Ecological Opportunity from Innovation, not Islands, Drove the Anole Lizard Adaptive Radiation

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Abstract.—Islands are thought to facilitate adaptive radiation by providing release from competition and predation. Anole lizards are considered a classic example of this phenomenon: different ecological specialists ("ecomorphs") evolved in the Caribbean Greater Antilles (Cuba, Hispaniola, Jamaica, and Puerto Rico), resulting in convergent assemblages that are not observed in mainland Latin America. Yet, the role of islands in facilitating adaptive radiation is more often implied than directly tested, leaving uncertain the role of biogeography in stimulating diversification. Here, we assess the proposed "island effect" on anole diversification using Bayesian phylogenetic comparative methods that explicitly incorporate rate heterogeneity across the tree and demonstrate two cases of would be false positives. We discovered that rates of speciation and morphological evolution of island and mainland anoles are equivalent, implying that islands provide no special context for exceptionally rapid diversification. Likewise, rates of evolution were equivalent between island anoles that arose via *in situ* versus dispersal-based mechanisms, and we found no evidence for island-specific rates of speciation or morphological evolution. Nonetheless, the origin of *Anolis* is characterized by a speciation pulse that slowed over time—a classic signature of waning ecological opportunity. Our findings cast doubt on the notion that islands catalyzed the anole adaptive radiation and instead point to a key innovation, adhesive toe pads, which facilitated the exploitation of many arboreal niches sparsely utilized by other iguanian lizards. The selective pressures responsible for arboreal niche diversification differ between islands and the mainland, but the tempo of diversification driven by these discordant processes is indistinguishable. [*Anolis*; Caribbean; key innovation; morphological evolution; RevBayes; speciation.]

Islands are widely viewed as cradles for biodiversity because of the inherent ecological opportunity, a surplus of underutilized resources, supplied by their simplified biotas (Losos and Ricklefs 2009; Gillespie et al. 2011; Mahler et al. 2010). Ecological opportunity may result from 1) ecological release from incumbent competitors/predators (i.e., following extinction or colonization of a novel habitat) or 2) evolution of a key innovation (e.g., wings or pharyngeal jaws) that unlocks access to novel ecological space (Simpson 1953; Schluter 2000; Stroud and Losos 2016). Therefore, islands are poised to provide a setting highly amenable for rapid diversification by providing release from competition and predation compared to more saturated continental communities (Schluter 1988). The disproportionate representation of island lineages among key examples of adaptive radiation supports this idea (Losos and Ricklefs 2009). Such examples include Darwin's finches on the Galápagos, Hawaiian honeycreepers and silverswords, Malagasy vangas, and Caribbean anoles (Lack 1947; Carlquist 1974; Grant and Grant 2008; Losos 2009; Lerner et al. 2011; Reddy et al. 2012). Geographic transitions to isolated environments are often paired with additional sources of ecological opportunity, such as the evolution of a key innovation (Jønsson et al. 2012) or a suite of innovations (Salzburger et al. 2005; Burress and Wainwright 2019). It is unclear how several putative catalysts might interact to promote adaptive radiation.

A central feature of adaptive radiation is the fast rate of evolutionary change, both in terms of species proliferation and in ecological, morphological, and/or functional diversification. Simpson (1953, p. 223),

for example, described adaptive radiation as rapid divergence of a lineage into numerous species that occupy different niches. This insight prompted a generation of emphasis on the tempo of trait evolution during adaptive radiation (Freckleton and Harvey 2006; Mahler et al. 2010; Yoder et al. 2010; Stroud and Losos 2016). Likewise, elevated rates of speciation, particularly early in the radiation, are widely viewed as a key signal of adaptive radiation (Rabosky and Lovette 2008; Glor 2010; Mahler et al. 2010; Derryberry et al. 2011; Burress and Tan 2017). Given the ecological opportunity afforded by islands, rates of trait evolution and speciation should be correspondingly high. Yet, strong conceptual support for island effects on diversification has been met with equivocal empirical support. Whereas some studies recover faster species multiplication and trait evolution in island lineages (e.g., Lovette et al. 2002; Millien 2006; Garcia-Porta et al. 2016), others have found no effect of islands or even faster rates in continental lineages (e.g., Bromham and Woolfit 2004; Arbogast et al. 2006; Raia and Meiri 2011; Takayama et al. 2018; Salazar et al. 2019). Such ambiguity has cast doubt on the role of biogeography (and, correspondingly, ecological opportunity) in deciphering the causes and consequences of adaptive radiation. Discovering the mechanisms that sculpt adaptive radiation requires pinpointing the appropriate scale at which it unfolds and disentangling the relative roles of biogeography and phenotypic innovation in driving diversification.

One crucial limitation of previous tests of "island effects" on diversification is failing to account for rate heterogeneity. In most methods, a null model in

which rates are constant across a lineage is compared to an alternative model in which the rate varies according to the state of the discrete character of interest (Beaulieu and O'Meara 2014). Given this methodological approach, an isolated bout of diversification in an island assemblage, for example, could be interpreted as a broader signal of an "island effect" because all rate variation is attributed to the island state. There are solutions for estimating the impact of a discrete character on speciation (Beaulieu and O'Meara 2016), but until recently analyses of trait evolution have remained problematic (May and Moore 2020). Likewise, univariate methods ignore that traits associated with complex phenotypes (e.g., anole lizard ecomorphs) have correlated evolutionary histories rather than independent histories. It is unclear how much these methodological limitations have led to over emphasizing or obfuscating the effect of islands on diversification, and subsequently limited exploration of alternative factors in driving adaptive radiation.

