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

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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 relationship to macrohabitat (vegetation), use of structural microhabitat (perch height) and congeneric competition for two distantly related Lesser Antillean anole clades: the *Anolis bimaculatus* and *Anolis roquet* series. We collected univariate and geometric morphometric data from 254 individuals across 22 species to test the hypotheses that functional morphology should covary with both vegetation and perch height and that the presence of a competitor may disrupt such covariation. Our data showed predictable associations between morphology and macrohabitat on single-species islands but not when a congeneric competitor was present. The outcomes of competition differed between series, however. In the *A. bimaculatus* series, species with a sympatric congener diverged in claw and toepad traits consistent with functional predictions, whereas *A. roquet* series anoles showed either no association between habitat and morphology or the opposite pattern. Our results demonstrated 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.

ADDITIONAL KEYWORDS: *Anolis* – Caribbean – ecomorphology – geometric morphometrics – phenotypic evolution.

INTRODUCTION

Variation in functional traits with direct consequences on performance 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 & Thomson, 2009; Sletvold & 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 and sometimes opposing selective pressures, potentially leading to inconsistent patterns of morphological adaptation with respect to a single ecological variable (Gómez, 2004; Templeton & 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

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agent of selection is often linked to divergence in microhabitat use between sympatric species (Toft, 1985; Ziv *et al.*, 1993; Robertson, 1996; Schluter, 2000; Buckley & Roughgarden, 2005a), 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 & 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 being 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 & 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), whereas 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 among Greater Antillean anoles (Losos, 1990b; Glossip & Losos, 1997; Beuttell & Losos, 1999; Elstrott & Irschick, 2004; Yuan *et al.*, 2019). For example, more arboreal (higher-perching) ecomorphs have wider toepads, more lamellae and more curved claws in comparison to more terrestrial (lower-perching) ecomorphs (Losos, 1990b; Glossip & Losos, 1997; Beuttell & Losos, 1999; Elstrott & Irschick, 2004; Yuan *et al.*, 2019). Additionally, twig anoles, whose structural habitat use is characterized predominantly 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 owing 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, in contrast, 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 *Anolis bimaculatus* series from the Greater Antilles 16.8–27.8 Mya and the *Anolis roquet* series from the South American mainland 23.8–39.1 Mya (Underwood, 1959; Thorpe *et al.*, 2018). The *A. 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 *A. 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. 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 that ecological patterns on single-species islands can be disrupted on two-species islands in this system, probably 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 & Roughgarden, 2005b). 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. 1; Rummel & Roughgarden, 1985; Losos, 1990a; Buckley & Roughgarden, 2005a). Two-species islands also exhibit partitioning of vertical habitat space in the *A. bimaculatus* series, with the smaller species being more terrestrial in comparison to the larger species, and partitioning of microclimate in the *A. roquet* series, with the smaller species perching in warmer microclimates in comparison to the larger species (Roughgarden *et al.*, 1981; Buckley & Roughgarden, 2005a). Additionally, experimental removal of either *A. bimaculatus* or *Anolis schwartzi* on Sint Eustatius improved the fitness of the remaining species (Rummel & Roughgarden, 1985), the presence or absence of *Anolis pogus* changes perching behaviour and fitness in *Anolis gingivinus* (Roughgarden *et al.*, 1984), and the introduction of *Anolis cristatellus* to Dominica resulted in perch height partitioning with the native *Anolis*
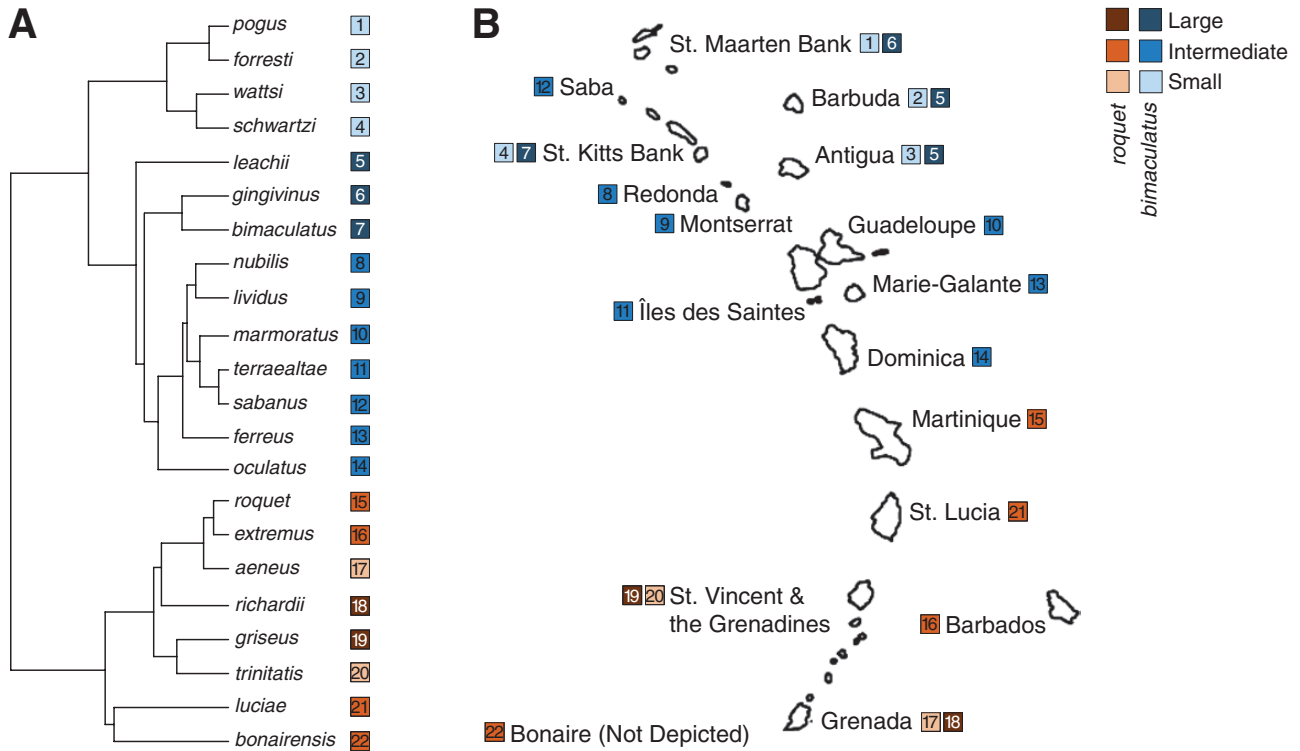
Figure 1. A, phylogeny of Lesser Antillean *Anolis* pruned from Poe *et al.* (2017). Each species is coded by subgeneric series and body size classification by colour. Branch lengths have been transformed for ease of viewing and are not biologically meaningful. B, map of the islands of the Lesser Antilles, 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 composed of St Eustatius, St Kitts and Nevis, and the St Maarten Bank is composed of Anguilla, St Maarten and St Barthélemy. Endemic anoles are denoted for each island or bank by numerical codes corresponding to the phylogeny.

