Convergence and Divergence from Populations to Species:
Phenotypic Evolution of Caribbean *Anolis* Lizards

By

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Abstract

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This dissertation is primarily focused on understanding the generation and maintenance of phenotypic diversity through ecological selection. Natural selection acts on the phenotype because the phenotype lies at the interface between an organisms genotype and its environment. Thus, the study of phenotypic diversity is central to our understanding of evolution. I have primary addressed questions of phenotypic evolution using the radiations of Caribbean *Anolis* lizards.

Chapter I of my dissertation examines if claw and toepad morphology formed an integrated phenotype correlated with microhabitat partitioning in Greater Antillean anoles. The Greater Antilles forms an exceptional system to study convergent evolution due to the repeated evolution of structural microhabitat specialist 'ecomorphs'. As locomotor traits associated with clinging performance, claw and toepad traits are likely highly relevant to partitioning of vertical arboreal habitat. I found that correlative selection did drive the evolution of claw and toepads as an integrated phenotype to optimize performance on specific microhabitats. Additionally, rates of evolution were coupled between claws and toepads across most species, except twig specialists which experienced a dramatic reduction in claw structure. Thus, this study provides a convincing case study for correlative selection facilitating ecological divergence between species.

Chapter II studies claw and toepad integration in the context of the species depauperate Lesser Antillean anole fauna. These anoles represent broad habitat generalists with only one or two species per island. Broadly, claw and toepad morphology correlated with overall island habitat availability on one species islands, but not two species islands. Here, I found that *Anolis bimaculatus* series anoles closely-related to the Greater Antillean adaptive radiations followed predictable patterns of divergence on two species islands in that they partitioned vertical habitat space and showed associated phenotypic integration between claws and toepads. However, the distantly-related *A. roquet* series anoles did not show predictable patterns of divergence on two species islands and a decoupling of claw and toepad traits. These results suggest that phylogenetic history may influence the capacity for adaptive divergence.

Chapter III tests for parallel intraspecific patterns of divergence across environmental gradients in nine species of *A. bimaculatus* series anoles inhabiting the northern Lesser Antilles. Species within the *A. bimaculatus* series are broadly generalist and occur widely throughout their native islands. Thus, each encounters a wide range of environmental variation ranging from xeric coastal scrub to montane rainforests. I found that patterns of morphological divergence across these environmental gradients were idiosyncratic. It is possible that due to many-to-one mapping of form to function, adaptation to environmental gradients can be achieved through different ecologically-relevant traits. However, strong patterns of convergence did emerge for some traits, notably dorsal coloration.

Chapter IV examines the phenomenon of species richness-genetic diversity in the context of island biogeography and extends this framework to include phenotype diversity. Specifically, I examined the relative roles of island size, distance from mainland, environmental variance, and topographic complexity across the Lesser Antilles. I partitioned biogeographical effects across species, phenotypic, and genetic diversity using both native and introduced herpetofauna. I found that island size correlates with both species richness and genetic diversity in all contexts. Secondary island characteristic effects on species and genetic diversity differed between groups likely due to differences in their natural history. Phenotypic diversity was not correlated with tested island variables in all cases suggesting that macroecological forces which shape species and genetic diversity are decoupled from phenotypic diversity.

For my family and friends who got me through this.

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Finally, I thank the anoles because without them this dissertation would not exist.

PREFACE

Phenotypic variation represents a fundamental axis of biological diversity. It is the phenotype upon which natural selection directly acts and, thus, the phenotype which lies at the interface between an organism's genetics and its environment. In short, without heritable phenotypic variation natural selection would not occur. Therefore, understanding the generation and maintenance of phenotypic diversity is central to the pursuit of evolutionary biology. It is from this perspective that I approach the work presented in this dissertation.

Convergent evolution, including its subcase parallel evolution, provides an exceptional opportunity to study environment-phenotype interactions because it offers biological replication in natural systems. As an aside, the terms convergence and parallelism have often has inconsistent definitions in the literature and have been subject to debate as to the degree that they represent distinct phenomena (Arendt and Reznick 2008; Losos 2011; Conte et al. 2012; Pearce 2012). Parallelism is often applied with the assumption that closely related species should have a evolved from a similar initial phenotypic or genetic state, whereas convergence assumes that they have not (Arendt and Reznick 2008). However, the ancestral states do not necessarily conform to these assumptions, nor are they often known. Here, I follow the framework presented by Arendt and Reznick (2008) in considering convergence and parallelism a singular phenomenon of independent evolution of a phenotype. Thus, in most chapters only the term convergence is employed. The use of the terms parallelism and convergence in Chapter III serve only to distinguish between within clade and between clade comparisons respectively. Regardless, replicated evolution has also captured the interest of generations of biologists because it implies a degree of predictability in evolution, whether through natural selection leading phenotypes toward common adaptive peaks or through shared evolutionary constraints (Losos 2011). Although the particular selective environments which generate convergence may vary, a primary focus of this dissertation is the study of convergent selection generated through divergent selection. That is, when similar selective environments lead to divergence at multiple evolutionary scales (i.e. between species or populations) such that the pattern of divergence is itself convergent.

I address questions of phenotypic evolution using two study systems: the Greater and Lesser Antillean anoles. The Greater Antilles is host to the remarkable repeated adaptive radiations of anoles, which have formed the basis for a rich literature in the study of evolution (Losos 1990, 2009; Mahler et al. 2013). These adaptive radiations are characterized by the convergent evolution of 'ecomorphs' which exhibit similar ecologies, behaviors, and morphologies (Williams 1972; Losos 1990b; Losos et al. 1998; Kolbe et al. 2011). These ecomorphs represent a classic case of convergent evolution, in this case due to competition driven habitat partitioning. Thus, the Greater Antilles represents a compelling system in which to study convergent phenotypic evolution in detail. Compared to the complex communities of the Greater Antilles, the Lesser Antillean anole fauna is depauperate. Every island is host to one or at most two species of anole (Underwood 1959; Lazell 1972). These anoles are broad generalists, which occur throughout the entirety of their native islands (Lazell 1972; Losos and de Queiroz 1997). This simplified system allows for more direct comparisons of islands with and without specific environmental pressures.

In the following chapters, I present an empirical examination of ecological selection as a driver of both intraspecific and interspecific phenotypic diversity using Caribbean anoles as a study system. Specifically, Chapters I and II focus on the evolution of convergent morphologies in response to habitat partitioning between species of Greater and Lesser Antillean anoles respectively. Chapter III aims to detect parallel patterns of phenotypic divergence across similar environmental gradients using Lesser Antillean anoles. Finally, Chapter IV extends this framework toward understanding the macroecological forces that may drive similar patterns across levels of diversity: species, phenotypic, and genetic. Together, this dissertation builds our understanding of the degree to which similar environmental selective agents drive similar patterns of phenotypic evolution across populations and species.

CHAPTER I

Phenotypic integration between claw and toepad traits promotes microhabitat specialization in the *Anolis* adaptive radiation

This manuscript has previously been published.

Citation:

Abstract

The performance of an organism in its environment frequently depends more on its composite phenotype than on individual phenotypic traits. Thus, understanding environmental adaptation requires investigating patterns of covariation across functionally-related traits. The replicated adaptive radiations of Greater Antillean *Anolis* lizards are characterized by ecological and morphological convergence, thus providing an opportunity to examine the role of multiple phenotypes in microhabitat adaptation. Here, we examine integrated claw and toepad morphological evolution in relation to habitat partitioning across the adaptive radiations of Greater Antillean anoles. Based on analysis of 428 specimens from 57 species, we found that different aspects of claw morphology were associated with different perch dimensions, with claw height positively associated with perch diameter and claw curvature positively associated with perch height. Patterns of integration also varied across claw and toepad traits, likely driven by correlative selection for performance on smoother and rougher substrates. Finally, rates of evolution differed between claw and toepad traits, with claw length evolving faster than all other traits despite having no predicted functional importance. Our results highlight the multivariate nature of phenotypic adaptation and suggest that phenotypic integration across Greater Antillean anoles is driven by fine-scale correlative selection based on structural habitat specialization.

Introduction

Natural selections acts upon whole organism performance, as determined through multivariate trait complexes (Arnold 1983; Schluter and Nychka 1994; Wainwright and Reilly 1994) and often involving performance tradeoffs between multiple aspects of an organism's phenotype (Reznick and Ghalambor 2001; Ghalambor et al. 2003). Therefore, correlative selection often leads to phenotypic integration, or patterns of covariation in functionally-related traits, that maximizes performance across otherwise independent traits (Zelditch 1988; Schluter and Nychka 1994; Endler 1995; Pigliucci 2003). Such selection-mediated phenotypic integration may be particularly prevalent during adaptive radiations, allowing clades to utilize previously inaccessible ecological space (Miller 1949; Monteiro and Nogueira 2010; Stroud and Losos 2016).

The replicated adaptive radiations of *Anolis* lizards on the Greater Antilles display remarkable convergent evolution in both habitat use and morphology (Williams 1972; Losos et al. 1998; Losos 2009). The primary axis of divergence in structural habitat use is facilitated by convergent evolution of overall body plans, including body size, limb dimensions, head dimensions, and adhesive toepad morphology producing highly integrated whole organism phenotypes within the radiations (Losos 1990b; Losos et al. 1998; Beuttell and Losos 1999; Kolbe et al. 2011). Based on this ecological, behavioral, and morphological convergence, the Greater Antilles anoles are classified into six ecomorphs, named for their utilization of vertical microhabitat space: grass-bush, trunk-ground, trunk, trunk-crown, crown-giant, and twig anoles (Williams 1972; Losos et al. 1998; Losos 2009). This pattern of convergence indicates strong multi-trait selection associated with structural habitat use among Greater Antillean anoles. Functional studies have demonstrated the utility of several convergent phenotypes in exploitation of the structural habitat (Losos and Sinervo 1989; Losos 1990b; Beuttell and Losos 1999; Elstrott and Irschick 2004; Crandell et al. 2014). Yet, the functional linkage between traits that might facilitate phenotypic integration in a correlative selection framework is not always straightforward, and finer-scale phenotypic covariation may be masked by gross morphology.

Here, we examine the integrated evolution of two traits whose functions should be highly linked in anoles: the adhesive toepad and the claw. Both toepads and claws occur in all species of anoles except *A. onca,* which lacks toepads. In the adaptive radiation of *Anolis* lizards, adhesive toepads are thought to be a key innovation which allowed them to occupy broader arboreal niche space relative to species without toepads (Irschick et al. 2006; Losos 2009). Certainly, Greater Antillean anoles display remarkable convergent evolution in toepad traits related to habitat use (Macrini et al. 2003; Schaad and Poe 2010), and toepads are functionally important for clinging ability (Elstrott and Irschick 2004; Irschick et al. 2006; Crandell et al. 2014). However, our understanding of the role of claws in habitat partitioning by anoles is limited (Losos 2009; Crandell et al. 2014). Yet, in other arboreal species, claws are often ecologically important to arboreality even when adhesive toepads are present (Zani 2000; Vanhooydonck et al. 2005; Song et al. 2016). Toepads are adapted to provide adhesion to smoother surfaces due to increased surface area contact between setae and underlying substrates (Vanhooydonck et al. 2005; Gillies et al. 2014), whereas the interlocking performance of claws is thought to be facilitated by surface texture (Cartmill 1974). Therefore, previous authors have suggested, although never empirically tested, that integration in claws and toepad traits may have contributed to habitat partitioning by

allowing anoles to efficiently navigate a variety of surface textures more effectively than toepads alone would have (Elstrott and Irschick 2004; Crandell et al. 2014).

Across vertebrates, the morphology of claws often reflects their specialized functionality (Tulli et al. 2009, 2016; Birn-Jeffery et al. 2012). For instance, tree-climbing and branch-perching birds have greater claw curvature than terrestrial species (Feduccia 1993), a pattern that is broadly shared across squamate reptiles as well (Zani 2000; Tulli et al. 2009; D'Amore et al. 2018). Greater claw curvature facilitates climbing by improving penetrative and interlocking performance with climbing surfaces (Cartmill 1974). Arboreal lizards also have taller claws compared to terrestrial lizards, yet claw height and curvature are associated with different aspects of clinging performance (Zani 2000). Claw height improves clinging performance on rougher surfaces but not smoother surfaces across squamate reptiles, whereas claw curvature improves clinging performance on smoother surfaces (Zani 2000; Tulli et al. 2011). Therefore, correlative selection should lead to phenotypic integration between toepad traits, which provide adhesion to smoother surfaces, and claw curvature but not claw height.

Although another aspect of claw morphology, length, may act as an extension of the toe in more terrestrial species, allowing for greater surface area contact and propulsive force when running on flat surfaces (Glen and Bennett 2007; Tulli et al. 2009; Birn-Jeffery et al. 2012), claw length does not affect clinging performance on any surface (Zani 2000; Tulli et al. 2011) and thus should not be under correlative selection with toepad traits related to adhesive performance or other functionally relevant claw traits. Phenotypic integration is also expected to be linked to the rate of evolution across integrated traits (Frédérich et al. 2014; Sherratt et al. 2017). Because traits that are under strong selection and biomechanical constraint often have lower rates of evolution (Adams et al. 2017a), sets of integrated biomechanical traits should evolve more slowly than those not under correlative selection. Therefore, we expect that rates of evolution should be similar across integrated claw and toepad traits but not traits lacking ecological relevance in our study system.

To test these hypotheses about how a multivariate trait complex evolves in response to correlative selection, we examine a suite of claw and toepad characters to study integrated trait evolution in relation to habitat use throughout the adaptive radiations of Greater Antillean anoles. We characterize patterns of claw variation from 57 *Anolis* species to address four major questions that examine the importance of claw and toepad traits at different scales of ecological divergence: (I) Are claw height and curvature correlated with greater arboreality as predicted by functional assays? (II) Is claw morphology associated with microhabitat usage in Greater Antillean anoles? (III) Is there phenotypic integration between toepads and claw curvature but not height, suggesting correlative selection? (IV) Do rates of morphological evolution covary between claw and toepad traits, as predicted for evolution under biomechanical constraint?

Methods

Sampling

We collected morphological data from preserved museum specimens maintained by the Museum of Vertebrate Zoology (University of California, Berkeley), the California Academy of Sciences (San Francisco, CA), and the National Museum of Natural History (Smithsonian Institution, Washington, DC) (Appendix I). We sampled 428 adult males representing 57 species. Our sampling includes at least one species from every ecomorph present on each Greater Antillean island (45 species) plus seven 'unique' Greater Antillean species not belonging to an ecomorph class. We also included the mainland species *A. carolinensis* as a trunk-crown ecomorph because it represents a back-colonization from the Greater Antilles to the mainland and retains traits characteristic of Greater Antillean trunk-crown anoles (Losos 2009). Lastly, because only one truly terrestrial species exists on the Greater Antilles, *A. barbouri*, we included four mainland leaf litter anoles to examine differences between terrestrial and arboreal species: *A. nitens, A. humilis, A. uniformis*, and *A. quaggulus* (Köhler et al. 2006; Losos 2009). Due to ecological and evolutionary differences between the mainland and Greater Antillean anole assemblages (Loses, 2009), these mainland anoles were not included in analyses other than the terrestrial-arboreal comparisons.

Morphological Measurements

After measuring snout-vent length (SVL) for all specimens as a proxy for body size, we imaged the fourth hind toepad for each specimen using a Dino-Lite Digital Microscope (Model AM4115ZT) or an EPSON V19 flatbed scanner (Fig 1.1). We also sagittally flattened and imaged the fourth hind claw using a Dino-Lite Digital Microscope. The fourth hind digit was chosen because it is the longest digit and has been the predominate focus of morphological and functional studies in anoles (Losos 1990b; Macrini et al. 2003; Kolbe et al. 2011; Mahler et al. 2013; Crandell et al. 2014). Using tpsdig2 (Rohlf 2006), we measured claw height, claw length, and claw curvature from digital images following Zani (2000) so that our data would be comparable to previous studies. Briefly, we measured claw height as the height at the base of the claw, and calculated claw curvature as

$$curvature = 57.296\left(2\sin^{-1}\left(\frac{(2A^2B^2+2B^2C^2+2A^2C^2-A^4-B^4-C^4)^{0.5}}{2AB}\right)\right),$$

where *A* is the distance from the ventral base of the claw to the vertex of the ventral curve, *B* is the distance from the ventral vertex to the tip of the claw, and *C* is the distance from the ventral base of the claw to the tip of the claw (Zani 2000). We calculated claw length as the sum of distances *A* and *B* (Fig 1.1). For toepad measurements, we defined the toepad as beginning where the next distal lamella is wider than the previous lamella. We counted the number of lamellae, following this definition, and measured toepad width as the widest point of the toepad. We could not measure some toepad traits for three specimens with damaged toepads. We did not measure toepad traits for the mainland leaf litter species because they were not needed for the relevant analyses.

We conducted all subsequent data analyses in R v3.3.3 (R Core Team 2017). For all analyses requiring phylogenetic information, we used the most recent comprehensive *Anolis* phylogeny (Poe et al. 2017), pruned to include only our focal taxa. We natural log-transformed all univariate measurements, except claw curvature, to achieve normality and homoscedasticity of our data. To quantify correlations with body size, we performed phylogenetic independent contrasts (PICs; (Felsenstein 1985) between log-transformed SVL and all other morphological and ecological traits. PICs use the underlying phylogeny to transform trait values to achieve statistical independence and identical distributions assuming Brownian motion (Felsenstein, 1985). We identified allometric scaling between claw traits and body size by comparing the 95% confidence intervals of slopes against one, to test for deviations from isometry, and against zero, to test for deviations from independence. For traits significantly correlated with body size, we regressed log-transformed traits against log-transformed SVL accounting for phylogeny (Revell 2009) using the 'phyl.resid' function in the *phytools* package (Revell 2017). We used residuals for all downstream analyses involving body-size correlated traits.

Because non-geometric data do not fully capture complex shape information, we also collected geometric morphometric data by characterizing claw shape using 30 semilandmarks placed along both the ventral and dorsal curves of the claw (Tinius and Russell 2017) and toepad shape using 50 semilandmarks following the outline of each toepad starting and ending on opposing proximate corners of the first toepad lamella. We placed semilandmark curves using tpsdig2. To remove non-shape features, we performed generalized Procrustes superimposition allowing semilandmarks to slide to minimize bending energy (Bookstein 1997) using the gpagen function in *geomorph* package (Adams et al. 2017b). Bending energy does not deform landmarks beyond the endpoints of the curve (Gunz and Mitteroecker 2013). For downstream analyses, we calculated mean shape values as the average coordinate position of each semilandmark for each species using the mshape function in *geomorph*.

Ecomorph Comparisons

To examine the association between structural habitat usage and claw morphology, we tested for the effects of ecomorph classification on univariate claw traits in Greater Antillean anoles using phylogenetically-corrected ANOVAs (Garland et al. 1993) implemented by the 'phylANOVA' function in *phytools*. If ANOVAs were significant, we then conducted *post hoc* pairwise comparisons between ecomorph categories. For multivariate claw shape, we analyzed the effects of ecomorph classification using Procrustes ANOVAs in a phylogenetic framework (Adams 2014a) implemented by the 'procD.lm' function in *geomorph*. We then calculated geometric morphometric shape disparity as the Procrustes variance for each ecomorph using the 'morphol.disparity' function in *geomorph*. To test whether levels of disparity differed between ecomorphs, we performed pairwise comparisons using absolute differences in Procrustes variances as test statistics compared against null distributions generated by permuting residuals across groups (Zelditch et al. 2012).

Arboreality and Perch Dimensions

Although ecomorph classification denotes differences in structural habitat use, no truly terrestrial ecomorph is present in the Greater Antilles and only a single 'unique' species, *A. barbouri*, can

be classified as terrestrial. Thus, to evaluate the effects of arboreal and terrestrial ecologies, we classified all Greater Antillean ecomorphs as arboreal and included mainland terrestrial species in comparisons between arboreal and terrestrial claw morphology. We compared terrestrial and arboreal species for each univariate claw trait using phylogenetically-corrected ANOVAs. For geometric morphometric claw shape, we tested for differences between terrestrial and arboreal species using Procrustes ANOVAs in a phylogenetic framework.

To examine the association between claw morphology and different characteristics of perch substrate, we compiled mean perch height and perch diameter estimates for 37 species (Losos and Sinervo 1989; Losos 1990a; Losos and Irschick 1996; Losos and de Queiroz 1997; Schettino et al. 2010). Perch data for the remainder of our study species were not readily available. As with morphological traits, if perch traits were significantly correlated with body size, we analyzed residuals after regressing the trait against log-transformed SVL. We then tested if log perch height and diameter were correlated with univariate claw traits using phylogenetic generalized least squares (PGLS). Next, we performed phylogenetic Procrustes regressions (Adams 2014a) to test for relationships between perch height and diameter with multivariate claw shape. We excluded twig, grass-bush, and crown-giant anoles from analyses of perch height because their highly specialized habitat utilizations are not principally differentiated by vertical perch height (Losos 2009). The remaining ecomorphs (trunk-ground, trunk, and trunk-crown anoles) represent different degrees of arboreality through their vertically structured use of tree trunk microhabitat.

Phenotypic Integration

To test for patterns of phenotypic integration across univariate traits, we performed PGLS between all combinations of univariate claw and toepad traits. We then estimated the degree of phenotypic integration between geometric morphometric claw and toepad shape, accounting for phylogeny, under Brownian motion by partial least squares (Adams and Felice 2014) as implemented by the 'phylo.integration' function in *geomorph*. To assess statistical significance of integration between geometric morphometric claw and toepad shapes, we compared our observed r_{PLS} against a null distribution of values generated by permuting claw data relative to toepad data.

Rates of Morphological Evolution

We examined the rate of morphological evolution for both univariate claw and toepad characteristics and multivariate shape traits. To test whether the rates of evolution are decoupled between toepads and claws, we fit both a single rate model and an independent rate model of continuous trait evolution under Brownian motion for all pairs of univariate traits and compared these fitted models using likelihood ratio tests (Adams 2013) implemented through the 'ratebytree' function in *phytools*. Because we used natural log-transformed values to standardize measurements, the variation in rate is the relative change, in proportion to the mean, for each trait.

To examine differences in rates of evolution across ecomorphs, we calculated net rates of morphological evolution for multivariate shape data for each ecomorph using the

'compare.evol.rates' function in *geomorph*. Due to the high dimensionality of geometric morphometric shape data, we followed the approach of (Adams 2014b), which uses the sum of squared distances between phylogenetically transformed data and the origin in multidimensional morphospace to estimate rates of evolution. We estimated the rates of evolution for toepad and claw shapes separately. The ratio between the rates of evolution was used as a test statistic, with the ratio between the minimum and maximum rate across ecomorphs used to determine overall ecomorph differences (Denton and Adams 2015). We estimated statistical significance using phylogenetic simulation under Brownian motion, assuming a common evolutionary rate across all species, to generate a null distribution of rate ratios.

Results

Body Size Correlations

We found that that both claw length ($F_{1,50}$ = 160.0, R^2 = 0.757, P < 0.001; slope = 1.20, 95% CI [1.01, 1.39]) and claw height ($F_{1,50}$ = 435.7, R^2 = 0.895, P < 0.001; slope = 1.24, 95% CI [1.12, 1.35]) scaled allometrically with body size, but claw curvature scaled independently of body size ($F_{1,52}$ = 3.667, R^2 = 0.050, P = 0.061; slope = 0.106, 95% CI [-0.01, 0.22]). Therefore, we corrected claw length and height, but not curvature, for body size in subsequent analyses.

Ecomorph Comparisons

Consistent with the anole ecomorph hypothesis, we found that both multivariate ($F_{5,40}$ = 3.24, P = 0.001; Fig 1.2A, B) and univariate claw shape were significantly predicted by ecomorph classification. For univariate traits, ecomorph classification significantly predicted relative height ($F_{5,40}$ = 10.35, P = 0.002), relative length ($F_{5,40}$ = 8.33, P = 0.004), and curvature of the claw ($F_{5,40}$ = 4.79, P = 0.046; Fig 1.3A-C). Consistent with previous work (Irschick and Losos 1998; Losos et al. 1998; Macrini et al. 2003; Schaad and Poe 2010), we found that toepad shape was predicted by ecomorph classification (all P < 0.05).

Subsequent *post hoc* pairwise tests found twig anoles significantly differed in multivariate claw shape from crown-giant (P = 0.003), grass-bush (P < 0.001), trunk-crown (P = 0.004), and trunk-ground anoles (P = 0.035). Trunk-crown anoles also significantly differed in multivariate claw shape from grass-bush (P = 0.035) and trunk-ground anoles (P = 0.033). For univariate measurements, claw curvature in twig anoles were significantly different from trunk-crown (P = 0.002) and trunk anoles (P = 0.023) and claw curvature in trunk-ground anoles was significantly different from trunk-crown anoles (P = 0.016). However, only twig anoles were significantly differentiated for both relative claw height and length (all P < 0.005) in *post hoc* pairwise comparisons (Fig 1.3).

We also found that levels of morphological disparity, or shape variance, differed across ecomorphs. Morphological shape disparity for claws was significantly greater in twig anoles than all other ecomorphs (all P < 0.05). Twig anoles had 2.8 to 4.7 times greater shape disparity for claws than other ecomorphs, whereas no other ecomorphs differed significantly from each other (all P > 0.05; Fig 1.2C).