Here, we investigate how two aspects of ecological opportunity—ecological release on islands and the evolution of key innovations—impacted the tempo of speciation and trait evolution in *Anolis* lizards, a classic example of adaptive radiation. Anoles are a diverse lineage (400+ species) of lizards distributed throughout the tropical and subtropical regions of the Western Hemisphere. Species packing is especially high in the Caribbean, particularly in the Greater Antilles (Cuba, Hispaniola, Jamaica, and Puerto Rico). Anoles in Caribbean Greater Antilles independently diversified into convergent assemblages comprised of similar structural microhabitat specialists (termed "ecomorphs") (Losos 2009). Such repeated evolution is strong evidence for adaptation and predictability in the evolutionary process (Schluter 2000; Losos 2011) and places considerable emphasis on islands as the critical prerequisite for exceptional radiation (Gavrilets and Losos 2009; Mahler et al. 2010). Relationships between ecology and morphology (Irschick et al. 1997), assemblage structure (Anderson and Poe 2019), and macroevolutionary features such as rates of morphological (Pinto et al. 2008; Poe et al. 2018) and physiological evolution (Velasco et al. 2016; Salazar et al. 2019) are generally different between islands and the mainland. In contrast, some evidence has pushed back on this paradigm, instead suggesting that island and mainland anoles underwent similar adaptive radiation (Poe and Anderson 2019). Nonetheless, the role of island biogeography has not been explicitly considered in the context of background rate heterogeneity that may have historically led to over emphasizing island effects on diversification. An alternative catalyst of adaptive radiation is key innovations—phenotypes that permit a lineage to interact with the environment in a novel way (Simpson 1949; Vermeij 1976; Hunter 1998). Anoles have several putative innovations—dewlaps that may function as a means of sexual selection (Sigmund 1983) or species recognition (Losos 1985; Ng and Glor 2011;

Lambert et al. 2013) and adhesive toe pads that facilitate the exploration of arboreal habitat (Elstrott and Irschick 2004; Bloch and Irschick 2005; Crandell et al. 2014; Yuan et al. 2019).

Here, we provide a thorough test of island effects on rates of anole diversification (hereafter diversification is meant to generally refer to both speciation and morphological evolution). The diversification of mainland species should be limited by competition and predation (Schluter 1988). Since islands provide release from both these constraints, diversification is predicted to be faster on islands (Gavrilets and Losos 2009; Stroud and Losos 2016). Previous work comparing rates of morphological evolution between island and mainland anoles have been mixed, finding support for "island effects" on the evolution of some traits but not others (Pinto et al. 2008; Thomas et al. 2009; Poe et al. 2018; Feiner et al. 2021). We revisit this classic framework using contemporary phylogenetic comparative methods but also test more subtle ways in which islands may influence adaptive radiation. Islands may also provide access to alternative speciation modes, specifically an enhanced capacity for dispersal-mediated speciation, since species are less geographically dispersed compared to those on larger land masses (i.e., the mainland; Losos and Schluter 2000). Among Caribbean island anoles, we compare diversification of species that arose *in situ* (a mechanism afforded by mainland and island ecosystems) on their host island to those that dispersed to their host island (a mechanism with enhanced access on islands). We predict that dispersal will be associated with faster diversification rates due to the abrupt nature of reproductive isolation created by this speciation mode. We also tested for island-specific effects on anole diversification owing to the diversity of islands throughout the Caribbean in terms of surface area and distance from the mainland (among many other features; Itescu et al. 2019). We predict that intrinsic characteristics of islands elicit different diversification rates in anoles (Losos and Ricklefs 2009; Rabosky and Glor 2010). During adaptive radiation, species arise as they occupy new niches (Simpson 1953, p. 223) and evolve associated adaptations (Givnish 2015). Therefore, rates of speciation and morphological evolution may be correlated across a clade that has undergone adaptive radiation. Factors that provide unique ecological opportunity and alter the adaptive landscape, such as islands, may elicit changes in this relationship. Correspondingly, we predict that island anoles will have a stronger relationship between speciation and morphological evolution. Lastly, we evaluate the diversification of anoles with respect to other closely related iguanian lizards in an effort to disentangle the effects of putative innovations in driving their adaptive radiation. Since both putative sister groups have dewlaps but lack adhesive toe pads (see details below), similar rates of diversification as anoles would point to the role of dewlaps as a key innovation that predated *Anolis*, whereas faster rates in anoles relative

to outgroups would implicate to adhesive toe pads as a key innovation coincident with the origin of *Anolis*. Both cases may or may not be paired with island effects.

