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Ecomorphology of *Anolis* lizards of the Choco′ region in Colombia and comparisons with Greater Antillean ecomorphs

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We analysed the ecomorphological relationships in four species of *Anolis* lizard that occur in the Choco′ region in Colombia. The region is one of the most diverse of the Neotropical lowlands. The species were assigned to traditionally recognized Greater Antillean ecomorph categories based on habitat use data. Principal component analyses were carried out to examine correlations between the morphological traits, body size, and habitat use. We found that species are separated in morphological space principally by body size and lamella number. Upon removal of the effect of body size, correlations between morphology and habitat use became apparent. However, when compared with Greater Antillean ecomorphs, we found little evidence of morphological convergence in species occupying similar habitats. The species of the Choco′ region are, however, clearly separated in the multidimensional morphological space from the Antillean taxa, and appear to form a separate cluster differentiating principally in body size and the number of lamellae. Mainland species clearly constitute an ecomorphological radiation but apparently this is independent of that of the West Indian fauna. More studies are needed to understand the causes for the independence of evolutionary trajectories on the mainland and the Greater Antilles, and to obtain a better understanding of the ecological and evolutionary processes underlying the radiation of these faunas.

ADDITIONAL KEYWORDS: adaptive radiation – body size – evolutionary divergence – morphological convergence – South America.

INTRODUCTION

Ecomorphology analyses the covariation between morphology and ecology in closely related species (Aerts *et al*., 2000) to test whether morphology may restrict or define habitat use, and to generate ecological predictions based on morphology (Garland & Losos, 1994; Losos, 1994b). Although ecological differences among species may be attributable to differences in, for example, body size, body size differences alone cannot explain the full complexity of the variation between organisms. Rather, specific ecological conditions such as habitat use appear to be reflected in the morphology and functional capacities of animals, which in turn suggests an adaptive component to the variation in morphology (Moermond, 1979; Losos, 1994a; Aerts *et al*., 2000). To determine whether variation in morphology is specifically tied in to the way of life of a species, the application of ecomorphological approaches is essential (Gould, 1975; Strauss, 1984). Thus, it is crucial to have an adequate understanding of the ecological conditions of species under study which can then be linked to the observed morphological differences.

Anolis lizards are a good model system to test ecomorphological hypotheses because they represent a striking adaptive radiation that occurred in the West Indies, and Central and Southern America, with high speciation rates *in situ* in the Greater Antilles

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Table 1. Microhabitat use categories, perch height and ecomorph assignments for each species of Choco′ *Anolis* analysed

Species	Microhabitat	Perch height (m)	Ecomorph*
Anolis latifrons	Arboreal (trunk, branches)	2–5	Trunk–crown
Anolis chloris	Arboreal (trunk)	0–5	Trunk
Anolis notopholis	Ground, bushes, grass	0–2	Grass–bush
Anolis macrolepis	Semi-aquatic	0	Semi-aquatic

*The assignment to ecomorph category is based in field data of the Choco′ region (see text).

(Williams, 1983; Losos, 1994a, 2004). Moreover, these lizards show a large variation in ecology, morphology, and behaviour, and occupy a great diversity of habitats (Losos, 1994a). *Anolis* lizards also show strong convergence, thus generating phylogenetically distant species sets that are similar in morphology, ecology, and behaviour, termed ecomorphs (Williams, 1983). The ecomorphs were principally identified for the Greater Antillean islands based on the covariation in morphology and ecology. Six classes of ecomorphs have been proposed: trunk–ground, trunk–crown, crown–giant, twig, grass–bush, and trunk. In the Lesser Antilles, however, these ecomorph designations do not always hold (but see also Beuttell & Losos, 1999). Surprisingly, the ecomorph concept has not been rigorously tested for mainland species assemblages. Irschick *et al*. (1997) did, however, evaluate the ecomorphological relationships in mainland species and compared these with Antillean taxa. Yet, in their analyses, species of very different regions were used rather than sympatric species assemblages for which the ecomorphological patterns are expected to be strongest.

The present study aimed to evaluate the relationship between limb morphology and habitat use in four sympatric species of *Anolis* lizards that occur in the Choco′ region of Colombia. Specifically, we tested whether the species of a mainland community show distinct specializations to habitat use. Additionally, we assigned these species to traditional Greater Antillean ecomorph groups based on ecological and morphological data, and tested whether these are indeed convergent with West Indian ecomorphs. Finally, we explored whether, and how, mainland and Greater Antillean *Anolis* are broadly convergent in morphological space.

