

LETTERS

Sexual dimorphism and adaptive radiation in *Anolis* lizards

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Sexual dimorphism is widespread and substantial throughout the animal world^{1,2}. It is surprising, then, that such a pervasive source of biological diversity has not been integrated into studies of adaptive radiation, despite extensive and growing attention to both phenomena^{1,3–7}. Rather, most studies of adaptive radiation either group individuals without regard to sex or focus solely on one sex. Here we show that sexual differences contribute substantially to the ecomorphological diversity produced by the adaptive radiations of West Indian *Anolis* lizards: within anole species, males and females occupy mostly non-overlapping parts of morphological space; the overall extent of sexual variation is large relative to interspecific variation; and the degree of variation depends on ecological type. Thus, when sexual dimorphism in ecologically relevant traits is substantial, ignoring its contribution may significantly underestimate the adaptive component of evolutionary radiation. Conversely, if sexual dimorphism and interspecific divergence are alternative means of ecological diversification, then the degree of sexual dimorphism may be negatively related to the extent of adaptive radiation.

Sexual dimorphism may increase the ecologically relevant variation within a community when sexes play ecologically differentiated roles. Sometimes, the ecological differences between sexes can be as great as those observed between coexisting species^{8–10}. By extension, in a community of sexually dimorphic species, members of the same sex may cluster ecologically regardless of species, or sexes and species may be interdigitated across the ecological spectrum. Either possibility will result in 'intersexual niche packing', which leads to an increase in the overall niche space occupied. This effect may be accentuated in the presence of ecological character release, and thus may be more pronounced in younger communities in which the paucity of species permits the sexes to differ to a greater extent^{8,10}.

Lizards of the genus *Anolis* are a particularly appropriate group in which to investigate the interaction of sexual and interspecific patterns. *Anolis* is a classic example of adaptive radiation, having experienced essentially independent radiations on each of the islands of the Greater Antilles (Cuba, Hispaniola, Jamaica and Puerto Rico), in each case producing a suite of species morphologically and behaviourally specialized to use different parts of the environment. For example, species that occupy open habitats have long legs, which provide great running and jumping capabilities. In contrast, those species which specialize on twigs have short legs that enhance manoeuvrability in their narrow and irregular habitat. Moreover, the same set of habitat specialists—termed ecomorphs and named for the part of the habitat they use (for example, crown-giant, grass-bush, trunk-crown, trunk-ground, and twig)—has evolved repeatedly across the four islands^{11,12}. In addition, anoles vary considerably in the extent of sexual dimorphism in body size^{8,13,14}, ranging from species in which the sexes are the same size to others in which adult

males are more than three times the mass of adult females, and in ecomorphologically relevant body proportions^{9,15}. Similarly, sexual differentiation in microhabitat use, diet and behaviour is substantial among West Indian anoles (see, for example, refs 9, 15; Supplementary Information). West Indian anoles thus contain extensive ecomorphological differentiation, both among species specialized to use different habitats within the adaptive radiations on each island and between sexes within these species.

The relative significance of adaptive radiation and sexual dimorphism can be examined in two ways. First, to quantify the extent to which ecomorphological variation is related to adaptive radiation and sexual dimorphism, and the interaction between them, we compared the relative importance of interspecific and intersexual variation in explaining morphological shape diversity using partial variance components from multivariate analysis of variance (MANOVA). This approach compares the degree to which the explanatory variables shape morphology, but cannot examine whether sexes occupy unique regions of morphological space (morphospace). Second, to test the hypothesis of intersexual 'niche packing'¹⁰, we used a non-parametric approach to compare the volume of ecological space or morphospace occupied by males alone as compared with the space occupied when both sexes are included in the analysis.

Both adaptive radiation and sexual dimorphism are substantial in anoles. Anole species using different microhabitats vary greatly in shape morphology, in agreement with previous studies¹⁶ (Fig. 1). Within species, the sexes differ in the same morphological traits that distinguish the ecomorphs, and for which the ecological significance of morphological variation is well-understood^{15,16}: adjusted for size, females have longer bodies and more toepad lamellae (see Methods) than males, whereas males have longer limbs (Fig. 1). In addition, the extent and form of dimorphism varies among the different ecomorph types (Fig. 1).