MATERIALS AND METHODS

Morphological Trait Data

We used an existing morphological data set that included femur length, head length, toe length, tail length, the number of lamellae (expanded toe pad scales), and snout-vent length (SVL) for 336 anole species (from Poe and Anderson 2019). Due to variable degrees of sexual dimorphism among species (Butler et al. 2007; Thomas et al. 2009), measurements were collected from adult males (Poe and Anderson 2019). Body size is associated with diet and habitat use (reviewed in Losos 2009). Relative femur length is strongly correlated with microhabitat use (e.g., Losos et al. 1994; Pounds 1988; Muñoz et al. 2015) as well as ecologically relevant performance, including sprint speed and jumping capacity (Losos and Sinervo 1989; Losos 1990). Tail length is also related to microhabitat use and locomotor performance; grass-bush anoles, for example, bear especially long tails associated with stability on compliant substrates like grasses (Irschick et al. 1997; Losos 1990). Head length is related to feeding ecology, as these lizards are gape-limited (Verwaijen et al. 2002). Toe length is associated with clinging ability (Zani 2000; Bloch and Irschick 2005). Anoles bear adhesive toe pads comprised of expanded toe pad scales (termed lamellae), each bearing a dense covering of sticky hairs, or setae, that help anoles cling to vertical substrates (Ruibal and Ernst 1965). The number of lamellae are positively correlated with clinging ability: higher-perching anoles, for example, often exhibit bigger toepads bearing more lamellae (Glossip and Losos 1997; Irschick et al. 1997; Stuart et al. 2014). All traits scaled strongly with body size (i.e., SVL); therefore, these traits were ln-transformed and regressed against ln-SVL using the phyl.resid function implemented in phytools (Revell 2012). For all subsequent phylogenetic comparative methods, we used a multivariate framework including femur length, tail length, toe length, head length, the number of lamellae, and snout-vent length.

We also examined several discrete characters related to biogeography and its broader implications. We followed the island and mainland designations for each species as reported by Poe and Anderson (2019), which considered native species distributions. These character states were mutually exclusive (i.e., no species occur on both the mainland and on islands). We also classified the Caribbean island species based on two alternative speciation modes: species that arose *in situ* on their host island (i.e., were nested within a clade endemic to that island) and species that dispersed to their host island without subsequent speciation (i.e., were nested within a clade from a different island). To facilitate these classifications, we estimated the stochastic ancestral state

history of the native island with the make.simmap function implemented in phytools (Revell 2012). During this procedure, we used a model that permitted each transition rate to be different (all-rates-different; model). We only classified species if the relevant internal nodes were resolved (i.e., >90% for a given state of the discrete character). Species that did not meet this threshold were excluded from this comparison. Lastly, we also considered that there may be island-specific effects on diversification due to inherent characteristics of islands such as their surface area or distance from the mainland (Losos and Ricklefs 2009; Rabosky and Glor 2010). We classified species by their island of origin as reported by Losos (2009).

For phylogenetic comparative methods, we used an existing phylogenetic tree (Mahler et al. 2010) that included 165 species (124 islands and 41 mainlands) that matched our data set; although, we demonstrate that our results are consistent with an alternative tree (Zheng and Wiens 2016) that included 191 species (124 islands and 67 mainlands) that matched out data set (results shown in the Supplementary material available on Dryad at http://dx.doi.org/10.25338/B8VH1S). The phylogenetic tree from Poe et al. (2017) was not used for phylogenetic comparative methods (although it contains a larger number of anole species) because all species did not have sequence data and discretized versions of the morphological characters were used in its construction. We evaluated the relative morphological disparity between island and mainland species using data sets pruned to match these phylogenetic trees to verify that similar relationships were observed regardless of the size of the data set. The morphological disparity was calculated using the disparity function implemented with the R package geiger (Harmon et al. 2008).

Phylogenetic Comparative Methods

To ensure that our morphological traits were ecologically relevant, particularly with regards to the diversification of Caribbean island anoles, we compared each trait among ecomorphs using phylogenetic Analysis of Variance (ANOVA) with a residual randomization permutation procedure (Collyer and Adams 2018) implemented in the geomorph R package (Adams and Otárola-Castillo 2013). Statistical significance was determined using 10k permutations. We determined the statistical significance of pairwise comparisons using the pairwise function implemented in the RRPP package (Collyer and Adams 2018).

We tested the effect of discrete characters on speciation rates using Hidden State-Dependent Speciation and Extinction models (HiSSE; Beaulieu and O'Meara 2016) implemented in RevBayes (Höhna et al. 2016). HiSSE models reduce the risk of falsely attributing rate heterogeneity with a character by introducing an unobserved (i.e., "hidden") character to the model that is uncorrelated with the observed character. We specified uniform incomplete taxon sampling based on a conservative estimate of 425 species of *Anolis*.

HiSSE models were run for 10k generations with two independent chains. Due to inherent difficulty estimating extinction rates with molecular phylogenies based on extant taxa (Rabosky 2010; Louca and Pennell 2020), we only interpret the impact of discrete characters on speciation rates.

We also tested the effect of discrete characters on rates of morphological evolution using Multiple State-Specific Rates of continuous character evolution (MuSSCRat; May and Moore 2020). To reduce the risk of erroneously attributing rate heterogeneity to the discrete character of interest, this model permits background rate variation (i.e., rate variation not attributed to the discrete character). This model also accommodates multivariate continuous characters to account for the correlated evolution of traits and simultaneously estimates discrete and continuous character histories (rather than estimating each sequentially). MuSSCRat models were run for 10k generations with 10% burnin. The model requires a prior on the number of rate shifts for the continuous characters. Therefore, we repeated analyses with different priors (10, 20, 30, and 40 shifts) to assess its impact on posterior estimates of key parameters and the posterior probability that rates were state-dependent. As further quality checks, we performed additional MuSSCRat analyses with an uncorrelated lognormal (UCLN) model (May and Moore 2020) in which the rates do not have a phylogenetic structure. To evaluate the role of rate heterogeneity in erroneously driving effects of discrete characters on rates of morphological evolution (i.e., false positives), we repeated all analyses with a reduced MuSSCRat model that did not permit rates to vary among branches (i.e., did not account for background rate variation).

