



Patterns of ecomorphological convergence among mainland and island *Anolis* lizards

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Differing selective pressures on islands versus the mainland may produce alternative evolutionary outcomes among closely related lineages. Conversely, lineages may be constrained to produce similar outcomes in different mainland and island environments, or mainland and island environments may not differ significantly. Among the best-studied island radiations are Caribbean *Anolis* lizards. Distinct morphotypes, or ‘ecomorphs’, have been described, and the same ecomorphs have evolved independently on each Greater Antillean island. The mainland *Anolis* radiation has received much less attention. We use a large morphological data set and a novel phylogenetic hypothesis to show that mainland *Anolis* did not evolve the same morphotypes as island *Anolis*, despite some island species being more closely related to mainland species than to island species that share their morphotype. A maximum of four of the six Caribbean ecomorphs were found to exist on the mainland, and just 15 of 123 mainland species are assignable to a Caribbean ecomorph. This result was insensitive to differing taxon samples and alternative phylogenetic hypotheses. Mainland convergence to a Caribbean ecomorph occurs only among species assigned to the grass-bush ecomorph. Thus, the ecomorphs that have evolved convergently multiple times in the Caribbean have not evolved in parallel on the mainland. These results are consistent with the hypothesis that mainland and island environments offer different selective pressures. © 2010 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2010, 101, 852–859.

ADDITIONAL KEYWORDS: adaptive radiation – convergent evolution – ecomorph – interspecific interactions – morphology – morphospace.

INTRODUCTION

Adaptive radiation and niche partitioning may occur differently in island versus mainland environments. Few studies have examined this inference at large evolutionary scales (Case, 1978; Case & Schwaner, 1993; Irschick *et al.*, 1997; Losos & Miles, 2002; Macrini, Irschick & Losos, 2003; Velasco & Herrel, 2007; Pinto *et al.*, 2008). The recognition that islands represent an unusual adaptive situation compared with mainland systems dates back to Darwin (1859). Classic examples of island radiations include Darwin’s finches (Lack, 1947; Grant, 1966; Schluter, 1988; Burns, Hackett & Klein, 2002), Hawaiian silverswords (Carlquist, 1965; Baldwin & Robichaux,

1995), and Caribbean *Anolis* lizards (Williams, 1983; Losos *et al.*, 1998; Losos, 2009). Mainland radiations include hummingbirds (Morony, Bock & Farrand, 1975; Feinsinger & Colwell, 1978; Bleiweiss, Kirsch & Matheus, 1997), Australian marsupials (Strickberger, 2000), and, perhaps less well documented, Central and South American *Anolis* lizards (Pounds, 1988; Nicholson *et al.*, 2005; Losos, 2009). Differences in competitors, dispersal, food resources, predator diversity and abundance, and greater selective pressure generally as a result of decreased geographic space on islands have each been implicated as explanations for greater competition on islands versus the mainland (e.g. Grant, 1966; Schluter, 1988; Irschick *et al.*, 1997; Losos, 2009).

The phenomenon of convergent evolution affords a convenient means to test island versus mainland evolutionary outcomes resulting from species radiations. Lineages that have independently evolved similar

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traits are assumed to have been subject to similar selection pressures (Futuyma, 2005). If mainland and island environments offer different selective pressures, then the niche space occupied by the evolutionary outcomes of adaptive radiations on the mainland should differ from those on islands. Conversely, if there is no 'island effect' then evolutionary convergence might produce repeated similar patterns in both island and mainland environments among close relatives. Comparison of closely related radiations within, versus between, island and mainland systems should disentangle the evolutionary effects of geography from clade-specific effects.

The lizard genus *Anolis* is a model system for mainland–island comparisons (Losos, 2009, and references therein). There are over 380 species of *Anolis* distributed among the Caribbean islands and mainland Central and South America (Poe, 2004; Nicholson *et al.*, 2005). Pinto *et al.* (2008) suggested that mainland *Anolis* slightly overlapped with their island counterparts in morphospace, and that mainland *Anolis* lineages evolved at different rates than island lineages. Thomas, Meiri & Philimore (2009) showed that body size evolved at different rates for different ecomorph classes (trunk-crown or trunk-ground versus other), and in island (small island, large island) and continental landmasses. Extensive morphological convergence has been demonstrated between island faunas of *Anolis* (Williams, 1983; Losos *et al.*, 1998), but the existence of such patterns has not been confirmed or refuted among mainland *Anolis* (Losos, 2009). Here, we test whether the patterns of convergence in ecomorphology observed among island *Anolis* are also evident in mainland *Anolis* radiations.

