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Original Article

Title: **Climatic niche attributes and diversification in *Anolis* lizards**

Running header: **Niche and speciation in lizards**

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ABSTRACT

Aim The aim of this study was to test the link between climatic niche dynamics and species diversification in *Anolis* on islands and on the mainland. We tested the hypotheses that lineages in warmer climates and with narrow climate niches diversified more than lineages in cold climates and with broad climate niches. We also tested the hypothesis that species-rich clades exhibit greater niche diversity than species-poor clades.

Location Neotropics

Methods We collated occurrence records for 328 *Anolis* species to estimate niche breadth, niche position and occupied niche space (as a proxy for niche diversity). We compared niche breadth between insular and mainland *Anolis* species and among *Anolis* clades, controlling for the potential confounding effect of range size. Using two approaches (clade-based and QuaSSE) we explore the association between niche metrics and diversification rates in *Anolis* lizards.

Results We found that Caribbean *Anolis* had a narrower niche breadth and niche space occupation compared to mainland anoles after controlling for range size differences. There was a significant association between niche traits (mean niche position and niche breadth) and diversification in anoles. Anole lineages with narrow niche breadths and that occupy warmer areas exhibited higher speciation rates than those with broader niche breadths that occupy cold areas. In the same way, clades with higher total diversification exhibit more niche diversity than clades with lower total diversification.

Main conclusions Climatic niche attributes play a role in anole diversification with some differences between mainland and insular anole lineages. Climatic niche differences between regions and clades likely are related to differences in niche evolutionary rates. This also suggest that climate plays a strong role in shaping species richness between and within mainland and islands.

Keywords *Anolis*, climate constraints, climatic space, evolution, Neotropics, niche breadth, niche diversification, niche specialization, lizards, species richness

INTRODUCTION

Species richness in a clade or region results from the interplay of ecological and evolutionary factors operating at different spatial and temporal scales (Wiens, 2011; Cornell, 2013). Species richness in a region can ultimately be explained by differences in diversification rates (i.e., speciation minus extinction) and dispersal events (Wiens & Donoghue, 2004; Wiens, 2011). Although species diversification is known to be influenced by ecological factors within a particular region (Wiens, 2011; Cornell, 2013; Machac *et al*., 2013), there is still little understanding of how variation in ecological factors affects species diversification, and thus species richness, across phylogenetic and geographic scales.

Ecology, diversification, and species richness are linked through the niche concept (Hutchinson, 1957; Soberón & Nakamura, 2009; Ricklefs, 2012). For instance, some recent studies have shown that speciation rates are coupled with rates of niche evolution (Rabosky, 2012a; Rabosky & Adams, 2012; Rabosky *et al*., 2013). Accordingly, clades displaying a high degree of species richness are expected to have greater niche diversity than clades with low species richness (Rabosky, 2012a; Ricklefs, 2012; Rabosky *et al*., 2013). This prediction is an expected outcome during adaptive radiation where slowdowns in diversification occur as ecological space is filled and species' niches become narrow due to competition (Schluter, 2000; Rabosky, 2009). In this way, niche divergence can drive cladogenesis. Alternatively, diversification may not be ecologically constrained but rather, time or area dependent (Wiens, 2011). In cases where cladogenesis is decoupled from niche evolution, we would expect lineages to have greater niche similarity and large niche breadths (Cornell, 2013). The above scenarios have been explored mostly using phenotypic traits related to habitat use (Schluter, 2000; Harmon *et al*., 2003). Only recently have some studies explored the role of coarse-grain climatic niche attributes in clade diversification (Kozak & Wiens, 2010; Pyron & Burbrink, 2012; Schnitzler *et al*., 2012; Machac *et al*., 2013; Wiens *et al*., 2013; Kostikova *et al*., 2014).

The climatic niche is defined as the set of climatic variables at a coarse-resolution with an influence on the intrinsic and instantaneous population growth rates of a species at a geographic scale (Soberón, 2007; Peterson *et al*., 2011). It is useful to establish whether climatic niche requirements can explain differences in species richness and diversification among regions and clades. This definition considers climatic niche as a population-level trait and not as an individual-level trait, which is implicit in definitions incorporating critical physiological boundaries. Accordingly, several studies have explored the link between climatic niche attributes and diversification (Kozak & Wiens, 2010; Schnitzler *et al*., 2012). For instance, Kozak & Wiens (2010) suggested that high rates of climatic-niche evolution might promote increases in diversification rates. However, a causal link between diversification rate and climatic niche evolution is difficult to establish (Schnitzler *et al*., 2012). In order to clarify the link between niche dynamics, diversification and species richness, clear predictions about how climatic niche attributes (e.g., niche space and niche breadth) facilitate increases or slowdowns in diversification rates are needed.

In this paper, first, we hypothesize a link between climatic niche metrics (i.e., niche position and niche breadth) and diversification in *Anolis* lizards. For niche position, we predict that lineages occupying warmer and drier areas (where anole diversity is higher; Algar & Losos, 2011; Losos, 2009) tend to diversify more than lineages adapted to cold and very humid conditions (where their diversity is lower). For niche breadth, we predict that clades composed of climatic niche specialist species (i.e., with narrow niche breadths) will have higher diversification rates than lineages composed of climatic niche generalist species (i.e., wide niche breadths) (Futuyma & Moreno, 1988; Cantalapiedra *et al*., 2011; Cadena *et al*., 2012; Wiens *et al*., 2013). This hypothesis predicts a negative relationship between diversification rates and niche breadth, a relationship that likely is mediated by climatic niche conservatism (Gómez-Rodríguez *et al*., 2015). Second, we hypothesize that clades with high species richness (and likely high diversification rates) will have a high degree of niche diversity (i.e., more occupied niche space) than clades poor in species (Ricklefs, 2012). This is consistent with a scenario where cladogenesis is driven by niche evolution rates (Harmon *et al*., 2003; Rabosky *et al*., 2013).

