Comparative Evolution of an Archetypal Adaptive Radiation: Innovation and Opportunity in *Anolis* Lizards

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abstract: Adaptive radiation is a widely recognized pattern of evolution wherein substantial phenotypic change accompanies rapid speciation. Adaptive radiation may be triggered by environmental opportunities resulting from dispersal to new areas or via the evolution of traits, called key innovations, that allow for invasion of new niches. Species sampling is a known source of bias in many comparative analyses, yet classic adaptive radiations have not been studied comparatively with comprehensively sampled phylogenies. In this study, we use unprecedented comprehensive phylogenetic sampling of *Anolis* lizard species to examine comparative evolution in this well-studied adaptive radiation. We compare adaptive radiation models within *Anolis* and in the *Anolis* clade and a potential sister lineage, the Corytophanidae. We find evidence for island (i.e., opportunity) effects and no evidence for trait (i.e., key innovation) effects causing accelerated body size evolution within *Anolis*. However, island effects are scale dependent: when *Anolis* and Corytophanidae are analyzed together, no island effect is evident. We find no evidence for an island effect on speciation rate and tenuous evidence for greater speciation rate due to trait effects. These results suggest the need for precision in treatments of classic adaptive radiations such as *Anolis* and further refinement of the concept of adaptive radiation.

Keywords: diversification, key innovation, opportunity, phylogeny, rates.

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Introduction

Adaptive radiation is a widely recognized pattern of evolutionary diversity (Simpson 1953; Mayr 1970). The phenomenon is characterized by rapid speciation resulting in evolution of disparate ecologies and morphologies (Schluter 2000). Adaptive radiation may occur whenever new ecological opportunities confront a lineage, including dispersal to novel or barren environments such as islands and evolution of "key innovations," traits that accelerate diversification by enabling evolutionary entry into novel ecological space (Simpson 1953). Other diversification triggers, such as climatic or competitive effects, are also possible (Simões et al. 2016). Classic island adaptive radiations include Galapagos finches, Hawaiian silverswords, and Caribbean *Anolis* lizards. Key innovations have been implicated in explosive radiations of birds (Mayr 1963), insects (Nicholson et al. 2014), and mammals (Hunter and Jernvall 1995), among other lineages.

Adaptive radiation in island forms is demonstrable only if it can be contrasted with comparable and presumably less adaptively radiated mainland lineages (Bronham and Woolfit 2004). Similarly, key innovation effects should be tested with reference to comparable species that lack the purported key innovation (Hunter and Jernvall 1995). But most studies of adaptive radiation do not include appropriate comparisons with comparably sampled lineages, habitats, or timescales (Futuyma 2003; Gavrilets and Losos 2009). For the adaptive radiation concept to be meaningful, lineages labeled as such should display faster speciation rates and greater

ecomorphological diversity than counterparts that lacked evolutionary access to comparable ecological opportunity (Pinto et al. 2008; Santos et al. 2011; Givnish 2015). More precisely, hypotheses of adaptive radiation should not constitute vague associations of the term with taxonomic groups or even clades but rather should be tied explicitly to reconstructed causal factors of geography, climate, or traits (Simões et al. 2016).

Anolis lizards (anoles) are an archetypal example of adaptive radiation (e.g., Freeman et al. 2013). Multiple ecomorphological types have evolved in the Greater Antilles (Williams 1983), in some cases convergently (Losos et al. 1998), and the nearly unstudied mainland forms may be equally diverse (Schaad and Poe 2010; Moreno-Arias and Calderón-Espinosa 2016). The clade *Anolis* includes two major predominantly mainland lineages and multiple island radiations in the Greater Antilles (Pinto et al. 2008). An initial mainland-island split in *Anolis* suggests comparable time for island and mainland evolution that has produced similar species diversity on islands ($n = 173$ species) and mainland ($n = 206$ species). Suggested outgroups to *Anolis* such as Corytophanidae and *Polychrus* are found exclusively on the mainland. These factors make *Anolis* an ideal system for testing potential island effects of adaptive radiation.

Males of nearly all species of *Anolis* possess a dewlap, an extensible gular pouch used mainly for intraspecific signaling. This trait has been suggested as a key innovation for the *Anolis* lineage (Losos 2009) and is lacking in the potential sister clade of *Anolis*, the Corytophanidae (Pyron et al. 2013). A test of the key innovation hypothesis for the adaptive radiation of *Anolis* is possible by comparing phenotypic and diversification rates in dewlapped and dewlapless lineages, including both *Anolis* and additional dewlapless lineages such as corytophanids.

