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The cold-climate hypothesis is the main and most supported explanation of the evolution of viviparity among reptiles. This hypothesis sustains that viviparity arose as a means to save eggs from an increased mortality in nests linked with low temperatures. In this sense, some authors have stated that viviparity could constitute an evolutionary constraint. However, the link between evolutionary constraints and the evolution of ecological niches has not been well studied. Here, we study the climatic niche evolution of a group of viviparous lizards from North America to test whether the diversification of the group is linked with Phylogenetic Niche Conservatism (PNC). We evaluated phylogenetic signals and trait evolution, besides a reconstruction of ancestral climate tolerances, and did not find PNC in the ecological niche of the species in the group. Surprisingly, we did not find conservatism in any bioclimatic variables associated with temperature; we only had evidence of conservatism in Precipitation Seasonality (Bio15) and Precipitation of Coldest Quarter (Bio19). Analysis of relative disparity through time (DTT) indicates high divergence around 4.0 MYA and 0.65 MYA that coincides with orogenic and glacial periods. There is no evidence that climatic niche differentiation was the main factor in the diversification of the studied group. Orogenic and glacial periods probably promote cycles of the availability of new territories and isolation, which could promote the rapid accumulation of ecological differences between the species of the group.
Climatic niche evolution in the viviparous *Sceloporus torquatus* group (Squamata: Phrynosomatidae).

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Background

The actual distribution of species has been explained as the interaction of historical processes such as vicariance and dispersal, and shallow time processes that include ecological factors, such as habitat filtering, biotic interactions like competition or predation, and niche partitioning (Sexton et al. 2009; Nyári & Reddy, 2013). We refer to the niche or ecological niche of the species to be those biotic and abiotic variables that allow the persistence of populations (Hutchinson, 1957). At the same time, ecological components are important for speciation process, as reproductive isolation could appear by the evolution of barriers to gene flow due to divergent natural selection (Mayr, 1947; Pavey et al., 2010; Nosil, 2012). This kind of speciation implies changes in the ecological niche, but ecological niches are multidimensional, and it is unlikely that every dimension evolves in the same way (Schluter, 1996; Ackerly, 2003; Duran et al., 2013). There are other cases where the reproductive isolation is conditioned by a combination of ecological constraints and a vicariance process (e.g. geographic barriers), where species could retain some ancestral requirements that limit the adaptation to the climatic conditions imposed by the barrier (Wiens & Graham, 2005). The tendency of related species to retain their ancestral requirements or niches through time is described as Phylogenetic Niche Conservatism (PNC) (Boucher et al., 2014), and has been commonly studied by measuring the Phylogenetic Signal (PS). PS is the tendency for related species to resemble each other more than they resemble species drawn at random from the phylogenetic tree (Blomberg & Garland 2002), and for some authors, this is enough to verify PNC (Wiens et al., 2010b). However, some revisions have highlighted the theoretical problems with the PNC concept and the practical difficulties related to how to measure it (Revell et al., 2008; Münkemüller et al., 2015). Some authors argue that PNC is a process and some that is a pattern, while other researchers argue that PNC can be either a process or a pattern depending on how the research questions are raised (Losos, 2008; Wiens et al., 2010b). Additionally, the concept of PNC by itself cannot explain anything but can result from several processes (i.e. genetic constraints or stabilizing selection) (Losos, 2008); however, some authors argue that a combination or interaction between niche evolution and niche conservatism shape the biogeographic patterns observed in many species (Wiens & Donoghue, 2004), as well as the functional diversification of lineages.
and niche similarity of phylogenetically related species (Culumber & Tobler, 2016).

Nevertheless, the relationship of some constraints or shared biases in the production of phenotypic variability with niche evolution is barley known (Maynard Smith et al., 1985). Similar correlated responses are expected in organisms that share similar constraints; thereby, the interaction of this constraints and natural selection produce phenotype-environment correlations (Losos, 2011). In this regard, the viviparity among reptiles has been linked to cold climates, because it provides a selective advantage that prevents the death of embryos in the nest caused by low temperatures (Tinkle & Gibbons, 1977; Shine, 1985; Lambert & Wiens, 2013), and could be considered a phylogenetic constraint (Tinkle & Gibbons, 1977; Uller, 2003).

For example, there is evidence that viviparity among phrynosomatid lizards constrained some life-history traits (Zúñiga-Vega et al., 2016). Thus, we expected that viviparous species share environmental affinities that could lead to a stabilized selection and, as a consequence, show PNC, at least in some characteristics linked with breeding season, and for instance with cold environments.

The viviparity among squamata (lizards and snakes) has evolved from oviparity around 100 times (Blackburn, 2000; 2015) and has been a model system for testing many evolutionary hypotheses about the origin of viviparity between vertebrates (Lambert & Wiens, 2013). A group of lizards suitable for evolutionary studies about niche evolution and viviparity is the genus Sceloporus, which is widely distributed in North America and contains around 70 viviparous species distributed in five groups (Wiens & Reeder, 1997; Méndez-de la Cruz et al., 1998), and for which there is molecular and phylogenetic information for almost all recognized species along with a wide occurrence database (Wiens & Reeder, 1997; Leaché, 2010; Wiens et al., 2010a; Leaché et al., 2016).

We assume that given the hypothesis about the development of viviparity in reptiles being linked with low temperatures, this could constrain the niche evolution between viviparous species. In this study, using the viviparous Sceloporus torquatus group as model organisms, we aim to: (1) assess whether niche evolution is phylogenetically constrained between viviparous species of the group, (2) test whether similarities in environmental tolerances between species
and the phylogenetic relationship predicts PNC; and (3) test whether most important bioclimatic variables used as niche descriptors show PNC.

The *torquatus* group (Smith, 1938) is distributed from the southern United States southward into Guatemala (Martínez-Méndez & Méndez de la Cruz, 2007). Throughout its distribution, the group occurs in mountain ranges with temperate conditions, but also in semi-desert and tropical environments (e.g. *S. serrifer*). The group is diagnosed by a series of osteological and scutelation (meristic) characters, but perhaps its main external characteristic is the nuchal collar formed for dark scales lined with lighter or white scales (Smith, 1938; 1939; Wiens & Reeder 1997), with sizes that ranges from 56 mm in SVL (snout-vent length) to 130 mm in SVL (field notes of NMM). The great amount of the species of the group have saxicolous habits with the exception of some populations of *S. serrifer* in Usumacinta basin and in Yucatan peninsula; in this last, the species can toggle between boulders and only certain species of tropical trees (field observations of NMM). There is evidence that population demography could influence the climatic niche evolution of the species (Jakob *et al.*, 2010), and in turn body size can influence the demography of the species (Sibly & Brown, 2007; Fernández-Chacón *et al.*, 2015).

For this reason, and in order to avoid additional confounding factors, we focused only in *torquatus* group analyses without including *grammicus* and *megalepidurus* groups (which are its viviparous sister groups), because the differences in sizes and habits between them could be high. The species of the *grammicus* group have a maximum SVL of around 76 mm and have primary arboreal habits, although the organism can inhabit cracks in rocks in many populations and even can be found in walls and rock fences. On the other hand, the species of *megalepidurus* are smaller, with an SVL of around 55 mm and use agave and yucca leaves as refuges (field notes of NMM). Nonetheless, in a future study of niche evolution, we will include these two additional groups along with data on size, habits and specific thermal preferences.

