Climatic niche evolution in the viviparous *Sceloporus torquatus* group (Squamata: Phrynosomatidae).

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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.

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1 **Background**

2 The actual distribution of species has been explained as the interaction of historical processes

3 such as vicariance and dispersal, and shallow time processes that include ecological factors,

4 such as habitat filtering, biotic interactions like competition or predation, and niche partitioning

5 (Sexton *et al.* 2009; Nyári & Reddy, 2013). We refer to the niche or ecological niche of the

6 species to be those biotic and abiotic variables that allow the persistence of populations

7 (Hutchinson, 1957). At the same time, ecological components are important for speciation

8 process, as reproductive isolation could appear by the evolution of barriers to gene flow due to

9 divergent natural selection (Mayr, 1947; Pavey *et al.*, 2010; Nosil, 2012). This kind of speciation

10 implies changes in the ecological niche, but ecological niches are multidimensional, and it is

11 unlikely that every dimension evolves in the same way (Schluter, 1996; Ackerly, 2003; Duran *et*

12 *al*., 2013). There are other cases where the reproductive isolation is conditioned by a

13 combination of ecological constraints and a vicariance process (*e.g.* geographic barriers), where

14 species could retain some ancestral requirements that limit the adaptation to the climatic

15 conditions imposed by the barrier (Wiens & Graham, 2005). The tendency of related species to

16 retain their ancestral requirements or niches through time is described as Phylogenetic Niche

17 Conservatism (PNC) (Boucher *et al.*, 2014), and has been commonly studied by measuring the

18 Phylogenetic Signal (PS). PS is the tendency for related species to resemble each other more

19 than they resemble species drawn at random from the phylogenetic tree (Blomberg & Garland

20 2002), and for some authors, this is enough to verify PNC (Wiens *et al.,* 2010b). However, some

21 revisions have highlighted the theoretical problems with the PNC concept and the practical

22 difficulties related to how to measure it (Revell *et al*., 2008; Münkemüller *et al*., 2015). Some

23 authors argue that PNC is a process and some that is a pattern, while other researchers argue

24 that PNC can be either a process or a pattern depending on how the research questions are

25 raised (Losos, 2008; Wiens *et al.,* 2010b). Additionally, the concept of PNC by itself cannot

26 explain anything but can result from several processes (i.e. genetic constraints or stabilizing

27 selection) (Losos, 2008); however, some authors argue that a combination or interaction

28 between niche evolution and niche conservatism shape the biogeographic patterns observed in

29 many species (Wiens & Donoghue, 2004), as well as the functional diversification of lineages

30   and niche similarity of phylogenetically related species (Culumber & Tobler, 2016).

31   Nevertheless, the relationship of some constraints or shared biases in the production of

32   phenotypic variability with niche evolution is barley known (Maynard Smith *et al.,* 1985). Similar

33   correlated responses are expected in organisms that share similar constraints; thereby, the

34   interaction of this constraints and natural selection produce phenotype-environment

35   correlations (Losos, 2011). In this regard, the viviparity among reptiles has been linked to cold

36   climates, because it provides a selective advantage that prevents the death of embryos in the

37   nest caused by low temperatures (Tinkle & Gibbons, 1977; Shine, 1985; Lambert & Wiens,

38   2013), and could be considered a phylogenetic constraint (Tinkle & Gibbons, 1977; Uller, 2003).

39   For example, there is evidence that viviparity among phrynosomatid lizards constrained some

40   life-history traits (Zúñiga-Vega *et al.*, 2016). Thus, we expected that viviparous species share

41   environmental affinities that could lead to a stabilized selection and, as a consequence, show

42   PNC, at least in some characteristics linked with breeding season, and for instance with cold

43   environments.

44   The viviparity among squamata (lizards and snakes) has evolved from oviparity around 100

45   times (Blackburn, 2000; 2015) and has been a model system for testing many evolutionary

46   hypotheses about the origin of viviparity between vertebrates (Lambert & Wiens, 2013). A

47   group of lizards suitable for evolutionary studies about niche evolution and viviparity is the

48   genus *Scelopurus,* which is widely distributed in North America and contains around 70

49   viviparous species distributed in five groups (Wiens & Reeder, 1997; Méndez-de la Cruz *et al*.,

50   1998), and for which there is molecular and phylogenetic information for almost all recognized

51   species along with a wide occurrence database (Wiens & Reeder, 1997; Leaché, 2010; Wiens *et*

52   *al*., 2010a; Leaché *et al.,* 2016).

53   We assume that given the hypothesis about the development of viviparity in reptiles being

54   linked with low temperatures, this could constrain the niche evolution between viviparous

55   species. In this study, using the viviparous *Sceloporus torquatus* group as model organisms, we

56   aim to: (1) assess whether niche evolution is phylogenetically constrained between viviparous

57   species of the group, (2) test whether similarities in environmental tolerances between species

58   and the phylogenetic relationship predicts PNC; and (3) test whether most important

59   bioclimatic variables used as niche descriptors show PNC.

60   The *torquatus* group (Smith, 1938) is distributed from the southern United States southward

61   into Guatemala (Martínez-Méndez & Méndez de la Cruz, 2007). Throughout its distribution, the

62   group occurs in mountain ranges with temperate conditions, but also in semi-desert and

63   tropical environments (e.g. *S. serrifer*). The group is diagnosed by a series of osteological and

64   scutelation (meristic) characters, but perhaps its main external characteristic is the nuchal collar

65   formed for dark scales lined with lighter or white scales (Smith, 1938; 1939; Wiens & Reeder

66   1997), with sizes that ranges from 56 mm in SVL (snout-vent length) to 130 mm in SVL (field

67   notes of NMM). The great amount of the species of the group have saxicolous habits with the

68   exception of some populations of *S. serrifer* in Usumacinta basin and in Yucatan peninsula; in

69   this last, the species can toggle between boulders and only certain species of tropical trees

70   (field observations of NMM). There is evidence that population demography could influence

71   the climatic niche evolution of the species (Jakob *et al.*, 2010), and in turn body size can

72   influence the demography of the species (Sibly & Brown, 2007; Fernández-Chacón *et al.,* 2015).

73   For this reason, and in order to avoid additional confounding factors, we focused only in

74   *torquatus* group analyses without including *grammicus* and *megalepidurus* groups (which are

75   its viviparous sister groups), because the differences in sizes and habits between them could be

76   high. The species of the *grammicus* group have a maximum SVL of around 76 mm and have

77   primary arboreal habits, although the organism can inhabit cracks in rocks in many populations

78   and even can be found in walls and rock fences. On the other hand, the species of

79   *megalepidurus* are smaller, with an SVL of around 55 mm and use agave and yucca leaves as

80   refuges (field notes of NMM). Nonetheless, in a future study of niche evolution, we will include

81   these two additional groups along with data on size, habits and specific thermal preferences.

82   To achieve the stated objectives, we constructed a phylogeny of the group and used a

83   phyloclimatic analysis that implies the use of occurrence data and bioclimatic information in a

84   phylogenetic comparative context to: (1) evaluate the phylogenetic signal of the species'

85   ecological niche and the bioclimatic variables used to construct it, (2) fit macroevolutionary

86   models for the most important bioclimatic variables for the group, (3) investigate the history of

87   ecological niche occupancy and accumulation, (4) investigate ancestral tolerances, and (5)

88   calculate the niche disparity through time.

89

90   **MATERIALS AND METHODS**

91   Data sources

92   Occurrence data were obtained from The Global Biodiversity Information Facility (GBIF;

93   http://www.gbif.org/), HERPENET (http://www.herpnet.org), Comisión Nacional para el

94   Conocimiento y Uso de la Biodiversidad (CONABIO; https://www.gob.mx/conabio) and field

95   notes of main author. We removed occurrence records that constituted misidentifications,

96   mistakes on coordinates (i.e. points on the sea) and with similar coordinates. To minimize

97   spatial autocorrelation, we randomly removed occurrences within 0.5 km of each other in order

98   to obtain localities in distinct grids to match the spatial resolution of environmental layers (30

99   arc second). For environmental layers, we used bioclim layers at a 30 arc second resolution (1

100   km x 1 km) and monthly and annual maximum and minimum temperatures and precipitation

101   levels available from the WorldClim database 1.4 (http://www. worldclim.org), as well monthly

102   and annual potential evapotranspiration (PET) and aridity available from http://www.cgiar-

103   csi.org/data/global-aridity-and-pet-database (Zomer *et al*., 2008). All layers were clipped to the

104   general limits species' group distribution.

