

1 Original Article

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

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

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29 **ABSTRACT**

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

36 **Location** Neotropics

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

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

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

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

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60 INTRODUCTION

61 Species richness in a clade or region results from the interplay of ecological and
62 evolutionary factors operating at different spatial and temporal scales (Wiens,
63 2011; Cornell, 2013). Species richness in a region can ultimately be explained by
64 differences in diversification rates (i.e., speciation minus extinction) and dispersal
65 events (Wiens & Donoghue, 2004; Wiens, 2011). Although species diversification
66 is known to be influenced by ecological factors within a particular region (Wiens,
67 2011; Cornell, 2013; Machac *et al.*, 2013), there is still little understanding of how
68 variation in ecological factors affects species diversification, and thus species
69 richness, across phylogenetic and geographic scales.

70 Ecology, diversification, and species richness are linked through the niche
71 concept (Hutchinson, 1957; Soberón & Nakamura, 2009; Ricklefs, 2012). For
72 instance, some recent studies have shown that speciation rates are coupled with
73 rates of niche evolution (Rabosky, 2012a; Rabosky & Adams, 2012; Rabosky *et*
74 *al.*, 2013). Accordingly, clades displaying a high degree of species richness are
75 expected to have greater niche diversity than clades with low species richness
76 (Rabosky, 2012a; Ricklefs, 2012; Rabosky *et al.*, 2013). This prediction is an
77 expected outcome during adaptive radiation where slowdowns in diversification
78 occur as ecological space is filled and species' niches become narrow due to
79 competition (Schluter, 2000; Rabosky, 2009). In this way, niche divergence can
80 drive cladogenesis. Alternatively, diversification may not be ecologically
81 constrained but rather, time or area dependent (Wiens, 2011). In cases where
82 cladogenesis is decoupled from niche evolution, we would expect lineages to

83 have greater niche similarity and large niche breadths (Cornell, 2013). The above
84 scenarios have been explored mostly using phenotypic traits related to habitat use
85 (Schluter, 2000; Harmon *et al.*, 2003). Only recently have some studies explored
86 the role of coarse-grain climatic niche attributes in clade diversification (Kozak &
87 Wiens, 2010; Pyron & Burbrink, 2012; Schnitzler *et al.*, 2012; Machac *et al.*, 2013;
88 Wiens *et al.*, 2013; Kostikova *et al.*, 2014).

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

105 In this paper, first, we hypothesize a link between climatic niche metrics
106 (i.e., niche position and niche breadth) and diversification in *Anolis* lizards. For
107 niche position, we predict that lineages occupying warmer and drier areas (where
108 anole diversity is higher; Algar & Losos, 2011; Losos, 2009) tend to diversify more
109 than lineages adapted to cold and very humid conditions (where their diversity is
110 lower). For niche breadth, we predict that clades composed of climatic niche
111 specialist species (i.e., with narrow niche breadths) will have higher diversification
112 rates than lineages composed of climatic niche generalist species (i.e., wide niche
113 breadths) (Futuyma & Moreno, 1988; Cantalapiedra *et al.*, 2011; Cadena *et al.*,
114 2012; Wiens *et al.*, 2013). This hypothesis predicts a negative relationship
115 between diversification rates and niche breadth, a relationship that likely is
116 mediated by climatic niche conservatism (Gómez-Rodríguez *et al.*, 2015). Second,
117 we hypothesize that clades with high species richness (and likely high
118 diversification rates) will have a high degree of niche diversity (i.e., more occupied
119 niche space) than clades poor in species (Ricklefs, 2012). This is consistent with a
120 scenario where cladogenesis is driven by niche evolution rates (Harmon *et al.*,
121 2003; Rabosky *et al.*, 2013).

122 We test these hypotheses for *Anolis* lizards, which occur mainly in the
123 Caribbean islands and on the mainland from Mexico to southern Brazil. They are
124 species-rich on both the islands (~160 species) and the mainland (~230 species;
125 Table 1). The evolutionary history of Caribbean *Anolis* has been subjected to
126 intense research in the last several decades (Losos, 2009). There is evidence that
127 their diversification in the Greater Antilles is related to island size and colonizing

128 time, with speciation rates declining over time as a function of area (Rabosky &
129 Glor, 2010). This pattern suggests that regional species richness in the Greater
130 Antilles is controlled by area and potentially by competitive interactions (Losos &
131 Schluter, 2000; Rabosky & Glor, 2010). Specifically, we predict that *Anolis* lizards
132 with narrow climatic niches and specialization toward particular climate regimes
133 have diversified more than those that tolerate a wide range of climate conditions
134 (Kozak & Wiens, 2010).

