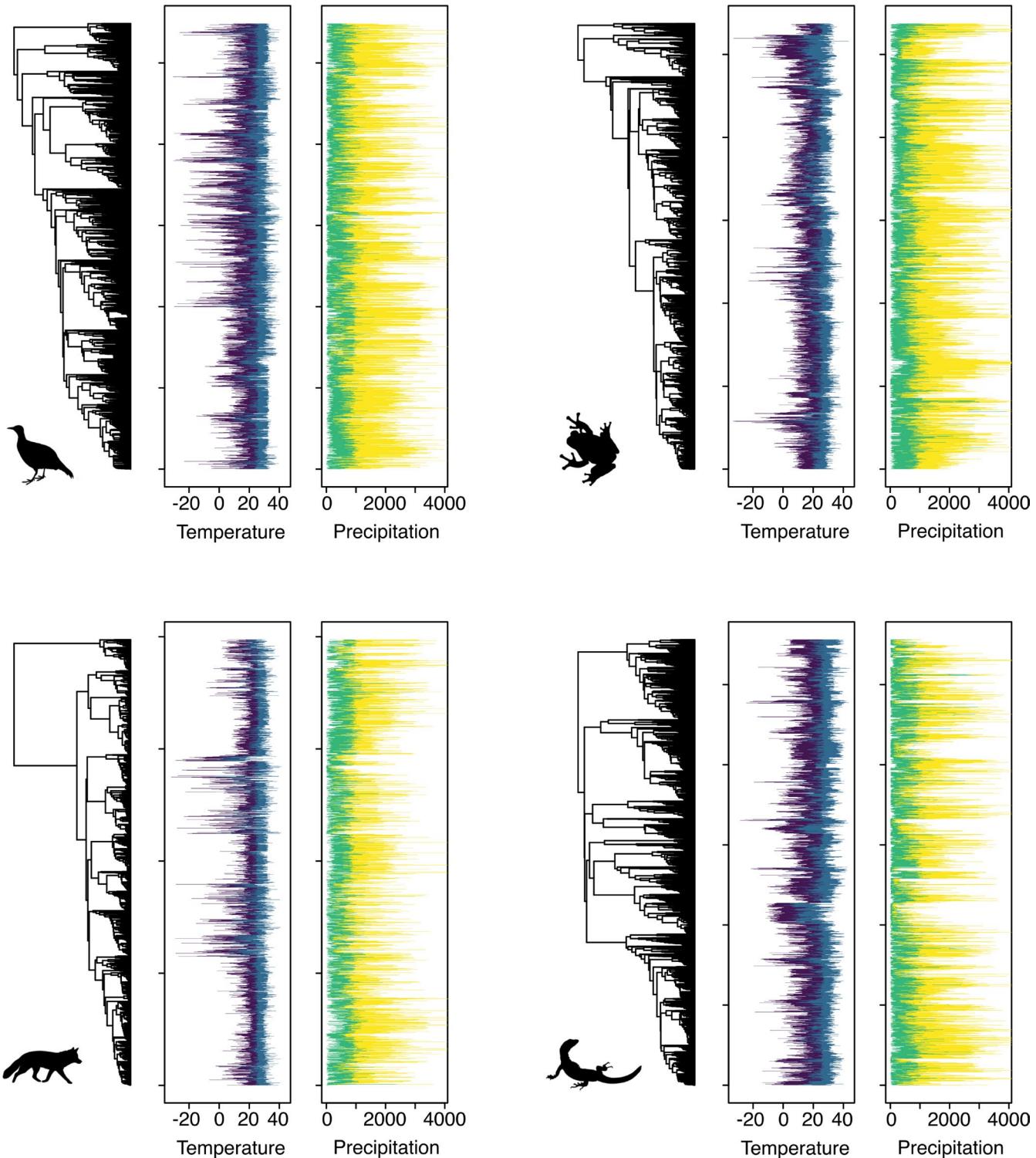


FIGURE 2 Variation in climatic niche breadth across terrestrial vertebrates (birds, amphibians, mammals, and squamates). Each horizontal line represents the niche breadth across the range of a given species, with different colors indicating the difference between the lower limit (minimum annual temperature/precipitation in the driest month) and the more typical condition (mean annual temperature/annual precipitation); and between the latter and the upper limit (maximum average temperature/precipitation in the wettest month)

proportion to their relative prevalence. Indeed, Meyer and Pie (2018) demonstrated that environmental prevalence was a better predictor of species richness in a variety of ecto- and endotherm taxa,

explaining more of the geographical variation in species richness than the climatic variables themselves (e.g., annual mean temperature). In the context of climatic niches, several studies have recently