We test these hypotheses for *Anolis* lizards, which occur mainly in the Caribbean islands and on the mainland from Mexico to southern Brazil. They are species-rich on both the islands (~160 species) and the mainland (~230 species; Table 1). The evolutionary history of Caribbean *Anolis* has been subjected to intense research in the last several decades (Losos, 2009). There is evidence that their diversification in the Greater Antilles is related to island size and colonizing time, with speciation rates declining over time as a function of area (Rabosky & Glor, 2010). This pattern suggests that regional species richness in the Greater Antilles is controlled by area and potentially by competitive interactions (Losos & Schluter, 2000; Rabosky & Glor, 2010). Specifically, we predict that *Anolis* lizards with narrow climatic niches and specialization toward particular climate regimes have diversified more than those that tolerate a wide range of climate conditions (Kozak & Wiens, 2010).

In this paper, we compare climatic niche attributes in *Anolis* between regions and clades, to assess whether niche position and specialization have driven diversification in these lizards. We evaluate the available climatic space in each region to explore patterns of niche occupation in *Anolis* clades inhabiting the islands and the mainland. Although there are substantial niche differences between insular and mainland anoles, niche traits were associated with cladogenesis in both anole faunas.

MATERIALS AND METHODS

Anolis **records**

We mapped 13,580 georeferenced locality records for 328 *Anolis* species from the Caribbean islands (145 species, 3,134 locality records) and the mainland (183 species, 10,445 locality records), drawn from the Global Biodiversity Information Facility (GBIF, http://gbif.org), HerpNET (http://www.herpnet.org/), Algar and Losos (2011), Ochoa-Ochoa & Flores-Villela (2006) and other databases not publicly available (e.g., GK database). Some herpetological collections for which *Anolis* locality data is not available via the Internet (e.g., GBIF or HerpNet), namely

ICN (Colección de Anfibios y Reptiles, Instituto de Ciencias Naturales, Bogotá Colombia), MHUA (Museo de Herpetología de la Universidad de Antioquia, Medellin, Colombia), and QCAZ (Colección de Anfibios y Reptiles, Pontificia Universidad Católica de Ecuador, Quito, Ecuador) were georeferenced using national gazetteers and the point-georeferencing method with a spatial precision of ~1 km (Chapman & Wieczorek, 2006). We carefully revised each record in our database and eliminated erroneous, doubtful and duplicate records (i.e., identical records from two or more sources).

Climatic niche metrics in *Anolis* lizards

We estimated the climatic niche represented by temperature and precipitation variables drawn from the WorldClim database (Hijmans *et al*., 2005) using the occurrence records of 328 species. Our climatic niche estimates encompass the realized niche as is common in GIS approaches (Peterson *et al*., 2011). To estimate the niche breadth for each *Anolis* species, we used maximum Mahalanobis distances (Rotenberry et al., 2006); a statistical technique for ecological niche modelling based on presence-only records (Peterson *et al*., 2011). The Mahalanobis distance measures the space between two points in a *n*-dimensional coordinate system accounting for unequal variances and correlation between variables (Xian *et al*., 2008). Distances are simply calculated as a standardized difference between the value of any point (i.e., a species' record) and the mean values from all points from the climate space (Rotenberry *et al*., 2006). Also, we estimated niche breadth using Euclidean distances and ran a correlation of niche breadth between both distance methods, which was highly significant ($p < 0.0001$).

We characterized the available climatic space for each region in which each clade occurs. For each island in the Greater Antilles we extracted values for bioclimatic variables for all pixels (1 km^2 pixel size). For the mainland, we generated a minimum convex polygon for Middle American and South American anole records with a buffer of 1,000 km in each area. Note that here Middle America refers to the countries of Central America and Mexico. This polygon potentially represents at least the dispersal or movement area for mainland anole species (Peterson & Soberón, 2012; Saupe *et al*., 2012). We clipped all bioclimatic rasters using this polygon and extracted values for all 19 variables from a random set of pixels (>100,000 pixels of 1 km^2 each for South America, and >25,000 pixels of 1 km^2 each for Middle America). We conducted a Principal Components Analysis (PCA) with all 19 bioclimatic variables from species records and points from each region (see Appendix S1 in Supporting Information). For each anole species we calculated the mean of the scores of the first PC as an estimate of niche position. Finally, we calculated range size for each species as the area within the minimum convex polygon (MCP) enclosing all records for individual species and for anole clades. The MCP was only used to calculate range sizes, which were used as covariates for comparisons of niche breadth between clades and regions.

Phylogenetic estimation

We generated a time-calibrated phylogeny using an *Anolis* dataset extracted from a recent Squamata phylogeny (Pyron *et al*., 2013). Our anole tree comprises 207 anole species, representing 53% of the total number of recognized anole species (Uetz, 2014). Although sampling was very complete for the Caribbean anole species (87%, 19 species missing), and was very incomplete for the mainland species (76 species, 32% of all known species). We also included 32 outgroups based on the topological position of *Anolis* in the Iguania phylogeny (Townsend *et al*., 2011). The assembled matrix included 233 taxa and 12,896 sites corresponding to 9 genes included in Pyron *et al*. (2013). We used their alignment to maintain consistency among studies. We used only two calibration points due to the low availability of fossil samples. First, using a normal distribution prior we calibrated the root with the crown-group pleurodont iguanian *Saichangurvel* (Conrad & Norell, 2007) from the Late Campanian (70.6 ± 0.6 Ma; Townsend *et al*., 2011). Second, a lognormal prior with a minimum age of 23 Ma was used to calibrate the *Anolis chlorocyanus* group based an unnamed fossil from the Dominican Republic putatively assigned to this clade (de Queiroz *et al*., 1998). We placed this anole fossil at the stem of the *chlorocyanus* group (*A. aliniger*, *A. chlorocyanus*, *A. coelestinus*, *A. singularis*) following Nicholson *et al.* (2012). We implemented a relaxed clock method with uncorrelated rates among branches using the software BEAST 1.8.0 (Drummond *et al*., 2012). We did not implement a highly parameterized partitioned analysis as the ingroup (*Anolis*) is represented almost entirely by one single gene (ND2). As suggested by jModeltest v.2