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

142 **MATERIALS AND METHODS**

143 ***Anolis* records**

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

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

159

160 **Climatic niche metrics in *Anolis* lizards**

161 We estimated the climatic niche represented by temperature and precipitation
162 variables drawn from the WorldClim database (Hijmans *et al.*, 2005) using the
163 occurrence records of 328 species. Our climatic niche estimates encompass the
164 realized niche as is common in GIS approaches (Peterson *et al.*, 2011). To
165 estimate the niche breadth for each *Anolis* species, we used maximum
166 Mahalanobis distances (Rotenberry *et al.*, 2006); a statistical technique for
167 ecological niche modelling based on presence-only records (Peterson *et al.*,
168 2011). The Mahalanobis distance measures the space between two points in a n -
169 dimensional coordinate system accounting for unequal variances and correlation
170 between variables (Xian *et al.*, 2008). Distances are simply calculated as a
171 standardized difference between the value of any point (i.e., a species' record)
172 and the mean values from all points from the climate space (Rotenberry *et al.*,

173 2006). Also, we estimated niche breadth using Euclidean distances and ran a
174 correlation of niche breadth between both distance methods, which was highly
175 significant ($p < 0.0001$).

176 We characterized the available climatic space for each region in which each
177 clade occurs. For each island in the Greater Antilles we extracted values for
178 bioclimatic variables for all pixels (1 km² pixel size). For the mainland, we
179 generated a minimum convex polygon for Middle American and South American
180 anole records with a buffer of 1,000 km in each area. Note that here Middle
181 America refers to the countries of Central America and Mexico. This polygon
182 potentially represents at least the dispersal or movement area for mainland anole
183 species (Peterson & Soberón, 2012; Saupe *et al.*, 2012). We clipped all bioclimatic
184 rasters using this polygon and extracted values for all 19 variables from a random
185 set of pixels (>100,000 pixels of 1 km² each for South America, and >25,000 pixels
186 of 1 km² each for Middle America). We conducted a Principal Components
187 Analysis (PCA) with all 19 bioclimatic variables from species records and points
188 from each region (see Appendix S1 in Supporting Information). For each anole
189 species we calculated the mean of the scores of the first PC as an estimate of
190 niche position. Finally, we calculated range size for each species as the area
191 within the minimum convex polygon (MCP) enclosing all records for individual
192 species and for anole clades. The MCP was only used to calculate range sizes,
193 which were used as covariates for comparisons of niche breadth between clades
194 and regions.

195

196 **Phylogenetic estimation**

197 We generated a time-calibrated phylogeny using an *Anolis* dataset extracted from
198 a recent Squamata phylogeny (Pyron *et al.*, 2013). Our anole tree comprises 207
199 anole species, representing 53% of the total number of recognized anole species
200 (Uetz, 2014). Although sampling was very complete for the Caribbean anole
201 species (87%, 19 species missing), and was very incomplete for the mainland
202 species (76 species, 32% of all known species). We also included 32 outgroups
203 based on the topological position of *Anolis* in the Iguania phylogeny (Townsend *et*
204 *al.*, 2011). The assembled matrix included 233 taxa and 12,896 sites
205 corresponding to 9 genes included in Pyron *et al.* (2013). We used their alignment
206 to maintain consistency among studies. We used only two calibration points due
207 to the low availability of fossil samples. First, using a normal distribution prior we
208 calibrated the root with the crown-group pleurodont iguanian *Saichangurvel*
209 (Conrad & Norell, 2007) from the Late Campanian (70.6 ± 0.6 Ma; Townsend *et al.*,
210 2011). Second, a lognormal prior with a minimum age of 23 Ma was used to
211 calibrate the *Anolis chlorocyanus* group based on an unnamed fossil from the
212 Dominican Republic putatively assigned to this clade (de Queiroz *et al.*, 1998). We
213 placed this anole fossil at the stem of the *chlorocyanus* group (*A. aliniger*, *A.*
214 *chlorocyanus*, *A. coelestinus*, *A. singularis*) following Nicholson *et al.* (2012). We
215 implemented a relaxed clock method with uncorrelated rates among branches
216 using the software BEAST 1.8.0 (Drummond *et al.*, 2012). We did not implement a
217 highly parameterized partitioned analysis as the ingroup (*Anolis*) is represented
218 almost entirely by one single gene (ND2). As suggested by jModeltest v.2