To achieve the stated objectives, we constructed a phylogeny of the group and used a phyloclimatic analysis that implies the use of occurrence data and bioclimatic information in a phylogenetic comparative context to: (1) evaluate the phylogenetic signal of the species’ ecological niche and the bioclimatic variables used to construct it, (2) fit macroevolutionary
models for the most important bioclimatic variables for the group, (3) investigate the history of ecological niche occupancy and accumulation, (4) investigate ancestral tolerances, and (5) calculate the niche disparity through time.

MATERIALS AND METHODS

Data sources

Occurrence data were obtained from The Global Biodiversity Information Facility (GBIF; http://www.gbif.org/), HERPENET (http://www.herpnet.org), Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (CONABIO; https://www.gob.mx/conabio) and field notes of main author. We removed occurrence records that constituted misidentifications, mistakes on coordinates (i.e. points on the sea) and with similar coordinates. To minimize spatial autocorrelation, we randomly removed occurrences within 0.5 km of each other in order to obtain localities in distinct grids to match the spatial resolution of environmental layers (30 arc second). For environmental layers, we used bioclim layers at a 30 arc second resolution (1 km x 1 km) and monthly and annual maximum and minimum temperatures and precipitation levels available from the WorldClim database 1.4 (http://www.worldclim.org), as well monthly and annual potential evapotranspiration (PET) and aridity available from http://www.cgiar-csi.org/data/global-aridity-and-pet-database (Zomer et al., 2008). All layers were clipped to the general limits species’ group distribution.

Ecological niche modeling

Because of the large number of layers, we performed a preliminary analysis with MaxEnt v.3.4.1 (Phillips et al. 2006; Phillips & Dudik 2008) for all species using all layers and using default settings with a cloglog output. Using a jackknife test implemented in MaxEnt, we chose only those variables with high relative importance (10 for each species). In order to avoid collinearity and model overfitting, we extracted the environmental information for each grid cell from this reduced set of layers to perform a Pearson correlation. We retained only layers with low correlation (r < 0.75), and in the case of highly correlated variables, we chose, wherever was
possible, the layers that measured extreme conditions as they condition the range limits of
species (Sexton *et al.*, 2009), and also the most biologically meaningful layers according to the
biology of this group of species. This species-group has a fall-winter reproduction cycle, with
relationship between local extinctions and the increase in temperatures by global warming in
the reproductive season (Sinervo *et al.* 2010). The most evident layers with a biological
meaning for this species-group were those related to the fall and winter, which is the driest and
coldest season for almost the entire distribution range of studied species. Finally, we chose 11
layers: Max Temperature of Warmest Month (Bio5), Mean Diurnal Range (Bio2), Mean
Temperature of Wettest Quarter (Bio8), Mean Temperature of Driest Quarter (Bio9),
Precipitation Seasonality (Bio15), Precipitation of Warmest Quarter (Bio18), Precipitation of
Coldest Quarter (Bio19), Average Potential Evapotranspiration in May (PET5), Average
precipitation in May (Prec5), Average precipitation in October (Prec10), and Average maximum
temperature in January (Tmax1). The clip of layers, the extraction of climatic information and
Pearson correlation were performed using R (R Core Team, 2017) and Raster library (Hijmans,
2017).

The final MaxEnt analysis for each species was performed using default settings with cloglog
output and 10 replicate runs using different random seeds with 80% of the localities for model
training and 20% for model testing. For statistical evaluation, we used threshold-independent
receiver operating characteristic (ROC) analyses (Phillips *et al.*, 2006), where we examined the
area under ROC curve (AUC) across the 10 replicates and considered a mean AUC value ≥ 0.7 as
evidence that the model had discriminatory ability that was better than random (Swets, 1988;
Peterson *et al.*, 2011). Because ROC analyses in theory must be used with true absences and
not with pseudo-absences or background points, like that used in MaxEnt and weighed up as
the same errors of omission and commission (Lobo *et al.*, 2007), we additionally did partial ROC
analyses (Peterson *et al.*, 2008) that account for a user-defined maximum acceptable error of
omission. We performed partial ROC analyses with Tool for Partial-ROC (Narayani, 2008) using
50% of the evaluation points resampled in 1000 bootstrap runs and with a fixed error of
commission ≤ 5% (*1-omission threshold* > 0.95). Then, a Z test was achieved to determine
whether partial AUC proportions were better than random (AUC = 1.0).
Phylogeny of *Sceloporus torquatus* group

Leaché *et al.* (2016) estimated a phylogenomic tree of *Sceloporus* genus confirming the monophyly of *torquatus* group in relation to *megalepidurus* group by resolving some taxonomic inconsistencies due to fewer loci being used in previous studies and rapid radiations of some groups of species (Leaché, 2010; Wiens *et al*., 2010); unfortunately, they only included 15 species and probably misidentified two species. The specimen UTAR 39870 referred to *S. serrifer* from south Texas, which is recuperated like sister species of *S. cyanogenys* in the phylogenomic tree of Leaché *et al.* (2016). According to Martínez-Méndez & Méndez de la Cruz (2007), this corresponds to *S. cyanogenys*, with no close relationship with *S. serrifer* populations from Guatemala and the Yucatan peninsula in Mexico. Likewise, specimen UWBM 6636, identified as *S. mucronatus*, is probably *S. omiltemanus* because the organism was collected around ten kilometers east of the typical locality (Smith, 1939) and there is evidence that this species does not have a close phylogenetic relationship with *S. mucronatus* (Martínez-Méndez & Méndez de la Cruz, 2007).

In order to estimate the phylogeny of the *Sceloporus torquatus* group and include the maximum amount of species, we decided to use sequences for four mitochondrial genes (12S, 16S, Nd4, and ND1), and four nuclear genes (RAG1, BDNF, R35, and, PNN) that were retrieved from GenBank (Table S1) from the 23 species recognized for the group, including a new species (MX14-4) from central west Mexico and three species of *grammicus* group as the out-group (*S. grammicus*, *S. heterolepis* and *S. palaciosi*). As previously highlighted, we used the *grammicus* group, which is the second out-group of *torquatus*, because of problems of monophyly of *torquatus* with respect to *megalepidurus*, its sister group (Leaché, 2010; Wiens *et al*., 2010a; Leaché *et al*., 2016).