Anolis on the Greater Antilles have evolved specialized morphologies that correlate with the use of particular structural microhabitats (Rand & Williams, 1969; Williams, 1972, 1983; Losos, 2009). Williams (1972) used the term 'ecomorph' to define these correlations as a set of 'species with the same structural habitat/niche, similar in morphology and behavior, but not necessarily close phylogenetically.' Six Caribbean ecomorph classes are recognized and named for the microhabitat that they occupy: trunk-crown, trunk-ground, grass-bush, crown-giant, trunk, and twig. Losos *et al.* (1998) used the unweighted pair group method with arithmetic mean (UPGMA) to show that members of an ecomorph class cluster in morphological space, regardless of geography or phylogeny. In other words, some Caribbean *Anolis* species are more similar morphologically to *Anolis* from independent radiations on other islands than they are to their geographically or phylogenetically close congeners.

The independent evolution of ecomorphs on the Greater Antilles indicates convergent adaptation among island *Anolis* (Williams, 1983; Losos *et al.*,

1998; Leal, Knox & Losos, 2002). Each ecomorph has evolved at least twice, and may have evolved independently on each of the Greater Antilles (Losos *et al.*, 1998). Our question is whether adaptive radiations on the mainland produced the same ecomorphs that are found in the Caribbean. The presence of Caribbean ecomorphs on the mainland would suggest the lack of an 'island effect', whereas their absence would be compatible with the hypothesis that mainland and island radiations are shaped by different selective pressures. The shared phylogenetic history of mainland and island *Anolis* [e.g. the mainland Norops clade is more closely related to island forms than to the mainland Dactyloa group; see Nicholson *et al.*, 2005: fig. 1; and see Fig. S1 for our use of the informal group names Dactyloa and Norops (based on invalid genera erected by Guyer and Savage, 1986)] suggests that mainland–island differences are interpretable as environmental rather than lineage effects (Pinto *et al.*, 2008). This shared evolutionary history is especially useful for testing ecomorph evolution, as some island species assigned to ecomorph classes are more closely related to mainland species than to species assigned to their same ecomorph class (e.g. the Jamaican radiation includes four ecomorphs and forms a clade with the mainland Norops species, independent from other ecomorphs; Fig. S1; see also Losos, 2009).

Irschick *et al.* (1997) suggested that morphology and ecology in mainland *Anolis* might be decoupled, or at least related differently, in mainland versus Caribbean *Anolis*. Of the five mainland *Anolis* species for which ecological data were available to Irschick *et al.*, the mainland species that were morphologically similar to Caribbean *Anolis* differed ecologically from their Caribbean analogues (Irschick *et al.*, 1997). In this paper we use morphology as a proxy for ecomorph class (see Harmon *et al.*, 2005), because morphology and ecology are strongly linked in Caribbean *Anolis* (Losos, 2009; and references above). Thus, we are testing whether the same morphotypes, rather than ecomorphs, occur on the mainland as in the Caribbean. Still, we will frequently use the term 'ecomorph' below, as the absence of Caribbean morphotypes on the mainland falsifies the existence of Caribbean ecomorphs there (i.e. the '-morph' part of the test fails). The finding of morphological similarity on the mainland is compatible with (but does not prove) the same ecomorphs having evolved on the mainland. The ecology of nearly all mainland species remains to be tested.

We used a large morphological data set of Caribbean and mainland *Anolis* to explore the degree to which mainland *Anolis* fit the Caribbean ecomorph concept. We used a predictive multiple discriminant function analysis (DFA) and a new phylogenetic esti-