Arboreality and Perch Dimensions

We found significant differences in both multivariate claw shape ($F_{2,54}$ = 3.36, P = 0.016; Fig 1.4) and univariate claw curvature ($F_{1,55}$ = 16.22, P = 0.001) between arboreal and terrestrial anoles. Consistent with predictions from previous functional studies (Zani 2000), claw curvature was greater in arboreal species compared to terrestrial species. However, we found no significant differences between arboreal and terrestrial species for either relative claw height ($F_{1,55}$ = 0.17, P = 0.865) or length ($F_{1,55}$ = 1.86, P = 0.205; Fig 1.4).

Perch diameter was significantly correlated with body size ($F_{1,35}$ = 6.95, P = 0.012), whereas perch height was not correlated with body size ($F_{1,20}$ = 0.79, P = 0.384). Thus, we corrected perch diameter, but not perch height, for body size in tests for correlations between claw morphology and perch dimensions. We did not find a significant positive correlation between log perch height and relative claw height ($F_{1,20}$ = 1.33, P = 0.262), claw length ($F_{1,20}$ = 1.07, P = 0.313), or claw curvature ($F_{1,20}$ = 3.06, P = 0.080), although the latter did approach significance. We did find a significant positive correlation between relative perch diameter and relative claw height ($F_{1,35}$ = 3.99, P = 0.046) but not relative claw length ($F_{1,35}$ = 1.94, P = 0.316) or claw curvature ($F_{1,35}$ = 0.02, P = 0.877) (Fig 1.3D-I). For multivariate claw shape, we found that log perch height was significantly associated with claw morphology ($F_{1,20}$ = 5.90, R^2 = 0.286, P = 0.006), but relative perch diameter was not ($F_{1,35}$ = 1.51, R^2 = 0.041, P = 0.213). Finally, we found that perch height predicted toepad morphology (all P < 0.05).

Phenotypic Integration

We found significant signals of phenotypic integration between some univariate toepad and claw traits. As predicted, claw curvature was positively correlated with toepad traits (relative lamellae: $F_{1,51}$ = 4.765, P = 0.033; relative toepad width: $F_{1,51}$ = 4.283, P = 0.044; Fig 1.5), and we found no correlation between univariate toepad traits and claw height or width (P > 0.05). For our geometric morphometric data, we recovered a significant signal of phenotypic integration between claw and toepad shape (r_{PLS} = 0.691, P = 0.001; Fig 1.5).

Rates of Morphological Evolution

Comparing rates of morphological evolution between toepad and claw traits, we found no significant differences between relative lamellae number, relative toepad width, relative claw height, and claw curvature (Table 1.1). However, relative claw length evolved faster than all of these traits. We also found that evolutionary rates for the overall shapes of toepads (σ_1^2/σ_2^2 = 6.222, σ_{all}^2 = 1.30x10^{-3}, P = 0.008) and claws (σ_1^2/σ_2^2 = 7.0684, σ_{all}^2 = 1.70x10^{-3}, P = 0.001) significantly differed among ecomorphs (Fig 1.6). Toepad shape in crown-giant anoles evolved faster than in all other ecomorphs except twig anoles (Table 1.2), and no other ecomorphs differed significantly in the rate of toepad shape evolution. For claw shape, both crown-giant and twig anoles evolved significantly faster than grass-bush, trunk, and trunk-ground anoles (Table 1.3), and the rate of claw evolution was significantly slower in trunk anoles compared to all other ecomorphs (Table 1.3).

Discussion

Anoles adaptively radiated on each of the four Greater Antillean islands by vertically partitioning structural habitat (Williams 1972; Losos 2009), and adhesive toepads have been proposed as a key innovation that promoted diversification (Irschick et al. 2006; Losos 2009). Our analyses suggest that not just toepads but a complex evolutionary interplay between toepad and claw traits was involved in adaptation to arboreal environments and allowed for diversification by increasing access to arboreal niche space.

Are claw height and curvature associated with greater arboreality?

Arboreal habitats exert different selection on locomotor traits compared to terrestrial habitats because arboreal species must traverse vertical surfaces (Richardson 1942; Cartmill 1974; Glen and Bennett 2007). We found that arboreal anoles have more curved claws relative to terrestrial species (Fig 1.4), consistent with the pattern of claw curvature and arboreality in other squamate reptiles (Zani 2000; Tulli et al. 2009, 2011; D'Amore et al. 2018) and in birds (Feduccia 1993; Zeffer et al. 2003; Glen and Bennett 2007; Birn-Jeffery et al. 2012). We also observed this pattern, at finer levels of differentiation, when comparing species with different degrees of arboreality, either between ecomorph specialists (i.e. trunk-crown vs. trunk-ground ecomorphs; Fig 1.3C) or between species utilizing different perch heights (claw curvature vs. perch height; Fig 1.3F). One study of within-species variation in an anole (*A. cybotes*) also found reduced claw curvature associated with lower perch height (Wollenberg et al. 2013). However, our results contradict those previously reported in mainland anoles (Crandell et al. 2014). Yet, we note that curvature values reported in Crandell et al. (2014) are inconsistent with our data as well as those shown for other taxa (Birn-Jeffery et al. 2012; Wollenberg et al. 2013). For example, we measured a mean curvature of 100.27±4.6 degrees in *A. humilis*, whereas Crandell et al. (2014) reported 34.67±1.0 degrees. Therefore, we believe the results of Crandell et al. (2014) are likely to be inaccurate. Due to the widespread nature of the pattern of greater claw curvature in more arboreal species, some have hypothesized that curved claws provide functional benefits on vertical surfaces, whereas flattened claws provide functional benefits on horizontal surfaces (Glen and Bennett 2007; Tulli et al. 2009; Birn-Jeffery et al. 2012).The dramatically flattened claws of terrestrial anoles relative to arboreal species and performance assays demonstrating that more curved claws facilitate increased clinging force on vertical surfaces (Zani 2000; Dai et al. 2002; Tulli et al. 2011; Song et al. 2016) provide strong evidence that claw curvature plays an adaptive role in habitat utilization.

Contrary to patterns observed in varanid lizards (D'Amore et al. 2018) and squamates more broadly (Zani 2000; Tulli et al. 2009), we did not find evidence of differences in relative claw height between arboreal and terrestrial anoles. Because the ancestral state of anoles is arboreal rather than terrestrial (Losos 2009), taller claws in terrestrial species may reflect retention of the ancestral condition, particularly if thinner claws do not offer performance benefits for terrestrial locomotion. If the ancestral claw height of anoles was sufficient to withstand the forces exerted by climbing, selection may not have favored subsequent evolution of claw height.

Beyond differences between arboreal and terrestrial species, our data suggest that different aspects of claw morphology are associated with different aspects of perch substrates. Greater

claw height was correlated with greater average perch diameter, whereas greater claw curvature was correlated with greater average perch height (Fig 1.3). Because bark texture is often smoother higher in trees (Ferrenberg et al. 2013), highly curved claws may be favored in species with greater perch heights due to their increased performance on smoother substrates (Zani 2000; Tulli et al. 2011). Similarly, the positive relationship between claw height and perch diameter may be because taller claws improve performance on rougher surfaces (Zani 2000; Tulli et al. 2011) common in trees of larger diameter (Ferrenberg et al. 2013).

Is claw morphology associated with microhabitat usage in Greater Antillean anoles?

Anole ecomorphs are characterized by convergent ecologies, behavior, and morphologies related to microhabitat use (Williams 1972; Losos et al. 1998). Hence, the repeated evolution of anoles into ecomorph classes on each of the Greater Antillean islands provides an opportunity to examine the importance of claw and toepad traits at a finer level of niche divergence: vertical habitat partitions. Consistent with the convergence of other morphological traits (Williams, 1972; Losos, 2009; Kolbe et al. 2011), we found that ecomorph classification is associated with claw morphology for both univariate and multivariate shape analyses (Fig 1.2-1.4), suggesting that claws are ecologically important for microhabitat partitioning.

Differences in claw shape were most pronounced in twig anoles which were characterized by reduced (shorter and thinner, relative to body size) and flattened claws (Fig 1.3). These results are consistent with other morphological studies across Greater Antillean anoles, which demonstrate that twig anoles have the most derived body plans of all anole ecomorphs, including elongate bodies and heads, reduced limbs, altered gaits, and in some cases prehensile tails (Hedges and Thomas 1989; Losos 1990b; Diaz et al. 1996; Beuttell and Losos 1999; Huyghe et al. 2007). Because twig anoles make use of a highly derived habitat relative to many other anole species – narrow twigs rather than tree trunks and large branches – these behavioral and morphological phenotypes likely represent a high degree of habitat specialization. The attachment capabilities of claws through frictional interlocking is partly determined by the relative size of surface protrusions and claw height (Song et al. 2016); thus, maintaining taller claws may be unnecessary in twig anoles due to the highly reduced diameter of their preferred perches. Loss of function is common in traits that do not provide fitness benefits in particular populations or species (Fong et al. 1995) and may explain the rapid evolutionary rate of claws, but not toepads, in twig anoles (Table 1.2, 1.3; Fig 1.6) through release from biomechanical constraint (Adams et al. 2017a; Sherratt et al. 2017). Although claw loss has never been observed in anoles, dramatic claw reduction and even complete loss is observed in toepad-bearing geckos (Russell and Bauer 2008; Khannoon et al. 2015). Still, we cannot rule out the possibility that reduced claw morphology is beneficial to twig anoles either through improved functional interactions with thin perches or because relatively larger claws are deleterious to their mode of locomotion, for instance by interfering with toepad function.

Although less pronounced than differences between twig anoles and all other ecomorphs, Trunk-Ground anoles also significantly differ from trunk-crown anoles in claw curvature and overall shape (Fig 1.2-1.4). These differences may reflect trade-offs in claw morphology due to relative performance on different substrates. Highly curved claws have been shown to be important for clinging in arboreal species (Zani 2000; Tulli et al. 2011), whereas flattened claws may facilitate

propulsive force when running on flat surfaces in terrestrial species (Glen and Bennett 2007; Tulli et al. 2009; Birn-Jeffery et al. 2012). Thus, trunk-ground anoles may have flatter claws because they benefit from sacrificing clinging performance for greater ground sprint speed, although empirical tests confirming the relationship between flattened claws and ground sprint performance are still lacking in squamate reptiles.

Is there phenotypic integration between claw and toepad traits?

Our results support the hypothesis that covariation between toepad traits and claw curvature results from correlative selection due to microhabitat use. Consistent with predictions based on functional studies of fine scale claw and toepad morphology (Zani 2000; Tulli et al. 2011; Crandell et al. 2014), we observe strong covariation between traits adapted to similar functions and a lack of covariation between traits adapted to different functions. Specifically, we observe phenotypic integration across fine-scale claw and toepad attributes associated with performance on either rough or smooth surfaces. Claw curvature is positively correlated with toepad width and lamella number, likely representing adaptation for performance on smoother surfaces. Previous work has shown that greater claw curvature, greater toepad size, and more lamellae are all associated with increased clinging performance particularly on smoother surfaces (Zani 2000; Vanhooydonck et al. 2005; Tulli et al. 2011; Gillies et al. 2014). Conversely, the lack of correlation between toepad traits and claw height or length in Greater Antillean anoles may be a product of differential selection due to their different individual functions. Claw height and toepad characteristics may be evolutionarily decoupled because greater claw height predominantly improves function on rougher surfaces where toepads are less effective (Zani 2000; Song et al. 2016), thus reducing correlative selection. Similarly, claw length does not affect clinging performance on any surface (Zani 2000; Tulli et al. 2011) and, thus, is likely not under correlative selection with toepad traits related to adhesive performance. Still, overall elongation of the claw appears to be correlated with elongation of toepads or, at least, reduced toepad width in respect to length (Fig 1.2A). We lack a functional hypothesis for this observed pattern because no relevant performance consequences have yet been demonstrated for claw or toepad elongation.

Alternatively, patterns of integration may also be driven by genetic or developmental linkage between toepads and claw curvature but not between toepads and other claw dimensions. However, across vertebrates the formation of terminal digit structures is controlled by developmental programs distinct from the remainder of the digit (Casanova and Sanz-Ezquerro 2007), with several genes only expressed in digit tips (Macias et al. 1997; Sanz-Ezquerro and Tickle 2003). Additionally, tip development is often unimpeded by disruptions to the developmental pathways controlling formation of the proximate and medial portions of digits (Baur et al. 2000; Kraus et al. 2001). Consequently, strong developmental linkage between toepad and claw structures is unlikely to produce our observed relationships. Therefore, we suggest that patterns of phenotypic integration across Greater Antillean anoles are driven by correlative selection based on differential performance on specific attributes of the structural habitat rather than underlying developmental linkage.

Do rates of evolution covary between claw and toepad traits?

In addition to our morphological results, our analyses of evolutionary rates also support the hypothesis that claws and toepads are functionally integrated. Across ecomorphs, the rates of evolution for both claw and toepad shape were similar, except for the faster rate of claw shape evolution relative to toepads in twig anoles (Fig 1.6). The only trait that had a significantly different rate of evolution was claw length, which evolved faster than all other claw and toepad traits (Table 1.1). Because biomechanically constrained traits experience strong selection, they often have slower rates of evolution (Hertz et al. 2013; Adams et al. 2017a). Thus, the faster rate of evolution in claw length is likely due to its lack of biomechanical importance in arboreal anoles (Zani 2000). Similarly, the faster rate of claw evolution in twig anoles relative to toepads may be due to release from biomechanical restraint given their highly specialized form and locomotion.

Although diversifying selection can drive higher rates of morphological evolution in traits such as those under sexual selection (Arnegard et al. 2010; Klaczko et al. 2015), high rates of morphological evolution are not always necessary to produce corresponding shifts in functional performance, particularly in ecologically constrained traits (Gunderson et al. 2018). Small changes can produce large functional differences in some traits but not others. Thus, it may be inappropriate to expect the magnitude of trait divergence to map directly onto changes in performance. For instance, relatively small and evolutionarily slow changes in physiology have been shown to play an important role in thermal habitat partitioning in Greater Antillean anoles (Gunderson et al. 2018). The slower rate of evolution for ecologically important traits (i.e. claw and toepad morphology) observed here suggests that rapid, large changes in morphology are not required to generate corresponding shifts in performance and, subsequently, ecological diversity.

The relative lack of variation in evolutionary rates across ecomorphs, except crown-giants and twigs (Table 1.2, 1.3), suggests that microhabitat use is not strongly associated with variation in morphological diversity. Faster rates of claw evolution in crown-giants and twig anoles is consistent with their more derived overall body plans (Williams 1972; Beuttell and Losos 1999; Losos 2009) and may be linked to their more derived habitat use. However, grass-bush anoles do not show increased rates of evolution as would be expected if differences in habitat use and overall body plan strongly predicted rates of claw and toepad evolution. In agamid lizards, saxicolous and arboreal lineages have slower rates of evolution, suggesting that these ecologies constrain morphological evolution (Collar et al. 2010). Similar constraints may explain the relatively slower rates of morphological evolution observed for claws and toepads in most ecomorphs of anoles. However, semi-arboreal agamids evolve faster (Collar et al. 2010), whereas trunk-ground and grass-bush anoles do not, suggesting that the influence of microhabitat use on rates of diversification is not universal.

Conclusion

Vertical habitat partitioning is a hallmark of the adaptive radiations of Greater Antillean anoles and is associated with a suite of convergent morphological adaptations characterized by ecomorph classification (Williams 1972; Losos et al. 1998; Losos 2009). We provide evidence

that, at broad levels of ecomorphological divergence, claw morphology is similarly associated with macrohabitat (terrestrial and arboreal) and microhabitat (arboreal habitat partitions) use in Greater Antillean anoles and that patterns of covariation in claw and toepad morphology are likely driven by correlative selection. In particular, the association of claw morphology with perch dimensions, arboreality, and ecomorph generally align with predictions from previous performance studies in other squamates (Zani 2000; Tulli et al. 2011). Moreover, we also demonstrate that, at a finer scale, specific claw traits are differentially associated with toepad traits and microhabitat features, leading to a pattern of phenotypic integration among traits that is strongly associated with their functional roles. Specifically, correlative selection for performance on smoother surfaces likely drove the integration of claw curvature with toepad traits (and associations between claw curvature and perch height), whereas selection for claw height on rougher surfaces likely led to it being decoupled from toepad traits, which have limited functional roles on rougher surfaces (Zani 2000; Tulli et al. 2011). Additional functional studies are necessary to confirm the adaptive value of claw shape variation and to tease apart alternative hypotheses about the evolution of claws. Nevertheless, our results suggest that claws, in conjunction with toepads, are likely to have directly facilitated access to greater arboreal niche space and structural habitat partitioning across the replicated adaptive radiations of *Anolis* lizards and, thus, highlight the multivariate nature of adaptive phenotypic evolution.

