

SHARED AND UNIQUE FEATURES OF DIVERSIFICATION IN GREATER ANTILLEAN *ANOLIS* ECOMORPHS

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Abstract.—Examples of convergent evolution suggest that natural selection can often produce predictable evolutionary outcomes. However, unique histories among species can lead to divergent evolution regardless of their shared selective pressures—and some contend that such historical contingencies produce the dominant features of evolution. A classic example of convergent evolution is the set of *Anolis* lizard ecomorphs of the Greater Antilles. On each of four islands, anole species partition the structural habitat into at least four categories, exhibiting similar morphologies within each category. We assessed the relative importance of shared selection due to habitat similarity, unique island histories, and unique effects of similar habitats on different islands in the generation of morphological variation in anole ecomorphs. We found that shared features of diversification across habitats were of greatest importance, but island effects on morphology (reflecting either island effects per se or phylogenetic relationships) and unique aspects of habitat diversification on different islands were also important. There were three distinct cases of island-specific habitat diversification, and only one was confounded by phylogenetic relatedness. The other two unique aspects were not related to shared ancestry but might reflect as-yet-unmeasured environmental differences between islands in habitat characteristics. Quantifying the relative importance of shared and unique responses to similar selective regimes provides a more complete understanding of phenotypic diversification, even in this much-studied system.

Key words.—Adaptive radiation, *Anolis*, convergent evolution, diversification, ecomorphology, historical contingency, morphometrics, natural selection.

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One of the most remarkable features in evolutionary biology is the striking phenotypic convergence among taxa that inhabit similar environments. Such examples of convergent evolution suggest that natural selection can often produce predictable evolutionary outcomes (Harvey and Pagel 1991; Robinson and Wilson 1994; Conway Morris 1998; Losos et al. 1998; Schluter 2000; Melville et al. 2006). However, each species has its own distinct and unique historical path; the idiosyncrasies and contingencies of each species' course can lead to divergent evolution even for species occupying identical selective environments (Pianka 1986; Cadle and Greene 1993; Price et al. 2000; Gould 2002). Factors that may lead to distinct evolutionary trajectories of species occupying similar environments include differences in clade-specific factors (e.g., genetic variances and covariances among traits), chance historical events (e.g., genetic drift), and cryptic environmental differences (past or present disparity in selection) (e.g., Harvey and Pagel 1991; Cadle and Greene 1993; Schluter 1996; Price et al. 2000; Gould 2002; McGuigan et al. 2005).

Due to the combined influences of shared selective regimes and unique histories, we expect to frequently observe both shared and unique features of diversification when multiple species experience common selective pressures (e.g., Winemiller 1991; Travisano et al. 1995; Huey et al. 2000; Matos et al. 2002; Langerhans and DeWitt 2004). But which mechanism (shared selection vs. unique history) is generally more important in determining evolutionary patterns? Understanding the relative importance of shared selective regimes and unique histories in generating phenotypic outcomes is critical to elucidating the relative generality or peculiarity in evolutionary diversification (e.g., Irschick et al. 1997; Huey et

al. 2000; Matos et al. 2002; Van Buskirk 2002; Vanhooydonck and Irschick 2002; Langerhans et al. 2003; Ruzzante et al. 2003; Blackledge and Gillespie 2004; Langerhans and DeWitt 2004; Hendry et al. 2006).

Anolis lizard ecomorphs of the Greater Antilles represent a classic example of convergent evolution: similar sets of habitat specialists have evolved independently on each island (Williams 1983; Losos et al. 1998; Jackman et al. 1999; Nicholson et al. 2005). On each of the four Greater Antillean islands, anoles have partitioned the structural habitat into at least four categories; species in the same category on different islands exhibit similarities in morphology, ecology, and behavior (e.g., Williams 1983; Mayer 1989; Losos 1990). To date, research has focused on phenotypic convergence of anoles in similar habitats (e.g., Williams 1983; Losos 1990; Losos et al. 1998; Beuttell and Losos 1999; Elstrott and Irschick 2004; Harmon et al. 2005). However, the relative importance of unique histories in producing divergent phenotypes is currently unknown in this system.

