

Phylogeny, biogeography and island effect drive differential evolutionary signals in mainland and island lizard assemblages

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The means by which assemblages of closely related species form and persist have become a primary focus in evolution and ecology. Comparative studies of island and mainland assemblages may provide novel insight into assemblage evolution. The isolation and relative simplicity of islands may foster distinct evolutionary rates and endpoints relative to mainland areas. Adaptive radiations on islands are expected to result in assemblages that include close phylogenetic relatives but are phenotypically diverse, whereas predator- and competitor-rich mainland environments may produce phenotypically uniform assemblages. Here we use a nearly complete phylogeny and morphological data for 336 species of *Anolis* lizards to test for differences in phenotypic and phylogenetic structure in 91 mainland versus 76 island assemblages. We present three main conclusions: (1) both mainland and island assemblages comprise close relatives that are phenotypically similar; (2) mainland assemblages tend to be more clustered than island assemblages according to both phylogenetic and phenotypic measures; and (3) differences in degree of phenotypic clustering between mainland and island assemblages are not explained by differences in phylogenetic clustering alone. We interpret these results in terms of biogeography and differences between mainland and island environments.

ADDITIONAL KEYWORDS: assembly rules – community structure – comparative evolution – island biogeography – lizards.

INTRODUCTION

The isolation and relative simplicity of island environments has made them popular study arenas in evolution and ecology (Schoener, 1968; Carlquist, 1974; Warren *et al.*, 2015). Whereas some studies embrace islands as exemplars of general evolutionary principles (e.g. Emerson, 2002; Emerson & Gillespie, 2008), others have emphasized the distinctness of islands relative to mainland environments (e.g. Barton, 1996; Millien, 2006). Immigration to island environments is relatively restricted, and a dearth of predators and competitors is thought to promote adaptive radiation of invading lineages (MacArthur & Wilson, 1967; Schluter, 1988; Harmon & Gibson, 2006). Conversely, mainland environments are considered to be relatively species-rich and older, so evolution is thought to proceed more slowly, or at least differently, in mainland environments relative to islands. Some studies have

compared evolution in mainland and islands systems (e.g. Schluter, 1988; Harmon & Gibson, 2006; Millien, 2006; Pinto *et al.*, 2008; Schaad & Poe, 2010; Hernández-Salinas *et al.*, 2014), with mixed results on whether evolutionary outcomes consistently differ.

The formation, structure and history of species assemblages have become primary foci of evolutionary ecology (e.g. Swenson *et al.*, 2007; Graham *et al.*, 2009; Eiserhardt *et al.*, 2013), and islands may provide novel insight into assemblage evolution (e.g. Gillespie, 2004; Emerson & Gillespie, 2008; Warren *et al.*, 2015). Climate, competition, habitat and predator–prey dynamics interact at a local scale in the context of greater biogeographic processes, including speciation, immigration, emigration and extinction, to form an assemblage (Eiserhardt *et al.*, 2013). These forces may result in ‘clustered’ assemblages of similar species or ‘dispersed’ assemblages of dissimilar species, where operationalization of these terms occurs via morphological, ecological and/or phylogenetic metrics (Webb *et al.*, 2002). Clustering within a community is

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traditionally interpreted as indicating some filtering mechanism whereby only similar species may inhabit the studied area, whereas dispersion is commonly thought to signal competition (Weiher *et al.*, 1998; Kunstler *et al.*, 2012). Recent work (e.g. Mayfield & Levine, 2010; Gerhold *et al.*, 2015; Cadotte & Tucker, 2017) has shown these interpretations to be facile and has questioned the utility of phylogenetic clustering as a proxy measure for ecological processes.

Hypothesized differences between island and mainland environments might result in differing patterns of clustering in island versus mainland assemblages. For example, adaptive radiations on islands would be expected to produce assemblages with a high degree of phylogenetic clustering; whereas mainland faunas, not hindered by overwater dispersal, may form assemblages with relatively greater phylogenetic dispersion. Although there is ongoing interest in island evolution as a means to understand general evolutionary principles (Warren *et al.*, 2015), no large-scale study has yet compared community structure between mainland and island environments.

Anolis lizards (anoles) are classic study organisms in community evolution, adaptive radiation and mainland–island comparisons of evolution (e.g. Williams, 1972; Losos *et al.*, 1998; Rabosky & Glor, 2010; Hernández-Salinas *et al.*, 2014). *Anolis* is a remarkably diverse Neotropical genus with ~400 species exhibiting exceptional morphological and ecological variation (Losos, 2009). Adaptive radiation and inter-island dispersal have produced assemblages of predictable ecomorphological types that stratify by habitat specialization in the well-studied Greater Antilles (Williams, 1972). There is some evidence that the mainland anole fauna is as diverse as its island counterpart with respect to phylogeny and morphology (Schaad & Poe, 2010; Moreno-Arias & Calderon-Espinosa, 2016), and that evolution may have proceeded differently on the mainland versus islands (Velasco & Herrel, 2007; Pinto *et al.*, 2008; Thomas *et al.*, 2009; Algar & Losos, 2011; Velasco *et al.*, 2015; but see Poe *et al.*, 2018). Anole communities on the mainland are nearly unstudied (for examples of single-assemblage or single-area analyses, see: Velasco & Herrel, 2007; Moreno-Arias & Calderon-Espinosa, 2016), and comparative assemblage studies have been precluded by the lack of comprehensive phylogenetic, morphological and community content datasets for *Anolis*.