To assess the correlation between rates of speciation and morphological evolution, we estimated tip rates (i.e., species-specific rates of diversification; Harvey and Rabosky 2018; Title and Rabosky 2019). Tip rates are an estimate of the present-day evolutionary rate of a lineage (Title and Rabosky 2019). We first estimated branch-specific rates of speciation using a birth–death–shift process (Höhna et al. 2019) implemented in RevBayes (Höhna et al. 2016). This model is similar to Rabosky (2014), except that the model uses a finite number of rate categories to approximate a continuous distribution of diversification rates. We specified eight rate categories during the analysis. The Markov chain Monte Carlo (MCMC) was run for 10k generations with 10% burnin. We estimated branch-specific rates of morphological evolution using MuSSCRat (May and Moore 2020). Because there were no cases in which the discrete character affected the evolution of the continuous characters (see below), we used the branch-specific background rates (i.e., rate variation not attributed to the discrete character) estimated from the MuSSCRat model to calculate tip rates. Tip rates are not phylogenetically independent, so we used phylogenetic generalized least squares to assess the evolutionary correlation between rates of speciation and morphological evolution using

the gls function implemented with ape (Paradis and Schliep 2019) and nlme (Pinheiro et al. 2020).

We were also interested in how anole speciation rates compared to their close relatives. The identity of the sister group of *Anolis* remains unresolved; therefore, we compared two candidate sister taxa based on existing phylogenetic hypotheses—casquehead lizards (Corytophanidae; Pyron et al. 2013) and bush anoles (*Polychrus*; Zheng and Wiens 2016). Both of these lizard groups are superficially similar to *Anolis* in their morphology, arboreal ecology, and distribution in the Neotropics (Vitt and Lacher 1981; Vieira et al. 2005; Torres-Carvajal et al. 2017). Importantly, both groups have gular folds similar (though not functionally equivalent) to the *Anolis* dewlap (Ord et al. 2015) but lack adhesive toe pads. The Pyron et al. (2013) phylogenetic tree was not time-calibrated; therefore, branch lengths were transformed to relative time using the chronopl function implemented in the R package ape (Paradis and Schliep 2019). Both phylogenetic trees were pruned to include only *Anolis* and their respective sister group. We estimated speciation rates across both phylogenetic trees using a birth–death–shift process (Höhna et al. 2019) as described above. To determine if previous reports of speciation rates that have declined overtime on each of the major islands (Rabosky and Glor 2010) could instead be attributed to toe pads (i.e., across the entire genus), we assessed speciation rates through time using an episodic birth–death model (Höhna 2015). The episodic birth–death model permits speciation rates two vary among a specified number of time intervals. During this analysis, we used 10 time intervals and assumed uniform incomplete taxon sampling. To hone in on the impact of the origin of *Anolis* in moderating the tempo of evolution, we repeated these analyses excluding and including the outgroup.

RESULTS

The morphological disparity is higher in island anoles than in mainland species, regardless of the phylogenetic scale of the data set ($N = 165$, 191, or 334; Supplementary Fig. S1 available on Dryad), ranging from 1.6- to 1.7-fold difference. Most traits were, as expected, effective at distinguishing the Caribbean island ecomorphs (Supplementary Fig. S2 available on Dryad). Specifically, snout-vent-length, femur length, toe length, and tail length varied among ecomorphs; head length and the number of lamellae, by contrast, did not vary among ecomorphs (Supplementary Table S1, available on Dryad). Island and mainland anoles do not differ in rates of speciation (Fig. 1a) or in rates of morphological evolution (posterior probability = 0.14 to 0.17; Fig. 1b).