We postulate three possible causes of phenotypic divergence among species occupying similar habitats. First, an island effect may exist such that across habitats, species on one island are consistently different from their counterparts on other islands (e.g., perhaps insect prey or tree diameters differ among islands). Second, phylogenetic effects may exist such that members of one clade exhibit consistent differences from members of another clade. Third, species inhabiting a particular habitat may experience unique events and situations in the course of their evolution that affect those species differently than other species on their own island or species in the same habitat on other islands.

We examined the extent to which species in similar habitats

across islands have diverged phenotypically, and we attempted to assess the relative importance of these three putative causes of divergence. However, to a large (but not complete) extent, island and phylogenetic effects are confounded because large clades have radiated on each island. Thus, although island effects per se might be an important evolutionary source of variation, we anticipated that distinguishing them from phylogenetic effects would be difficult. Nonetheless, using a molecular phylogeny, we attempted to disentangle island and phylogenetic effects on evolutionary divergence.

MATERIALS AND METHODS

Data Collection

Four ecomorph categories of anoles are found on each of the Greater Antillean islands, named for the particular habitat the lizards occupy (trunk-ground, trunk-crown, twig, and crown-giant; two other ecomorph categories do not occur on all four islands). We investigated variation in morphology of anoles (independent of size) belonging to these four ecomorph categories. We examined morphological characters that have traditionally been used in distinguishing ecomorphs and appear to represent adaptations for enhanced locomotor performance in particular structural habitats (e.g., limb lengths), as well as characters rarely investigated that might relate to other fitness-related functions (e.g., head shape; for further discussion of the functional significance of these characters see Beuttell and Losos 1999).

We examined morphology of 27 species of *Anolis* representing all four ecomorphs from all four Greater Antillean islands (Cuba, Hispaniola, Jamaica, Puerto Rico). Some ecomorph categories were represented by more than one species per island. Species were chosen based on specimen availability. Using digital calipers, we measured snout-vent length (SVL), forelimb length, hindlimb length, pectoral girdle width, pelvic girdle width, toepad width, head depth, jaw length, and jaw width. Measurements were taken on 375 adult male individuals ($\bar{x} = 13.9$ specimens per species; range = 1–58). Three species were represented by only one individual; however, each of these species belonged to an ecomorph category that was represented by other species from the same island for which we measured multiple specimens. One additional measurement for each species, number of subdigital lamellae on the second and third phalanges of pedal digit IV, was taken from a previous study (Losos et al. 1998). All morphological variables were ln-transformed for statistical analysis. To examine size-independent morphology, we calculated the residual value of each variable regressed against SVL and used mean values for species in all analyses.

Statistical Analysis

We employed a statistical approach that explicitly examines the importance of shared responses to similar environments regardless of history, unique histories among islands regardless of environment, and history-dependent responses to similar environments in generating phenotypic variation (see Langerhans and DeWitt 2004). With this approach, we can simultaneously quantify the importance of both shared

and unique features of evolutionary diversification. Specifically, we conducted multivariate analysis of variance (MANOVA) using the nine morphological variables to investigate the relative effects of shared selective regimes (habitat), unique island histories (island), and unique effects of similar habitats on different islands (interaction between habitat and island) on anole morphology. We used Wilks's partial η^2 (measure of partial variance explained by a particular factor; multivariate approximation of $SS_{\text{effect}}/[SS_{\text{effect}} + SS_{\text{error}}]$) to compare the relative importance of the three factors in the model (see appendix of Langerhans and DeWitt 2004). MANOVA generates canonical variates for each factor that describe morphological variation designed to have optimal correlation with a given factor. Thus, canonical axes of this model describe the nature and magnitude of the association between anole morphology and each of the three factors. We examined these canonical axes to interpret the nature of morphological differences between groups. Statistical analysis was conducted using JMP software (ver. 5.1, SAS Institute, Inc., Cary, NC).