Figures and Tables

Figure 1.1 Representative photos of Greater Antillean anole claws taken using a Dino-Lite Digital Microscope. One species from each ecomorph is depicted with 0.5mm scale bar (TG = trunk-ground; TR = trunk; TC = trunk-crown; GB = grass-bush; TW = twig; CG = crown-giant). Bottom panels: (left) photo of toepad and claw of an anole and (right) diagram of univariate measurements of claw morphology adapted from Zani (2000). Variables A, B, and C follow eq. 1, h = claw height.
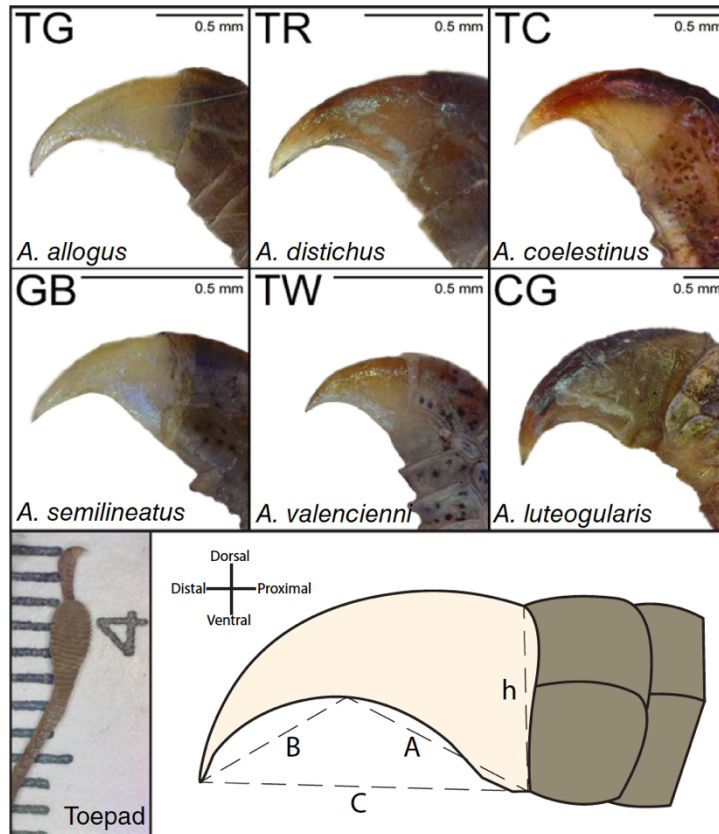
Figure 1.2 (A) Plot of the first and second Procrustes principal components for geometric morphometric claw shape across Greater Antillean anoles. Each data point represents a single species. Minimum convex hulls for each ecomorph and warp grids for extreme values of PC1 are displayed. (B) Mean claw shapes for each ecomorph. Points represent mean positions for individual semi-landmarks. (C) Morphological shape disparity represented as Procrustes variances for each ecomorph (* $P < 0.05$). All plots are color coded by ecomorph. Unique anoles were not compared in plots B and C. Abbreviations: CG = crown-giant; TC = trunk-crown; TR = trunk; TG = trunk-ground; GB = grass-bush; TW = twig.
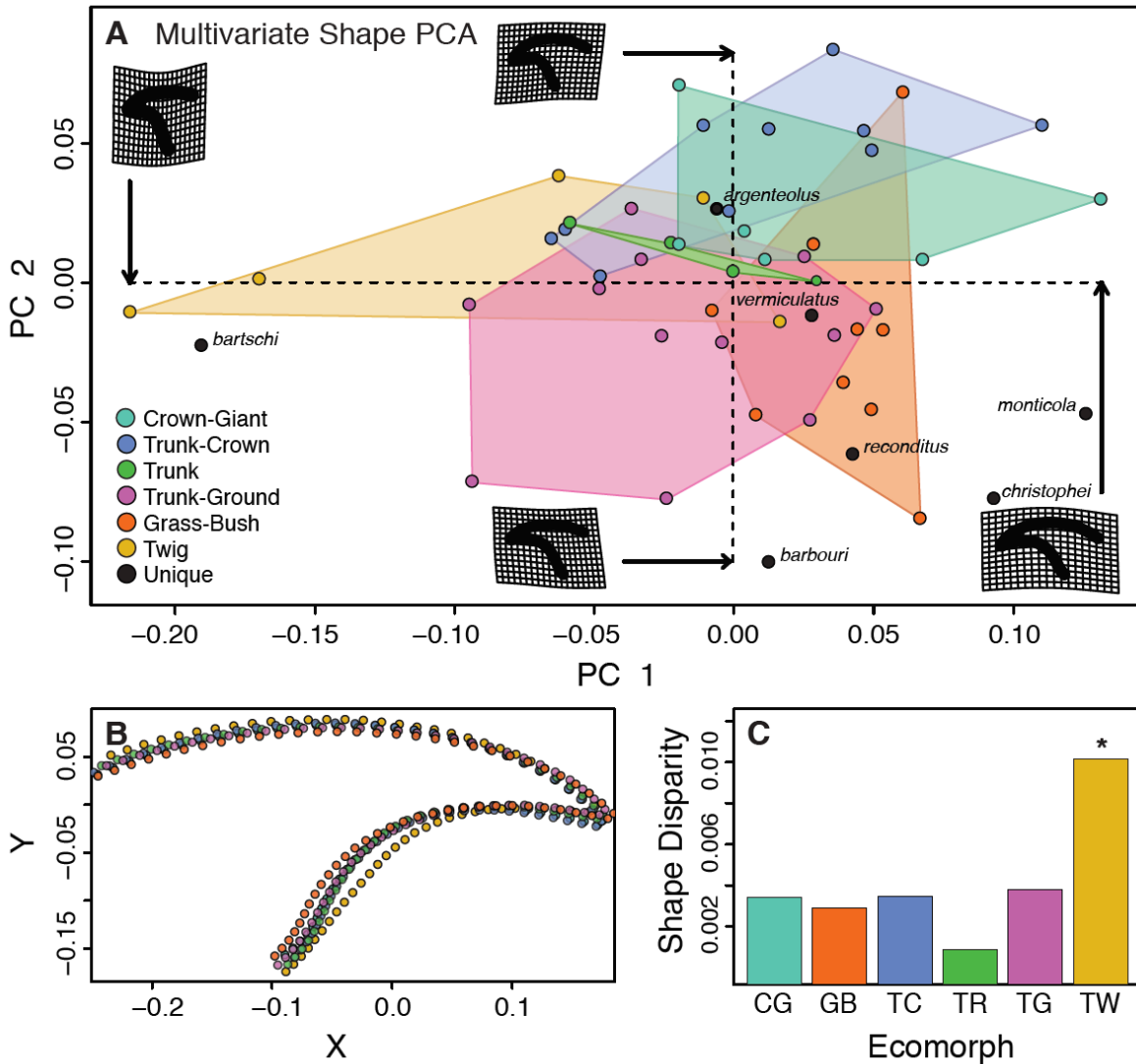
Figure 1.3 (A-C) Boxplots of univariate measures of claw morphology for each ecomorph (* *P* < 0.05; ** *P* < 0.01; *** *P* < 0.001). (D-I) Relationship between perch dimensions and claw traits. Crown-Giant, Grass-Bush, and Twig anoles are not included in models of perch height. For all plots, body size correct claw height and length are represented by residuals of regressions for each trait against SVL. Unique anoles are not depicted. Abbreviations: CG = crown-giant; TC = trunk-crown; TR = trunk; TG = trunk-ground; GB = grass-bush; TW = twig.
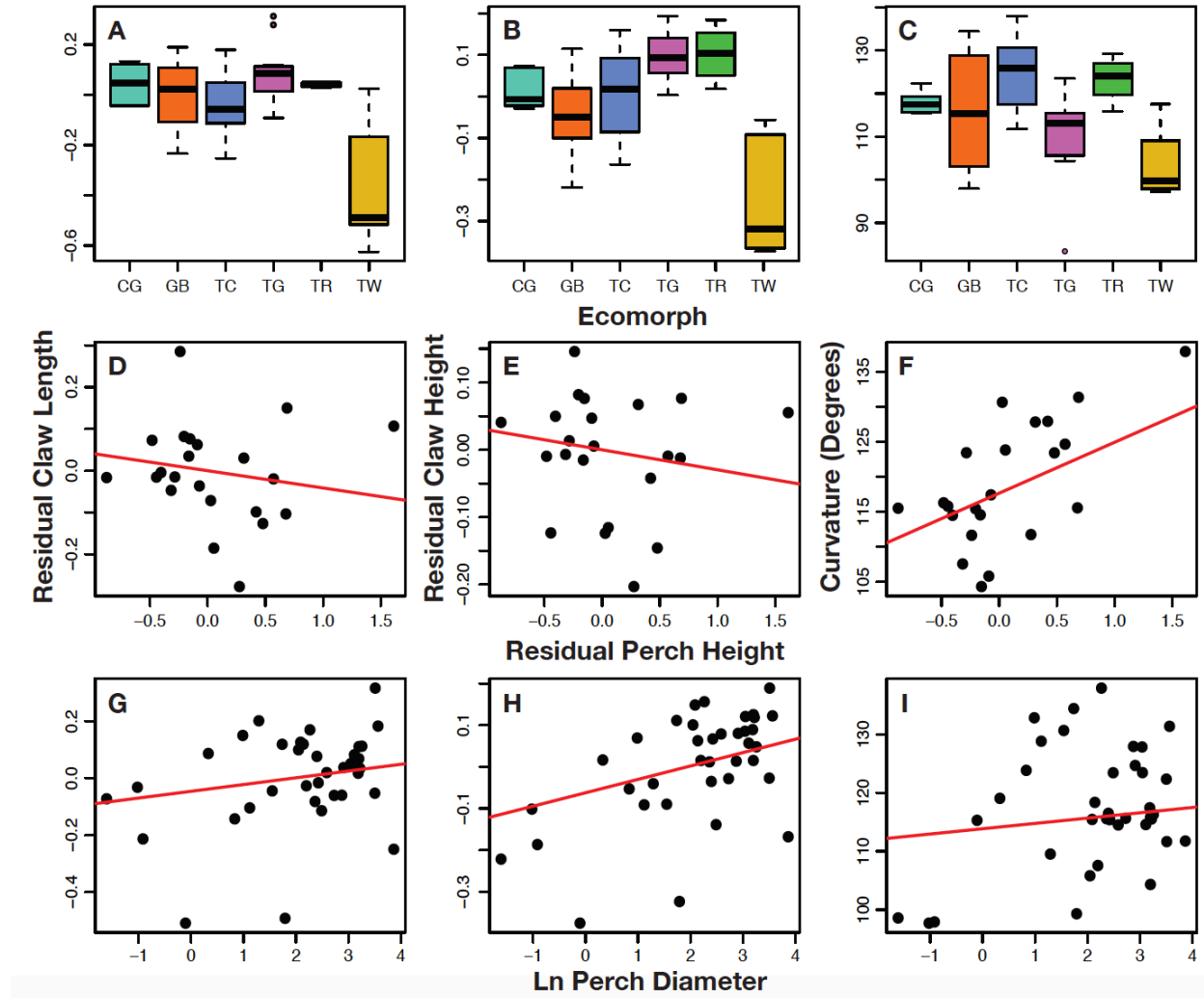
Figure 1.4 PCA plot of first and second principal components for univariate claw measurements. Convex hulls are depicted for each Greater Antillean ecomorph and terrestrial species (both Greater Antillean and mainland) are labelled. Insets: (A) Superimposed means of geometric morphometric shape for terrestrial and arboreal species; (B) Boxplots of claw curvature measurements for arboreal and terrestrial species (*** $P < 0.001$).
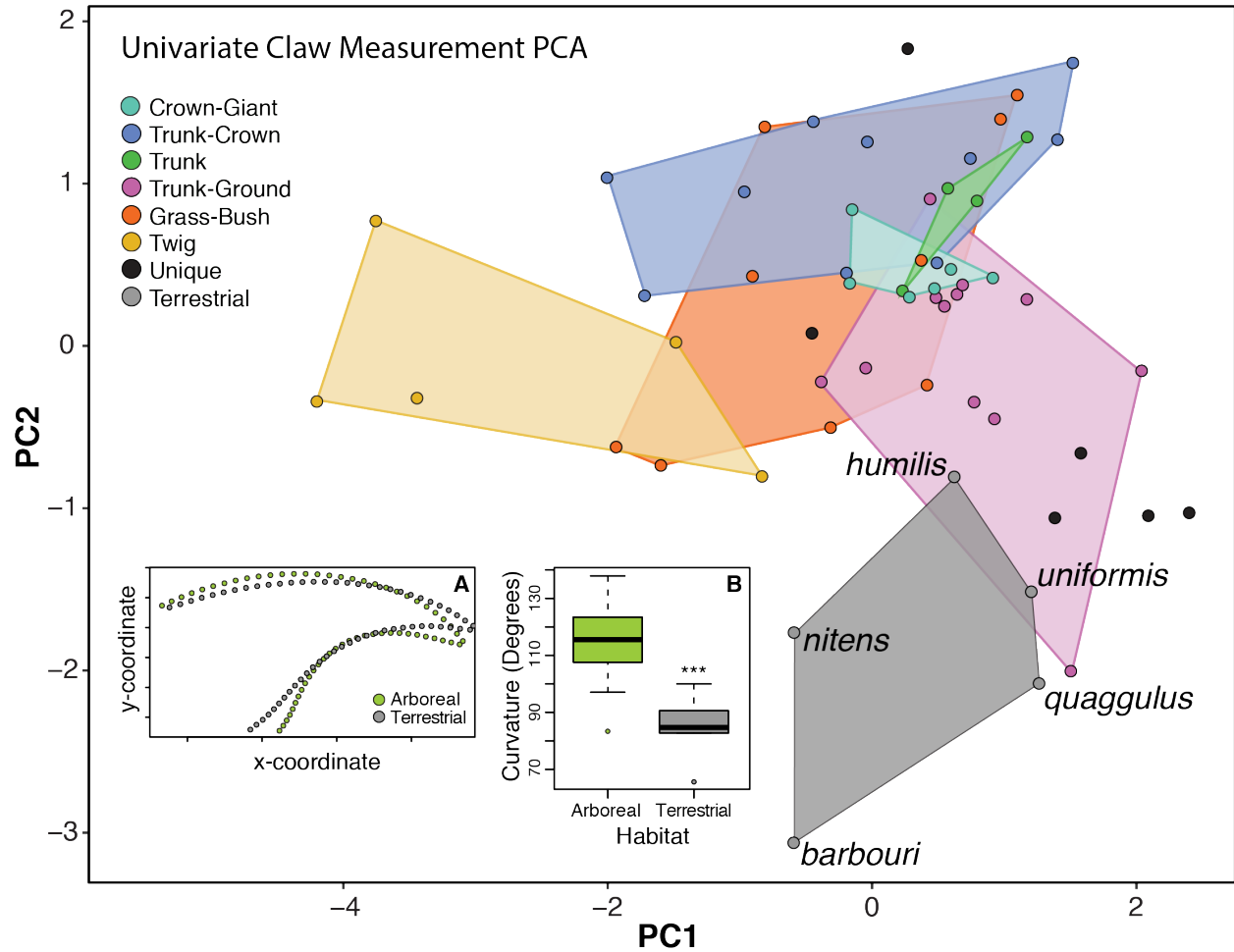
Figure 1.5 (A) Partial least squares plot of phenotypic integration between overall claw and toepad traits ($r_{PLS} = 0.691$, $P = 0.001$). Warp grids depict extreme shapes for each trait. Positive correlation between claw curvature and both (B) body size-corrected lamellae number and (C) body size-corrected toepad width. Body size-corrected values are residuals from regressing log trait values on log SVL.
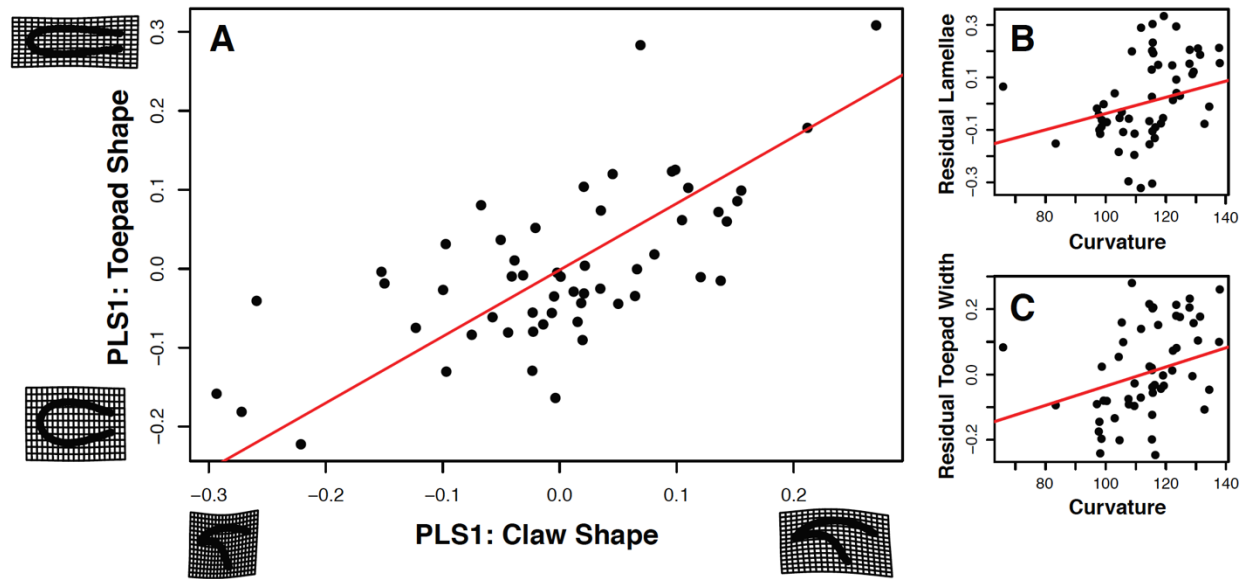
Figure 1.6 Estimated rates of evolution for claw (left, light) and toepad (right, dark) multivariate shape. Significant differences among rates are denoted by letters: lower case for claws and upper case for toepads. P-values are indicated in Table 1.2 and 1.3. Solid line represents overall rate of evolution for claw shape and dashed line represents overall rate of evolution for toepad shape.
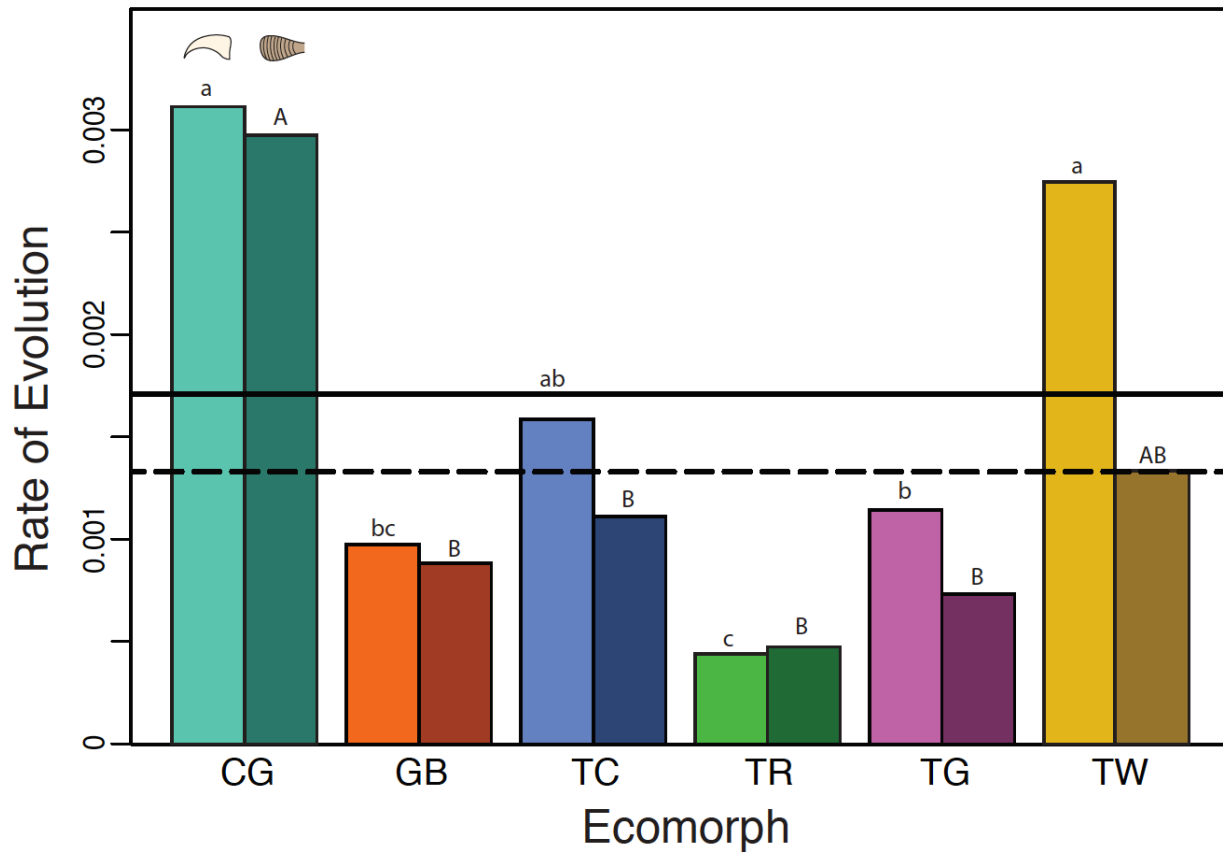
Table 1.1 Pairwise comparisons of evolutionary rate between univariate toepad and claw traits. Likelihood ratio tests were conducted to compare a single rate model with an independent two-rate model of phenotypic evolution. Estimated independent rate of evolution for each trait is denoted on the diagonal. *P*-values from likelihood ratio tests are shown in the lower off-diagonal with statistically significant values bolded. Likelihood ratios are shown in the upper off-diagonal.

	Lamellae	TPW	CH	CL	Curvature
Lamellae	4.0×10^{-4}	0.015	0.531	7.783	0.586
TPW	0.903	4.0×10^{-4}	0.368	8.451	0.415
CH	0.466	0.544	3.0×10^{-4}	12.25	0.001
CL	**0.005**	**0.003**	**<0.001**	9.0×10^{-4}	12.40
Curvature	0.444	0.520	0.970	**<0.001**	3.0×10^{-4}

TPW = toepad width; CH = claw height; CL = claw length

Table 1.2 Pairwise comparisons of evolutionary rate for multivariate toepad shape across ecomorphs. The estimate rate of evolution for each ecomorph is denoted on the diagonal. The overall rate of evolution, $\sigma_{all}^2 = 1.30 \times 10^{-3}$. *P*-values for comparisons of rate ratios between ecomorphs are denoted on the off-diagonal. Significant comparisons are bolded.

	CG	GB	TC	TR	TG	TW
CG	2.95×10^{-3}					
GB	**0.010**	8.53×10^{-4}				
TC	**0.023**	0.550	1.09×10^{-3}			
TR	**0.001**	0.246	0.105	4.74×10^{-4}		
TG	**0.001**	0.644	0.238	0.412	7.17×10^{-4}	
TW	0.121	0.357	0.711	0.067	0.206	1.31×10^{-3}

CG = Grown-Giant; TC = Trunk-Crown; TR = Trunk; TG = Trunk-Ground; GB = Grass-Bush; TW = Twig.

Table 1.3 Pairwise comparisons of evolutionary rate for multivariate claw shape between ecomorphs. The estimated rate of evolution for each ecomorph is on the diagonal. The overall rate of evolution is $\sigma_{all}^2 = 1.70 \times 10^{-3}$. *P*-values for comparisons of rate ratios between ecomorphs are below the off-diagonal. Significant comparisons are bolded.

	CG	GB	TC	TR	TG	TW
CG	3.13×10^{-3}					
GB	**0.003**	9.95×10^{-4}				
TC	0.075	0.154	1.60×10^{-3}			
TR	**0.001**	0.057	**0.003**	4.43×10^{-4}		
TG	**0.005**	0.676	0.278	**0.018**	1.14×10^{-3}	
TW	0.760	**0.011**	0.172	**0.001**	**0.033**	2.74×10^{-3}

CG = Grown-Giant; TC = Trunk-Crown; TR = Trunk; TG = Trunk-Ground; GB = Grass-Bush; TW = Twig.

CHAPTER II

Habitat use, competition, and phylogenetic history shape the evolution of claw and toepad morphology in Lesser Antillean anoles

This manuscript has previously been published.

Citation:

Abstract

Ecologically functional traits are the product of several, at times opposing, selective forces. Thus, ecomorphological patterns can be disrupted locally by biotic interactions such as competition and may not be consistent across lineages. Here, we studied the evolution of claws and toepads in relation to macrohabitat (vegetation), use of structural microhabitat (perch height), and congeneric competition for two distantly-related Lesser Antillean anole clades: the *bimaculatus* and *roquet* series. We collect univariate and geometric morphometric data from 254 individuals across 22 species to test the hypotheses that (1) functional morphology should covary with both vegetation and perch height and that (2) the presence of a competitor may disrupt such covariation. Our data show predictable associations between morphology and macrohabitat on single-species islands but not when a congeneric competitor is present. The outcomes of competition differ between series, however. In the *bimaculatus* series, species with a sympatric congener diverge in claw and toepad traits consistent with functional predictions, whereas *roquet* series anoles show either no association between habitat and morphology or the opposite pattern. Our results demonstrate that ecomorphological patterns across macrohabitats can be disrupted by competition-driven microhabitat partitioning and that specific morphological responses to similar ecological pressures can vary between lineages.

Introduction

Variation in functional traits with direct performance consequences should reflect divergence along ecologically-relevant axes of an organism's niche. The study of these traits in closely-related species can sometimes reveal the primary axes of diversification within a clade, such as the coevolution of plant-pollinator relationships through correlated mouthparts and nectary lengths (Nilsson 1988; Muchhala and Thomson 2009; Sletvold and Ågren 2010) or the partitioning of seed type through beak shape in Darwin's finches (Schluter *et al.*, 1985; Grant & Grant, 2006). However, functional traits also often reflect the composite effects of multiple, sometimes opposing selective pressures, potentially leading to inconsistent patterns of morphological adaptation with respect to a single ecological variable (Gómez 2004; Templeton and Shriner 2004; Bischoff et al. 2006; Petrů et al. 2006).

Generalized adaptation to environmental variation can be confounded by localized biotic interactions, such as competition or predation, if such interactions drive changes in habitat use at local scales (Bischoff et al. 2006). In particular, competition as an agent of selection is often linked to divergence in microhabitat use between sympatric species (Toft 1985; Ziv et al. 1993; Robertson 1996; Schluter 2000a; Buckley and Roughgarden 2005b), which may disrupt macrohabitat-scale patterns that would otherwise occur in allopatry. For example, the dominant selective force acting on the cruciferous plant, *Biscutella didyma*, switches from precipitation to competition in more complex communities (Petrů et al. 2006). Previous theoretical work has also posited that geographically-restricted competition can disrupt patterns of clinal environmental adaptation by promoting discrete phenotypic clustering (Doebeli and Dieckmann 2003; Leimar et al. 2008). Thus, landscape-level patterns of morphological adaptation to environmental differences within and among species may be disrupted if competition results in partitioning along additional ecological axes.

The repeated adaptive radiations of *Anolis* lizards in the Greater Antilles are characterized primarily by competition-driven structural microhabitat partitioning (Schluter 1994; Losos 2009), with microhabitat usage associated with a suite of ecological and morphological differences, leading to the categorization of these species into convergent 'ecomorph' classes (i.e. crown-giant, trunk-crown, trunk, trunk-ground, twig, and grass-bush; (Williams 1972; Losos 1990b; Beuttell and Losos 1999; Herrel et al. 2008; Kolbe et al. 2011). In particular, both claws and toepads play important roles in facilitating exploitation of arboreal habitats (Losos, 1990b; Zani, 2000; Yuan *et al.*, 2019). Adhesive toepads improve climbing performance by adhering to vertical surfaces through Van der Waals forces (Autumn et al. 2002), while claws operate by interlocking with climbing substrates (Cartmill, 1974; Dai *et al.*, 2002). Functional studies have demonstrated that more highly curved claws, wider toepads, and more subdigital lamellae improve clinging ability in squamate reptiles (Zani, 2000; Elstrott & Irschick, 2004; Tulli *et al.*, 2011; Crandell *et al.*, 2014), and differences in competition-driven microhabitat use across ecomorphs are strongly reflected in both claw and toepad morphology in Greater Antillean anoles (Losos 1990b; Glossip and Losos 1997; Beuttell and Losos 1999; Elstrott and Irschick 2004; Yuan et al. 2019). For example, more arboreal (higher perching) ecomorphs have wider toepads, more lamellae, and more curved claws compared to more terrestrial (lower perching) ecomorphs (Losos 1990b; Glossip and Losos 1997; Beuttell and Losos 1999; Elstrott and Irschick 2004; Yuan et al. 2019). Additionally, twig anoles, whose structural habitat use is

predominantly characterized by perch diameter rather than perch height, have highly derived morphologies, including flattened, reduced claws (Yuan *et al.*, 2019). Yet, decoupling the effects of competition from environmental adaptation is difficult in the Greater Antilles due to its complex anole communities with numerous sympatric species. How functional traits would evolve in the absence of interspecific competitors is, therefore, difficult to study. The species depauperate Lesser Antillean anole fauna, on the other hand, presents a simplified system in which to examine the dynamics of an evolutionary radiation.

The Lesser Antilles is a chain of volcanic islands colonized independently by two distantly related lineages of anoles: the *bimaculatus* series from the Greater Antilles 16.8-27.8 Ma and the *roquet* series from the South American mainland 23.8-39.1Ma (Underwood 1959; Thorpe et al. 2018). The *bimaculatus* series, the clade endemic to the Leeward Islands, is nested within the Greater Antillean radiations (Poe et al. 2017; Thorpe et al. 2018). In contrast, the independent colonization of the Windward Islands by the *roquet* series from the South American mainland, whose fauna does not represent an adaptive radiation (Irschick *et al.*, 1997), provides an opportunity to examine the influence of phylogenetic history on adaptive evolution.

Across the Lesser Antilles, each island is inhabited by one or two endemic anoles (Fig 2.1). Thus, the Lesser Antilles represents a simplified community and allows for comparisons between the presence and absence of a congeneric competitor. Previous studies suggest ecological patterns on single-species islands can be disrupted on two-species islands in this system, likely by competition. For example, bioenergetic models that are highly predictive of abundance on one-species islands perform poorly for two-species islands, suggesting competitive interactions (Buckley and Roughgarden 2005a). Additionally, on two-species islands, anoles display divergence in body size. Each two-species island has one large-bodied and one small-bodied anole species, whereas single-species islands have an intermediate-sized anole (Fig 2.1; Rummel & Roughgarden, 1985; Losos, 1990a; Buckley & Roughgarden, 2005a). Two-species islands also exhibit partitioning of vertical habitat space in the *bimaculatus* series with the smaller species more terrestrial compared to the larger species and of microclimate in the *roquet* series with the smaller species perching in warmer microclimates compared to the larger species (Roughgarden *et al.*, 1981; Buckley & Roughgarden, 2005a). Additionally, experimental removal of either *Anolis bimaculatus* or *A. schwartzi* on Sint Eustatius improved fitness of the remaining species (Rummel and Roughgarden 1985), the presence or absence of *A. pogus* changes perching behavior and fitness in *A. gingivinus* (Roughgarden *et al.,* 1984), and the introduction of *A. cristatellus* to Dominica resulted in perch height partitioning with the native *A. oculatus* (Dufour *et al.*, 2017). Taken together, the body of direct and indirect evidence strongly supports the hypothesis of strong competitive interactions maintaining habitat partitioning across the radiation. Thus, the Lesser Antilles provide an opportunity to study not only the effects of competition on adaptation, by comparing one and two species anole communities, but also how phylogenetic history influences evolutionary responses to similar biotic and abiotic pressures.

Here, we conduct a comparative analysis of claw and toepad morphology among 22 species of Lesser Antillean anoles to determine how habitat use, species interactions, and phylogenetic history shape the evolution of these ecologically important traits. Specifically, we investigate five questions about the forces driving the evolution of these functional traits in this system. (I) Are claw and toepad morphologies associated with both macro (overall vegetation) and

microhabitat (perch use) use across Lesser Antillean anoles? (II) Are habitat associations with claw and toepad morphology consistent between one and two species islands? (III) Do two-species islands show evidence of divergence in claw and toepad morphology consistent with habitat partitioning? (IV) Are ecological patterns of claw and toepad morphology consistent between the *bimaculatus* and *roquet* series? And (V) are patterns of divergence on two-species islands consistent with divergence between sympatric ecomorphs in the Greater Antilles?

Methods

Sampling

We collected morphological measurements of preserved museum specimens (Appendix II) housed in the Museum of Vertebrate Zoology (University of California, Berkeley, CA), the California Academy of Sciences (San Francisco, CA), the Museum of Comparative Zoology (Harvard University, Cambridge, MA), and the National Museum of Natural History (Smithsonian Institution, Washington, DC). We also measured eight *Anolis lividus* individuals that we collected from Montserrat in May 2018. In total, we sampled 254 adult male anoles representing 22 species from the Lesser Antilles. Our sampling includes all six sympatric species pairs occurring in the Lesser Antilles and 11 of 15 species from single-species islands, which we hereafter refer to as 'solitary' anoles. This sampling represents eight of nine species from the *roquet* series and 14 of 17 from the *bimaculatus* series (Fig 2.1). All specimens had known collection localities within their native range except *A. aeneus* for which only specimens from an introduced population of Trinidad were available. Although male and female anoles often exhibit ecological differences (Schoener 1967; Malhotra and Thorpe 1997), most studies have focused on male anoles, limiting the number of females anoles in collections. Hence, we examined only male specimens for this study, and further work is required to understand the morphological evolution of female anoles.