Anolis is a classic adaptive radiation, but it is not clear whether the diversity of this clade is attributable to geographic (i.e., island), trait (i.e., key innovation), or some other effects. Alternatively as a null hypothesis, the radiation may not be exceptional. Here we test for an island effect in adaptive radiation by comparing speciation rates and rates of morphological evolution in mainland and island forms. We test for a key innovation effect by comparing speciation rates and rates of morphological evolution in dewlapped and dewlapless forms. We consider the dewlap to constitute a key innovation in the sense that it opens up new avenues for variation that may facilitate speciation. Namely, variation in this sexual signaling organ may accelerate partitioning of habitat (via differential detection of alternative dewlaps) and/or evolution of mate preference (via variation in dewlap color, size, and employment during display). We analyze all *Anolis* species described as of June 1, 2014, and all species of Corytophanidae in speciation rate analyses, and we analyze 336 species of *Anolis* and all species of Corytophanidae in phenotypic rate analyses.

Our unprecedented sampling of *Anolis* and its potential sister group allows for testing of hypotheses of diversification as well as a fuller treatment of phenotypic evolution and avoids the perils of phylogenetic undersampling for comparative methods (e.g., Ackerly 2000).

Material and Methods

Data

We collected three characters of morphology from one to 15 specimens of 336 species of *Anolis* (a recent study [Armstead and Poe 2015] suggests that $n = 1$ is an adequate sample size for our purposes) and all nine species of Corytophanidae. These data are uploaded to the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.6v5hq (Poe et al. 2017). Body size (snout vent length [SVL]) was measured from tip of snout to anterior edge of cloaca. Size of head scales (HS) was measured as number of scales across the snout at the level of the second canthal scales. Relative femoral length (FL, a measure of hind limb length) was measured from ventral longitudinal midline laterally to knee and scaled by SVL. That is, hind limb length was scored in units of SVL. There is no single correct way to scale measurements based on overall size (see Packard and Boardman 1988). Many authors use residuals from linear regression on body size instead of our approach of simply dividing by body length. However, for our data, our approach gives results that are nearly completely correlated with body size residuals (example shown in fig. S1; figs. S1, S2 are available online). Therefore, we adopt our approach for practical reasons (e.g., it is not necessary to perform a new regression every time new data are added). Characters were ln-transformed prior to comparative analyses: species means for SVL and HS were ln-transformed, and species mean ratios for FL/SVL were ln-transformed. We selected these three traits for study because they are known to be functionally important in lizards. For example, limb length correlates with microhabitat use (e.g., Irschick 2002), scale size is related to dessication rate (e.g., Soule 1966; Wegener et al. 2014), and body size affects many if not most life-history traits (e.g., Peters 1983).

These three characters were analyzed individually rather than under dimension-reducing procedures such as principal component analysis (PCA) because of the difficulty with biological interpretation of PCs (e.g., Karr and Martin 1981; James and McCulloch 1990; e.g., in the current case, subsets of *Anolis* species analyzed separately give vastly different PC loadings; results not shown) and recent work demonstrating biases inherent to the use of PCs in phylogenetic comparative studies (Revell 2009) that are not corrected by currently suggested modeling techniques (Uyeda et al. 2015).

For our comparative analyses we used phylogenetic estimates from Poe et al. (2017), who analyzed all 379 spe-

cies of *Anolis* known in 2014. One to 100 of Poe et al.'s post-burn-in trees from their MrBayes analyses were used for comparative analyses (see below). These samples were used (rather than the entire post-burn-in sample) due to limitations of computing power. Publicly available supercomputing resources (e.g., the CIPRES cluster) do not offer the comparative programs used here, and our comparative analyses are extraordinarily time-consuming on standard desktop computers. Trees were analyzed including all *Anolis* species (for speciation analyses) or pruned to match our comparative morphological data set (for phenotypic analyses). That is, we used Poe et al.'s (2017) MrBayes trees rather than their BEAST trees.

Some of our analyses were performed on the *Anolis* clade together with its potential sister clade, the Corytophanidae (Pyron et al. 2013). *Anolis* and Corytophanidae have been scored for few shared phylogenetic characters, and we do not possess tissues of the two corytophanid species not included in the most comprehensive phylogenetic analysis including this group (Pyron et al. 2013). Therefore, we grafted corytophanid species to our *Anolis* trees for our comparative analyses that included both *Anolis* and Corytophanidae. We added the seven corytophanid species included by Pyron et al. (2013) to analyzed trees according to the Pyron et al. topology. We included the two corytophanid species not analyzed by Pyron et al., adding *Corytophanes hernandezi* as sister species to *Corytophanes cristatus* and *Laemanctus serratus* as sister to *Laemanctus longipes*. We added this corytophanid topology to trees from Poe et al. (2017) and used Mesquite (Maddison and Maddison 2014) to vary branch lengths to assess the effects of uncertainty in this parameter on our comparative analyses (see below).

Species were categorized as mainland or island forms according to their native ranges. Species were categorized as dewlapped or dewlapless according to our observations of male specimens and literature records. Island/mainland and dewlap/dewlapless information is available in table A1 (tables A1, S1–S4 are available online).