To examine the effects of phylogenetic relationships on our MANOVA results, we used sequences for 121 anole species and one outgroup (*Polychrus acutirostris*) from a 1481-bp mitochondrial DNA region that spanned the protein coding regions ND1 to COI, including the complete ND2 gene, the origin of light-strand replication, and five tRNAs; all sequences used were previously published (Nicholson et al. 2005 and references therein) and are available on GenBank (<http://www.ncbi.nlm.nih.gov/Genbank/>). We analyzed sequences using the GTR + I + Γ model, selected using hierarchical likelihood-ratio testing with the program MrModelTest version 1.0b (Nylander 2002). We then conducted a Bayesian analysis using the program MrBayes 3 (Ronquist and Huelsenbeck 2003), with four chains for 1,000,000 generations and selecting one tree every 5000 generations for the posterior distribution. Likelihoods of the trees in the Bayesian analysis reached a plateau at around 50,000 generations; to be conservative, we discarded results from the first 100,000 burn-in generations. This resulted in a posterior distribution of 180 trees. We formed a consensus of these trees with branch lengths using MrBayes 3. This tree was constructed without assuming a molecular clock; therefore, we made it ultrametric using penalized likelihood as implemented in the program r8s (Sanderson 2002). We first identified the least-squares smoothing parameter (to the nearest 0.1 \log_{10} unit) using cross-validation ($\log_{10}[\text{smoothing parameter}] = 0.7$). We then used this smoothing parameter for the penalized-likelihood tree linearization procedure, checking the local stability of the solution by starting three searches with different initial random guesses, and ensuring that they all converged on the same answer (Sanderson 2002). Branch lengths were scaled to relative time by arbitrarily setting the root node to an age of 100. We then pruned out all but the 27 species included in this study, resulting in the tree presented in Figure 1.

To estimate support for topological relationships among species used in this study, we used the posterior distribution of 180 trees obtained from the Bayesian analysis. We pruned all but the 27 species of interest from each of these trees and then used the resulting pruned tree distribution to define sup-