Morphological Measurements

For each specimen, we measured snout-vent length (SVL) as a proxy for body size, and we measured univariate claw traits following the protocol from Zani (2000). In brief, we imaged the fourth hind toepad and sagittally flattened claw for each specimen using a Dino-Lite Digital Microscope (Model AM4115ZT). Toepads were flattened against plexiglass to reduce deformities introduced during specimen preparation. Using claw images, we measured claw height, claw length, and claw curvature in tpsdig2 (Rohlf 2006). Following Zani (2000), claw height was defined as the height at the base of the claw, and we calculated claw curvature as

$$curvature = 57.296\left(2\sin^{-1}\left(\frac{(2A^2B^2 + 2B^2C^2 + 2A^2C^2 - A^4 - B^4 - C^4)^{0.5}}{2AB}\right)\right),$$

where *A* was the distance from the claw's ventral base to the ventral curve vertex, *B* was the distance from the claw's ventral curve vertex to the tip, and *C* was the distance from the claw's ventral base to the tip. We calculated claw length as the sum of measurements *A* and *B* (Fig 2.2). For toepad measurements, we defined the toepad as beginning where the next distal lamella is

wider than the previous lamella. Following this definition, we counted the number of lamellae and measured toepad width at the widest point of the toepad (Fig 2.2).

We also collected geometric morphometric data in tpsdig2 following the protocol of Tinius and Russell (2017). In brief, we characterized claw shape using 30 equidistant semilandmarks following each of the dorsal and ventral curves of the claw (Fig 2.2). We then removed non-shape features using generalized Procrustes superimposition implemented in the R package *geomorph* (Adams et al. 2017b). We allowed semilandmarks to slide along curves to minimize bending energy (Bookstein 1997), which does not deform landmarks beyond the endpoints of the curve (Gunz and Mitteroecker 2013). For downstream analyses, we calculated mean shape values for each species as the average coordinate position of each semilandmark. We also performed a principal component analysis (PCA) on univariate claw measurements and a Procrustes PCA on mean shape value data across our sampled species to visualize variation in morphospace.

Allometric Analyses

We conducted all subsequent data analyses in R v3.3.3 (R Core Team 2017). To incorporate information on phylogenetic relatedness, we used the most recent comprehensive *Anolis* phylogeny (Poe et al. 2017) and pruned it to include only our focal taxa (Fig 2.1A). To achieve normality and homoscedasticity of our data, we natural log transformed all univariate measurements except claw curvature, which was already homoscedastic and normally distributed. We tested the effects of body size using phylogenetic independent contrasts (PICs; Felsenstein, 1985) of ln-SVL with all univariate morphological traits. To determine whether univariate claw and toepad traits scaled allometrically, isometrically, or independently with body size, we used the 95% confidence intervals of slopes from the PICs. Slopes of one indicate isometry, greater than one indicate allometry, and zero indicate independence for one dimensional traits. If a trait scaled significantly with body size, we regressed the natural log transformed trait against phylogenetically-informed ln-SVL (Revell 2009) using the 'phyl.resid' function in the *phytools* package (Revell 2017). We retained residuals as body size corrected measurements for downstream analyses. Long-term specimen preservation can potentially influence morphological measurements from museum collection. Although modern collection are largely standardized in preservation technique, previous work has documented a small and asymptotic amount of shrinkage in body size in lizards due to fixation in 10% formalin and storage in 70% ethanol, primarily because of initial contraction in soft tissues (Vervust et al. 2009) Hard and keratinized tissues such as claws and toepads, however, should be resistant to distortion. Nevertheless, to account for any potential influences of SVL shrinkage on body size corrected measurements, we conducted all analyses both with and without the SVL correction proposed by Vervust et al. (2009): SVL + SVL * 0.037.

Between Series and Radiation Comparisons

We examined differences in claw and toepad morphology between *roquet* and *bimaculatus* series anoles using phylogenetic ANOVAs to compare all univariate traits (Garland et al. 1993) in *phytools* and using phylogenetic Procrustes ANOVAs to compare multivariate claw shape (Adams 2014a) in *geomorph*. Additionally, we tested for differences in overall shape disparity in

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claw shape between series using the 'morphol.disparity' function in *geomorph*, which performs pairwise comparisons using absolute differences in Procrustes variances as test statistics compared against null distributions generated by permuting residuals across groups (Zelditch *et al.*, 2012). To place the Lesser Antillean anole fauna within the context of the wider *Anolis* radiation, we compared our data with previously published claw and toepad data for the adaptive radiations of Greater Antillean anoles (Yuan et al. 2019). Specifically, we tested for differences between Greater Antillean ecomorphs and Lesser Antillean anoles using phylogenetic ANOVAs and Procrustes ANOVAs followed by *post hoc* pairwise comparisons. Finally, we performed a principal component analyses on univariate claw measurements to visualize the placement of Lesser Antillean anoles within Greater Antillean claw morphospace.

Phenotypic Integration, Habitat Use, and Morphology

To parse the effects of phylogenetic history and competition on morphological adaptation, we conducted all subsequent analyses using five subsets of the data: all Lesser Antillean anoles, only solitary anoles, only two-species island anoles, only the *roquet* series, and only the *bimaculatus* series. On two species islands, one species is always smaller and more terrestrial, while the other is larger and more arboreal; the smaller, more terrestrial species form a clade that is reciprocally monophyletic with all other more arboreal species in the *bimaculatus* series (Fig 2.1A), potentially confounding ecological and phylogenetic signals. Therefore, we conducted analyses both considering and disregarding the underlying phylogeny when analyzing the all species dataset and the *bimaculatus* series dataset. To test for phenotypic integration, defined as covariation between functionally-related traits, we examined correlations between all combination of univariate claw and toepad traits using phylogenetic generalized least squares (PGLS) implemented in *phytools*.

To examine the effect of environmental habitat variation (macrohabitat) on claw and toepad morphology, we used normalized difference vegetation index (NDVI) data layers from NASA's Moderate Resolution Imaging Spectroradiometer (MODIS). Because many specimens predate available NDVI data, we use modern NDVI as a proxy for the vegetation likely experienced on each island. To capture broad variation in vegetation structure over time, we averaged 250m resolution NDVI data across collection localities from 2010-2015 using the *MODIStools* package in R (Koen 2019) for each species. Due to the 1995 Soufrière Hills eruption on Montserrat, which dramatically altered the landscape of the island, we excluded museum specimens of *A. lividus* from NDVI analyses because post-eruption values of NDVI are unlikely representative of the habitat from which these specimens were originally collected. Instead, we used only modern *A. lividus* samples collected in 2018 from localities not directly impacted by pyroclastic flows. To assess microhabitat use, we amassed perch height and diameter data for 16 species from Losos & de Queiroz (1997). We performed PGLS between all morphological traits and habitat metrics: perch diameter, perch height, and NDVI. For multivariate claw shape, we conducted phylogenetic Procrustes regressions (Adams 2014a) between multivariate claw shape and all habitat metrics. Finally, to characterize more fine-scale shape differences, we summarized multivariate claw shape variation using principal component analysis and examined correlations between the first two principal components explaining 90.6% of variance and habitat metrics using phylogenetic regressions.

Results

Body Size and Claw Morphospace

Results for all analyses were entirely consistent between preservation shrinkage-corrected and uncorrected SVL. Thus, we report only uncorrected results here. We found that all claw and toepad traits, except claw curvature (PIC: $F_{1,19} = 1.26$, $R^2 = 0.013$, $P = 0.275$, slope = 0.11, 95% CI [-0.09, 0.31]) correlated with body size (all $F_{1,19} > 8.41$, $R^2 > 0.270$, $P < 0.01$). Claw height (slope = 1.26, 95% CI [1.11, 1.42]), claw length (slope = 1.36, 95% CI [1.11, 1.61]), and lamella number (slope = 0.38, 95% CI [0.11, 0.66]) scaled allometrically with body size, whereas toepad width scaled isometrically with body size (slope = 1.24, 95% CI [0.94, 1.53]). Therefore, we corrected all traits except claw curvature for body size in subsequent analyses.

Multivariate claw shape variation was characterized by relative claw length and height (Procrustes PC1: 80.1% of variation) and claw curvature (Procrustes PC2: 10.5% of variation; Fig 2.3A). For univariate data, PC1 explained 56.2% of total variation and was primarily characterized by claw height and length, whereas PC2 explained 27.3% of univariate claw variation and was primarily characterized by claw curvature (Fig 2.4A).

Between Series and Radiation Comparisons

We found no significant differences between the *bimaculatus* and *roquet* series in any univariate claw or toepad traits (all $P > 0.05$). The directionality of univariate claw and toepad trait divergence between larger and smaller species on two-species islands was generally not consistent between series except for claw height (Fig 2.3D-E), although divergence between *A. wattsi* and *A. leachii* still showed inverse directionality compared to all other species pairs for claw height. Additionally, there was no significant difference between series in multivariate claw shape (phylogenetic Procrustes ANOVA: $F_{1,20} = 0.009$, $R^2 < 0.001$, $P = 0.851$; Fig 2.3A) nor shape disparity (morphological disparity: $P = 0.336$).

In comparisons with Greater Antillean ecomorphs, we found that Lesser Antillean anoles had relatively longer (*posthoc* t-test: T = 5.746; *d.f.* = 25; $P = 0.001$), taller (T = 6.817; *d.f.* = 25; $P = 0.001$), and more curved claws (T = 3.382; *d.f.* = 25; $P = 0.040$) compared to the twig ecomorph (Fig 2.4), the set of species with slender bodies and short limbs that specialize on twig and small branch habitat. Lesser Antillean anoles also differ in multivariate shape from Greater Antillean twig (*post hoc* permutation test: distance = 0.096; permutations = 9999; $P = 0.005$) and grass-bush anoles (distance = 0.059; permutations = 9999; $P = 0.037$). However, Lesser Antillean anoles did not significantly differ from any other Greater Antillean ecomorphs (*post hoc* t-test: all $P > 0.05$). Thus, Lesser Antillean anoles occupy claw morphospace similar to the Greater Antillean ecomorphs that occupy arboreal trunk habitats (i.e. trunk-ground, trunk, trunk-crown, and crown-giant). For toepad traits, Lesser Antillean anoles had relatively wider toepads than grass-bush (*post hoc* t-test: T = 4.996; *d.f.* = 29; $P = 0.008$) and twig (T = 3.597; *d.f.* = 25; $P = 0.024$) anoles and relatively more lamellae than grass-bush (T = 3.709; *d.f.* = 29; $P = 0.046$) and trunk-ground anoles (T = 5.962; *d.f.* = 32; $P = 0.008$).

We found no evidence of phenotypic integration between phylogenetically-informed toepad and claw morphology; no toepad traits were correlated with claw traits (PGLS: all $P > 0.05$). Additionally, claw curvature was not correlated with other claw traits (length: $F_{1,20} = 0.08$, $P = 0.779$; height: $F_{1,20} = 0.06$, $P = 0.810$). However, relative toepad width was positively correlated with relative lamella number ($F_{1,20} = 11.90$, $P = 0.003$), and relative claw length was positively correlated with claw height ($F_{1,20} = 12.08$, $P = 0.002$). Our results were consistent when analyzing only solitary species, only two-species islands, and each series independently, except that relative claw height and length were not significantly correlated in *roquet* series anoles ($F_{1,6} = 0.57$, $P = 0.450$). When not accounting for phylogeny, we found claw curvature was also positively correlated with relative lamella number ($F_{1,20} = 7.62$, $P = 0.012$) across all species. For *bimaculatus* series anoles, we found that both relative lamella number ($F_{1,12} = 718.69$, $P < 0.001$) and claw height ($F_{1,12} = 7.38$, $P = 0.019$) were positively correlated with claw curvature when not accounting for phylogeny. All other results were consistent whether analyses were informed by phylogeny or not.

Across all species, on two-species islands, and within each series, NDVI was not significantly correlated with any phylogenetically-informed claw or toepad traits (PGLS: all $P > 0.05$). However, for solitary anoles, NDVI was positively correlated with claw curvature ($F_{1,9} = 6.41$, $P = 0.032$) and multivariate claw shape PC2, which characterizes claw curvature ($F_{1,9} = 8.86$, $P = 0.016$; Fig 2.5). Our results for all species and the *bimaculatus* series were consistent with these when not phylogenetically-informed. Additionally, we found that no claw or toepad traits were correlated with perch dimensions (height and diameter) across Lesser Antillean anoles or within the *bimaculatus* series ($P > 0.05$) when accounting for phylogeny. However, we found that within the *roquet* series claw curvature was negatively correlated with perch height ($F_{1,5} = 10.50$, $P = 0.023$; Fig 2.6) and a negative correlation between claw height and ln-perch diameter approached significance ($F_{1,5} = 6.04$, $P = 0.057$). For solitary anoles, lamella number was positively correlated with perch height ($F_{1,5} = 7.47$, $P = 0.041$). When not accounting for phylogeny, we found that claw curvature (ANOVA: $F_{1,15} = 5.11$, $R^2 = 0.205$, $P = 0.039$), toepad width ($F_{1,15} = 5.52$, $R^2 = 0.220$, $P = 0.033$), and lamella number ($F_{1,15} = 5.81$, $R^2 = 0.231$, $P = 0.029$) were positively correlated with ln-perch height across Lesser Antillean anoles (Fig 2.6). The same traits were also positively correlated in *bimaculatus* series anoles when not accounting for phylogeny (claw curvature: $F_{1,6} = 5.74$, $R^2 = 0.345$, $P = 0.043$; toepad width: $F_{1,6} = 10.66$, $R^2 = 0.518$, $P = 0.011$; lamella number: $F_{1,6} = 6.89$, $R^2 = 0.396$, $P = 0.030$) as was claw shape PC2 ($F_{1,6} = 6.21$, $R^2 = 0.433$, $P = 0.047$). All other results were consistent between phylogenetically-informed and uninformed analyses.

Discussion

The lack of significant correlations for claw and toepad traits with habitat use in Lesser Antillean anoles, as a whole, is contrary to the strong relationships for these traits observed across a broad range of taxa, from mammals (Cartmill 1974; Tulli et al. 2016) to birds (Feduccia 1993; Birn-Jeffery et al. 2012) to squamate reptiles, including other anole assemblages (Zani 2000; Macrini et al. 2003; Tulli et al. 2009; D'Amore et al. 2018; Yuan et al. 2019). Both Greater Antillean and

mainland anole species show positive relationships between perch height and toepad width, lamella number (Irschick *et al.*, 1997; Macrini *et al.*, 2003; Crandell *et al.*, 2014), and claw curvature (Yuan et al. 2019). We contend that the lack of an overall relationship between claw morphology and habitat use in Lesser Antillean anoles is likely due to the interplay between phylogenetic history and two competing agents of selection: performance in different macrohabitats, characterized by NDVI, and competition driven microhabitat partitioning of perch sites. Thus, our results are consistent with interactions between potential agents of selection shaping observable ecomorphological patterns. Selective forces limited to a subset of species, in this case competition, can prevent ecomorphological patterns that may otherwise occur across a radiation.

Macrohabitat-morphology associations

On single-species islands, anoles inhabiting more densely vegetated islands had greater claw curvature, suggesting that macrohabitat type influences claw morphology as predicted. Low NDVI islands, such as Bonaire, Saba, and Redonda, are dominated by arid habitat and low lying vegetation (Stoffers 1956; Howard 1962; Lazell 1972; De Freitas et al. 2005), which may select for flatter claws due to the reduced availability of arboreal relative to terrestrial habitat. Flattened claws are thought to improve performance in terrestrial habitats while decreasing clinging performance in arboreal habitats (Zani 2000; Glen and Bennett 2007; Tulli et al. 2009; Birn-Jeffery et al. 2012). Thus, overall claw shape on single-species islands is likely reflective of performance tradeoffs in different structural habitats available on each island.

Toepad morphology was not correlated with NDVI, perch height, or perch diameter across Lesser Antillean anoles as a whole, suggesting that it may not play an essential role in differential performance across vegetation types. Yet, strong relationships with structural habitat use have been documented in both Greater Antillean and mainland anoles (Losos, 1990b; Glossip & Losos, 1997; Crandell *et al.*, 2014; Yuan *et al.* 2019), indicating that toepads should be functionally relevant in Lesser Antillean species, at least in relation to perch height if not vegetation types. Indeed, toepad traits did correlate with perch height, as predicted, in *bimaculatus* series anoles, at least when not accounting for phylogenetic relatedness (Fig 2.6). However, toepad traits did not correlate with either perch height or diameter in *roquet* series anoles. Because the strength of interaction between toepads and surfaces is mediated through the microscopic setae that compromise lamellae (Autumn et al. 2002; Hagey et al. 2014), ecological differences in the *roquet* series may be driven largely by changes in setal properties rather than in lamellae. Experiments have shown that adhesive force can increase without changes to macroscale lamellar properties in both anoles and geckos (Hagey et al. 2014; Dufour et al. 2019), although the precise mechanism for this change is unknown and warrants future study. Thus, confounding morphological patterns between the *bimaculatus* and *roquet* series likely mask the relationship between structural microhabitat use and toepad traits when examining Lesser Antillean anoles altogether.

Competition disrupts morphology-macrohabitat associations

Because of fitness tradeoffs, overall phenotypic evolution can be driven largely by a dominant selective pressure leading to patterns contrary to functional predictions in response to other

environmental variables (Gómez 2004; Templeton and Shriner 2004; Bischoff et al. 2006; Petrů et al. 2006). Indeed, we found that the relationship between vegetation type and claw curvature was lost when including two-species islands (Fig 2.5). On all two-species islands, both species co-occur throughout most, if not all, of their ranges (Lazell 1972), and there is strong evidence for niche partitioning in either microclimate or structural microhabitat, supporting the hypothesis that competition is an important driver of evolution (Schoener and Gorman 1968; Rummel and Roughgarden 1985; Buckley and Roughgarden 2005b). Thus, we propose that the lack of macrohabitat-morphology associations on two-species islands is due to the confounding effects of interspecific competition. Specifically, in allopatry, species can utilize all potentially available ecological space. Thus, selection should favor performance reflective of their overall habitat as observed on single-species islands. However, if competition constrains the availability of ecological niche space on two-species islands, such as through partitioning of vertical habitat space, species may not conform to the predicted ecomorphological patterns in response to macrohabitat because they cannot fully utilize habitat space compared to species evolving in allopatry. Instead, phenotypic evolution of claw and toepad traits should reflect narrower specialization on a subset of available microhabitats.

Additionally, previous work has shown that when interspecific competition is weaker, intraspecific competition can generate parallel patterns of niche partitioning between sexes in Greater Antillean anoles (Butler *et al.,* 2007). Although we examined only males in this study, future investigations of habitat partitioning between sexes may provide greater insight into the differences between one and two-species islands.

Differences between series in morphology-microhabitat associations

For the *bimaculatus* series anoles, although correlations between microhabitat use and morphology are lost when accounting for phylogeny, these habitat-morphology associations are consistent with other anole radiations and functional expectations. Specifically, *bimaculatus* series anoles show positive correlations of claw curvature, toepad width, and lamella number with perch height, consistent with both Greater Antillean and Mainland anoles (Irschick et al. 1997; Macrini et al. 2003; Yuan et al. 2019). These traits have also all been shown to improve performance in arboreal habitats across squamate reptiles (Losos 1990b; Zani 2000; Elstrott and Irschick 2004; Tulli et al. 2011; Crandell et al. 2014). Smaller, more terrestrial species within the *bimaculatus* series also had more similar claw morphology to trunk-ground and grass-bush anoles than their more trunk-crown like congeners (Fig 2.3B-E, 2.4A). Because the more terrestrial anoles form a reciprocally monophyletic clade with more arboreal species in the *bimaculatus* series (Fig 2.2A), signals of selection could be indistinguishable from phylogenetic signal. Still, we cannot rule out that the relationships of claw and toepad traits with perch height represent a purely phylogenetic artifact, particularly as the *wattsi* group's (*A. forresti, A. pogus, A. schwartzi,* and *A. wattsi*) more terrestrial life history is likely to have evolved just once in their common ancestor.

The *roquet* series anoles did not exhibit evidence of morphological adaptation to habitat consistent with expectations. Rather, we found that *roquet* series anoles showed a negative relationship between claw curvature and perch height and no relationships between toepad traits and perch height or diameter (Fig 2.6). These patterns are contrary not only to those observed

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across the *bimaculatus* series but also to the general pattern across Greater Antillean anoles (Losos 1990b; Glossip and Losos 1997; Macrini et al. 2003; Yuan et al. 2019) and squamates more broadly (Zani 2000; Tulli et al. 2009, 2011; D'Amore et al. 2018) as well as predictions from functional studies (Zani 2000; Crandell et al. 2014). Additionally, patterns of divergence on two-species islands in the *roquet* series were often the converse of those observed on two-species islands in the *bimaculatus* series (Fig 2.3). Within the *roquet* series, the larger species on two-species islands had flatter claws, smaller toepads, and fewer lamellae compared to their smaller congeners. Unlike Greater Antillean and *bimaculatus* series anoles, *roquet* series anoles do not partition vertical habitat on multi-species islands (Roughgarden et al. 1981; Buckley and Roughgarden 2005b). Therefore, divergent selection for traits associated with vertical habitat partitioning is likely to be weaker within the *roquet* series. Although *roquet* series anoles do partition thermal microhabitat on two-species islands, we lacked adequate data to formally test the effects of thermal microhabitat across Lesser Antillean anoles.

Why *roquet* series anoles do not exhibit vertical habitat partitioning, and associated morphological divergence, is unclear. However, whereas the *bimaculatus* series is descended from the Greater Antillean radiation, the *roquet* series colonized the Lesser Antilles from the South American mainland. Different lineages may be more or less capable of responding along axes that facilitate diversification in response to similar ecological opportunities (Wellborn and Langerhans 2015). Given the widespread convergence of vertical habitat partitioning across the Greater Antilles but not the mainland (Irschick et al. 1997), *bimaculatus* series anoles may have a greater evolutionary predisposition for such divergence compared to the *roquet* series. Differing evolutionary dynamics may also be expected given the *bimaculatus* and *roquet* series last shared a common ancestor at the base of the crown group of anoles, estimated to approximately 31-65 Ma (Blankers et al. 2012; Prates et al. 2015; Poe et al. 2017; Román-Palacios et al. 2018). Although convergent responses to similar ecological pressures can occur between distantly-related species, such as flower shape with pollinator specificity in angiosperms (Dafni et al. 1990; Papadopulos et al. 2013) and body shape with pelagic swimming in fishes (Donley et al. 2004), the overall likelihood of convergent evolution decreases in more distantly related clades (Conte et al. 2012). Still, convergent claw morphology in response to arboreality has been observed across more highly-divergent taxa including primates (Cartmill 1974; Smith and Smith 2013), birds (Feduccia 1993; Glen and Bennett 2007; Birn-Jeffery et al. 2012), and other squamate reptiles such as geckos, skinks, and varanids (Zani 2000; Tulli et al. 2009, 2011; D'Amore et al. 2018). Therefore, the *roquet* series anoles appear to violate an otherwise widespread ecomorphological pattern across squamates. Nevertheless, our results suggest a hypothesis that different phylogenetic histories influenced how each anole series responded to similar ecological pressures in the Lesser Antilles. Future work may clarify if these differences explain the overall lower diversity of *Dactyloa* clade anoles to which the *roquet* series belongs.

Conclusion

Overall, our results suggest that the evolution of ecologically-relevant claw and toepad traits in Lesser Antillean anoles has been shaped not only by their functional role in habitat use but also the confounding effects of interspecific competition and phylogenetic history. The *bimaculatus* and *roquet* series show consistent morphology-macrohabitat associations on single-species

islands (Fig 2.5), but this pattern is disrupted in both series by contrasting effects of competition-driven microhabitat partitioning on two-species islands (Fig 2.3). Thus, we demonstrate that predictable ecomorphological patterns can be disrupted by species-specific effects of competition but that the outcomes of this disruption may differ between clades. Whereas the *bimaculatus* series shows patterns of microhabitat partitioning and subsequent morphological divergence consistent with Greater Antillean anoles (Yuan et al. 2019), claw and toepad traits appear to be decoupled from structural microhabitat use, as characterized by perch height and diameter, in the *roquet* series (Fig 2.6). Thus, our data indicate the capacity for strong morphological responses to similar environmental pressures may differ between clades, which may have consequences for adaptive diversification either by constraining or facilitating effective niche exploitation. Differences between the *bimaculatus* and *roquet* series anoles on the Lesser Antilles suggest that the Greater Antillean lineages may have been especially primed to adaptively radiate through their hallmark partitioning of vertical habitat.