MATERIAL AND METHODS

Study area and species

The Colombian Pacific Coast region (Choco′ region) is the stretch of land between the Pacific Ocean and Cordillera Occidental of the Andes. More specifically, it ranges from the west of the mouth of the Atrato River, near Panama, to the Mataje River bordering north-western Ecuador (Rangel-Ch & Aguilar, 1993). The Colombian departments represented are primarily Chocó, Valle del Cauca, Cauca, and Nariño. The region is composed of lowlands, with elevations rarely exceeding 600 m, and highlands, which are usually above 600 m. There are three major landforms: (1) plains of recent alluvium; (2) low hills formed by relatively recent stream dissection of Tertiary and Pleistocene sediments; and (3) complex mountainous areas of Mesozoic rocks (West, 1957).

The anole fauna in the region can be divided into three faunistic components distributed in the north, middle, and south of the region (Castro, 1988). Each one of these communities is composed of species that are widely distributed, as well as species with a narrow distribution (i.e. endemics). We investigated species that occur in the central zone of the Chocó region and focused on four species of a community comprising ten species. We chose these species because they represent the greatest ecological diversity in the community (Castro, 1988) and are most amenable to field research. Of the four, three species could be readily assigned to traditional ecomorph categories (trunk, trunk–crown, grass–bush) and one was classified as semi-aquatic, a habitat also occupied by *Anolis* lizards in the West Indies and Central America, but not considered a true ecomorph (Leal, Knox & Losos, 2002). The information on the habitat use was taken, principally, from Castro (1988) and complemented with personal observations in various localities in the region (Velasco, 2003; J. A. Velasco, field observ.; Table 1).

Morphological measurements

Nine morphological measurements were taken for individuals of four species of *Anolis* (*Anolis notopholis*, *Anolis chloris*, *Anolis latifrons*, and *Anolis macrolepis*) in the Choco′ region in Colombia, South

Table 2. Means ± standard deviation of the morphological variables (mm) quantified for the four Chocó *Anolis* species

Variables	*Anolis latifrons* ($N = 15$)	*Anolis chloris* ($N = 24$)	*Anolis notopholis* ($N = 23$)	*Anolis macrolepis* ($N = 20$)
Snout–vent length	97.19 ± 5.46	46.00 ± 0.85	44.74 ± 0.44	51.83 ± 1.36
Humerus	26.60 ± 1.95	8.81 ± 0.24	7.49 ± 0.09	9.29 ± 0.26
Ulna	26.07 ± 1.96	7.97 ± 0.23	7.25 ± 0.13	8.36 ± 0.22
Femur	19.15 ± 0.93	10.56 ± 0.26	12.44 ± 0.15	14.41 ± 0.34
Tibia	18.50 ± 0.92	11.07 ± 0.21	12.90 ± 0.16	13.84 ± 0.31
Metatarsus	18.77 ± 0.88	15.09 ± 0.27	17.91 ± 0.30	17.77 ± 0.42
Metacarpus	31.78 ± 3.57	7.70 ± 0.16	7.59 ± 0.10	8.48 ± 0.30
Longest toe	21.30 ± 1.42	8.77 ± 0.16	10.13 ± 0.10	9.39 ± 0.23
Lamella number	24.05 ± 1.42	18.23 ± 0.14	15.87 ± 0.14	16.11 ± 0.39

America. All individuals were adults (both males and females), with the exception of the data for *A. latifrons* which also included some subadult individuals. The specimens are deposited in the UVC (Colección de Anfibios y Reptiles, Universidad del Valle, Cali-Colombia). The morphological variables were: snout–vent length (SVL), humerus length, ulna length, femur length, tibia length, metatarsal and metacarpal length, length of the longest toe on the hind foot, and lamella number under phalanges II and III of the longest toe of the hind foot. All measurements were taken twice with dial calipers (± 0.1 mm). The mean of both measurements was calculated and used in all further analyses. When a difference of more than 5% was noted between two measurements, a third measurement was taken (Irschick *et al*., 1997; Bickel & Losos, 2002). For comparative purposes, data on hindlimb length, femur length, tibia length, metatarsal length, longest toe length, and number of lamellae under phalanges II and III of toe longest, collected by A.H. for Greater Antillean lizards were also used. For a broad comparison with both other mainland and Caribbean anoles, a more restricted data set, including SVL, body mass, forelimb length, hindlimb length, tail length (only in specimens with intact tails) and the number of lamellae under phalanges II and III of the longest toe on the hind foot was assembled based on both data available in the literature (Losos, 1990; Irschick *et al*., 1997) and previously unpublished data (for a list of species, see Appendix).