MANOVA identifies microhabitat use (=ecomorph type) as the most important source of variation within the *Anolis* radiations (Table 1). However, differences between sexes are also highly significant and explain a substantial proportion of the variation as well (Table 1). Moreover, the ecomorph by sexual dimorphism interaction is significant, indicating that sexual differences in shape take on different forms in different ecomorph types (Fig. 1). These effects are not reduced when phylogeny is taken into account (all MANOVA effects significant at $P < 0.001$, Table 1).

Analyses of morphospace packing reveal that sexual dimorphism is responsible for a large proportion of the total ecomorph niche space occupied. As expected (based on previous studies), the ecomorphs occupy largely non-overlapping portions of multivariate morphospace. However, we demonstrate here that sexes within ecomorphs also occupy unique regions of morphospace (Fig. 2, Table 2 and Supplementary Information). Only 14% of occupied cells in

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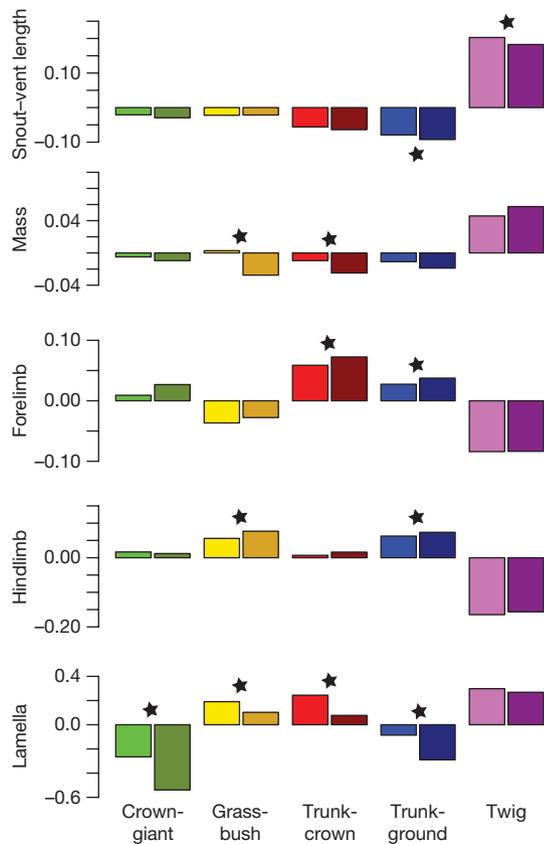


Figure 1 | Shape dimorphism among the ecomorphs. Relative means for ecomorphs (colours; defined at bottom) and sexes (light, females; dark, males) for shape morphology variables (*y*-axes). Ecomorph-sex means are adjusted for all other effects in the ANOVA models (LSMEANS option in Proc GLM in the SAS statistical language; see Methods), and plotted relative to the grand mean (centred at 0). Stars indicate significant sexual differences within ecomorphs. Sexual dimorphism in body length (snout-vent length) occurs in ecomorphs with the shortest and longest bodies, dimorphism in forelimbs in ecomorphs with the longest forelimbs, and dimorphism in hindlimbs in ecomorphs with the longest hindlimbs. All ecomorphs are dimorphic in lamella number, except twig anoles, which have the greatest lamella numbers relative to body size.

morphospace contain both male and female individuals. By contrast, females uniquely occupy 45% of morphospace and males uniquely occupy 36% of morphospace. Thus, sexual dimorphism significantly increases the density of morphospace occupied by the anole radiations ($P = 0.0048$): a 59% increase if the morphospace volume of both sexes is compared to that of only females, and an 88% increase compared to the male-only volume. This result remains significant

Table 1 | MANOVA results for shape morphology

Effect	Wilks' λ	F-value	P-value	<i>p</i>	<i>q</i>	<i>r</i>	η^2
Non-phylogenetic shape dimorphism							
Sex	0.599	78.78	<0.0001	5	1	1	40%
Ecomorph	0.00906	328.84	<0.0001	5	4	4	69%
Sex \times ecomorph	0.838	5.35	<0.0001	5	4	4	4%
Species(ecomorph)	0.135	31.04	<0.0001	5	10	5	33%
Shape dimorphism adjusted for phylogeny							
Sex	0.594	80.52	<0.0001	5	1	1	41%
Ecomorph	0.0167	253.34	<0.0001	5	4	4	64%
Sex \times ecomorph	0.794	7.07	<0.0001	5	4	4	6%
Species(ecomorph)	0.205	23.20	<0.0001	5	10	5	27%