(Guindon & Gascuel 2003; Darriba *et al*., 2012) we used the GTRGI model of evolution for the entire dataset. We initiated two runs starting from a random tree and ran these for 40 million generations sampling every 1,000 following a burn-in of 2 million generations. The number of generations required to reach stationarity was determined by examining marginal probabilities in Tracer v1.6 (Rambaut *et al*., 2014). For each run, the posterior sampling of trees yielded an effective sample size (ESS) of >200 for all parameter models. Both runs were combined as they gave similar results, and node and branch parameters were summarized on the maximum clade credibility tree (see Fig. S1 in Appendix S2). The resulting tree was very similar in topology to recent phylogenetic estimates of *Anolis* lizards using the same datasets (Mahler *et al*., 2010; Nicholson *et al*., 2012; Gamble *et al*., 2014; Prates *et al.*, 2015). In particular, Prates *et al.* (2015) generated a calibrated tree for a subset of *Anolis* species (some species from *Dactyloa* clade, *Anolis carolinensis* and some species from *Norops* clade) using three fossils as calibration points and lying outside of the *Anolis* ingroup (one in the root, and two inside the outgroup). Their estimated dates for the most recent common ancestor (MRCA) of *Anolis* are very similar to our estimated dates (see Prates *et al*., 2015).

Climatic niche attributes and diversification in *Anolis* lizards

i) The clade-based approach

We implemented a clade-based approach to correlate occupied climatic niche space with species richness. Nicholson *et al*. (2012, their figure 4) recognized eight clades in the *Anolis* phylogeny and raised them to the rank of genus (but see

Poe, 2013). We used these same names as clades to compare niche attributes. Although the criteria to delimit these clades is arbitrary, the same problem occurs with the use of recognized taxa of a given rank (e.g., family or genus level); additionally, some of these clade names for anoles have been used by some herpetologists for almost three decades (Guyer & Savage, 1986; Savage, 2002). We separated the *Norops* clade into three: Cuban *Norops*, Jamaican *Norops* and mainland *Norops*, and also split the *Dactyloa* clade: Lesser Antillean *Dactyloa* and mainland *Dactyloa* (Table 1). We obtained species richness data for each clade from Nicholson *et al*. (2012). For each clade, we calculated occupied niche space as the summed variances of the first four PC scores (see above). This measure of occupied niche space can be considered a proxy for niche diversity, analogous to the measures of morphological variance used in studies of morphological disparity (Foote, 1997; Wainwright, 2004; Ricklefs, 2012). We can use the species richness (ln species richness) of anole clades as a direct estimator of the total diversification in each clade (the Ω estimator in Rabosky, 2009) because anole clade diversity was not correlated with age ($R^2 = 0.30$, $p = 0.124$) (Rabosky, 2009, 2012b; Rabosky & Adams, 2012). In addition, we calculated net diversification rates for each anole clade using the method-of-moments estimator (Magallón & Sanderson, 2001), based on the crown-group age (obtained from our calibrated tree) and the total number of described species for each clade, and using two values for relative extinction rate (0.9 and 0.1). We tested for a relationship between occupied niche space, clade area (log10 geographical area) and species richness (ln species richness) and net diversification rates in *Anolis* clades using a path analysis. We repeated the same analysis using only insular clades. This approach allowed us to incorporate all of the anole species for which we had compiled climate data.

ii) The QuaSSE approach

We implemented a quantitative-state speciation and extinction model (QUASSE; FitzJohn, 2012) to correlate niche attributes (mean niche position and niche breadth) with diversification rates (FitzJohn, 2010). The QuaSSE approach uses a maximum likelihood method to evaluate whether a distribution of continuous character states is associated with higher or lower speciation rates (FitzJohn, 2010). This method has been used previously to find associations between climate and diversification rates in other taxonomic groups (Pyron & Wiens, 2013; Kostikova *et al*., 2014). We explored whether mean niche position and niche breath were associated with speciation rates in *Anolis* lizards. These niche metrics describe the ecological niche of a species across a set of environmental axes (Schoener, 1989; Thuiller *et al*., 2005). The QuaSSE approach identifies whether lineages exhibiting lower or higher niche positions/broader or narrower niche breadths are correlated with higher speciation rates in *Anolis*.

We generated four models in which speciation rates were fitted according to a particular function: (i) constant function (trait variation has no influence on speciation rate); (ii) linear function (a linear increase in a trait is associated with a linear increase in speciation rate); (iii) a sigmoid function (there is an association between speciation rates and a continuous trait exhibiting a sigmoidal function), and (iv) a modal function (where intermediate values for a trait are associated with a higher speciation rate). In addition, we generated another set of models, but assuming a directional trend in the evolution of the particular trait (FitzJohn, 2012). We kept extinction rates constant among models because QuaSSE is known for its difficulty detecting differences in extinction rates (FitzJohn, 2010). We conducted the same analysis but only for the Caribbean species by pruning all mainland species from the phylogeny. We did not conduct a specific analysis for mainland species only due to the limited taxon sampling for these species (see above). Models were compared using the Akaike Information Criterion (Burnham & Anderson, 2002) and we selected as the best models those with the lowest AIC scores (Burnham & Anderson, 2002). As QuaSSE calculations are quite complex and computationally extensive (FitzJohn, 2012), we only performed a QuaSSE analysis for each variable with the best topology selected from our BEAST analysis. Therefore, we were not able to evaluate the potential effects of phylogenetic uncertainty on correlations between speciation rates and niche traits. Finally, we performed a rarefaction analysis for the Caribbean anole tree to evaluate the impact of missing species on the QuaSSE analysis. We randomly pruned species in a sequence of percentages (10%, 15%, 20%, 25%, 30%, 35%, 40%, 45% and 50%) and generated a QuaSSE analysis for each dataset with these pruned trees. The aim was to evaluate whether QuaSSE is sensitive to missing species and therefore to explore the potential impact of taxon incompleteness on the association between traits and diversification (see Appendix S3).

RESULTS

Anole climatic niches

The first two axes of the PCA explained 46.6% and 22.4% of the total variance of climatic variables in *Anolis* lizards (69% in total). Both axes were mainly related to temperature variables (see Appendix S1). The first axis was mainly associated with the minimum temperature of the coldest month (bio 6) and the second axis was mainly associated with the maximum temperature of the warmest month (bio 5; see Appendix S1). We used the mean PC scores of the first axis for each species as a metric of average niche position.