The alignment of each locus was performed using Clustal X ver. 2.1 (Larkin *et al*., 2007); the loci were then concatenated and refined by eye into Mesquite ver. 3.2 (Maddison & Maddison, 2017). We considered 21 partitioning schemes: by gene region of 12S, 16S and Nd4-tRNAs, and by codon position of the rest of nuclear and mitochondrial loci. To determine the best substitution model for each data partition we used jModeltest ver. 2 (Darriba *et al*., 2012)
based on the corrected Akaike Information Criterion (AIC). The models with a parameter for invariant sites (I) in addition to among site-heterogeneity (Γ) were not considered because the correlation of these two parameters does not allow its independent optimization (Sullivan et al., 1999; Rannala, 2002). Phylogenetics relationships of torquatus group were assessed using Maximum Likelihood (ML) and Bayesian inference (BI). ML analysis was performed in RAxML ver. 8.1. (Stamatakis, 2014) using GTA+ Γ, and base frequencies which were estimated and optimized for the partitioning scheme listed above with 1000 non-parametric bootstrap replicates using the rapid-bootstrapping algorithm. BI was performed using MrBayes ver. 3.2.6 (Ronquist et al., 2012) with partitioned data using models suggested by jModeltest; when the model was not implemented in MrBayes, we used the nearest and most inclusive model (parameter rich) for analyses. Four Metropolis-coupled MCMC chains were run for 10 million generations with trees sampled every 1000 iterations using default temperatures for chain heating. After a burn-in of 25%, as determined by visualizing posterior distributions of the parameter values in Tracer ver. 1.6 (Rambaut et al., 2014), we generated a 50% majority-rule consensus tree with SumTrees ver. 3.3.1, which is part of the Python library DendroPy (Sukumaran & Holder, 2010). The edition and plot of phylogenetic tree with posterior probabilities and bootstrap proportions was assessed using the package ape (Paradise et al., 2004) in R (R Core Team, http://www.r-project.org/) (Fig. 1).

In order to get a dated phylogeny for the subsequent phyloclimatic analyses, we used the R package ape (Paradis et al., 2004) to edit the original tree. First, those species excluded from niche analysis were pruned using the drop.tip function; then, the tree was made ultrametric and node ages were estimated with a semi-parametric method based on penalized likelihood using the chronos function with default settings (fig. 2). We used the divergence between former torquatus and poinsetti clades (8.24-12.65 MYA) as calibration points obtained from the phylogenomic analysis of Leaché et al. (2016), and the divergence between Sceloporsus serrifer and S. prezygus (1.58-6.35 MYA) obtained from the phylogeographic analysis of Martínez-Méndez et al. (2015).
Phylogenetic signal of climatic variables and testing for Phylogenetic Niche Conservatism

Despite the criticisms about PNC following Münkemüller *et al.* (2015), we assumed for simplicity the over-simplification of the reality that species niches can be described by single continuous traits (in this case bioclimatic variables), and adopted two practical positions to investigate the presence of PNC: 1) PS can be used to measure PNC only if the analyzed character evolves under a Brownian motion (BM), namely trait changes along the phylogeny of a group occurs as a random walk with a constant increase of variance and an expected mean equal to zero (Felsenstein, 1985); and 2) if under the exploration of alternative evolutionary models such as the Ornstein-Uhlenbeck (OU) model, where traits evolve to an adaptive optimum (Butler & King, 2004), we obtained support for a single optimum with high selection strength, or under support for the multi-optima OU model we obtained relatively few peak shifts. To achieve the above, first we calculated the environmental mean for the chosen bioclimatic variables for each species using the package phyloclim (Heibl & Calenge, 2015), and then we tested for PS using the package phytools (Revell, 2012) by calculating Blomberg’s K (K) (Blomberg *et al*., 2003) with 1000 simulations and Pagel’s lambda (λ) (Pagel, 1999) using maximum likelihood. Blomberg’s K (K) is a scaled ratio of the variance of the data between species and the mean squared error based on the variance-covariance matrix of the phylogeny under a BM expectation, whose values range from zero to infinity, where K>1 indicates a strong PS with the variance distributed between clades, and K<1 indicates weak PS with variance within clades (Blomberg *et al*., 2003; Münkemüller *et al*., 2012). Pagel’s λ is a scaling parameter for the phylogeny that measures the correlation of the observed trait data between species under a BM, whose values ranges from 0 or no correlation to 1 or correlation between species, suggesting that phylogenetic relationships predict well the pattern of trait evolution (BM process), and different degrees of phylogenetic signal are included in 0 < λ < 1 values (Pagel, 1999; Münkemüller *et al*., 2012). At the same time, we used the R package Geiger (Harmon *et al*., 2008) to tested for four alternative models of trait evolution of bioclimatic layers: (1) Brownian Motion (BM); (2) Ornstein-Uhlenbeck (OU), as we pointed out models with the evolution of a trait around an optimal value (Butler and King 2004), however this should not be interpreted as stabilizing the selection in comparative studies (Cooper *et al*., 2017); (3) Early
Burst (EB) or rapid evolution of a trait followed by stasis (Harmon et al., 2010); and (4) Pagel’s delta (δ) (Pagel, 1999), which models changes on rates of evolution through time, where δ < 1 is indicative of a slowdown on the recent evolution of the group and trait evolution is concentrated in the base of the phylogenetic tree, and δ > 1 indicates that recent evolution was fast and trait evolution is concentrated in the tips of the tree. The identification of a best fitting model of evolution was by means of log likelihood and AICc, where the model with the higher log likelihood and lower AICc has the better fit (Hurvich & Tsai, 1989). Additionally, to choose between models, we followed Burnham and Anderson (2002; 2004), who pointed out that models with ΔAIC < 2 (AIC differences) are more or less equivalent; models with ΔAIC within 4-7 are distinguishable; and models with ΔAIC > 10 are different. Then, we compared the ΔAIC between the model with lower AICc and the rest of the models and established that: ΔAIC < 2 = e (equivalent models); ΔAIC ≥ 2 and < 7 = * (more or less distinguishable models); ΔAIC ≥ 7 and < 10 = ** (distinguishable models); and ΔAIC ≥ 10 = *** (different models). Following the recommendations of Münkemüller et al. (2015), the white Noise (WN) model that is equivalent to no phylogenetic signal was not considered, because it has the same pattern of an OU model with strong attraction strength (tends to infinity).

We also performed a test under a multiple-optima OU framework to infer location, magnitude and the number of possible adaptive shifts using the R package bayou (Uyeda & Harmon, 2014), which uses a reversible-jump Bayesian method to test for multiple optima. We first established a prior function with a half-Cauchy distribution prior for α and σ², a normal prior for θ, a conditional Poisson for the number of shifts and a maximum of one shift per branch. We run two chains for 2 x10⁶ generations, sampling every 200 steps. After discarding the first 50% of generations as burn in, the convergence was assessed using Gelman and Rubin’s R statistic (R ≤ 1.1).

To explore the presence of PS in patterns of niche overlap (niche evolution), we used the modification of Warren et al. (2008) for the age-range correlation (ARC) proposed by Turelli & Fitzpatrick (2006). This method used a linear regression of node age given the niche overlap of the species, where a positive or negative significant correlation is an indication of PS in niche
evolution, and can also be used to investigate speciation mode. For this purpose, we calculated
the niche overlap by means of Schoener’s $D$ and Warren’s $I$ statistics (modification of Hellinger
distance $I$), which range from 0 for no overlap to 1 for total overlap (Warren et al., 2008). Given
that Schoener’s $D$ makes assumptions about species densities that are probably incorrect if
there are significant differences with $I$ statistic ($I$ tended to yield high values than $D$) (Warren et
al., 2008), we chose Warren’s $I$ statistic for correlation, and 1000 iterations for a Monte Carlo
resampling of overlap matrix was used to determine the significance of the analyses. Niche
overlap statistics and ARC analyses were performed using the package phyloclim (Heibl &
Calenge, 2015).