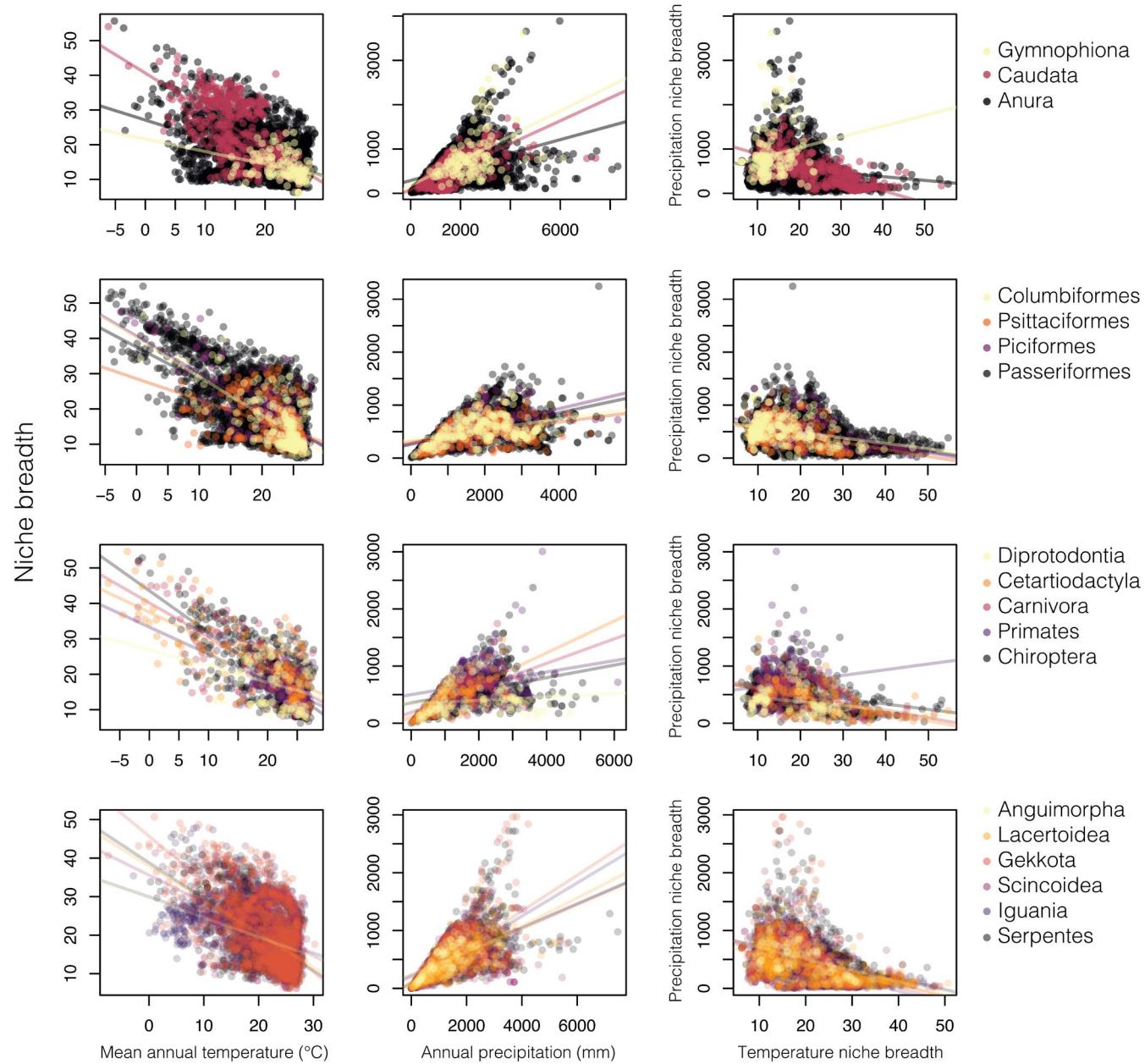


FIGURE 3 Relationship between the position along each niche axis (temperature on the left column, precipitation on the right column) and niche breadth for amphibians, birds, mammals, and squamates. Temperature niche breadth was calculated across the range of each species as the difference between the mean temperature in the warmest and coldest months. Likewise, precipitation niche breadth was calculated as the difference in average precipitation between the wettest and the driest months