Niche breadth between insular and mainland *Anolis* lizards and among *Anolis* clades

Caribbean *Anolis* species did not have lower niche breadth values than their mainland counterparts (Fig. 1a; $F_{1, 330} = 3.32$, $p < 0.069$). However, after controlling for geographical range size effects, niche breadths do differ between regions (ANCOVA; $F_{1, 308} = 4.24$, $p < 0.040$). Furthermore, we did not find any differences in niche breadth between clades (Fig. 1b; $F_{10, 321} = 1.57$, $p < 0.114$), but we did detect differences after controlling for range size differences (ANCOVA; $F_{10, 299} = 2.35$, $p = 0.011$).

Occupied niche space in *Anolis* clades and available climate space

Comparisons of occupied niche space with available climate conditions across regions revealed that the occupation of niche space differed strikingly between insular and mainland lineages (Fig. 2 and 3). Insular anole clades seem to occupy almost all climate conditions available on each of the Greater Antilles islands, except Jamaica (Fig. 2). In contrast, mainland anoles occupy only a portion of all available climate conditions both in Middle America and South America. The *Norops* clade occupies a larger thermal and water niche space than *Dactyloa* does in Middle America, but in South America both clades occupy similar portions of the niche space (Fig. 3).

The clade-based approach

Path analysis revealed a significant correlation between species richness (total diversification) and occupied niche space for all anole clades (R=0.71, *p*=0.015; Fig. 4a). Furthermore, occupied niche space had an indirect influence on species richness through clade area (partial r = 0.79). Average niche breadth was not correlated with species richness (R=0.02, *p*=0.950; Fig. 4b), nor did it have any indirect influence on species richness through clade area (partial r = 0.22). For insular clades, niche attributes (occupied niche space and average niche breadth) were not correlated with species richness (Fig. 4c,d). Similar results were obtained using net diversification rates for *Anolis* clades (see Fig. S2 in Appendix S2). This suggests that our results are robust to differences in the diversification metrics used (i.e., total diversification and net diversification rates).

The QuaSSE approach

We found an association between niche attributes (niche position and niche breadth) and speciation rates for all *Anolis* lizards (Table 2). For niche position and niche breadth, we found that the best model was one with a humped directional trend (Table 2, Fig. 5 upper; though according to AIC values for niche breadth this model had no more support than the linear model with a directional trend). This suggests that speciation rates are higher in lineages occupying warmer areas and for lineages with very narrow niches and some with large niches. For Caribbean anoles, we found that the best model for niche position was one with a directional linear trend (Table 2, Fig. 5 bottom left; again, comparing AIC values for this model had no more support than the hump model with a directional trend). The best model for niche breadth for Caribbean anoles was one with a humped directional trend (Table 2; Fig. 5 bottom right). This suggests that speciation rates are higher in Caribbean anole lineages occupying warmer regions and with very small niches than in lineages occupying cold climates and with large niches. Finally, the association between niche traits and speciation rates for Caribbean *Anolis* lizards found here was stable to the different percentage of random taxon pruning (see Appendix S3). Therefore our QuaSSE analyses were robust to the taxonomic incompleteness in our dataset.

DISCUSSION

In this study, we found evidence of an association between niche traits and cladogenesis in *Anolis* lizards. First, we found that anole species occurring in warmer and drier regions tend to diversify more than species in humid and cold regions. This result was consistent for mainland and Caribbean anole species. In particular, Caribbean anole clades tend to occupy all available climate space in comparison with mainland anoles. This suggests that Caribbean clades are not likely constrained by an inability to expand their climatic niche limits, but rather, by the limited Caribbean climate space (Algar & Mahler, 2015). In fact, Caribbean species might not be prevented from inhabiting cold conditions by evolutionary constraints on cold tolerance, which can evolve quickly (Leal & Gunderson, 2012; Muñoz *et al*., 2014), but rather by climatic availability in the region (Algar & Mahler, 2015). The limited climatic space, coupled with the high species richness of these clades, suggests substantial niche overlap in insular species, though this may be mediated in part by narrower niche breadths. Furthermore, the high degree of similarity in niche traits for Caribbean anoles, suggests that climate niche convergence might be a widespread phenomenon across the Greater Antilles, as found for phenotypic traits (Losos *et al*., 1998; Mahler *et al*., 2013). This pattern might be the result of a combination of reduced climatic space in the region and a strong effect of stabilizing selection on climatic niches (Sedio *et al*. 2013; Wüest *et al*., 2015).

Mainland clades occupy only a portion of the climatic space within their accessible area (Peterson *et al*., 2011), but these clades still exhibited greater niche breadth and broader niche space values than insular clades. Mainland clades may have been prevented from exploiting the complete available climate space either because of insufficient time for niche diversification (though this is unlikely for the *Dactyloa* clade given its age: 30 Ma; see Table 1), inability to adapt to extreme climate conditions, strong biotic interactions, or dispersal constraints. As mainland anole species tend be absent from regions with extreme temperatures (e.g., mountaintops exceeding 3,000 m or desert areas) anoles may have physiological constraints that prevent them from inhabiting regions with these extreme climate conditions. However, whether mainland anoles are more limited in range by current climate, dispersal limitations or biotic interactions than Caribbean anoles are (Algar *et al*., 2013), remains unknown.

We found strong evidence of a negative relationship between niche breadth and diversification rates. This suggests that niche specialization, particularly toward warmer and drier climates, has driven anole diversification. This association between niche specialization and cladogenesis suggest a strong role of climate in anole diversification. Similar results have been found in lampropeltine snakes, for which lineages occurring in warm conditions had higher speciation rates (Pyron & Burbrink, 2012). Finally, we found that clades with higher species richness tend to exhibit more niche diversity (occupied niche space) than species-poor clades. These results support the hypothesis that cladogenesis is coupled with climate niche divergence in *Anolis* lizards (Rabosky 2012a, Rabosky *et al*., 2013). Recently, Gómez-Rodríguez *et al*. (2015) suggested that a negative relationship between niche width and diversification rates would be expected under a scenario of niche conservatism (Wiens, 2004). In contrast, they suggested that a positive relationship would be expected under a scenario of climatic niche divergence (Moritz *et al*., 2000). However, it is not clear how these niche conservatism or niche divergence patterns can shape diversification dynamics at regional scales. In our opinion, the evolutionary mechanisms underlying the correlation between climatic niche traits and speciation dynamics are still unknown.