Predicted Niche Occupancy and ancestral tolerances

To reconstruct the evolutionary history of niche tolerance or Predicted Niche Occupancy (PNO),
we used the methodology of Evans et al. (2009). This method relates the distribution of
suitability of the Maxent analyses of all species to each bioclimatic variable in order to obtain a
unit area histogram of suitability, which represents the tolerance (occupancy) of the species at
a given bioclimatic variable (PNOs profiles). Later, the PNOs and pruned phylogenetic tree were
used to estimate the ancestral tolerance of nodes to each bioclimatic variable, using 1000
random iterations from PNOs profiles and a maximum likelihood method. Additionally, we used
the weighted means of PNOs in a phylogenetic Principal Components Analysis (pPCA; Revell,
2009) to explore a possible climatic differentiation or geographic association between species
and clades; however, this method assumes that all traits evolved under a multivariate BM
process (Revell, 2009; Uyeda et al., 2015). PNO profiles and ancestral tolerances were
calculated using the package phyloclim (Heibl and Calenge, 2015), and pPCA was performed
with the package phytools (Revell, 2012).

Finally, we used an analysis of relative Disparity Through Time (DTT) (Harmon et al. 2003) to
explore the time pattern of niche evolution and how the niche disparity is distributed among or
within subclades. Here, the disparity is the average of the squared Euclidian distance of
weighted mean values of PNOs among all pairs of species (pairwise differences), and relative disparity is the disparity within a clade divided by the disparity of the entire phylogenetic tree. The DTT is calculated as the mean relative disparity of all clades whose ancestral lineages were present in each speciation event. Then, a null or expected DTT distribution is made with simulated data under a BM model of evolution. The expected DTT and observed DTT of each subclade were plotted against divergence times to obtain a DTT plot. The results of DTT analyses were quantified using the morphological disparity index (MDI), which is the difference between the observed and expected DTT. Positive MDI values indicate a disparity distributed within subclades or a recent evolution of the trait with divergence between subclades. Conversely, negatives values indicate a disparity distributed between subclades and early evolution of the trait or conservatism within more deep clades (Evans et al., 2009). We present MDIs for total phylogeny and for former poinsettii and torquatus clades. The DTT analyses were performed using the package geiger (Harmon et al., 2008) with 1000 simulations and a confidence level of 0.95.

RESULTS

Ecological niche modeling

The presence data of Sceloporus sp. (MX14-4), S. lineolateralis, and S. macdougalli were excluded from niche analyses because these species had a reduced amount of useful points after depuration (< 5). For all of the remaining species, the mean AUC scores were > 0.75, which were statistically significant with AUC proportions of partial ROC analyses > 1; then, the ecological niche models (Fig. S1) were considered suitable for use as inputs in the subsequent analyses.
Phylogeny of the *Sceloporus torquatus* group

The phylogeny of the *torquatus* group is basically similar to previous studies (Wiens and Reeder, 1997; Martínez-Méndez & Méndez de la Cruz, 2007; Leaché *et al*., 2016) with two main clades that correspond to the former *poinsettii* and *torquatus* groups Leaché, 2010; Wiens *et al*., 2010); here, we refer to these two clades as *poinsettii* and *torquatus* clades to avoid confusion with the total *torquatus* group, both of which have strong support (*poinsettii* clade: PP = 1, BSP = 100%; *torquatus* clade: PP = 0.99, BSP = 99%). However, as we pointed out previously, there are some differences between our phylogeny and that of Leaché *et al*., 2016: (1) the probable misidentification of *S. omiltemanus* as *S. mucronatus*, where Wiens & Reeder (1997) and Martínez-Méndez & Méndez de la Cruz (2007) reported the non-monophyly of *S. mucronatus* subspecies, and the last authors proposed that *S. mucronatus omiltemanus* should be elevated to full species status; (2) the consideration of UTAR 39870 from Texas as *S. serrifer*, since according with Martínez-Méndez & Méndez de la Cruz (2007) the populations from Texas and Northeast of Mexico were considered to be *S. serrifer plioporus* for Olson (1987), being synonymized into *S. cyanogenys*; (3) we included the new specimen MX14-4 (*Sceloporus* sp.), which was resolved as a sister species of *S. melanogaster* with a strong support only for Bayesian analyses (PP = 1, BSP < 75%) (Fig. 1).

Phylogenetic signal of climatic variables and testing for Phylogenetic Niche Conservatism

The tests of PS indicated that only Precipitation Seasonality (Bio15) has significant support (Table 1), with a moderate to weak PS and with the variance distributed within clades (K = 0.9789271, p = 0.003), thereby suggesting a high correlation of the data with a BM process (λ = 0.8990152, p = 0.009). The above coincides with the test of alternative models of evolution (Table 2), where only Bio15 shows weak support for BM evolution, because the difference between alternative models is just over two (ΔAIC = 2.0003). The other bioclimatic layer that shows a BM evolution with the lower AICc are not distinguishable from other models of evolution or even are equivalent (*i.e.* BM and δ are equivalents in Bio2 and Tmax1). Similarly
only Precipitation of Coldest Quarter (Bio19) presents evidence of an OU model of evolution; however, the selection strength is relatively weak ($\alpha = 0.597$; Table S3). Probably, this implies a weak PNC of the Bio19 variable in the alternative interpretation of Münkemüller et al. (2015), where PNC is indicated by relative strong selection strength and one or relatively few adaptive peak shifts. The other bioclimatic layers with OU showing lower values of AICc are not distinguishable from other models. Noteworthy, in all cases, Pagel’s delta ($\delta$) was > 1 (Table 2), indicating a tendency in trait evolution to be concentrated in the tips of the tree. Likewise, the multi optima OU method implemented in Bayou fails to correctly detect the location and magnitude of adaptive shifts (Table S4 and Figure S2), because the mean number of shifts was nine (K=9) and parameters are correctly estimated only if the number of shifts is not large (K > 25% the number of tips) (Uyeda and Harmon, 2014).

Niche overlap values (Fig. 3) are on average low (Schoener’s $D$ and Warren’s $I$ statistics < 0.4) for all species and for *torquatus* and *poinsettii* clades. Similarly, only a few pairs of species show moderate-to-high values (Table 3), such as *Sceloporus cyanstictactus* vs. *S. ornatus caeruleus* (Warren’s $I = 0.907$). However, none of these are sister or close relative species with the exception of the small clade formed by *S. cyanogenys* + (*S. oberon* + *S. ornatus ornatus*), which shows values of Warren’s $I$ statistics ranging from 0.753 to 0.894. The arc-range correlation (ARC) shows no significant correlation between niche overlap at internal nodes and divergence time (Fig. 4), and fails to detect PS in niche evolution in all the bioclimatic layer used, which is consistent with the lack of PS for almost all of the bioclimatic layers individually tested, except for Bio15.