When exploring the island radiation in greater detail, we found that the rate of speciation (Fig. 1c) and morphological evolution (PP = 0.18–0.33; Fig. 1d) also does not differ based on speciation mode (*in situ* vs. dispersal). Similarly, rates of speciation are equivalent
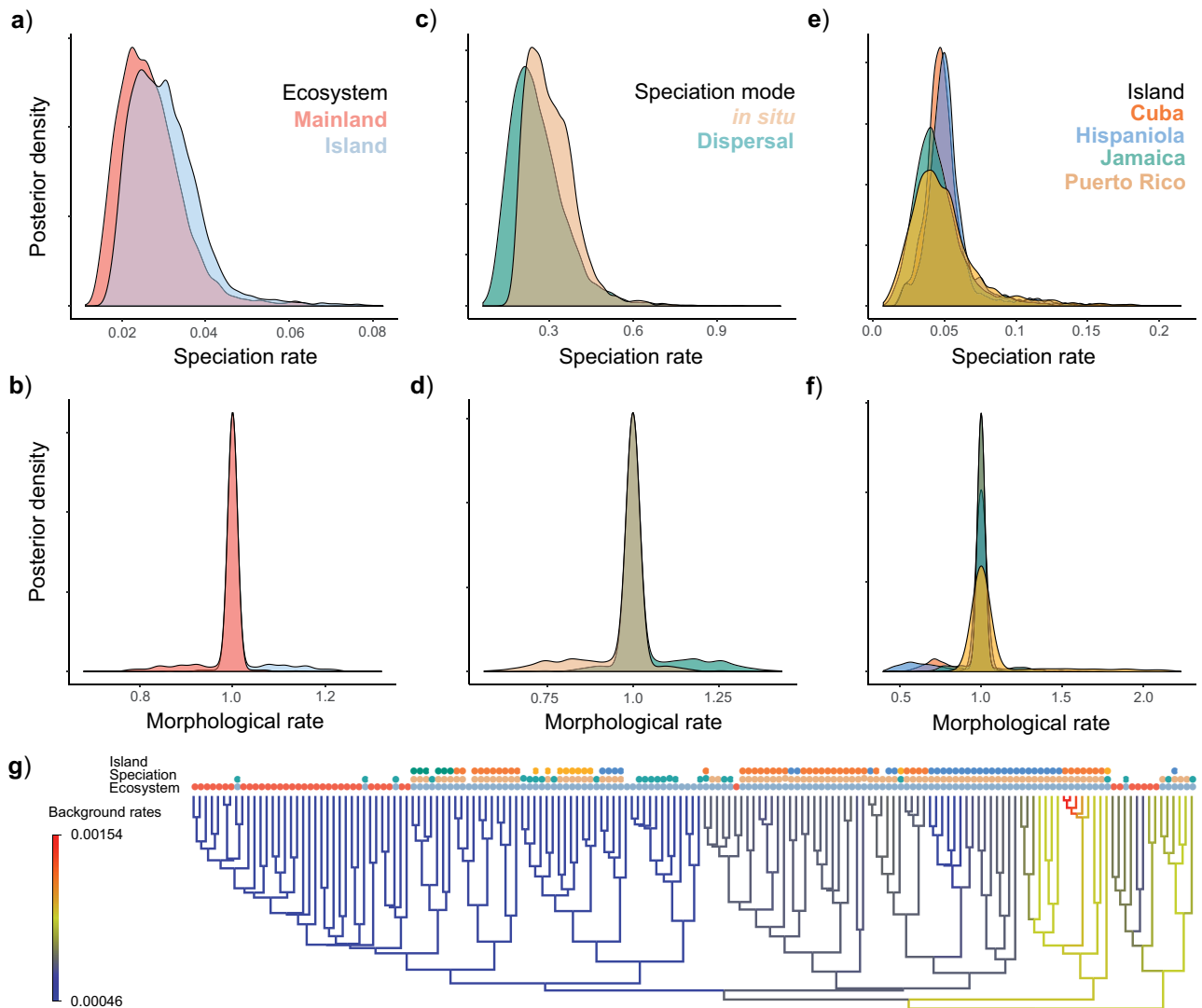
FIGURE 1.   Lack of island effects on anole diversification. Rates of speciation and morphological evolution between a, b) islands and the mainland, c, d) modes of speciation, and e, f) Caribbean islands. Background rates of morphological evolution across the anole phylogeny (g). The distributions of character states are depicted by circles along the tips of the phylogeny.

among the four major Caribbean islands (Fig. 1e), as are rates of morphological evolution (PP = 0.261; Fig. 1f). Background variation in the rate of morphological evolution (i.e., variation not attributed to ecosystem type) consisted of isolated bouts of elevated rates, particularly in a small clade of Cuban crown-giant species (Fig. 1g). Posterior estimates of key parameters were consistent across runs with different priors or varied as expected in response to priors (Supplementary Figs. S3–S5 available on Dryad; Moore et al. 2016; May and Moore 2020). Rates of speciation and morphological evolution are correlated across the anole phylogeny ($r = 0.199; t = 7.69; P < 0.0001$), but geography (island vs. mainland) had no effect on the slope of the line fit to this correlation (based on Akaike Information Criterion; Fig. 2). These results were consistent when repeated with a larger data set that matches the Zheng and Wiens (2016) phylogenetic tree (Supplementary Figs. S6

and S7 available on Dryad) and using an uncorrelated lognormal (UCLN) model (Supplementary Fig. S8 available on Dryad). If rate heterogeneity was ignored, however, then island anoles had 2.4-fold faster rates of morphological evolution than those on the mainland (PP = 1.0) and species that arose via dispersal had 1.9-fold faster rates than those that arose *in situ* on their host island (PP = 0.978; Supplementary Fig. S9 available on Dryad), highlighting two cases of averted false positives by accounting for background rate variation.

Anoles exhibit faster speciation rates than closely related iguanian lizards that possess gular folds but lack adhesive toe pads (Fig. 3a,b). On average, anole speciation rates were 1.9-fold faster than *Polychrus* and 3.8-fold faster than Corytophanidae. Speciation rates varied episodically through time, including a pulse of elevated rates following the origination of *Anolis* before declining towards the present (Fig. 3c,d).
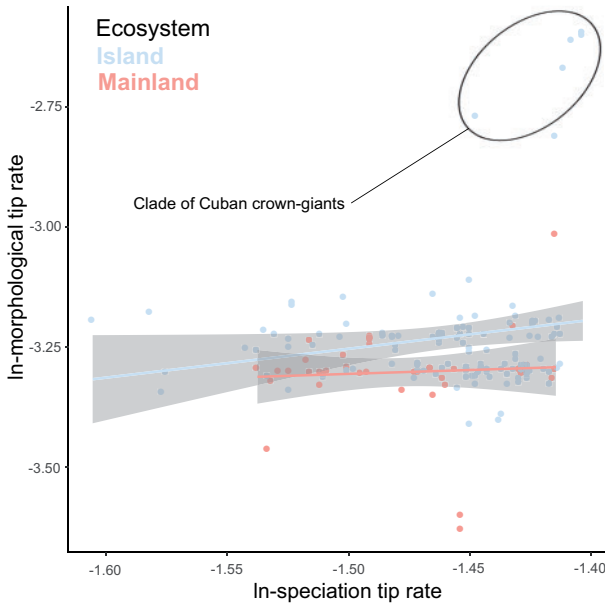
FIGURE 2. Relationship between rates of speciation and morphological evolution among anoles. Best-fit lines correspond to island and mainland species to depict their similar slopes.