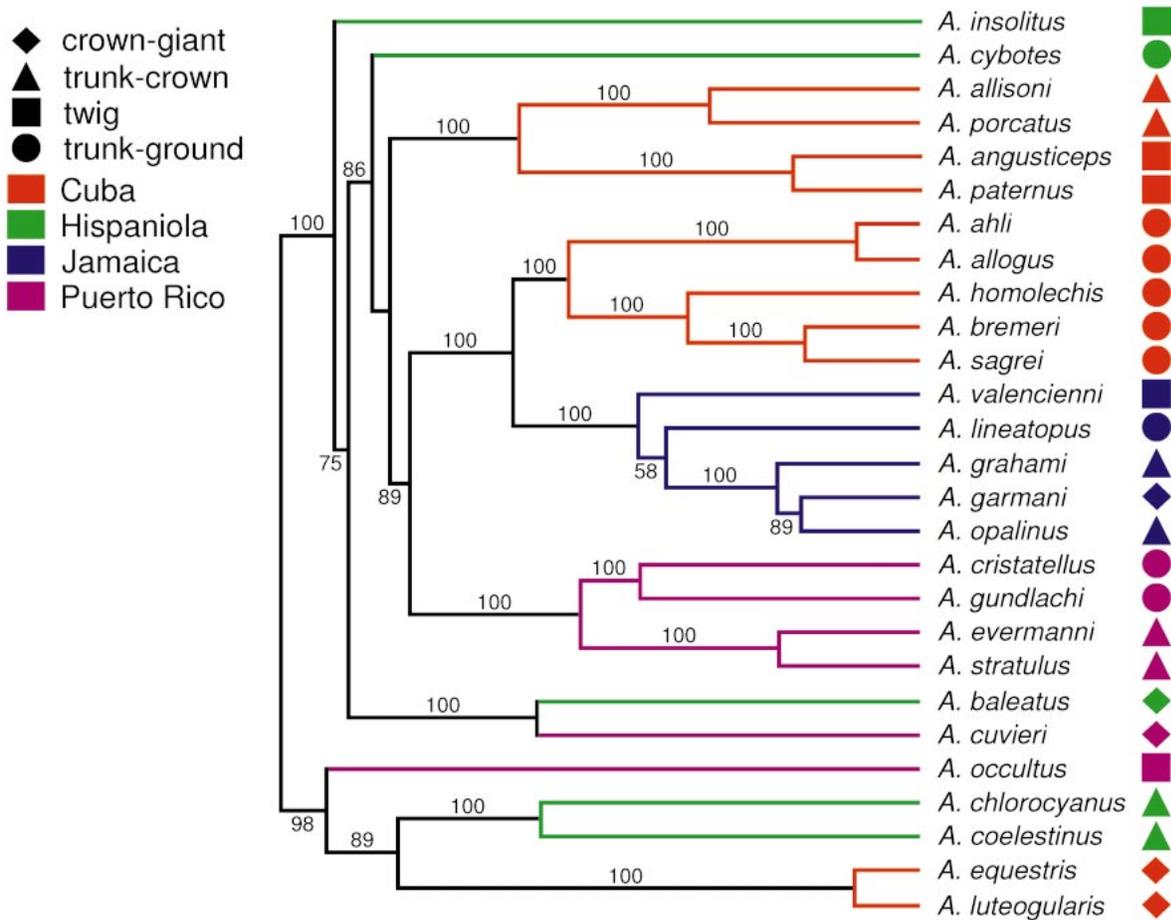


FIG. 1. Phylogeny of *Anolis* used in the study. Island of origin and ecomorph category are given for each species. Numbers represent Bayesian posterior probabilities for each node in the pruned tree topology. Branch lengths are relative, with the distance from the root to the tips arbitrarily set to 100 units.

port for nodes in our presented phylogeny. We generated a majority-rule consensus tree from this set of trees in PAUP* (Swofford 2002) and calculated support values as the proportion of pruned trees that included each clade in our phylogeny. We then used the pruned ultrametric tree to calculate the phylogenetic distance separating each pair of species on the tree using the program PDAP (Garland et al. 1993). This matrix of pairwise patristic distances was used in statistical analyses described below.

To examine how our results might have been influenced by phylogenetic relatedness, we conducted partial Mantel tests using the program PASSAGE (Rosenberg 2001). These analyses evaluated the correlation between two matrices, while statistically holding a third matrix constant (Smouse et al. 1986; Manly 1991; Thorpe 2002; Harmon et al. 2005). Significance was assessed by comparing the z -statistic of the actual matrices to the z -statistics from 9999 random permutations. All distance matrices used in partial Mantel tests represented distances in a particular variable between all species pairs. We examined the correlation between morphological distance—defined as the Mahalanobis distance using canonical axes derived from a given factor in the MANOVA—and a design matrix describing a particular factor in

the model (i.e., habitat, island, or their interaction), while holding the patristic distance matrix constant. Thus, we tested the matrix correlation between morphological distance and our variable of interest, controlling for phylogeny. Design matrices for main effects reflected whether species pairs were from the same or different habitat (or island; assigned 0 or 1). Design matrices for interaction terms can be much more complex. We calculated this design matrix by conducting a singular value decomposition of the interaction effect (predicted values from a MANOVA including only the interaction term) and extracting the pairwise distances (Golub and Van Loan 1996).

