CONVERGENCE AND THE MULTIDIMENSIONAL NICHE

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Abstract.—Convergent evolution has played an important role in the development of the ecological niche concept. We investigated patterns of convergent and divergent evolution of Caribbean *Anolis* lizards. These lizards diversified independently on each of the islands of the Greater Antilles, producing the same set of habitat specialists on each island. Using a phylogenetic comparative framework, we examined patterns of morphological convergence in five functionally distinct sets of morphological characters: body size, body shape, head shape, lamella number, and sexual size dimorphism. We find evidence for convergence among members of the habitat specialist types for each of these five datasets. Furthermore, the patterns of convergence differ among at least four of the five datasets; habitat specialists that are similar for one set of characters are often greatly different for another. This suggests that the habitat specialist niches into which these anoles have evolved are multidimensional, involving several distinct and independent aspects of morphology.

Key words.—*Anolis*, convergent evolution, ecomorphology, geometric morphometrics, Mantel test.

Convergent evolution of the traits of species occupying similar environments is generally considered to be evidence of adaptation (McLennan and Brooks 1993; Pagel 1994; Larson and Losos 1996; Schluter 1988, 2000). Observations of convergent evolution played an important historical role in Grinnell's (1917, 1924) development of the ecological niche concept. Indeed, Grinnell viewed convergent evolution as evidence that niches exist independent of the species that occupy them (e.g., Grinnell 1917, 1924). Hutchinson (1959) reoriented thinking about the niche by suggesting that the niche is a property of species rather than of the environment. In this sense, niches change during the process of evolution; convergence implies that selection in similar environments has led to convergent evolution of species' niches. Another of Hutchinson's important contributions to niche theory was his concept of the multidimensional niche, the idea that organisms interact with the environment along many biotic and abiotic niche dimensions (Hutchinson 1957). However, this idea has not been fully integrated into discussions of convergence and the niche (but see Green 1971). The question this raises in the context of convergence is the extent to which species converge along multiple niche dimensions.

Early niche theorists described examples of niche convergence, but differed regarding the dimensionality of the niches involved. Certainly, Grinnell considered the niche to be multidimensional (see Schoener 1989), including factors related to habitat, diet, and predators, strongly suggesting that he considered convergence to be in multiple dimensions as well. On the other hand, Elton (1927), whose views on the niche were also influential, emphasized single niche dimensions, suggesting, for example, that arctic foxes and hyenas each occupy the same niche because they both eat birds' eggs. Since then, the issue has received little attention. Even canonical examples of convergence, such as dolphins and ichthyosaurs or jerboas and kangaroo rats, may be cases in which the species have converged in response to one particular aspect of the environment (in both of these cases, locomotor demands presented by the environment), while retaining differences along other significant niche dimensions. Many oth-

er recent examples of convergence focus on adaptation of a limited set of traits to particular aspects of the environments, for example, teeth: (Ben-Moshe et al. 2001); limb length: (McCracken et al. 1999).

The issue of the dimensionality of convergence is complicated by the fact that trait convergence could potentially be multidimensional in two distinct senses. First, multiple organismal traits could be converging in a coordinated response to a single aspect of the environment; however, this would not reflect a truly multidimensional environmental effect (Green 1971). Alternatively, different organismal traits could be converging in response to different aspects of the environment, each acting independently. In this second case, convergence of multiple traits would reflect the multidimensionality of the niche itself.

If we focus on species that have convergently evolved into only two environments, then distinguishing between these two forms of multidimensional convergence is not possible; even if these species have converged in multiple traits, it is impossible to distinguish the possibilities that the multiple convergent traits are coordinated adaptive responses to a single environmental axis or that they are independent adaptive responses to multiple aspects of the environment. However, if one studies a set of species in which subsets of species have converged into at least three different environments, then identifying the existence of multiple, independent dimensions is possible by comparing patterns of divergence between sets of morphological traits among these different environments (Fig. 1). For example, if all measured traits are reacting to a single environmental factor, then patterns of similarity among convergent groups will be identical for all traits (Fig. 1A). In contrast, if traits are responding to multiple, independent environmental factors, patterns of similarity will differ among different dimensions (Fig. 1B). For example, in terms of one aspect of the niche, Environments B and C may be more similar to each other than either is to Environment A; traits affected by that aspect of the niche would then be expected to be most similar when comparing species from environments B and C (e.g., trait 1 in Fig. 1B).
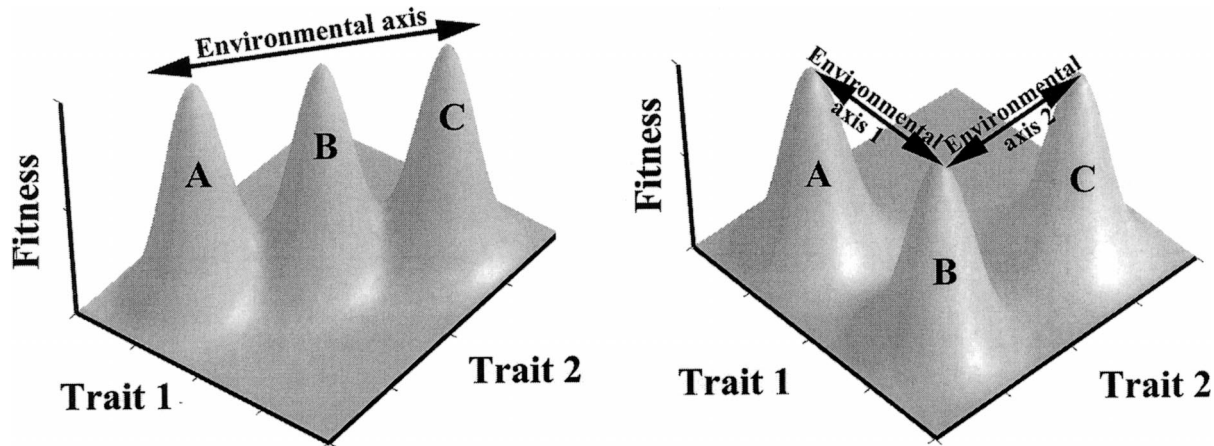
FIG. 1. Possible relationships between ecological and morphological characters for species in three different environments (A, B, and C). (A) Both traits are linearly related to variation in one environmental factor. In this case, the patterns of divergence among the three environments are the same along each trait axis. (B) Traits are related to variation in two independent environmental factors, and patterns of divergence differ between the two trait axes.

If in another aspect of the niche, Environments A and B are the most similar, then sets of traits associated with this second aspect of the niche are expected to be most similar between environments A and B (e.g., trait 2 in Fig. 1B).

Our method is thus an extension of the classic approach to the study of convergence. Just as convergent evolution of similar phenotypes in the same environment suggests that the phenotype is adaptive in that environment, discrepant patterns of convergence among different aspects of the phenotype across multiple environments can distinguish whether the convergence is occurring in response to one or multiple selective aspects of the environment.

An underlying assumption in this sort of analysis is that morphological variation among species corresponds to ecological variation. This is a standard assumption of ecomorphological studies and one that has been the focus of intensive study in many groups (e.g., Wainwright and Reilly 1994). Two secondary assumptions are that for each trait, the relationship between morphology and ecology is a linear one, and that ecomorphological relationships for one trait are independent of those for a second trait. These latter assumptions have been investigated much less often; in the Discussion, we explore the extent to which violation of these assumptions may affect the conclusions that may be drawn.