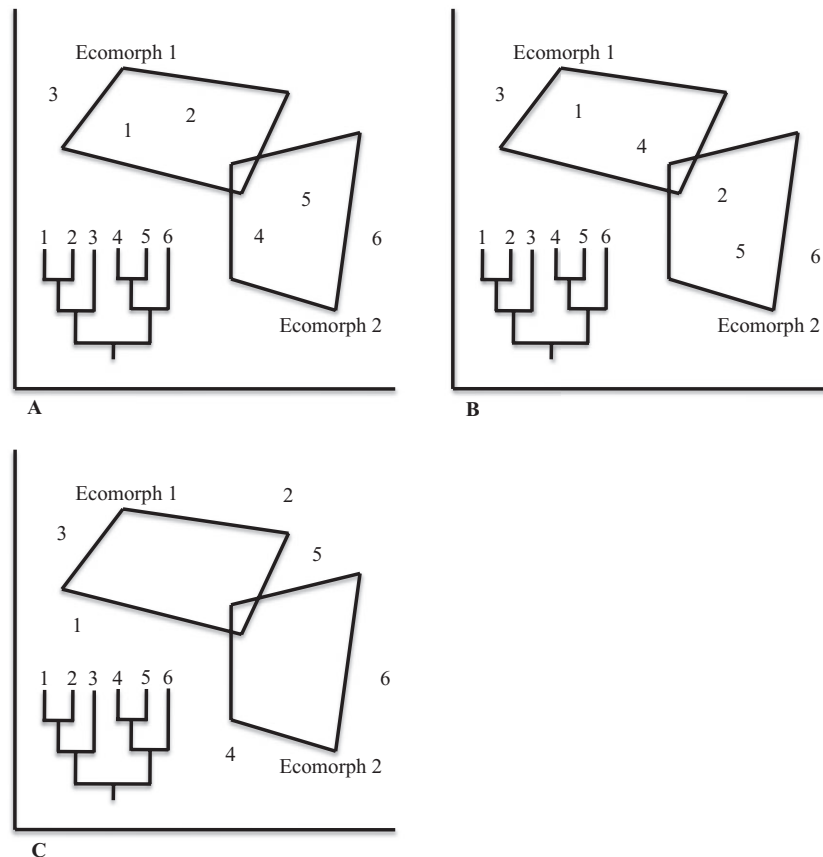


Figure 1. Three hypothetical outcomes of mainland *Anolis* species occupation of Caribbean morphospace. A hypothetical phylogeny for six mainland species is shown along with minimum convex polygons representing the morphological space occupied by two Caribbean ecomorphs. A, mainland and Caribbean species occupy the same morphospace, and mainland species show no convergence of ecomorphs within mainland lineages; B, mainland and Caribbean species occupy the same morphospace, with convergence of ecomorphs within mainland lineages; C, mainland and Caribbean species occupy different morphospace.

mate to test three hypotheses: (1) mainland *Anolis* can be classified into the same ecomorph classes as Caribbean *Anolis*, but show no convergence within the mainland; (2) mainland *Anolis* can be classified into the same ecomorph classes as Caribbean *Anolis* and show convergence within the mainland; (3) mainland *Anolis* occupy different morphospace than Caribbean *Anolis*. These three hypotheses are depicted graphically in Figure 1.

MATERIAL AND METHODS

MORPHOLOGICAL DATA AND PHYLOGENETIC RELATIONSHIP

We examined 255 of the approximately 380 species of *Anolis* ($n = 1-15$ specimens/species). Of the species we examined, 132 were Caribbean and 123 were from mainland Central and South America. The Caribbean species in this study include those from the Greater

Antilles that have previously been assigned to ecomorph classes (Williams, 1983; Losos *et al.*, 1998; Losos, 2009), as well as all other Greater and Lesser Antillean species not assigned to any ecomorph class.

We used digital calipers and stereomicroscopes to collect the morphological data, and supplemented this with data from original species descriptions from Williams *et al.* (1995). The characters analysed include: mean snout-vent length (SVL), as a measure of body size; sexual size dimorphism (SSD), measured as maximum female SVL divided by maximum male SVL; mean femur length (FL); mean head length (HL); median number of lamellae under the second and third digit of the fourth hind toe (L); median number of scales across the snout between the second canthals (SNSC); and median ratio of tail length to SVL (TR). Variation in some of these morphological characters has been shown to reflect variation in the ecology of *Anolis* lizards (Harmon *et al.*, 2005, and

references therein). These morphological characters differ from those originally used to identify the Caribbean ecomorphs (Irschick *et al.*, 1997; Losos *et al.*, 1998), in that we use HL, SNSC, SSD, different treatments of hindlimb length and tail length, and do not include body mass.

We used two separate sets of phylogenetic estimates for analysis of evolutionary changes to ecomorph class among mainland species. The first set of trees is 1344 optimal topologies resulting from parsimony analysis of 255 species and eight out-groups using morphological characters (Poe, 2004; S. Poe, unpubl. data), mitochondrial DNA (mtDNA) sequences, and nuclear ITS DNA (nDNA) sequences. The second set is a sample of 1501 topologies obtained from the post burn-in phase of a Markov Chain Monte Carlo Bayesian analysis of 189 *Anolis* species and two out-groups scored for mtDNA (reanalysis of data from Nicholson *et al.*, 2005).