105   Ecological niche modeling

106   Because of the large number of layers, we performed a preliminary analysis with MaxEnt v.3.4.1

107   (Phillips *et al.* 2006; Phillips & Dudik 2008) for all species using all layers and using default

108   settings with a cloglog output. Using a jackknife test implemented in MaxEnt, we chose only

109   those variables with high relative importance (10 for each species). In order to avoid collinearity

110   and model overfitting, we extracted the environmental information for each grid cell from this

111   reduced set of layers to perform a Pearson correlation. We retained only layers with low

112   correlation (r < 0.75), and in the case of highly correlated variables, we chose, wherever was

113   possible, the layers that measured extreme conditions as they condition the range limits of

114   species (Sexton *et al.*, 2009), and also the most biologically meaningful layers according to the

115   biology of this group of species. This species-group has a fall-winter reproduction cycle, with

116   relationship between local extinctions and the increase in temperatures by global warming in

117   the reproductive season (Sinervo *et al*. 2010). The most evident layers with a biological

118   meaning for this species-group were those related to the fall and winter, which is the driest and

119   coldest season for almost the entire distribution range of studied species. Finally, we chose 11

120   layers: Max Temperature of Warmest Month (Bio5), Mean Diurnal Range (Bio2), Mean

121   Temperature of Wettest Quarter (Bio8), Mean Temperature of Driest Quarter (Bio9),

122   Precipitation Seasonality (Bio15), Precipitation of Warmest Quarter (Bio18), Precipitation of

123   Coldest Quarter (Bio19), Average Potential Evapotranspiration in May (PET5), Average

124   precipitation in May (Prec5), Average precipitation in October (Prec10), and Average maximum

125   temperature in January (Tmax1). The clip of layers, the extraction of climatic information and

126   Pearson correlation were performed using R (R Core Team, 2017) and Raster library (Hijmans,

127   2017).

128   The final MaxEnt analysis for each species was performed using default settings with cloglog

129   output and 10 replicate runs using different random seeds with 80% of the localities for model

130   training and 20% for model testing. For statistical evaluation, we used threshold-independent

131   receiver operating characteristic (ROC) analyses (Phillips *et al.*, 2006), where we examined the

132   area under ROC curve (AUC) across the 10 replicates and considered a mean AUC value ≥ 0.7 as

133   evidence that the model had discriminatory ability that was better than random (Swets, 1988;

134   Peterson *et al.*, 2011). Because ROC analyses in theory must be used with true absences and

135   not with pseudo-absences or background points, like that used in MaxEnt and weighed up as

136   the same errors of omission and commission (Lobo *et al.*, 2007), we additionally did partial ROC

137   analyses (Peterson *et al.*, 2008) that account for a user-defined maximum acceptable error of

138   omission. We performed partial ROC analyses with *Tool for Partial-ROC* (Narayani, 2008) using

139   50% of the evaluation points resampled in 1000 bootstrap runs and with a fixed error of

140   commission ≤ 5% (*1-omission threshold* > 0.95). Then, a Z test was achieved to determine

141   whether partial AUC proportions were better than random (AUC = 1.0).

142   Phylogeny of *Sceloporus torquatus* group

143   Leaché *et al.* (2016) estimated a phylogenomic tree of *Sceloporus* genus confirming the

144   monophyly of *torquatus* group in relation to *megalepidurus* group by resolving some taxonomic

145   inconsistencies due to fewer loci being used in previous studies and rapid radiations of some

146   groups of species (Leaché, 2010; Wiens *et al.*, 2010); unfortunately, they only included 15

147   species and probably misidentified two species. The specimen UTAR 39870 referred to *S.*

148   *serrifer* from south Texas, which is recuperated like sister species of *S. cyanogenys* in the

149   phylogenomic tree of Leaché *et al*. (2016). According to Martínez-Méndez & Méndez de la Cruz

150   (2007), this corresponds to *S. cyanogenys,* with no close relationship with *S. serrifer* populations

151   from Guatemala and the Yucatan peninsula in Mexico. Likewise, specimen UWBM 6636,

152   identified as *S. mucronatus,* is probably *S. omiltemanus* because the organism was collected

153   around ten kilometers east of the typical locality (Smith, 1939) and there is evidence that this

154   species does not have a close phylogenetic relationship with *S. mucronatus* (Martínez-Méndez

155   & Méndez de la Cruz, 2007).

156   In order to estimate the phylogeny of the *Sceloporus torquatus* group and include the

157   maximum amount of species, we decided to use sequences for four mitochondrial genes (12S,

158   16S, Nd4, and ND1), and four nuclear genes (RAG1, BDNF, R35, and, PNN) that were retrieved

159   from GenBank (Table S1) from the 23 species recognized for the group, including a new species

160   (MX14-4) from central west Mexico and three species of *grammicus* group as the out-group (*S.*

161   *grammicus*, S*. heterolepis* and *S. palaciosi*). As previously highlighted, we used the *grammicus*

162   group, which is the second out-group of *torquatus,* because of problems of monophyly of

163   *torquatus* with respect to *megalepidurus*, its sister group (Leaché, 2010; Wiens *et al.*, 2010a;

164   Leaché *et al.,* 2016).

165   The alignment of each locus was performed using Clustal X ver. 2.1 (Larkin *et al*., 2007); the loci

166   were then concatenated and refined by eye into Mesquite ver. 3.2 (Maddison & Maddison,

167   2017). We considered 21 partitioning schemes: by gene region of 12S, 16S and Nd4-tRNAs, and

168   by codon position of the rest of nuclear and mitochondrial loci. To determine the best

169   substitution model for each data partition we used jModeltest ver. 2 (Darriba *et al.,* 2012)

170   based on the corrected Akaike Information Criterion (AIC). The models with a parameter for

171   invariant sites (I) in addition to among site-heterogeneity (Γ) were not considered because the

172   correlation of these two parameters does not allow its independent optimization (Sullivan *et*

173   *al.,* 1999; Rannala, 2002). Phylogenetics relationships of *torquatus* group were assessed using

174   Maximum Likelihood (ML) and Bayesian inference (BI). ML analysis was performed in RAxML

175   ver. 8.1. (Stamatakis, 2014) using GTA+ Γ, and base frequencies which were estimated and

176   optimized for the partitioning scheme listed above with 1000 non-parametric bootstrap

177   replicates using the rapid-bootstrapping algorithm. BI was performed using MrBayes ver. 3.2.6

178   (Ronquist *et al.*, 2012) with partitioned data using models suggested by jModeltest; when the

179   model was not implemented in MrBayes, we used the nearest and most inclusive model

180   (parameter rich) for analyses. Four Metropolis-coupled MCMC chains were run for 10 million

181   generations with trees sampled every 1000 iterations using default temperatures for chain

182   heating. After a burn-in of 25%, as determined by visualizing posterior distributions of the

183   parameter values in Tracer ver. 1.6 (Rambaut *et al.*, 2014), we generated a 50% majority-rule

184   consensus tree with SumTrees ver. 3.3.1, which is part of the Python library DendroPy

185   (Sukumaran & Holder, 2010). The edition and plot of phylogenetic tree with posterior

186   probabilities and bootstrap proportions was assessed using the package ape (Paradise *et al.,*

187   2004) in R (R Core Team, http://www.r-project.org/) (Fig. 1).