Figures

Figure 2.1 (A) Phylogeny of Lesser Antillean *Anolis* pruned from Poe et al. (2017). Each species is coded by sub-generic series and body size classification by color. Branch lengths have been transformed for ease of viewing and are not biologically meaningful. (B) Map of the islands of the Lesser Antilles, excluding the Leeward Antilles (Aruba, Curaçao, and Bonaire). Minor islets are not shown. For readability, multi-island banks are labelled only by bank names. The St. Kitts Bank is comprised of St. Eustatius, St. Kitts, and Nevis and the St. Maarten Bank is comprised of Anguilla, St. Maarten, and St. Barthélemy. Endemic anoles are denoted for each island or bank by numerical codes corresponding to the phylogeny.
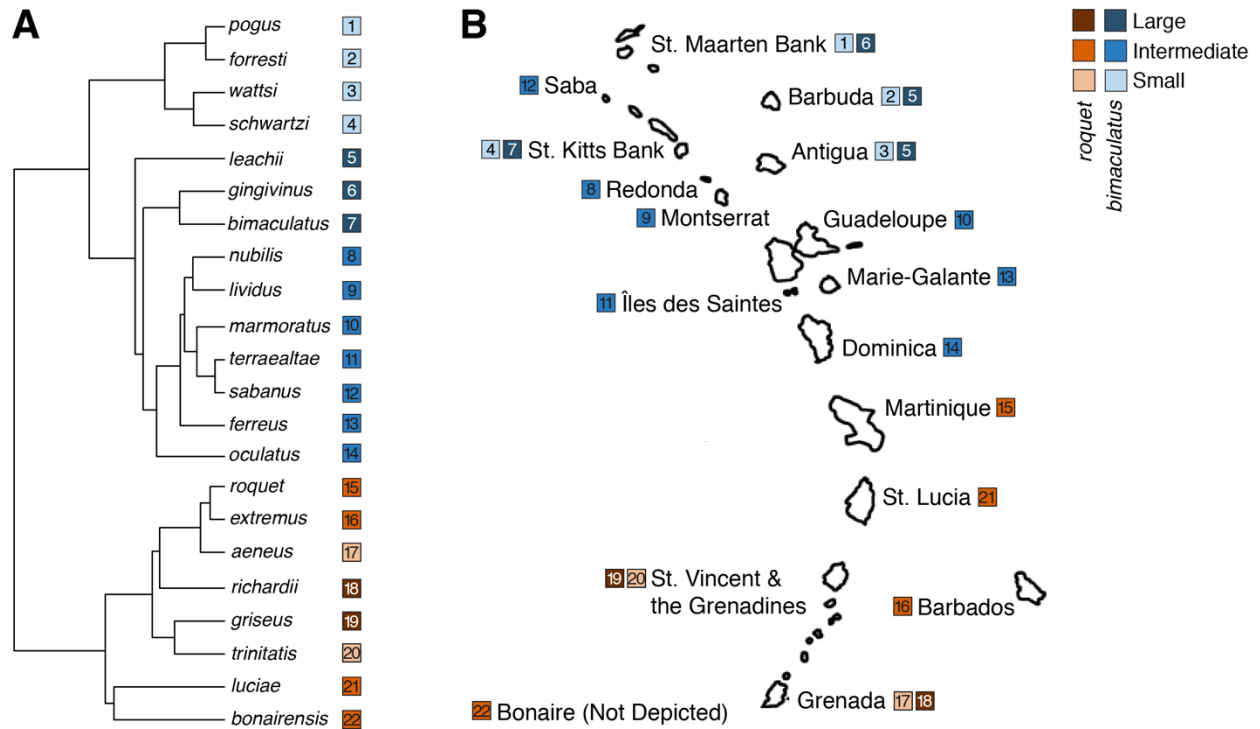
Figure 2.2 (A) Diagram showing univariate measurements for claw morphology. Claw length is determined as A+B, height as H, and curvature as $57.296\left(2\sin^{-1}\left(\frac{(2A^2B^2+2B^2C^2+2A^2C^2-A^4-B^4-C^4)^{0.5}}{2AB}\right)\right)$.

Univariate measurements taken as described in Zani (2000). (B) Example of geometric morphometric semilandmark placement along the ventral and dorsal curves of the claw. (C) Diagram depicting toepad measurements: toepad width taken at the widest point and lamellae count.
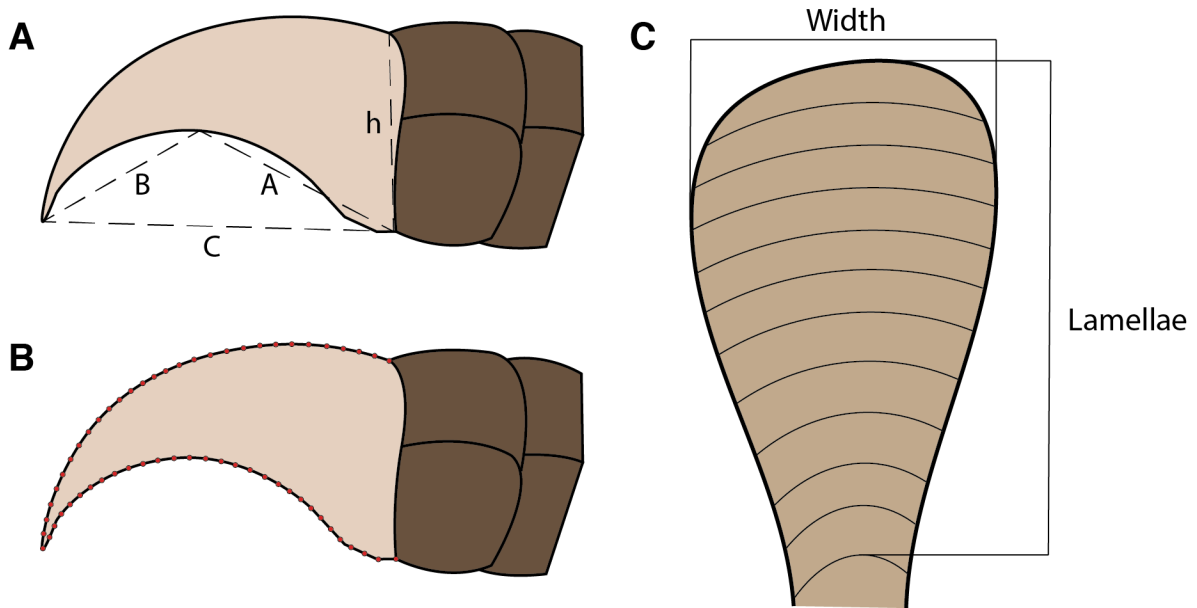
Figure 2.3 (A) Plot of multivariate claw shape principal components 1 and 2. All species are coded by series and size classification. Warp grids representing extremes of PC1 are depicted. (B-E) Pairwise comparisons between large and small species on two-species islands for select univariate traits (relative claw height, claw curvature, relative toepad width, and relative lamella number). a – *aeneus*; b – *bimaculatus*; f – *forresti*; gi – *gingivinus*; gr – *griseus*; l – *leachii*; p – *pogus*; r – *richardii*; s – *schwartzi*; t – *trinitatis*; w – *wattsi*.
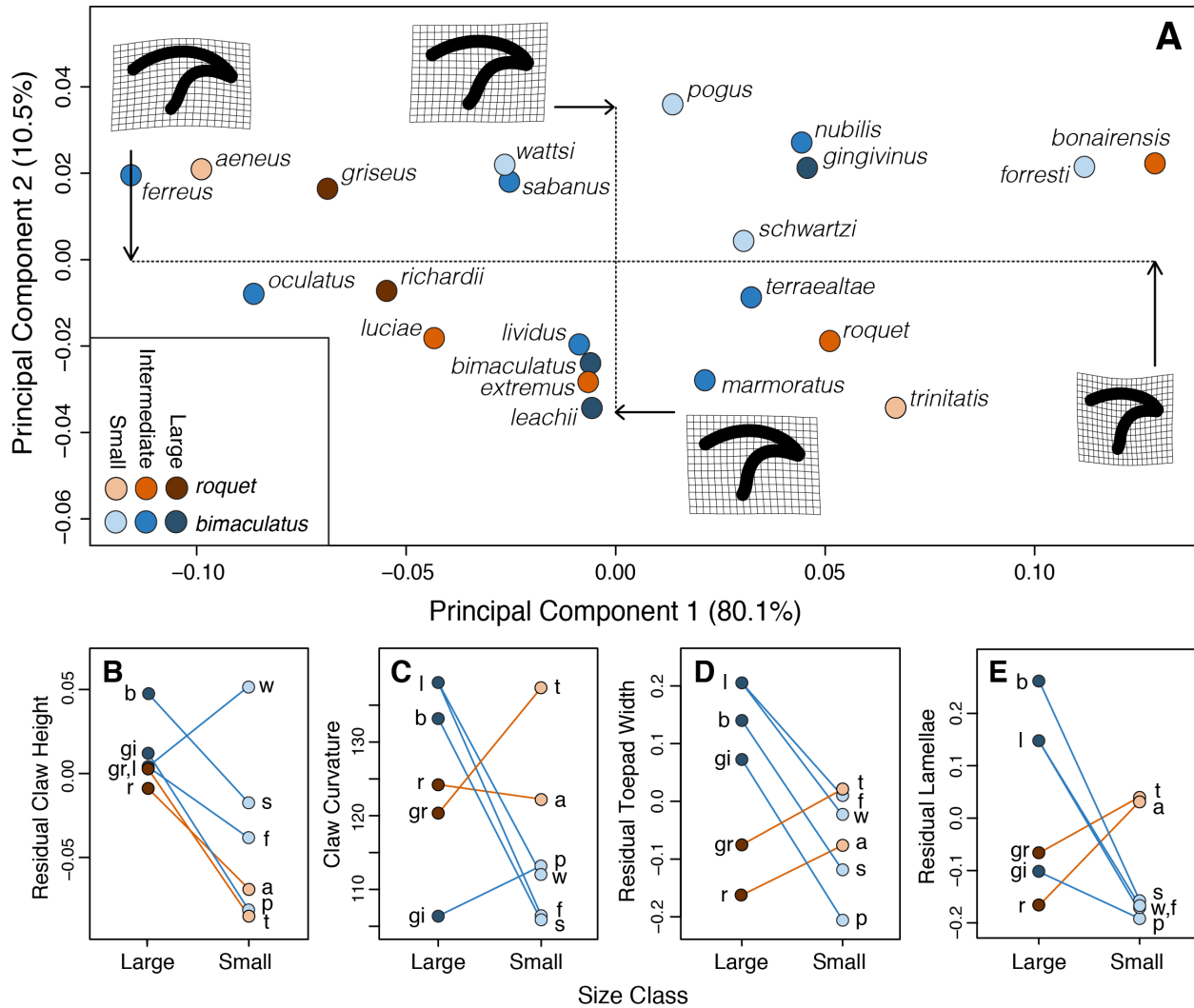
Figure 2.4 (A) Plot of principal components 1 and 2 for all univariate claw measurements (claw curvature and relative claw height and length) across both Greater and Lesser Antillean anoles. For Greater Antillean anoles, only minimum convex polygons are displayed for each ecomorph classification. All sampled Lesser Antillean species are shown coded by body size classification. (B-D) Boxplots depicting relative claw height, claw curvature, and relative lamella number for each ecomorph compared to Lesser Antillean species as a whole. LA = Lesser Antillean, CG = crown-giant, TC = trunk-crown, TR = trunk, TG = trunk-ground, GB = Grass-Bush, TW = twig.
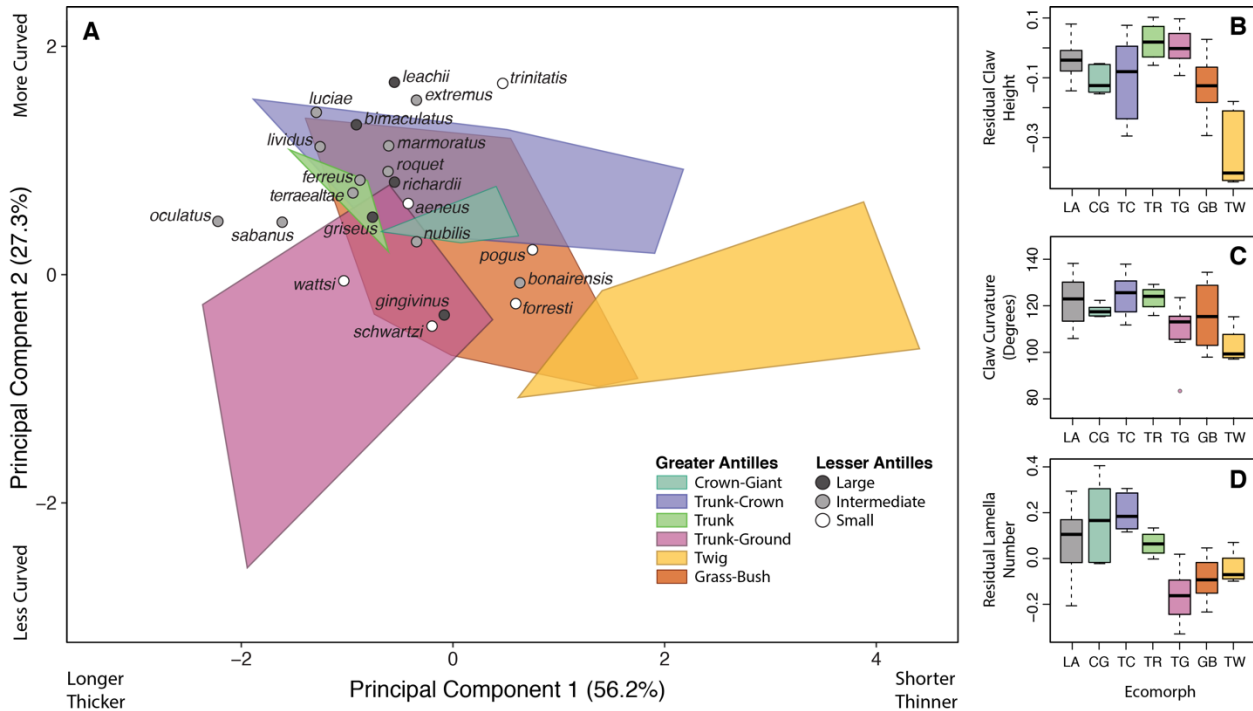
Figure 2.5 The relationship between both claw curvature and multivariate claw shape PC2 (which also characterizes ventral claw curvature) with ln NDVI for (A) all Lesser Antillean species sampled and (B) only species from single-species islands. Claw shape PC2 is depicted by unfilled circles and claw curvature is depicted by black filled circles. All data points represents the species mean values. Correlations were significant for both traits for species from singly-species islands, whereas correlations only approached significance across all sampled species.
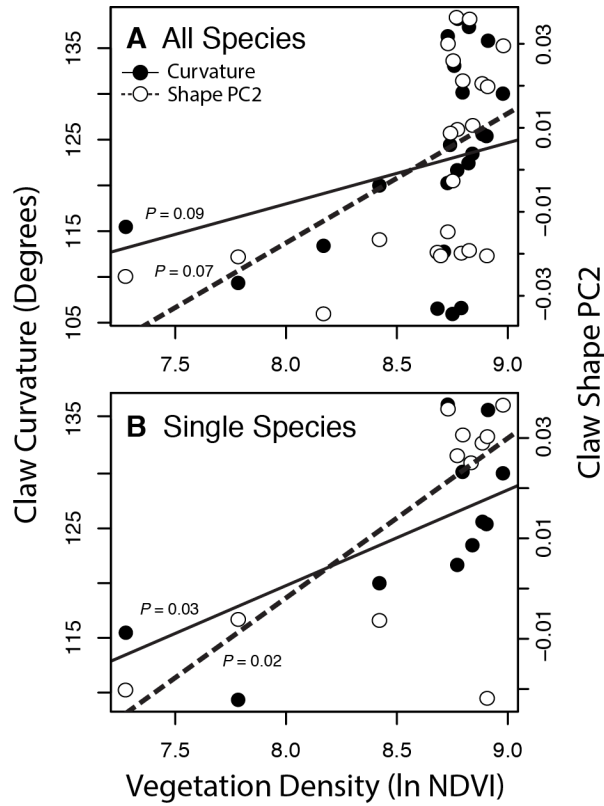
Figure 2.6 Plots of morphological correlates with perch height: (A) Claw curvature, (B) relative toepad width, and (C) relative lamellae number. Plots include regression lines for all species, only the *bimaculatus* series, and only the *roquet* series if relationships were statistically significant. Non-significant relationships are not depicted. We did not perform uninformed tests when examining only the *roquet* series.
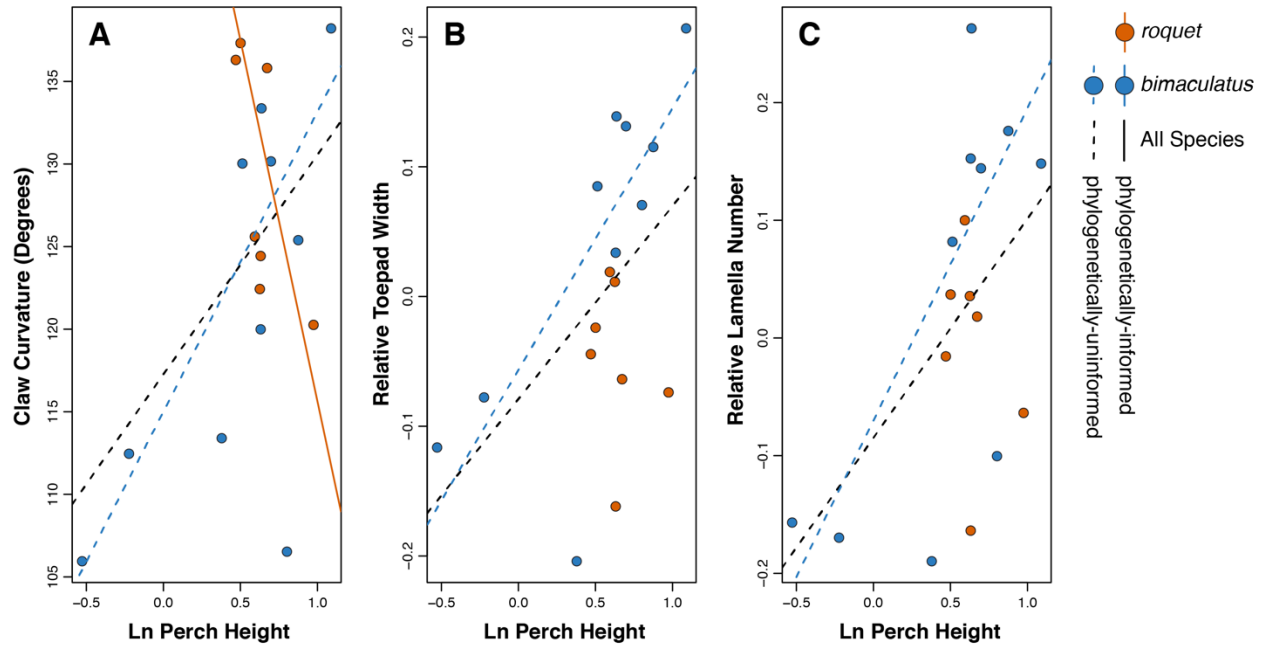
CHAPTER III

Parallel color and idiosyncratic morphological responses to environmental variation across
Lesser Antillean anoles

Abstract

Species whose ranges encompass substantial environmental variation should experience heterogeneous selection potentially generating local adaptation. When ecologically similar species experience similar environments, parallel covariation between phenotype and environment across species provide strong evidence for adaptation. Lesser Antillean anoles provide an excellent system to study parallel local adaptation because most species are widespread generalists occurring throughout environmentally heterogenous island landscapes. I leveraged this natural replication to test the hypothesis that phenotype (morphology and coloration) is consistently associated with environment across species. Specifically, I tested for parallel covariation across nine species of *bimaculatus* series anoles and compare our results with findings from the distantly related *roquet* series. I showed parallel patterns of color variation associated with climatological and habitat variation across *bimaculatus* series anoles consistent with patterns previously observed across the *roquet* series. Conversely, I did not find a signal of parallel morphological covariation with environment. My results show that phenotypic response to environment can be idiosyncratic for many traits. However, I also demonstrate a striking case of convergent local adaptation in dorsal color between two distantly related clades.

Introduction

Organisms with ranges encompassing broad environmental variation experience heterogeneity in the strength and agents of selection across populations. In response to variation in selection, such organisms may evolve either broadly generalist phenotypes to maximize average fitness across different habitats (McPeek 1996; Merilaita et al. 1999; Kassen 2002) or locally-adapted specialist forms (Richards et al. 2005; Bolnick et al. 2007; Webster et al. 2011; Taylor et al. 2018). In the latter case, selection should lead to strong correlations between ecologically-relevant phenotypic variation and corresponding environmental variation. Thus, studies of phenotype-environment associations across space can provide insight into how broadly distributed species adapt to varied environments across their ranges. In particular, parallel signals of phenotype-environment correlations across multiple species provide strong support for adaptive evolution in response to environmental conditions (Schluter 2000b; Harrod et al. 2010).

Climatological variation plays a fundamental role in determining where species occur and how they adapt to local environmental conditions (Laine 2008; Normand et al. 2009; Lasky et al. 2014; Rolland et al. 2018). Although direct effects of climate on organisms are primarily physiological (i.e. thermoregulatory and osmoregulatory), these physiological responses are often mediated through morphology (Peters and Peters 1986). For instance, broad patterns of morphological variation in response to climate, such as Bergmann's rule (larger body size in cooler habitats), were formulated to describe endothermic responses to thermal environmental gradients (Bergmann 1848). Temperature variation can also pose strong constraints for ectotherms because their basic biological functions are explicitly tied to environmental temperatures (Cossins and Bowler 1987; Hochachka and Somero 2002; Rolland et al. 2018), but support for Bergmann's rule across ectotherms including insects, amphibians, and reptiles is equivocal (Mousseau 1997; Ashton 2002; Ashton and Feldman 2007; Adams and Church 2008; Shelomi 2012; Muñoz et al. 2014; Womack and Bell 2020). Regional differences in coloration may also reflect adaptation to differences in thermal environment in a wide range of organisms. For example, darker color is associated with cooler climates and increased rates of heat absorption across a range of ectotherms (Jong et al. 1996; Vences et al. 2002; Clusella-Trullas et al. 2009; Stuart-Fox et al. 2017), and locally adapted coloration may be associated with increased physiological performance and overall fitness (Clusella Trullas et al. 2007).

Climate can also influence aspects of an animal's morphology indirectly by shaping vegetation and, therefore, available structural habitat. Theory predicts that organisms should adapt to the most readily available resources (Morris 2011); consequently, for species that experience broadly different structural environments, locomotor traits associated with habitat use should vary with respect to the most locally abundant vegetation types (Calsbeek 2008; Harrod et al. 2010; Webster et al. 2011; Taylor et al. 2018; Ennen et al. 2019). For example, an arboreal generalist species may by necessity behave more terrestrially in dry scrubland habitat than in rainforest habitat and subsequently undergo morphological shifts to optimize locomotor performance. Indeed, in the ornate tree lizard (*Urosaurus ornatus*) different morphologies are associated with populations in boulder versus tree dominated habitats, with boulder-dwelling lizards experiencing directional selection for longer hindlimbs (Taylor et al. 2018). Similarly, predator avoidance strategies such as cryptic coloration should reflect the dominant background color as determined by the structural environment. For example, color and pattern morphs reflect host

plant species to optimize background matching in *Timema cristinae* walking sticks (Nosil 2007) and background reef structure color in *Tridacna crocea* giant clams (Todd et al. 2009). In some species, however, cryptic coloration instead reflects a generalist phenotype to minimize trade-offs in different habitats (Merilaita et al. 1999, 2001) or is optimized to the habitat with the greatest predation pressure (Houston et al. 2007). Systems that exhibit parallelism across closely-related species and convergence across distantly-related species provide opportunities to investigate the predictability and generalizability of these phenotypic responses to environment.

The Lesser Antillean islands form an oceanic chain extending from southeast of Puerto Rico to South America (Fig 3.1). The volcanic history of these islands generated topographic complexity associated with dramatic, yet predictable, differences in climate and habitat despite the relatively limited geographic size of each island (Fig 3.2). Generally, the low-lying areas around the fringes of the islands contain xeric scrub and dry forests, whereas high elevation interiors are characterized by elfin and rain forests. Additionally, the windward side of each island typically experiences greater climatic variation than the leeward side. Two clades of anoles independently colonized the Lesser Antilles, the *bimaculatus* series (17 species) from the Greater Antilles and the *roquet* series (9 species) from the South American mainland, with one or two species endemic to each island (Underwood 1959; Lazell 1972). These two clades diverged ~49-59 Ma (Prates et al. 2015; Poe et al. 2017; Román-Palacios et al. 2018) and are divided by the Martinique Passage, with the *bimaculatus* series native to the Leeward Islands north of the passage and the *roquet* series native to the Windward Islands in the south. In all cases, these *Anolis* species occur broadly throughout their native islands and, therefore, experience wide-ranging climatic and habitat variation despite their small ranges (Fig 3.2).

Morphologically, most Lesser Antillean species appear to be arboreal generalists (Losos and de Queiroz 1997), yet many species within the *roquet* series also show high levels of parallel intraspecific morphological and dorsal color variation that correlates with the local abiotic environment (Lazell 1972; Thorpe et al. 2015). This variation is primarily genetically determined (Thorpe et al. 2005) and persists despite high levels of gene flow between populations (Stenson et al. 2002). Across the *roquet* series, coastal xeric forms are pale in coloration, while montane mesic forms are bright green or blue (Lazell 1972; Thorpe et al. 2015). The *roquet* series anoles also display parallel divergence in ventral scale number, head dimensions, and toe length (Thorpe et al. 2015) (Fig 3.3). Existing comparative data within the *bimaculatus* series are limited to two species, *Anolis marmoratus* and *Anolis oculatus*. Both species show patterns consistent with the *roquet* series in coloration, but morphological convergence in response to environment is less clear (Malhotra and Thorpe 1997; Muñoz et al. 2013; Thorpe et al. 2015). Although phenotypic plasticity can produce patterns consistent with local adaptation, common garden experiments in *A. oculatus* demonstrate that these differences are heritable (Thorpe et al. 2005). Consequently, the current data suggest that some, but not all, traits have evolved convergently between the two distantly-related series in response to shared patterns of environmental variation. However, the prevalence of this pattern across most of the Leeward Island species (*bimaculatus* series) has not yet been documented. To understand the extent of potential convergence, we studied whether phenotypic divergence covaries with both climate and vegetation across nine species of *A. bimaculatus* series anoles (Fig 3.1). Specifically, I addressed two questions: (I) Is phenotypic variation (morphology and coloration) associated with geographic or environmental (climate and vegetation) variation in *A. bimaculatus* series anoles?