Rates of Speciation

We tested whether speciation rates differed between island and mainland species and between species possessing and lacking a male dewlap, using the BiSSE method (Maddison et al. 2007) implemented in Mesquite (Maddison and Maddison 2014). We compared the likelihood of a model with separate speciation rates for conditions (mainland vs. island, dewlap vs. no dewlap) to a model where speciation rate was fixed across the tree, for two samples of trees: 100 trees of Poe et al.'s (2017) post-burn-in sample, including all *Anolis* species but not corytophanids, and Poe et al.'s (2017) maximum clade credibility (MCC) tree, with 10 randomly perturbed sets of branch lengths for the corytophanid topology.

We performed these comparisons with nuisance parameters (extinction rate, character state transition rate) constrained to be constant across the tree (there is no evidence that these parameters vary between mainland and island clades). Recent cautions concerning BiSSE-type methods (Maddison and Fitzjohn 2015) are not likely to apply to our results (i.e., the problem is one of type I error, but our results are nonsignificant).

As a check on our Mesquite BiSSE results, we also tested for variation in speciation rate using computational paradigms and computer programs different than described above. We analyzed the BEAST tree of Poe et al. (2017) using BAMM (Rabosky 2014). The BAMM analyses were generated using Markov chain Monte Carlo for 50×10^6 generations and using prior parameters generated from the tree using the setBAMMpriors function from the BAMMtools R package as follows: expected number of shifts = 1, speciation rate prior = 2.714, speciation shift prior = 0.017, extinction rate prior = 2.71. We tested for rate differences across the tree and visualized rate comparisons using macroevolutionary cohort analysis (Rabosky et al. 2014). We also separated the tree into mainland *Dactyloa*, mainland *Draconura*, and island lineages (as in Pinto et al. 2008) and compared rates of speciation across these lineages. Finally, we used FiSSE (Rabosky and Goldberg 2017) to test for differences in speciation rate in dewlapped versus dewlapless lineages across the 10 trees including the corytophanid outgroups. FiSSE analyses were generated using the R script provided by Rabosky in the GitHub repository.

Phenotypic Evolution

We tested whether body size, relative hind limb length, and head scale size evolved at different rates on islands versus mainland and in species that possess versus lack a male dewlap using the noncensored approach of O'Meara et al. (2006) implemented in the program Brownie. We analyzed 10 post-burn-in trees from Poe et al. (2017), pruned to include the 336 species scored for the three traits, and added all corytophanid species under the above-discussed topology with varying branch lengths. Models were compared using the Akaike information criterion corrected for sample size (AICc). Ancestral geographies (mainland vs. island) and male dewlap conditions (presence vs. absence) were reconstructed using likelihood in Brownie.

Results

Phylogenetic estimates from Poe et al. (2017) show a minimum of 12–14 dispersals between mainland and island environments in *Anolis*, thus demonstrating the suitability of *Anolis* for mainland-island comparisons. The clade *Anolis* includes two major mainland lineages and multiple island

radiations among the Greater Antilles, with an initial mainland-island split in *Anolis* suggesting comparable time for island and mainland evolution (Pinto et al. 2008). In all Brownie reconstructions, a male dewlap evolved once at the base of the *Anolis* tree and was lost in the lineage leading to sister species *Anolis bartschi* and *Anolis vermiculatus*; a male dewlap is absent in all corytophanids. Figure 1 shows example trait distributions for mainland/island and dewlapped/dewlapless lineages on Poe et al.'s (2017) MCC tree with outgroup corytophanids added.

Mainland and island lineages were found not to differ in speciation rate according to BiSSE analyses (Maddison et al. 2007), regardless of whether the corytophanid outgroups were included. Differences in ln-likelihoods for one- and two-rate models ranged from 0 to 0.004 across 100 trees when anoles were analyzed alone and from 0 to 0.003 across 10 analyzed trees when corytophanids were included. These results were reinforced by the BAMM analyses, wherein mainland and island lineages did not differ in speciation rate (fig. S2). Both mainland and island lineages showed a gradual decrease in speciation rate over time (fig. 2).

Models of phenotypic evolution that allowed for different rates for mainland and island lineages were significantly favored over single-rate models in one of the six trait-trees combinations (three characters × two sets of trees). When *Anolis* was analyzed alone (i.e., without corytophanids), rates of body length evolution were significantly higher in island lineages (mean rate within mainland lineages = 0.61; mean rate within island lineages = 1.09; fig. 3; table S1). This difference in rates of body size evolution is not evident when corytophanids are included, nor is it obtained in other traits (fig. 3; table S2).

Results of speciation-rate analyses in dewlapped versus dewlapless lineages were equivocal. Dewlapped lineages consistently displayed higher speciation rates than dewlapless lineages according to BiSSE analyses (mean rate for dewlapped lineages = 42.2; mean for dewlapless lineages = 28.3; $P = .005$, Wilcoxon paired test comparing rates for each of 10 trees). However, support for one- versus two-rate models was not significant for any particular tree according to likelihood score (ln-likelihoods for one- and two-rate models ranged from 0 to 0.4 across 10 analyzed trees)—a result reinforced by the finding of a lack of support for two-rate models in FiSSE analyses (results available in table S3). All dewlap analyses were performed only on trees including corytophanids. Because only two of 379 *Anolis* species lack a male dewlap, dewlap-related diversification analyses are not informative for analyses of the *Anolis* lineage alone.