STATISTICAL AND PHYLOGENETIC ANALYSES

We natural log-transformed the seven morphological characters and conducted a predictive multiple DFA using these traits as discriminant variables, and using Caribbean ecomorph classes, as defined by Losos (2009), as the categorical grouping variable. We included 87 Caribbean ecomorph species for building a predictive model for ecomorph membership classification (Table S1). We assessed whether mainland species could be assigned to Caribbean ecomorphs based on two criteria: (1) the assigned probability of ecomorph membership according to DFA; and (2) the squared distance from the DFA centroid of an ecomorph polygon. Mainland species assigned to a Caribbean ecomorph with at least 99% probability were considered to be candidate species for ecomorph class assignment. Of the mainland species assigned with 99% probability, we accepted as designated ecomorphs only those species that had a lower squared distance from the centroid of an ecomorph compared with the Caribbean ecomorph representative species with the greatest squared distance from the centroid of that ecomorph. That is, if the squared distance value of a particular mainland species assigned to an ecomorph with 99% probability was greater than that of the greatest *a priori* assigned Caribbean species in that ecomorph class, we rejected the assignment of that mainland species to the ecomorph class. As a more conservative approach, we also performed this analysis using a 95% cut-off with the same squared distance criterion.

To further test mainland ecomorph class assignment, we reanalysed all mainland species using DFA, but restricted the Caribbean species used to construct the predictive model to only a single member of each

clade where an ecomorph has evolved independently. Where possible we chose ecomorph species such that at least one representative from each of the Greater Antilles was included. This sampling scheme resulted in 23 Caribbean species being *a priori* assigned to an ecomorph (Table S2). This additional analysis was conducted to assess whether there was an effect of phylogenetic pseudoreplication when including all Caribbean ecomorph species.

We mapped the evolution of Caribbean ecomorphs among mainland *Anolis* lineages using MacClade (Maddison & Maddison, 2000) and our two sets of phylogenetic estimates. We constructed a data matrix wherein species were assigned a score of 0 if they were Caribbean or if they were from the mainland but had not been assigned to an ecomorph by our approach. Scores of 1 (trunk-ground), 2 (trunk-crown), 3 (grass-bush), 4 (twig), 5 (crown-giant), and 6 (trunk) were assigned to mainland species that were classified to Caribbean ecomorphs by our criteria, and the character was considered to be unordered. We used the MacClade 'chart state changes' function to count the number of changes to each Caribbean ecomorph class among mainland species. We summed the average number of changes to each ecomorph class across all reconstructions among all 1344 most parsimonious trees, and among all 1501 Bayesian post burn-in trees. This count indicates the degree of convergence (i.e. the number of evolutionarily independent transitions) to each Caribbean ecomorph class within mainland lineages.

To summarize, we are examining the evolution of Caribbean ecomorphs on the mainland using eight combinations of variables: two sets of phylogenetic trees (parsimony and Bayesian, to allow for differing taxonomic coverage and methods, and mtDNA versus combined data sets), two DFA percentile cut-offs for assignment to ecomorph class (99 and 95%, so as to allow statistical leniency and conservatism of group membership), and two sets of designated Caribbean ecomorph species to dictate group membership (all assigned species and species from phylogenetically independent radiations, to control for phylogenetic pseudoreplication).

RESULTS

Of the 87 Caribbean species *a priori* assigned to ecomorphs (Table S1), six (6.9%) were classified differently by our DFA method compared with the original ecomorph classification when all Greater Antillean species were included (*Anolis dolichocephalus* Williams, 1963, grass-bush to trunk-crown; *Anolis evermanni* Stejneger, 1904, trunk-crown to trunk-ground; *Anolis isolepis* Cope, 1861, trunk-crown to twig; *Anolis jubar* Schwartz, 1968, trunk-ground to trunk; *Anolis*

mestrei, Barbour & Ramsden, 1916, trunk-ground to trunk; *Anolis valencienni* Duméril & Bibron, 1837, twig to trunk-crown). Of the Caribbean ecomorph species correctly reassigned to their *a priori* ecomorph, 17 (19.5%) were reassigned with less than 95% confidence. The 'incorrect' assignments among Caribbean ecomorphs in this paper may have resulted from differing analytical techniques (DFA versus UPGMA in previous studies), alternative scaling approaches (in most previous studies, characters were scaled with SVL before analysis; we allowed the DFA to incorporate size as just another variable for all variables except tail length, for which data were collected in terms of body length), or different morphological characters relative to previous studies (we include HL, SNSC, and SSD, different treatments of hindlimb length and tail length, and do not include body mass; Irschick *et al.* 1997; Losos *et al.* 1998). Analysis using 23 Caribbean ecomorph species from phylogenetically independent radiations (Table S2) resulted in no misclassifications, and all species were reassigned to their original ecomorph class with at least 99% confidence.