Here, we use extensive, ground-truthed documentation of species composition in mainland and island assemblages, a morphological dataset of 336 species, and a nearly complete phylogeny to test for differences in morphological and phylogenetic structure in mainland versus island assemblages of *Anolis*. We first test for differences in clustering patterns of mainland and island assemblages using simple summary statistics. These initial analyses detected differences in mainland

and island clustering patterns, so we performed an ANCOVA to further test for a mainland–island effect of morphological clustering while controlling for phylogenetic clustering. The paucity of information regarding mainland assemblages of anoles makes hypothesis formulation difficult. As a first pass, we predicted that island assemblages would be (1) more phylogenetically clustered than mainland assemblages due to the known prevalence of adaptive radiations in the Greater Antilles, and (2) more morphologically dispersed than mainland assemblages due to the known presence of multiple ecomorphological types within some Caribbean assemblages.

METHODS

DATA

We compiled species composition data for 76 island and 91 mainland assemblages comprising two or more species from throughout the range of *Anolis*. We considered an assemblage to constitute a set of species that were sympatric within a radius of approximately 1 km. Because of concerns regarding pseudoreplication (e.g. Hurlbert, 1984), we stipulated that not more than one species be shared between assemblages. However, multiple assemblages may share a single wide-ranging species (e.g. *A. biporcatus*). Approximately 60% of these assemblages were ‘ground-truthed’ by tallying species composition during the course of fieldwork from 2003 to 2015. The remaining 40% of assemblages include well-sampled and well-known localities such as those described in Powell & Henderson (2012). Assemblage information is presented in [Supporting Information, Appendix S1](#).

Our analyses of phylogenetic structure of assemblages incorporated the Maximum Clade Credibility tree from Poe *et al.* (2017) pruned to include only the 336 species for which we have morphological data. We examined variability of phylogenetic clustering metrics across a sample of 100 trees from Poe *et al.*'s (2017) Bayesian post-burnin sample. We note that because the phylogeny of Poe *et al.* (2017) includes morphological data, some readers may be concerned with potential circularity regarding measures of phylogenetic and morphological distances. However, we are confident the inclusion of these morphological characters (46 of 24 925 characters) will not bias our findings.

We collected data for nine morphological characters from one to 15 specimens of 336 species of *Anolis* [Armstead & Poe (2015) suggests $N = 1$ is an adequate sample size for our purposes]. Body size (snout vent length, SVL) was measured from tip of snout to anterior edge of cloaca. Hindlimb length (HLL) was measured from ventral longitudinal midline laterally to knee as thigh is extended from the body at a right angle. Head length (HDL) was measured from tip of snout to anterior extent

of ear opening. Tail length (TAL) was measured from posterior edge of the cloaca. Toe length (TOL) was measured for the fourth (i.e. largest) toe from the base of the toe out to the tip of the claw. Size of head scales (HSC) was measured as number of scales across the snout at the level of the second canthal scales. Ventral (VSC) and dorsal (DSC) scales were counted longitudinally for a distance of 5% of SVL; dorsal scales were counted at the midline of the body, ventral scales were counted at midbelly (~1/3 the distance between cloaca and axillae). Toe lamellae (LAM) were counted in the manner of Williams *et al.* (1995).

Several traits (HLL, HDL, TAL and TOL) are strongly correlated with overall size and thus these traits were collected in units of SVL. Ratios are often considered undesirable for size correction (e.g. Packard & Boardman, 1988) so many authors use residuals from linear regression on some measure of body size (e.g. body length or first principal component score) instead of our approach. However, for our data, body size ratios are nearly completely correlated with body length residuals (example shown in Supporting Information, Fig. S1), so we use ratios for practical reasons, e.g. it is not necessary to perform a new regression every time a new datapoint (species) is added.

Herein we focus on results from individual traits, but acknowledge that composite treatments of morphology are possible (e.g. principal components, Mahalanobis distances) and favoured by some. We have reservations about using these composite measures due to known phylogenetic effects (Revell, 2009) and the difficulty with correcting for these (Uyeda *et al.*, 2015), as well as additional effects that indicate other biases. All such composite corrections implicitly assume constancy of trait relationships across included species, but this assumption clearly seems to be violated in the current case. For example, principal component (PC) scores are vastly different when calculated separately for mainland and island species (results not shown). Furthermore, in addition to these bias issues, results from individual traits are much more easily interpretable than PC scores. Given these reservations, we feel it is more informative to present results from individual traits and interpret these in light of expected trait correlations (with phylogeny, body size, etc.) than to present biased, uninterpretable PC scores.

METRICS OF ASSEMBLAGE STRUCTURE

One problem inherent in studies of this kind is the assignment of appropriate species pools from which null communities can be sampled. We opted to include the entire *Anolis* clade for the following reasons: (1) we felt it important to test for, and establish, the biogeographic aspects of assemblage structure; (2) designation of null species pools is necessarily equivocal (e.g. the Sierra Maestra of Cuba or the entire Island of Cuba are both

potentially valid subgroup assignments); and (3) ad hoc assignment of subgroups or species pools entails problematic issues of justification and incorporated assumptions. For similar reasons, we chose not to assume that any one species is more or less likely to be part of an assemblage based on aspects of its natural history. Moreover, many of the species included in the present study are poorly known and weighting the likelihood of one species coexisting with another on the basis of abundance or dispersal ability may, again, introduce assumptions that would likely bias our results.