(II) Do species in *bimaculatus* series anoles exhibit parallel patterns of phenotypic divergence similar to those of the *A. roquet* series? My results allowed us to examine the degree of repeatability in intraspecific responses to environmental variation across both closely and distantly-related species.

Methods

Color Data

I collected dorsal and ventral skin coloration data for five species in the field between 2018 and 2020: *A. bimaculatus* (N = 28)*, A. gingivinus* (N = 33), *A. lividus* (N = 33), *A. oculatus* (N = 27), and *A. schwartzi* (N = 31). I photographed the dorsum and venter of live individuals with a SpyderCHECKR 24 color standard (Datacolor, Lucerne, Switzerland) under standardized lighting conditions in a Foldio2 portable studio (Orangemonkie, San Diego, CA) using an Olympus TG-5 digital camera (Olympus Corporation, Tokyo, Japan). Five individuals of *A. lividus* were only photographed dorsally. Because anoles are capable of color change in response to stress and temperature, I acclimated all individuals to common ambient temperature (~26-28°C) in opaque cloth bags for at least two hours. Each individual was photographed immediately upon removal from the cloth bag to minimize handling time. I color corrected all photographs in Adobe Lightroom Classic 7.3.1 (Adobe Inc., Mountain View, CA) using the SpyderCHECKR add-on. I measured color in red-green-blue (RGB) space and achromatic grayscale by averaging values for each channel across 2,500 pixels in four areas: throat, ventral mid-trunk, dorsal shoulder, and dorsal waist.

I also calculated the overall color distance between specimens using the R package *colordistance* (Weller and Westneat 2019). I quantified the RGB value for every pixel on dorsal images between the posterior attachment of the hindlimb and the base of the skull excluding limbs. Unlike averaging values for subsets of pixels, this method could only be applied to dorsal color due to issues with consistent positioning of lizards during photography. I excluded the limbs, head, and tail due to inconsistencies in their orientations across images. Ventral images were excluded because limb orientation prevented consistently unobstructed images of the full venter. Next, I constructed histograms of the distribution of pixels across 27 color bins using the getImageHist() function. Finally, I calculated the earth mover's distance between each histogram to quantify pairwise distances in color space. Earth mover's distance determines the minimum 'work' required to transform one distribution to another.

Morphological Measurements

I measured the morphology of 883 adult males from nine *bimaculatus* series anole species (*Anolis bimaculatus, Anolis gingivinus, Anolis leachii, Anolis lividus, Anolis marmoratus, Anolis oculatus, Anolis sabanus, Anolis schwartzi,* and *Anolis wattsi*) (Fig 3.1) using museum species and specimens I collected from the field. Museum specimens were from the National Museum of Natural History (Smithsonian Institution, Washington, DC), the Museum of Comparative Zoology (Harvard University, Cambridge, MA), and the Museum of Vertebrate Zoology (University of California, Berkeley, CA; Appendix III). I collected additional specimens of *A.*

bimaculatus, A. lividus, and *A. schwartzi* from the field during 2018-2019. All field-collected specimens were accessioned in the Museum of Vertebrate Zoology or donated to the Government of Saint Kitts and Nevis. In total, I sampled 106 *A. bimaculatus,* 88 *A. gingivinus,* 37 *A. leachii,* 198 *A. lividus,* 106 *A. marmoratus,* 161 *A. oculatus,* 64 *A. sabanus,* 49 *A. schwartzi,* and 74 *A. wattsi.*

For each individual, I measured 16 morphological characters. First, I measured snout-vent-length (SVL) and counted ventral scales along a 5mm medial transect through the midpoint of the trunk. I then imaged the 4th hind toe and sagittally flattened claws using an AM4115ZT Dino-Lite Digital Microscope (AnMo Electronics Corporation, New Taipei City, Taiwan) and skeletal structure by digital x-ray. I collected morphological measurements from digital images using ImageJ (Schneider et al. 2012). Specifically, I measured femur length, tibia length, radius length, humerus length, 4th metatarsal length, skull width, skull length, shoulder width, and pelvic girdle width from x-rays. For 4th hind toes, I measured toepad width, lamella number, claw height, claw length, and claw curvature. Toepads were defined as starting where the toe begins to widen (i.e. the next most distal lamellae is wider). Claw measurements follow protocols from Zani (2000) and have been previously implemented in anoles (Crandell et al. 2014; Yuan et al. 2019, 2020b). Due to variation in specimen quality, I could not measure all traits for every specimen. I natural log transformed all traits, except claw curvature, to achieve normality. For traits that significantly correlated with body size, I regressed ln-transformed values against ln-transformed body size and retained the residuals.

Environmental Data

Where GPS records were not available for museum specimens, I georeferenced specimens based on available locality information in order to assign environmental data. I downloaded all 19 bioclimatic variables from WorldClim2 (Fick and Hijmans 2017) at 1km resolution. I assessed overall bioclimatic variation across islands by performing a raster PCA including all 19 BIOCLIM layers for the entire region. I then summarized and visualized range-wide PC1 and PC2 values for each island or island bank inhabited by my study species. I also downloaded three years (2017-2019) of enhanced vegetation index (EVI) data layers from NASA's Moderate Resolution Imaging Spectroradiometer (MODIS) (Didan 2015) at 250m resolution. To account for tropical seasonality, I divided EVI data into dry (January through June) and wet seasons (July through December) and averaged values for each season across years. I then extracted environmental variables by sampling locality for each species from all 21 data layers. To reduce the dimensionality of my data and because environmental variables often covary, I conducted PCAs on all extracted environmental variables. Finally, I performed Horn's parallel analyses (Horn 1965) to determine PCs to retain for downstream analyses.

Data Analyses

I tested the prediction that coloration is correlated with either dry season EVI (vegetation) or mean annual temperature (BIO1) across *bimaculatus* series anoles for the five species with color data. A correlation with EVI would support the hypothesis of cryptic coloration, whereas a correlation with BIO1 would support a hypothesis of thermal adaptation. I conducted all coloration analyses at the individual level. Because coloration is likely to covary between body

regions, I conducted principal component analyses (PCA) for all measured body regions. PCAs were performed for RGB and achromatic grayscale data separately. I then conducted ANOVAs to test the effect of dry season EVI and mean annual temperature (BIO1) on retained PCs for each color dataset. I expect that anoles should be paler and brighter in drier, hotter habitats across these species, similar to the previously characterized *bimaculatus* series species *A. oculatus* and *A. marmoratus* (Thorpe et al. 2015).

Next, I tested whether my study species conformed to inverse Bergmann's rule, using individual-level variation. Because Bergmann's rule directly applies to body size, only full-size adults were used in analyses. I identified animals at maximum body size using characteristic bone fusion in limb joints (Maisano 2002). All other traits were either independent of or adjusted for body size and, thus, are not expected to be biased by growth stage. Hence, all adult individuals were used in downstream analyses for all traits besides body size. I fit linear mixed models to individual-level data with collection locality as a random factor using the package *lme4* (Bates et al. 2014). To examine Bergmann's rule within each species, I regressed body size against mean annual temperature (BIO1). Because seasonality has been alternatively proposed as the underlying mechanism of Bergmann's rule (Boyce 1978; Murphy 1985), I also regressed body size against annual temperature range (BIO7). To assess overall covariation between morphology and environment, I first performed principal component analyses for all morphological variables except SVL separately for each species and retained PCs. I then averaged all values for each sampling locality for downstream analyses. Next, I tested for correlations between retained, locality-level morphological and environmental PCs using linear regressions.

To test for phenotypic isolation-by-distance (IBD) and isolation-by-environment (IBE), I implemented multiple matrix regression with randomization (MMRR) analyses (Wang 2013). MMRR conducts multiple linear regressions on distance matrices, using a permutation procedure to calculate significance values because of the non-independence of pairwise values in distance matrices. For each model, I fit morphological or earth mover's color distances separately as response variables and retained environmental PCs and Euclidean geographic distances as predictor variables. I calculated significance using 999 permutations of the response variables. I performed MMRR analyses starting with all predictor variables and conducted variable selection by backwards elimination removing the lowest coefficient variable and refitting the model until only significant variables remained.

Results

Color and environment

My results support both the thermoregulatory and cryptic color function hypotheses. To represent intraspecific color variation, I retained one to three chromatic and one to two achromatic PCs for each species. Retained chromatic PCs accounted for 63.2-88.8% of total variation, while retained achromatic PCs accounted for 61.5-85.0% of total variation per species (Fig 3.4). I found that both chromatic and achromatic PC1 were correlated with mean annual temperature for *A. lividus* (chromatic: $F_{1,25} = 17.19$, $P < 0.001$; achromatic: $F_{1,25} = 17.02$, $P < 0.001$), *A. gingivinus* (chromatic: $F_{1,30} = 4.43$, $P = 0.044$; achromatic: $F_{1,30} = 5.13$, $P = 0.031$), *A.*

oculatus (chromatic: $F_{1,24}$ = 18.95, P < 0.001; achromatic: $F_{1,29}$ = 19.69, P < 0.001), and *A. schwartzi* (chromatic: $F_{1,29}$ = 16.14, P < 0.001; achromatic: $F_{1,29}$ = 8.06, P = 0.008). Additionally, both chromatic and achromatic PC1 were correlated with dry season EVI for *A. lividus* (chromatic: $F_{1,25}$ = 9.00, P = 0.006; achromatic: $F_{1,25}$ = 8.89, P = 0.006), *A. gingivinus* (chromatic: $F_{1,30}$ = 5.65, P = 0.024; achromatic: $F_{1,30}$ = 9.77, P = 0.004), and *A. oculatus* (chromatic: $F_{1,24}$ = 12.69, P = 0.001; achromatic: $F_{1,29}$ = 15.67, P < 0.001). In all significant cases, individuals in hotter, drier habitats were relatively yellower than those from wetter, drier habitats (Fig 3.4). All other tests were not significant (P > 0.05).

My MMRR color analyses were generally congruent with results from PC analyses. I found a signature of color-based IBD for only one species, whereas I found a signature of IBE for four of five species examined (Table 3.1). The best-fit MMRR model for *A. lividus* included environmental PC1 and PC2 (F = 55.91, r^2 = 0.176, P < 0.001). For *A. oculatus* (F = 27.75, r^2 = 0.074, P < 0.001) and *A. gingivinus* (F = 92.53, r^2 = 0.150, P < 0.001), I retained only environmental PC1 in MMRR analyses. I found dorsal color distance was significantly associated with both environmental PC1 and geographic distance for *A. schwartzi* (F = 49.20, r^2 = 0.176, P < 0.001). Conversely, no models were significant for *A. bimaculatus*, although PC2 was marginally significance (F = 10.96, r^2 = 0.028, P = 0.056).

Morphology and environment

Support for consistent phenotype-environment associations was mixed across species and traits (Fig 3.3). My data support the pattern of reverse Bergmann's rule *sensu stricto* for two species: *A. lividus* (χ^2 = 18.25, P < 0.001) and *A. gingivinus* (χ^2 = 7.87, P = 0.005). Additionally, I found body size negatively correlated with annual temperature range in *A. oculatus* (χ^2 = 5.18, P = 0.023) and marginally in *A. wattsi* (χ^2 = 3.75, P = 0.054) and *A. marmoratus* (χ^2 = 3.59, P = 0.058). However, for the remaining five species, body size did not correlate with either mean annual temperature or annual temperature range (all P > 0.05).

I found significant morphology-by-environment correlations in four species: *A. lividus, A. oculatus, A leachii,* and *A. bimaculatus*. I retained environmental PC1 (temperature and precipitation) and PC2 (seasonality and EVI), which together explained 74.9-86.3% of variance for each island. Temperature and precipitation were inversely related in all cases. I retained between one and four PCs for each species explaining 38.2-76.4% of total morphological variance for each species (Table 3.2). I found that environmental PC1 was correlated with morphological PC1 for *A. bimaculatus* ($F_{2,24}$ = 2.93, R^2 = 0.197, P = 0.025) and *A. lividus* ($F_{2,34}$ = 5.37, R^2 = 0.240, P = 0.002) (Table 3.2, Fig 3.3). I recovered an association between environmental PC2 and *A. oculatus* morphological PC3 ($F_{2,24}$ = 5.49, R^2 = 0.257, P = 0.005) and *A. leachii* morphological PC4 ($F_{2,12}$ = 3.83, R^2 = 0.288, P = 0.018) (Table 3.2, Fig 3.3). In all other species, morphological PCs were not correlated with environmental PCs (all P > 0.05).

Results from MMRR analyses were mostly congruent with PC analyses. My MMRR models had no significant predictors for *A. gingivinus, A. leachii, A. marmoratus, A. sabanus, A. schwartzi,* and *A. wattsi* (all P > 0.05) suggesting a lack of both morphological IBD and IBE in these species. However, a MMRR model of only environmental PC2 trended toward significance for *A. leachii* (F = 15.13, R^2 = 0.128, P = 0.056). I recovered a signal of phenotypic IBE due to

environmental PC1, but not IBD, for *A. lividus* (F = 65.37, r^2 = 0.090, *P* = 0.036) (Table 3.3). For *A. oculatus*, the best-fit, MMRR recovered the effect of geographic distance and environmental PC2 (F = 20.19, r^2 = 0.104, *P* = 0.014). Finally, MMRR showed effects of geographic distance and environmental PC1 on phenotypic distance for *A. bimaculatus* (F = 33.39, r^2 = 0.161, *P* = 0.028) (Table 3.3).

Discussion

I found mixed support for parallel phenotypic responses to environment across *bimaculatus* series anoles. Coloration exhibited a strong signal of parallelism in response to habitat as predicted. Comparatively, I did not recover consistent signals of parallel morphological evolution associated with environment. Although four out of nine species exhibited a signal of overall morphological covariation with environment, the specific traits involved and the directionality of their associations were idiosyncratic. Thus, I contend that color is under strong and consistent local selection both within and across species, whereas morphology is not.

Parallel patterns of color variation

The only trait that consistently covaried with the environment was coloration (Table 3.1). Specifically, individuals from hotter, drier regions were yellower in all study species except *A. bimaculatus* (Fig 3.4). Individuals from xeric populations were also generally brighter except in the case of *A. gingivinus,* in which mesic populations were brighter. Comparable color divergence across a range of taxa has been linked to differences in either thermal performance (Forsman 2000; Clusella Trullas et al. 2007) or background matching driven by predator avoidance (Hargeby et al. 2005; Niu et al. 2017; Barrett et al. 2019). Whether color divergence between xeric and mesic populations in Lesser Antillean anoles is driven by thermal physiology or predator avoidance is unclear because habitat is consistently correlated with climate across islands. However, my MMRR results suggest that temperature and precipitation are the primary correlates of color differentiation, which is consistent with a thermoregulatory role (Table 3.1). Nevertheless, these hypotheses are not necessarily mutually exclusive, particularly because different aspects of coloration can affect thermal performance and camouflage (Smith et al. 2016; Stuart-Fox et al. 2017; Kraemer et al. 2019). Performance studies of color morphs, as well as physiological and predator optical modeling, would help disentangle selective pressures leading to this parallel divergence in coloration along xeric-mesic gradients.

Alternatively, differences in color may reflect neutral divergence and underlying population genetic structure. Color differences have traditionally been used to denote subspecies in Lesser Antillean anoles (Lazell 1972). However, all existing studies contradict the population structure hypothesis. Previous work has shown that color phenotypes are not associated with genetic structure in at least two *bimaculatus* series species: *A. oculatus* (Malhotra and Thorpe 2000; Stenson et al. 2002) and *A. marmoratus* (Muñoz et al. 2013). Additionally, color divergence does not map onto phylogeographic structure in any *roquet* series species (Thorpe et al. 2015). Instead, environmentally structured color polymorphism persists despite high levels of historical and contemporary gene flow in all previously studied species (Malhotra and Thorpe 2000; Stenson et al. 2002; Muñoz et al. 2013). Thus, although I do not have genetic data for all of my

study species, I propose that repeated color divergence is best explained by ecological selection with gene flow.

Idiosyncratic patterns of morphological variation

I did not recover evidence for parallel local adaptation in morphology across *bimaculatus* series anoles. Four species did show morphological covariation with environment, although no morphological traits covaried consistently with environment or geographic distance (Table 3.2, Fig 3.3). When morphological traits were correlated with environmental variation among populations of a given species, the directionality of that correlation sometimes matched predictions from functional studies. For example, I found that traits associated with clinging performance (e.g. claw curvature, lamella number, and hindlimb length) shifted predictably in *A. lividus* that occupy more densely vegetated habitats (Macrini et al. 2003; Crandell et al. 2014; Yuan et al. 2019) (Fig 3.3). Many of these traits are known to be at least partly genetically determined in anoles (Thorpe et al. 2005). Thus, several traits may be locally adapted in specific species, but not broadly throughout the clade. Still, other traits exhibited opposing patterns of covariation with environmental variables between species and several species showed no detectable pattern in morphology. For example, *A. bimaculatus* limb length was greater in rainforests despite longer limbs being associated with poorer climbing performance in anoles (Losos 1990b). Lack of local adaptation in morphology does not appear to be correlated with overall environmental variance because it occurs in species on both larger, more heterogeneous islands (e.g. Guadeloupe) and smaller, more homogeneous islands (e.g. Saba and the St. Martin Bank) (Fig 3.3). It is possible that I could not detect a signal of environmental correlation on smaller islands due to environmental layers not adequately capturing fine scale heterogeneity. However, I did recover evidence of local color adaptation on smaller islands such as *A. gingivinus* on St. Martin indicating adequate resolution of environmental data.

Idiosyncratic morphological responses to environment may be due to many-to-one functional mapping allowing some traits to be locally adapted in the absence of the predicted pattern in other related traits (Wainwright et al. 2005). That is, because selection acts on whole organism performance, similar performance gains may be realized through adaptive shifts in different subsets of functionally related traits. This may explain opposing patterns of variation across some traits in species that exhibit a signal of morphological covariation with environment overall. However, this mechanism is unlikely to explain why several species exhibited no signal of covariation between their morphology and environment.

A macroevolutionary study of anoles found that historical climate shifts rather than current environmental variables drove body size evolution across the wider clade (Velasco et al. 2020). Therefore, the morphology of species that exhibited no relationship with current climate may instead reflect historical climatic conditions. Yet, anoles are also capable of rapid phenotypic evolution in response to climatic events (Campbell-Staton et al. 2017; Donihue et al. 2018; Dufour et al. 2019). Studies of environmental stability through time could provide further insight into the forces that shaped observed patterns of phenotypic variation.

Finally, the strength of environmental selection may also vary across species. Weaker local selection produces weaker performance trade-offs across the range, thereby potentially favoring

the generation of generalist phenotypes. Weak selection can also allow otherwise maladaptive traits to persist through gene flow (García-Ramos and Kirkpatrick 1997; Rolshausen et al. 2015). Relatively strong selection is probably necessary to maintain local phenotypic differences in the face of high levels of observed gene flow within small islands (Stenson et al. 2002; Muñoz et al. 2013). Further functional studies are required to differentiate between these hypotheses.

Comparison with the distantly-related roquet clade

My data support broad convergence in color, but not morphology, between the distantly related *roquet* and *bimaculatus* series anoles. Still, other than *A. lividus* and the previously studied *A. marmoratus* (Thorpe et al. 2015), my study species did not exhibit the color extremes observed in the *roquet* series. Nevertheless, these differences in color are consistent in directionality with those observed between xeric and mesic populations across species in the distantly-related *roquet* series (Thorpe et al. 2015). Thus, we demonstrate dorsal coloration is locally-tuned across most species of Lesser Antillean anoles regardless of clade. The lack of parallel within radiation divergence in morphology for the *bimaculatus* series (Fig 3.3) suggests that selection across xeric-mesic gradients is either stronger and more consistent for color or morphological evolution is more constrained in the *bimaculatus* series.

Interspecific morphological variation is more predictably partitioned in *bimaculatus* series than *roquet* series anoles. For example, at the species level, variation in claw and toepad morphology is predicted by average island vegetation and structural habitat use for the *bimaculatus* series, but not the *roquet* series (Yuan et al. 2020b). We observed the converse at the intraspecific level, where only the *roquet* series showed predictable population-level divergence across habitats. The reason that morphological partitioning does not extend from the intraspecific to the interspecific level in Lesser Antillean anoles is unclear. However, this may suggest that functional morphology across the *bimaculatus* series is indeed tuned to species-wide generalist phenotypes rather than locally adapted. Interspecific patterns may also have been obscured by locally adapted intraspecific variation in the *roquet* series.

Conclusion

In summary, the pattern of parallel evolution is weaker in the *A. bimaculatus* series compared to that observed in the *A. roquet* series. Unlike the *A. roquet* series, no morphological traits consistently covaried with environment across the *A. bimaculatus* series (Table 3.2). Furthermore, in five out of nine *bimaculatus* series species I detected no signature of covariation between morphology and the environment consistent with selection for broadly generalist phenotypes rather than localized specialization. Nevertheless, my results demonstrate that a single trait, dorsal coloration, exhibits remarkable parallel intraspecific divergence associated with climate across two distantly-related clades.