188   In order to get a dated phylogeny for the subsequent phyloclimatic analyses, we used the R

189   package ape (Paradis *et al.,* 2004) to edit the original tree. First, those species excluded from

190   niche analysis were pruned using the *drop.tip* function; then, the tree was made ultrametric

191   and node ages were estimated with a semi-parametric method based on penalized likelihood

192   using the *chronos* function with default settings (fig. 2). We used the divergence between

193   former *torquatus* and *poinsetti* clades (8.24-12.65 MYA) as calibration points obtained from the

194   phylogenomic analysis of Leaché *et al.* (2016), and the divergence between *Sceloporsus serrifer*

195   and *S. prezygus* (1.58-6.35 MYA) obtained from the phylogeographic analysis of Martínez-

196   Méndez *et al.* (2015).

197

198   Phylogenetic signal of climatic variables and testing for Phylogenetic Niche Conservatism

199   Despite the criticisms about PNC following Münkemüller *et al*. (2015), we assumed for

200   simplicity the over-simplification of the reality that species niches can be described by single

201   continuous traits (in this case bioclimatic variables), and adopted two practical positions to

202   investigate the presence of PNC: 1) PS can be used to measure PNC only if the analyzed

203   character evolves under a Brownian motion (BM), namely trait changes along the phylogeny of

204   a group occurs as a random walk with a constant increase of variance and an expected mean

205   equal to zero (Felsenstein, 1985); and 2) if under the exploration of alternative evolutionary

206   models such as the Ornstein-Uhlenbeck (OU) model, where traits evolve to an adaptive

207   optimum (Butler & King, 2004), we obtained support for a single optimum with high selection

208   strength, or under support for the multi-optima OU model we obtained relatively few peak

209   shifts. To achieve the above, first we calculated the environmental mean for the chosen

210   bioclimatic variables for each species using the package phyloclim (Heibl & Calenge, 2015), and

211   then we tested for PS using the package phytools (Revell, 2012) by calculating Blomberg's K (K)

212   (Blomberg *et al*., 2003) with 1000 simulations and Pagel's lambda (λ) (Pagel, 1999) using

213   maximum likelihood. Blomberg's K (K) is a scaled ratio of the variance of the data between

214   species and the mean squared error based on the variance-covariance matrix of the phylogeny

215   under a BM expectation, whose values range from zero to infinity, where K>1 indicates a strong

216   PS with the variance distributed between clades, and K<1 indicates weak PS with variance

217   within clades (Blomberg *et al*., 2003; Münkemüller *et al*., 2012). Pagel's λ is a scaling parameter

218   for the phylogeny that measures the correlation of the observed trait data between species

219   under a BM, whose values ranges from 0 or no correlation to 1 or correlation between species,

220   suggesting that phylogenetic relationships predict well the pattern of trait evolution (BM

221   process), and different degrees of phylogenetic signal are included in 0 < λ < 1 values (Pagel,

222   1999; Münkemüller *et al*., 2012). At the same time, we used the R package Geiger (Harmon *et*

223   *al*., 2008) to tested for four alternative models of trait evolution of bioclimatic layers: (1)

224   Brownian Motion (BM); (2) Ornstein-Uhlenbeck (OU), as we pointed out models with the

225   evolution of a trait around an optimal value (Butler and King 2004), however this should not be

226   interpreted as stabilizing the selection in comparative studies (Cooper *et al.,* 2017); (3) Early

227   Burst (EB) or rapid evolution of a trait followed by stasis (Harmon *et al.,* 2010); and (4) Pagel's

228   delta (δ) (Pagel, 1999), which models changes on rates of evolution through time, where δ < 1 is

229   indicative of a slowdown on the recent evolution of the group and trait evolution is

230   concentrated in the base of the phylogenetic tree, and δ > 1 indicates that recent evolution was

231   fast and trait evolution is concentrated in the tips of the tree. The identification of a best fitting

232   model of evolution was by means of log likelihood and AICc, where the model with the higher

233   log likelihood and lower AICc has the better fit (Hurvich & Tsai, 1989). Additionally, to choose

234   between models, we followed Burnham and Anderson (2002; 2004), who pointed out that

235   models with ΔAIC < 2 (AIC differences) are more or less equivalent; models with ΔAIC within 4-7

236   are distinguishable; and models with ΔAIC > 10 are different. Then, we compared the ΔAIC

237   between the model with lower AICc and the rest of the models and established that: ΔAIC < 2 =

238   *e* (equivalent models); ΔAIC ≥ 2 and < 7 = * (more or less distinguishable models); ΔAIC ≥ 7 and

239   < 10 = ** (distinguishable models); and ΔAIC ≥ 10 = *** (different models). Following the

240   recommendations of Münkemüller *et al*. (2015), the white Noise (WN) model that is equivalent

241   to no phylogenetic signal was not considered, because it has the same pattern of an OU model

242   with strong attraction strength (tends to infinity).

243   We also performed a test under a multiple-optima OU framework to infer location, magnitude

244   and the number of possible adaptive shifts using the R package bayou (Uyeda & Harmon, 2014),

245   which uses a reversible-jump Bayesian method to test for multiple optima. We first established

246   a prior function with a half-Cauchy distribution prior for α and σ^2, a normal prior for θ, a

247   conditional Poisson for the number of shifts and a maximum of one shift per branch. We run

248   two chains for 2×10^6 generations, sampling every 200 steps. After discarding the first 50% of

249   generations as burn in, the convergence was assessed using Gelman and Rubin´s R statistic (R ≤

250   1.1).

251   To explore the presence of PS in patterns of niche overlap (niche evolution), we used the

252   modification of Warren *et al.* (2008) for the age-range correlation (ARC) proposed by Turelli &

253   Fitzpatrick (2006). This method used a linear regression of node age given the niche overlap of

254   the species, where a positive or negative significant correlation is an indication of PS in niche

255   evolution, and can also be used to investigate speciation mode. For this purpose, we calculated

256   the niche overlap by means of Schoener's *D* and Warren's *I* statistics (modification of Hellinger

257   distance *I*), which range from 0 for no overlap to 1 for total overlap (Warren *et al*., 2008). Given

258   that Schoener's *D* makes assumptions about species densities that are probably incorrect if

259   there are significant differences with *I* statistic (*I* tended to yield high values than *D*) (Warren *et*

260   *al*., 2008), we chose Warren's *I* statistic for correlation, and 1000 iterations for a Monte Carlo

261   resampling of overlap matrix was used to determine the significance of the analyses. Niche

262   overlap statistics and ARC analyses were performed using the package phyloclim (Heibl &

263   Calenge, 2015).

264

265   Predicted Niche Occupancy and ancestral tolerances

266   To reconstruct the evolutionary history of niche tolerance or Predicted Niche Occupancy (PNO),

267   we used the methodology of Evans *et al.* (2009). This method relates the distribution of

268   suitability of the Maxent analyses of all species to each bioclimatic variable in order to obtain a

269   unit area histogram of suitability, which represents the tolerance (occupancy) of the species at

270   a given bioclimatic variable (PNOs profiles). Later, the PNOs and pruned phylogenetic tree were

271   used to estimate the ancestral tolerance of nodes to each bioclimatic variable, using 1000

272   random iterations from PNOs profiles and a maximum likelihood method. Additionally, we used

273   the weighted means of PNOs in a phylogenetic Principal Components Analysis (pPCA; Revell,

274   2009) to explore a possible climatic differentiation or geographic association between species

275   and clades; however, this method assumes that all traits evolved under a multivariate BM

276   process (Revell, 2009; Uyeda *et al*., 2015). PNO profiles and ancestral tolerances were

277   calculated using the package phyloclim (Heibl and Calenge, 2015), and pPCA was performed

278   with the package phytools (Revell, 2012).

279   Finally, we used an analysis of relative Disparity Through Time (DTT) (Harmon *et al*. 2003) to

280   explore the time pattern of niche evolution and how the niche disparity is distributed among or

281   within subclades. Here, the disparity is the average of the squared Euclidian distance of

282 weighted mean values of PNOs among all pairs of species (pairwise differences), and relative

283 disparity is the disparity within a clade divided by the disparity of the entire phylogenetic tree.

284 The DTT is calculated as the mean relative disparity of all clades whose ancestral lineages were

285 present in each speciation event. Then, a null or expected DTT distribution is made with

286 simulated data under a BM model of evolution. The expected DTT and observed DTT of each

287 subclade were plotted against divergence times to obtain a DTT plot. The results of DTT

288 analyses were quantified using the morphological disparity index (MDI), which is the difference

289 between the observed and expected DTT. Positive MDI values indicate a disparity distributed

290 within subclades or a recent evolution of the trait with divergence between subclades.

291 Conversely, negatives values indicate a disparity distributed between subclades and early

292 evolution of the trait or conservatism within more deep clades (Evans *et al*., 2009). We present

293 MDIs for total phylogeny and for former *poinsettii* and *torquatus* clades. The DTT analyses were

294 performed using the package geiger (Harmon *et al*., 2008) with 1000 simulations and a

295 confidence level of 0.95.

296

297 **RESULTS**

298 Ecological niche modeling

299 The presence data of *Sceloporus sp*. (MX14-4), *S. lineolateralis*, and *S. macdougalli* were

300 excluded from niche analyses because these species had a reduced amount of useful points

301 after depuration (< 5). For all of the remaining species, the mean AUC scores were > 0.75, which

302 were statistically significant with AUC proportions of partial ROC analyses > 1; then, the

303 ecological niche models (Fig. S1) were considered suitable for use as inputs in the subsequent

304 analyses.