STATISTICAL ANALYSES

First, all morphological data were $\log_{10}$-transformed to fulfil assumptions of normality and homoscedasity. To test for differences among the four Choco′ species, multivariate analyses of variance were used. To explore morphological variation of the four species a principal component analysis was performed. To remove effects of body size, the residuals of the regressions of the $\log_{10}$-transformed morphological variables against $\log_{10}$-transformed SVL were calculated. The residuals values were then used as the input in a new principal component analysis to explore variation in shape among the four species.

We explored morphological convergence between Choco′ and West Indian *Anolis* using principal component analyses using residual data morphological data and SVL as input. To explore whether the Choco′ lizards were typical for mainland anoles, we then assembled a larger data set based on literature data (see Appendix). Again, residuals were calculated and used as input for a factor analysis with varimax rotation. To visualize differences between ecomorph groups in the three data sets (mainland, Caribbean, and Chocó), we calculated the Euclidian distances for the group means using the factor scores of the first three factors. To explore ecomorphological relationships in the larger data set, factor scores on the first two factors (together representing most of the variation in the data set) were regressed against two typical indicators of habitat use in *Anolis*: perch height and perch diameter.

RESULTS

Table 2 lists the means and standard deviations of the morphological variables for the four mainland species. The species that exhibits the greatest morphological variation is *A. latifrons* (Table 2). Species differed significantly in multivariate space (multivariate analysis of variance: Wilk's $\lambda = 0.001$, $F_{27,205} = 67.32$, $P < 0.01$). The PCA analysis separated the species by body size and shape with more than 95% of the variance being explained by the first two

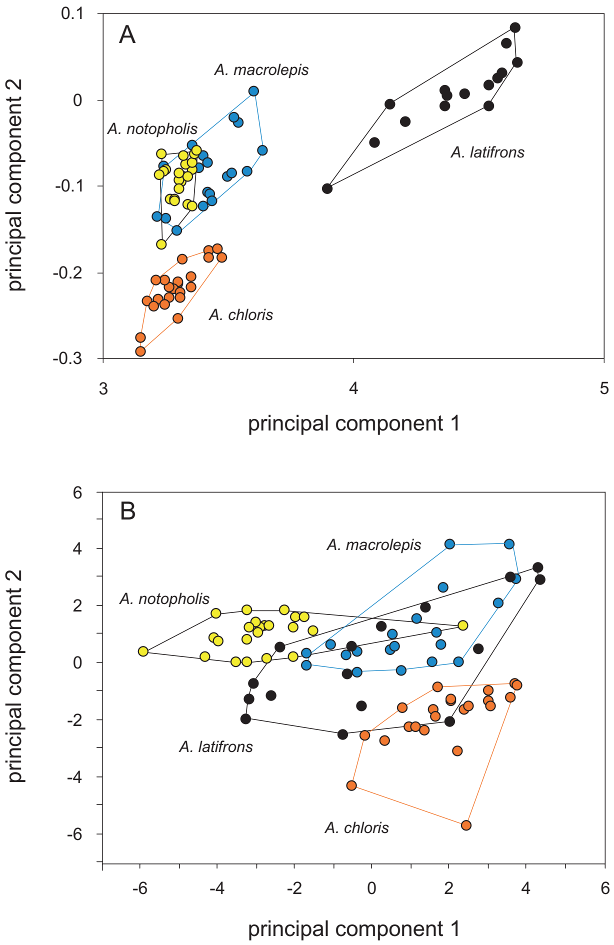

Figure 1. A, the position of the species of the Choco′ region in the morphological space as indicated by principal component analysis conducted on the raw data. B, the position of species of the Choco′ region in morphological shape defined by principal component analysis using size-adjusted data.

Table 3. Loadings on principal components for species of Choco′ region

Variables	PC I	PC II
Snout–vent length	0.341	–0.026
Humerus	0.332	–0.299
Ulna	0.335	–0.190
Femur	0.332	0.361
Tibia	0.338	0.287
Metatarsus	0.335	0.318
Metacarpus	0.339	–0.019
Longest toe	0.336	0.229
Lamella number	0.311	–0.713
Eigenvalue	8.44	0.30
% Variance	93.73	3.31

Table 4. Loadings on principal components axes for species of Choco′ region using size-adjusted (residual) data

Variables	PC I	PC II	PC III	PC IV
Humerus	0.007	–0.571	–0.239	0.288
Ulna	–0.063	–0.504	–0.416	0.255
Femur	–0.398	0.331	–0.184	0.524
Tibia	–0.523	0.137	0.028	0.341
Metatarsus	–0.518	–0.091	0.071	–0.293
Metacarpus	–0.306	–0.419	0.008	–0.399
Longest toe	–0.443	–0.056	0.238	–0.216
Lamella number	0.008	–0.324	0.820	0.412
Eigenvalue	36.04	22.53	12.05	9.26
% Variance	2.88	1.80	0.96	0.74

principal components (Fig. 1A; Table 3). The first PC explained 93.7% of the morphological variance across the four species. The second PC, a shape component, explained only 3.3% of the variation in the data. All the morphological variables included in the analysis loaded similarly on the first PC which appears to separate *A. latifrons* from the other three species. Lamella number loaded strongly on the second principal component and mainly separates *A. chloris* from the others (Fig. 1A).