oculatus (Dufour *et al.*, 2017). Taken together, the body of direct and indirect evidence strongly supports the hypothesis that competitive interactions maintain 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 the following five questions about the forces driving the evolution of these functional traits in this system.

1. Are claw and toepad morphologies associated with both macro- (overall vegetation) and microhabitat (perch use) use across Lesser Antillean anoles?
2. Are habitat associations with claw and toepad morphology consistent between one- and two-species islands?

3. Do two-species islands show evidence of divergence in claw and toepad morphology consistent with habitat partitioning?
4. Are ecological patterns of claw and toepad morphology consistent between the *A. bimaculatus* and *A. roquet* series?
5. Are patterns of divergence on two-species islands consistent with divergence between sympatric ecomorphs in the Greater Antilles?

MATERIAL AND METHODS

SAMPLING

We collected morphological measurements from preserved museum specimens (Supporting Information, Table S1) housed in the Museum of Vertebrate Zoology (University of California, Berkeley, Berkeley, CA, USA), the California Academy of Sciences (San Francisco, CA, USA), the Museum of Comparative Zoology (Harvard University, Cambridge, MA, USA) and the National Museum of Natural History (Smithsonian Institution, Washington, DC, USA).

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 (Supporting Information, Table S2). Our sampling includes all six sympatric species pairs occurring in the Lesser Antilles and 11 of 15 species from single-species islands, which we refer to hereafter as 'solitary' anoles. This sampling represents eight of nine species from the *A. roquet* series and 14 of 17 from the *A. bimaculatus* series (Fig. 1). All specimens had known collection localities within their native range except *Anolis aeneus*, for which only specimens from an introduced population on Trinidad were available. Although male and female anoles often exhibit ecological differences (Schoener, 1967; Malhotra & Thorpe, 1997), most studies have focused on male anoles, limiting the number of females anoles in collections. Hence, we examined only male specimens for the present study, and further work is required to understand the morphological evolution of female anoles.

MORPHOLOGICAL MEASUREMENTS

For each specimen, we measured the 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:

$$\text{Curvature} = 57.296 \left\{ 2\sin^{-1} \left[\frac{\left(\begin{array}{c} 2A^2B^2 + 2B^2C^2 \\ + 2A^2C^2 - A^4 \\ -B^4 - C^4 \end{array} \right)^{0.5}}{2AB} \right] \right\},$$

where A was the distance from the ventral base of the claw to the ventral curve vertex, B was the distance from the ventral curve vertex of the claw to the tip, and C was the distance from the ventral base of the claw to the tip. We calculated claw length as the sum of measurements A and B (Fig. 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).