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308   Phylogeny of the *Sceloporus torquatus* group

309   The phylogeny of the *torquatus* group is basically similar to previous studies (Wiens and Reeder,

310   1997; Martínez-Méndez & Méndez de la Cruz, 2007; Leaché *et al*., 2016) with two main clades

311   that correspond to the former *poinsettii* and *torquatus* groups Leaché, 2010; Wiens *et al*.,

312   2010); here, we refer to these two clades as *poinsettii* and *torquatus* clades to avoid confusion

313   with the total *torquatus* group, both of which have strong support (*poinsettii* clade: PP = 1, BSP

314   = 100%; *torquatus* clade: PP = 0.99, BSP = 99%). However, as we pointed out previously, there

315   are some differences between our phylogeny and that of Leaché *et al*. (2016): (1) the probable

316   misidentification of *S. omiltemanus* as *S. mucronatus*, where Wiens & Reeder (1997) and

317   Martínez-Méndez & Méndez de la Cruz (2007) reported the non-monophyly of *S. mucronatus*

318   subspecies, and the last authors proposed that *S. mucronatus omiltemanus* should be elevated

319   to full species status; (2) the consideration of UTAR 39870 from Texas as *S. serrifer*, since

320   according with Martínez-Méndez & Méndez de la Cruz (2007) the populations from Texas and

321   Northeast of Mexico were considered to be *S. serrifer plioporus* for Olson (1987)*,* being

322   synonymized into *S. cyanogenys*; (3) we included the new specimen MX14-4 (*Sceloporus* sp.),

323   which was resolved as a sister species of *S. melanogaster* with a strong support only for

324   Bayesian analyses (PP = 1, BSP < 75%) (Fig. 1).

325

326   Phylogenetic signal of climatic variables and testing for Phylogenetic Niche Conservatism

327   The tests of PS indicated that only Precipitation Seasonality (Bio15) has significant support

328   (Table 1), with a moderate to weak PS and with the variance distributed within clades (K =

329   0.9789271, *p* = 0.003), thereby suggesting a high correlation of the data with a BM process (λ =

330   0.8990152, *p* = 0.009). The above coincides with the test of alternative models of evolution

331   (Table 2), where only Bio15 shows weak support for BM evolution, because the difference

332   between alternative models is just over two (ΔAIC = 2.0003). The other bioclimatic layer that

333   shows a BM evolution with the lower AICc are not distinguishable from other models of

334   evolution or even are equivalent (*i.e*. BM and δ are equivalents in Bio2 and Tmax1). Similarly

335   only Precipitation of Coldest Quarter (Bio19) presents evidence of an OU model of evolution;

336   however, the selection strength is relatively weak (α = 0.597; Table S3). Probably, this implies a

337   weak PNC of the Bio19 variable in the alternative interpretation of Münkemüller *et al*. (2015),

338   where PNC is indicated by relative strong selection strength and one or relatively few adaptive

339   peak shifts. The other bioclimatic layers with OU showing lower values of AICc are not

340   distinguishable from other models. Noteworthy, in all cases, Pagel's delta (δ) was > 1 (Table 2),

341   indicating a tendency in trait evolution to be concentrated in the tips of the tree. Likewise, the

342   multi optima OU method implemented in Bayou fails to correctly detect the location and

343   magnitude of adaptive shifts (Table S4 and Figure S2), because the mean number of shifts was

344   nine (K=9) and parameters are correctly estimated only if the number of shifts is not large (K >

345   25% the number of tips) (Uyeda and Harmon, 2014).

346   Niche overlap values (Fig. 3) are on average low (Schoener's *D* and Warren's *I* statistics < 0.4)

347   for all species and for *torquatus* and *poinsettii* clades. Similarly, only a few pairs of species show

348   moderate-to-high values (Table 3), such as *Sceloporus cyanstitctus vs*. *S. ornatus caeruleus*

349   (Warren's *I* = 0.907). However, none of these are sister or close relative species with the

350   exception of the small clade formed by *S. cyanogenys* + (*S. oberon* + *S. ornatus ornatus*), which

351   shows values of Warren's *I* statistics ranging from 0.753 to 0.894. The arc-range correlation

352   (ARC) shows no significant correlation between niche overlap at internal nodes and divergence

353   time (Fig. 4), and fails to detect PS in niche evolution in all the bioclimatic layer used, which is

354   consistent with the lack of PS for almost all of the bioclimatic layers individually tested, except

355   for Bio15.

356

357   Predicted Niche Occupancy and ancestral tolerances

358   The PNO profiles (Fig. 5) show a high heterogeneity in some bioclimatic variables, with species

359   occupying different sections of parameter space and with different levels of specificity in

360   climatic tolerance, as denoted by the breadths of the profiles. However, some overlapping

361   peaks that indicate similar climatic tolerance between few species are found in all bioclimatic

362   layers, but are especially important in Average Potential Evapotranspiration in May (Pet5) and

363   in the Precipitation of the Coldest Quarter (Bio19). Also, Bio19 has an overall breadth of PNO

364   profile that is the narrowest of all bioclimatic layers, which is consistent with the OU model of

365   evolution with a single optimum detected for this bioclimatic layer (Table 2). It is also important

366   to note the case of *Sceloporus serrifer,* which shows the more extreme values in Mean

367   Temperature of Wettest Quarter (Bio8) and in Mean Temperature of Driest Quarter (Bio9) PNO

368   profiles. The plots of history of evolution of climatic tolerances (Fig. 6) show no pattern

369   between the two main clades, with crossing branches from different clades for all bioclimatic

370   variables indicating divergent evolution, and only some nearly overlapping nodes being

371   recovered, indicating some grade of convergent climatic origins. However, these plots were

372   built under the assumption of BM evolution, so only the plot for Bio15 would have a non-biased

373   interpretation; nevertheless, the means are close and the density of climate tolerance is more

374   or less narrow for each species on Prec10, Bio9, Bio18 and Bio19. In the case of the Bio19 plot,

375   despite the assumptions that BM evolution is clear, there is a trend consistent with an OU

376   model with a single optimum, with the exception of the branch of *Sceloporus serrifer* and *S.*

377   *prezygus* in Bio19, that show major divergent evolution.

378   Phylogenetic PCA (pPCA) shows no pattern or separation between clades (Figure S3), with some

379   species being more influenced by Bio2 and Pet5 (*S. cyanogenys*, *S. ornatus ornatus*, *S. poinsetti*,

380   *S. jarrovii*) and others more influenced by Bio15 and Prec5 (*S. aureolus*, *S. mucronatus*); again, *S.*

381   *serrifer* shows the more divergent niche influenced mainly by Bio9 and Bio19. Owing to the

382   pPCA analysis not showing an evident pattern or separation between clades, a phylogenetic

383   MANOVA analysis was not necessary to confirm any significant differences. Nevertheless, this

384   method is useful for visualizing divergence across phylomorphospace; the interpretation of the

385   contribution of each trait has to be taken with caution because of the assumption of BM

386   evolution of all traits and other statistical bias (Uyeda *et al*., 2015).

387   The analysis of relative disparity through time (DTT) shows (Fig. 7) that almost all bioclimatic

388   layers have a zero disparity in internal (deep) nodes, indicative of early conservatism in major

389   clades, with the exception of Bio9 and Bio15; also, all bioclimatic layers show significantly ($P <$

390   0.05) higher levels of disparity through time than expected by null model (dotted line in Fig. 7),

391   with some peaks indicating higher divergence in recent nodes, consistent with evolution within

392   clades. As noted above, Bio15 shows weak support for a BM evolution and the DDT plot

393   confirms this, because only in some points in the past was this bioclimatic variable close to a

394   BM process. In general, the higher levels of disparity in DTT in all bioclimatic layers are

395   concentrated in subclades in relative times that range from 0.3 to 0.8, which corresponds with

396   changes around the last 6.6 MYA. The maximum peaks in most of the bioclimatic variables,

397   except for Bio8 and Prec10, are detected at around 4.0 MYA (relative time of 0.5) and 0.65 MYA

398   (relative time of 0.75). The bioclimatic variable Bio8 (Mean Temperature of Wettest Quarter)

399   only presents the 0.65 MYA peak. On the other hand, Prec10 (Average precipitation in October)

400   presents a maximum peak at around 4.0 MYA and two small peaks at around 7.9 MYA (relative

401   time of 0.2) and 1.9 MYA (relative time of 0.65), which are barely significantly lower than the

402   null model; this is indicative of disparity distributed between subclades at that time. The values

403   of MDI (Table 4) for the total tree are positive in all cases, suggesting some niche evolution

404   within subclades and niche conservatism between subclades, or that the ecological disparity

405   tends to be distributed within subclades rather than between subclades. The same pattern is

406   observed with MDI values for former *torquatus* and *poinsettii* clades, with the exception of

407   Prec10 for both former clades, and Tmax1 for the *torquatus* clade, showing negative values,

408   indicating niche conservatism within clades and niche evolution between clades.