DISCUSSION

We challenge an existing adaptive radiation paradigm that has been conspicuously island-centric, and instead show that diversification among Caribbean island anoles has been consistent with those on the mainland. There is widespread phenotypic convergence between the island and mainland anoles (Poe and Anderson 2019), including mainland analogs of the trunk-crown, trunk-ground, grass-bush, and twig ecomorphs (Schaad and Poe 2010; Losos et al. 2012; Moreno-Arias, and Calderon-Espinosa 2016). The extensive parallel evolution of microhabitat specialists on the Caribbean islands (Losos 2009; Mahler et al. 2013) may have simply been a more

visible theatre for their adaptive radiation to play out than in the more saturated forest communities of the Latin American mainland.

Islands as Drivers of Adaptive Radiation

In some cases, there is a strong "island effect" on speciation, as in Malagasy vangas (Reddy et al. 2012). For aquatic organisms, lakes function like islands insofar as they are isolated and discrete ecosystems. There is a strong lake effect on speciation in cichlid fishes when lakes are colonized by riverine lineages (Seehausen 2006; Burress and Tan 2017). Here, we found no effect of islands on speciation rates. Anole assemblages exhibit long-term stability on Caribbean islands insofar as their present day ecomorphological diversity has persisted since the Miocene (Sherratt et al. 2015). There has also been parallel declines to equilibrium on most islands (Rabosky and Glor 2010). These patterns may explain the lack of an island effect on rates of speciation.

Since rates of speciation and phenotypic evolution may be correlated across species-rich radiations (Rabosky et al. 2013), islands may be expected to have a similar influence on both. Specialization of beak morphology, particularly the evolution of stout or curved bills, drives speciation in the island and continental birds (Conway and Olsen 2019). But, island effects on bird diversification are known to be variable and dependent upon intrinsic features of clades that colonize islands (Lovette et al. 2002). In particular, finches, honeycreepers, and vangas have diversified extensively on islands (Lerner et al. 2011; Reddy et al. 2012) and tend to be more morphologically diverse than their mainland relatives (Losos and Ricklefs 2009; Tokita et al. 2017). We find that anoles are more morphologically diverse on islands (Supplementary Fig. S1 available on Dryad), but that this discrepancy does not appear to have arisen via faster rates of evolution on islands (Fig. 1).
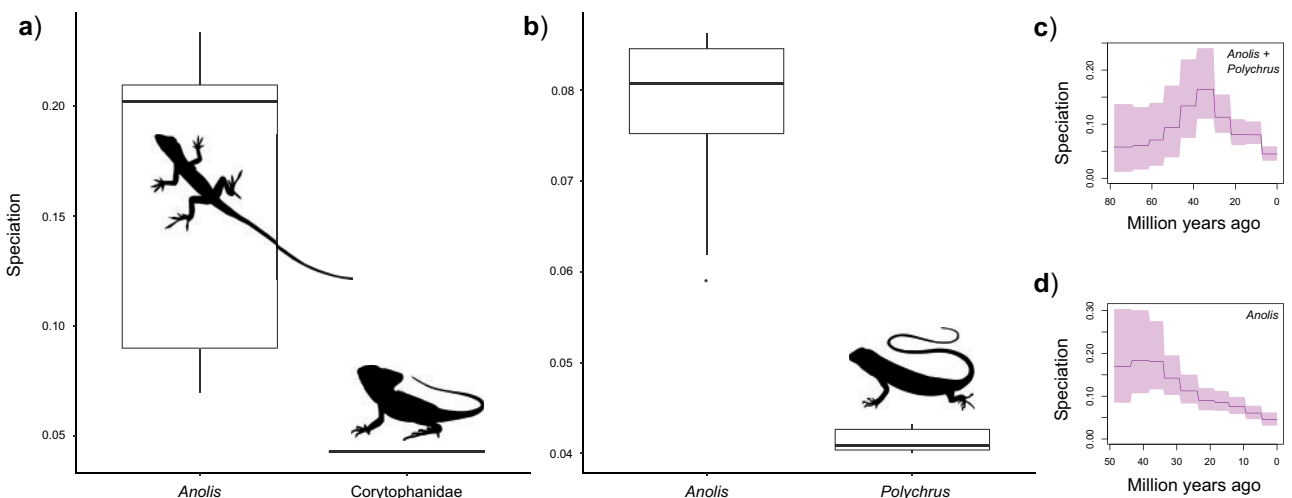

FIGURE 3. Speciation rates of *Anolis* and closely related iguanian lizards that have gular folds but lack adhesive toe pads (a, b). c) Pulse of speciation following the origin of *Anolis* and d) subsequent decline through time.

Rather, there is some redundancy in ecomorphs between islands and the mainland, hinting at deeper levels of ecomorphological convergence (Schaad and Poe 2010; Losos et al. 2012; Poe and Anderson 2019). Morphological diversification in anoles appears to parallel patterns observed in East African Rift Lake cichlids, which evolved extreme versions of ecomorphs, but their corresponding phenotypes are largely a recycling of those already found in riverine assemblages (Seehausen 2015).