Models of phenotypic evolution that allowed for different rates for dewlapped and dewlapless lineages were strongly favored over single-rate models for body size, with body size evolving much faster in dewlapless (i.e., corytophanid) lineages (mean rate within dewlapped lineages = 0.84; mean rate within dewlapless lineages = 10.49; fig. 4; table S4). Two-rate models were not favored for relative hind limb or head scale traits (fig. 4); rates of change were comparable for these traits in dewlapped and dewlapless lineages (table S4).

Discussion

Geography, Traits, and Speciation Rates

One of the hallmarks of adaptive radiation is rapid speciation (Schluter 2000). Rates of diversification in Greater Antillean anoles have been shown to decline over time, possibly indicating gradual ecological saturation of island communities after an initial burst of speciation (Rabosky and Glor 2010). Our results show that a similar pattern is operating in mainland forms (fig. 2), and overall rates of speciation are not significantly elevated on islands relative to mainland in *Anolis* (fig. S2). Isolated areas such as islands and lakes are known areas of rapid speciation (Carlquist 1974), but so are the Andes (Hughes and Eastwood 2006) and the Cordillera Central of Central America (Savage 2002) where *Anolis* have also diversified extensively. The Andes (Garzione et al. 2008) and the Cordillera Central (Denyer et al. 2000) developed rapidly and are home to many *Anolis* species with microendemic distributions (Köhler 2008). Speciation rates in *Anolis* may be elevated relative to other clades by virtue of their occurrence in two speciation hot spots, islands and rapid geologic uplifts. The decrease in speciation rate over time seen in both island and mainland forms is consistent with parallel processes of species saturation (Rabosky and Glor 2010) occurring in both areas. Alternatively, the constancy of rate decrease across the tree, among distinct lineages in disparate environments (figs. 2, S2), may indicate some artefactual effect.