We also examined whether phylogenetic relatedness might explain particular unique features of diversification revealed by the interaction term. To accomplish this, we obtained phylogeny-free morphological distances between all species pairs and tested the association between these distances and several specific effects identified by the interaction term from the MANOVA. Specifically, we regressed Mahalanobis distance (using canonical axes derived from the interaction term) on patristic distance and obtained the residual values (identical to the first step of a partial Mantel test). These data were then tested for their association with the predictions made

TABLE 1. Results of MANOVA examining morphological variation among 27 species of Greater Antillean *Anolis* lizards. *F*-ratios were approximated using Wilks's Λ values. Partial variance explained by each effect was estimated using Wilks's partial η^2 . Values marked with an asterisk remained significant after accounting for phylogenetic relationships.

Test for	Factor	<i>F</i>	df	<i>P</i>	Partial variance explained
Shared diversification	habitat	13.92	27, 9.4	0.0001*	97.3%
Island histories	island	3.31	27, 9.4	0.0295	89.9%
Unique diversification	habitat \times island	3.05	81, 28.4	0.0007*	80.4%

from the interaction term of the MANOVA. If phylogeny did not account for particular unique aspects of diversification, distances between certain species pairs (those implicated by the nature of the interaction term effects) should be greater than other species pairs chosen at random, with the constraint that they occupy the same habitat. For example, the interaction term of the MANOVA might reveal that the effect of the trunk-ground habitat on morphology differed between Cuba and the other islands. To examine whether phylogeny accounted for this effect, we would compare the average phylogeny-free morphological distance between Cuban trunk-ground species and other trunk-ground species to the average distance for a random set of an equal number of species pairs that reside in the same habitat. To determine significance, we repeated the procedure 9999 times, comparing the observed average distance to the permuted average distance each time. Because the interaction term could describe multiple effects, we conducted a test of each specific effect.

RESULTS

MANOVA revealed significant effects for all factors (Table 1). Most of the morphological variance among anole species was explained by the MANOVA model, as reflected by the high partial η^2 -values (Table 1). Based on significance values and estimates of partial η^2 , the habitat term (i.e., shared morphological differences among habitats on each island) was the most important factor associated with anole morphology. This suggests that natural selection has repeatedly produced similar morphological outcomes within similar habitats. Island effects were also evident, revealing consistent differences among species in similar habitats as a function of island of occurrence. Furthermore, the interaction term revealed significant effects, indicating aspects of habitat divergence unique to species occupying particular islands. Partial η^2 -values suggested that island effects were of slightly larger magnitude than unique features of diversification.

Evaluation of canonical axes revealed that the effect of habitat involved most aspects of morphology and largely matched previous findings (e.g., fewer toe lamellae and longer hindlimbs in trunk-ground anoles; more toe lamellae in trunk-crown anoles; shorter hindlimbs in twig anoles; see Losos 1990; Beuttell and Losos 1999; Harmon et al. 2005; Appendix). Island effects on morphology primarily involved pectoral width, jaw width, and head depth and did not result from any peculiar island. Rather, all four islands were implicated in generating island effects (Appendix). These results suggest that island histories influenced certain aspects

of anole morphology, regardless of the habitats particular anoles occupy.

Three distinct causes for the significance of the interaction term were evident (Fig. 2, Appendix): (1) the Puerto Rican crown-giant anole differed in morphology (narrower pectoral width, deeper head, wider pelvic width) from crown-giant anoles on other islands; (2) twig anoles from Jamaica and Hispaniola differed in morphology (deeper head, narrower pelvic width) from twig anoles on Cuba and Puerto Rico; and (3) Cuban trunk-crown anoles differed in morphology (wider jaw, shorter hindlimbs) from other trunk-crown anoles. Thus, island-specific aspects of habitat diversification primarily involved head shape and pelvic width, and was observed in all habitat types except the trunk-ground habitat.

When we controlled for phylogenetic relationships among species, the habitat term and the interaction term both remained significant, but island effects were no longer evident (Table 2). This indicated that effects of island history could be statistically explained by their association with phylogeny (i.e., island history and phylogeny are confounded). Thus, either phylogenetic effects or some other factor(s) associated with island of occurrence influenced anole morphology; however, which source played a larger causal role cannot be determined due to the extent of covariation between phylogeny and island history. By examining each of the three major aspects described by the interaction term, we found that one aspect was no longer significant after adjusting for phylogeny: Cuban trunk-crown anoles differed from other trunk-crown anoles in certain aspects of morphology due to their resemblance to their sister taxa, Cuban twig anoles (see Fig. 1, canonical axis 2 in Fig. 2). However, the other two unique features of habitat diversification remained highly significant even after controlling for phylogenetic relationships.