Fig 3.1 Elevation map of the Leeward Islands and species included in this study. Island banks with shared species are labelled as a group: St. Kitts Bank (St. Eustatius, St. Kitts, and Nevis) and St. Maarten Bank (St. Martin, St. Barthelemy, and Anguilla).
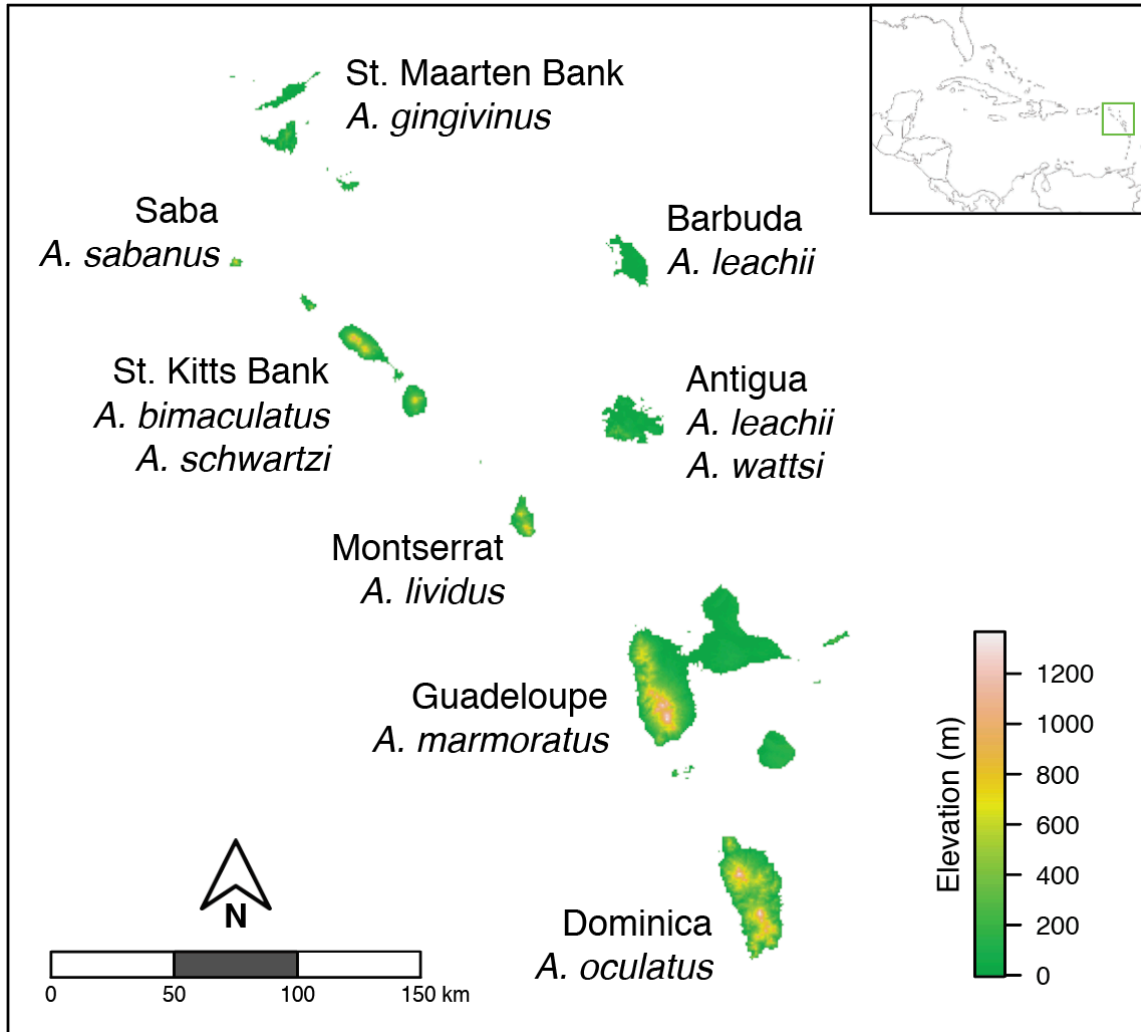
Fig 3.2 (A-B) Violin plots including mean and standard deviation of environmental PC1 (temperature and precipitation) and PC2 (seasonality) for each sampled island. Island banks with shared species are grouped together: Antigua Bank (Antigua and Barbuda), St. Kitts Bank (St. Eustatius, St. Kitts, and Nevis), and St. Maarten Bank (St. Martin, St. Barthelemy, and Anguilla). Martinique and Grenada from the *roquet* series are shown for comparison. Although climatic variance differs between island banks, all islands contain both xeric scrub and rainforest habitats. Island banks showing morphology-environment covariation for at least one species are denoted by diamonds and color-environment covariation by circles. We did not collect color data for species on either Saba or the Antigua Bank. Evidence for covariation on Guadeloupe (color), Martinique, and Grenada (color and morphology) is based on Thorpe et al. (2015). (C-F) Dot plots of locality sampling for four species superimposed on violin plots of range-wide environmental PC1.
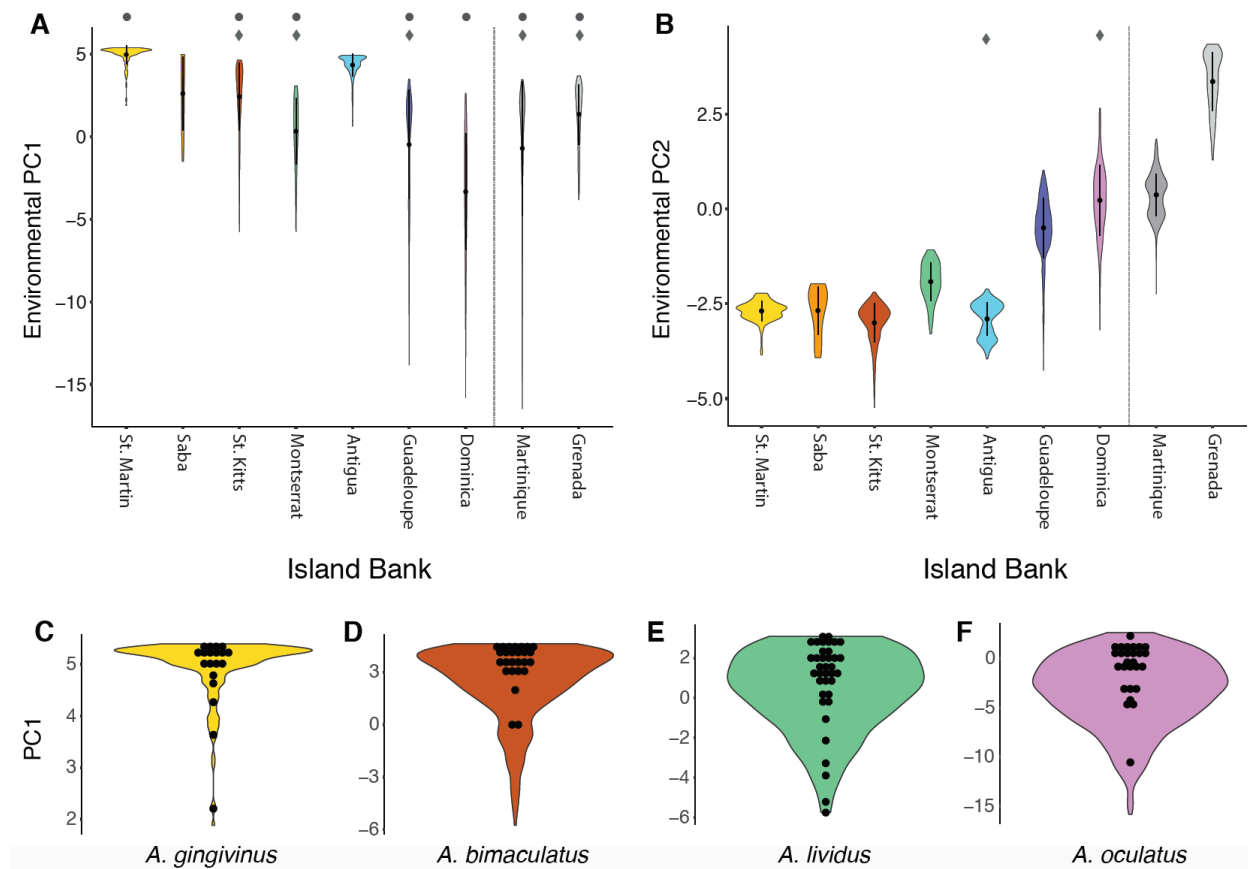
Fig 3.3 Summary of morphological covariation with either environmental PC1 (temperature and precipitation) or PC2 (seasonality and EVI). Predicted covariation with PC1 based on *roquet* series anoles from Thorpe et al. (2015). For PC1, blue cells denote positive correlation with precipitation and negative with temperature. For PC2, blue cells denote positive correlation with seasonality and EVI. In all cases, yellow cells denote the opposite correlation and grey no correlation. °marginally significant relationship with body size, $0.10 < P < 0.05$.
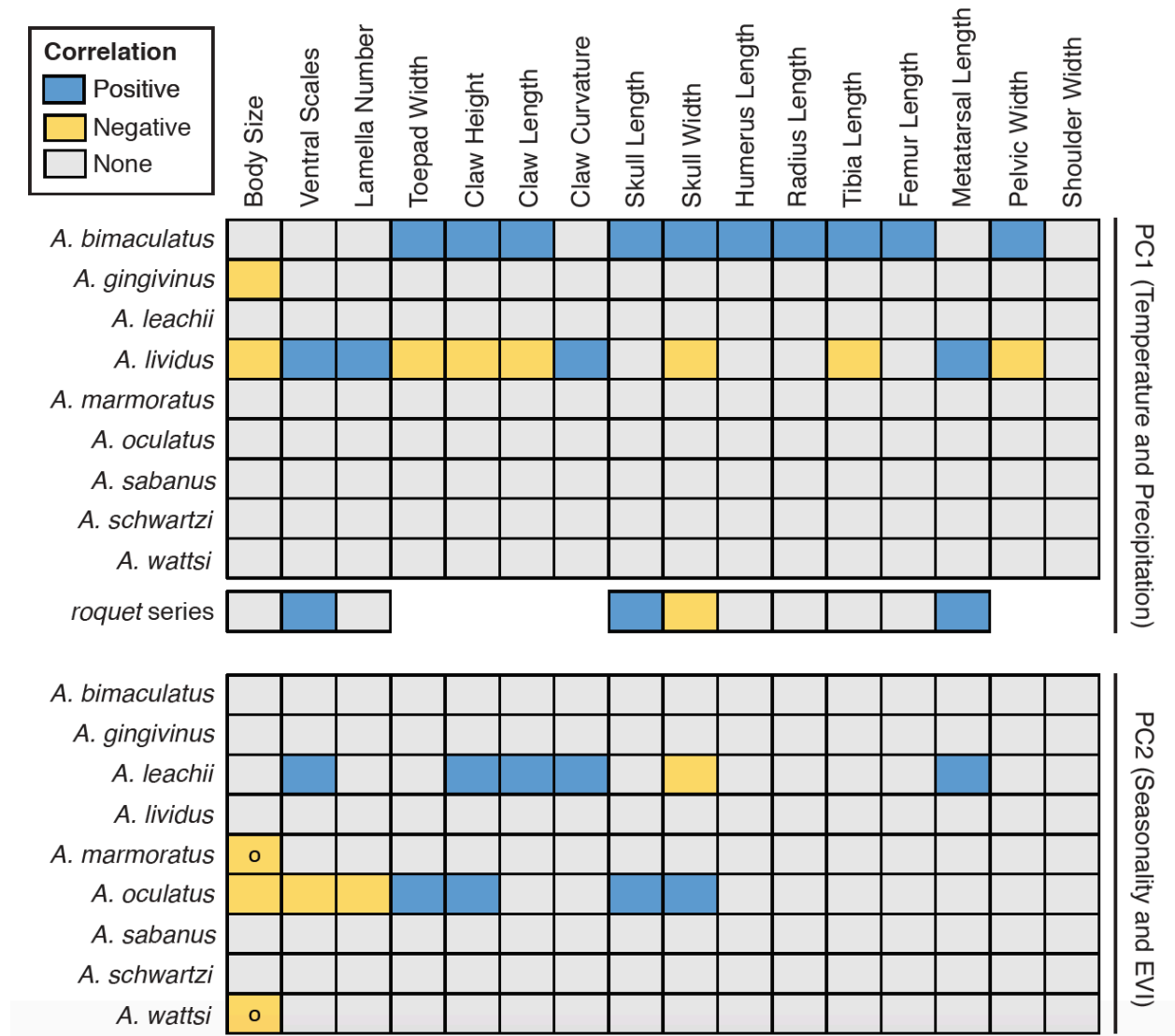
Fig 3.4 First two principal components of chromatic values for the five species in this study. Points are colored by mean annual temperature (BIO1) of sampling locality. Representative dorsal head photographs collected from three sites are shown for *A. lividus*.
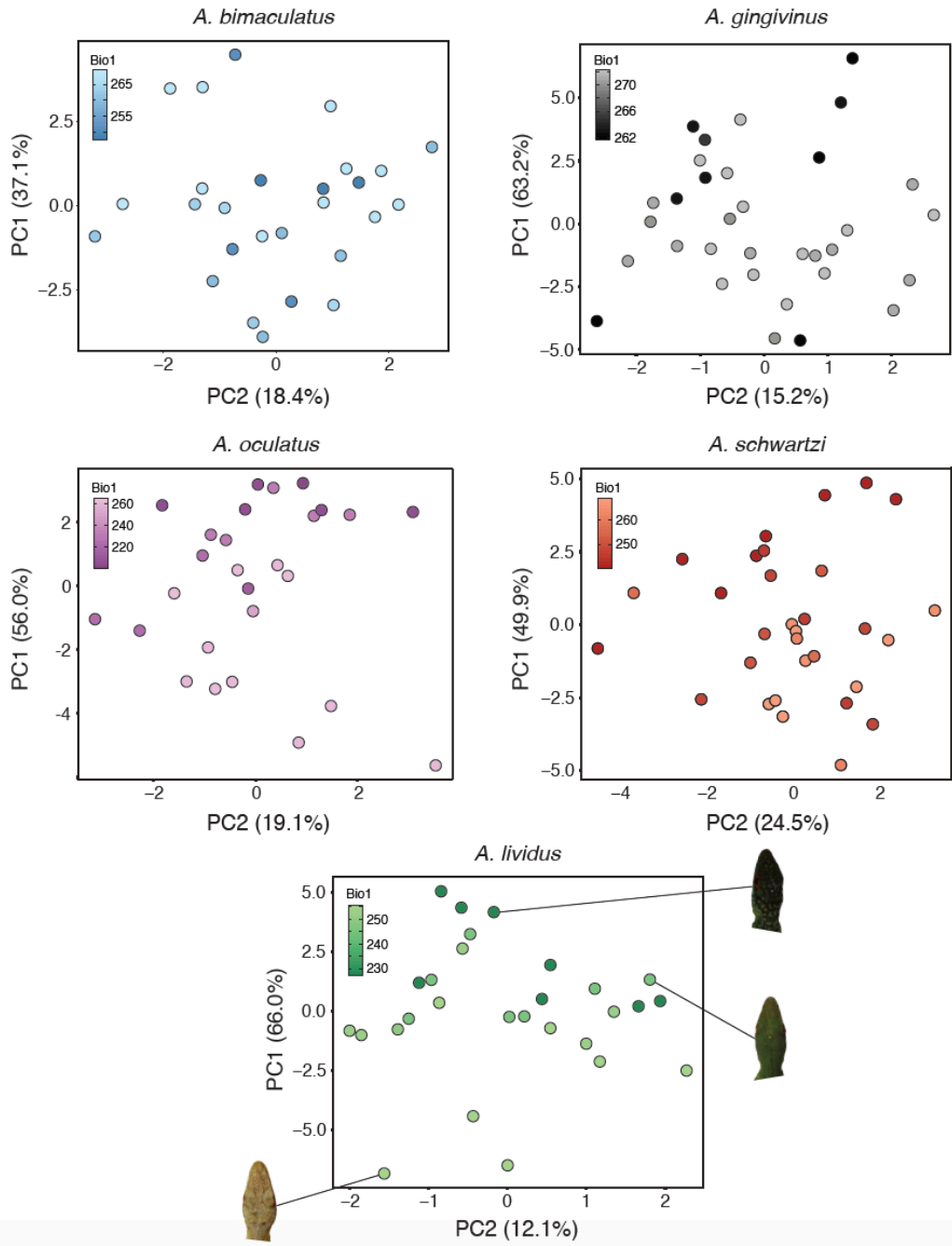
Table 3.1 Results of MMRR analyses testing for correlations between dorsal color distance and geographic and environmental distances in (I) *A. lividus,* (II) *A. oculatus,* (III) *A. bimaculatus,* (IV) *A. schwartzi,* and (V) *A. gingivinus.* In each test, we used dorsal color earth mover's distance as the response variable. Only the final models with predictor variables retained following a backward elimination procedure are shown. For each model, model significance and variance explained (r^2) are denoted along with individual coefficients and *P*-values for each retained predictor variables.

I. *A. lividus* (r^2 = 0.176, *P* < 0.001)		
	Coefficient	*P*
PC1	0.268	0.005
PC2	0.296	0.007
II. *A. oculatus* (r^2 = 0.074, *P* < 0.001)		
	Coefficient	*P*
PC1	0.271	< 0.001
III. *A. bimaculatus* (r^2 = 0.028, *P* = 0.056)		
	Coefficient	*P*
PC2	0.168	0.056
IV. *A. schwartzi* (r^2 = 0.176, *P* < 0.001)		
	Coefficient	*P*
Geography	-0.106	0.043
PC1	0.409	< 0.001
V. *A. gingivinus* (r^2 = 0.150, *P* < 0.001)		
	Coefficient	*P*
PC1	0.387	< 0.001

Table 3.2 Loadings for morphological PCA with percent variation explained. Only retained morphological PCs found to be significantly correlated with environmental variation are shown.

	A. bimaculatus PC1 (33.4%)	*A. leachii* PC4 (12.6%)	*A. lividus* PC1 (24.8%)	*A. oculatus* PC3 (11.8%)
Claw curvature	-0.045	0.323	-0.214	0.004
Claw length	-0.311	0.519	0.290	-0.086
Claw height	-0.298	0.516	0.303	-0.242
Toepad width	-0.290	-0.088	0.351	-0.377
Lamellae number	-0.136	-0.145	-0.210	0.479
Skull width	-0.276	-0.221	0.338	-0.345
Skull length	-0.346	0.016	-0.087	-0.275
Shoulder length	0.090	-0.076	-0.192	0.131
Pelvic Width	-0.344	-0.149	0.378	-0.021
Humerus length	-0.338	-0.001	0.035	0.057
Radius length	-0.239	0.037	-0.086	0.040
Femur length	-0.237	-0.140	-0.067	0.141
Tibia length	-0.352	-0.120	0.348	0.137
4th metatarsal length	-0.140	0.250	-0.246	0.090
Ventral scale number	0.125	0.394	-0.338	0.546

Table 3.3 Results for significant MMRR analyses of (I) *A. lividus,* (II) *A. oculatus,* and (III) *A. bimaculatus* using morphological distance as the response variable. Only the final model with predictor variables retained following a backward elimination procedure are shown. For each model, model significance and variance explained (r^2) are denoted. Additionally, coefficients and *P*-values for individual retained variables are shown.

I. *A. lividus* ($r^2 = 0.090$, *P* = 0.036)		
	Coefficient	*P*
PC1	0.299	0.036
II. *A. oculatus* ($r^2 = 0.104$, *P* = 0.014)		
	Coefficient	*P*
Geography	0.263	0.009
PC2	0.322	0.016
III. *A. bimaculatus* ($r^2 = 0.161$, *P* = 0.028)		
	Coefficient	*P*
Geography	0.147	0.026
PC1	0.358	0.042

CHAPTER IV

The island biogeography of interspecific and intraspecific diversity in Lesser Antillean herpetofauna

Abstract

Species diversity of islands are a product of colonization and extinction. Theoretically, these processes have genetic corollaries in gene flow and genetic drift. For example, both colonization and gene flow should be dependent on distance to the mainland and extinction and genetic drift should both be dependent on island size. Thus, these processes should generate species-genetic diversity correlations (SGDCs). Additionally, similar processes may also drive the evolution of another aspect of biological diversity on islands, the phenotype. Yet, studies of SGDCs have not been extended to the study of phenotypes. Here, I test whether species, genetic, and phenotypic diversity are correlated with the same island characteristics. Specifically, I examined diversity across both introduced and native Lesser Antillean amphibians and reptiles. I found a positive relationship between island size and both species and genetic diversity. The pattern was consistent between native and introduced species and between amphibians and reptiles. Thus, my results support the broad generalizability of island area as a driver of multiple levels of biological organization. Beyond island area, factors driving both species and genetic diversity differed between taxa. Finally, I found that phenotypic diversity was decoupled from island variables driving species and genetic diversity suggesting different macroecological forces generate or constrain phenotypic variation.

Introduction

Classic island biogeography posits that species richness is a product of colonization (as a function of distance to the mainland) and extinction (as a function of island size) (MacArthur and Wilson 1967). Theoretically, these factors could also influence intraspecific variation (Vellend 2003). Immigration should introduce new genetic variation to island populations in the short-term, and homogenize island and mainland populations in the long-term. The process of loss and fixation through genetic drift is also potentially analogous to extinction in cases where population size correlates with island size. Thus, these parallel processes driving interspecific and intraspecific variation have been proposed to drive the phenomenon of species-genetic diversity correlations (SGDCs) (Vellend 2003, 2005; Vellend and Geber 2005). However, the generality and directionality of species-genetic diversity relationships has been debated (Taberlet et al. 2012; McGlaughlin et al. 2014; Laroche et al. 2015; Lamy et al. 2017). For example, models incorporating high mutation rates predict negative SGDCs (Laroche et al. 2015). We can also imagine that in systems with high levels of endemism external gene flow should be eliminated potentially decoupling species-genetic diversity relationships for endemic species. Additionally, studies of SGDCs have long neglected an important component of biological diversity, the phenotype. Though being generated through an interaction between genotype and the environment, quantitative phenotypic diversity *per se* may not lend itself neatly to classical island biogeography.

Extensions on classic island biogeography have incorporated other aspects of islands in explaining species diversity such as those that promote *in situ* diversification (Losos and Schluter 2000). For example, prominent proposed underlying causes of the species-area relationship include habitat (Ricklefs and Lovette 1999; Fox and Fox 2000; Báldi 2008; Kallimanis et al. 2008), climatic (Dewar and Richard 2007; Ohlemüller et al. 2008), and topographic variation (Hortal et al. 2009; Steinbauer et al. 2012; Irl et al. 2015), though these island characteristics are often correlated. However, the relative effects of island environmental characteristics differ across groups and are often tied to specific differences in natural history (e.g. dispersal capabilities, specialization, population density, etc.) (Ricklefs and Lovette 1999). Such island characteristics should increase diversification if they promote local adaptation or otherwise act as barriers to gene flow, although environmental variation may also facilitate species diversity simply through colonization by expanding ecological niche availability (Kallimanis et al. 2008). These mechanisms should also generate intraspecific genetic diversity separately from any external immigration based processes. Similarly, overall phenotypic variation may be constrained or relaxed depending on the strength of natural selection (Scharloo et al. 1967). Indeed, environmental variation should act on phenotypes upstream of any genetic consequences. Partitioning the factors which influence diversification at the species and population levels can provide insight into their similarities and differences.

The Lesser Antilles is a classic system for the study of island biogeography (Ricklefs and Lovette 1999). The region is characterized by a volcanic island arc which formed at the Lesser Antilles subduction zone. Thus, the entirety of the Lesser Antilles is comprised by oceanic islands and has never been connected to the adjacent landmasses. Lesser Antillean communities were originally formed by overseas colonization from either the Greater Antilles or South America and exhibit high levels of endemism (Censky and Kaiser 1999). Here, I examined the

relationship between island characteristics (i.e. island area, distance to mainland, and habitat, climatic, and topographic variation) and species, phenotypic, and genetic diversity in both native and introduced communities of amphibians and reptiles. Specifically, I tested the relative effects of island characteristics and if similar island variables influenced diversity across levels of biological organization.

Methods

Environmental and Species Richness Data

I collected data for 25 islands in the Lesser Antilles ranging in size from 0.05 km^2 (Little Scrub) to 1630 km^2 (Guadeloupe; Fig 4.1, Table 4.1). My sampling includes every island in the Lesser Antilles inhabited by at least one endemic amphibian or reptile. I excluded all other islands. For each island, I determined total amphibian and reptile species richness, total island area, geographic distance to the mainland, topographic complexity, and climatic and habitat variation. I treated the small archipelago of Îles des Saintes, compromised of eight satellite islets of Guadeloupe, as single island for the purposes of my analyses due to its shared fauna and geologic history (Vaurie 1961; Thorpe et al. 2008a). To generate species lists of amphibians and reptiles, I compiled species accounts from the CaribHerp database as of 11 September 2019 (http://www.caribherp.org) (Table 4.2). I verified the CaribHerp data against literature, field guides, and local government checklists where possible. I downloaded island-wide climatic data from the WorldClim 2 dataset at 1km resolution (Fick and Hijmans 2017). I performed raster PCA using all bioclimatic variables to assess patterns of covariation throughout the Lesser Antilles. Overall variation (84.2%) primarily consisted of two principal components. I selected two representative variables for analyses based on highest loadings for the first two PCs: mean annual temperature (BIO1) and isothermality (BIO3). For each retained bioclimatic variable, I calculated island-wide coefficients of variation. I compiled the inverse Simpson's index of habitat types reported by (Ricklefs and Lovette 1999) as a proxy for habitat variation. Ricklefs and Lovette (1999) did not calculate values for all islands included in this study due to a lack of comparable vegetation maps for the smaller (<10km^2) islands. Finally, I determined topographic complexity by calculating the standard deviation of slope (SD$_{slope}$) from 90m resolution Shuttle Radar Topography Mission digital elevation models. Standard deviation of slope was used a proxy for surface ruggedness because its performance is relatively robust to scale (Grohmann et al. 2011).

Phenotypic and Genetic Data

I assessed intraspecific diversity using the radiations of *Anolis* lizards and *Sphaerodactylus* geckos. Across the Lesser Antilles, both of these genera display high levels of endemism, are generally ubiquitous throughout islands where they occur, and are present on most (*Sphaerodactylus*) or all (*Anolis*) study islands. These genera have also been subject to extensive study allowing for access to comparative genetic and phenotypic datasets (Stenson et al. 2004; Thorpe et al. 2008a; Surget-Groba and Thorpe 2012; Thorpe et al. 2015; Martin et al. 2015; Vuillaume et al. 2015; Yuan et al. 2020a,b). To study if results extend to introduced species, I

also collected *Eleutherodactylus johnstonei*, a frog native to Montserrat but widely introduced throughout the Lesser Antilles (Kaiser 1997).

To assess phenotypic diversity, I analyzed two previously published *Anolis* morphological datasets. First, I downloaded the dataset of Yuan et al. (2020b) comprised of six traits (snout-vent length, toepad width, lamella number, and claw height, width, and curvature) for 254 adult males from 20 species inhabiting 20 islands. Claw and toepad traits have demonstrated locomotor function in *Anolis* lizards associated with structural habitat variation (Losos 1990b; Zani 2000; Crandell et al. 2014; Yuan et al. 2019). Second, I assessed a broader morphological dataset for 16 traits (snout-vent length, ventral scale number, femur length, tibia length, radius length, humerus length, 4th metatarsal length, skull width, skull length, shoulder width, pelvic girdle width, toepad width, lamella number, and claw height, width, and curvature) across 883 adult males and nine species inhabiting 15 of my sampled islands (Chapter III). Due to differences in the species and traits examined resulting in only partially overlapping sampling, I analyzed each data set separately. For each dataset, I calculated overall morphological disparity, or the Procrustes variance in multivariate trait space, for each species-island combination using the 'morphol.disparity' function in *geomorph* (Adams and Otárola-Castillo 2013). Although this function was built for geometric morphometric landmark data, morphological disparity can be calculated for any scaled multivariate data by assuming each trait represents a point in morphospace rather than landmark coordinates.