409

410   **DISCUSSION**

411   Current ecological niche of *torquatus* group and viviparity

412   Some of the layers chosen for estimation of the ecological niche of *torquatus* group had an

413   evident link with the current fall-winter reproductive cycle of viviparous lizards (*i.e.,*

414   Precipitation of Coldest Quarter (Bio19), Average maximum temperature in January (Tmax1),

415   and Average precipitation in October (Prec10)). Likewise, Mean Temperature of Driest Quarter

416   (Bio9) matched with late fall (November) and winter in the Mexican Plateau (Central Mexico)

417   and Chihuahuan Desert zone (Willmott & Matsuura, 2001; http://www. worldclim.org), where

418   many of the species of the *torquatus* group can be found. Moreover, despite a lack of data

419   about the biology of the reproduction and demography of the whole group, the remaining

420   layers could have some direct relevance in some phases of life history; for example, Average

421   Potential Evapotranspiration in May (PET5), Average precipitation in May (Prec5), Max

422   Temperature of Warmest Month (Bio5) and Precipitation of Warmest Quarter (Bio18), could be

423   linked with the survival of the offspring, because parturition in some species of the group has

424   been reported to occur between late April and early May (Guillette & Méndez-de la Cruz, 1993;

425   Méndez-de la Cruz *et al.*, 1998; Feria-Ortiz *et al.*, 2001; Villagrán-Santa Cruz *et al.,* 2009), and

426   the warmest month coincides with April, May or June in many occurrence sites of the group.

427   Watson *et al*. (2014) found that Max Temperature of Warmest Month (Bio5) is frequently the

428   best predictor of viviparous populations of *Phyrnosoma*, *Sceloporus* and *Plestiodon* in North

429   America. However, there is an absence of studies on the thermal susceptibility of the young,

430   but we assume that because of their small size, they could be more susceptible than adults to

431   overheating and dehydration, meaning that the temperature and humidity range of their

432   activity period should be lower, which would be a limitation for the establishment of

433   populations in certain areas, although these zones have conditions within the limits of

434   tolerance for adults. It would be necessary to carry out studies on thermoregulation and

435   locomotor performance of young and sub-adults to determine the role that these stages would

436   have in the establishment of populations. Likewise, Mean Temperature of Wettest Quarter

437   (Bio8) could be related to ovary cycle, because vitellogenesis in species of this group has been

438   reported to occur throughout the spring and fall (Guillette & Méndez-de la Cruz 1993; Méndez-

439   de la Cruz *et al*., 1998; Feria-Ortiz *et al*., 2001; Villagrán-Santa Cruz *et al.,* 2009), which is the

440   wettest period in almost all distribution areas of the group, and is linked with the abundance of

441   food necessary for the accumulation of yolk proteins in follicles (Feria-Ortiz *et al*., 2001). The

442   ovary cycle is highly conservative at different altitudes in many *Sceloporus* species;

443   nevertheless, the testicular cycle is not conservative and shows shifts related to altitude

444   (Villagrán-Santa Cruz *et al.,* 2009), and is possibly linked to the temperature needed for the

445   proper development of testicles, accessory sexual structures, and sperm maturation (Pearson,

446   *et al.,* 1976; Van Damme *et al.,* 1987; Villagrán-Santa Cruz, *et al.,* 1994). Therefore, the variation

447 and plasticity in reproduction cycles needs to be evaluated, especially in males, in order to

448 determinate the climatic requirements and the importance in the distribution of the species.

449 Likewise, the Mean Diurnal Range (Bio2) and Precipitation Seasonality (Bio15) has been

450 reported with a high relevance in the evolution of climatic niches in squamata reptiles (Pie *et*

451 *al.,* 2017). Probably, this result is due to these bioclimatic layers reflecting the extreme

452 conditions of both temperature and humidity, and it has been pointed out that extreme

453 climatic conditions could determine the range limits of species (Sexton *et al*., 2009).

454

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

456 Our analyses show a moderate to high niche divergence with no PNC in the ecological niche

457 models of the *torquatus* group species, and only two bioclimatic variables show weak evidence

458 of conservatism (Bio15 and Bio19). In general, the lack of PS and poor fit to the BM model in

459 almost all bioclimatic variables and ecological niches suggest that the evolution of habitat

460 preferences or requirements evolve quickly, causing the inability to detect PS and the absence

461 of PNC. The above is sustained by the changes in rate evolution showing a high heterotachy

462 among almost all bioclimatic variables, as demonstrated in DTT plots. Probably, the changes in

463 the rate of trait evolution masked the PS, which coincides with the high heterotachy detected in

464 the squamata phylogeny and the poor statistical fit to BM in the niche evolution of many

465 reptiles (Pie *et al*., 2017). With regard to Bio15 (Precipitation Seasonality) and Bio19

466 (Precipitation of Coldest Quarter), these bioclimatic variables possibly highlight the importance

467 of the extreme conditions in precipitation for the *torquatus* group and for squamata in general

468 (Pie *et al.,* 2017), because these are a measure of the variability and amount (in reproduction

469 season) of rainfall in a locality (http://www. worldclim.org). Also, although this species occurs in

470 sites with different levels of annual precipitation, the precipitation is concentrated in the same

471 season (Willmott & Matsuura, 2001; http://www. worldclim.org). The single optimum OU

472 model of evolution for Bio19 could be interpreted as evidence of stabilizing selection (Hansen,

473 1997), although some authors do not recommend the use of this term to refer to the evolution

474 around an optimal value (Cooper *et al*., 2017). We have to be careful in affirming that a single

475   optimum OU process is the best model for Bio19, since the multiple-optima OU analyses fail

476   because of the size of the sample. We think that the narrow overall breadth of the PNO profile

477   for Bio19, which is indicative of similar levels of tolerance for all species of the group, is indirect

478   evidence of a single optimum OU process. This is the only bioclimatic variable that is directly

479   linked to the fall-winter reproductive cycle that seems to be conserved, and for what almost all

480   species of this group have similar requires. Surprisingly, we expect that bioclimatic layers linked

481   with temperature could have PS and PNC, as temperature during breeding season is the

482   principal factor to estimate the extinction probabilities by global warming in lizards (Sinervo, *et*

483   *al.,* 2010). It is possible that the great amount of species in the group have not been thoroughly

484   explored throughout the entire climatic space that could be occupied, or that microclimatic

485   conditions in refuges could probably be more important for these species, as long as hours of

486   restriction (hours in refuges to avoid overheating) in the reproductive season remains < 4

487   (Sinervo *et al*., 2010); also, Bio15 and Bio19 remain between certain limits. For example, *S.*

488   *serrifer,* which despite having preferred temperatures similar to other species of the group,

489   occurs in different habitats, but is only present in Yucatan peninsula where there are some

490   kinds of trees or artificial refuges, like walls and rock fences, which provide suitable thermal

491   conditions to spend night and hours of restriction (Martínez-Méndez *et al*., 20015). Thus, we

492   think that the microclimate in refuges and thermoregulatory behavior could allow this species

493   to explore beyond typical montane sites and contribute to the no PNC detection in bioclimatic

494   variables linked with temperature. In this sense, extensive ecophysiological, phylogeographic

495   and thermal ecology studies on the species of the group remains necessary, in order to

496   determine its fundamental niche and its thermal requirements, and to measure the effect of

497   biotic interactions and historic factors in its distribution.

498   The low niche overlap values between sister species could be an additional indicator of no niche

499   conservatism, in contrast to the results of Warren *et al*. (2008), who found moderate and high

500   niche overlap and conservatism in many sister species of butterflies, birds and mammals in

501   Mexico. The low niche overlap values in the *torquatus* group is not an exception; for example,

502   some studies with freshwater fishes of North America and Mexico show that some clades

503   present high niche overlap and conservatism, while others shows high niche diversification and

504   low niche overlap (McNyset, 2009; Culumber & Tobler, 2016). There is similar evidence that

505   sister species of tropical plethodontids salamanders tend to have divergent climatic niches

506   compared to temperate sister species (Kozak & Wiens 2007). Some studies have highlighted the

507   importance not only of the niche overlap in the understanding of diversification but also the

508   sympatry and range overlap of sister or closely related species, because some models of

509   speciation consider competition for resources to drive sympatric speciation, and ecological

510   differentiation to arise to prevent competition (Rundle & Nosil, 2005; Nosil, 2012).