219 (Guindon & Gascuel 2003; Darriba *et al.*, 2012) we used the GTRGI model of
220 evolution for the entire dataset. We initiated two runs starting from a random tree
221 and ran these for 40 million generations sampling every 1,000 following a burn-in
222 of 2 million generations. The number of generations required to reach stationarity
223 was determined by examining marginal probabilities in Tracer v1.6 (Rambaut *et*
224 *al.*, 2014). For each run, the posterior sampling of trees yielded an effective
225 sample size (ESS) of >200 for all parameter models. Both runs were combined as
226 they gave similar results, and node and branch parameters were summarized on
227 the maximum clade credibility tree (see Fig. S1 in Appendix S2). The resulting tree
228 was very similar in topology to recent phylogenetic estimates of *Anolis* lizards
229 using the same datasets (Mahler *et al.*, 2010; Nicholson *et al.*, 2012; Gamble *et al.*,
230 2014; Prates *et al.*, 2015). In particular, Prates *et al.* (2015) generated a calibrated
231 tree for a subset of *Anolis* species (some species from *Dactyloa* clade, *Anolis*
232 *carolinensis* and some species from *Norops* clade) using three fossils as
233 calibration points and lying outside of the *Anolis* ingroup (one in the root, and two
234 inside the outgroup). Their estimated dates for the most recent common ancestor
235 (MRCA) of *Anolis* are very similar to our estimated dates (see Prates *et al.*, 2015).

236

237 **Climatic niche attributes and diversification in *Anolis* lizards**

238 *i) The clade-based approach*

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

242 Poe, 2013). We used these same names as clades to compare niche attributes.
243 Although the criteria to delimit these clades is arbitrary, the same problem occurs
244 with the use of recognized taxa of a given rank (e.g., family or genus level);
245 additionally, some of these clade names for anoles have been used by some
246 herpetologists for almost three decades (Guyer & Savage, 1986; Savage, 2002).
247 We separated the *Norops* clade into three: Cuban *Norops*, Jamaican *Norops* and
248 mainland *Norops*, and also split the *Dactyloa* clade: Lesser Antillean *Dactyloa* and
249 mainland *Dactyloa* (Table 1). We obtained species richness data for each clade
250 from Nicholson *et al.* (2012). For each clade, we calculated occupied niche space
251 as the summed variances of the first four PC scores (see above). This measure of
252 occupied niche space can be considered a proxy for niche diversity, analogous to
253 the measures of morphological variance used in studies of morphological disparity
254 (Foote, 1997; Wainwright, 2004; Ricklefs, 2012). We can use the species richness
255 (ln species richness) of anole clades as a direct estimator of the total
256 diversification in each clade (the Ω estimator in Rabosky, 2009) because anole
257 clade diversity was not correlated with age ($R^2 = 0.30$, $p = 0.124$) (Rabosky, 2009,
258 2012b; Rabosky & Adams, 2012). In addition, we calculated net diversification
259 rates for each anole clade using the method-of-moments estimator (Magallón &
260 Sanderson, 2001), based on the crown-group age (obtained from our calibrated
261 tree) and the total number of described species for each clade, and using two
262 values for relative extinction rate (0.9 and 0.1). We tested for a relationship
263 between occupied niche space, clade area (log₁₀ geographical area) and species
264 richness (ln species richness) and net diversification rates in *Anolis* clades using a

265 path analysis. We repeated the same analysis using only insular clades. This
266 approach allowed us to incorporate all of the anole species for which we had
267 compiled climate data.

268 *ii) The QuaSSE approach*

269 We implemented a quantitative-state speciation and extinction model (QUASSE;
270 FitzJohn, 2012) to correlate niche attributes (mean niche position and niche
271 breadth) with diversification rates (FitzJohn, 2010). The QuaSSE approach uses a
272 maximum likelihood method to evaluate whether a distribution of continuous
273 character states is associated with higher or lower speciation rates (FitzJohn,
274 2010). This method has been used previously to find associations between climate
275 and diversification rates in other taxonomic groups (Pyron & Wiens, 2013;
276 Kostikova *et al.*, 2014). We explored whether mean niche position and niche
277 breadth were associated with speciation rates in *Anolis* lizards. These niche metrics
278 describe the ecological niche of a species across a set of environmental axes
279 (Schoener, 1989; Thuiller *et al.*, 2005). The QuaSSE approach identifies whether
280 lineages exhibiting lower or higher niche positions/broader or narrower niche
281 breadths are correlated with higher speciation rates in *Anolis*.