demonstrated that their rate of evolution in general proceeds in a fairly constant rate during the history of different taxa, as the prevalence of different climatic regimes becomes available over the course of their diversification (Duran et al., 2013; Duran & Pie, 2015; Pie et al., 2017). Likewise, we argue here that the observed variation in climatic niche breadth might simply mirror the climatic template of environmental prevalence rather than intrinsic physiological constraints. Indeed, it is important to note that the definition of benign and inhospitable environments with respect to climate is often circular, given that they are determined by the relative occurrence of

different species with respect to more “typical” conditions based indirectly on their geographical distributions rather than on physiological first principles. This becomes evident when one simply plots the relationship between niche breadth across niche axis for the entire globe based on WorldClim environmental layers (Figure 5), in which we observe a distribution of climatic conditions remarkably similar to those found across terrestrial vertebrates (Figure 2). This suggests that environmental tolerances have evolved in response to environmental prevalence of different climatic regimes, as opposed to being the cause of the underlying distribution of different lineages.

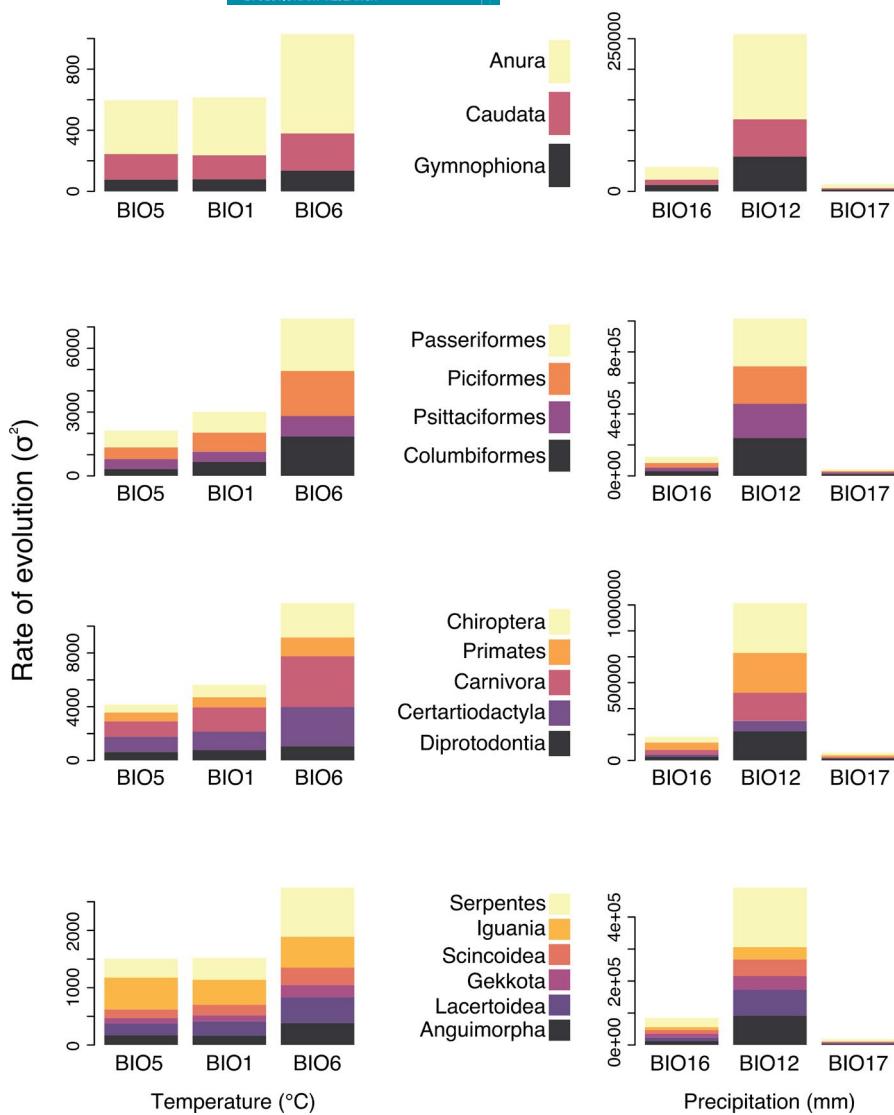


FIGURE 4 Rates of evolution of the mean bioclimatic variables for each of the studied lineages. BIO1 = annual mean temperature; BIO5 = maximum temperature of warmest month; BIO6 = minimum temperature of coldest month; BIO12 = annual precipitation; BIO16 = precipitation of wettest quarter; BIO17 = precipitation of driest quarter. Bars correspond to the median of estimated rates across 1000 alternative topologies

One corollary of this hypothesis is that the commonly observed variation in traits such as minimum and maximum critical temperatures of different organisms are not themselves the result of inherent physiological constraints, but rather reflect the history of selective regimes during their evolution.