Our study is the first to examine how climatic niches vary among *Anolis* lizards at large phylogenetic and geographical scales, and how climatic niche traits are related to species diversification. We found that Caribbean and mainland anoles exhibit striking differences in niche traits (after controlling for range size effects) and these are correlated with speciation rates. Specifically, we found that lineages with narrow niches and that are specialized to warmer areas have diversified more than lineages with large niches and specialized to cold regions. Niche differences in insular and mainland anoles suggest that different evolutionary processes (niche divergence or niche conservatism) might be operating between regions, as in the case of ecomorphological traits (Pinto *et al*., 2008). However, it is crucial that a more comprehensive phylogeny for mainland anoles be incorporated to corroborate these findings using comparative phylogenetic methods. Finally, our study found interesting macroecological and macroevolutionary patterns, but more research is necessary to identify the potential evolutionary mechanisms driving these patterns.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Results of the Principal Components Analysis for 19 bioclimatic variables.

Appendix S2 Supplementary figures.

Appendix S3 Effects of missing species on the QuaSSE analysis.

Biosketch

Julián A. Velasco is carrying out his Ph.D studies at the Instituto de Biología, Universidad Nacional Autónoma de México. His doctoral research focuses on understanding the ecological and evolutionary processes responsible for species richness gradients and diversification in *Anolis* lizards. He addresses several evolutionary and ecological topics using a combination of conceptual and methodological approaches including niche modelling, geospatial analysis, historical biogeography and macroecology.

Author contributions: JAV conceived the ideas and analysed the data; EMM, OFV and AGA, and ACA provided feedback and contributed ideas; ACA, GK and OFV collected the occurrence records for *Anolis* species; JMD performed the phylogenetic analysis; JAV led the writing and had the approval of all the authors.

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Tables

Table 1. Clades recognized in *Anolis* radiation, species richness, range size (log10 km^2), age, net diversification rates (Net div. rates; extinction fraction 0.9/0.1), occupied niche space (Occ. niche space), niche breadth (log10) and distribution.

Clade	Species richness	Range size	Age (Ma)	Net divers. rates	Occ. niche space	Niche breadth	Distribution
Anolis	44	5.095	30.090	0.054/0.102	3.076	1.542	Bahamas, Cayman islands, Cuba, Hispaniola, south of Florida.
Lesser Antilles *Dactyloa*	9	3.210	25.510	0.021/0.059	1.34	1.513	Southern Lesser Antilles.
Mainland *Dactyloa*	83	7.053	30.980	0.072/0.122	16.496	2.640	Lower Central America and South America.
Audantia	9	4.921	22.860	0.023/0.059	7.968	1.779	Hispaniola and satellite islands.
Chamaelinorops	16	4.863	30.850	0.028/0.067	7.432	1.704	Hispaniola and satellite islands.
Ctenonotus	36	4.945	30.870	0.047/0.093	5.2	1.779	Bahamas, Hispaniola, Puerto Rico, Virgin Islands, Northern Lesser Antilles.
Deiroptyx	21	5.270	32.100	0.033/0.073	4.861	1.704	Cuba, Hispaniola, Puerto Rico.
Xiphosurus	11	5.170	30.030	0.021/0.057	4.199	1.736	Cuba, Hispaniola, Puerto Rico and satellite islands.

Cuban *Norops*	18	5.110	28.950	0.029/0.068	1.986	2.640	Cuba.
Jamaican *Norops*	7	4.090	25.270	0.016/0.049	2.575	1.382	Jamaica.
Mainland *Norops*	150	7.140	32.310	0.090/0.142	14.148	2.707	Middle and South America.

Table 2. QuaSSE models of the relationship between climatic niche metrics (niche position and niche breadth) and speciation rates in all *Anolis* and only Caribbean *Anolis* lizards. Best-fitting models according to delta AIC (Akaike information criterion) values are in bold. Pars: Number of parameters; lnL: ln Likelihood; AIC: Akaike Information Criterion; ΔAIC: Delta AIC; Weights: model weights.

			Niche position				Niche breadth			
	Model	Pars	lnL	AIC	ΔAIC	Weights	lnL	AIC	ΔAIC	Weig
All *Anolis*	Minimal	3	-937.95	1881.9	48	0.00	-683.31	1372.6	45	0.0
	Linear	4	-937.89	1883.8	50	0.00	-683.22	1374.5	47	0.0
	Sigmoidal	6	-937.06	1886.1	52	0.00	-682.91	1377.8	51	0.0
	Hump	6	936.28	1884.5	51	0.00	-682.81	1377.6	50	0.0
	Linear (drift)	**5**	-917.36	1844.7	11	0.00	**-659.16**	**1328.3**	**1**	**0.2**
	Sigmoidal (drift)	7	-917.92	1849.8	16	0.00	-662.35	1338.7	12	0.0
	Hump (drift)	**7**	**-909.91**	**1833.8**	**0**	**0.38**	**-656.58**	**1327.2**	**0**	**0.3**

Caribbean *Anolis*	Minimal	3	-652.3	1310.5	24	0.00	-391.7	789.5	16	0.0
	Linear	4	-652.2	1312.5	26	0.00	-391.7	791.4	18	0.0
	Sigmoidal	6	-651	1314	27	0.00	-391.7	795.3	22	0.0
	Hump	6	-649.4	1310.8	24	0.00	-391.7	795.3	22	0.0
	Linear (drift)	**5**	**-638.4**	**1286.8**	**0**	**0.38**	-391.4	792.7	20	0.0
	Sigmoidal (drift)	**7**	-641.2	1296.3	9	0.00	**-379.5**	**773.1**	**0**	**0.3**
	Hump (drift)	**7**	**-637.2**	**1288.3**	**1**	**0.23**	-391.7	797.3	24	0.0

Figure Legends

Figure 1. Box plots of niche breadth values for Caribbean and mainland *Anolis* species (a) and *Anolis* clades (b). Niche breadth was estimated using maximum Mahalanobis distances to the niche centroid for 19 bioclimatic variables in a multidimensional climatic niche space. *Dactyloa* LA: *Dactyloa* Lesser Antilles.