282 We generated four models in which speciation rates were fitted according to a
283 particular function: (i) constant function (trait variation has no influence on
284 speciation rate); (ii) linear function (a linear increase in a trait is associated with a
285 linear increase in speciation rate); (iii) a sigmoid function (there is an association
286 between speciation rates and a continuous trait exhibiting a sigmoidal function),

287 and (iv) a modal function (where intermediate values for a trait are associated with
288 a higher speciation rate). In addition, we generated another set of models, but
289 assuming a directional trend in the evolution of the particular trait (FitzJohn, 2012).
290 We kept extinction rates constant among models because QuaSSE is known for
291 its difficulty detecting differences in extinction rates (FitzJohn, 2010). We
292 conducted the same analysis but only for the Caribbean species by pruning all
293 mainland species from the phylogeny. We did not conduct a specific analysis for
294 mainland species only due to the limited taxon sampling for these species (see
295 above). Models were compared using the Akaike Information Criterion (Burnham &
296 Anderson, 2002) and we selected as the best models those with the lowest AIC
297 scores (Burnham & Anderson, 2002). As QuaSSE calculations are quite complex
298 and computationally extensive (FitzJohn, 2012), we only performed a QuaSSE
299 analysis for each variable with the best topology selected from our BEAST
300 analysis. Therefore, we were not able to evaluate the potential effects of
301 phylogenetic uncertainty on correlations between speciation rates and niche traits.
302 Finally, we performed a rarefaction analysis for the Caribbean anole tree to
303 evaluate the impact of missing species on the QuaSSE analysis. We randomly
304 pruned species in a sequence of percentages (10%, 15%, 20%, 25%, 30%, 35%,
305 40%, 45% and 50%) and generated a QuaSSE analysis for each dataset with
306 these pruned trees. The aim was to evaluate whether QuaSSE is sensitive to
307 missing species and therefore to explore the potential impact of taxon
308 incompleteness on the association between traits and diversification (see
309 Appendix S3).

310 **RESULTS**

311 **Anole climatic niches**

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

319

320 **Niche breadth between insular and mainland *Anolis* lizards and among *Anolis*** 321 **clades**

322 Caribbean *Anolis* species did not have lower niche breadth values than their
323 mainland counterparts (Fig. 1a; $F_{1,330} = 3.32, p < 0.069$). However, after
324 controlling for geographical range size effects, niche breadths do differ between
325 regions (ANCOVA; $F_{1,308} = 4.24, p < 0.040$). Furthermore, we did not find any
326 differences in niche breadth between clades (Fig. 1b; $F_{10,321} = 1.57, p < 0.114$),
327 but we did detect differences after controlling for range size differences (ANCOVA;
328 $F_{10,299} = 2.35, p = 0.011$).

329

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

331 Comparisons of occupied niche space with available climate conditions across
332 regions revealed that the occupation of niche space differed strikingly between

333 insular and mainland lineages (Fig. 2 and 3). Insular anole clades seem to occupy
334 almost all climate conditions available on each of the Greater Antilles islands,
335 except Jamaica (Fig. 2). In contrast, mainland anoles occupy only a portion of all
336 available climate conditions both in Middle America and South America. The
337 *Norops* clade occupies a larger thermal and water niche space than *Dactyloa*
338 does in Middle America, but in South America both clades occupy similar portions
339 of the niche space (Fig. 3).

340

341 **The clade-based approach**

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

353 **The QuaSSE approach**

354 We found an association between niche attributes (niche position and niche
355 breadth) and speciation rates for all *Anolis* lizards (Table 2). For niche position and

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

372 **DISCUSSION**

373 In this study, we found evidence of an association between niche traits and
374 cladogenesis in *Anolis* lizards. First, we found that anole species occurring in
375 warmer and drier regions tend to diversify more than species in humid and cold
376 regions. This result was consistent for mainland and Caribbean anole species. In
377 particular, Caribbean anole clades tend to occupy all available climate space in

378 comparison with mainland anoles. This suggests that Caribbean clades are not
379 likely constrained by an inability to expand their climatic niche limits, but rather, by
380 the limited Caribbean climate space (Algar & Mahler, 2015). In fact, Caribbean
381 species might not be prevented from inhabiting cold conditions by evolutionary
382 constraints on cold tolerance, which can evolve quickly (Leal & Gunderson, 2012;
383 Muñoz *et al.*, 2014), but rather by climatic availability in the region (Algar & Mahler,
384 2015). The limited climatic space, coupled with the high species richness of these
385 clades, suggests substantial niche overlap in insular species, though this may be
386 mediated in part by narrower niche breadths. Furthermore, the high degree of
387 similarity in niche traits for Caribbean anoles, suggests that climate niche
388 convergence might be a widespread phenomenon across the Greater Antilles, as
389 found for phenotypic traits (Losos *et al.*, 1998; Mahler *et al.*, 2013). This pattern
390 might be the result of a combination of reduced climatic space in the region and a
391 strong effect of stabilizing selection on climatic niches (Sedio *et al.* 2013; Wüest *et*
392 *al.*, 2015).