All of our results were qualitatively similar; therefore, we present here only the results using the largest taxonomic sample (i.e. 1344 parsimony trees with ecomorphs designated using all Caribbean ecomorph species) and the 99 and 95% prediction cut-offs for DFA membership. We list results from the other six combinations of variables in the online material. Among the 123 mainland *Anolis* species, nine (7.3%) were assigned to a Caribbean ecomorph class with 99% confidence or better, and met the squared distance criterion of being closer to the ecomorph centroid than the furthest actual assigned Caribbean ecomorph species (Table 1). Of the mainland species assigned to an ecomorph class, seven were classified as grass-bush, one as trunk-crown, and one as twig. No mainland species were assigned to the crown-giant or trunk ecomorph classes (Tables S3 and S4).

Our phylogenetic analysis of the number of evolutionary independent derivations of Caribbean ecomorph class among mainland lineages revealed an average of nine independent transitions to a Caribbean ecomorph (Table 1; see Tables S5–S7 for the results of additional analyses). Convergence to an ecomorph class among mainland species occurred only within the grass-bush ecomorph (Table 1).

DISCUSSION

Few mainland *Anolis* lineages have evolved to resemble Caribbean ecomorph classes, in spite of the close phyletic relationship between some Caribbean ecomorph species and some mainland species (Poe, 2004; Nicholson *et al.* 2005; Losos, 2009). Under all eight analyses, a maximum of only four out of six

Table 1. Number of mainland species assigned to a Caribbean ecomorph class when including all *a priori* assigned Caribbean ecomorph *Anolis* species, and estimated number of evolutionary changes to each Caribbean ecomorph class among mainland *Anolis* species. Evolutionary changes of mainland species to Caribbean ecomorph class averaged among 1344 most parsimonious trees

Ecomorph	Number of mainland species assigned to Caribbean ecomorph (99/95%)	Number of evolutionary changes to ecomorph within mainland lineages (99/95%)
Grass-bush	7/4	7/9
Trunk-crown	1/0	1/1
Twig	1/0	1/1
Trunk-ground	0/2	0/2
Crown-giant	0/0	0
Trunk	0/0	0

The assignment to an ecomorph is based on discriminant function analysis (99 or 95% confidence), and meeting the criteria of falling within the greatest squared distance to the centroid of an *a priori* assigned Caribbean species in that ecomorph.

Caribbean ecomorphs can be shown to occur on the mainland, and up to 15 out of 123 mainland species are assigned to a Caribbean ecomorph class (Table 1; Tables S3–S7). These results demonstrate that adaptive radiations among *Anolis* result in different evolutionary outcomes on islands compared with the mainland (see also, Irschick *et al.* 1997; Pinto *et al.* 2008). With the exception of the grass-bush ecomorph, each ecomorph class includes only between one and four assigned mainland species (Table 1; Tables S3 and S4). Thus, the extensive convergent evolution of ecomorphs among Caribbean islands is not occurring in parallel on the mainland among the few Caribbean ecomorphs that have evolved there. Although the well-known ecomorph phenomenon observed among Caribbean *Anolis* is not a uniquely island phenomenon, we have shown that the evolution of ecomorphs first identified in the Caribbean is clearly largely restricted to the Caribbean.

The results presented here show that mainland and island systems may produce different evolutionary outcomes, even among close island and mainland relatives (Fig. S1) in a lineage – the *Anolis* lizards – famous for convergence (Losos *et al.* 1998; Freeman, 2005). The lack of a lineage effect in our results is perhaps most obvious in the comparison of the Jamaican island *Anolis grahami* Gray, 1845 radiation, with its mainland sister Norops radiation. In this comparison, the island *A. grahami* clade results

in four ecomorphs among six of seven species (86% of species are ecomorph species), whereas the mainland *Norops* sister clade results in 12 ecomorph species among 78 total species (15%; Fig. S1).