The shape analysis retained four principal components together explaining 79% of the variation in shape (Table 4). Whereas the distal hindlimb segments loaded strongly on the first principal component, forelimb dimensions were strongly and correlated with the second component. The number of lamellae, on the other hand, was strongly correlated with the third principal component and femur length was the only variable to load somewhat strongly on the fourth principal component. Separation along the first component principally separated *A. chloris* from *A. notopholis*, with the trunk anole *A. chloris* having relatively short distal hindlimb segments (Fig. 1B). Interestingly, species were better defined along the second principal component, suggesting that differences among species in forelimb dimensions were strong with the arboreal species (*A. chloris* and *A. latifrons*) having relatively longer forelimbs than the more terrestrial ones (*A. macrolepis* and *A. notopholis*; Fig. 1B).

The comparison of the Choco′ with Caribbean anoles shows a strong separation in morphospace both when using raw or size-corrected data (Fig. 2A, B). The nonsize adjusted principal component analysis explained more of 95% of the variance on the first two components. Because all variables load equally

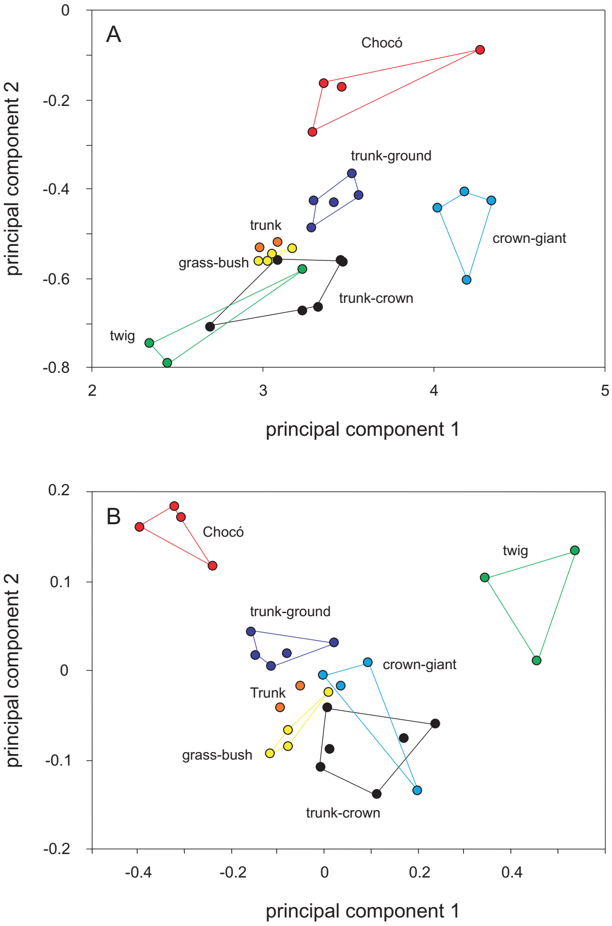

Figure 2. A, the distribution of species both mainland and Antilles in the morphological space defined by principal component analysis using means data by species. The red outline correspond to species of the Choco′ region. B, the distribution of species (both mainland and Antilles) in the morphological space defined by principal component analysis using size-adjusted data. Each one of the mainland species was assigned to an ecomorph category based on preliminary data with respect to habitat use.

Table 5. Loadings on the first two principal components for both Choco′ region and Caribbean *Anolis*

Variables	PC I	PC II
Snout–vent length	0.387	–0.242
Femur	0.405	0.054
Tibia	0.404	0.118
Metatarsal	0.345	0.531
Longest toe	0.396	–0.025
Hindlimb	0.402	0.198
Lamella number	0.294	–0.777
Eigenvalue	5.98	0.73
% Variance	85.39	10.36

Table 6. Loadings on the first four principal components for all species (Choco′ region and Caribbean) using size-adjusted data