393 Mainland clades occupy only a portion of the climatic space within their
394 accessible area (Peterson *et al.*, 2011), but these clades still exhibited greater
395 niche breadth and broader niche space values than insular clades. Mainland
396 clades may have been prevented from exploiting the complete available climate
397 space either because of insufficient time for niche diversification (though this is
398 unlikely for the *Dactyloa* clade given its age: 30 Ma; see Table 1), inability to adapt
399 to extreme climate conditions, strong biotic interactions, or dispersal constraints.
400 As mainland anole species tend to be absent from regions with extreme

401 temperatures (e.g., mountaintops exceeding 3,000 m or desert areas) anoles may
402 have physiological constraints that prevent them from inhabiting regions with
403 these extreme climate conditions. However, whether mainland anoles are more
404 limited in range by current climate, dispersal limitations or biotic interactions than
405 Caribbean anoles are (Algar *et al.*, 2013), remains unknown.

406 We found strong evidence of a negative relationship between niche breadth
407 and diversification rates. This suggests that niche specialization, particularly
408 toward warmer and drier climates, has driven anole diversification. This
409 association between niche specialization and cladogenesis suggest a strong role
410 of climate in anole diversification. Similar results have been found in lampropeltine
411 snakes, for which lineages occurring in warm conditions had higher speciation
412 rates (Pyron & Burbrink, 2012). Finally, we found that clades with higher species
413 richness tend to exhibit more niche diversity (occupied niche space) than species-
414 poor clades. These results support the hypothesis that cladogenesis is coupled
415 with climate niche divergence in *Anolis* lizards (Rabosky 2012a, Rabosky *et al.*,
416 2013). Recently, Gómez-Rodríguez *et al.* (2015) suggested that a negative
417 relationship between niche width and diversification rates would be expected
418 under a scenario of niche conservatism (Wiens, 2004). In contrast, they suggested
419 that a positive relationship would be expected under a scenario of climatic niche
420 divergence (Moritz *et al.*, 2000). However, it is not clear how these niche
421 conservatism or niche divergence patterns can shape diversification dynamics at
422 regional scales. In our opinion, the evolutionary mechanisms underlying the

423 correlation between climatic niche traits and speciation dynamics are still
424 unknown.

425 Our study is the first to examine how climatic niches vary among *Anolis*
426 lizards at large phylogenetic and geographical scales, and how climatic niche
427 traits are related to species diversification. We found that Caribbean and mainland
428 anoles exhibit striking differences in niche traits (after controlling for range size
429 effects) and these are correlated with speciation rates. Specifically, we found that
430 lineages with narrow niches and that are specialized to warmer areas have
431 diversified more than lineages with large niches and specialized to cold regions.
432 Niche differences in insular and mainland anoles suggest that different
433 evolutionary processes (niche divergence or niche conservatism) might be
434 operating between regions, as in the case of ecomorphological traits (Pinto *et al.*,
435 2008). However, it is crucial that a more comprehensive phylogeny for mainland
436 anoles be incorporated to corroborate these findings using comparative
437 phylogenetic methods. Finally, our study found interesting macroecological and
438 macroevolutionary patterns, but more research is necessary to identify the
439 potential evolutionary mechanisms driving these patterns.

440

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451

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649 **Supporting Information**

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

651

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

654

655 **Appendix S2** Supplementary figures.

656 **Appendix S3** Effects of missing species on the QuaSSE analysis.

657

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659

660 **Biosketch**

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

668

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

673

674 Editor: Kostas Triantis

675 Tables

676 Table 1. Clades recognized in *Anolis* radiation, species richness, range size (log₁₀ km²), age, net diversification rates (Net
 677 div. rates; extinction fraction 0.9/0.1), occupied niche space (Occ. niche space), niche breadth (log₁₀) and distribution.
 678

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

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

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

Model	Pars	Niche position					Niche breadth			
		lnL	AIC	Δ AIC	Weights	lnL	AIC	Δ AIC	Weig	
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	
<i>All Anolis</i> 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	

	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
Caribbean <i>Anolis</i>	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