Although it was not among the main objectives of our study, one intriguing result of our study was the remarkable variation among clades in their rates of climatic niche evolution (Table S3). For instance, there was at least one order of magnitude difference between rates of climatic niche evolution among taxa, with most of these differences reflecting the distinction between ectotherms (anurans and squamates) and endotherms (mammals and birds) (Table S3). However, these differences were not completely congruent between temperature and precipitation axes. For instance, Cetartiodactyla showed the fastest rates of evolution in all temperature axes (BIO1, BIO5 and BIO6), yet their rates of evolution in precipitation axes were slower than all other endotherms, and slower than several ectotherm taxa as well (see also Jezkova & Wiens, 2016; Rolland et al., 2018). These patterns suggest that understanding the causes of such dramatic differences in rates of climatic niche

evolution and their impact on the evolution of climatic niche breadth is likely to become a particularly interesting area for future studies.

The lack of association between speciation rates and either temperature, precipitation or the corresponding niche breadths is intriguing, given previous studies (e.g., Castro-Insua et al., 2018; Moen & Wiens, 2017; Pie, 2016; Schnitzler et al., 2012). For instance, it has been hypothesized that temperature might have a direct effect on mutation rates and, ultimately, on speciation rates (Allen et al., 2002, 2006; Rohde, 1992). Although there is some evidence for a link between mutation rates and temperature (e.g., Gillman et al., 2009; Gillman et al., 2010; Gillman et al., 2011; Wright et al., 2011, but see Weir & Schlüter, 2011), a causal relationship between mutation rates and speciation is yet to be established (but see Dugo-Cota et al., 2015). Alternatively, one could argue that higher temperatures would be associated with larger populations, which in turn, could lead to higher speciation rates, yet the predictions from the metabolic theory have not been shown to be general (e.g., Cassemiro & Diniz-Filho, 2010; Hawkins et al., 2007). In the case of climatic niche breadth, Gómez-Rodríguez et al. (2015) provided five alternative arguments for its potential relationship with diversification, namely