We also collected geometric morphometric data in tpsdig2, following the protocol of Tinius & 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). We then removed non-shape features using generalized Procrustes superimposition implemented in the R package *geomorph* (Adams & Otárola-Castillo, 2013). 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 & 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 components analysis (PCA) on univariate claw measurements and a Procrustes PCA on mean shape value data across our sampled species to visualize the variation in morphospace.

ALLOMETRIC ANALYSES

We conducted all subsequent data analyses in R v.3.3.3 (R Core Team 2018). 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. 1A). To achieve normality and homoscedasticity of our data, we carried out natural logarithmic transformation of 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 (CIs) of slopes from the PICs. Slopes of one indicate isometry, greater than one allometry and zero independence for one-dimensional traits. If a trait scaled significantly with body size, we regressed the natural logarithmically transformed trait against phylogenetically informed ln-SVL (Revell, 2009) using the 'phyl.resid' function in the *phytools* package (Revell, 2012). We retained residuals as body size-corrected measurements for downstream analyses. Long-term specimen preservation can potentially influence morphological measurements from museum collections. Although modern collections are largely standardized in preservation technique, previous work has documented a small and asymptotic amount of shrinkage in body size in lizards owing to fixation in 10% formalin and storage in 70% ethanol, primarily because of initial contraction of the soft tissues (Vervust *et al.*, 2009). Hard and keratinized tissues, such as claws and toepads, however, should
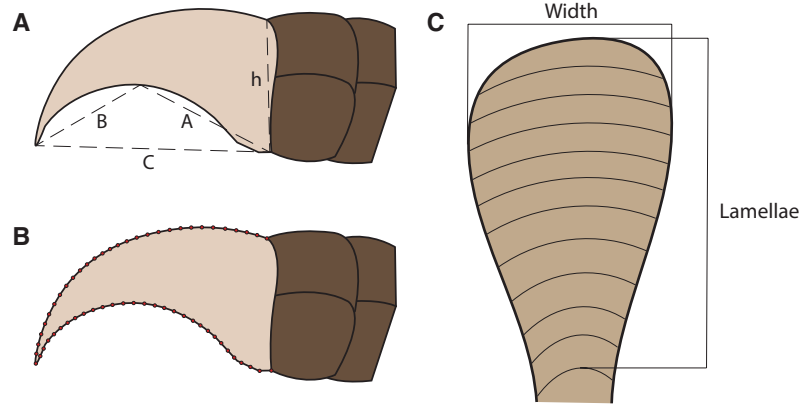
Figure 2. A, diagram showing univariate measurements for claw morphology. Claw length is determined as $A + B$, height as h, and curvature as: $57.296 \left\{ 2\sin^{-1} \left[\frac{(2A^2B^2 + 2B^2C^2 + 2A^2C^2 - A^4 - B^4 - C^4)^{0.5}}{2AB} \right] \right\}$. Univariate measurements were taken as described by 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 at the widest point and lamellae count beginning where the next distal lamellae is wider than the previous.

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 BETWEEN-RADIATION COMPARISONS

We examined differences in claw and toepad morphology between *A. roquet* and *A. 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, 2014) in *geomorph*. Additionally, we tested for differences in overall shape disparity in 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 PCA 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 *A. roquet* series; and only the *A. bimaculatus* series. On two-species islands, one species is always smaller and more terrestrial, whereas the other is larger and more arboreal; the smaller, more terrestrial species forms a clade that is reciprocally monophyletic with all other more arboreal species in the *A. bimaculatus* series (Fig. 1A), potentially confounding ecological and phylogenetic signals. Therefore, we conducted analyses both considering and disregarding the underlying phylogeny when analysing the all-species dataset and the *A. bimaculatus* series dataset. To test for phenotypic integration, defined as covariation between functionally related traits, we examined correlations between all combinations 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). Given that many specimens pre-date available NDVI data, we use modern NDVI as a proxy for the vegetation likely to be experienced on each island. To capture broad variation in vegetation structure over time, we averaged 250 m resolution NDVI data across collection localities from 2010 to 2015 using the *MODIStools* package in R (Koen,

2019) for each species. Owing 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 to be 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, 2014) between multivariate claw shape and all habitat metrics. Finally, to characterize more fine-scale differences in shape, we summarized multivariate claw shape variation using Procrustes PCA and examined correlations between the first two principal components (PCs) 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)] were 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 number of lamellae [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. 3A). For univariate data, PC1 explained 56.2% of total variation and was characterized primarily by claw height and length, whereas PC2 explained 27.3% of univariate claw variation and was characterized primarily by claw curvature (Fig. 4A; Supporting Information, Table S3).