Phylogenetic and morphological clustering of each *Anolis* community was inferred in Phylocom 4.2 (Webb *et al.*, 2008). Mean phylogenetic distance (MPD) was calculated for each community and compared to values obtained from 100 000 randomly generated null communities of the same size using Phylocom's COMSTRUCT. We used a null model in which species were equiprobably sampled without replacement from all 336 species. Raw MPD values and *P* values were retained for comparative analyses. We calculated morphological clustering within each assemblage for each trait using mean trait distance (MTD) among the species in an assemblage in Phylocom's COMTRAIT. We determined significance with the same null sampling approach used for phylogenetic clustering, and retained both raw and *P* values for analysis. We used 'rankHi' *P* values for phylogenetic clustering and 'rankLow' *P* values for morphological clustering so that low or high *P* values had comparable interpretations for assemblages. That is, under this scheme, low *P* values indicate clustering for both phylogenetic and morphological analyses.

We tested for overall trends in dispersion among assemblages in morphology and phylogeny by comparing rankHi/Low *P* values to 0.5 using a Wilcoxon Rank Sum Test. For example, if a significant majority of *P* values for dispersion in body size of mainland assemblages are less than 0.5, we may infer that mainland assemblages tend to include species of similar body size.

COMPARISONS OF ISLAND AND MAINLAND ASSEMBLAGE STRUCTURE

We performed several analyses to test for relationships and biases in our data that may need to be accounted for in analyses. We tested for correlations of number of taxa per assemblage versus MPD, number of taxa per assemblage versus MTD (for each of the nine traits) and MPD versus MTD (for each of the nine traits) using the Spearman's signed ranks test, linear regression and graphical visualization. Comparisons were made using both raw MTD and MPD values, and rankHi/Low *P* values for these metrics.

We tested for differences in phylogenetic clustering (MPD) and in morphological clustering (MTD) between mainland and island assemblages using a

Mann–Whitney U test. For analyses of both MTD and MPD, we performed separate analyses using raw values and rankHi/Low P values as assemblage data points.

In order to assess the effects of mainland versus island assemblage status on morphological clustering while allowing for the correlation between MTD and MPD (see below), we performed an analysis of covariance (ANCOVA) of assemblages using dependent variable MTD (i.e. dispersion in each of nine morphological traits) and independent variables MPD and location assignment (mainland or island). Some of our analysed variables appear to be non-normally distributed. Therefore, we performed analyses using Box–Cox transformation of raw MTD and MPD values. For each trait, we constructed ANCOVA models where MTD and MPD were transformed with separate power parameters for each. Values for the power transformations were determined by maximum likelihood under the ANCOVA model.

Statistical analyses were performed in R 3.3.2 and checked in Stata (Statacorp, 2011). We discuss our results in terms of raw MTD or MPD when referencing general pattern as these raw values are closely tracked by the rankHi/Low P values recovered in our null comparisons and we believe the raw values allow for better discrimination of differences between mainland and island assemblages.

RESULTS

TESTS FOR BIASES IN THE DATA

Spearman's signed ranks tests of MPD and MTD versus number of taxa returned non-significant results for all comparisons ($P = 0.237$ – 0.896 ; Supporting Information, Table S1). Consequently, we did not account for number of taxa per assemblage in our analyses despite a greater number of species per mainland assemblage (island mean = 3.76, mainland mean = 4.59; $P = 0.007$). Spearman's signed ranks tests documented positive correlations between MTD and MPD values for hindlimb length ($P = 0.045$), head length ($P < 0.0001$), toe length ($P = 0.042$), tail length ($P = 0.005$), dorsal scale number ($P < 0.0001$) and lamellae number ($P < 0.0001$) (Supporting Information, Table S1). Therefore, we incorporated MPD as a covariate in ANCOVA analyses testing for a mainland–island effect on MTD.

COMPARISONS OF ASSEMBLAGE STRUCTURE

Mainland assemblages are more phylogenetically clustered than island assemblages (Fig. 1; mean = 0.091 and 0.105, respectively; $P < 0.0001$). Both mainland and island assemblages tend to be phylogenetically clustered relative to null models generated in COMSTRUCT (mean = 0.072 and 0.228, respectively; $P < 0.0001$ for

each; Supporting Information, Fig. S2). Little variation in MPD results was observed across the 100 sampled post-burnin Bayesian trees (average standard deviation in MPD across assemblages = 0.009), so all presented results are based on the MCC tree.

Mean trait distances (MTD, a measure of phenotypic clustering) were significantly lower (more clustered) in mainland assemblages than island assemblages for head length (mean MTD = 0.013 and 0.028, respectively; $P < 0.0001$), tail length (mean MTD = 0.254 and 0.416, respectively; $P < 0.0001$) and lamellae (mean MTD = 2.851 and 4.473, respectively; $P = 0.0007$). However, MTD values were significantly higher (more dispersed) in mainland assemblages than island assemblages for hindlimb length (mean MTD = 0.036 and 0.031, respectively; $P = 0.022$) and head scale size (mean MTD = 1.866 and 0.981, respectively; $P < 0.0001$). Comparisons of clustering in SVL ($P = 0.355$), ventral scale size ($P = 0.483$) and dorsal scale size ($P = 0.342$) were nonsignificant. Figure 2 summarizes these results for raw MTD values.