DISCUSSION

Evolutionary biologists aim to understand the relative magnitudes of shared selective regimes, unique histories, and the interaction between these two evolutionary sources of diversification (e.g., Irschick et al. 1997; Huey et al. 2000; Matos et al. 2002; Van Buskirk 2002; Ruzzante et al. 2003; Blackledge and Gillespie 2004; Hendry et al. 2006). Nonetheless, the explicit quantification and evaluation of the importance and nature of these mechanisms rarely has been attempted (Langerhans and DeWitt 2004). Here we simultaneously quantified evolutionary sources of phenotypic variation and found that shared selective regimes within similar habitats, unique island/phylogenetic histories, and unique responses to similar habitats on different islands have all played

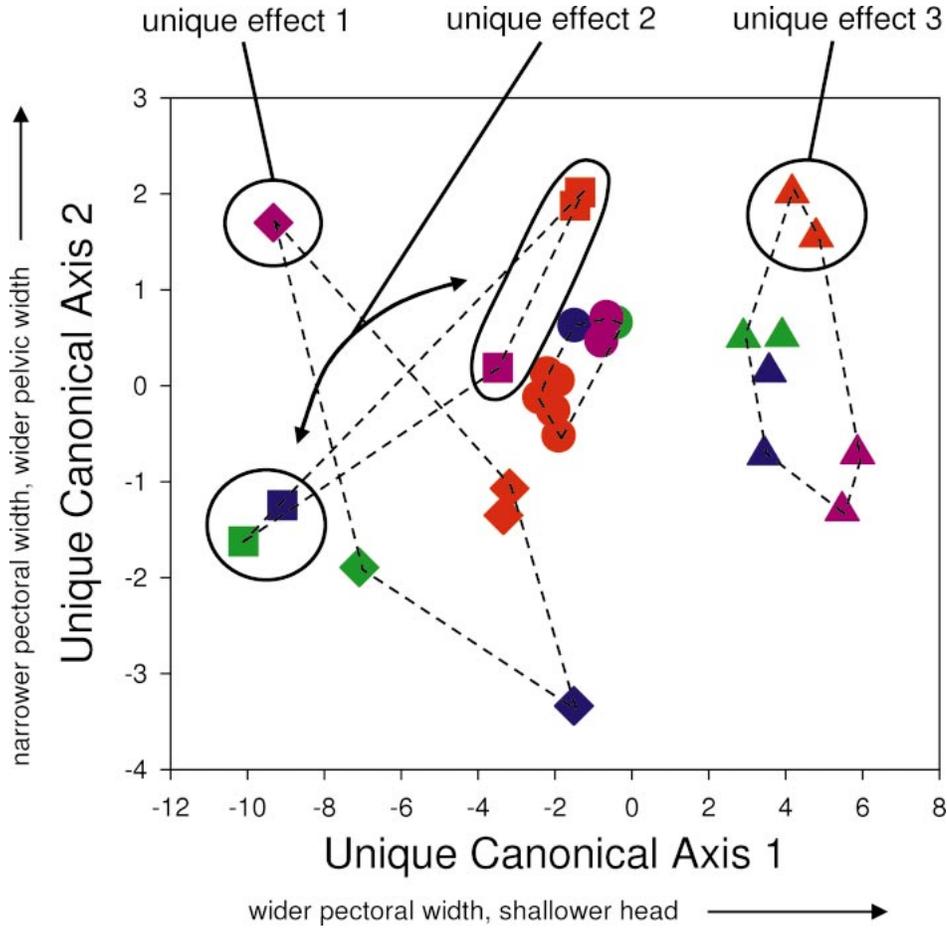


FIG. 2. Morphological variation along the first two canonical axes derived from the interaction term (habitat × island) of the MANOVA. Convex polygons (dashed lines) delineate each ecomorph category. Highlighted unique effects represent the three distinct cases identified by the interaction term. Symbols as in Figure 1.

significant roles in generating morphological variation in Greater Antillean *Anolis* ecomorphs.