Predicted Niche Occupancy and ancestral tolerances

The PNO profiles (Fig. 5) show a high heterogeneity in some bioclimatic variables, with species occupying different sections of parameter space and with different levels of specificity in climatic tolerance, as denoted by the breadths of the profiles. However, some overlapping peaks that indicate similar climatic tolerance between few species are found in all bioclimatic
layers, but are especially important in Average Potential Evapotranspiration in May (Pet5) and in the Precipitation of the Coldest Quarter (Bio19). Also, Bio19 has an overall breadth of PNO profile that is the narrowest of all bioclimatic layers, which is consistent with the OU model of evolution with a single optimum detected for this bioclimatic layer (Table 2). It is also important to note the case of *Sceloporus serrifer*, which shows the more extreme values in Mean Temperature of Wettest Quarter (Bio8) and in Mean Temperature of Driest Quarter (Bio9) PNO profiles. The plots of history of evolution of climatic tolerances (Fig. 6) show no pattern between the two main clades, with crossing branches from different clades for all bioclimatic variables indicating divergent evolution, and only some nearly overlapping nodes being recovered, indicating some grade of convergent climatic origins. However, these plots were built under the assumption of BM evolution, so only the plot for Bio15 would have a non-biased interpretation; nevertheless, the means are close and the density of climate tolerance is more or less narrow for each species on Prec10, Bio9, Bio18 and Bio19. In the case of the Bio19 plot, despite the assumptions that BM evolution is clear, there is a trend consistent with an OU model with a single optimum, with the exception of the branch of *Sceloporus serrifer* and *S. prezygus* in Bio19, that show major divergent evolution.

Phylogenetic PCA (pPCA) shows no pattern or separation between clades (Figure S3), with some species being more influenced by Bio2 and Pet5 (*S. cyanogenys, S. ornatus ornatus, S. poinsetti, S. jarrovi*) and others more influenced by Bio15 and Prec5 (*S. aureolus, S. mucronatus*); again, *S. serrifer* shows the more divergent niche influenced mainly by Bio9 and Bio19. Owing to the pPCA analysis not showing an evident pattern or separation between clades, a phylogenetic MANOVA analysis was not necessary to confirm any significant differences. Nevertheless, this method is useful for visualizing divergence across phylomorphospace; the interpretation of the contribution of each trait has to be taken with caution because of the assumption of BM evolution of all traits and other statistical bias (Uyeda et al., 2015).

The analysis of relative disparity through time (DTT) shows (Fig. 7) that almost all bioclimatic layers have a zero disparity in internal (deep) nodes, indicative of early conservatism in major clades, with the exception of Bio9 and Bio15; also, all bioclimatic layers show significantly (P <
higher levels of disparity through time than expected by null model (dotted line in Fig. 7), with some peaks indicating higher divergence in recent nodes, consistent with evolution within clades. As noted above, Bio15 shows weak support for a BM evolution and the DDT plot confirms this, because only in some points in the past was this bioclimatic variable close to a BM process. In general, the higher levels of disparity in DTT in all bioclimatic layers are concentrated in subclades in relative times that range from 0.3 to 0.8, which corresponds with changes around the last 6.6 MYA. The maximum peaks in most of the bioclimatic variables, except for Bio8 and Prec10, are detected at around 4.0 MYA (relative time of 0.5) and 0.65 MYA (relative time of 0.75). The bioclimatic variable Bio8 (Mean Temperature of Wettest Quarter) only presents the 0.65 MYA peak. On the other hand, Prec10 (Average precipitation in October) presents a maximum peak at around 4.0 MYA and two small peaks at around 7.9 MYA (relative time of 0.2) and 1.9 MYA (relative time of 0.65), which are barely significantly lower than the null model; this is indicative of disparity distributed between subclades at that time. The values of MDI (Table 4) for the total tree are positive in all cases, suggesting some niche evolution within subclades and niche conservatism between subclades, or that the ecological disparity tends to be distributed within subclades rather than between subclades. The same pattern is observed with MDI values for former *torquatus* and *poinsettii* clades, with the exception of Prec10 for both former clades, and Tmax1 for the *torquatus* clade, showing negative values, indicating niche conservatism within clades and niche evolution between clades.

**DISCUSSION**

Current ecological niche of *torquatus* group and viviparity

Some of the layers chosen for estimation of the ecological niche of *torquatus* group had an evident link with the current fall-winter reproductive cycle of viviparous lizards (*i.e.*, Precipitation of Coldest Quarter (Bio19), Average maximum temperature in January (Tmax1), and Average precipitation in October (Prec10)). Likewise, Mean Temperature of Driest Quarter (Bio9) matched with late fall (November) and winter in the Mexican Plateau (Central Mexico) and Chihuahuan Desert zone (Willmott & Matsuura, 2001; http://www.worldclim.org), where
many of the species of the torquatus group can be found. Moreover, despite a lack of data about the biology of the reproduction and demography of the whole group, the remaining layers could have some direct relevance in some phases of life history; for example, Average Potential Evapotranspiration in May (PET5), Average precipitation in May (Prec5), Max Temperature of Warmest Month (Bio5) and Precipitation of Warmest Quarter (Bio18), could be linked with the survival of the offspring, because parturition in some species of the group has been reported to occur between late April and early May (Guillette & Méndez-de la Cruz, 1993; Méndez-de la Cruz et al., 1998; Feria-Ortiz et al., 2001; Villagrán-Santa Cruz et al., 2009), and the warmest month coincides with April, May or June in many occurrence sites of the group. Watson et al. (2014) found that Max Temperature of Warmest Month (Bio5) is frequently the best predictor of viviparous populations of Phyrnosoma, Sceloporus and Plestiodon in North America. However, there is an absence of studies on the thermal susceptibility of the young, but we assume that because of their small size, they could be more susceptible than adults to overheating and dehydration, meaning that the temperature and humidity range of their activity period should be lower, which would be a limitation for the establishment of populations in certain areas, although these zones have conditions within the limits of tolerance for adults. It would be necessary to carry out studies on thermoregulation and locomotor performance of young and sub-adults to determine the role that these stages would have in the establishment of populations. Likewise, Mean Temperature of Wettest Quarter (Bio8) could be related to ovary cycle, because vitellogenesis in species of this group has been reported to occur throughout the spring and fall (Guillette & Méndez-de la Cruz 1993; Méndez-de la Cruz et al., 1998; Feria-Ortiz et al., 2001; Villagrán-Santa Cruz et al., 2009), which is the wettest period in almost all distribution areas of the group, and is linked with the abundance of food necessary for the accumulation of yolk proteins in follicles (Feria-Ortiz et al., 2001). The ovary cycle is highly conservative at different altitudes in many Sceloporus species; nevertheless, the testicular cycle is not conservative and shows shifts related to altitude (Villagrán-Santa Cruz et al., 2009), and is possibly linked to the temperature needed for the proper development of testicles, accessory sexual structures, and sperm maturation (Pearson, et al., 1976; Van Damme et al., 1987; Villagrán-Santa Cruz, et al., 1994). Therefore, the variation
and plasticity in reproduction cycles needs to be evaluated, especially in males, in order to
determinate the climatic requirements and the importance in the distribution of the species.
Likewise, the Mean Diurnal Range (Bio2) and Precipitation Seasonality (Bio15) has been
reported with a high relevance in the evolution of climatic niches in squamata reptiles (Pie et
al., 2017). Probably, this result is due to these bioclimatic layers reflecting the extreme
conditions of both temperature and humidity, and it has been pointed out that extreme
climatic conditions could determine the range limits of species (Sexton et al., 2009).