Variables	PC I	PC II	PC III	PC IV
SVL ($\log_{10}$)	0.000	0.000	–1	0.000
Femur	–0.464	–0.107	–0.000	0.228
Tibia	–0.468	–0.118	–0.000	0.018
Metatarsal	–0.392	0.295	0.000	–0.661
Longest toe	–0.392	–0.433	–0.000	0.445
Hindlimb	–0.468	–0.014	–0.000	–0.269
Lamella number	0.198	–0.837	–0.000	–0.490
Eigenvalue	4.32	1.01	1.00	0.51
Variance	61.71	14.43	14.29	7.32

strong on the first component, this should again be interpreted as a size axis. The second component showed strong correlations with both lamella number (negative) and metatarsal length (positive; Table 5). Not unexpectedly, differences between species from the Chocó and the Caribbean were mostly situated along the second principal component with species from the Chocó having fewer lamellae but longer metatarsi than Caribbean *Anolis*. Among the Caribbean anoles, ecomorphs are distinct along both the size and shape axes (Fig. 2A), as has been demonstrated previously (Losos, 1990).

The principal component analysis using size-adjusted data shows a better separation between regions and within traditional ecomorphs. The first four axes accounted for 97.7% of the variation in the data set (Table 6). The first component showed moderately negative loadings of all limb dimensions. The second and third components are largely explained by variation in lamella number and SVL, respectively. Interestingly, even when using size-adjusted data, the species from the Choco′ region are separated completely from the Caribbean species in multivariate space and do not appear to converge onto ecomorph categories as observed in the Caribbean species. Additionally, the distribution of the Choco′ region *Anolis* in morphological space is reduced when compared to Caribbean *Anolis* lizards (Fig. 2).

However, when examining a data set with fewer variables but a much greater number of mainland *Anolis* species, it becomes apparent that the Choco′ species are extremes even among mainland *Anolis* lizards (Fig. 3). A factor analysis performed on the residual data retained two factors together explaining 63% of the variation in the data. Whereas residual limb dimensions and residual body mass loaded

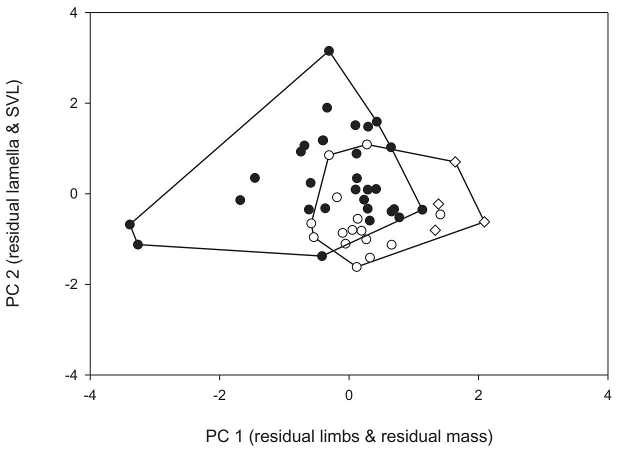

Figure 3. Distribution of mainland (white symbols) and Caribbean (filled circles) *Anolis* species in morphological shape space as indicated by the first two regression factors. Although there appears to be a clear separation among the two radiations on the first shape axis, there is considerable overlap between mainland and Caribbean species in on the second factor. Note how the Choco′ *Anolis* (white diamonds) are morphological extremes even for mainland *Anolis*. Although shape variation among Caribbean anoles is markedly greater than among mainland anoles, mainland species are under represented in the sample.