Caribbean lizards in the genus *Anolis* represent an ideal opportunity to examine the question of the dimensionality of niche convergence. Anoles have radiated independently on each of the four islands of the Greater Antilles (Cuba, Hispaniola, Jamaica, and Puerto Rico) and have produced, on each island, species morphologically specialized to use a diversity of habitat types (termed ''ecomorphs'' and named for the part of the environment they most frequently utilize, e.g., ''trunk-ground,'' ''twig'' [Williams 1983; Mayer 1989; Losos 1992]). Most remarkably, nearly the same set of ecomorphs has evolved on all four Greater Antillean islands.

Previous studies have validated the assumption that morphological and ecological variation are correlated among species (e.g., Lister 1976; Losos 1990a; Losos and de Queiroz 1997). Moreover, functional studies indicate that these con-

vergent features (e.g., limb lengths, lamella dimensions) confer functional advantages appropriate for movement and position maintenance in the particular structural habitat in which each species resides (e.g., Irschick et al. 1996; Irschick and Losos 1998, 1999; Macrini et al. 2003). Nonetheless, ecomorph convergence may reflect more than adaptation for locomotion in different structural habitats. The habitats to which these anoles adapt differ in a variety of ways other than substrate diameter and texture, including food type and availability, predator pressure, and visibility (which in turn might affect intraspecific territorial behavior, antipredator behavior, and mate choice). It is conceivable that these other environmental factors might also affect the convergent evolution of ecomorphs in Caribbean anoles. Previous studies of convergence in *Anolis* have focused on particular sets of traits (e.g., limb length: Losos 1990a; Beuttell and Losos 1999; toepad dimensions: Glossip and Losos 1997; Beuttell and Losos 1999; Macrini et al. 2003; sexual size dimorphism: Butler et al. 2000; head dimensions: Beuttell and Losos 1999; body size: Beuttell and Losos 1999), but previous work has not investigated differences in the patterns of ecomorph convergence between these different sets of morphological characters.

To investigate patterns of ecomorph convergence and divergence in anoles, we examined five character systems: body size, which has been shown to affect many aspects of anole biology, including energetics, locomotion, and prey size (Naganuma and Roughgarden 1990 and references therein); limb dimensions, which affect sprinting and jumping capabilities and position maintenance (Losos 1990a; Irschick and Losos 1998); lamella number, which affects the ability to grasp smooth and irregular surfaces (Losos 1990a; Irschick et al. 1996; Glossip and Losos 1997); head dimensions, which may affect prey type and shape (Schoener 1968; Schoener and Gorman 1968) or intraspecific interactions (more territorial species may have larger heads to enhance fighting ability [Stamps 1977; Herrel et al. 1996]); and sexual size dimorphism, which may relate to extent of territoriality, intrasexual
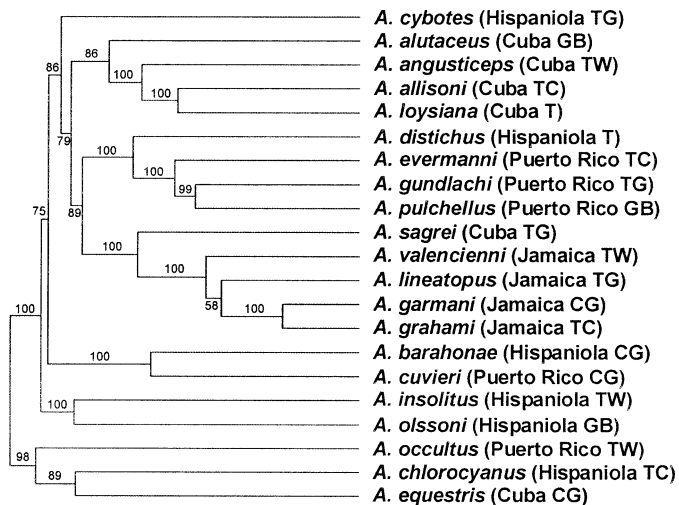
FIG. 2. Phylogenetic tree used in this study. Branch lengths are relative, with the distance from the root to the tips arbitrarily set at 100 units. The island where each species can be found is noted, and ecomorph categories are abbreviated as follows: TW, twig; CG, crown-giant; TC, trunk-crown; T, trunk; GB, grass-bush; TG, trunk-ground. Bayesian posterior probabilities for the pruned tree topology are given above each node.

resource partitioning, or sex-specific adaptation (Schoener 1967; Butler et al. 2000; Losos et al. 2003a).

We test two hypotheses for these character systems. First, we predict that species that have independently occupied the same habitat type have convergently evolved similar states in each character system. Such convergence, as discussed above, suggests that trait evolution has occurred adaptively with respect to the environment. Second, if convergence is truly multidimensional, with different character sets responding to different aspects of the environment, then we predict that patterns of convergence will differ significantly among these character systems. Thus, patterns of divergence among ecomorph categories will differ among character systems.

MATERIALS AND METHODS

We examined 21 species chosen to be a representative sample of all ecomorphs from each of the four Greater Antillean islands (Fig. 2), with each ecomorph-island combination represented by one species. Species were chosen based on specimen availability. On each island, each ecomorph type is almost always represented by members of a single clade (Jackman et al. 1999); hence, choice of species does not affect the phylogenetic structure of the analysis. We focused on five sets of characters: body size, linear measurements of body shape, three-dimensional landmark coordinates from the head, lamella number, and sexual size dimorphism. Data for sexual size dimorphism and lamella counts were taken from the literature (see below); for the other character sets, in most cases, two adult male individuals from each species were measured, although only one specimen was available for *A. evermanni* and *A. barahonae*.

Body Size

For each specimen, we used a ruler to measure snout-vent length (SVL) from the tip of the snout to the anterior end of the cloaca, which we used as the measure of overall body size. When two individuals were measured for a species, the average SVL was used. The SVL measurements we used in this study correlate highly ($r = 0.993$) with male SVL estimates for these species in a previous study that used much larger sample sizes (Butler et al. 2000).

Body Shape

To quantify body shape, we first used a ruler to externally measure tail length from the anterior end of the cloaca to the tip of the tail. Only individuals with fully intact tails were measured. Some of these individuals had tails with regenerated portions; in such cases, only those individuals with fully regrown tails were used. If only one of the two individuals for a particular species had a fully intact, nonregenerated tail, the measurement for this lizard was used as the tail length for the species. We then made the following measurements for each lizard from radiographs using the computer-driven imaging system MorphoSys (Meacham 1993): pelvis width (measured at the widest point of the pelvis); lengths of the humerus, ulna, femur, and tibia; length of the metacarpal on the digit III of the foreleg; and lengths of the metatarsal and first phalanx on digit IV of the hindleg. Whenever possible, measurements were made on the right side of the body. Each lizard was measured twice and these repeated measurements checked for consistency. Any measurement showing more than a 5% difference between measurements was repeated; otherwise, multiple measurements from a single individual were averaged. All repeated measures were then averaged to get a single value for each measurement for each individual. For species with two individuals measured, measurements were averaged, and the mean species value for each measurement used for all subsequent statistical analyses. All morphological measurements were carried out by the same person (LJH).