511   Complementarily, many events of allopatric speciation are not associated with ecological

512   divergence, which can lead to a signal of niche conservatism (Peterson, 2011). According to

513   Losos (2008), it is necessary to carefully identify niche similitudes as PNC, because conservatism

514   emerges in this case as a side result of a historic process where no related species share the

515   same geographic range. In this sense, some evidence supports the ecological differentiation in

516   sympatric speciation (Bush & Smith, 1998), whereas other studies underestimate its role, even

517   finding that the geographic overlap between clades in some species restricts diversification

518   (Kozak & Wiens 2010). Future studies should focus on whether the interaction with other

519   species of lizards could influence the evolution of the niche of these species. On the other hand,

520   in agreement with the general pattern found when analyzing the individual layers, the absence

521   of significant correlation between niche overlap at internal nodes and divergence time in the

522   Arc-Range Correlation (ARC) analyses is an indication of the absence of PS in the niche

523   evolution of the *torquatus* group, at least with the layers used to build the ecological niche, and

524   is also evidence that climatic niche differentiation (ecological divergence) was not the main

525   factor in the diversification of the *torquatus* group.

526   The Predicted Niche Occupancy (PNOs) profiles shows a high heterogeneity in the levels of

527   climatic tolerance, which indicates radiation over the spectrum of the ecological space

528   represented for the bioclimatic variables that were analyzed. Nevertheless, there were some

529   overlapping peaks indicating similar tolerances in some species, although similar tolerances are

530   not shared for the same species in each bioclimatic variable, and no sister species share similar

531   tolerances in all cases, except for Bio19, which is linked with the fall-winter reproductive cycle.

532   The most different tolerances in PNO profiles were observed in *S. serrifer*, which can be

533   explained by the fact that this species occurs in habitats ranging from highlands to almost the

534   sea level. Accordingly, the PNO profiles suggest distinct ecological preferences and some

535   degree of ecological differentiation between most of the species without groups of sister

536   species sharing the same ecological niche, as confirmed by pPCA analyses.

537   The plots of the history of evolution of climatic tolerances show that only some species have

538   some grade of convergent climatic origins for a number of bioclimatic variables, with most of

539   the species showing different magnitudes of divergent evolution. Also, the rate of change in

540   climatic tolerances through the time is different between species for each bioclimatic variable.

541   For example, Bio19 shows the lowest magnitude of final divergence between the species of the

542   group, except for the clade formed by *S. serrifer* and *S. prezygus*. This pattern suggests the lack

543   of niche conservatism for a long period of time. The analysis of relative Disparity Through Time

544   (DTT) and MDI values indicates that the ecological disparity tends to be distributed within

545   subclades rather than between subclades, with high divergence in recent nodes. The rapid

546   accumulation of ecological diversity has come about in the last 6.6 MYA, concentrating at

547   around 4.0 MYA and 0.65 MYA. The first peak seems to coincide with the high diversification

548   rate in different groups of organisms that occurred during the Pliocene-Pleistocene epochs in

549   America (Graham, 1999; Morrone, 2010; Bryson & Riddle, 2012; Licona-Vera & Ornelas, 2017),

550   which was attributed to orogenic processes that produced vicariant barriers like mountains,

551   rivers etc., and climatic changes (Bryson and Riddle, 2012; Mastretta-Yanes, *et al*., 2015). The

552   second peak coincides with the Pre-Illinoian glacial period around 0.62-0.67 MYA (Rutter *et al*.,

553   2012).

554   Thereby, the evidence of a lack of niche conservatism, and the recent accumulation of

555   ecological diversity could be associated with the possible geographic and climatic isolation

556   throughout speciation, which could promote the rapid accumulation of ecological differences

557   between species of the group (Culumber & Tobler, 2016). This pattern coincides with the

558   results of Pie *et al*. (2017), who found an extensive rate of heterogeneity in climatic niche

559   evolution of squamates with shifts involving accelerations concentrated in its recent

560   evolutionary history.

561 **CONCLUSIONS**

562 Our results indicate a lack of PNC in the niche evolution of *torquatus* group with the possible

563 exception of two bioclimatic variables, and only one linked with viviparity. This is evidence that

564 possible constraints associated with viviparity are not sufficient to explain the niche evolution

565 of the group. Even though most of the layers used to build the actual niche of the group could

566 be linked with viviparous reproduction, the species have evolved quite different tolerances to

567 them, with the exception of Bio19. However, the availability of new climatically heterogeneous

568 territories with the subsequent filling of that new environmental niche, and posterior cycles of

569 isolation during orogenic and glacial periods, could build the pattern we observed.

570 Nevertheless, as we pointed out, the physiology required and the use of refuges needs to be

571 evaluated to elucidate the most accurate niche evolution of the group.

572

577

578 **DATA AVAILABILITY**

579 The following information was supplied regarding data availability: The Ecological niche models

580 of the species of *Sceloporus torquatus* group were supplied as Figure S1. Phylogenetic trees

581 showing the position of adaptive shifts under reversible-jump Bayesian method implemented in

582 bayou were supplied as Figure S2. GenBank accession numbers were supplied as Table S1.

583 Occurrence data were supplied as XLSX archive as Table S2. Model parameters estimated for

584 Brownian Motion (BM), Ornstein-Uhlenbeck (OU), Early Burst (EB) and Pagel's delta (δ) for each

585 bioclimatic variable were supplied as Table S3, and Model parameters estimated for bayou

586 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.

Bioclimatic layer	Blomberg's K		Pagel's lambda (λ)			
	K	p	λ	logL	logL0	p
Mean Diurnal Range (Bio2)	0.7517042	0.077	0.7819658	-99.89475974	-100.4653185	0.285
Max Temperature of Warmest Month (Bio5)	0.6093276	0.332	8.06E-05	-111.5609569	-111.560767	1
Mean Temperature of Wettest Quarter (Bio8)	0.5832248	0.454	8.06E-05	-114.1056264	-114.1054896	1
Mean Temperature of Driest Quarter (Bio9)	0.6055844	0.365	6.61E-05	-113.7234086	-113.7232676	1
Precipitation Seasonality (Bio15)	0.9789271	0.003	0.8990152	-92.01841259	-95.39007416	0.009
Precipitation of Warmest Quarter (Bio18)	0.6265125	0.307	8.06E-05	-138.5466181	-138.5465873	1
Precipitation of Coldest Quarter (Bio19)	0.5298510	0.683	8.06E-05	-106.0601306	-106.0598546	1
Average Potential Evapo-Transpiration in May (PET5)	0.9362418	0.245	8.06E-05	-96.86246779	-96.86234353	1
Average precipitation in May (Prec5)	0.9021397	0.127	0.1542047	-109.9063051	-110.0433045	0.6
Average precipitation in October (Prec10)	0.8961354	0.168	8.06E-05	-113.3965164	-113.3962213	1
Average maximum temperature in January (Tmax1)	0.7792041	0.515	0.7215720	-117.5890078	-117.4820999	1

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.