Mode and tempo in the evolution of ecological niche of *torquatus* group

Our analyses show a moderate to high niche divergence with no PNC in the ecological niche
models of the *torquatus* group species, and only two bioclimatic variables show weak evidence
of conservatism (Bio15 and Bio19). In general, the lack of PS and poor fit to the BM model in
almost all bioclimatic variables and ecological niches suggest that the evolution of habitat
preferences or requirements evolve quickly, causing the inability to detect PS and the absence
of PNC. The above is sustained by the changes in rate evolution showing a high heterotachy
among almost all bioclimatic variables, as demonstrated in DTT plots. Probably, the changes in
the rate of trait evolution masked the PS, which coincides with the high heterotachy detected in
the squamata phylogeny and the poor statistical fit to BM in the niche evolution of many
reptiles (Pie et al., 2017). With regard to Bio15 (Precipitation Seasonality) and Bio19
(Precipitation of Coldest Quarter), these bioclimatic variables possibly highlight the importance
of the extreme conditions in precipitation for the *torquatus* group and for squamata in general
(Pie et al., 2017), because these are a measure of the variability and amount (in reproduction
season) of rainfall in a locality (http://www.worldclim.org). Also, although this species occurs in
sites with different levels of annual precipitation, the precipitation is concentrated in the same
season (Willmott & Matsuura, 2001; http://www.worldclim.org). The single optimum OU
model of evolution for Bio19 could be interpreted as evidence of stabilizing selection (Hansen,
1997), although some authors do not recommend the use of this term to refer to the evolution
around an optimal value (Cooper et al., 2017). We have to be careful in affirming that a single
The optimum OU process is the best model for Bio19, since the multiple-optima OU analyses fail because of the size of the sample. We think that the narrow overall breadth of the PNO profile for Bio19, which is indicative of similar levels of tolerance for all species of the group, is indirect evidence of a single optimum OU process. This is the only bioclimatic variable that is directly linked to the fall-winter reproductive cycle that seems to be conserved, and for what almost all species of this group have similar requires. Surprisingly, we expect that bioclimatic layers linked with temperature could have PS and PNC, as temperature during breeding season is the principal factor to estimate the extinction probabilities by global warming in lizards (Sinervo, et al., 2010). It is possible that the great amount of species in the group have not been thoroughly explored throughout the entire climatic space that could be occupied, or that microclimatic conditions in refuges could probably be more important for these species, as long as hours of restriction (hours in refuges to avoid overheating) in the reproductive season remains < 4 (Sinervo et al., 2010); also, Bio15 and Bio19 remain between certain limits. For example, S. serrifer, which despite having preferred temperatures similar to other species of the group, occurs in different habitats, but is only present in Yucatan peninsula where there are some kinds of trees or artificial refuges, like walls and rock fences, which provide suitable thermal conditions to spend night and hours of restriction (Martínez-Méndez et al., 20015). Thus, we think that the microclimate in refuges and thermoregulatory behavior could allow this species to explore beyond typical montane sites and contribute to the no PNC detection in bioclimatic variables linked with temperature. In this sense, extensive ecophysiological, phylogeographic and thermal ecology studies on the species of the group remains necessary, in order to determine its fundamental niche and its thermal requirements, and to measure the effect of biotic interactions and historic factors in its distribution.

The low niche overlap values between sister species could be an additional indicator of no niche conservatism, in contrast to the results of Warren et al. (2008), who found moderate and high niche overlap and conservatism in many sister species of butterflies, birds and mammals in Mexico. The low niche overlap values in the torquatus group is not an exception; for example, some studies with freshwater fishes of North America and Mexico show that some clades present high niche overlap and conservatism, while others shows high niche diversification and
low niche overlap (McNyset, 2009; Culumber & Tobler, 2016). There is similar evidence that
sister species of tropical plethodontids salamanders tend to have divergent climatic niches
compared to temperate sister species (Kozak & Wiens 2007). Some studies have highlighted the
importance not only of the niche overlap in the understanding of diversification but also the
sympatry and range overlap of sister or closely related species, because some models of
speciation consider competition for resources to drive sympatric speciation, and ecological
differentiation to arise to prevent competition (Rundle & Nosil, 2005; Nosil, 2012).
Complementarily, many events of allopatric speciation are not associated with ecological
divergence, which can lead to a signal of niche conservatism (Peterson, 2011). According to
Losos (2008), it is necessary to carefully identify niche similitudes as PNC, because conservatism
emerges in this case as a side result of a historic process where no related species share the
same geographic range. In this sense, some evidence supports the ecological differentiation in
sympatric speciation (Bush & Smith, 1998), whereas other studies underestimate its role, even
finding that the geographic overlap between clades in some species restricts diversification
(Kozak & Wiens 2010). Future studies should focus on whether the interaction with other
species of lizards could influence the evolution of the niche of these species. On the other hand,
in agreement with the general pattern found when analyzing the individual layers, the absence
of significant correlation between niche overlap at internal nodes and divergence time in the
Arc-Range Correlation (ARC) analyses is an indication of the absence of PS in the niche
evolution of the torquatus group, at least with the layers used to build the ecological niche, and
is also evidence that climatic niche differentiation (ecological divergence) was not the main
factor in the diversification of the torquatus group.

The Predicted Niche Occupancy (PNOs) profiles shows a high heterogeneity in the levels of
climatic tolerance, which indicates radiation over the spectrum of the ecological space
represented for the bioclimatic variables that were analyzed. Nevertheless, there were some
overlapping peaks indicating similar tolerances in some species, although similar tolerances are
not shared for the same species in each bioclimatic variable, and no sister species share similar
tolerances in all cases, except for Bio19, which is linked with the fall-winter reproductive cycle.
The most different tolerances in PNO profiles were observed in S. serrifer, which can be
explained by the fact that this species occurs in habitats ranging from highlands to almost the
sea level. Accordingly, the PNO profiles suggest distinct ecological preferences and some
degree of ecological differentiation between most of the species without groups of sister
species sharing the same ecological niche, as confirmed by pPCA analyses.

The plots of the history of evolution of climatic tolerances show that only some species have
some grade of convergent climatic origins for a number of bioclimatic variables, with most of
the species showing different magnitudes of divergent evolution. Also, the rate of change in
climatic tolerances through the time is different between species for each bioclimatic variable.
For example, Bio19 shows the lowest magnitude of final divergence between the species of the
group, except for the clade formed by S. serrifer and S. prezygus. This pattern suggests the lack
of niche conservatism for a long period of time. The analysis of relative Disparity Through Time
(DTT) and MDI values indicates that the ecological disparity tends to be distributed within
subclades rather than between subclades, with high divergence in recent nodes. The rapid
accumulation of ecological diversity has come about in the last 6.6 MYA, concentrating at
around 4.0 MYA and 0.65 MYA. The first peak seems to coincide with the high diversification
rate in different groups of organisms that occurred during the Pliocene-Pleistocene epochs in
America (Graham, 1999; Morrone, 2010; Bryson & Riddle, 2012; Licona-Vera & Ornelas, 2017),
which was attributed to orogenic processes that produced vicariant barriers like mountains,
rivers etc., and climatic changes (Bryson and Riddle, 2012; Mastretta-Yanes, et al., 2015). The
second peak coincides with the Pre-Illinoian glacial period around 0.62-0.67 MYA (Rutter et al.,
2012).