The degree of clustering relative to null distributions generated in COMTRAIT was significant for seven traits among mainland assemblages and five traits among island assemblages. Mainland assemblages

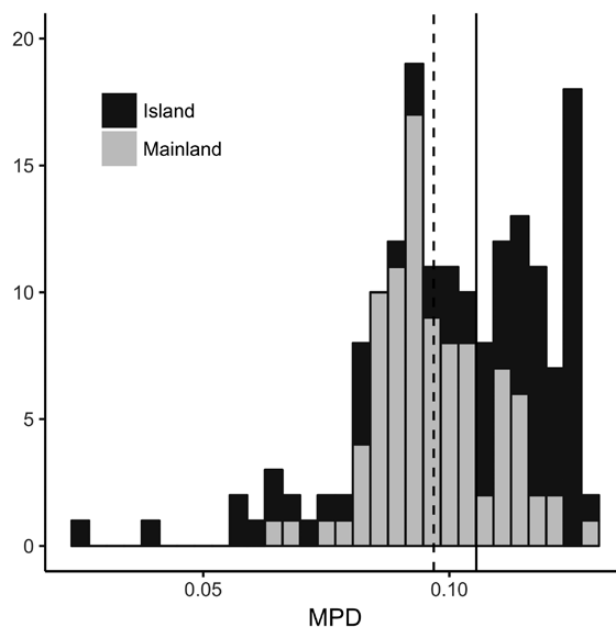


Figure 1. A histogram illustrating the distribution of mean phylogenetic distances (MPD) for island and mainland assemblages. Larger values indicate phylogenetic dispersion (assemblages comprising distantly related species) and smaller values indicate phylogenetic clustering (assemblages comprising closely related species). Solid and dashed vertical lines indicate mean MPD for island and mainland assemblages, respectively.