BETWEEN-SERIES AND BETWEEN-RADIATION COMPARISONS

We found no significant differences between the *A. bimaculatus* and *A. 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. 3D, E), although divergence between *Anolis wattsi* and *Anolis leachii* still showed inverse directionality in comparison 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. 3A) or shape disparity (morphological disparity: $P = 0.336$).

In comparisons with Greater Antillean ecomorphs, we found that Lesser Antillean anoles had relatively longer (post-hoc *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; $P = 0.040$) in comparison to the twig ecomorph (Fig. 4), the set of species with slender bodies and short limbs that specialize on twig and small branch habitat. Lesser Antillean anoles also differed 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 differ significantly from any other Greater Antillean ecomorphs (post-hoc *t*-test: all $P > 0.05$). Thus, Lesser Antillean anoles occupied claw morphospace similar to the Greater Antillean ecomorphs that occupied 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 anoles ($t = 3.597$; d.f. = 25; $P = 0.024$) 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; $P = 0.008$).

PHENOTYPIC INTEGRATION, HABITAT USE AND MORPHOLOGY

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 the relative number of lamellae ($F_{1,20} = 11.90$, $P = 0.003$), and relative claw length was positively correlated with claw height ($F_{1,20} = 12.08$, $P = 0.002$). Our results were consistent when analysing only solitary species, only two-species islands and each series independently, except that relative claw height and length were not significantly correlated in *A. roquet* series anoles ($F_{1,6} = 0.57$,
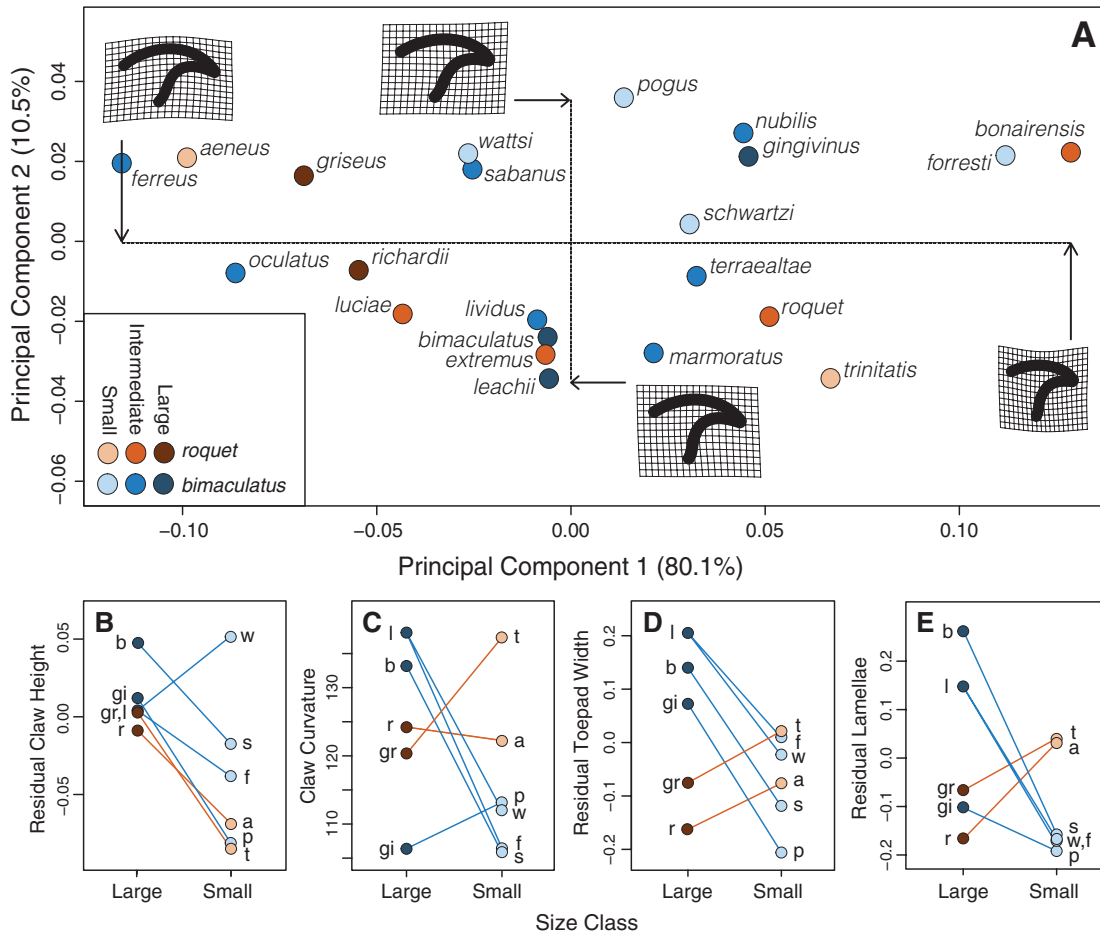
Figure 3. A, plot of multivariate claw shape principal components 1 and 2. All species are coded by series and size classification. Warp grids representing extremes of principal component 1 are depicted. B–E, pairwise comparisons between large and small species on two-species islands for select univariate traits (relative claw height, claw curvature, relative toepad width and relative number of lamellae). Abbreviations: a, *Anolis aeneus*; b, *Anolis bimaculatus*; f, *Anolis forresti*; gi, *Anolis gingivinus*; gr, *Anolis griseus*; l, *Anolis leachii*; p, *Anolis pogus*; r, *Anolis richardii*; s, *Anolis schwartzi*; t, *Anolis trinitatis*; w, *Anolis wattsi*.