Bioclimatic layer	Model	lnL	AICc	Parameters
Mean Diurnal Range (Bio2)	BM	-100.17936	204.9587	2
	δ=2.36	-99.57843	206.420	3 *e*
	OU	-99.69645	206.6561	3 *e*
	EB	-100.17937	207.6219	3 *
Max Temperature of Warmest Month (Bio5)	OU	-111.5608	230.3848	3
	δ=2.89	-112.2142	231.6915	3 *e*
	BM	-114.4009	233.4019	2 *
	EB	-114.4009	236.0650	3 *
Mean Temperature of Wettest Quarter (Bio8)	OU	-114.1055	235.4742	3
	δ=3.00	-114.8895	237.0421	3 *e*
	BM	-117.4305	239.4610	2 *
	EB	-117.4305	242.1242	3 *
Mean Temperature of Driest Quarter (Bio9)	OU	-113.6033	234.4698	3
	δ=2.99	-113.7634	234.790	3 *e*
	BM	-115.6251	235.8502	2 *e*
	EB	-115.6251	238.5134	3 *
Precipitation Seasonality (Bio15)	BM	-92.12050	188.8410	2
	δ=1.68	-91.78905	190.8413	3 *
	OU	-91.97477	191.2127	3 *
	EB	-92.12050	191.5042	3 *
Precipitation of Warmest Quarter (Bio18)	OU	-138.3016	283.8663	3
	δ=2.89	-138.4062	284.0756	3 *e*
	BM	-139.976	284.5520	2 *e*
	EB	-139.976	287.2152	3 *
Precipitation of Coldest Quarter (Bio19)	OU	-106.0001	219.2634	3
	δ=2.91	-107.0695	221.4021	3 *
	BM	-109.8923	224.3847	2 *
	EB	-109.8924	227.0479	3**
Average Potential Evapo-Transpiration in May (PET5)	BM	-97.56074	199.7215	2
	δ=2.96	-96.75241	200.7680	3 *e*
	OU	-96.82442	200.9120	3 *e*
	EB	-97.56075	202.3847	3 *
Average precipitation in May (Prec5)	OU	-109.7262	226.7155	3
	δ=2.97	-109.9754	227.2140	3 *e*
	BM	-111.6583	227.9166	2 *e*
	EB	-111.6583	230.5797	3 *
Average precipitation in October (Prec10)	OU	-112.7530	232.7692	3
	δ=2.89	-112.9429	233.1489	3 *e*
	BM	-114.9227	234.6692	2 *e*
	EB	-114.9227	237.1086	3 *
Average maximum temperature in January (Tmax1)	BM	-117.7130	240.0260	2
	δ=2.78	-116.8464	240.9560	3 *e*
	OU	-117.0573	241.3778	3 *e*
	EB	-117.7130	242.6892	3 *

Table 3 (on next page)

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*.

ID	Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1	*Sceloporus aureolus*	NA	0.146	0.321	0.060	0.059	0.098	0.195	0.351	0.033	0.139	0.131	0.476	0.117	0.290	0.101	0.002	0.443	0.157	0.407	0.368
2	*Sceloporus binocularis*	0.341	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
3	*Sceloporus bulleri*	0.613	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
4	*Sceloporus ornatus caeruleus*	0.175	0.567	0.219	NA	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
5	*Sceloporus cyanogenys*	0.168	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
6	*Sceloporus cyanostitctus*	0.237	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	0.673	0.069	0.083	0.045	0.160	0.114
7	*Sceloporus dugesii*	0.452	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
8	*Sceloporus insignis*	0.638	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
9	*Sceloporus jarrovii*	0.159	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
10	*Sceloporus melanogaster*	0.414	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
11	*Sceloporus minor*	0.349	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
12	*Sceloporus mucronatus*	0.768	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
13	*Sceloporus oberon*	0.292	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
14	*Scelporus omiltemanus*	0.576	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
15	*Sceloporus ornatus ornatus*	0.273	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
16	*Sceloporus poinsettii*	0.013	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
17	*Sceloporus prezygus*	0.759	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
18	*Sceloporus serrifer*	0.351	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
19	*Sceloporus sugillatus*	0.673	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
20	*Sceloporus torquatus*	0.642	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

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.

Bioclimatic layer	MDI value		
	Total tree	*torquatus* Clade	*poinsettii* Clade
Mean Diurnal Range (Bio2)	0.177	0.062	0.165
Max Temperature of Warmest Month (Bio5)	0.445	0.253	0.425
Mean Temperature of Wettest Quarter (Bio8)	0.365	0.390	0.285
Mean Temperature of Driest Quarter (Bio9)	0.331	0.283	0.256
Precipitation Seasonality (Bio15)	0.199	0.463	0.069
Precipitation of Warmest Quarter (Bio18)	0.198	0.420	0.081
Precipitation of Coldest Quarter (Bio19)	0.299	0.187	0.269
Average Potential Evapo-Transpiration in May (PET5)	0.151	0.032	0.090
Average precipitation in May (Prec5)	0.141	0.149	0.159
Average precipitation in October (Prec10)	0.027	-0.119	-0.010
Average maximum temperature in January (Tmax1)	0.157	-0.080	0.140

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.
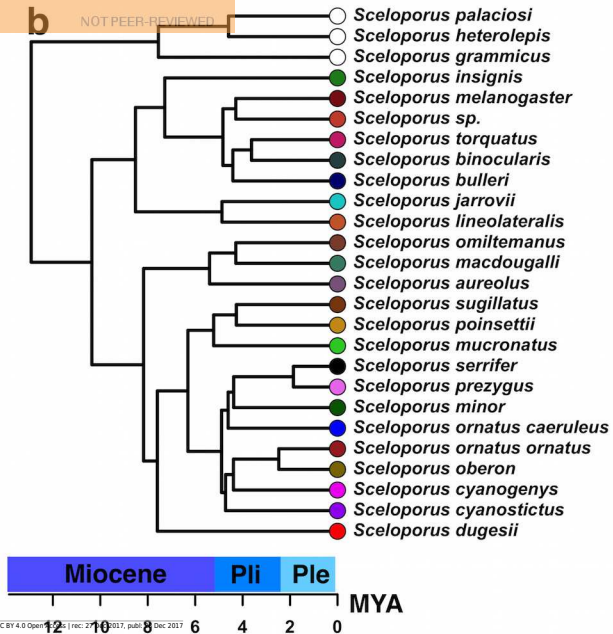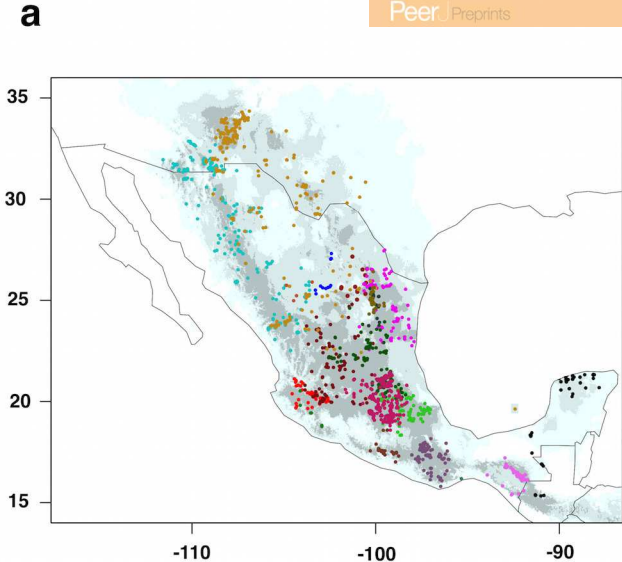
Figure 3(on next page)

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 (25th and 75th percentiles) around the median, whiskers delimit ≈ 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.
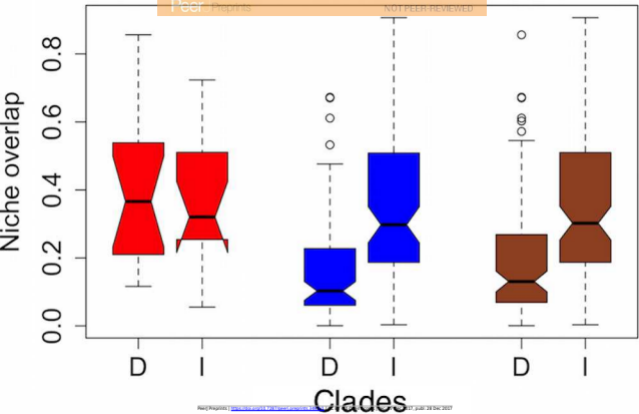
Figure 4 (on next page)

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.
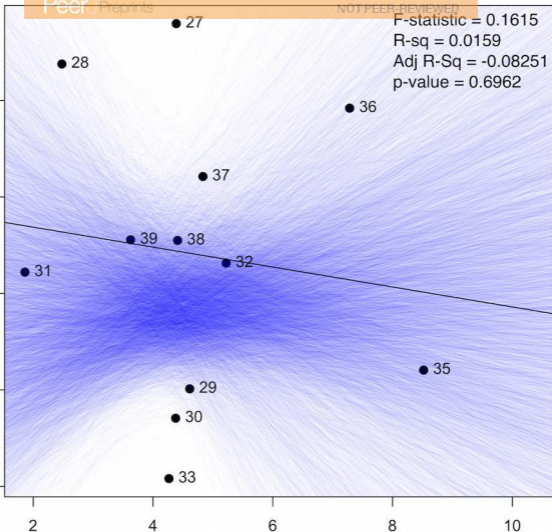
Figure 5(on next page)