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688 Figure Legends

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

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

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

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

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

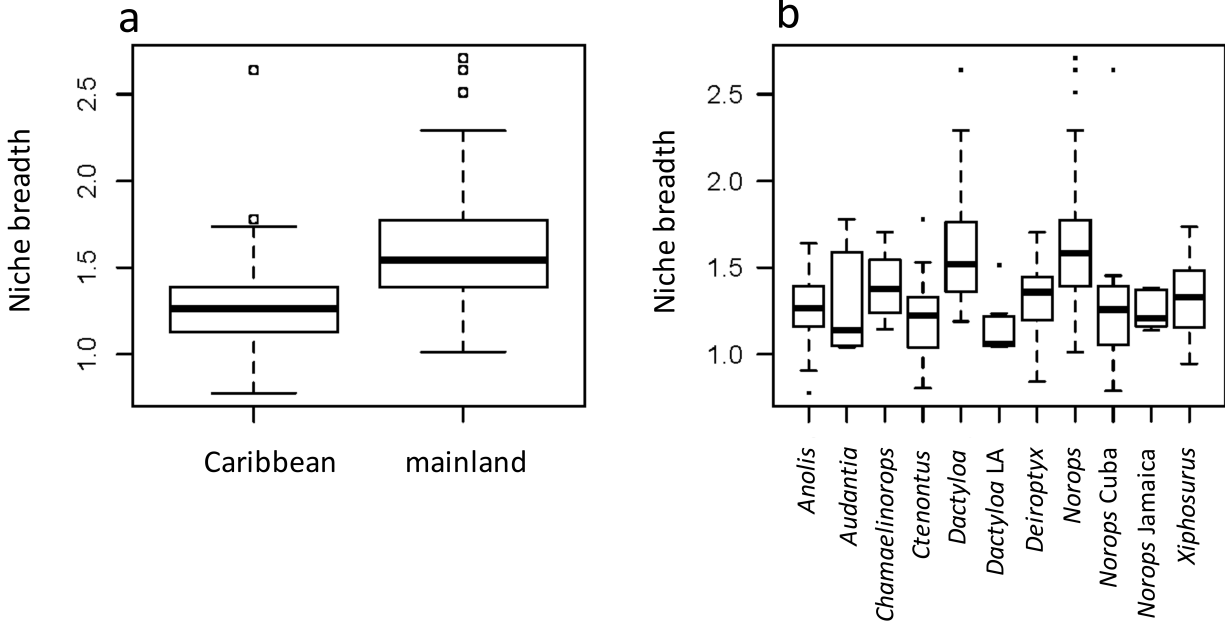