This possibility of elevated speciation rates in *Anolis* relative to other lizard lineages receives only tenuous support from our comparison of dewlapped and dewlapless lineages. This comparison is essentially one of *Anolis* and its possible sister clade Corytophanidae, as all corytophanids lack a dewlap and almost all *Anolis* species possess one. We did not find differences in speciation rate in dewlapped (i.e., *Anolis*) and dewlapless (i.e., Corytophanidae) forms according to BiSSE or FiSSE analyses, but we are cautious in accepting this result for three reasons. First, the statistical power of BiSSE to detect differences in speciation rate is low in cases like ours with fewer than 400 taxa (Davis et al. 2013). Second, we note that although individual trees do not show significant differences between dewlapped and dewlapless lineages, there is a general trend of faster rates in dewlapped forms across trees (10 of 10 analyzed trees in BiSSE, nine of 10 trees in FiSSE show this pattern; table S3). Finally, we make the obvious observation that the *Anolis* clade includes significantly more species than either of its currently hypothesized sister clades, corytophanids
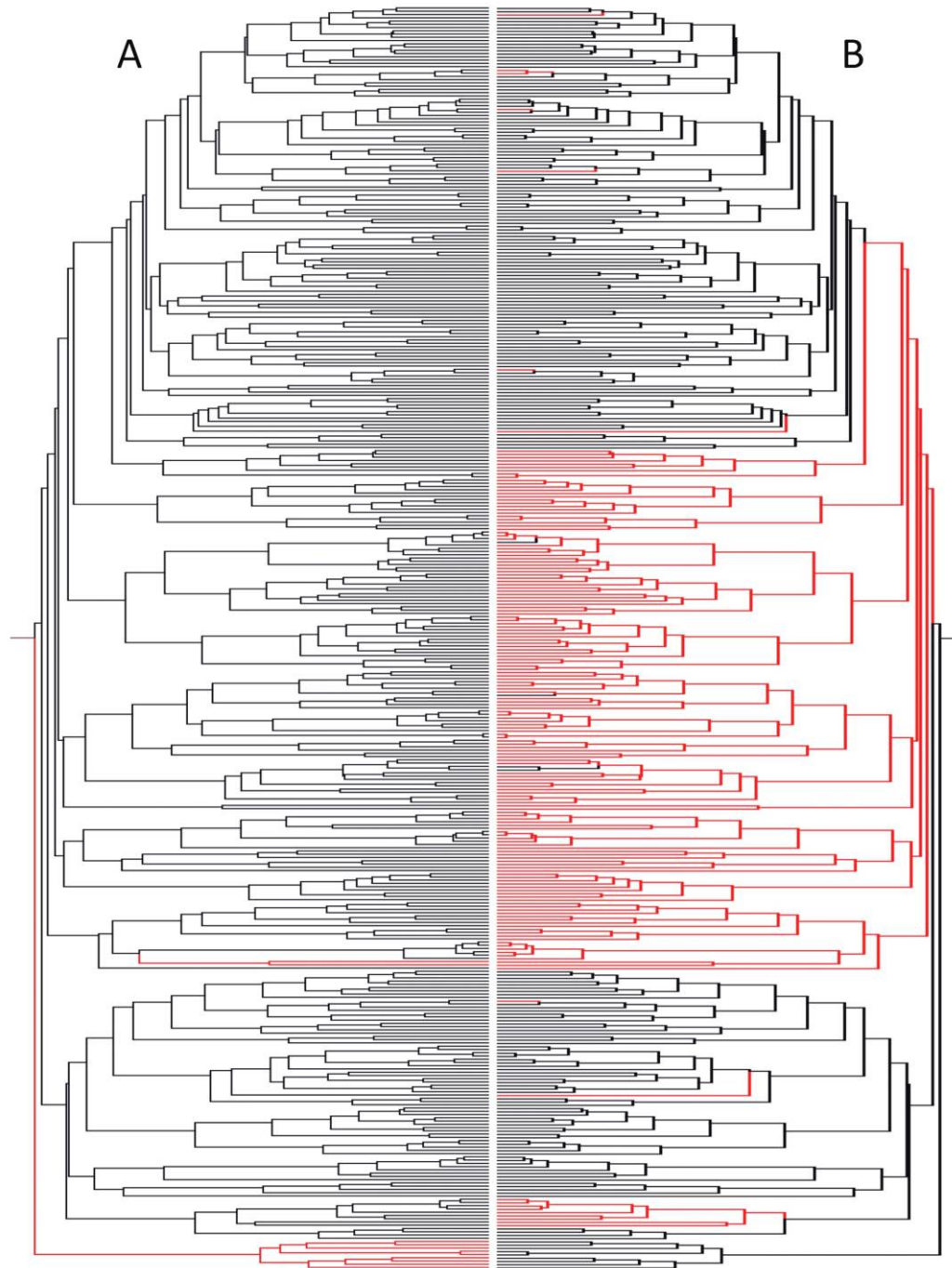
Figure 1: Phylogenetic estimate of 379 species of *Anolis* and nine outgroup species of Corytophanidae, maximum clade credibility tree of Poe et al. (2017) with outgroups. *A*, Lineages in which species possess a dewlap in males are black; those lacking a dewlap are red. *B*, Island lineages are red; mainland lineages are black. Ancestral states were reconstructed using parsimony for purposes of visualization. All analyses in the article were done using likelihood reconstructions.
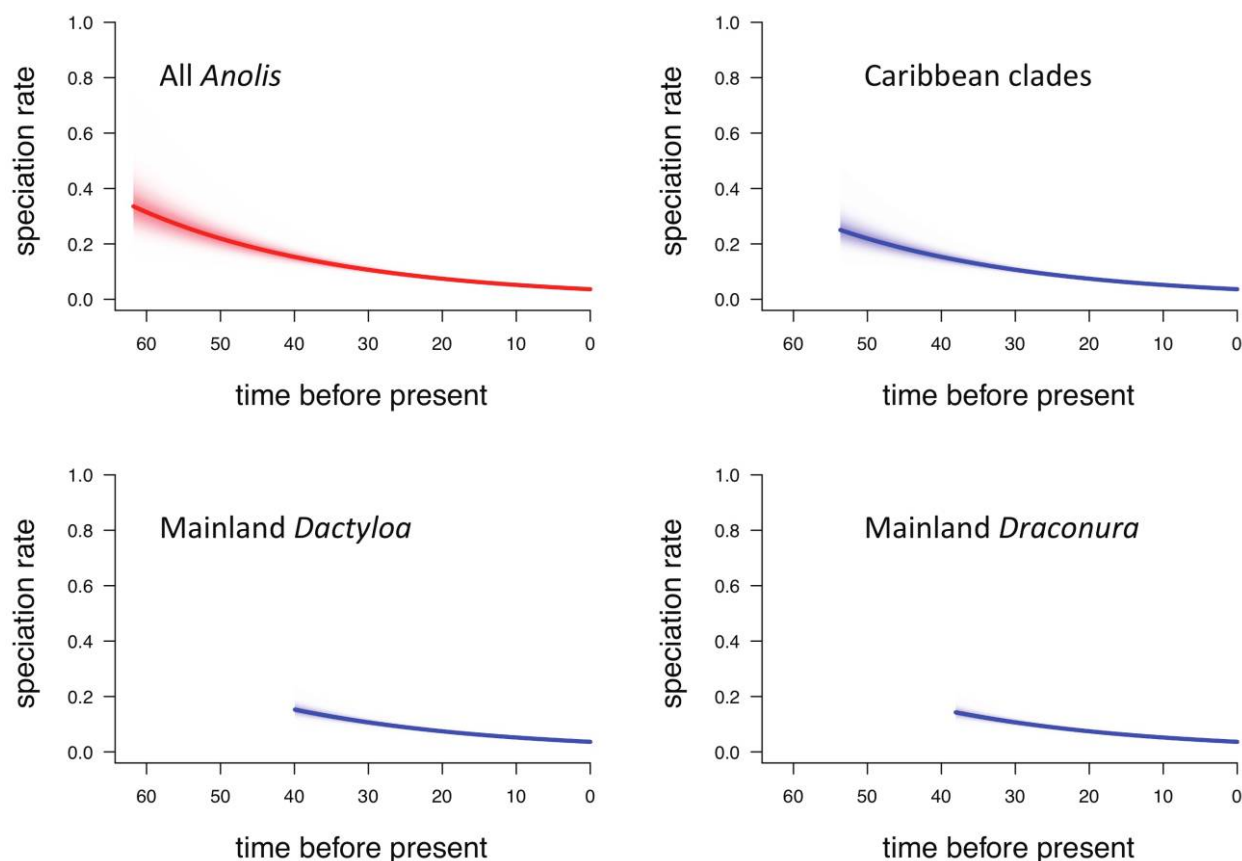
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Figure 2: Rates of speciation over time for predominantly Caribbean and two predominantly mainland clades in *Anolis*.