$P = 0.450$). When not accounting for phylogeny, we found that claw curvature was also positively correlated with the relative number of lamellae ($F_{1,20} = 7.62$, $P = 0.012$) across all species. For *A. bimaculatus* series anoles, we found that both the relative number of lamellae ($F_{1,12} = 718.69$, $P < 0.001$) 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. 5). Our results for all species and for the *A. 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 *A. bimaculatus* series ($P > 0.05$) when accounting for phylogeny. However, we found that within the *A. roquet* series claw curvature was negatively correlated with perch height ($F_{1,5} = 10.50$, $P = 0.023$; Fig. 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, the number of lamellae 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 the
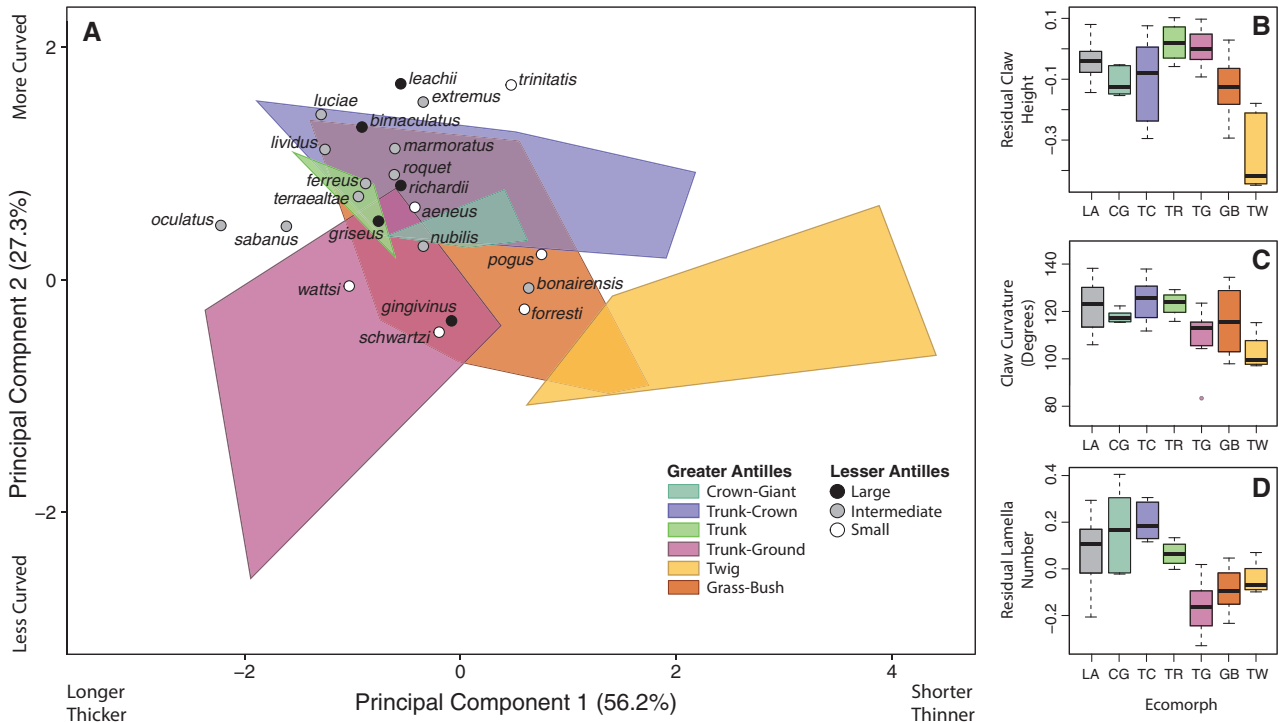
Figure 4. A, plot of principal components 1 and 2 for all univariate claw measurements (claw curvature and relative claw height and length) across both Greater and Lesser Antillean anoles. For Greater Antillean anoles, only minimum convex polygons are displayed for each ecomorph classification. All sampled Lesser Antillean species are shown coded by body size classification. B–D, boxplots depicting relative claw height, claw curvature and relative number of lamellae for each ecomorph compared with Lesser Antillean species as a whole. Abbreviations: CG, crown–giant; GB, grass–bush; LA, Lesser Antillean; TC, trunk–crown; TG, trunk–ground; TR, trunk; TW, twig.