Clarifying equivalent rates of diversification among biogeographic contexts urges a re-examination of the factors that theoretically accelerate evolution on islands. Islands are thought to provide release from predation (Schluter 1988). Yet, our findings suggest that anoles have diversified similarly on islands as on the mainland, despite these different selection pressures. Predation is often viewed as having a negative effect on ecological opportunity, specifically by restricting species' ability to exploit new niches (Schluter 1988). However, adaptive radiation may proceed under strong predation pressure on islands, evidenced by the diversification of Hawaiian stick spiders (Gillespie et al. 2018) that have employed crypsis to avoid detection by predators (Oxford and Gillespie 2001). Predation also promoted adaptive radiation of stick insects by imposing divergent selection for host-specific crypsis (Nosil and Crespi 2006). Mainland anoles are less colorful and less active than island anoles (Losos 2009), likely in response to different degrees of predation pressure. Anoles have several antipredator adaptations, including tail autonomy, color crypsis, and avoidance behavior (reviewed in Losos 2009), which may help them negotiate predation risk, and subsequently dilute the effects of variable predation pressures on islands and the mainland.

Islands are also thought to provide release from incumbent competitors on the mainland (Schluter 2000). Competition is often viewed as having a constraining effect on diversification; however, competition may drive adaptive radiation. For example, competition drives beak size evolution in Galápagos finches (Schluter et al. 1985). In anoles, competition for perches drives morphological diversification (Stuart et al. 2014; Yuan et al. 2020). In both these cases, the need to reduce competition by partitioning resources led to an increase in ecological diversity. Therefore, differences in assemblage saturation between the island and mainland anoles may not have manifested as different patterns of diversification.

Niches are multidimensional and adaptive radiation may unfold in a manner that engages with many of these dimensions, either simultaneously (Harmon et al. 2005; Muñoz and Losos 2018) or sequentially (Streelman and Danley 2003). Islands may differentially interact with some of these dimensions. While morphology is strongly tied to microhabitat specialization (Losos 2009; Mahler et al. 2013), physiology may represent another dimension subject to island effects (Salazar et al. 2019) due to strong associations with environmental variation and behavior (Hertz et al. 2013; Velasco et al. 2016; Gunderson and Mahler 2018; Muñoz et al. 2014; Muñoz and Losos 2018; Muñoz and Bodensteiner 2019). Therefore, the macroevolutionary signatures that manifest with morphology may erode when subjected to a broader, more multidimensional phenotypic exploration.

Extinction is expected to play a central role in driving the evolutionary dynamics of island biota over time (MacArthur and Wilson 1963, 1967; Losos and Ricklefs 2009; Rosindell and Harmon 2013). We did not estimate extinction rates due to inherent issues (Rabosky 2010) and the extended implications (Louca and Pennell 2020) of using phylogenies based on extant taxa. Thus, any discrepancies in extinction between island and mainland anoles would be a source of variation not considered that could lead to differences between island and mainland anoles.

The Role of Key Innovation in Spurring Adaptive Radiation

Our findings point to a broader *Anolis*-wide adaptive radiation, rather than one that is restricted to the Caribbean islands. Key innovations have periodically spurred bouts of diversification by allowing the lineage in which they evolve to interact with the environment in a novel way. There are many examples of such innovation across the tree of life, including adhesive silk in spiders that enhanced their ability to capture prey (Bond and Opell 1998), modified pharyngeal jaws in some acanthomorph fishes that facilitated feeding on prey protected by hard shells (Liem 1973; Wainwright et al. 2012), insect wings that enhanced their ability to disperse to isolated habitats (Nicholson et al. 2014), and alternative photosynthetic pathways that reduced water loss in arid environments (Silvestro et al. 2014). Anoles share several putative key innovations that may have promoted their diversification, including highly controllable dewlaps and adhesive toe pads. Dewlaps function as visual signals that could theoretically spur species diversification via sexual selection (Sigmund 1983), similar to male egg-spots and sexual dichromatism in African lake cichlids (Salzburger et al. 2005; Wagner et al. 2012). Alternatively, dewlaps may function as signals of species recognition (Losos 1985), particularly as a mechanism for reinforcement following secondary contact (Ng and Glor 2011; Lambert et al. 2013). Some anole species are polymorphic in terms of dewlap color (MacGuigan et al. 2016), which may reflect local adaptation for signal visibility under different light conditions (Leal and Fleishman 2002, 2004; Muñoz et al. 2013, Fleishman et al. 2020). These potential dewlap functions may explain species richness but lack a clear role in promoting morphological evolution and adaptation to different microhabitats, as ecomorphs have not converged on similar dewlaps (Nicholson et al. 2007). Poe et al. (2018) suggested that dewlaps led to faster rates of speciation in anoles, but candidate sister lineages of anoles also have gular folds used for visual

signaling (albeit less robust; Ord et al. 2015), suggesting it is an unlikely key innovation underpinning the anole adaptive radiation.