or *Polychrus*, as measured by, for example, the test of Slowinski and Guyer (1993). These caveats suggest that the hypothesis of elevated speciation rates in *Anolis*, while not currently supported, is worthy of continued consideration.

Geography, Traits, and Rates of Phenotypic Evolution

Rates of phenotypic evolution are purported to be especially high in adaptive radiations on islands (Bronham and Woolfit 2004; Santos et al. 2011). Our results show some support for this hypothesis, as rates of evolution of body length were found to be significantly higher on islands when the *Anolis* clade was analyzed alone. Body length obviously reflects overall size of an individual, a trait that affects perhaps most properties of organisms from cellular to ecological levels (Peters 1983; Schmidt-Nielson 1984). The other tested traits, relative hind limb length, which is associated with perch use in *Anolis* (e.g., Irschick 2002), and size of head scales, which is associated with hydric function (e.g., Soule and Kerfoot 1966), did not differ in rate of change across mainland and island lineages. Because of the extensive biological effects of body size, it is difficult to pinpoint what kinds of selective

pressures may be operating differently on islands versus mainland in *Anolis*. Broadly, elevated rates of phenotypic evolution due to geographic opportunity are hypothesized to be due to absence of predators and release from competitors allowing the use of new habitats or resources (Carlquist 1974; Schluter 1988; Stroud and Losos 2016). *Anolis* lizards of the Caribbean are famous for stratifying habitat according to body size (e.g., Schoener 1969; Williams 1983), a phenomenon that could be due to island forms evolving to fill open niches (Mahler et al. 2010).

Our body length results within *Anolis* might be interpreted as consistent with some of the results of Mahler et al. (2010), who found high initial rates of change for body size (and limb length) of Greater Antillean *Anolis* followed by decreasing rates as anole lineages accumulated. Island *Anolis* likely experienced rapid initial evolution of body size in the absence of congeners and other similar lizards (Mahler et al. 2010), whereas mainland *Anolis* evolved in areas where multiple diurnal arboreal lizards such as corytophanids, iguanids, and tropidurids were likely already present. The existence of these competing lizard groups may have prevented the explosive body size evolution that apparently
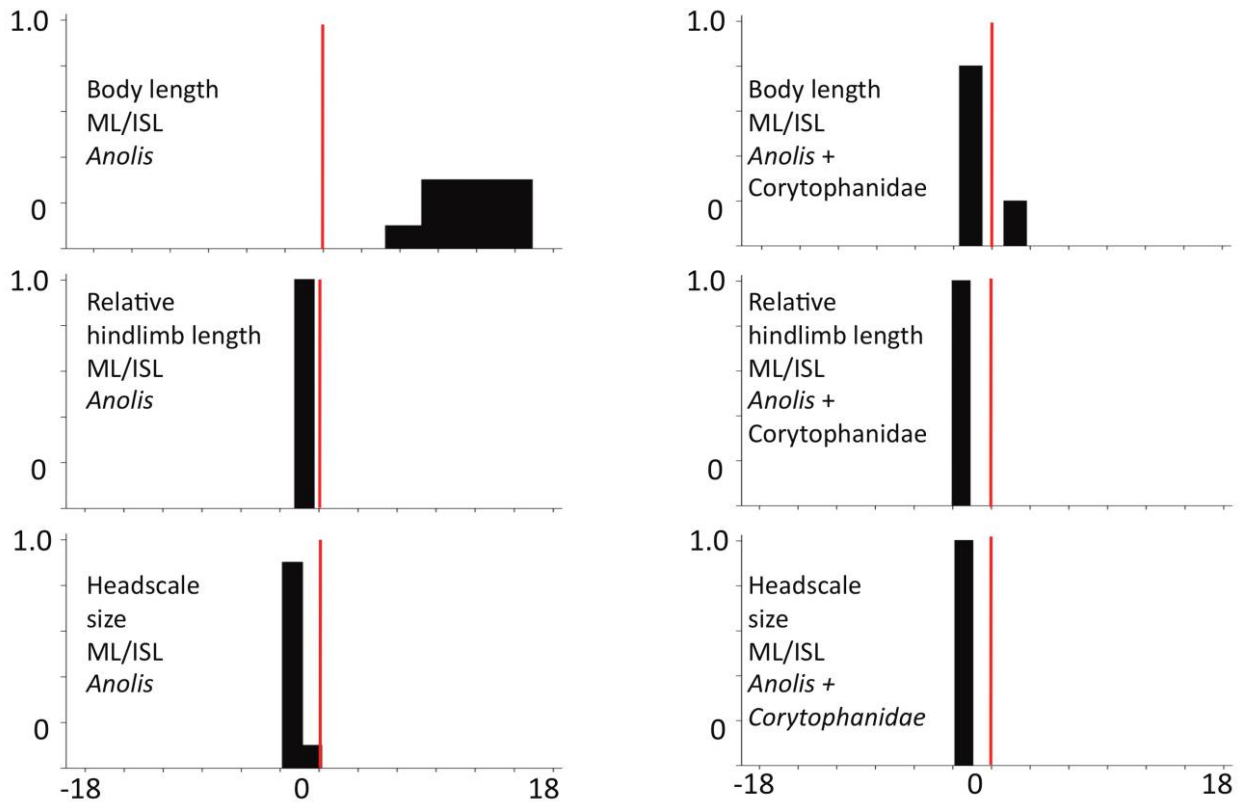
Figure 3: Comparisons of corrected Akaike information criterion (AICc) values for one- versus two-rate models for morphological evolution in *Anolis* analyzed alone and with Corytophanidae. Distributions show ΔAICc between models of evolution for three morphological traits for each evaluated tree. Single-rate Brownian motion models are compared to models allowing separate rates for mainland and island lineages (ML/ISL). Large positive values indicate favorability of the two-rates model. The vertical line is at 0, indicating equal support for each model.