Thereby, the evidence of a lack of niche conservatism, and the recent accumulation of
ecological diversity could be associated with the possible geographic and climatic isolation
throughout speciation, which could promote the rapid accumulation of ecological differences
between species of the group (Culumber & Tobler, 2016). This pattern coincides with the
results of Pie et al. (2017), who found an extensive rate of heterogeneity in climatic niche
evolution of squamates with shifts involving accelerations concentrated in its recent
evolutionary history.
CONCLUSIONS

Our results indicate a lack of PNC in the niche evolution of *torquatus* group with the possible exception of two bioclimatic variables, and only one linked with viviparity. This is evidence that possible constraints associated with viviparity are not sufficient to explain the niche evolution of the group. Even though most of the layers used to build the actual niche of the group could be linked with viviparous reproduction, the species have evolved quite different tolerances to them, with the exception of Bio19. However, the availability of new climatically heterogeneous territories with the subsequent filling of that new environmental niche, and posterior cycles of isolation during orogenic and glacial periods, could build the pattern we observed. Nevertheless, as we pointed out, the physiology required and the use of refuges needs to be evaluated to elucidate the most accurate niche evolution of the group.

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DATA AVAILABILITY

The following information was supplied regarding data availability: The Ecological niche models of the species of *Sceloporus torquatus* group were supplied as Figure S1. Phylogenetic trees showing the position of adaptive shifts under reversible-jump Bayesian method implemented in bayou were supplied as Figure S2. GenBank accession numbers were supplied as Table S1. Occurrence data were supplied as XLSX archive as Table S2. Model parameters estimated for Brownian Motion (BM), Ornstein-Uhlenbeck (OU), Early Burst (EB) and Pagel’s delta (δ) for each bioclimatic variable were supplied as Table S3, and Model parameters estimated for bayou analyses were supplied as Table S4.
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Table 1 (on next page)

Results of tests for phylogenetic signal of bioclimatic variables used in the study by means of Blomberg’s K (K) and Pagel’s lambda (λ) values.
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<td></td>
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<td>p</td>
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<td>logL</td>
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Table 2 (on next page)

Performance of alternative evolution models for each bioclimatic variable.

The differences between the model with lower AICc and the rest of the models are indicated with fallow abbreviations: e equivalent models; * more or less distinguishable models; ** distinguishable models; and *** different models.
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<th>Bioclimatic layer</th>
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<td>Average maximum temperature in January (Tmax1)</td>
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<td>BM</td>
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<td>EB</td>
<td>-117.7130</td>
<td>242.6892</td>
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Pairwise comparisons of niche overlap indices in terms of Schoener’s $D$ and Warren’s $I$.

The upper triangle contains values of $D$ and lower triangle contains values of $I$. 
<table>
<thead>
<tr>
<th>ID</th>
<th>Species</th>
<th>ID</th>
<th>Species</th>
<th>ID</th>
</tr>
</thead>
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<tr>
<td>1</td>
<td><em>Sceloporus aureolus</em></td>
<td>0</td>
<td>0.146 0.321 0.060 0.098 0.195 0.351 0.303 0.139 0.131 0.476 0.117 0.290 0.101 0.002 0.443 0.157 0.407 0.368</td>
<td></td>
</tr>
<tr>
<td>2</td>
<td><em>Sceloporus binocularis</em></td>
<td>0.341</td>
<td>NA 0.184 0.262 0.577 0.325 0.118 0.179 0.158 0.252 0.362 0.234 0.731 0.073 0.477 0.032 0.137 0.118 0.186 0.256</td>
<td></td>
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<tr>
<td>3</td>
<td><em>Sceloporus bulleri</em></td>
<td>0.613</td>
<td>0.427 NA 0.077 0.085 0.112 0.432 0.594 0.122 0.286 0.192 0.313 0.145 0.310 0.128 0.007 0.200 0.130 0.370 0.326</td>
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</tr>
<tr>
<td>4</td>
<td><em>Sceloporus ornatus caeruleus</em></td>
<td>0.175</td>
<td>0.567 NA 0.219 0.264 0.670 0.083 0.142 0.226 0.167 0.158 0.103 0.221 0.033 0.611 0.069 0.056 0.033 0.101 0.111</td>
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</tr>
<tr>
<td>5</td>
<td><em>Sceloporus cyanogenys</em></td>
<td>0.168</td>
<td>0.838 0.253 0.518 NA 0.269 0.065 0.089 0.099 0.178 0.266 0.118 0.533 0.019 0.427 0.005 0.060 0.061 0.081 0.140</td>
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</tr>
<tr>
<td>6</td>
<td><em>Sceloporus cyanostictus</em></td>
<td>0.237</td>
<td>0.614 0.273 0.907 0.553 NA 0.100 0.210 0.232 0.155 0.134 0.116 0.287 0.074 0.069 0.083 0.045 0.160 0.114</td>
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</tr>
<tr>
<td>7</td>
<td><em>Sceloporus dugesii</em></td>
<td>0.452</td>
<td>0.325 0.735 0.236 0.202 0.264 NA 0.432 0.060 0.376 0.175 0.233 0.086 0.198 0.103 0.002 0.081 0.047 0.261 0.294</td>
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<tr>
<td>8</td>
<td><em>Sceloporus insignis</em></td>
<td>0.638</td>
<td>0.415 0.856 0.327 0.233 0.399 0.745 NA 0.116 0.362 0.209 0.289 0.135 0.395 0.180 0.004 0.246 0.117 0.515 0.324</td>
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<tr>
<td>9</td>
<td><em>Sceloporus jarrovii</em></td>
<td>0.159</td>
<td>0.397 0.320 0.458 0.288 0.452 0.185 0.294 NA 0.135 0.097 0.057 0.123 0.017 0.174 0.204 0.026 0.020 0.106 0.055</td>
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<tr>
<td>10</td>
<td><em>Sceloporus melanogaster</em></td>
<td>0.414</td>
<td>0.545 0.572 0.402 0.384 0.403 0.674 0.669 0.366 NA 0.500 0.269 0.198 0.100 0.209 0.007 0.084 0.038 0.285 0.460</td>
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<tr>
<td>11</td>
<td><em>Sceloporus minor</em></td>
<td>0.349</td>
<td>0.645 0.425 0.405 0.536 0.380 0.429 0.468 0.290 0.784 NA 0.288 0.298 0.054 0.215 0.005 0.078 0.063 0.190 0.489</td>
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<tr>
<td>12</td>
<td><em>Sceloporus mucronatus</em></td>
<td>0.768</td>
<td>0.485 0.605 0.307 0.298 0.318 0.507 0.583 0.258 0.558 0.567 NA 0.180 0.154 0.147 0.010 0.242 0.102 0.453 0.621</td>
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<tr>
<td>13</td>
<td><em>Sceloporus oberon</em></td>
<td>0.292</td>
<td>0.937 0.363 0.510 0.820 0.565 0.254 0.341 0.332 0.478 0.582 0.417 NA 0.050 0.438 0.020 0.135 0.130 0.140 0.199</td>
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<tr>
<td>14</td>
<td><em>Sceloporus omitteanus</em></td>
<td>0.576</td>
<td>0.207 0.586 0.107 0.068 0.187 0.458 0.671 0.090 0.273 0.138 0.356 0.158 NA 0.058 0.001 0.252 0.069 0.378 0.158</td>
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<tr>
<td>15</td>
<td><em>Sceloporus ornatus ornatus</em></td>
<td>0.273</td>
<td>0.788 0.323 0.855 0.717 0.894 0.272 0.386 0.428 0.445 0.495 0.386 0.753 0.178 NA 0.056 0.102 0.082 0.128 0.152</td>
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<tr>
<td>16</td>
<td><em>Sceloporus poinsettii</em></td>
<td>0.013</td>
<td>0.121 0.033 0.190 0.036 0.201 0.008 0.018 0.475 0.053 0.048 0.064 0.091 0.003 0.187 NA 0.001 0.001 0.008 0.009</td>
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<tr>
<td>17</td>
<td><em>Sceloporus prezygus</em></td>
<td>0.759</td>
<td>0.341 0.448 0.156 0.177 0.205 0.233 0.499 0.130 0.294 0.269 0.534 0.321 0.514 0.276 0.016 NA 0.222 0.280 0.167</td>
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<tr>
<td>18</td>
<td><em>Sceloporus serrifer</em></td>
<td>0.351</td>
<td>0.309 0.348 0.105 0.198 0.128 0.161 0.271 0.087 0.174 0.234 0.324 0.340 0.190 0.245 0.005 0.496 NA 0.085 0.062</td>
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</tr>
<tr>
<td>19</td>
<td><em>Sceloporus sugillatus</em></td>
<td>0.673</td>
<td>0.431 0.642 0.278 0.220 0.352 0.539 0.785 0.280 0.581 0.425 0.702 0.358 0.659 0.335 0.042 0.533 0.208 NA 0.425</td>
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</tr>
<tr>
<td>20</td>
<td><em>Sceloporus torquatus</em></td>
<td>0.642</td>
<td>0.532 0.602 0.321 0.349 0.337 0.585 0.607 0.236 0.723 0.745 0.847 0.463 0.357 0.406 0.068 0.415 0.220 0.668 NA</td>
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</table>
Table 4 (on next page)