Figure 2. Occupied climate niche space for Caribbean anole clades in each one of the Greater Antilles islands. Light grey points represent the available climate conditions in each island extracted from each pixel (see text for details).

Figure 3. Occupied climate niche space for mainland anole clades in Middle America and South America. Light grey points represent the available climate conditions in each mainland region extracted from a random sample of pixels (see text for details)

Figure 4. Direct and indirect effects of climatic niche traits (occupied niche space and niche breadth) on species richness for all anole clades (a,b), and only for insular clades (c,d). Statistically significant correlation coefficients are in bold ($p < 0.05$).

Figure 5. Relationships between niche traits (mean niche position and niche breadth) and speciation rates for all anoles lizards (upper) and Caribbean anoles only (bottom) using the QuaSSE approach. Dotted lines represent alternative models according to delta AIC values (see table 2).

Figure 1

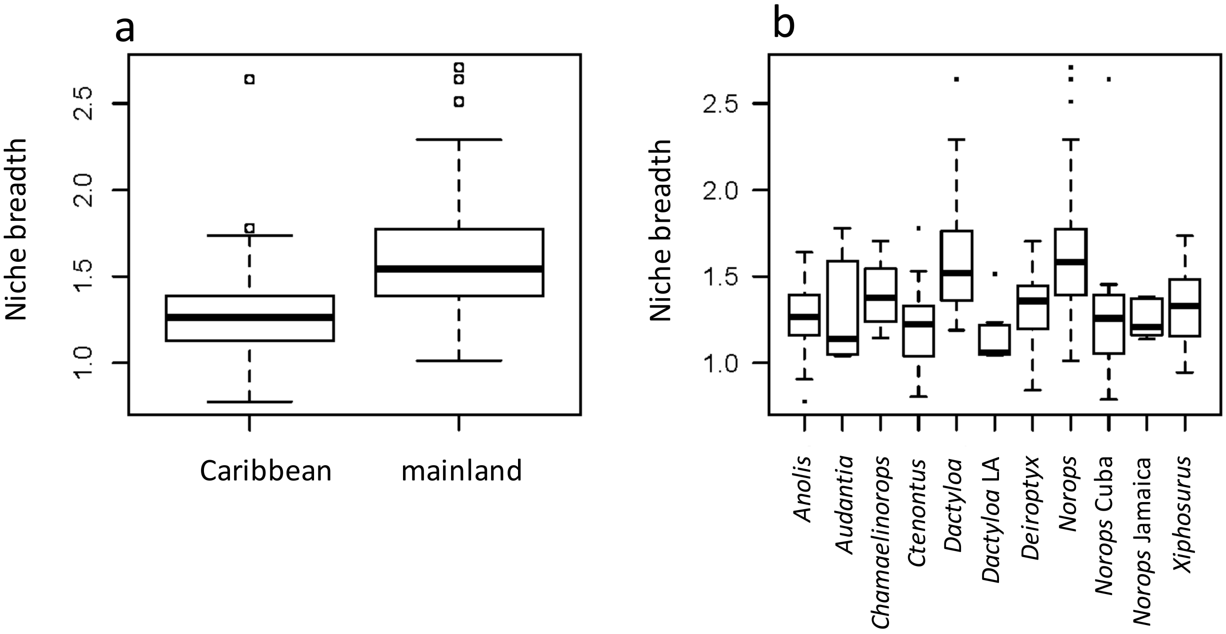

a
Niche breadth
1.0
1.5
2.0
2.5
Caribbean
mainland
b
Niche breadth
1.0
1.5
2.0
2.5
Anolis
Audantia
Chamaelinorops
Ctenontus
Dactyloa
Dactyloa LA
Deiroptyx
Norops
Norops Cuba
Norops Jamaica
Xiphosurus