number of lamellae ($F_{1,15} = 5.81$, $R^2 = 0.231$, $P = 0.029$) were positively correlated with ln-perch height across Lesser Antillean anoles (Fig. 6). The same traits were also positively correlated in *A. bimaculatus* series anoles when not accounting for phylogeny (claw curvature: $F_{1,6} = 5.74$, $R^2 = 0.345$, $P = 0.043$; toepad width: $F_{1,6} = 10.66$, $R^2 = 0.518$, $P = 0.011$; number of lamellae: $F_{1,6} = 6.89$, $R^2 = 0.396$, $P = 0.030$), 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, the number of lamellae (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 to be attributable 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 might otherwise occur across a radiation.

MACROHABITAT–MORPHOLOGY ASSOCIATIONS

On single-species islands, anoles inhabiting more densely vegetated islands had greater claw curvature, suggesting that the type of macrohabitat influences claw morphology, as predicted. Low-NDVI islands,
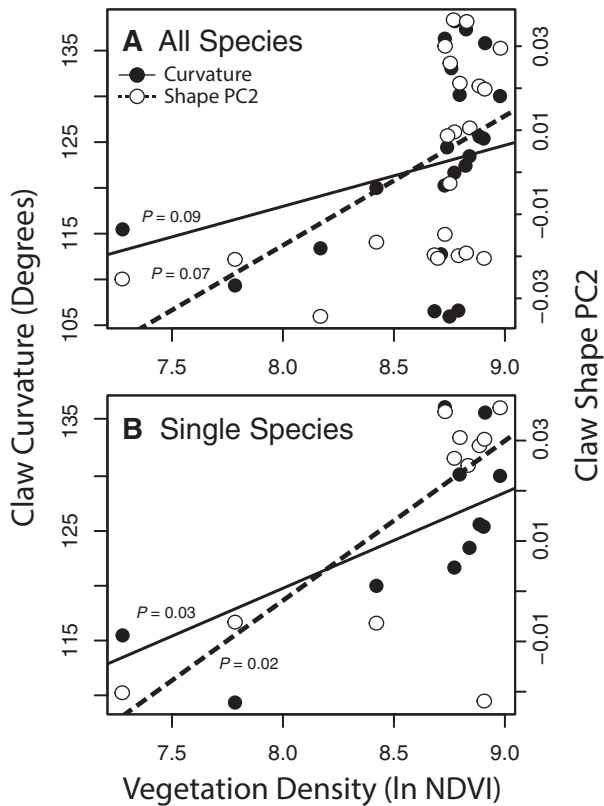
Figure 5. A, B, the relationship between both claw curvature and multivariate claw shape principal component 2 (PC2; which also characterizes ventral claw curvature) with the natural logarithm of normalized difference vegetation index (NDVI) for all Lesser Antillean species sampled (A) and only species from single-species islands (B). Claw shape PC2 is depicted by open circles and claw curvature is depicted by filled circles. All data points represent the species mean values. Correlations were significant for both traits for species from single-species islands, whereas correlations approached significance only across all sampled species.

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 might select for flatter claws owing 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 & Bennett, 2007; Tulli *et al.*, 2009; Birn-Jeffery *et al.*, 2012). Thus, overall claw shape on single-species islands is likely to be reflective of performance trade-offs 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 might not play

an essential role in differential performance across vegetation types. Nonetheless, 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 relationship to perch height if not vegetation types. Indeed, toepad traits were correlated with perch height, as predicted, in *A. bimaculatus* series anoles, at least when not accounting for phylogenetic relatedness (Fig. 6). However, toepad traits were not correlated with either perch height or diameter in *A. roquet* series anoles. Given that the strength of interaction between toepads and surfaces is mediated through the microscopic setae that compose the lamellae (Autumn *et al.*, 2002; Hagey *et al.*, 2014), ecological differences in the *A. roquet* series might 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 *A. bimaculatus* and *A. roquet* series are likely to mask the relationship between structural microhabitat use and toepad traits when examining Lesser Antillean anoles altogether.