Morphological disparity index (MDIs) for total phylogeny and for former *poinsettii* and *torquatus* clades.

The morphological disparity index (MDI) value represent the overall difference in disparity between the observed and the unconstrained null hypothesis, MDIs > 0 indicate niche evolution and MDIs < 0 indicate niche conservatism.
<table>
<thead>
<tr>
<th>Bioclimatic layer</th>
<th>MDI value</th>
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<td>Total tree</td>
<td><em>torquatus</em></td>
<td><em>poinsettii</em></td>
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<tr>
<td></td>
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<td>Clade</td>
<td>Clade</td>
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<td>Mean Diurnal Range (Bio2)</td>
<td>0.177</td>
<td>0.062</td>
<td>0.165</td>
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<td>Max Temperature of Warmest Month (Bio5)</td>
<td>0.445</td>
<td>0.253</td>
<td>0.425</td>
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<td>Mean Temperature of Wettest Quarter (Bio8)</td>
<td>0.365</td>
<td>0.390</td>
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<td>Mean Temperature of Driest Quarter (Bio9)</td>
<td>0.331</td>
<td>0.283</td>
<td>0.256</td>
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<td>Precipitation Seasonality (Bio15)</td>
<td>0.199</td>
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<td>0.069</td>
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<td>Precipitation of Warmest Quarter (Bio18)</td>
<td>0.198</td>
<td>0.420</td>
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<td>Precipitation of Coldest Quarter (Bio19)</td>
<td>0.299</td>
<td>0.187</td>
<td>0.269</td>
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<tr>
<td>Average Potential Evapo-Transpiration in May (PET5)</td>
<td>0.151</td>
<td>0.032</td>
<td>0.090</td>
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<tr>
<td>Average precipitation in May (Prec5)</td>
<td>0.141</td>
<td>0.149</td>
<td>0.159</td>
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<tr>
<td>Average precipitation in October (Prec10)</td>
<td>0.027</td>
<td>-0.119</td>
<td>-0.010</td>
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<tr>
<td>Average maximum temperature in January (Tmax1)</td>
<td>0.157</td>
<td>-0.080</td>
<td>0.140</td>
</tr>
</tbody>
</table>
Figure 1 (on next page)

Phylogenetic tree of *Sceloporus torquatus* group from Bayesian analysis of combined nuclear and mitochondrial DNA sequences.

Nodes with posterior probability values ≥ 0.5 and bootstrap values ≥ 50% are shown.
Figure 2 (on next page)

Current distribution and ultrametric time calibrated tree of species of the *Sceloporus torquatus* group.

(a) For illustrative purposes only, we show the ecological niche of the *Sceloporus torquatus* group constructed with all species records using the same layers used for the analyses of each species. Darker colors indicate higher environmental suitability, and colored dots in the map show the localities for each species before the final debugging (to get localities in distinct grids and without climatic outliers); also, each color corresponds with the same species in the calibrated tree. (b) Ultrametric time calibrated tree of *S. torquatus* group.
Notched boxplots for niche overlap indices in terms of Schoener’s \( D \) (D) and Warren’s \( I \) (I) for the former clades *torquatus* (red) and *poinsettii* (blue), and for total tree (brown).

The indices vary between 0 (no overlap) to 1 (complete overlap). Boxes delimit interquartile ranges (25\(^{th}\) and 75\(^{th}\) percentiles) around the median, whiskers delimit \( \approx 2 \) standard deviations, dotted line indicated maximum and minimum values, and the outliers are represented with circles. Each notch represents the confidence interval of 95\% for the median, and lack of overlap between notches is evidence of significant differences between medians.
**Figure 4** (on next page)

Linear regression of the age-range correlation (ARC).

Abscissa axis corresponds with node age and ordinate axis with Warren’s I niche overlap index. Blue lines correspond with regression lines from Monte Carlo randomization.
F-statistic = 0.1615
R-sq = 0.0159
Adj R-Sq = -0.08251
p-value = 0.6962
Figure 5 (on next page)

Predicted niche occupancy (PNO) profiles for *Sceloporus torquatus* species group.

Horizontal axes represent the bioclimatic variable parameter and vertical axes indicate the total suitability of the bioclimatic variable index for each species over its geographic distribution. Overlapping peaks indicate similar climatic tolerances, and the breadth of the profile indicates the climatic tolerance specificity. Species names consisting of the four letters of the species epithets, except for *Sceloporus ornatus caeruleos* (caeru).
History of evolution of climatic tolerances for *Sceloporus torquatus* species group.

The chronogram topology of the group is projected into niche parameter space (y-axis), and mean climatic tolerances based on 100 random samples of the PNO profiles are represented at internal nodes. Crossing branches of the phylogenetic tree indicate convergent niche evolution among taxa from different clades, and overlapping internal nodes indicate convergent climatic origins. A vertical dashed line indicates the 80% central density of climate tolerance for each species, and the point of the same color indicates the mean. Species names consist of the first three or four letters of the species epithets.
Plots of accumulation of relative disparity through time (DTT) for climatic tolerances in the *Sceloporus torquatus* species group.

The plot summarizes the distribution of the relative disparity through time (solid line) compared with mean disparity as simulated under 1000 replicates of an unconstrained model of Brownian Evolution (dashed line).