All of the above measurements were natural log-transformed prior to analysis. Species means for each body measurement were regressed on ln(SVL) and the residuals were used in a principal components analysis (PCA) to generate independent body shape axes. SVL itself was not retained for this analysis; thus, axes represent size-removed body shape variables. We carried out this analysis on the covariance matrix of the data, and we retained all PC axes that explained more variation than that expected under a broken-stick model (Frontier 1976).

Head Shape

We generated three-dimensional landmark coordinates for 14 landmarks on the external head of each lizard using a Polhemus Navigation 3-Space digitizer (Hildebolt and Vannier 1988). Of these landmarks, 10 were repeated on the right and left side of each lizard and four were along the midline of the head (Fig. 3). The 14 landmarks were defined at the following points (numbers correspond to points labeled in Fig. 3): (1) anterior-most point of nostril; (2) anterior corner of front two postrostral scales (midline point); (3) point on top of head where scales between supraorbital semicircles converge into two rows (midline point); (4) posterior-most point where large scales between interparietal and supraor-
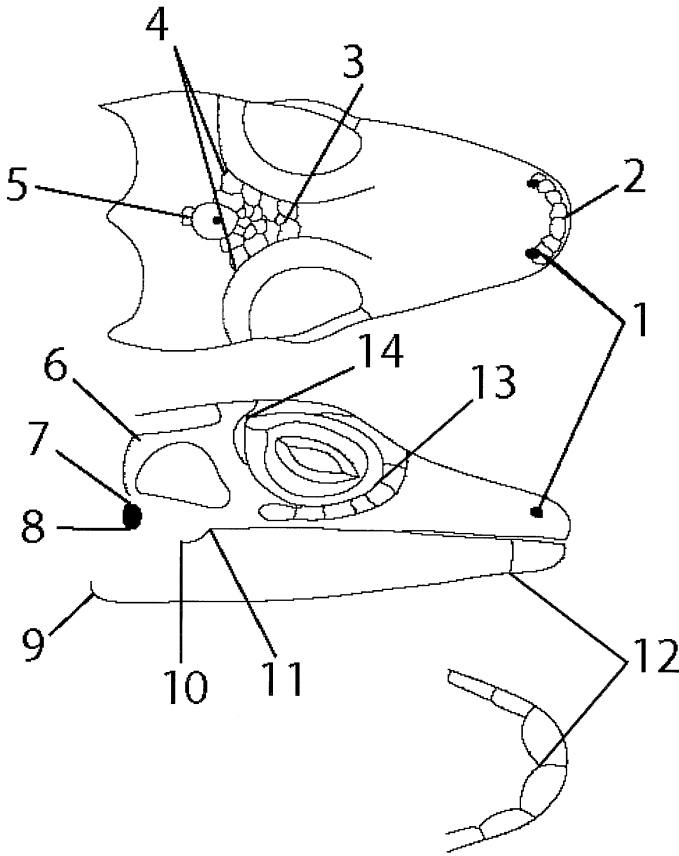
FIG. 3. Landmarks used for the morphometric analysis of anole head shape. Locations of landmarks are described in Materials and Methods.

bital semicircles meet semicircles; (5) posterior-most point of interparietal scale (midline point); (6) anterior-most point of inner temporal scale row; (7) ventral-most point of ear opening; (8) dorsal-most point of ear opening; (9) posterior-most point on back of lower jawbone, in line with plane formed by the bottom of the lower jaw; (10) posterior-most point of lips; (11) posterior-most point of jaw opening; (12) posterior corner of front two infralabial scales (midline point); (13) posterior-dorsal corner of subocular eye ridge, in line with eyelid; and (14) anterio-dorsal corner of superciliary eye ridge, in line with eyelid. Each specimen was digitized twice by the same person (LJH). We removed asymmetry by averaging landmarks from the right and left sides of each specimen (Klingenberg et al. 2002). We did this by superimposing each specimen with its reflection across the x-y plane using generalized Procrustes analysis (Gower 1975), and finding the mean of these two shapes (Klingenberg et al. 2002). For this procedure, the ten landmarks on each side of the head (1, 4, 6, 7, 8, 9, 10, 11, 13, and 14) were matched with the corresponding reflected landmark from the other side of the head, while the four landmarks along the midline (2, 3, 5, and 12) were matched with themselves. This resulted in a set of bilaterally symmetric three-dimensional landmark points.

Because each head was measured twice, we superimposed the symmetric three-dimensional landmarks from each of the two measurement sets using generalized Procrustes analysis (Gower 1975), and generated a mean set of landmarks for each individual in the program Morpheus (Slice 2000). Similarly, for the species with two representatives, mean landmarks from each of the two individuals were superimposed, and a set of mean landmarks obtained for each species. We then used the mean species' landmarks to generate a generalized least squares Procrustes reference form for the 21 anole species used in this study and calculated three-dimensional partial warp scores for each species based on this reference using the program IMP (Sheets 2003). Because size differences were removed during superimposition, differences in these scores represent differences in head shape between species.

We then used the partial warp scores in a principal components analysis to calculate relative warp scores for each species using the program IMP (Sheets 2003). We retained all relative warp axes that explained more variation than that expected under a broken-stick model (Frontier 1976). These axes could still reflect allometric differences in head shape among species; to test for such relationships, we used linear regression of ln(SVL) on each significant relative warp axis. For all relative warp axes with a significant allometric component, we repeated all relevant analyses using both the raw warp scores and residuals obtained by regressing the warp scores on ln(SVL). For visualization, we generated three-dimensional geometric representations of the shape changes implied by each of these significant PC axes using the program Morpheus (Slice 2000). We also created files, available online only (at http://dx/doi.org/10.1554/04-038.1.s1), that allow three-dimensional visualization of changes in head shape along the PC axes and between ecomorph categories.

Lamella Number and Sexual Size Dimorphism

Data for lamella counts for 17 of the 21 species in this study were taken from Glossip and Losos (1997), who counted the number of lamellae underlying the third and fourth phalanges of the fourth digit of the hindlimb using a dissecting microscope. We counted lamellae in the same way for the other four species (average counts: A. alutaceus: 17.2; A. loysiana: 17.5; A. allisoni: 30.0; and A. barahonae: 31.0). These counts were ln-transformed for normality, and size was removed by taking the residuals from a regression on ln(SVL). Sexual size dimorphism (SSD), calculated as log(male SVL/female SVL) and based on measurements of large collections of museum specimens (Schoener 1969, 1970), was obtained from Butler et al. (2000). Butler et al. (2000) did not include a SSD value for A. barahonae, but we substituted the value given for A. ricordi, because these two species are closely related (Nicholson et al. 2005) and were formerly treated as subspecies.

Statistical Analysis

Because only two specimens were measured per species for these analyses, we calculated the repeatability of measurements on different individuals within species, i.e., the repeatabilities of species' mean values. For the head shapes, we calculated repeatabilities on relative warp axes derived from the three-dimensional coordinates of all measured in-

dividuals. In principle, these axes could differ from the warp axes derived from the species means, which are used in the remainder of the analyses presented here. However, visual inspection of the variation described on these axes revealed that this was not the case; rather, these three axes closely correspond to the three warp axes used in the analyses below. For the SVL and body shape data, we calculated repeatabilities on the raw measurement data. We carried out all repeatability calculations in JMP version 5.1 (SAS Institute 2003).

Each of the five morphological data sets was used to calculate matrices of species differences. For each dataset, these matrices were composed of squared Euclidean distance between the mean values for each pair of species.