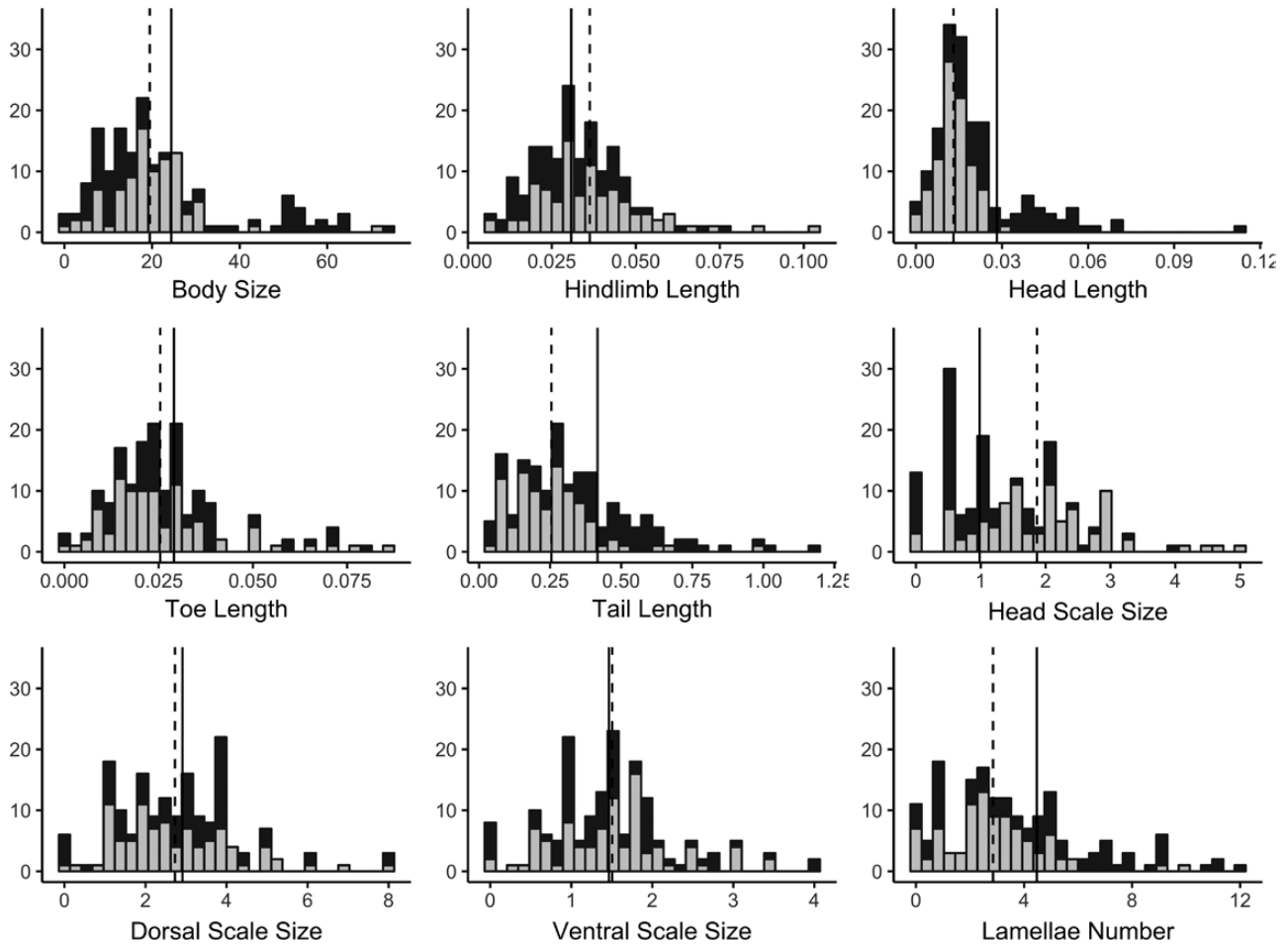


Figure 2. Histograms illustrating distributions of MTD for tested traits for island (black) and mainland (gray) assemblages. Solid and dashed vertical lines indicate mean MTD for island and mainland assemblages, respectively. Larger values indicate dispersion of MTD values within an assemblage, whereas smaller values indicate clustering (i.e. that species within assemblages tend to be nonrandomly similar in the tested trait).

demonstrate greater than expected clustering in body size, head, toe and tail length, ventral scale and lamellae number, and head scale size ($P < 0.001$); neither dispersion nor clustering were detected in hindlimb length or dorsal scale number ($P > 0.05$). For island assemblages clustering was detected in body size, hindlimb length, ventral scale and lamellae number, and head scale size ($P < 0.05$). Overdispersion of traits relative to null distributions was observed in island assemblages for head and tail length ($P < 0.0001$); neither clustering nor dispersion was detected for toe length or dorsal scale number ($P > 0.05$). Results for our COMTRAIT analysis are summarized in [Supporting Information, Figure S3](#).

Our ANCOVA indicated a significant model and strong effect of MPD on MTD for head and toe length, dorsal scale size and lamellae number ($P \leq 0.037$; [Table 1](#) and [Fig. 3](#)). A significant mainland-island

effect was recovered in hindlimb, head, and tail length and head scale size ($P \leq 0.0014$; [Table 1](#)).

DISCUSSION

We present three main conclusions from our analyses of phylogenetic and morphological clustering patterns in *Anolis* assemblages. First, mainland and island assemblages are both phylogenetically and morphologically clustered. That is, anole assemblages include close relatives that are morphologically similar. Second, mainland assemblages tend to be more clustered than island assemblages in phylogenetic and morphological metrics. Third, differences in the degree of morphological clustering between mainland and island assemblages are not explained by differences in phylogenetic

Table 1. Results of ANCOVA using Box-Cox transformed data presented with mean values obtained from MTD for each trait. Traits are: body size (SVL), hindlimb length (HLL), head length (HDL), toe length (TOL), tail length (TAL), ventral scale number (VSC), dorsal scale number (DSC), lamellae number (LAM) and head scale size (HSC). A phylogenetic effect was observed in HDL, TOL, TAL, DSC and LAM and a mainland–island effect was observed in HLL, HDL, TAL and HSC and are indicated in bold text

Trait	Mean (Isla.; Main.)	ANCOVA (MPD; IM; Overall)
SVL	24.40; 19.48	0.993; 0.602; 0.05
HLL	0.031; 0.036	0.098; 0.0014 ; 0.941
HDL	0.028; 0.013	<0.0001 ; <0.0001 ; 0.086
TOL	0.029; 0.025	0.019 ; 0.505; 0.0009
TAL	0.416; 0.254	0.037 ; <0.0001 ; 0.234
VSC	1.464; 1.505	0.583; 0.502; 0.263
DSC	2.912; 2.726	0.009 ; 0.411; 0.663
LAM	4.473; 2.851	<0.0001 ; 0.159; 0.358
HSC	0.981; 1.866	0.655; <0.0001 ; 0.458

clustering alone. Indeed, ANCOVA results show a significant mainland–island effect for some traits even when accounting for the demonstrated correlation of phylogenetic and morphological clustering.

CLUSTERED ASSEMBLAGES

We posit that the general trend of clustering in both phylogenetic and morphological structure in *Anolis* assemblages largely reflects biogeographical constraint to species dispersal and phylogenetic constraint to trait evolution. The coexistence of closely related species indicates some degree of geographic lability in historical distributions of species (e.g. [Chesser & Zink, 1994](#); [Losos & Glor, 2003](#); [Fitzpatrick & Turelli, 2006](#)). However, physiographic barriers and dispersal filters should constrain the movement of species in such a way that speciation events will usually occur on a limited geographic scale ([Weir & Price, 2011](#); [Wiens *et al.*, 2011](#)) and contributions to an assemblage should come from source pools that are both geographically and phylogenetically proximal ([Mittelbach & Schemske, 2015](#)). This scenario is born out in our results, where the distribution of MPD values indicates assemblages tend to comprise close relatives ([Fig. 1](#)).

Geographic aspects of speciation and assemblage structure also have an environmental component. Environmental conditions are likely to be similar in geographically proximate areas, and similar environments should beget similar selective pressures. Because most source pools are composed of geographic and phylogenetic neighbours, common environmental

conditions should act similarly on trait evolution in source pools that form an assemblage and further contribute to the pattern of morphological clustering observed here. In sum, viewed from a broad geographic perspective, anole assemblages tend to comprise closely related, biogeographically constrained species, and covariance of geography, phylogeny and environment contributes to the general trend of morphological clustering within anole assemblages.