The commonness of the grass-bush ecomorph on the mainland ($n = 11$ species) in our results may reflect the cladewide ubiquity of this ecomorph. Alternatively, it may be an artifact of the most morphologically extreme species *a priori* classified as the grass-bush ecomorph possessing an extraordinarily large squared distance to the centroid relative to other Caribbean ecomorphs (49.3 for grass-bush versus 8.3–18.7 for other ecomorphs; Table S3). This result suggests great diversity among Caribbean *Anolis* assigned to the grass-bush ecomorph, and a concomitant bias towards inclusion of mainland *Anolis* within this group according to our criteria. The variation among grass-bush species is reduced in our second analysis using independent clades of Caribbean ecomorph species (Tables S4, S6 and S7).

The limited morphological overlap of mainland and island species (Pinto *et al.* 2008) coupled with the relative dearth of island ecomorphs on the mainland (Table 1) suggests the possibility that there are other 'ecomorphs' on the mainland that do not occur in the Caribbean. For example, many of the mainland giant (> 100 mm SVL) *Anolis*, even those from separate phyletic lineages (i.e. alpha and beta; Etheridge, 1959), form a morphological group separate from island giants and other mainland species (Fig. S2). This 'mainland giant' group may turn out to be a novel ecomorph upon further study. It is important to note that the Caribbean ecomorphs were not identified *a posteriori* according to the results of some objective statistical analysis, but rather were defined *a priori* based on decades of accumulated information on morphology, ecology, and behaviour by Ernest Williams, Stanley Rand, and many others (Losos *et al.* 1998: note 12, p 2117; Losos, 2009). We are nowhere near gaining the body of knowledge that would enable comparable inferences about mainland species. This paper may be a first step in attempts to objectively identify morphological (and eventually ecological) 'types' of *Anolis* on the mainland.

These results offer some support for each of the hypotheses in Figure 1, but clearly favour hypothesis 3: mainland and island *Anolis* occupy largely non-overlapping morphospace. Although convergence to Caribbean ecomorphs appears uncommon within the mainland, our finding of 15 mainland species converging on Caribbean morphospace supports hypothesis 1. The pattern among grass-bush *Anolis* supports hypothesis 2 in some of the analyses in this study, which may indicate a single shared mainland-island grass-bush ecomorph or a bias towards this ecomorph inherent in our criteria because of the liberal *a priori*

designation of Caribbean species as grass-bush ecomorphs. Regardless, these results suggest that morphological convergence is proceeding differently in mainland versus island radiations. Future work on the ecology of mainland *Anolis* and the potential existence of novel mainland ecomorphs will offer further insight into differences and similarities in mainland and island radiations.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1. One of 1344 optimal topologies from parsimony analysis of 252 *Anolis* species and eight out-groups used in our analysis of evolutionary changes to an ecomorph class among mainland species.

Figure S2. Principal components (PC) plot showing the position in morphospace of mainland giant (> 100 mm snout–vent length) *Anolis* (solid circles) and Caribbean crown-giant ecomorph species (solid squares), and minimum convex polygons.

Table S1. All Caribbean *Anolis* species *a priori* assigned to an ecomorph class used in discriminant function analysis (see text).

Table S2. Twenty-three Caribbean *Anolis* species from independent phylogenetic radiations used in ecomorph assignment analyses (see text).

Table S3. Mainland *Anolis* species assigned to a Caribbean ecomorph class using discriminant function analyses and squared distance criteria when including all Caribbean *Anolis* species in the analysis (Table S1; see text).

Table S4. Mainland *Anolis* species assigned to a Caribbean ecomorph class using discriminant function analyses and squared distance criteria when including only 23 Caribbean *Anolis* species from independent phylogenetic radiations *a priori* assigned to ecomorph classes (Table S2; see text).

Table S5. Number of mainland species assigned to a Caribbean ecomorph class when including all *a priori* assigned Caribbean ecomorph species, and estimated number of evolutionary changes to each Caribbean ecomorph class among mainland species assuming 99 and 95% confidence.

Table S6. Number of mainland species assigned to a Caribbean ecomorph class when including only 23 Caribbean ecomorph species from independent phylogenetic lineages, and estimated number of evolutionary changes to each Caribbean ecomorph class among mainland species.

Table S7. Number of mainland species assigned to a Caribbean ecomorph class when including only 23 Caribbean ecomorph species from independent phylogenetic lineages, and estimated number of evolutionary changes to each Caribbean ecomorph class among mainland species.

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