To adjust for patterns of phylogenetic covariance in these data, we used a phylogeny of *Anolis* constructed for 121 species of mainly Caribbean species plus one outgroup, *Polychrus acutirostris*. We used sequences from a 1481 base pair 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 [Jackman et al. 1999, 2002; Glor et al. 2003; Losos et al. 2003a] and available on GenBank [http://www.ncbi.nlm.nih.gov/Genbank/]). We analyzed these sequences using the GTR + I + Γ model, selected using hierarchical likelihood ratio testing using the program MrModelTest version 1.0b (Nylander 2002). We then used these data in 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. The likelihoods of the trees in the Bayesian analysis reached a plateau at around 50,000 generations; we conservatively 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 180 trees with branch lengths, again 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 ($\log_{10}$(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 insuring 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 21 species included in this study, resulting in the tree represented in Figure 2. To estimate support for the topological relationships among the 21 species of interest in this study, we used the posterior distribution of 180 trees obtained from the Bayesian analysis. We pruned all but the 21 species of interest from each of these 180 trees, and then used the resulting pruned tree distribution to define support 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. Finally, we used the pruned

TABLE 1. Results of Mantel tests for phylogenetic autocorrelation.

Matrix	Z	r	P
Body size	1487.17	0.25	0.03
Body shape	2589.88	0.13	0.14
Head shape	40.41	0.09	0.23
Lamellae	160.20	0.05	0.31
Sexual size dimorphism	105.29	0.16	0.05

ultrametric tree to create a phylogenetic distance matrix using the program PDAP (Garland et al. 1993). The terms in the matrix represented the patristic distance separating each pair of species on the tree.

We tested for phylogenetic effects by conducting a Mantel test of each of these five morphological matrices against the phylogenetic distance matrix (Bohning-Gaese et al. 2003) using the program Passage (Rosenberg 2001). In all cases, significance was assessed by comparing the *z*-statistic of the actual matrices to the *z*-statistics from 9999 random permutations. Two of these five tests were significant (Table 1). Thus, to factor out the confounding effects of these phylogenetic relationships, we used three-way Mantel tests controlling for phylogeny in the remainder of the matrix correlation tests (Thorpe 2002; Thorpe and Stenson 2003).

We then tested the hypothesis of ecomorph convergence in each of the five morphological data sets. To do this, we used three-way Mantel tests to examine whether the six ecomorph categories were significantly distinct from each other in each of the five data sets. We first created an "ecomorph difference" matrix by setting each element to equal one if the two species being compared were different ecomorphs and zero if they were the same ecomorph. We then determined whether each of the five morphological datasets differed between ecomorphs; in terms of the Mantel test, this would mean that the morphological distance separating two species was related to whether the species were in the same or different ecomorph categories. Thus, we compared each morphological difference matrix to the ecomorph difference matrix with the phylogenetic distance matrix held constant. We used the distance matrices to carry out three-way Mantel tests using the program Passage (Rosenberg 2001), again assessing significance using 9999 random permutations.

As an alternative test for ecomorph differences, we conducted analyses of variance (ANOVA) or multivariate analyses of variance (MANOVA) on each dataset to test the hypothesis that ecomorph categories differed in morphology. To account for phylogenetic relatedness, we conducted phylogenetic ANOVAs and MANOVAs (Garland et al. 1993; Glor et al. 2003) by first calculating the standard *F*-statistic (ANOVA) or Wilks' lambda values (MANOVA) for each dataset. We then accounted for phylogenetic relatedness by generating null distributions of the *F*-statistic or Wilks' lambda value for each dataset by simulating 9999 datasets on the phylogenetic tree using a Brownian motion model of phenotypic evolution. For these simulations, the sigma parameter for the Brownian motion model, which determines the rate of evolution for each character, was taken as the maximum-likelihood value estimated from the data (Schluter et al. 1997; Purvis and Webster 1999). Each axis of the multivariate datasets was simulated independently. Statistical *P*-values were

TABLE 2. Repeatabilities of species' means for measurements used in this study.

Dataset	Measurement	Repeatability
Size	Snout-vent length	0.993
Body shape	Humerus	0.995
	Ulna	0.987
	Metacarpal	0.982
	Pelvis width	0.993
	Femur	0.995
	Tibia	0.993
	Metatarsal	0.988
	First phalanx on hind foot	0.987
	Tail length	0.976
Head shape	Relative warp 1	0.951
	Relative warp 2	0.892
	Relative warp 3	0.934

TABLE 3. Principal component loadings for body shape.

Variable (residuals)	PC Axis 1	PC Axis 2
Humerus	0.121	0.068
Ulna	0.175	0.089
Metacarpal	0.129	0.101
Pelvis width	0.064	0.085
Femur	0.143	−0.001
Tibia	0.215	0.013
Metatarsal	0.206	−0.005
First phalanx on hind foot	0.213	0.013
Tail length	0.182	−0.256
Eigenvalue	0.254	0.096
% Variance explained	66.4	25.2

calculated as (number of simulated F-statistics or Wilks' lambda values that were more extreme than that for the data + 1)/(total number of simulations + 1). These calculations were carried out in a c-program (phmanova.c, available from the authors) that was compiled under the GNU compiler gcc (Free Software Foundation, http://gcc.gnu.org).

Even if each dataset is able to discriminate between the six different ecomorphs, the relative similarities and differences between particular pairs of ecomorphs might differ in each dataset. To identify particular pairs of ecomorph categories discriminated by each dataset, we carried out post hoc tests for significant differences between each possible pair of ecomorph categories in each dataset. We first found the Euclidean distance between the centroids of each pair of ecomorph categories in each morphospace. We then used the 9999 simulated datasets from the ANOVA/MANOVA simulations to calculate a null distribution of these between-ecomorph centroid distances. We tested the hypothesis that the between-ecomorph distance was not any greater than expected by chance by comparing the actual distance between that pair of ecomorph categories to the corresponding null distribution. This analysis was repeated for each pair of ecomorph categories in each of the five datasets. A P-value for this test was calculated as (number of simulated distances greater than the actual distance + 1)/(number of simulations + 1). These calculations were again carried out in the c program described above.

Given that variation among some of the morphological categories is correlated, we then asked how many independent linear descriptions of ecomorph variation there are among the five datasets. To quantify differences among the datasets, we first investigated whether interspecific variation in one morphological dataset was related to variation in a second morphological dataset. We did this by testing for relationships between all possible pairs of the five morphological datasets, holding phylogeny constant in each case. These tests were again carried out in the program Passage (Rosenberg 2001), with significance determined by 9999 random permutations. We also used all five datasets together in a matrix multiple regression. To account for phylogenetic nonindependence, we regressed the values from the six difference matrices (body size, body shape, head shape, lamellae, sexual size dimorphism, and ecomorph differences) on

the phylogenetic difference matrix and calculated residuals for each matrix. We then regressed the five morphological residual matrices on the ecomorph residual matrix in a multiple matrix regression using the program Permute! (Legendre et al. 1994; Casgrain 2001). This analysis was used to determine which morphological data sets added significant information about ecomorph differences.

RESULTS

All species' mean measurements used in this study were highly repeatable (Table 2). All repeatabilities are greater than 95% except head shape relative warp axes 1 and 3, which still show relatively high repeatabilities of around 90% (Table 2).