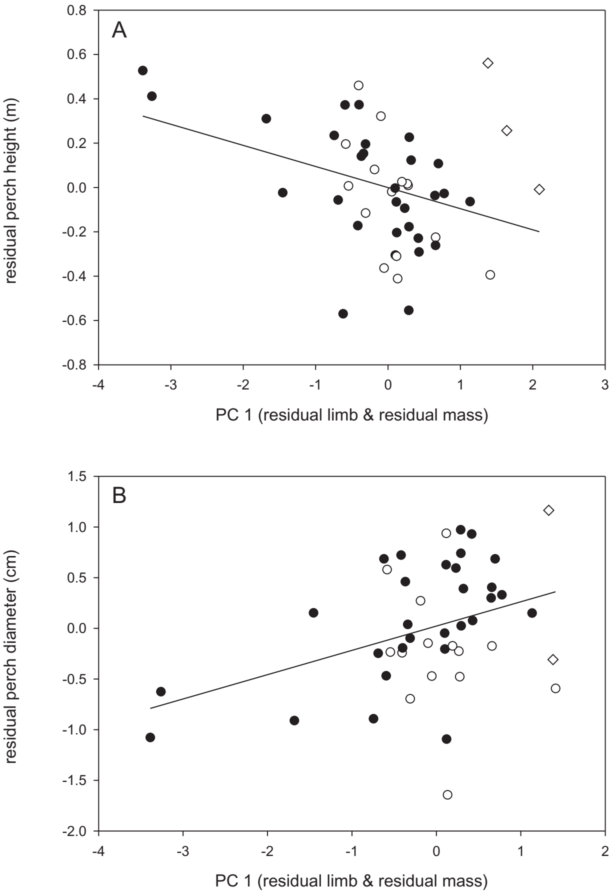

Figure 4. Correlations between limb shape and habitat use in *Anolis* lizards. A, a clear negative correlation is apparent between perch height and limb shape across all species in the data set. Note that the correlation is no longer significant when examining the mainland species separately. Filled symbols, Caribbean species; open symbols, mainland species; Choco′ *Anolis* is represented by diamonds. B, a strong positive correlation is apparent between limb shape and perch diameter across all species. Again, the relationship is no longer significant when excluding the Caribbean species from the analysis. Filled symbols, Caribbean species; open symbols, mainland ; Choco′ *Anolis* is represented by diamonds.

strongly on the first principal component, residual lamella number and SVL loaded strongly on the second principal component. On average, the overlap between both groups is considerable, especially on the second principal component (Fig. 3). Inspection of the Euclidian distances between groups, however, indicates that morphological differences are greatest between Caribbean twig anoles and crown giants compared with all other groups (Table 7).

Interestingly, the relations among morphological shape (as represented by factor 1) and a number of typical indicators of habitat use in *Anolis* lizards such as perch height and perch diameter are generally similar (analyses of covariance showed no difference between groups in perch height or perch diameter; all $P > 0.05$) for both mainland and Caribbean *Anolis* lizards (Fig. 4A, B). Whereas perch height is negatively correlated with relative limb dimensions (i.e. lizards with relatively shorter limbs perch higher up; $r = 0.35$; $P = 0.017$), perch diameter is strongly and positively correlated with relative limb dimensions across all species ($r = 0.37$; $P = 0.013$). However, the variation in relative limb dimensions appears to be much smaller for mainland *Anolis* lizards than for the Caribbean radiation, rendering the relationships between habitat use and morphology nonsignificant when examining mainland lizards only (Fig. 4A, B). Correlations between the second factor and our two indicators of habitat use were nonsignificant.

DISCUSSION

THE IMPORTANCE OF BODY SIZE AND SHAPE

Previous work has demonstrated that differences in body size are an important component of morphological variation in *Anolis* lizard communities.

Table 7. Euclidian distances between ecomorph groups

	Sample size (number of species)															
	1	4	2	4	1	1	1	3	3	1	5	8	1	5	6	4
Mainland crown giant	0.00															
Caribbean crown giant	1.60	0.00														
Mainland grass–bush	3.08	3.41	0.00													
Caribbean grass–bush	2.97	2.89	0.86	0.00												
Chocó grass–bush	3.72	3.76	2.11	2.18	0.00											
Mainland semi-aquatic	2.05	3.00	1.49	1.90	2.98	0.00										
Chocó semi-aquatic	2.93	3.10	1.42	1.49	0.91	2.12	0.00									
Mainland trunk	2.90	2.97	0.74	0.40	2.46	1.64	1.72	0.00								
Caribbean trunk	2.92	2.69	1.20	0.53	1.85	2.15	1.22	0.91	0.00							
Chocó trunk	3.30	3.25	1.56	1.46	0.75	2.52	0.53	1.77	1.10	0.00						
Mainland trunk–crown	1.97	2.61	1.40	1.51	3.03	0.66	2.13	1.24	1.80	2.44	0.00					
Caribbean trunk–crown	2.76	2.01	2.10	1.28	2.74	2.61	2.14	1.49	1.08	2.03	2.08	0.00				
Chocó trunk–crown	1.73	2.37	2.51	2.55	2.24	2.08	1.66	2.64	2.32	2.09	2.22	2.68	0.00			
Mainland trunk–ground	2.83	3.27	0.50	1.10	1.83	1.33	1.06	1.07	1.26	1.35	1.38	2.19	2.07	0.00		
Caribbean trunk–ground	2.27	2.20	1.43	1.05	1.81	1.83	1.02	1.26	0.75	1.17	1.57	1.25	1.60	1.24	0.00	
Caribbean twig	3.65	3.43	2.80	2.41	4.58	2.94	3.83	2.17	2.78	3.85	2.35	2.40	4.30	3.15	3.06	0.00

Euclidean distances are based on group means of the factors scores of the first three significant factors.