COMPETITION DISRUPTS MORPHOLOGY–MACROHABITAT ASSOCIATIONS

As a result of fitness trade-offs, overall phenotypic evolution can be driven largely by a dominant selective pressure leading to patterns contrary to functional predictions based upon other environmental variables (Gómez, 2004; Templeton & 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. 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 & Gorman, 1968; Rummel & Roughgarden, 1985; Buckley & Roughgarden, 2005a). Thus, we propose that the lack of macrohabitat–morphology associations on two-species islands is attributable to the confounding effects of interspecific competition. Specifically, in allopatry, species can use all potentially available ecological space. Thus, selection should favour performance reflective of their overall habitat, as observed on single-species islands. However, if
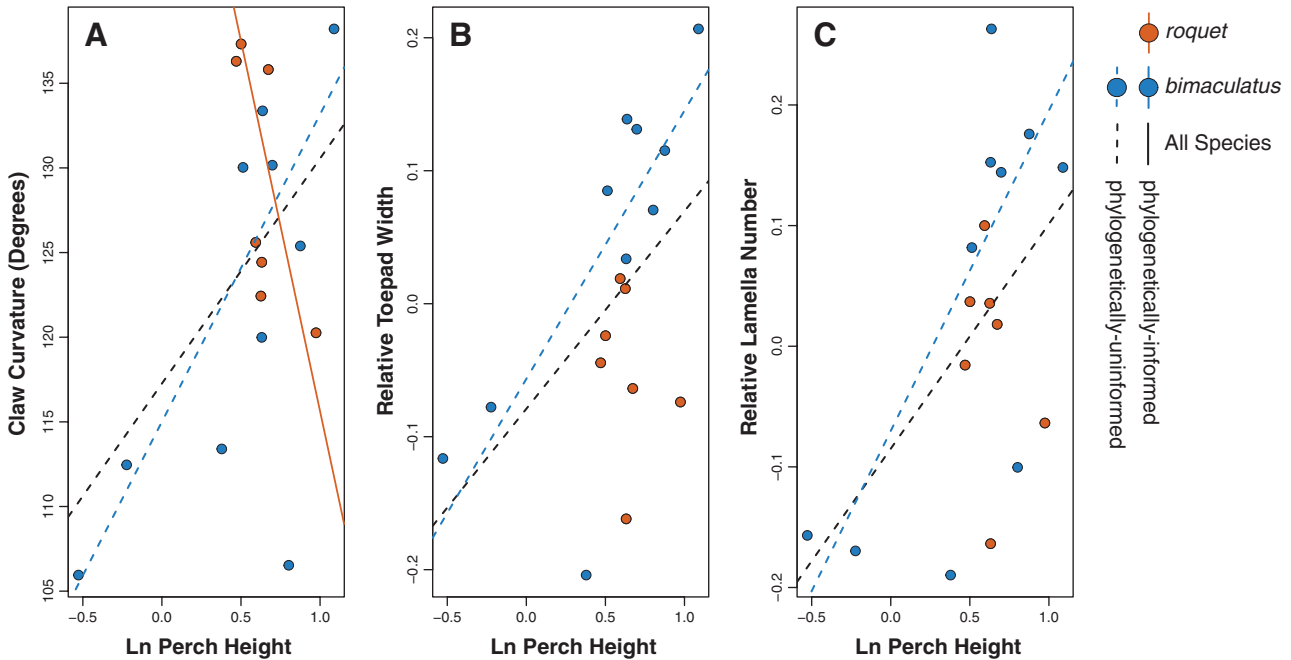
Figure 6. Plots of morphological correlates with perch height: claw curvature (A), relative toepad width (B) and relative number of lamellae (C). Plots include regression lines for all species, for only the *A. bimaculatus* series and for only the *A. roquet* series, if relationships were statistically significant. Non-significant relationships are not shown. We did not perform uninformed tests when examining only the *A. roquet* series.

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 use habitat space fully in comparison 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 the present study, future investigations of habitat partitioning between sexes might provide greater insight into the differences between one- and two-species islands.

DIFFERENCES BETWEEN SERIES IN MORPHOLOGY–MICROHABITAT ASSOCIATIONS

For *A. 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, *A. bimaculatus* series anoles show positive

correlations of claw curvature, toepad width and the number of lamellae 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 & Irschick, 2004; Tulli *et al.*, 2011; Crandell *et al.*, 2014). Smaller, more terrestrial species within the *A. bimaculatus* series also had more similar claw morphology to trunk–ground and grass–bush anoles than their more trunk–crown like congeners (Figs 3B–E, 4A). Given that the more terrestrial anoles form a reciprocally monophyletic clade with more arboreal species in the *A. bimaculatus* series (Fig. 2A), signals of selection could be indistinguishable from phylogenetic signal. Nevertheless, we cannot rule out the possibility that the relationships of claw and toepad traits with perch height represent a purely phylogenetic artefact, particularly given that the more terrestrial life history of the *A. wattsi* group (*A. forresti*, *A. pogus*, *A. schwartzi* and *A. wattsi*) is likely to have evolved only once, in their common ancestor.