For body shape, the first two PCA axes explained more variation than expected under the broken-stick model. These axes together explain 91.6% of body shape variation among these species and are clearly interpretable, with the first axis measuring relative limb and tail lengths, with higher values corresponding to species with long limbs and tails relative to their size (Table 3). The second axis is loaded most heavily on tail length, although it also contrasts relative forelimb length with relative tail length (Table 3).

Head shape varied among the species included in this study (Fig. 4). For head shape, the first three relative warp axes explained more variation (68.2%) than expected under the broken-stick model (proportion of variation explained by PC axis 1: 41.1%, PC axis 2: 15.9%, PC axis 3: 11.2%). Two of the three PC axes were significantly correlated with lnSVL (PC axis 1: $r = −0.29$, $P = 0.2$; PC axis 2: $r = −0.56$, $P = 0.009$; PC axis 3: $r = −0.55$, $P = 0.01$), and thus could represent allometric aspects of head shape. Aligned coordinates representing changes along these axes are presented in Figure 5, which shows a three-dimensional representation of the shape deformation described by each axis. PC axis 1 contrasts short, broad heads (low values of PC1) with longer, narrow heads. PC axis 2 describes deformations in the angle defined by the top of the head relative to the back of the jaw and the tip of the snout; small values of PC2 correspond to species with more strongly peaked heads, viewed from the side, whereas large values of PC2 correspond to species with flatter heads. PC axis 3 is a more complicated shape change; large values of PC3 correspond to landmarks on top of the head moving farther apart and the tip of the snout moving ventrally and posteriorly relative to the rest of the head. In-

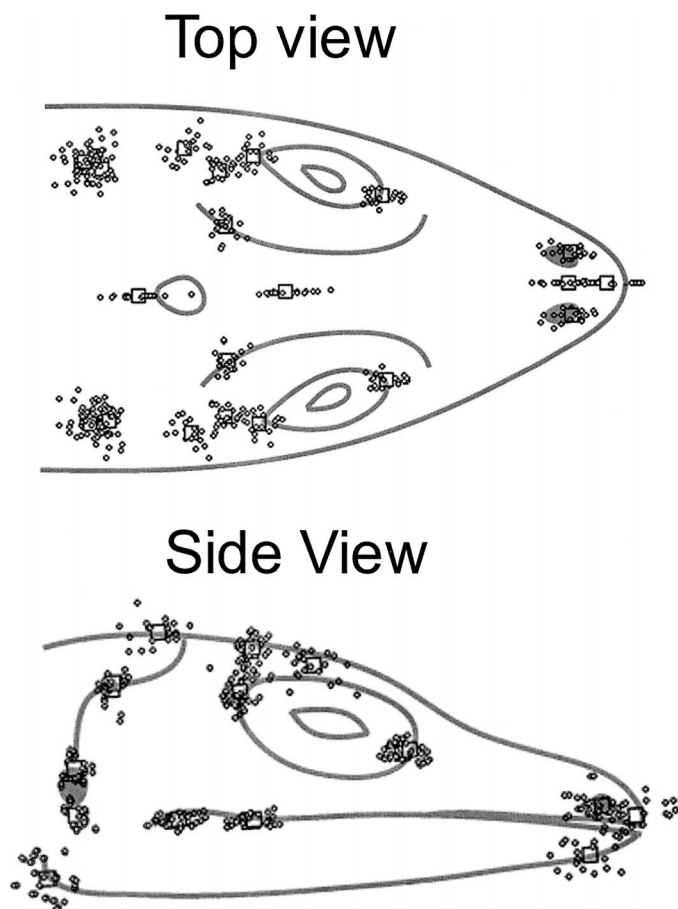## Top view

Side View

FIG. 4. Aligned three-dimensional head landmarks for the 21 species used in this study. The points represent individual species' values and the squares represent the least squares Procrustes reference form for all species.

teractive three-dimensional representations of these diagrams are available online (http://dx.doi.org/10.1554/04-038.1.s1).

Species are typically more similar to each other in morphological space when they are members of the same ecomorph class than when they belong to different classes (Fig. 6) even when phylogeny is taken into account (Table 4). Significant differences among ecomorph categories in head shape remain even when allometric effects are removed by using residuals from lnSVL for the 2nd and 3rd partial warp axes ($r = 0.23$, $P < 0.0001$). This result is confirmed by the phylogenetic ANOVAs and MANOVAs, which show that ecomorph categories are significantly distinct in each of the five morphological datasets (SVL: $P = 0.0001$; body shape: $P = 0.0001$; head shape: $P = 0.0003$; lamellae: $P = 0.0011$, SSD: $P = 0.0006$). This relationship for head shape remains significant when residuals from lnSVL are used for head shape partial warp axes 2 and 3 ($P = 0.0004$).

Differences between the datasets in the way ecomorph categories are differentiated from each other are reflected in the post hoc tests of pairwise ecomorph differences (Table 5). For example, the two most divergent ecomorphs in terms of lamella number, trunk-ground, and trunk-crown, are not significantly different in SSD and body shape (Table 5, Figs. 6, 7). Additionally, trunk and grass-bush anoles are almost iden-

tical in the extent of SSD and similar in lamella counts, but significantly different in head shape (Table 5, Figs. 6, 7). Furthermore, every possible pairwise comparison of ecomorph categories is significantly distinct in at least one morphological dataset (Table 5). These differences are also illustrated in Figure 7, which is a graphical depiction of the results of these post hoc tests of ecomorph differences. Although all five datasets reveal distinct ecomorph clusters, each dataset has a distinct pattern of divergence among the six ecomorphs (Fig. 7). These results are not qualitatively changed when residuals from lnSVL are used for head shape partial warp axes 2 and 3 (results not presented).

Controlling for phylogeny, pairwise correlations among size, body shape, head shape, lamellae, and SSD are significant for only two of ten comparisons, body shape-head shape and body shape-SSD (explaining only 13% and 6% of the variation in these datasets, respectively; Table 4). This result is corroborated by the matrix multiple regression, which shows a significant ecomorph effect for SVL, body shape, lamella number, and SSD ($r^2 = 0.31$, Table 6). Again, these results are qualitatively unchanged when residuals from lnSVL are used for head shape partial warp axes 2 and 3 (results not presented).

DISCUSSION

The Caribbean anole radiation is characterized by the repeated evolution of the same set of habitat specialists—ecomorphs—on each of the four islands of the Greater Antilles (Williams 1983; Mayer 1989; Losos et al. 1998). Our results reveal, in agreement with previous studies (see Introduction), that convergence among members of each ecomorph category occurs in all five morphological datasets we examined: body size, body shape, head shape, lamella number, and sexual size dimorphism. However, the particular sets of ecomorph categories that are statistically distinguishable differ among each of the five datasets. Furthermore, interecomorph variation in at least four of these character sets is independent of the other character sets, suggesting that each character set represents adaptation to different aspects of the environment, thus supporting the hypothesis of multidimensional convergence in Caribbean anoles.

Adaptive Basis of Character Convergence

We found convergence in five distinct character systems. Two of these systems, body shape and lamella number, have been shown to relate to aspects of the structural habitat matrix which differ among ecomorphs (Williams 1972; Moermond 1979a,b; Losos 1990b, 1994). The other three character systems, body size, head shape, and sexual size dimorphism, are probably related to other aspects of the environment.