Here, we favour a biogeographic interpretation, but we note that environmental filtering, competition, predation and, as noted above, covariance of numerous other biotic and abiotic factors can produce patterns of assemblage clustering (see: [Vamosi *et al.*, 2009](#); [Mayfield & Levine, 2010](#); [Cadotte & Tucker, 2017](#)). Moreover, geographic lability of species and shifts in climatic or ecological regimes make it difficult to ascertain the processes responsible for assemblage formation based solely on analyses of the kind performed here. We hope that future work can elaborate from our pattern-based analyses to test more mechanistic explanations.

GREATER ANTILLEAN ECOMORPHS

The trend of phylogenetic and morphological clustering is largely upheld among assemblages containing Greater Antillean (GA) ecomorphs, long cited as exemplars of morphological diversity resulting from congeneric, competition-driven adaptive radiations ([Williams, 1972](#); [Losos, 1994](#)). This result suggests most GA assemblages, like most assemblages, comprise geographically and phylogenetically close relatives. However, among the 50 GA assemblages included in our analyses, we observe two notable departures from our null models: overdispersion of phylogenetic distances in several GA assemblages and overdispersion in two morphological traits. Eight assemblages occurring on Cuba, Hispaniola and Puerto Rico display phylogenetic overdispersion significantly greater than expected from null models (MPD = 0.125–0.127; RankHi MPD > 0.56), whereas all remaining GA assemblages are clustered (MPD < 0.125; RankHi MPD < 0.47). Six of these assemblages occur on Hispaniola, where departure from the pattern observed for anole assemblages in general (and those occurring on neighbouring islands), likely reflects the complex historical biogeography of Hispaniolan anoles ([Williams, 1976, 1983](#); [Mahler *et al.*, 2010](#); [Poe *et al.*, 2017](#)).

Two traits, head length and tail length, present greater than expected overdispersion for a significant portion of GA assemblages. Overdispersion of head size is centred on Cuba, where this pattern may be attributed to the island-wide sympatry of *Trachypilus* clade anoles, which possess short heads, and *carolinensis* group anoles, which possess long heads. Members