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).
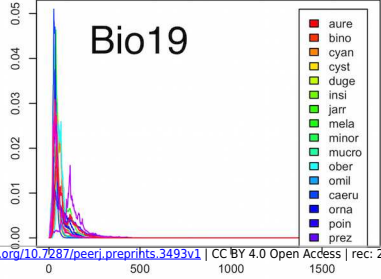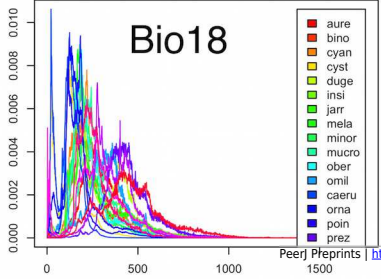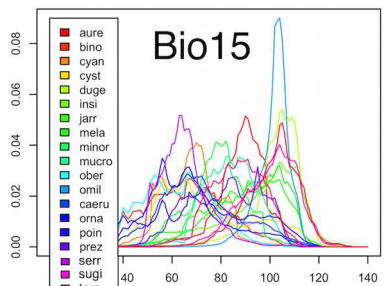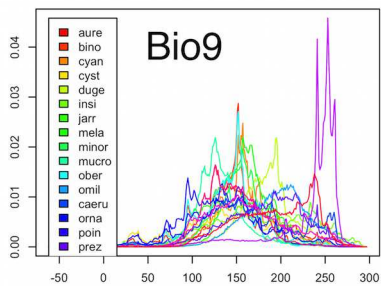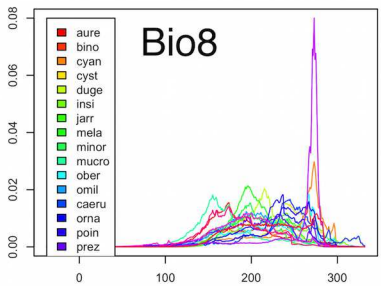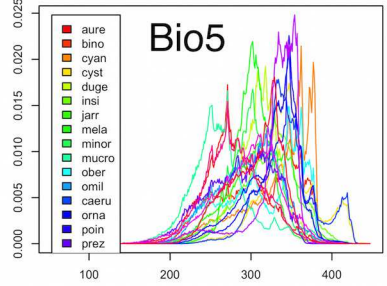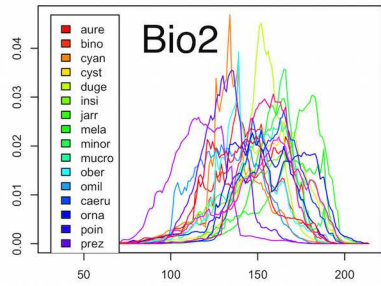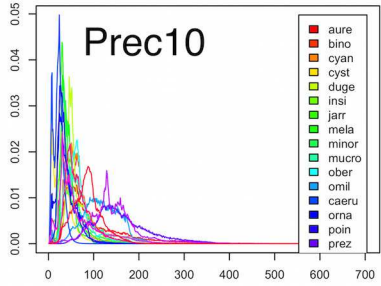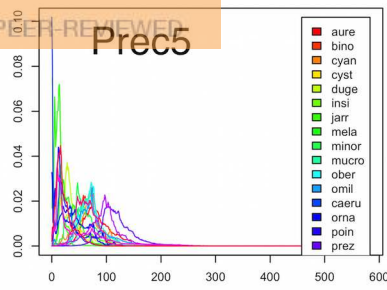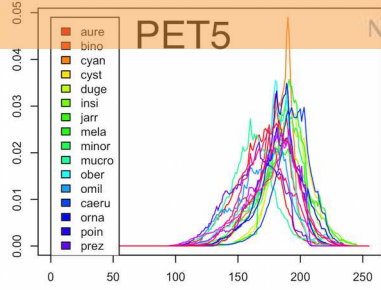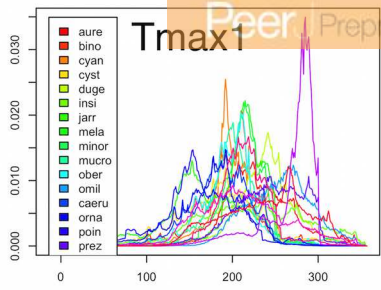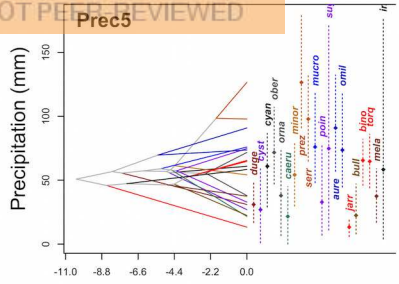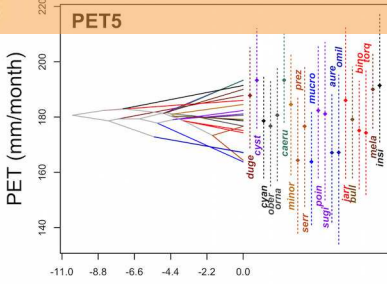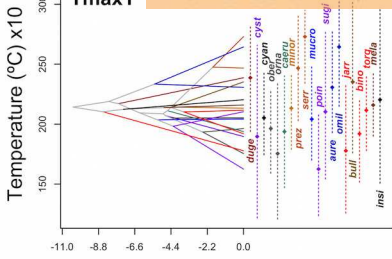
Figure 6 (on next page)

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.
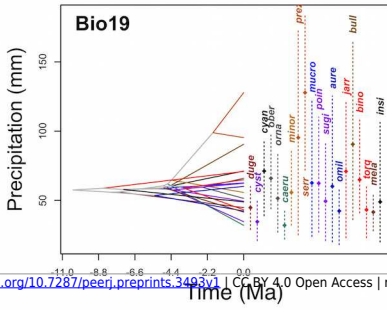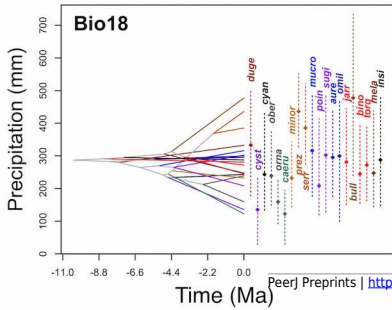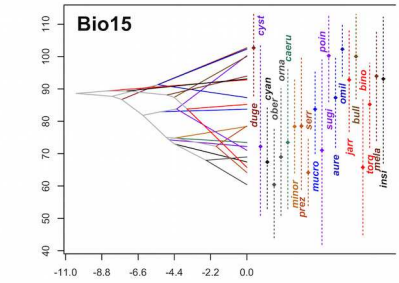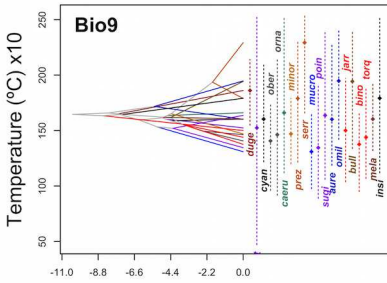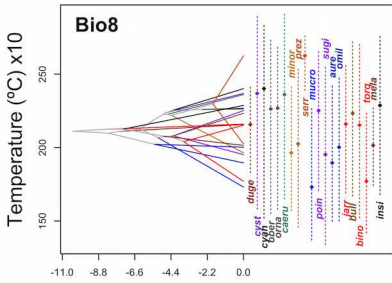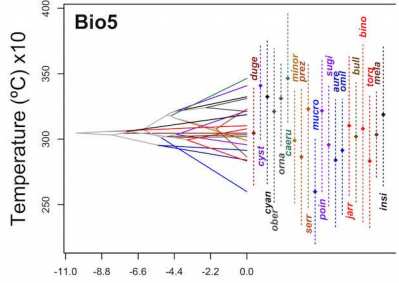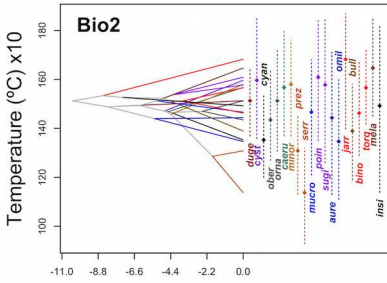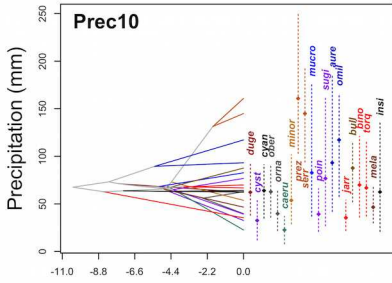
Figure 7(on next page)

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).