Body shape

Morphological differences among the ecomorph classes have primarily been interpreted as adaptations to using different structural habitats (Williams 1972; Moermond 1979a,b; Losos 1990b, 1994). Extensive morphological, behavioral, and performance studies have revealed that the body shape differences among ecomorphs reflect adaptations to

Head Alignment

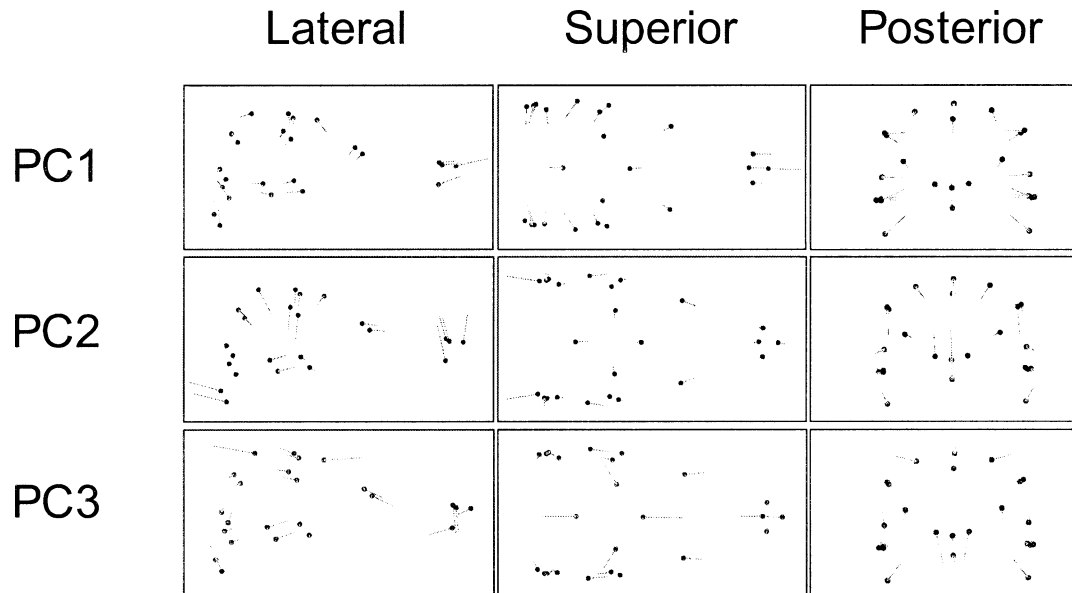| Lateral | Superior | Posterior |

FIG. 5. Deformations along the first three relative warp axes for anole head shapes. These diagrams represent the three-dimensional change in landmark configuration of anole heads that is represented by each of the first three relative warp axes. Circles represent the Procrustes mean head shape for species included in this study; lines represent deformations implied by high values along each PC axis (corresponding low values for each PC axis were left out of the figure for clarity).

differences in structural habitats. Behavioral studies (Moermond 1979a,b; see also Pounds 1988) have highlighted the different locomotor demands placed on lizards by the ''habitat matrix'' used by different ecomorphs. For example, trunk-ground anoles that occur on broad, uncluttered surfaces near the ground must be able to run and jump quickly, whereas twig species must be able to move with agility through a cluttered, three-dimensional habitat. Functional studies, in turn, have indicated how differences in morphological characteristics maximize performance abilities in these different environmental settings. For example, the long legs of trunk-ground anoles are an adaptation for greater sprint speed on broad surfaces, whereas the short legs of twig anoles provide the ability to move more easily on narrow surfaces (Losos and Sinervo 1989; Losos and Irschick 1996; Irschick and Losos 1999).

Lamella number

Our results indicate that even in terms of the structural habitat, the anole ecomorphs partition two distinct axes, one related to body shape, and the other to lamella number. Whereas limb length correlates with diameter of substrates used (Larson and Losos 1996), lamella number correlates with perch height (Glossip and Losos 1997). That these two aspects of the habitat are not correlated should not be surprising, as the trunk ground and grass-bush anoles both perch low to the ground, yet differ greatly in substrate diameter. A similar contrast exists between twig anoles and the other

arboreal ecomorphs, which are similar in perch height, but differ in perch diameter.

Body size

Differences in body size among ecomorph categories probably relate to many different ecological factors, such as energetics, locomotion (Peters 1983; Calder 1984; Naganuma and Roughgarden 1990), and perch height and diameter (Glossip and Losos 1997). The best studied of these relationships is the positive correlation between body size and prey size (Schoener 1967, 1970).

Head shape

With regard to differences in head shape, a variety of explanations—none mutually exclusive—could account for the ecomorph differences. Possible explanations include habitat specific differences in diet, habitat specific differences in aggressive or antipredator behavior, and crypsis. A lizard's head shape likely has functional consequences in terms of bite strength, which has been shown to be important for niche partitioning of lizards in the field (Herrel et al. 2001a; Verwaijen et al. 2002). Furthermore, bite force is positively related to head height in some species of lizards (Herrel et al. 2001b); theoretical models also suggest that lizards with wider heads and shorter lower jaws will have a stronger bite force relative to their head size (Herrel et al. 2001b). In our analyses, lizards with lower values of PC1 for head shape, as described above, have relatively wide, high heads with
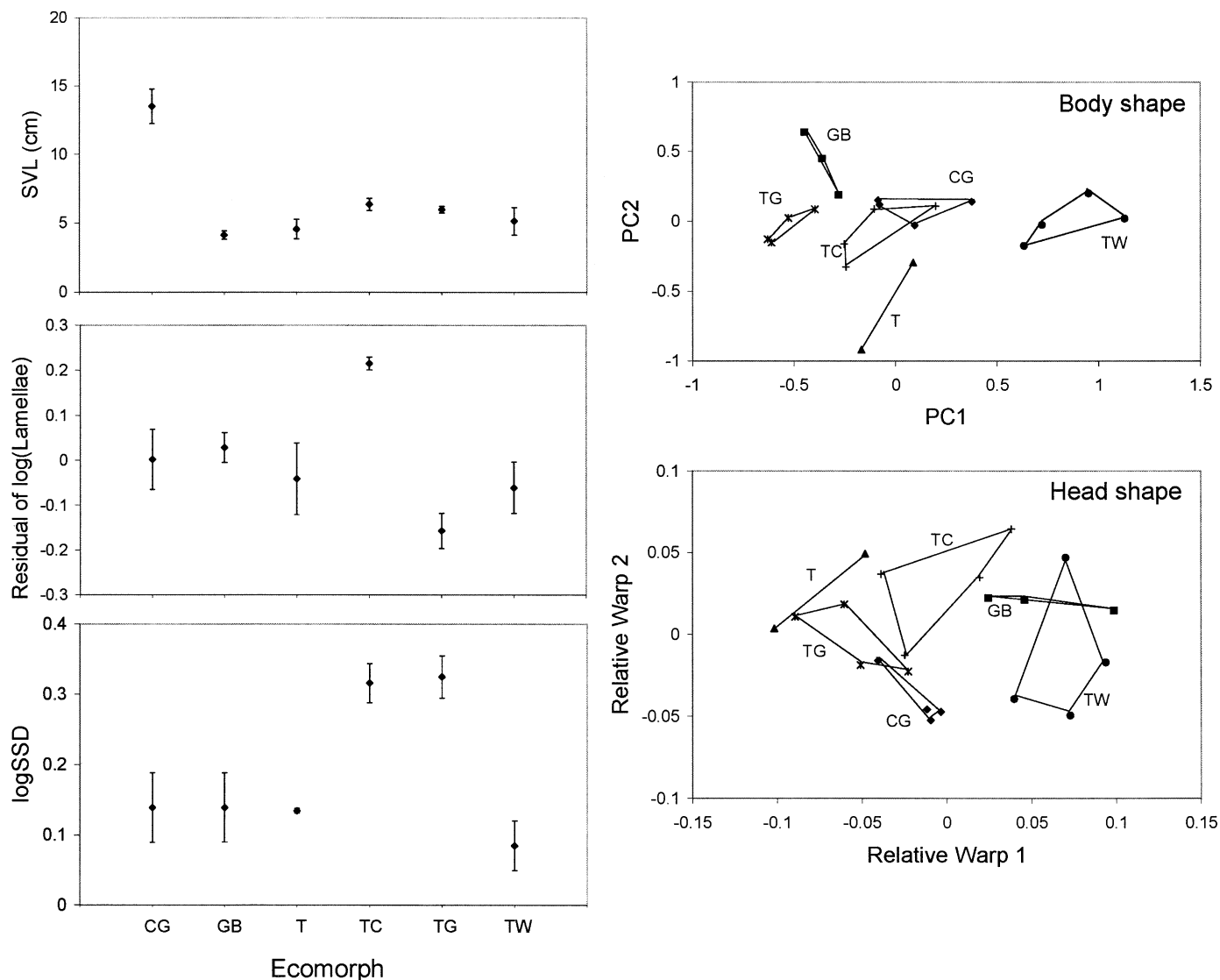
FIG. 6. Ecomorph groups in five different morphospaces. Ecomorphs abbreviated as follows: CG, crown-giant; GB, grass-bush; T, trunk; TC, trunk-crown; TG, trunk-ground; TW, twig.