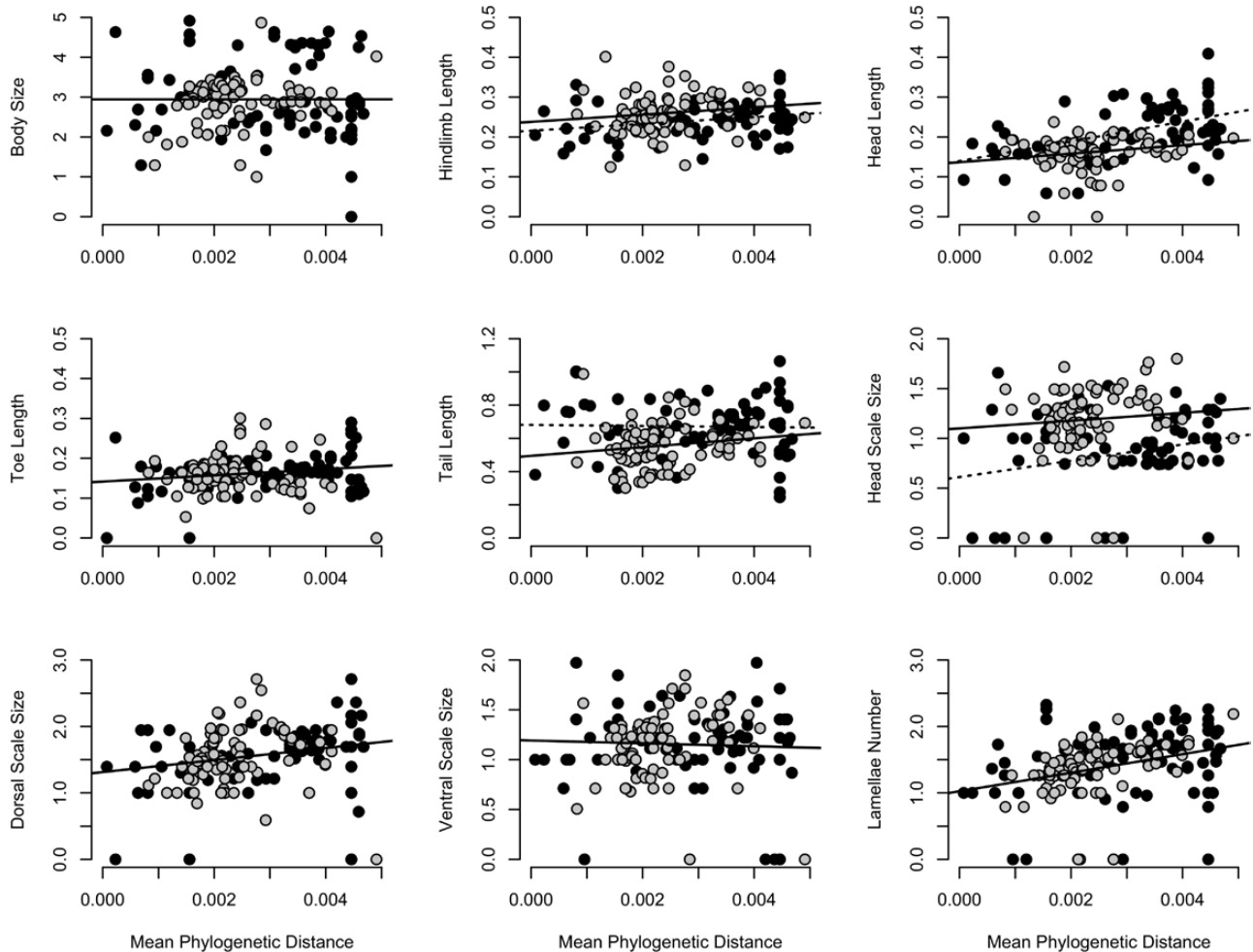


Figure 3. Linear regressions presented for mean trait distance (MTD) by mean phylogenetic distance (MPD) after Box-Cox transformation of tested traits for island (black) and mainland (grey) assemblages. Separate regression lines for island (solid) and mainland (dashed) assemblages are plotted to traits with a significant island-mainland effect and a single regression line is plotted when no significant island-mainland effect was detected.

of these clades also drive overdispersion of head size in several Bahamian and Cayman Island assemblages, which often comprise only a *Trachypilus* clade and a *carolinensis* group species. Twig and grass ecomorphs, found in most GA assemblages, contribute to overdispersion of tail length observed in numerous assemblages on multiple islands. Twig anoles are characterized by short tails, usually not much longer than body length, whereas grass anoles possess tails up to five times their body length. Five of the seven remaining traits tend to cluster within island assemblages and two (toe length and dorsal scale number) are not significantly different than null expectations. We note that, as demonstrated by [Losos *et al.* \(2003\)](#), species comprising an assemblage are likely able to coexist because of overdispersion along a single morphological, ecological or physiological axis. Although

we examine traits that should reflect ecological differences, we did not set out to address fine-scale aspects of niche complementarity that would necessitate the inclusion of ecological variables. Generally, covariance of phylogenetic, geographic and environmental factors seem to work toward constraining traits to remain similar among species in most assemblages (see above). However, congeneric, competition-driven adaptive radiation seems to have contributed to overdispersion of some traits in some assemblages ([Losos, 1994](#)).

MAINLAND–ISLAND CLUSTERING PATTERNS

Given the dynamics of island biotas in general – immigration, emigration, extinction and speciation rates driven by covariance of island isolation, size, age, resource availability and a dearth of predators and/

or competitors (Simpson, 1953; MacArthur & Wilson, 1967; Carlquist, 1974; Schluter, 1988, 2000; Harmon & Gibson, 2006) – and that much of the West Indian anole diversity is derived from intra-island adaptive radiations (Losos, 2009; Poe *et al.*, 2017), one might expect greater phylogenetic clustering in island assemblages. Yet, we identify a significantly greater degree of phylogenetic clustering in mainland assemblages. We note that, although significant, the effect size between mainland and island assemblages is extremely small and the mode for both island and mainland assemblages is identical. Consequently, island and mainland assemblages may be viewed as having similar degrees of clustering. In part, this result may be an artefact of sampling bias. Indeed, many of our studied mainland assemblages include only *Draconura* clade anoles and few contain both. Surely, one could bolster the mean mainland MPD value by sampling more assemblages, including both *Dactyloa* and *Draconura* clade anoles, and in doing so may or may not produce a more accurate comparison of phylogenetic clustering between mainland and island assemblages. However, we sought to minimize pseudoreplication by minimizing species overlap (see above). Alternatively, our result may accurately reflect the random interplay of factors by which species pools contribute to an assemblage.

One potential major implication of the latter scenario is that mainland lineages are somehow under relatively greater biogeographic constraint than island lineages. That is, biogeographic constraints on mainland assemblage structure (physiographical barriers, congeneric or intergeneric competitive exclusion, or some combination thereof) seem to be slightly more efficient in precluding distantly related anole taxa from coexisting in mainland systems than in island systems. This result is surprising, for two reasons. First, it suggests that mainland physiographic barriers to dispersal may be as formidable as overwater barriers to inter-island dispersal. Second, the mainland may harbour multiple localized adaptive radiations, as in the Greater Antilles. Vamوسي *et al.* (2009) suggest a scenario whereby a regional phylogeny occupying a large geographic area characterized by multiple, geographically discrete adaptive peaks may promote phylogenetic clustering. A scenario of this sort seems to have played out in both major mainland clades (see *Dactyloa* and *Draconura* clades in Poe *et al.*, 2017).