Among these three sources of variation, our results suggest that common selective pressures within similar habitats have been most important in producing the morphological patterns observed among Caribbean anoles. This finding is consistent with previous work on Greater Antillean *Anolis* lizards, a system that has become a model example of adaptive radiation (e.g., Williams 1983; Losos 1994; Losos et al. 1998; Schluter 2000; Streelman and Danley 2003), but further extends this work by establishing that shared morphological responses are of greater importance than island histories or island-specific responses to structural environments. More-

over, our results suggest that these alternative sources of morphological variation (i.e., island/phylogenetic histories and island-specific responses to similar environments) should not be ignored, as they represent significant aspects of diversity, albeit of lesser importance than shared selective regimes in this system.

We found that overall island effects on anole morphology were largely confounded by phylogenetic relatedness. Thus, while island histories influenced anole morphology, this may have resulted from island effects per se, phylogenetic effects, or a combination of both sources. Regardless of which evolutionary source underlying island histories was more important, our results indicate that the unique histories of anoles

TABLE 2. Significance of association between anole morphology and the following factors, controlling for phylogenetic relationships (patristic distance).

Source	P
Shared diversification (habitat)	0.0001
Island histories (island)	0.2438
Unique diversification (effect of habitat differed among islands)	0.0315
Unique effect 1 (crown-giant effect)	0.0019
Unique effect 2 (twig effect)	0.0001
Unique effect 3 (trunk-crown effect)	0.5168

on different islands influenced morphology, irrespective of habitat. One testable explanation for island effects on morphology is that island-specific *Anolis* community composition (i.e., number of ecomorph categories occupied by anoles: Cuba: six, Hispaniola: six, Puerto Rico: five, Jamaica: four) influences anole morphology, independent of habitat (Williams 1983; Beuttell and Losos 1999). However, we can reject this claim as morphological differences among islands were not associated with similarity in ecomorph composition (Mantel results: without controlling for phylogeny, $P = 0.26$; controlling for phylogeny, $P = 0.69$). Thus, the actual causes of morphological differences among islands remain unclear.

Island-specific features of habitat diversification were only partially associated with phylogeny. Cuban trunk-crown anoles exhibited wide jaws and short hindlimbs relative to other trunk-crown anoles. However, when phylogenetic relationships were considered, this finding was no longer significant. Cuban trunk-crown anoles are closely related to the wide-jawed, short-legged Cuban twig anoles, whereas trunk-crown anoles on other islands are not closely related to twig anoles. Hence, these unique characteristics of trunk-crown anoles on Cuba may reflect a phylogenetic effect resulting from shared evolutionary history with Cuban twig anoles.

Two of the three unique aspects of habitat divergence remained significant after controlling for phylogenetic effects, suggesting that mechanisms independent of shared ancestry are responsible for these results. These unique features may have arisen via differences in selection among similar habitats on different islands caused by as yet unknown differences in environmental characteristics (e.g., prey type, microclimate). In addition, unique aspects of habitat divergence might reflect differences in past selective regimes, random historical events (i.e., genetic drift), or differences in genetic variance-covariance matrices among species (e.g., Harvey and Pagel 1991; Schluter 1996; Gould 2002).