occurred in the Greater Antilles, which lack these competitors. Alternatively to or in concert with these factors, the greater number of potential lizard predators on the mainland may have limited anole evolution (Andrews 1979).

Pinto et al. (2008, table 4) also compared rates of phenotypic evolution in mainland and island *Anolis*. They found some traits to evolve more quickly in island anoles and other traits to evolve more quickly in one of the two predominantly mainland clades that they analyzed. Although there are similarities between their study and ours in the general questions asked and techniques used (e.g., incorporation of phylogeny, assessment of phenotypic evolution, use of Brownie [O'Meara 2006]), there are also differences in several aspects that preclude direct comparison of results. Pinto et al. (2008) performed PC analyses rather than analyzing individual traits, scaled their traits differently, and focused on mensural traits, whereas we included a trait of scalation. Pinto et al. (2008) divided mainland anoles into two groups (called M1, M2) corresponding to phylogenetically if not geographically distinct anole radiations (some M lineage species such as *Anolis gorgonae* evolved to live on islands,

and some island species such as *Anolis carolinensis* evolved to live on the mainland) and compared among island, M1, and M2 groups using the censored rate test in Brownie that compares clades; we compared mainland and island radiations using the noncensored test that compares parts of the tree reconstructed with particular traits (i.e., mainland and island) and thus does not require designation of "mainland" and "island" clades. Probably most importantly, we included more species in our analyses (177 vs. 35 mainland, 159 vs. 57 island). These differences in approach notwithstanding, some similarities in results emerged. In particular, our finding of lack of significant support for two-rate models in most cases is compatible with the general conclusion of Pinto et al. (2008) of comparable rates of phenotypic evolution in mainland and island species.

The main difference in conclusions between our study and the phenotypic rates results of Pinto et al. (2008) is that we find no support for greater rates of evolution on mainland versus island lineages for any trait in *Anolis*, whereas they noted two cases where one of their analyzed mainland clades underwent faster PC evolution relative to their island
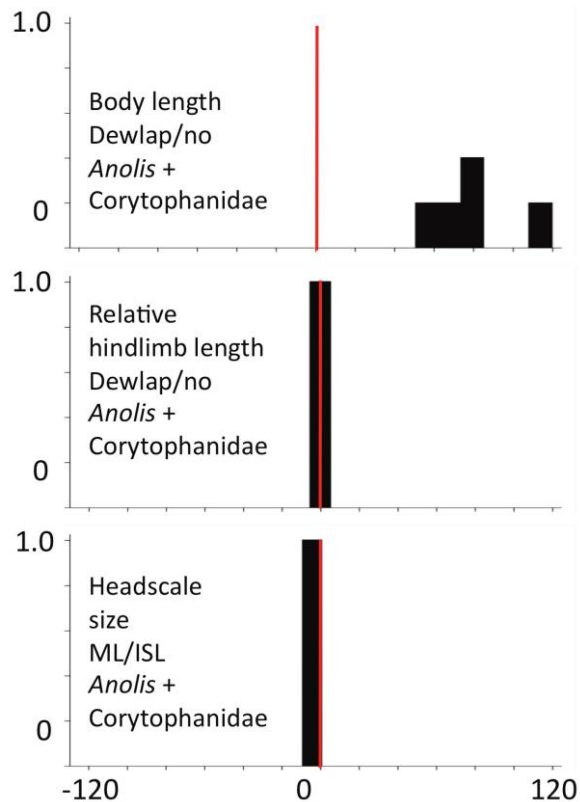
Figure 4: Comparisons of corrected Akaike information criterion (AICc) values for one- versus two-rate models for morphological evolution in *Anolis* and Corytophanidae. Distributions show ΔAICc between models of evolution for three morphological traits for each evaluated tree. Single-rate Brownian motion models are compared to models allowing separate rates for dewlapped and dewlapless lineages. Large positive values indicate favorability of the two-rates model. The vertical line is at 0, indicating equal support for each model.