Differences in body size may both allow and drive resource partitioning among species and can thus be an important structuring agent (Schoener, 1974; Losos, 1994a). The data for the *Anolis* lizards from the Choco′ region examined in the present study also revealed a significant variation in body size between species, suggesting that differences in body size play an important structuring role here as well. However, upon the removal of variation in body size between species, habitat-related variation in limb shape between species also becomes evident. For example, *A. chloris* (occupying mostly trunks) and *A. latifrons* (occupying the trunk–crown region) have a relatively greater number of subdigital lamellae in comparison with the more terrestrial *A. notopholis* and *A. macrolepis*. This is in agreement with other studies that have demonstrated that lamella number is a good predictor of arboreal habitat use for *Anolis* lizards (Glossip & Losos, 1997; De Queiroz, Chu & Losos, 1998; Macrini, Irschick & Losos, 2003). In addition, the two more arboreal species have front- and hindlimb pairs of more similar length, a condition that permits a more stable type of locomotion on narrow perches (Losos, 1990; Irschick & Losos, 1998, 1999). The two more terrestrial species, *A. notopholis* and *A. macrolepis* have relatively longer hindlimbs as has been observed for other lizards that principally occupy terrestrial habitats and rely on sprint speed rather than crypsis as a predator avoidance mechanism (Losos, 1994a; Losos *et al.*, 2000; Herrel, Meyers & Vanhooydonck, 2002).

In Caribbean *Anolis* lizards, body size also increases with preferred perch height (Losos, 1994a). In our data, we also observed a tendency for increasing body size with increasing perch height. A similar pattern of covariation of perch height and body size was observed for mainland species of various localities in both Central and South America (Irschick *et al.*, 1997). It is has been suggested that this tendency to increase body size with an increase in perch height is related to competitive interactions between species as has been documented for species pairs in the Lesser Antilles (Schoener, 1970; Losos, 1994a). This could be the case for the Chocó *Anolis* examined in the present study because they are part of a larger, more complex, and species rich community. However, further data on habitat use and morphology for all members of the community are needed to fully understand the role of body size in structuring the Chocó *Anolis* community.

Williams (1983) argued that the adaptive radiation of *Anolis* lizards in the Greater Antilles is largely due to the evolution of faunistic complexity in relation to island size and topographic diversity (i.e. the result of local adaptation to the wide diversity in available of habitats). He also suggested that Lesser Antillean *Anolis* species have not yet reached the level of differentiation of the Greater Antilles islands (in body size and shape and habitat use). This would in turn be reflected in a differentiation among species principally along the body size axis. However, the data from the present study indicate that morphological differentiation in the Chocó *Anolis* lizards is also more prominent in body size rather than shape, despite the great structural and vegetative complexity of the region (Gentry, 1986). Thus, pronounced differentiation in body size need not be the result of limited structural or habitat complexity *per se*.

ARE MAINLAND COMMUNITIES CONVERGENT WITH THE GREATER ANTILLES ECOMORPHS?

Our analyses of morphological convergence showed two general patterns. First, we observed two species groups, Choco′ region species and Caribbean species, with a differentiation in morphospace largely by differences in metatarsal length (Fig. 2). Body size, however, does not play a key role in the separation of the groups because the Choco′ species fall within of the range of sizes of the insular species. Second, when examining size-free variables, the separation among insular ecomorph groups and between the Antillean and Chocó groups generally becomes stronger. The separation between Choco′ species and Antilles species is largely due to hindlimb shape and lamella number. Interestingly, despite the fact that the Choco′ region species examined in the present study are the ecologically most diverse in the region, the area occupied in shape space appears to be constrained compared with Antillean *Anolis* lizards (Fig. 2B). Thus, at first sight, it appears that *Anolis* radiations from mainland regions have not reached the degree of morphological differentiation as observed for Greater Antillean anoles (Irschick *et al.*, 1997). However, this does not invalidate the application of the ecomorph concept to mainland faunas as indicated by the clear covariation between morphology and habitat use for the Chocó lizards included in the present study.