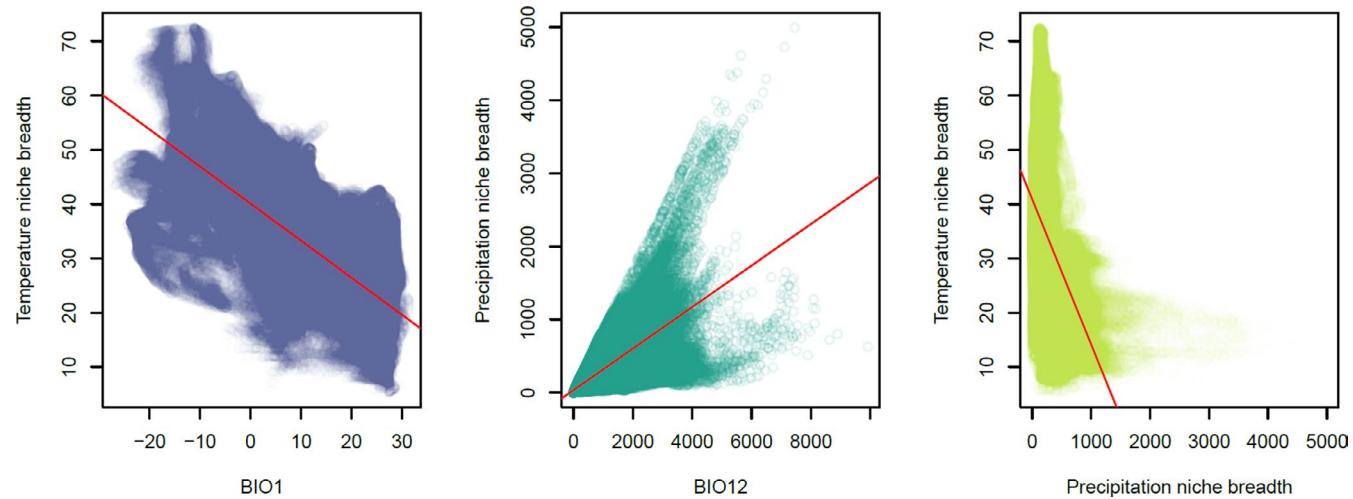


FIGURE 5 Relationships between climatic breadth and the corresponding environmental variable for temperature (a) and precipitation (b), as well as between climatic breadths of different axes (c) for all continents except Antarctica. Data were obtained from WorldClim (resolution of 10°). Temperature breadth was calculated as the difference between the mean temperature in the warmest and coldest months for each cell. Likewise, precipitation niche breadth was calculated as the difference in average precipitation between the wettest and the driest months. All associations between variables (Spearman rank correlations) are highly significant: a: $\rho = -0.74$, b: $\rho = 0.80$, c: $\rho = -0.45$, $p < 2.2e-16$ for all comparisons. Lines are based on linear regressions and are provided to facilitate visualization of the main trends in each plot

(H1) narrower niches increase diversification via speciation through niche conservatism; (H2) Wider niches increase diversification via increased speciation through niche divergence; (H3) Wider niches increase diversification via reduced extinction; (H4) Wider niches indirectly related to diversification via geographic extent; or (H5) Niche width of clades indirectly associated with diversification rate via separate geographic effects on niche widths and diversification rates (e.g., narrower niches and faster diversification rates in tropics) [see Gómez-Rodríguez et al. (2015) for details on the rationale of each hypothesis]. How can one reconcile our results with those of Gómez-Rodríguez et al. (2015)? Although there are some differences in the way we calculated climatic niche breadth, given that they are ultimately based on the same underlying data, we believe that such differences are unlikely to have caused the discrepancy in our conclusions. Rather, we believe that there are two non-exclusive explanations for the lack of association between climatic niche breadth and diversification in our study. First, the analyses by Gómez-Rodríguez et al. (2015) involved clade-level estimates of niche and lineage diversification and, therefore, involve relatively older divergence times. This argument is consistent with the observation by Gómez-Rodríguez et al. (2015) that the positive relationship found in their analysis was much stronger when analyzing family niche widths than with mean species widths. On the other hand, *ES-sim* tends to focus on more recent branches, which also tend to reflect more closely speciation rates rather than net diversification rates. Therefore, large-scale differences in climatic niches of major clades (e.g., above the family level) might lead to variation in diversification rates that would tend to become negligible at shallow evolutionary divergences. Second, by focusing on speciation rates, our analyses might overlook important differences in extinction rates, which might also (at least in part) explain the incongruence between our

results and those of Rolland and Salamin (2016). Teasing apart these alternatives is challenging, but future methodological advances, particularly those involving better treatment of extinction rates, might prove to be particularly revealing.

It is important to note that there are several limitations to the kinds of inference based on our results. First, we focused on temperature and precipitation variables because they are more easily available, particularly after the availability of WorldClim data. However, different organisms might be more severely limited by other niche axes that cannot be assessed based on our data, such as productivity and biotic interactions. Also, our approach was univariate, yet realized climatic space of a species is, by definition, not only limited by climatic conditions but by a combination of different factors such as biotic interactions and dispersal ability as well as thermal tolerance (Colwell & Rangel, 2009; Hutchinson, 1957). Therefore, the realized climatic space may not represent the full range of climatic conditions (i.e., the fundamental climatic niche) where a species can survive (Colwell & Rangel, 2009). Other factors, such as behavioral/physiological thermoregulation and microclimatic conditions might at times override the effects of large-scale environmental variables. Nevertheless, we believe that the coarse-grained view provided here might serve as a good first approximation to understand the relationship between climatic niche breadth and its relationship to lineage diversification. Moreover, our results underscore the potential of exploring further the relationship between environmental prevalence and interspecific patterns of niche breadth.

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AUTHORS' CONTRIBUTIONS

M.R.P. designed the study; M.R.P., R.D. and F.S.C. collected the data and conducted the analyses. M.R.P. wrote the first draft of the paper, M.R.P., R.D. and F.S.C. reviewed the final version of the paper.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

Table S1. Mean bioclimatic variables across the range of each species of the studied clades.

Table S2. Linear models of the relationship between niche breadth and their axes.

Table S3. Relationship between climatic niche variables and their breadths based on phylogenetic independent contrasts.

Table S4. Rates of evolution of average bioclimatic conditions across the range of species in each taxon.

Table S5. Tests of correlates of speciation rates in the studied taxa using ES-sim.

Figure S1. Rates of evolution of the mean bioclimatic variables for each of the studied lineages.

Figure S2. Correlation coefficients (ρ) of the relationship between speciation rates in the studied taxa using ES-sim.

Script S1. Code for test trait-dependent diversification using tip rate correlation (TRC).

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