Effects of island histories and island-specific features of habitat diversification primarily involved morphological characters not traditionally used in assessing ecomorph status (e.g., head shape, pelvic width, pectoral width). *Anolis* lizards are believed to be specialized for alternative substrata, requiring different morphologies related to locomotor performance (e.g., relative limb lengths, lamellae number) in different habitats (e.g., Williams 1983; Losos 1990; Irschick and Losos 1998; Losos et al. 1998), and our results demonstrating strong shared features of habitat diversification are consistent with this claim. However, the relationship between locomotor performance—or, more directly, fitness in alternative habitats—and the morphological features involved in unique aspects of habitat divergence is currently unknown. Thus, future work should assess the possible effects of unique morphological responses on fitness components and examine possible differences in habitat characteristics among islands.

The results of this study emphasize that there is more to the study of convergent evolution than simply the investigation of convergent patterns. Unique elements of morphological diversification were observed in all habitat types except the trunk-ground habitat. In this sense, anoles inhabiting the trunk-ground habitat appear to represent the most convergent set of *Anolis* ecomorphs, a result only revealed by explicitly assessing unique features of habitat divergence in

addition to the shared features. To advance our knowledge of replicated evolution among multiple groups of organisms, evolutionary biologists must move beyond simply examining the significance of shared responses to shared selective regimes. Understanding the factors that contribute to divergent evolution among species occupying shared selective regimes is essential if we are to fully appreciate the relative generality or peculiarity of evolutionary trends (e.g., Huey et al. 2000; Gould 2002; Matos et al. 2002; Van Buskirk 2002; Ruzzante et al. 2003; Langerhans and DeWitt 2004; Hendry et al. 2006).

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APPENDIX

Standardized canonical coefficients for each morphological variable, corresponding to canonical axes derived from each factor of the MANOVA (HD, head depth; JL, jaw length; JW, jaw width; TPW, toe pad width; LN, lamellae number; HL, hindlimb length; FL, forelimb length; PEL, pelvic width; PEC, pectoral width). These coefficients depict the standardized contribution of each morphological trait on each axis, controlling for all other traits. While nine canonical axes were derived for the interaction term, the first three axes captured most of the significant unique features of diversification; thus, we only present results from these three axes. Group differences represent the rank order of species groups relevant to each canonical axis (CG, crown-giant; TC, trunk-crown; TG, trunk-ground; TW, twig; C, Cuba; H, Hispaniola; J, Jamaica; P, Puerto Rico). Bars above groups indicate groups that are not significantly different from each other using Tukey's HSD test.

Source	HD	JL	JW	TPW	LN	HL	FL	PEL	PEC	Group differences
Habitat										
Canonical axis 1	-2.630	1.753	1.949	-2.208	2.543	2.099	-1.805	0.713	3.522	TW < CG < TG < TC
Canonical axis 2	0.413	-0.180	-0.337	0.090	-0.289	0.895	-0.142	0.693	-0.659	TW < TC < CG < TG
Canonical axis 3	0.345	0.102	-2.019	0.322	0.270	-0.014	1.010	-1.101	1.812	TW < TG < TC < CG
Island										
Canonical axis 1	-2.513	1.698	2.346	-2.129	2.220	2.160	-2.191	1.240	2.330	H < J < P < C
Canonical axis 2	0.721	0.191	-1.697	0.595	-0.879	1.301	-0.425	1.669	-2.019	J < C < H < P
Canonical axis 3	-0.263	0.448	-0.782	-0.462	1.018	1.026	0.090	-0.094	1.960	H < C < J < P
Habitat × island										
Canonical axis 1	-2.684	1.660	2.209	-2.224	2.546	1.762	-1.715	0.388	3.695	P-CG < H-CG < C-CG < J-CG J-TW < H-TW < P-TW < C-TW
Canonical axis 2	-0.298	0.333	1.301	-0.433	0.026	1.298	-1.549	1.745	-1.925	J-CG < H-CG < C-CG < P-CG H-TW < J-TW < P-TW < C-TW P-TC < J-TC < H-TC < C-TC
Canonical axis 3	-0.081	-0.458	1.699	-0.055	-0.146	-1.598	0.093	-1.044	-0.306	P-TC < H-TC < J-TC < C-TC