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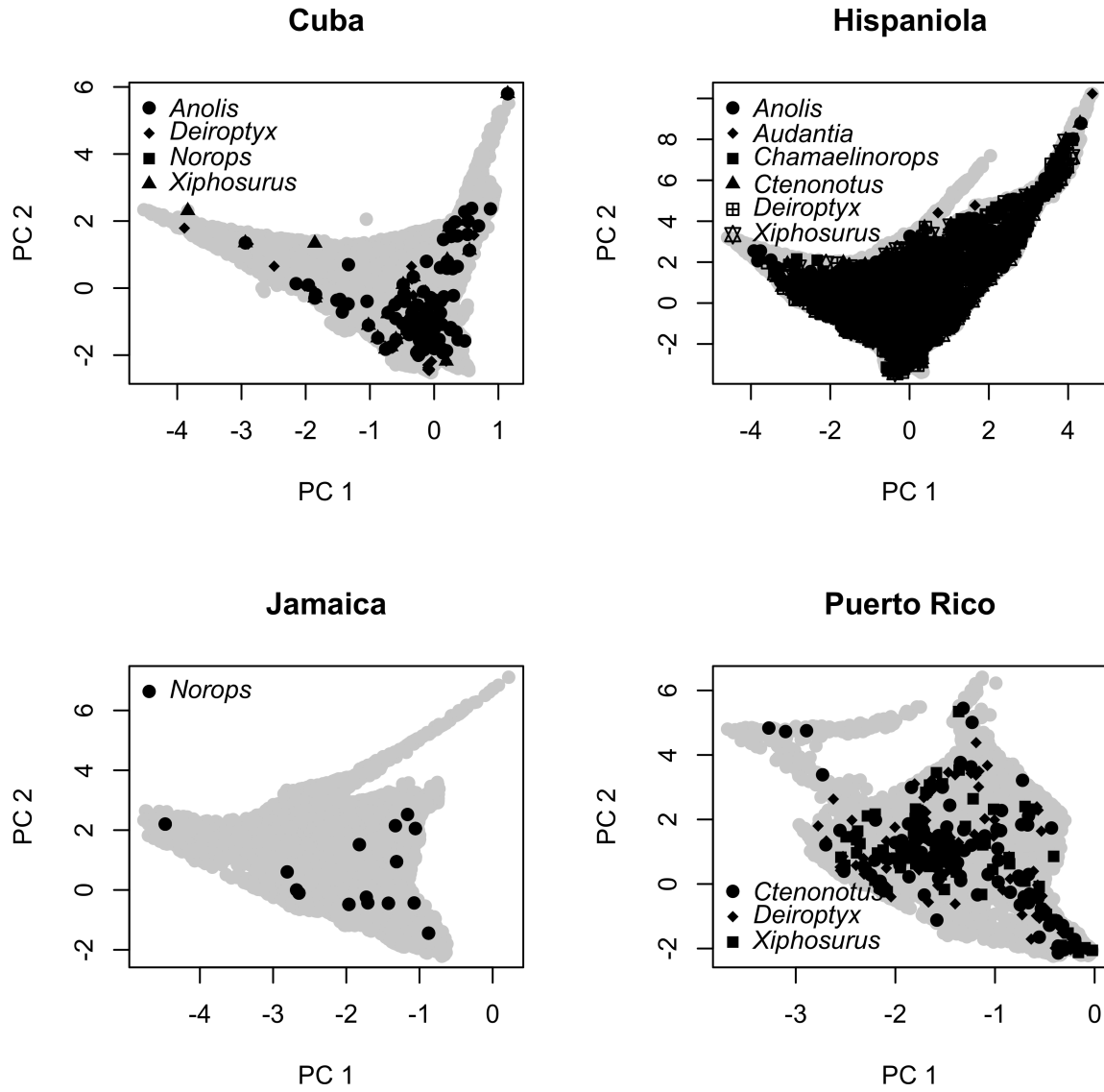
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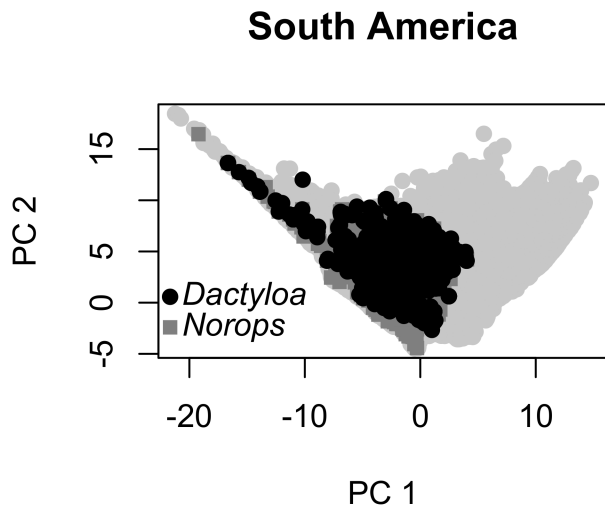
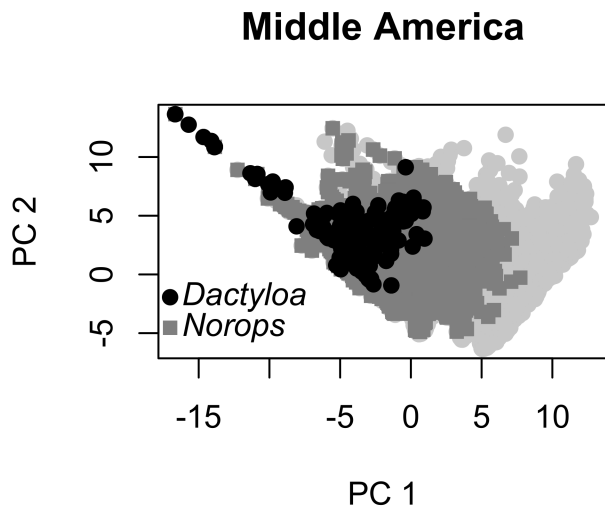
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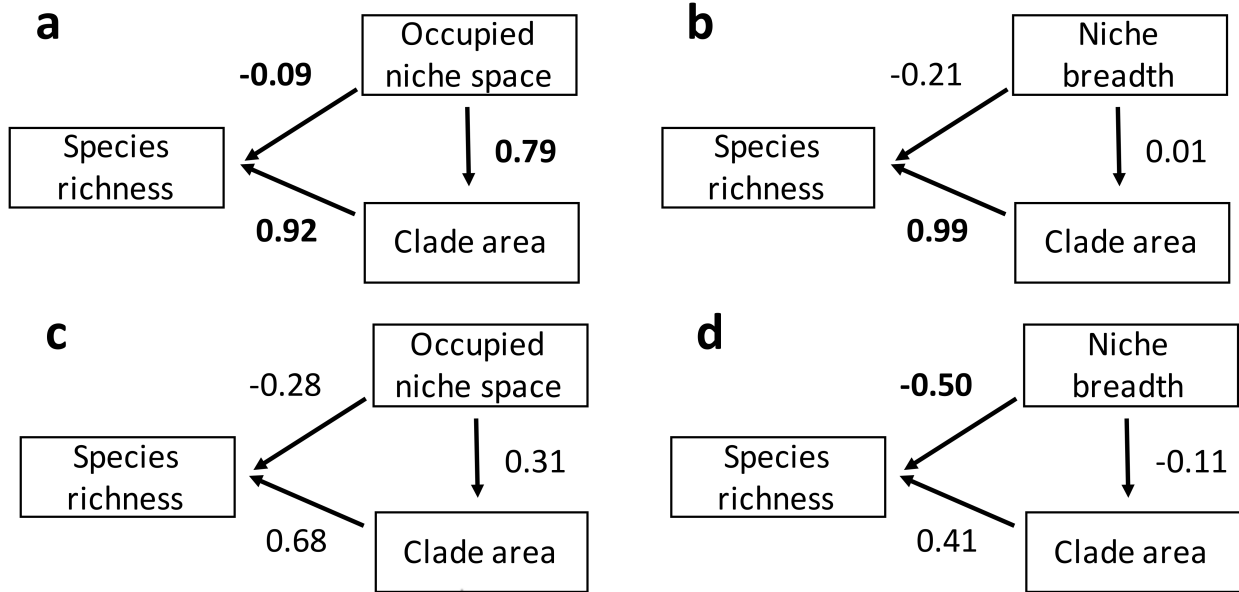
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725 Figure 4