Interestingly, the broad comparison of Antillean and mainland anoles indicates that mainland anoles are not morphologically constrained *per se* because they show a considerable morphological diversity that is almost as great that of Antillean anoles (despite the restricted number of mainland species included; see Appendix). Among Antillean anoles, however, it is principally the twig anoles and crown giants that appear to be driving much of the variation in morphology (Table 7; Vanhooydonck & Irschick, 2002). Unexpectedly, and although overlapping to some degree, differences among Antillean and mainland anoles in limb shape are great (Fig. 3B). Although this could partly be due to the different sources of the data included in the analysis (i.e. derived from measurements by different people), this is unlikely because mainland and Chocó lizards converge on the same region of morphospace. Moreover, differences between groups appear to be greatest between specific Caribbean ecomorphs (twig anoles and crown giants) and other groups, rather than between groups derived from different data sets. As a corollary, the evolutionary processes leading to differentiation of groups in different regions are not deterministic because the morphological diversification clearly has not followed similar trajectories in both species groups (Losos *et al.*, 1998). However, the covariation among morphology and ecology is convergent among both groups and appears to be largely determined by mechanical principles driving locomotor performance on specific substrates (Fig. 4). Thus, across all anoles, species perching higher have relatively shorter limbs, but species living on broader substrates have relatively longer limbs as has been demonstrated previously for Antillean *Anolis* lizards. However, as noted previously (Irschick *et al.*, 1997), patterns of ecomorphological variation do not appear to hold when examining mainland species by themselves. Again, this largely appears to be driven by the absence of extreme ecomorphs, such as twig anoles and crown giants, that drive much of the patterns of covariation observed in Antillean anoles (Table 7; Vanhooydonck & Irschick, 2002). However, more studies of mainland *Anolis* communities are needed to test the general principles of convergence among mainland and Antillean *Anolis* lizards. In addition, more studies focusing on the covariation in ecology, behaviour, and performance in these communities are needed to better understand the ecological and evolutionary processes driving the diversification of mainland anole faunas.

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APPENDIX

LIST OF SPECIES USED IN THE BROAD COMPARATIVE ANALYSIS

Genus	Species	Source
Anolis	*angusticeps*	Bahamas, Andros Island
Anolis	*auratus*	Irschick *et al*. (1997)
Anolis	*bahorucoensis*	Domenican Republic, Barahona peninsula
Anolis	*barahonae*	Domenican Republic, Barahona peninsula
Anolis	*biporcatus*	Irschick *et al*. (1997)
Anolis	*brevirostris*	Domenican Republic, Barahona peninsula
Anolis	*brunneus*	Bahamas, Acklins Island
Anolis	*capito*	Irschick *et al*. (1997)
Anolis	*carolinensis*	Louisiana, Good Hope field
Anolis	*carpenteri*	Irschick *et al*. (1997)
Anolis	*chloris*	Colombia
Anolis	*coelestinus*	Domenican Republic, Barahona peninsula
Anolis	*cristatellus*	Puerto Rico, El Verde
Anolis	*cristatellus*	Florida, Miami
Anolis	*cuvieri*	Puerto Rico, Cambalache forest
Anolis	*cybotes*	Domenican Republic, Barahona peninsula
Anolis	*distichus*	Domenican Republic, Barahona peninsula
Anolis	*distichus*	Florida, Miami
Anolis	*equestris*	Florida, Miami
Anolis	*evermanni*	Puerto Rico, El Verde
Anolis	*frenatus*	Irschick *et al*. (1997)
Anolis	*fuscoauratus*	Irschick *et al*. (1997)
Anolis	*garmani*	Jamaica, Discovery Bay
Anolis	*grahami*	Jamaica, Discovery Bay
Anolis	*gundlachi*	Puerto Rico, El Verde
Anolis	*humilis*	Irschick *et al*. (1997)
Anolis	*krugi*	Puerto Rico, El Verde
Anolis	*latifrons*	Colombia
Anolis	*lemurinus*	Irschick *et al*. (1997)
Anolis	*limifrons*	Irschick *et al*. (1997)
Anolis	*lineatopus*	Jamaica, Discovery Bay
Anolis	*macrolepis*	Colombia
Anolis	*meridionalis*	Irschick *et al*. (1997)
Anolis	*nitens*	Irschick *et al*. (1997)
Anolis	*notopholis*	Colombia
Anolis	*occultus*	Puerto Rico, El Yunque
Anolis	*olssoni*	Domenican Republic, Barahona peninsula
Anolis	*ortonii*	Irschick *et al*. (1997)
Anolis	*oxylophus*	Irschick *et al*. (1997)
Anolis	*pulchellus*	Puerto Rico, El Verde
Anolis	*punctatus*	Irschick *et al*. (1997)
Anolis	*sagrei*	Bahamas, Andros Island
Anolis	*sericeus*	Irschick *et al*. (1997)
Anolis	*sheplani*	Domenican Republic, Barahona peninsula
Anolis	*singularis*	Domenican Republic, Barahona peninsula
Anolis	*smaragdinus*	Bahamas, Staniel Cay
Anolis	*stratulus*	Puerto Rico, El Verde
Anolis	*trachyderma*	Irschick *et al*. (1997)
Anolis	valencienni	Jamaica, Discovery Bay