All shape variables are entered into the model as dependent variables. Independent variables included in the model are listed under 'Effect'. 'F-value', value from *F* distribution; *p*, number of dependent variables; *q*, number of independent degrees of freedom; *r*, minimum of *p* or *q*; η^2 , multivariate partial variance = $1 - \lambda^{1/r}$ (refs 28, 29); Species(ecomorph), species nested within ecomorph.

when closely related species of the same ecomorph are not included ($P = 0.0018$), or if the analysis is repeated using principal components analysis ($P = 0.017$). As with the MANOVA, the extent of intersexual divergence is a function of ecomorph type (Table 2, Fig. 2 and Supplementary Fig. 1): in some ecomorphs, sexes appear to have more exclusive clusters, whereas in others, the sexes form a mixed cluster.

The significant interaction between sexual dimorphism and microhabitat use suggests an interplay of the diversifying forces that act between sexes and species during anole adaptive radiation. The role of environmental factors in interspecific diversification is well-established³. Although not as widely appreciated, environmental context can be just as important in determining the degree to which males and females can diverge¹⁷⁻¹⁹. For example, food quality and dispersion may determine whether territorial mating systems are energetically feasible, and in particular, what degree of polygyny is possible, as has been suggested for African antelopes²⁰. Alternatively,

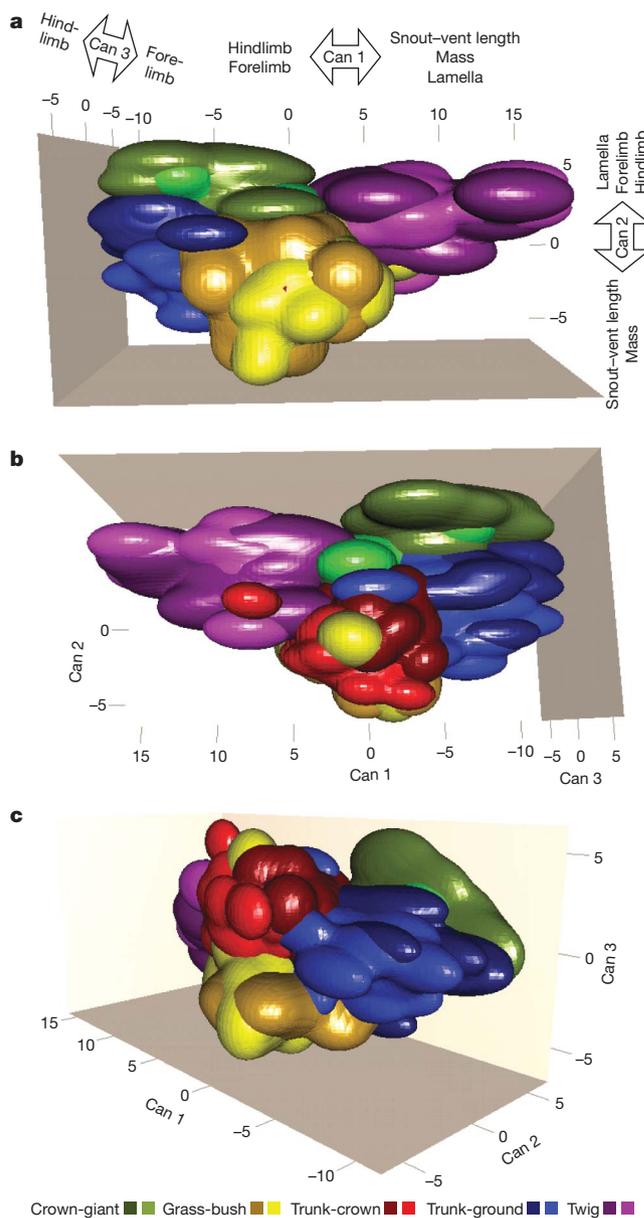


Figure 2 | Three-dimensional visualization of morphological space. Panels a-c show different views of the same three-dimensional density object. The plot is based on individual data with ecomorphs (colours; same as Fig. 1) and sexes (light, females; dark, males) indicated. Can 1-3 indicate canonical variate scores (see Methods).