Arboreal microhabitats played a central role during anole diversification (Losos 2009) and toe pads may have facilitated the exploitation of these niches by enhancing the grip and/or locomotor performance while traversing tree trunks, branches, and twigs (Elstrott and Irschick 2004; Bloch and Irschick 2005; Crandell et al. 2014; Yuan et al. 2019). Adhesive toe pads evolved independently in several lineages of lizards, including geckos, some skinks, and anoles (Irschick et al. 2006). There are some morphological differences in toe pads of the island and mainland anoles, but they maintain similar associations to habitat use (Macrini et al. 2003). The high morphological disparity exhibited by anoles when compared to other groups of lizards has been attributed to toe pads (Warheit et al. 1999; Losos 2009). The central role adhesive toe pads play in the use of vertical habitats is supported by the pattern that anoles and geckos with small toe pads or that lack toe pads tend to be terrestrial (Peterson 1983; Lamb and Bauer 2006; Nicholson et al. 2006), whereas more developed toe pads provide enhanced clinging ability (Irschick et al. 1996). While toe pads likely facilitated widespread use of arboreal habitats, some lizards evolved alternative solutions to the functional demands associated with moving along branches and twigs. For example, chameleons have their own suite of innovations, namely prehensile tails and highly modified grasping feet, which facilitate traversal along branches (Higham and Jayne 2004; Herrel et al. 2013).

Anoles have higher speciation rates than close relatives that have gular folds but lack adhesive toe pads (Fig. 3); this pattern suggests that toe pads, rather than dewlaps, have driven their adaptive radiation. While other life-history traits likely differ among these groups, generation time, an important predictor of speciation rate, is comparable between *Polychrus* and *Anolis* (i.e., less than a year; Andrews 1976; Vitt and Lacher 1981), albeit slightly longer in Corytophanids (i.e., about a year and a half; Van Devender 1982). Correspondingly, other features may have interacted with this innovation to spur faster speciation in anoles. Corytophanids and *Polychrus* share many characteristics with anoles, including their Neotropical distributions (Vieira et al. 2005; Torres-Carvajal et al. 2017) and preference for arboreal habitats (Vitt and Lacher 1981). In a manner analogous to anoles, *Polychrus* lizards have even colonized islands off the coast of South America (Murphy et al. 2017). In principle, these closely related lineages likely encountered many of the same ecological opportunities and selective pressures encountered by anoles but may not have had the necessary adaptations to exploit arboreal habitat to the degree achieved by anoles. There are many limitations when dealing with singular events, such as the origin of toe pads in anoles, but we demonstrate a classic signal of waning ecological opportunity—declining rates of speciation through time—across *Anolis*, thus associating this feature with the origin of toe pads (Fig. 3c,d). Importantly, our findings suggest that the pattern of declining rates of speciation (Rabosky and Glor 2010) and phenotypic evolution (Mahler et al. 2010) on the major Caribbean islands could be a broader signal attributable to innovation (Fig. 3c,d). More generally, we recognize that there are other phenotypically diverse and species-rich groups of lizards, such as skinks, liolaemids, and agamids (Collar et al. 2010; Rabosky et al. 2014; Pincheira-Donoso et al. 2015), suggesting toe pads are far from the only means to extensive diversification within the group.

Ecological opportunity can sometimes result from innovations and biogeography. For example, an innovation of the pharyngeal jaw apparatus enhanced the feeding repertoire of cichlids (Liem 1973) as well as wrasses and parrotfishes (Labridae; Liem and Sanderson 1986). Subsequently, there were dramatic "lake effects" and "coral reef effects" on the diversification of cichlids and labrids, respectively, as they invaded those environments (Seehausen 2006; Price et al. 2011; Burress and Tan 2017). Similarly, vangas experienced an initial pulse of diversification after colonizing Madagascar, followed by a subsequent pulse driven by an innovation in beak morphology (Jønsson et al. 2012). Anoles appear to differ from these other classic adaptive radiations in that adhesive toe pads enhanced their ability to traverse arboreal habitat (Elstrott and Irschick 2004; Bloch and Irschick 2005; Crandell et al. 2014; Yuan et al. 2019), but there was no subsequent "island effect" on diversification (Fig. 1). Whether these discrepancies are due to intrinsic features of each lineage, idiosyncrasies of their respective innovations, or historical contingencies remains to be tested.

CONCLUSIONS

Islands are ideal venues for studying how adaptive radiation unfolds (Losos and Ricklefs 2009; Gavrilets and Losos 2009), especially the predictability of the evolutionary process (Mahler et al. 2013) and diversification patterns of local assemblages (Rabosky and Glor 2010; Mahler et al. 2010; Reddy et al. 2012; Gillespie et al. 2018). Yet, our findings indicate that islands are no more remarkable than continental habitats for facilitating anole adaptive radiation. In particular, we demonstrate the importance of accommodating background rate variation, as several would-be "island effects" were driven by rate heterogeneity (Fig. 1 and Supplementary Fig. S9 available on Dryad). To understand the mechanisms of adaptive radiation, studies should ideally situate at the phylogenetic scale at which exceptional diversification manifests. In the case of anoles, rapid diversification characterizes the entire lineage, regardless of biogeographic context. Mainland communities are more saturated in terms of competitors and predators (Schluter 1988, 2000; Losos 2009), resulting in very different selective regimes than on islands. But, divergent mechanisms can often converge on similar evolutionary outcomes (Wainwright et al. 2005;

Burress et al. 2018; Conway and Olsen 2019; Muñoz 2019). In this regard, competition and predation may be viewed as robustly effective for adaptive radiation, either promoting diversification via intense selection (i.e., cryptic evolution on the mainland), or by providing ecological opportunity in their absence via enhanced resource availability (i.e., increased mobility on islands). In either scenario, the ability to exploit arboreal habitat via adhesive toepads was likely a critical prerequisite for the observed ecological and morphological diversity of the anole adaptive radiation.

SUPPLEMENTARY MATERIAL

Data available from the Dryad Digital Repository: http://dx.doi.org/10.25338/B8VH1S.

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