TABLE 4. Results of Mantel tests for differences in morphology between ecomorphs and for correlations between all pairwise comparisons of morphological data sets. Significance levels, as determined by 9999 matrix permutations, are indicated with asterisks (*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$).

Matrix 1	Matrix 2	Control matrix	Z	r
Body size	Ecomorph	Phylogeny	18.22***	0.26
Body shape	Ecomorph	Phylogeny	32.56***	0.33
Head shape	Ecomorph	Phylogeny	0.34***	0.28
Lamellae	Ecomorph	Phylogeny	1.47**	0.20
Sexual size dimorphism	Ecomorph	Phylogeny	1.02***	0.23
Body size	Body shape	Phylogeny	−23.82	−0.16
Body size	Head shape	Phylogeny	0.07	0.04
Body size	Lamellae	Phylogeny	−1.57	−0.15
Body size	Sexual size dimorphism	Phylogeny	−0.66	−0.10
Body shape	Head shape	Phylogeny	1.17***	0.46
Body shape	Lamellae	Phylogeny	−1.31	−0.09
Body shape	Sexual size dimorphism	Phylogeny	2.79**	0.30
Head shape	Lamellae	Phylogeny	0.006	0.03
Head shape	Sexual size dimorphism	Phylogeny	0.01	0.08
Lamellae	Sexual size dimorphism	Phylogeny	0.04	0.05

TABLE 5. Results of post-hoc tests of ecomorph differences in each of the five morphological data sets. Distance represents the Euclidean distance between the centroids of each pair of ecomorphs in the respective data space; significantly large distances, as determined from 9999 phylogenetic null simulations, are indicated with asterisks (*$P < 0.05$, **$P < 0.01$). Ecomorphs abbreviated as follows: CG, crown-giant; GB, grass-bush; T, trunk; TC, trunk-crown; TG, trunk-ground; TW, twig.

	Distance				
Contrast	SVL	Body shape	Head shape	Lamellae	SSD
CG-GB	1.18**	0.55	0.10	0.03	0.00006
CG-T	1.08**	0.71	0.10	0.04	0.005
CG-TC	0.75*	0.24	0.07	0.21	0.18*
CG-TG	0.80*	0.63	0.06	0.16	0.19*
CG-TW	1.00**	0.79	0.09	0.06	0.05
GB-T	0.09	1.08*	0.13*	0.07	0.005
GB-TC	0.43	0.56	0.07	0.19	0.18*
GB-TG	0.37	0.50	0.12*	0.19	0.19*
GB-TW	0.18	1.29**	0.04	0.09	0.05
T-TC	0.34	0.54	0.09	0.26	0.18*
T-TG	0.28	0.75	0.05	0.12	0.19*
T-TW	0.09	1.09*	0.15**	0.02	0.05
TC-TG	0.06	0.44	0.06	0.37**	0.01
TC-TW	0.25	0.96**	0.09*	0.28*	0.23**
TG-TW	0.19	1.40**	0.13**	0.10	0.24**

TABLE 6. Matrix multiple regression of morphological difference matrices on ecomorph difference matrix. Values reported are the standardized regression coefficient for each variable, along with P-values determined by 9999 random permutations of the matrices for each individual variable as well as the overall model.

Variable	b	P-value
SVL	0.36	0.0001
Body shape	0.33	0.0001
Lamellae	0.28	0.0001
SSD	0.14	0.013
Head shape	0.09	0.07
Overall model	—	0.0001

short lower jaws (Fig. 5), and thus are predicted to have higher bite forces relative to their head size. The ecomorphs with the lowest values of head shape PC1 are the trunk and trunk-ground anoles (Fig. 6); we predict that these two ecomorphs have the highest bite forces relative to their size. Further empirical work is needed to test this hypothesis. Additionally, more data are needed to identify how differences in bite force might relate to differences in habitat use (e.g., the extent of difference in prey hardness in different environments [Herrel et al. 1996, 2001a, b; Verwaijen et al. 2002] or the extent of difference in aggressive defense against pred-
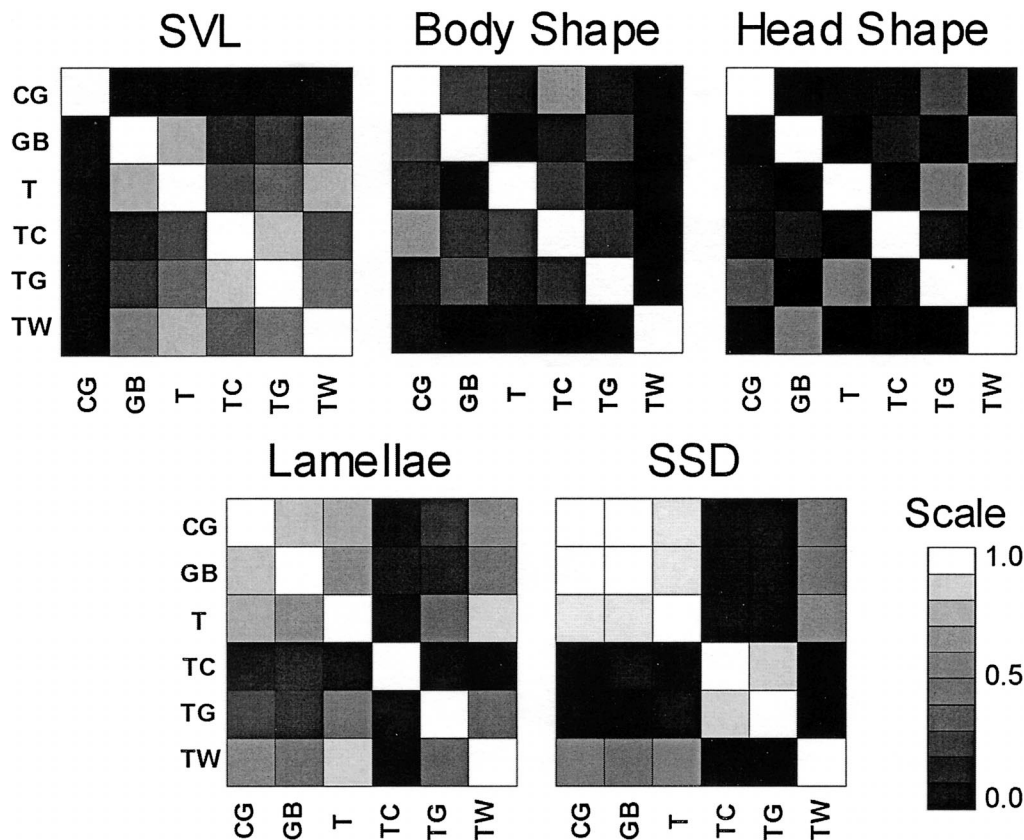