Figure 2

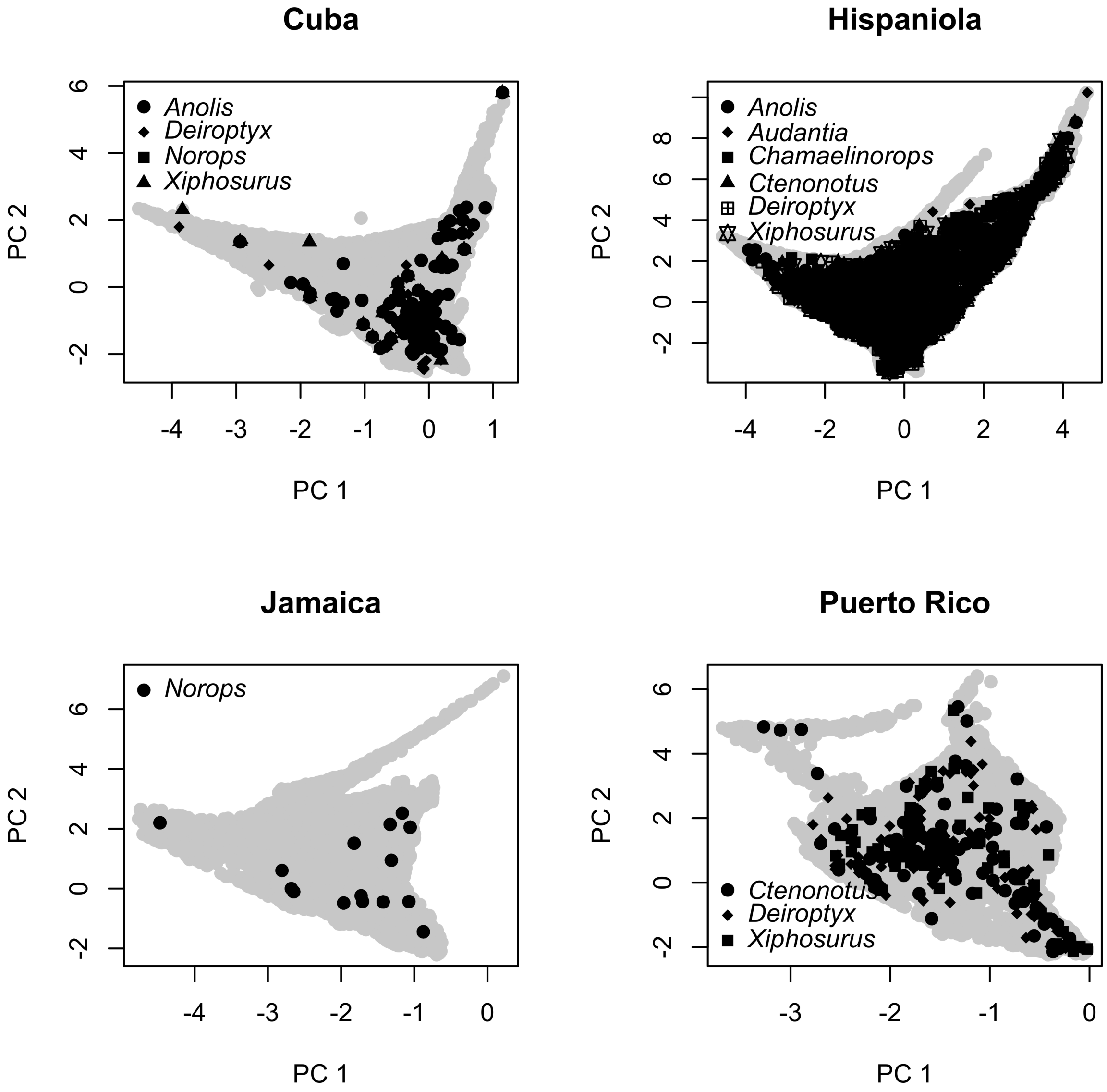

Cuba
Anolis
Deiroptyx
Norops
Xiphosurus
PC 2
PC 1
6
4
2
0
-2
-4
-3
-2
-1
0
1
Hispaniola
Anolis
Audantia
Chamaelinorops
Ctenonotus
Deiroptyx
Xiphosurus
PC 2
PC 1
8
6
4
2
0
-2
-4
-2
0
2
4
Jamaica
Norops
PC 2
PC 1
6
4
2
0
-2
-4
-3
-2
-1
0
Puerto Rico
Ctenonotus
Deiroptyx
Xiphosurus
PC 2
PC 1
6
4
2
0
-2
-3
-2
-1
0

Figure 3

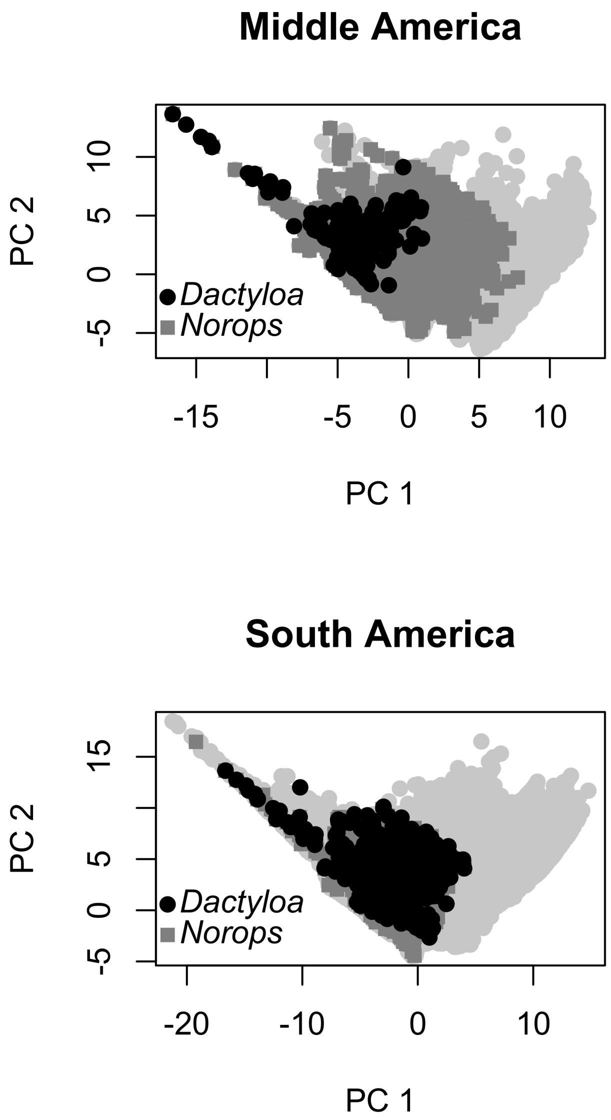

Middle America
PC 2
PC 1
-15
-5
0
5
10
-5
0
5
10
● Dactyloa
■ Norops
South America
PC 2
PC 1
-20
-10
0
10
-5
0
5
15
● Dactyloa
■ Norops