Although not explicitly tested in the present study, priority effects and taxon cycles may also drive difference in clustering. In such cases, species arriving early during assemblage formation are likely to be close relatives, from nearby source pools that are morphologically similar relative to species from more distant source pools. Subsequently, a priority effect similar to that outlined by Losos *et al.* (1993) may

exclude the recruitment of later arriving taxa into the assemblage. This phenomenon may act to maintain phylogenetic clustering and morphology may be constrained by phylogeny or may disperse only along a single axis. Thus, unless an assemblage is subject to frequent taxon cycles, it seems likely that clustering will be maintained. The existence of fewer active taxon cycles on the mainland could result in greater phylogenetic clustering in mainland faunas. Roughgarden & Pacala (1989) proposed a taxon cycle wherein islands harbouring solitary species are subject to invasion by a second species, which drives the incumbent to extinction through competition (for further discussions of this system, see: Losos, 1992; Roughgarden, 1992). This process of invasion and extinction results in two-species communities formed of distant relatives rather than by adaptive radiation. The greater complexity and stability of mainland systems (Schluter, 1988, 2000) might limit repeated invasion and thus preserve the contents of older adaptive radiations on the mainland. Further, the majority of assemblages with high MPD values comprise 2–4 species and occupy small islands (e.g. cays associated with Cuba, Hispaniola and The Bahamas) where such taxon cycles are likely common.

Our ANCOVA results indicate both a strong phylogenetic effect and a distinct mainland–island effects for several traits (Table 1; Fig. 3). We expected that any island effects would be manifest as greater dispersion in island communities, due to the presence of the famously diverse anole ecomorphs that comprise many Greater Antillean assemblages (Williams, 1983; Losos *et al.*, 1998; Losos, 2009). Indeed, head length and tail length display strong mainland–island effects and greater dispersion for island assemblages (see above discussion of these traits). However, head scale size and hindlimb length display relatively greater dispersion in mainland assemblages. Head scale size displays clustering in both island and mainland assemblages (RankLow MTD = 0.116 and 0.288, respectively; $P < 0.0001$), whereas hindlimb length tends to cluster in island assemblages but is randomly distributed in mainland assemblages (RankLow MTD = 0.409 and 0.496, respectively; $P = 0.0346$). These results may indicate greater competition (congeneric, intergeneric, or both) regarding these traits on the mainland, that variability of these traits is greater among source pools available to mainland assemblages than those available to island assemblages (i.e. greater variation within discrete mainland regions than within islands), that a greater abundance of predators in mainland systems (Siliceo-Cantero *et al.*, 2016) has promoted the evolution of multiple predator avoidance tactics that are manifest in these traits, or perhaps some other factor. Traditionally, these kinds of patterns are attributed to

greater perceived diversity and complexity in mainland environments (Schluter, 1988, 2000).

CONCLUSION

Our study represents the broadest taxonomic and geographic assessment of congeneric vertebrate assemblages to date. Our integrated assessment of assemblage composition, including a nearly complete phylogeny, ecologically important traits and phylogenetic correction, has allowed us to incorporate incumbent phylogenetic constraints to trait dispersion and identify broad-scale patterns arising from differential covariance of biotic and abiotic drivers of community assembly. Although we do not address the fine-scale drivers of assemblage structure directly, we hypothesize that anole assemblages experience biogeographic constraints to dispersal from source pools and phylogenetic constraints to trait evolution. These factors create anole assemblages that tend to be clustered in both phylogenetic and morphological structure.

We have identified unequivocal differences in the degree of clustering among mainland and island anole assemblages and demonstrate that differences in trait dispersion are not simply an artifact of phylogeny. The slight but significant difference in overall patterns of phylogenetic clustering implies mainland species pools experience greater constraints to dispersal than do species pools on islands, and that mainland *Anolis* evolution may be characterized by localized adaptive radiations as in the Greater Antilles. Differences in trait dispersion between mainland and island environments are not straightforwardly interpretable as reflecting general trends, as two traits are more dispersed on islands and two are more dispersed on the mainland. The more dispersed traits on islands may reflect the well-known ecomorphological diversity of Greater Antillean anoles and the suggested greater environmental complexity on the mainland constraining evolution via extrageneric competition. However, traits presenting greater dispersion in mainland assemblages may indicate that greater diversity of mainland systems may actually select for greater *Anolis* diversity in certain traits. These speculations may be tested with fine-scale approaches.

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SUPPORTING INFORMATION

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

Appendix 1. Assemblage information for 167 *Anolis* lizard communities including: name, location (country or region), mainland-island designation, and number of species.

Figure S1. An example case where size-correction by ratio and residual give the same results for our data. Data are from Armstead and Poe (2015), 10 individuals each of 13 species measured for limb and body length. Graph shows mean limb length/SVL ratio versus residuals from linear regression of ln mean SVL versus ln mean limb length. Data points are species. $R_2 = 0.98$ for regression of residual predicting ratio.

Figure S2. The distribution of rankHi P values generated from mean phylogenetic distances for island and mainland assemblages. Values less than 0.50 indicate clustering and values greater than 0.50 indicate dispersion. Solid and dashed vertical lines indicate means for island and mainland assemblages, respectively.

Figure S3. Distributions of rankLow P values generated from MTD of tested traits for island (dark grey) and mainland (light grey) assemblages. Solid and dashed vertical lines indicate means for island and mainland assemblages, respectively. Values less than 0.50 indicate clustering and values greater than 0.50 indicate overdispersion.

Table S1. P values obtained from Spearman's Rho tests for phylogenetic distance (MPD) by number of taxa (ntaxa) and nine morphological traits by MPD and ntaxa. Results indicate significant bias with respect to mean trait distance and MPD for most traits. Traits are: body size (SVL), hindlimb length (HLL), head length (HDL), toe length (TOL), tail length (TAL), ventral scale number (VSC), dorsal scale number (DSC), lamellae number (LAM), and head scale size (HSC).