FIG. 7. Differences between ecomorphs using each of the five morphological data sets. Plots represent differences between each pair of ecomorphs in the respective data space; shading is proportional to the P-value of the post hoc simulation test of differences between that pair of ecomorphs in that data space, with white indicating higher P-values and black indicating lower P-values (i.e., significant differences). Ecomorphs abbreviated as follows: CG, crown-giant; GB, grass-bush; T, trunk; TC, trunk-crown; TG, trunk-ground; TW, twig.

ators by different ecomorphs [Stamps 1977; Herrel et al. 1996]).

The observation that among-ecomorph differences in head shape are parallel to differences in body shape suggests that differences in both character sets are correlated with the same environmental factors. Thus, head shape differences could be adaptations to differences in structural habitat. For example, movement on narrow twigs might require both short limbs and narrow heads. Alternatively, head shape could be responding to a different selective factor that is related to differences in structural habitat among the ecomorphs. For example, predator avoidance might require narrow heads on narrow substrates to facilitate crypsis.

Sexual size dimorphism

Ecomorph categories also differ in degree of sexual size dimorphism: in trunk-ground and trunk-crown anoles, males are substantially larger than females, whereas, at the other extreme, twig anoles are nearly monomorphic. Currently three general hypotheses exist for the existence of sexual size dimorphism: sexual selection, intersexual resource competition, and different reproductive demands (Butler et al. 2000). Interecomorph variation in SSD suggests that the factors that regulate SSD vary among the ecomorph habitats (Butler et al. 2000). For example, certain habitats may make territoriality, and thus selection for large size in males, more likely. Conversely, the ability to partition resources intersexually may also vary among habitats. Although the data at hand do not allow them to be distinguished (Butler et al. 2000; Losos et al. 2003b), these hypotheses could be tested readily by future field studies.

Upon How Many Resource Axes Are the Anole Ecomorphs Convergent?

Patterns of divergence among ecomorph categories differ greatly among four of the five character systems (Table 5; Figs. 6, 7). For example, the crown-giant anoles are significantly larger than all other ecomorphs, whereas four of the five significant differences in body shape involve a twig anole as one of the ecomorphs being compared. Other axes separate different pairs of ecomorph categories, such that all pairs are significantly different along at least one axis. We have argued that this pattern suggests that the ecomorph phenomenon—divergence among ecomorph categories, but convergence among species in the same category—implies that multiple, independent environmental selective factors have been involved in anole diversification; in other words, that ecomorph ''niches'' are multidimensional.

This interpretation rests on two assumptions: that for a given trait system, morphological variation maps linearly onto ecological variation, such that the more different two ecomorph categories are morphologically, the more different they will be ecologically; and that the morphology-ecology relationship for one trait system is independent of that relationship for other traits. An alternative possibility is that the relationship between morphology and ecology is nonlinear or that the relationship of traits to the environment is not independent across traits (Emerson et al. 1990; Koehl 1996; Alfaro et al. 2004; Spezzano and Jayne 2004). Either rela-

tionship could in theory produce patterns like those observed. Consider first nonlinearity in the relationship between a trait and the environment. Suppose, for example, that habitats differed in prey size and that the relationship between head size and prey size was nonlinear because a minimum head size existed, such that head size remained constant even as prey size decreased below some threshold value. Suppose, further, that larger prey required faster lizards, and hence longer legs, but that this relationship was linear: among habitats, the bigger the prey, the longer the legs of lizards. In this example, even though only one environmental factor (prey size) varied among habitats, our approach would suggest the existence of multiple morphological dimensions because limb length and head shape would not perfectly covary among habitats. Similarly, if the effects of variation in two traits were not independent, then complex patterns might result. For example, if the capture of large prey required either large heads or long legs, but not both, then one would not observe perfect covariation in traits among habitats, even though only one aspect of the environment (prey size) varied among ecomorphs.

These considerations are certainly reasonable and worthy of further investigation. It is surprising how little we know about even well studied groups such as Caribbean anoles. More detailed functional and ecological studies (e.g., Spezzano and Jayne 2004) will provide greater insight into patterns of anole evolutionary diversification and will permit evaluation of these assumptions. Such studies would be most useful in comparing pairs of ecomorph categories that are similar in some morphological character sets but not others (Fig. 7). We do think it unlikely that a single environmental axis is responsible for the many and varied patterns of convergence we have discovered; however, it is certainly possible that the minimum of four separate axes may be an overestimate if the assumptions of linearity and independence turn out to be unwarranted.

Conclusions

Hutchinson (1957) emphasized the multidimensionality of the ecological niche. Consequently, we would expect that species that convergently occupy the same niche should exhibit convergence along multiple ecological axes. Here we have shown that the Caribbean anole radiation, one of the hallmark examples of convergent evolution, exhibits multidimensional phenotypic convergence. Moreover, this convergence includes not only features important for moving and maintaining position in different structural habitats, but also character systems related to diet and intersexual biological differences. These results would not surprise Joseph Grinnell, one of the pioneers of the niche concept, who emphasized the many dimensions of the niche, including spatial habitat, feeding, and antipredator adaptations (Grinnell 1917; Schoener 1989).

Although convergence in single traits is widely reported, the extent to which species have independently occupied the same niche along multiple ecological dimensions remains to be seen. The existence of true multidimensional convergence, as seen in anoles, sheds light on old debate of whether the concept of an ''empty niche'' is meaningful. This debate has

centered on niche definitions, and in particular whether the niche is a property of the species or its environment. For example, some have argued that the concept is an empty one, because the niche is a property of the species that occupies it, and one can think up countless possible niches that could exist (Lewontin 1985). One modern definition regards the niche as an irreducible product of the species-environment interaction (Chase and Leibold 2003). Our results suggest that in anoles, species' phenotypes are more closely related to their environments than to their ancestry. To the extent that multiple lineages converge on the same niche, then that niche would seem to be predetermined by the environment, calling forth through selection the same adaptive responses in these lineages. In this sense, when given a group of related species such as anoles, it might be meaningful to speak of empty niches. In such groups, the forces that deterministically result in evolution into particular niches may exist prior to the species that occupy them.

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