For the genetic dataset, I compiled *cytochrome b* mitochondrial sequence data for all three groups using both tissues collected from the field between 2018-2020 (N = 385) and publicly available sequences from Genbank (N = 624). In total, I collected sequences for 485 *Anolis,* 238 *Sphaerodactylus*, and 164 *E. johnstonei* (Appendix IV). For field collected tissues, I extracted whole genomic DNA from either tail, toe, or liver preserved in RNAlater using GeneJet DNA extraction kits (Thermo Scientific). I PCR-amplified cytochrome b using previously published primers for each species (Thorpe et al. 2008b; Surget-Groba and Thorpe 2012) and primer specific annealing temperatures (Table 4.3). In brief, I performed PCRs using 2 min initial denaturing at 94°C, followed by 35 cycles of 30s denaturing at 94°C, 30s annealing at primer specific temperature, 30s extension at 72°C, and then 5min final extension at 72°C. All reactions consisted of 1X standard *Taq* reaction buffer (NEB), 1.5mM MgCl2, 0.2mM dNTPs, 0.2μM of each primer, and 0.625U *Taq* polymerase (NEB). Following PCR, I purified amplicons using ExoSAP-IT (USB), performed cycle sequencing reactions using Big Dye v3.1 sequencing chemistry (Applied Biosystems), and sequenced Sephadex™ G-50 cleaned products on an ABI Automated 3730xl DNA Analyzer (Applied Biosystems). I then aligned all sequences using the MUSCLE algorithm (Edgar 2004) in AliView (Larsson 2014). Finally, to determine genetic diversity, I calculated nucleotide diversity (π) (Nei 1987) for each island-species combination using the *pegas* package in R (Paradis 2010).

Clade Origins

I inferred the origin of each native Lesser Antillean clade as either Greater Antillean or South American based upon available phylogenetic studies (Bergmann and Russell 2007; Heinicke et al. 2007; Camargo et al. 2009; Fenwick et al. 2009; Hedges et al. 2009; Gamble et al. 2014; Tucker et al. 2017; Thorpe et al. 2018). There are no known or hypothesized colonization routes

outside of the Greater Antilles and South America among Lesser Antillean herpetofauna. I assigned clade origins based upon the geographic distribution of their extant sister clade. For species with distributions outside the Lesser Antilles, I assigned origins based upon their non-Lesser Antillean range. Although the faunas of the Greater Antilles and the South American mainland are largely distinct, this method does not account for potential extinction. Nor do I distinguish the directionality of colonization (i.e. originating in the Lesser Antilles). However, both the Greater Antilles and South American mainland are orders of magnitude older land masses than the Lesser Antilles and cases of mainland back colonization are rare. Despite these limitation, these data can examine the relative contributions to Lesser Antillean fauna at a coarse level.

Data Analyses

I analyzed species richness for introduced and native amphibians and reptiles separately. Island area was natural log-transformed for all analyses. I then assessed the relative roles of island area, distance to the mainland, topographic complexity, and environmental variation across levels of diversity using generalized linear models (GLMs). To examine the influence of island characteristics on species richness, I fit GLMs with a quasi-Poisson distribution. I fit GLMs with a quasibinomial distribution for genetic diversity and a Gaussian distribution for phenotypic variance. For all models, I implemented a backwards variable selection procedure beginning with all predictors and removing the highest p-value predictors until only significant variables remain. To assess the proportion of variance explained by my final models, I calculated D^2, the amount of deviance explained (Guisan and Zimmermann 2000). Finally, I examined the relative contributions of the Greater Antilles and South America to the Lesser Antillean communities. I fit GLMs with a quasibinomial distribution to the proportion of Lesser Antillean communities assigned to each source fauna using distance to source as a predictor variable.

Results

Island area was positively correlated with habitat variation ($P = 0.019$), as well as the coefficients of variation for BIO1 and BIO3 (all $P < 0.001$). Thus, I corrected these variables for island area in downstream analyses. Island size did not correlate with SD_{slope} or distance to mainland (all $P > 0.05$). In all cases, island area was a significant predictor of species diversity (all $P < 0.05$; Table 4.4). Indeed, island area was the only variable retained for both introduced amphibian and reptiles richness. However, relative habitat diversity and variation in mean annual temperature were also associated with native reptile richness (habitat: $P < 0.001$; BIO1: $P = 0.026$) and SD_{slope} was associated with native amphibian diversity ($P = 0.028$). Similar to species diversity, genetic diversity was positively associated with island area for all datasets (all $P < 0.05$; Table 4.5). As with amphibian species diversity, genetic diversity in introduced *E. johnstonei* was also associated with SD_{slope} ($P = 0.006$). Although the genetic diversity of introduced populations (range = 0-0.0016, $\bar{\pi} = 0.0009$) was lower than the native Montserrat population ($\pi = 0.0105$). For *Anolis* and *Sphaerodactylus* lizard genetic diversity, only island area was retained. Phenotypic variance was not associated with any tested variables for both datasets (all P > 0.05). Finally, I found that the proportion of species inferred to have colonized from the Greater Antilles (Null Deviance = 9.78, Residual Deviance = 3.26, $D^2 = 0.666$, $P <$

0.001) and South America (Null Deviance = 9.78, Residual Deviance = 1.59, D^2 = 0.837, P < 0.001) was negatively correlated with distance from the respective source (Fig 4.1).

Discussion

My results are broadly consistent with previous studies that have demonstrated the species-area relationships across a wide variety taxonomic groups (MacArthur and Wilson 1967; Ricklefs and Lovette 1999; Losos and Schluter 2000; Russell et al. 2004; Valente et al. 2020). However, relationships between species richness and other island characteristics such as habitat variation differed across groups. Additionally, I found evidence for positive genetic diversity-area relationships in both native reptiles and an introduced amphibian indicating a broad influence of island area. Nevertheless, different island characteristics also appear to influence diversity at the interspecific and intraspecific level. Tested island variables did not correlate with intraspecific phenotypic diversity, suggesting a decoupling between the macroecology of phenotypic variation and both species and genetic diversity. Yet, phenotypic variance was strongly associated with genetic diversity despite a lack of parallel ecological correlates.

Species Diversity

Previous work which recovered an effect of area, elevation, and habitat on Lesser Antillean species richness grouped herpetofauna together (Ricklefs and Lovette 1999). However, my results suggest that amphibians and reptiles respond differently to island characteristics. Although both exhibit species-area relationships, native reptile diversity was predicted by habitat and climatic variation, whereas native amphibian diversity was predicted by topographic variation. Perhaps unsurprising given differences in natural history, patterns may be confounded by grouping disparate groups together.

Differences in drivers of species diversity across groups may be explained by mechanisms of community assembly. *In situ* diversification within *Eleutherodactylus* plays a major role in generating native amphibian across the Lesser Antilles representing over half the total amphibian diversity in the region. Additionally, total successful colonization events were likely substantially lower for amphibians than reptiles. Only four extant genera of amphibians are represented compared to 31 extant reptile genera. Phylogeographic studies support divergence along elevation gradients as the primary driver of *in situ* diversification in *Eleutherodactylus* frogs (Kaiser et al. 1994a,b; Kaiser 1996; Breuil 2002). My data are concordant with these studies as SD_{slope} was a significant predictor of native amphibian richness (Table 4.4). Conversely, there is limited evidence that *in situ* diversification was a major driver of reptile diversity in the Lesser Antilles. Rather, divergence in reptiles appears to have been primarily driven by isolation between islands (Thorpe et al. 2008b, 2018; Surget-Groba and Thorpe 2012; Martin et al. 2015; Tucker et al. 2017). Further, broad-ranging anole species do not exhibit reduced gene flow across habitat or elevational gradients in the Lesser Antilles (Thorpe and Stenson 2003; Stenson et al. 2004; Muñoz et al. 2013; Thorpe et al. 2015). Thus, the role of habitat in reptile community assembly is likely because it provided greater niche availability for colonizing species rather than promotion of speciation. My data supports findings that despite the

generalizable effects of island area, secondary correlates of species diversity vary between taxonomic groups (Ricklefs and Lovette 1999).

My data confirm the generalizability of the species-area relationship to introduced communities (Russell et al. 2004; Blackburn et al. 2008; Long et al. 2009) (Fig 4.2). Although species-area relationships are strong, I found no evidence for isolation as a driver of introduced species diversity. Evidence that geographic isolation is important in introduced communities is mixed (Blackburn et al. 2008; Long et al. 2009). Given the anthropogenic origins of introduced species, the effects of geographic distance should only occur when related to anthropogenic island connectivity. Thus, the lack of influence of distance to mainland is consistent with the Lesser Antilles' extensive anthropogenic interconnection dating back to 5800-2500 years BP (Napolitano et al. 2019; Nägele et al. 2020). Additionally, native species do not exhibit species-geographic isolation relationships. In the case of native species, I may not have detected an effect of distance to the mainland because diversification within the Lesser Antilles and colonization from the Greater Antilles dilutes mainland colonization. Indeed, the proportion of island communities derived from either the Greater Antilles and the South American mainland is proportional to the distance from each putative source (Fig 4.1). Only island area predicts the total number of introduced species suggesting that available geographic rather than ecological space makes islands more susceptible to invasion. My results suggest that in early phases of island colonization island area *per se* dominates. However, I did not account for anthropogenic activity, which is often predictive of introduced species richness (Russell et al. 2004; Blackburn et al. 2008). Data from native species also suggest that different dynamics begin to contribute to species diversity over evolutionary time.

Genetic Diversity

Similarly to species diversity, I recovered island area as a predictor of genetic diversity for all datasets suggesting parallel processes may influence biodiversity at multiple levels. In general, the species examined here are widely distributed throughout their native or introduced islands, thus island area should represent a reasonable proxy for the total area exploited by each species. Although some *Sphaerodactylus* species such as *S. fantasticus* on Dominica have restricted ranges, they represent a minor component of overall *Sphaerodactylus* diversity. Population size is also likely to be correlated with island area. Thus, genetic diversity may be linked to island area only insofar as larger islands have larger carrying capacities. However, I cannot disentangle these factors as population size data for most study species are lacking. Testing for differences in patterns of genetic diversity between broad-ranging low density and geographically-restricted high density populations may provide further insight into the influence of population size and area *per se.*

Beyond island area, I did not recover additional island characters as drivers of native reptile genetic diversity. Predictably, island distance to mainland was not associated with genetic diversity. Amphibians and reptiles exhibit a high degree of endemism across the Lesser Antilles (88% of amphibians and 93% of reptiles), which likely decouples genetic diversity from island isolation because most species cannot experience external gene flow. Although habitat and climatic variables accounted for native reptile species diversity, they did not affect the genetic diversity of *Anolis* and *Sphaerodactylus.* Although these groups both exhibit phenotypic

variation throughout their ranges associated with environmental variables (Muñoz et al. 2013; Thorpe et al. 2015; Yuan et al. 2020b) (see Chapter III), these do not generally correlate with underlying genetic structure (Thorpe and Stenson 2003; Stenson et al. 2004; Thorpe et al. 2008a). Rather, the lack of strong population genetic structure in these groups suggests environmental variation does not drive genetic differentiation despite its role in reptile species diversity. This further supports the hypotheses that the role of habitat and climatic variation in reptile species diversity is the promotion of colonization through greater niche availability rather than *in situ* divergence.

Phenotypic Diversity

My results suggest that overall phenotypic diversity is decoupled from macroecological drivers of species and genetic diversity. However, phenotypic diversity for a suite of integrated traits demonstrated to associate with habitat use (Yuan et al. 2019, 2020b) did tend toward significance with island area. I did not infer any measured habitat, climatic, or topographic variable to be associated with phenotypic diversity. Yet, individual phenotypic traits have been shown to be associated with some of these variables (Thorpe et al. 2015) (see Chapter III). It is possible that these single-trait, within island associations do not extend to indices of overall phenotypic variance. Additionally, unmeasured variables may explain overall phenotypic variation. For example, phenotypic variation may be more tuned to differences in microhabitat use or other axes of environmental variation not readily captured in island level datasets.

I did recover a strong effect of genetic diversity on phenotypic variation across all datasets. Despite documented phenotypic divergence along environment gradients, studies have not shown similar genetic divergence along these gradients (Thorpe and Stenson 2003; Stenson et al. 2004; Thorpe et al. 2008a; Muñoz et al. 2013). Yet, I recovered a correlation between overall genetic and phenotypic diversity. Taken together, these results suggest that while island-wide genetic and phenotypic diversity are correlated, they are not co-distributed across the landscape.

A difficulty with testing for phenotypic diversity is the differences in variability across traits and the inability to measure an organism's total phenotype. To address these issues, I tested multiple phenotypic datasets. The dataset of Yuan et al. (2020b) encompasses a small set of phenotypically integrated traits. That is, functionally-related traits which exhibit covariation. Comparatively, data from Chapter III represents a larger suite of traits meant to summarize the overall body plan of *Anolis* lizards. Still, these datasets are limited in overall scope. Yet, they highlight the possibility that phenotypic variation is driven by macroecological forces decoupled from those which may drive SGDCs. Further work is needed to develop our understanding the macroecology of phenotypic variation.

Conclusion

Overall, I found support for the pervasive role of island area in shaping biodiversity. However, these results did not extend to phenotypic diversity suggesting that different macroecological forces generate or constrain phenotypic variation. Beyond island area, my results emphasize that drivers of diversification not only differ between species, genetic, and phenotypic diversity, but

also differ across taxonomic groups. The relative ability of environmental variation to influence both interspecific and intraspecific diversity is likely tied to the particulars of natural history. Thus, the search for broad biogeographic patterns should take into account the particulars of a given focal clade.

Figures and Tables

Figure 4.1 Map of the Lesser Antilles. Islands included in this study are labelled. Inset plot depicts the relative proportion of Greater Antillean and South American species by ln distance to mainland South America.
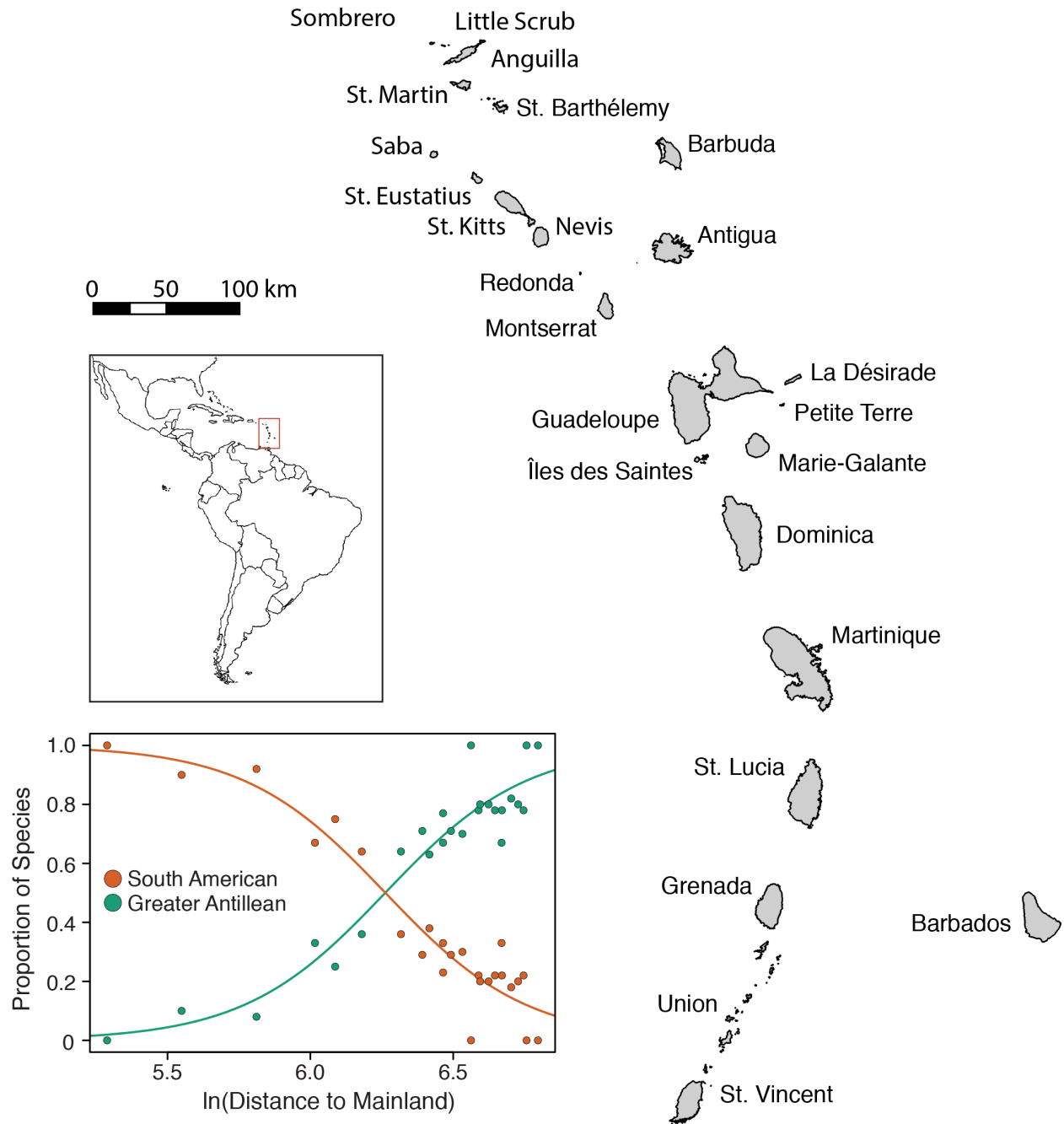
Figure 4.2 Scatterplots of island area and both interspecific (species richness) and intraspecific (genetic diversity and phenotypic variance) variation. Reptiles and amphibians are shown separately. For species richness, native and introduced values are denoted. For intraspecific variation, each analyzed dataset is labelled separately. Phenotypic variance was not analyzed for amphibians.
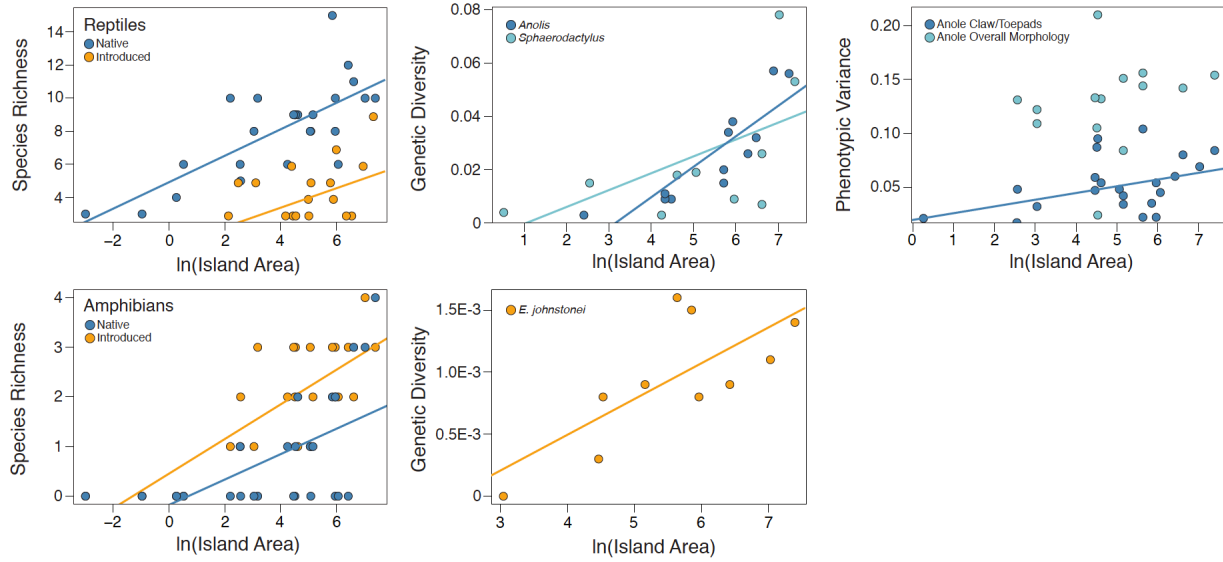
Table 4.1 Characteristics of islands included in this study: total area, standard deviation of slope (SD_{slope}), distance to mainland South America, coefficient of variance for mean annual temperature (BIO1), coefficient of variance for isothermality (BIO3), Simpson's index of habitat types (habitat), and island age.

Island	Area (km^2)	SD$_{slope}$	Mainland dist. (km)	BIO1 CV	BIO3 CV	Habitat
Anguilla	91	0.030	851	0.37	0.69	1
Antigua	281	0.103	727	1.33	0.89	1.14
Barbados	431	0.053	440	2.04	0.80	1.22
Barbuda	161	0.013	789	0.28	1.13	1
Dominica	750	0.157	554	7.26	1.12	2.79
Grenada	349	0.117	198	4.19	1.38	4.71
Guadeloupe	1630	0.132	642	6.11	1.88	3.73
Îles des Saintes	13	0.130	597	2.23	0.47	-
La Désirade	70	0.180	660	2.82	0.89	-
Little Scrub	0.05	0	860	0	0	-
Marie-Galante	158	0.070	612	1.57	0.63	1.12
Martinique	1130	0.131	483	5.87	1.03	3.08
Montserrat	101	0.145	687	4.77	1.02	2.61
Nevis	93	0.126	731	3.83	0.82	2.7
Petite Terre	1.68	0.007	642	0	0	-
Redonda	1.3	0.144	708	0	0	-
Saba	13	0.156	788	5.93	0.64	1.8
Sombrero	0.38	0.007	895	0	0	-
St. Barths	24	0.121	815	1.13	0.99	1
St. Eustatius	21	0.169	770	2.53	0.67	1.22
St. Kitts	174	0.146	753	5.75	1.13	2.9
St. Lucia	617	0.129	410	3.67	0.79	3.08
St. Martin	87	0.150	835	1.89	1.13	1.22
St. Vincent	389	0.140	334	6.80	0.92	3.27
Union	9	0.123	257	1.10	0.28	-

Table 4.2 Species richness data for amphibians and reptiles on each study island. Data for introduced and native species are presented separately.

Island	Amphibians			Reptiles		
	Native	Introduced	Total	Native	Introduced	Total
Anguilla	0	2	2	9	3	12
Antigua	0	3	3	8	2	10
Barbados	0	2	2	6	7	13
Barbuda	0	1	1	8	3	11
Dominica	3	2	5	11	3	14
Grenada	2	3	5	15	5	20
Guadeloupe	4	3	6	10	9	19
Iles des Saintes	1	1	2	6	5	11
La Désirade	1	2	3	6	3	9
Little Scrub	0	0	0	3	0	3
Marie-Galante	1	3	4	8	4	12
Martinique	3	4	6	10	6	16
Montserrat	2	1	3	9	3	12
Nevis	1	3	4	9	2	11
Petite Terre	0	0	0	6	1	7
Redonda	0	0	0	4	1	5
Saba	0	2	2	5	1	6
Sombrero	0	0	0	3	0	3
St Barths	0	3	3	10	5	15
St Eustatius	0	1	1	8	2	10
St Kitts	1	2	2	9	5	14
St Lucia	0	3	3	12	3	15
St Martin	0	3	3	9	6	15
St Vincent	2	2	4	10	4	14
Union	0	1	1	10	3	13

Table 4.3 Primers used for amplification of *cytochrome b* fragments in this study including primer specific annealing temperature and original citation.

Primer	Taxa	Sequence	Annealing Temp	Citation
MTA-S	*Anolis*	ATCTCAGCATGATGAAACTTCG	50	Thorpe et al. 2008
MTF-S	*Anolis*	TTTGGTTTACAAGACCAATG	50	Thorpe et al. 2008
rPro-1H3	*Sphaerodactylus*	TWAAAATKCTAGTTTTGGG	50	Surget-Groba and Thorpe 2013
cytb3R-2	*Sphaerodactylus*	GGTGGAATGYGATTTTATCTG	50	Surget-Groba and Thorpe 2013

Table 4.4 GLM results for species richness of introduced and native amphibians and reptiles. For each GLM, null deviance, residual deviance, and D^2 are shown in addition to coefficient and p-values for retained variables.

Introduced Amphibians (Null Dev. = 23.89, Resid. Dev. = 10.37, D^2 = 0.566)		
Variable	*Coefficient*	*p-value*
Area	0.267	< 0.001
Native Amphibians (Null Dev. = 39.91, Resid. Dev. = 15.87, D^2 = 0.602)		
Variable	*Coefficient*	*p-value*
Area	0.599	< 0.001
SD slope	16.48	0.028
Introduced Reptiles (Null Dev. = 38.31, Resid. Dev. = 18.56, D^2 = 0.516)		
Variable	*Coefficient*	*p-value*
Area	0.231	< 0.001
Native Reptiles (Null Dev. = 8.68, Resid. Dev. = 3.01, D^2 = 0.654)		
Variable	*Coefficient*	*p-value*
Area	0.079	0.013
BIO1	-0.059	0.026
Habitat	0.209	< 0.001

Table 4.5 GLM results for genetic diversity of introduced and native amphibians and reptiles. For each GLM, null deviance, residual deviance, and D^2 are shown in addition to coefficient and *p*-values for retained variables.

E. johnstonei (Null Dev. = 0.003, Resid. Dev. = 0.001, D^2 = 0.794)		
Variable	*Coefficient*	*p-value*
Area	0.273	0.028
SD slope	-25.42	0.006
Anolis (Null Dev. = 0.146, Resid. Dev. = 0.016, D^2 = 0.887)		
Variable	*Coefficient*	*p-value*
Area	0.640	< 0.001
Sphaerodactylus (Null Dev. = 0.272, Resid. Dev. = 0.163, D^2 = 0.402)		
Variable	*Coefficient*	*p-value*
Area	0.373	0.016

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Appendix II

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Personal Materials: MLY545; MLY546; MLY547; MLY551; MLY552

Appendix IV

Genbank accession numbers for all publicly available *Sphaerodactylus* and *Anolis* cytochrome b sequences included in Chapter IV.

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