Figure 4

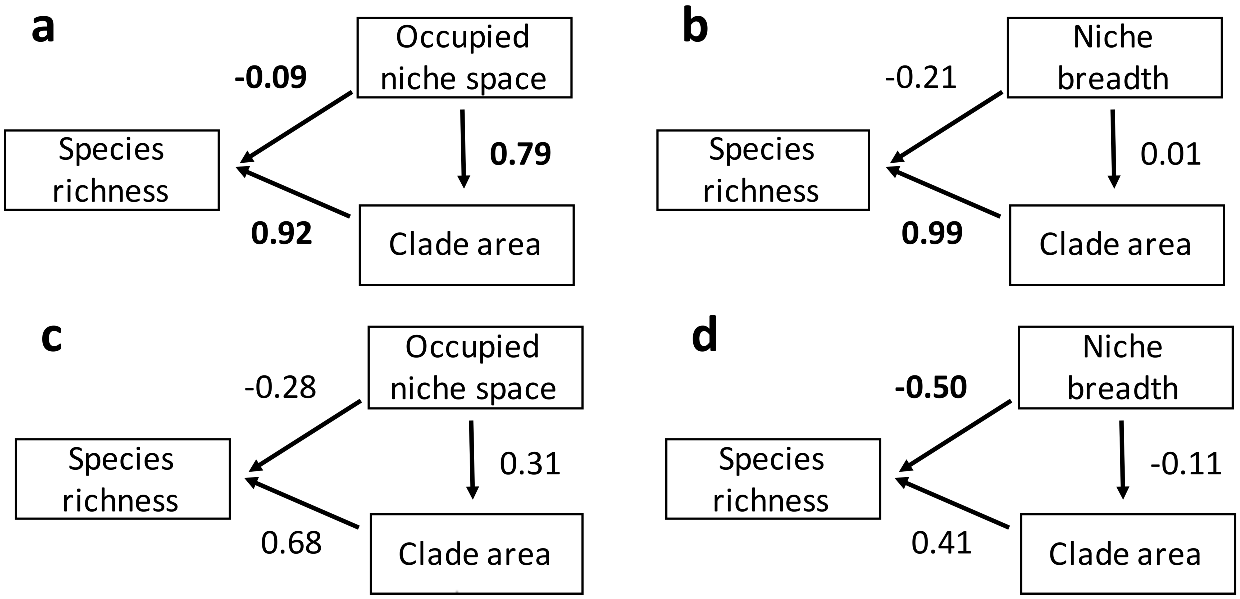
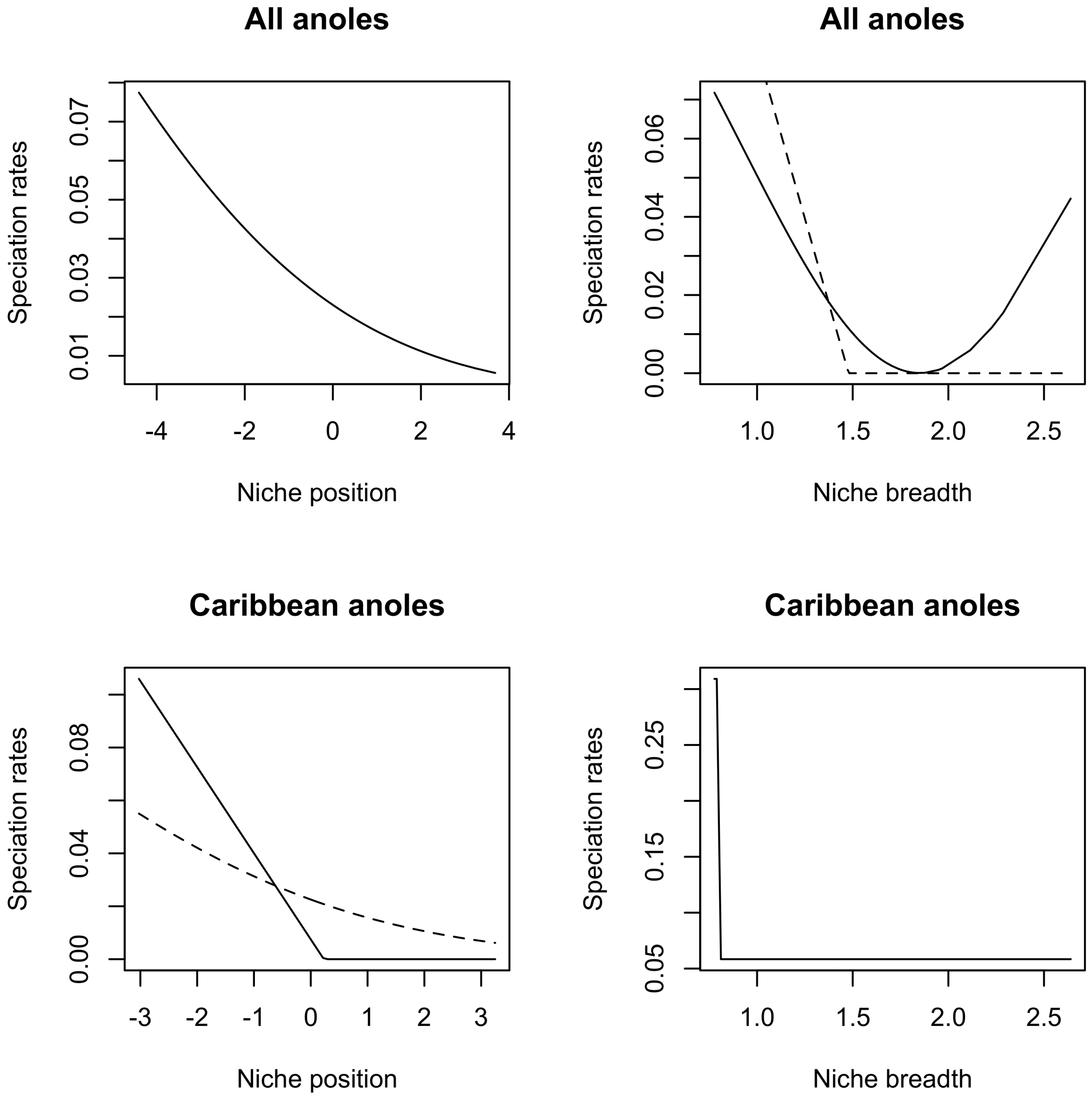

a
Occupied niche space
Species richness
Clade area
-0.09
0.79
0.92
b
Niche breadth
Species richness
Clade area
-0.21
0.01
0.99
c
Occupied niche space
Species richness
Clade area
-0.28
0.31
0.68
d
Niche breadth
Species richness
Clade area
-0.50
-0.11
0.41

Figure 5


All anoles
Speciation rates
0.01
0.03
0.05
0.07
-4
-2
0
2
4
Niche position
All anoles
Speciation rates
0.00
0.02
0.04
0.06
1.0
1.5
2.0
2.5
Niche breadth
Caribbean anoles
Speciation rates
0.00
0.04
0.08
-3
-2
-1
0
1
2
3
Niche position
Caribbean anoles
Speciation rates
0.05
0.15
0.25
1.0
1.5
2.0
2.5
Niche breadth