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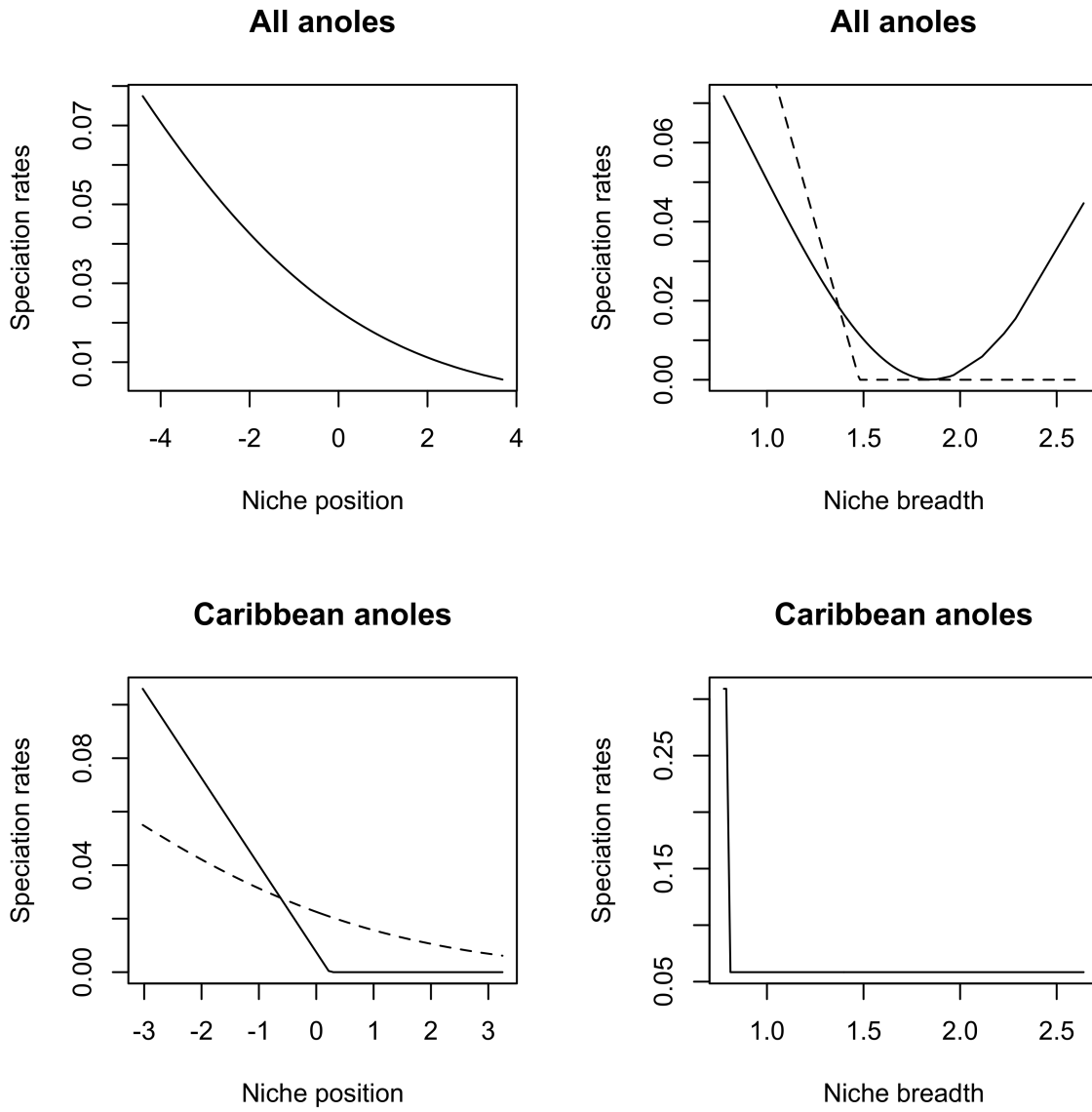
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731 Figure 5



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