species. Among the differences in these two studies listed above, the slight differences in questions asked (i.e., comparison of M1 to M2 to island in Pinto et al. versus comparison of mainland to island here) and the greater taxon sampling in our study seem the most likely explanations for these differences. That is, our results do not contradict Pinto et al.'s finding that a subset of the mainland radiation is evolving faster than the Caribbean radiation for some traits, and a difference in results between analyses including 35 (Pinto et al. 2008) versus 177 (this study) mainland species is unsurprising.

Our finding of a greater rate of body length evolution in island *Anolis* is consistent with expectation and interpretation of island *Anolis* as an adaptive radiation, but this difference in rate is erased when corytophanids are included in the analysis (fig. 3). This sampling dependence of results demonstrates the importance of scale in questions of evolutionary rate. It would be inaccurate to cite our results as

support for some general island rule of phenotypic change. Rather, these results invite a less general and more complex series of next questions involving the interaction of a particular lineage, the *Anolis*, with a particular set of environments, the islands of the Caribbean. The teasing apart of causal factors for geographic effects on phenotypic evolution is likely to be difficult and should benefit from both finer (e.g., comparison of *Anolis* on separate islands) and broader (e.g., inclusion of more of the squamate phylogeny) approaches.

Unlike our island-mainland tests, which gave limited support for a geographic effect, our dewlap tests failed to support a key-innovation effect on rates of phenotypic evolution. In fact, dewlapless lineages were found to display much higher rates of body length evolution than dewlapped lineages (fig. 4; table S4). This result of no dewlap effect is surprising, as it suggests that the *Anolis* clade, nearly all of whose members possess a male dewlap, does not display the classic phenotypic rate characteristics of an adaptive radiation. It is possible that some other predominantly *Anolis* trait such as expanded toepads may be found to be a key innovation for *Anolis*, but this result seems unlikely, as the distribution of expanded toepads is phylogenetically similar to that of male dewlap for the lineages analyzed here. Another possibility is that analyses conducted on a broader phylogenetic scale may find the dewlap (which is also present, though structurally different from *Anolis*, in lineages such as *Draco* and *Polychrus*) or some other trait (expanded toepads that differ structurally from those in *Anolis* are found in some gecko lineages; Gamble et al. 2012) to be key innovations. If such studies are to be rigorous, they must be done on greater phylogenetic and morphological samples of lizard species than are available today. In the meantime, until such studies can be undertaken, the status of *Anolis* as a classic adaptive radiation should not be unquestioned.

Conclusions

Recent reviews (Simões et al. 2016; Stroud and Losos 2016) have championed greater theoretical and operational precision in treatments of adaptive radiation. We tested for geographic (island) and key-innovation (male dewlap) effects on rates of speciation and phenotypic evolution in one of the classic adaptive radiations, the *Anolis* lizards. Our unprecedented phylogenetic and morphological sampling allowed rigorous examination of these possibilities and showed that island effects on body length evolution are evident within *Anolis*. However, continued interpretation of *Anolis* as an adaptive radiation is not straightforward. Island effects are not demonstrable when tested on a broader phylogenetic scale or on additional traits, and significantly heightened speciation rates were not unambiguously associated with hypothesized geographic or key-innovation triggers for *Anolis*.

Other archetypal adaptive radiations besides *Anolis* currently are explained by island effects (e.g., Galapagos finches [Grant 1986]), key innovations (e.g., Cenozoic mammals [Hunter and Jernvall 1995]), or some combination of these factors (e.g., cichlid evolution triggered by isolation in uninhabited lakes [Meyer et al. 1990] and highly evolvable jaw morphologies [Liem 1973]). Geographic, trait, and other effects should be tested in these and other hypothesized adaptive radiations. Studies of purportedly exceptional radiations should incorporate comprehensive phylogenetic information, reconstruction of hypothesized causal triggers, and appropriate comparisons with null, supposedly nonadaptive lineages that lack such triggers.

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