Table 2 | Morphospace niche-packing analysis

Ecomorph	Both sexes*				Males				Females			
	$N_{ind}†$	Tot _{cubes} ‡	Unique _{cubes} §	Unique %	N_{ind}	Tot _{cubes}	Unique _{cubes}	Unique %	N_{ind}	Tot _{cubes}	Unique _{cubes}	Unique %
Trunk-ground	166	95	78	27	79	51	34	12	87	57	32	11
Trunk-crown	150	76	72	25	63	38	26	9	87	47	37	13
Crown-giant	31	29	21	7	16	16	12	4	15	13	9	3
Grass-bush	88	65	57	20	43	36	23	8	45	38	26	9
Twig	58	43	43	15	19	16	10	3	39	33	27	9
All	493			94	220			36	273			45
Total cubes		289				154¶				182¶		

We compared the overlapping versus unique space occupied by ecomorphs and ecomorph-sex classes to assess the relative contributions to morphospace volume.

* 'Both sexes' refers to ecomorph analyses with sexes combined, whereas ecomorph-females and ecomorph-males separates each ecomorph class by sex.

† N_{ind} , number of individuals.

‡ Tot_{cubes}, the number of (morphospace volume) cubes filled by each sex, ecomorph or ecomorph-sex class; these cubes may contain individuals of more than one class. See Methods for details.

§ We measured unique_{cubes}, the volume occupied by each class. It is the volume of morphospace that is occupied solely by the given class relative to the entire volume occupied by all classes. Unique_{cubes} excludes those cubes which contain more than one class.

|| 'Unique %' refers to the percentage of cubes occupied by only the given class relative to the total number of cubes.

¶ Forty-seven cubes are occupied by both sexes.

males and females may evolve independent adaptations to better utilize non-overlapping regions of the relevant resource spectrum, as has been demonstrated for snakes and hummingbirds^{5,9,21}. The feasibility of such intersexual resource partitioning will be strongly determined by environmental context, so that greater dimorphism may result in some habitats more than in others.

Differences between the sexes in resource use have been documented in many *Anolis* species. In the present study, we find that intersexual differences in habitat use are great, and correlated with morphological dimorphism (Supplementary Information). In contrast to environmental factors, sexual selection probably plays a lesser role in driving the evolution of *Anolis* sexual dimorphism. Although sexual selection for large size in males as a means of obtaining large territories and the females they contain is commonly invoked as an explanation for lizard sexual dimorphism (reviewed in ref. 13), it is difficult to attribute the patterns observed here to that cause. For example, in those ecomorphs with significant shape dimorphism, males have lesser relative mass than females, shorter relative body length, and fewer lamellae. If anything, this pattern is opposite to what one might expect if dimorphism evolves to provide superior fighting ability in males.

An additional possibility is that the interplay of sexual and interspecific differentiation is not static, but rather that the interaction itself evolves during adaptive radiation. Anole diversification on Puerto Rico has produced more species than the radiation on Jamaica. Comparison of the extent of sexual dimorphism across these islands suggests how the interaction between sexual dimorphism and adaptive radiation may evolve during clade diversification. Previous work²² indicates that the degree of sexual size dimorphism in *Anolis* decreases with the number of sympatric congeners. Correspondingly, our results indicate that sexual dimorphism in shape is diminished on the more species-rich island (average multivariate s.d. computed by intersexual Mahalanobis distances averaged within island = 2.61 for Jamaica versus 1.95 for Puerto Rico; ANOVA, island effect, one-tailed $P = 0.032$; Supplementary Table 1). Thus, these results indicate that increased species diversity may constrain the magnitude of sexual size and shape dimorphism, in accord with ecological theory²³.

This finding suggests a model of how sexual dimorphism and adaptive radiation interact during biological diversification. Species are often observed to expand their niche breadth in the absence of competitors (the phenomenon of ecological release, reviewed in ref. 10). Some theoretical models suggest that this variation may be converted by disruptive selection into sexual dimorphism or distinct but monomorphic species^{23,24} (see also ref. 25). In anoles, data for one-species islands indicate that sympatric speciation does not occur²⁶ and that sexual dimorphism predominates²². As species richness accumulates, sexual dimorphism is decreased as intraspecific, intersexual dimorphism is converted into interspecific differentiation. This intriguing hypothesis could be directly tested by examining

shape and size dimorphism in areas into which non-native anoles have been recently introduced; at the extreme, nine anole species have been introduced to Florida and as many as four occur sympatrically with the native *Anolis carolinensis* (reviewed in ref. 27). If this hypothesis is correct, then we would expect to see dimorphism decrease as the number of introduced species increases.