The *A. roquet* series anoles did not exhibit evidence of morphological adaptation to habitat consistent with expectations. Instead, we found that *A. 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. 6). These patterns are contrary not only to those observed across the *A. bimaculatus* series but also to the general pattern across Greater Antillean anoles (Losos, 1990b; Glossip & 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) and to predictions from functional studies (Zani, 2000; Crandell *et al.*, 2014). Additionally, patterns of divergence on two-species islands in the *A. roquet* series were often the converse of those observed on two-species islands in the *A. bimaculatus* series (Fig. 3). Within the *A. roquet* series, the larger species on two-species islands had flatter claws, smaller toepads and fewer lamellae in comparison to their smaller congeners. Unlike Greater Antillean and *A. bimaculatus* series anoles, *A. roquet* series anoles do not partition vertical habitat on multispecies islands (Roughgarden *et al.*, 1981; Buckley & Roughgarden, 2005a). Therefore, divergent selection for traits associated with vertical habitat partitioning is likely to be weaker within the *A. roquet* series. Although *A. roquet* series anoles do partition thermal microhabitat on two-species islands, we lacked adequate data to test the effects of thermal microhabitat formally across Lesser Antillean anoles.

Why *A. roquet* series anoles do not exhibit vertical habitat partitioning, and associated morphological divergence, is unclear. However, the *A. bimaculatus* series is descended from the Greater Antillean radiation, whereas the *A. 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 & Langerhans, 2015). Given the widespread convergence of vertical habitat partitioning across the Greater Antilles but not the mainland (Irschick *et al.*, 1997), *A. bimaculatus* series anoles might have a greater evolutionary predisposition for such divergence in comparison to the *A. roquet* series. Differing evolutionary dynamics may also be expected given that the *A. bimaculatus* and *A. roquet* series last shared a common ancestor at the base of the crown group of anoles, estimated to ~31–65 Mya (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). Nonetheless, convergent claw morphology in response to arboreality has been observed across more highly divergent taxa, including primates (Cartmill, 1974;

Smith & Smith, 2013), birds (Feduccia, 1993; Glen & 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 *A. 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 might clarify whether these differences explain the overall lower diversity of *Dactyloa* clade anoles, to which the *A. roquet* series belongs.

CONCLUSIONS

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 by the confounding effects of interspecific competition and phylogenetic history. The *A. bimaculatus* and *A. roquet* series show consistent morphology–macrohabitat associations on single-species islands (Fig. 5), but this pattern is disrupted in both series by contrasting effects of competition-driven microhabitat partitioning on two-species islands (Fig. 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. The *A. bimaculatus* series shows patterns of microhabitat partitioning and subsequent morphological divergence consistent with Greater Antillean anoles (Yuan *et al.*, 2019), whereas claw and toepad traits appear to be decoupled from structural microhabitat use, as characterized by perch height and diameter, in the *A. roquet* series (Fig. 6). Thus, our data indicate that the capacity for strong morphological responses to similar environmental pressures may differ between clades, which may have consequences for adaptive diversification by either constraining or facilitating effective niche exploitation. Differences between the *A. bimaculatus* and *A. roquet* series anoles on the Lesser Antilles suggest that the Greater Antillean lineages might have been especially primed to radiate adaptively through their hallmark partitioning of vertical habitat.

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M.L.Y. conceived and developed the study with advice from I.J.W. and M.H.W. M.L.Y. and C.J. conducted fieldwork and collected morphological data. M.L.Y. analysed the data. M.L.Y. wrote the manuscript, with important contributions from all coauthors.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's website.

Table S1. Summary of all individual specimens examined in this study: collection, catalogue number and species.
Table S2. Summary statistics for each species. Body size classification, series, sample size (*N*), snout–vent length (SVL; in millimetres), claw height (CH; in millimetres), claw length (CL; in millimetres) claw curvature (in degrees), toepad width (TPW; in millimetres), number of lamellae, normalized difference vegetation index (NDVI), perch height (PH; in metres) and perch diameter (PD; in centimetres) are listed. The mean and SE are given for all relevant variables. Perch data are compiled from the literature (see main text).
Table S3. Loadings for principal components analysis of univariate claw measurements.

SHARED DATA

Data deposited in the Dryad digital repository (Yuan *et al*., 2019b; https://doi.org/10.6078/D10H4Z).