Islands have long served as a natural laboratory for studies of evolutionary diversification and adaptive radiation. However, whether phenomena characteristic of islands also occur in older and more biotically complex continental areas is an open question. The model that we propose is potentially general in scope, and could be an important explanation for patterns of ecologically driven sexual dimorphism. Assessment of the generality of this pattern, both among *Anolis* lizards and animals in general, will require integration of ecological and phylogenetic analyses.

METHODS

Data collection. We measured five morphometric characters from adults of both sexes of members of each ecomorph class on Puerto Rico and Jamaica (sample sizes, 3–29; mean, 16.4): mass, snout-to-vent length (SVL), fore- and hindlimb length (FOREL and HINDL), and sub-digital lamella number on the fourth toe of the hind foot (LAMN; lamellae are laterally expanded scales on the subdigital toepads). We used the natural logarithm of all variables; mass was first cube-root transformed to place it on a linear scale with length measurements. We used the geometric-mean method to separate size and shape¹⁵, with SIZE defined as the arithmetic mean of log-adjusted SVL, MASS, FOREL and HINDL (LAMN is not included as it does not scale intraspecifically, and only weakly interspecifically with size). Shape variables were calculated for each individual by taking the difference of each log-variable with SIZE.

Species mean values for morphology are presented in Supplementary Table 2. Previous studies have established that both interspecific and intersexual variation in these characters is adaptive with respect to differences in habitat use^{15,16}.

Multivariate shape analyses. We used ANOVA and MANOVA to test for effects of sex, ecomorph type, their interaction, and species nested within ecomorph type on shape variation (Proc Reg and Proc GLM in the SAS statistical language). Multiple comparisons were controlled at an experiment-wise error rate of 5% using the Tukey-Cramer method. The relative importance of each factor or interaction was estimated using components of partial variance explained by each term in the model^{28,29} (partial η^2 ; because they are partial variances, their sum can exceed 100%).

A phylogenetic version of these analyses was conducted using a molecular phylogeny for *Anolis* (Supplementary Fig. 2) and a phylogenetic GLS method described previously¹⁴. Briefly, this method uses Cholesky decomposition to normalize the variance-covariance matrix of dependent and independent variables by the expected similarity due to a brownian-motion model of evolution. We preserved individual variation by conducting the phylogenetic transformation on the individual data. To do so, we expanded the rows and columns of the phylogenetic similarity matrix by the numbers of individuals per species, and added an identity matrix. We then computed the square root of the matrix by Cholesky decomposition followed by the matrix inverse, as before. We used this matrix to post-multiply data matrices (rows = individuals, columns = dependent or independent variables). Ecomorph type, sex, and species nested within ecomorph type, all categorical variables, were effect coded¹⁴.

Niche filling analyses. We conducted separate analyses of niche filling for morphological and ecological data sets. For each data set, we used canonical variate analysis to reduce the dimensionality of our multiple-group data (as an alternative ordination method, we repeated these analyses using principal components analysis, which does not incorporate information on within-group covariance among shape variables; Supplementary Table 4). For the morphological analysis, the dependent variables were the shape morphology variables described above. The independent variables were the species-sex classes (loadings reported in Supplementary Table 3). We used individual canonical variate scores to test hypotheses of morphospace filling. We binned individual observations into cubes of morphospace defined by intervals of one canonical variate unit along canonical variate axes one to three. We measured the volume of morphospace occupied by male *Anolis* lizards by counting the number of cubes occupied by one or more individuals. We then measured the increase in volume attributable to adding females by counting the number of additional cubes filled when females were included. Significance was assessed by randomizing the sex of the individual within species using 20,000 permutations of the data. Code implementing this test in the R statistical language is available at <http://www2.hawaii.edu/~mbutler/software.html>. To account for any phylogenetic confounding, analyses were re-run after eliminating the two species whose closest relatives share the same ecomorph type (*Anolis pulchellus* and *Anolis stratulus*).

To visualize the position of the sexes and species in morphological space, we plotted 20% contours of the three-dimensional kernel density using the *ks* package written in R³⁰. The densities were computed using kernel discriminant analysis in three dimensions (using canonical variate scores Can 1–3) on ecomorph-sex groups.

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