

Convergent patterns of adaptive radiation between island and mainland *Anolis* lizards

JONATHAN M. HUIE^{1,2,*}, IVAN PRATES^{2,3}, RAYNA C. BELL^{2,4} and KEVIN DE QUEIROZ²

¹Department of Biological Sciences, The George Washington University, Washington, DC 20052, USA

²Department of Vertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, DC 20560, USA

³Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, MI 48109, USA

⁴Herpetology Department, California Academy of Sciences, San Francisco, CA 94118, USA

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Uncovering convergent and divergent patterns of diversification is a major goal of evolutionary biology. On four Greater Antillean islands, *Anolis* lizards have convergently evolved sets of species with similar ecologies and morphologies (ecomorphs). However, it is unclear whether closely related anoles from Central and South America exhibit similar patterns of diversification. We generated an extensive morphological data set to test whether mainland *Draconura*-clade anoles are assignable to the Caribbean ecomorphs. Based on a new classification framework that accounts for different degrees of morphological support, we found morphological evidence for mainland representatives of all six Caribbean ecomorphs and evidence that many ecomorphs have also evolved repeatedly on the mainland. We also found strong evidence that ground-dwelling anoles from both the Caribbean and the mainland constitute a new and distinct ecomorph class. Beyond the ecomorph concept, we show that the island and mainland anole faunas exhibit exceptional morphological convergence, suggesting that they are more similar than previously understood. However, the island and mainland radiations are not identical, indicating that regional differences and historical contingencies can lead to replicate yet variable radiations. More broadly, our findings suggest that replicated radiations occur beyond island settings more often than previously recognized.

ADDITIONAL KEYWORDS: anole – ecomorph – habitat – morphology – replicated radiation.

INTRODUCTION

A primary goal of evolutionary biology is to understand the causes of similar and dissimilar evolutionary outcomes. Adaptive radiation is the rise of diverse ecological and morphological forms, descended from a single common ancestor (Simpson, 1953; Schlüter, 2000; Losos, 2011; Gillespie *et al.*, 2020). This hallmark evolutionary process often works in tandem with convergence to produce repeated evolutions of similar form-function relationships. When different species occupy similar ecological niches, selection for similar functional attributes often leads to morphological convergence (Schlüter & Nagel, 1995; Losos, 2011; Santana & Cheung, 2016; Burress *et al.*, 2018; Moen, 2019). In some cases, repeated ecological

diversification leads to exceptional morphological convergence between entire radiations in distinct regions, as seen in African rift lake cichlids, Hawaiian spiders, stickleback fishes, Bonin Islands snails, Caribbean rain frogs and Caribbean anole lizards (Kocher *et al.*, 1993; Losos *et al.*, 1998; Rundle *et al.*, 2000; Chiba, 2004; Gillespie *et al.*, 2018; Dugo-Cota *et al.*, 2019). These replicated adaptive radiations illustrate the deterministic aspects of evolution. However, the generality of replicated radiations is not clear, as most recognized cases occur in insular and lacustrine systems, where neighbouring islands and lakes present similar environments (Schlüter, 2000; Losos, 2009; Prates & Singhal, 2020).

Comparisons of closely related taxa in island and mainland settings are useful for testing the pervasiveness of replicated adaptive radiations. Many factors differ between island and mainland

*Corresponding author. E-mail: jonathanmhuie@gmail.com

environments that might lead to disparate evolutionary outcomes. In general, islands present fewer competitor and predator species and more “unoccupied” niches compared to mainland environments, which tend to be older and often have more diverse and established communities (MacArthur & Wilson, 1967; Carlquist, 1974; Schlüter, 1988). However, recent studies suggest that some mainland environments provide ample opportunities, if not more, for physiological diversification than insular habitats (Velasco *et al.*, 2016, 2018; Salazar *et al.*, 2019). To test for convergent patterns of adaptive radiation, we can characterize diversification in closely related groups of species with similar ecologies across regions (Schluter, 1988; Irschick *et al.*, 1997; Bossuyt & Milinkovich, 2000; Schaad & Poe, 2010). The independent evolution of similar morphologies with strong ties to ecology would suggest that island and mainland lineages are evolving under similar selective regimes and support the hypothesis of convergent adaptive radiations. By contrast, the absence of morphological convergence in mainland lineages would suggest that replicated radiations are primarily restricted to island settings.

Anole lizards (*Anolis*) provide an exemplary system for investigating convergent evolution and adaptive radiation (Losos, 2009). In the Greater Antilles, anoles have radiated four times on four different islands, where they repeatedly evolved habitat specialists with similar morphological adaptations (Losos *et al.*, 1998). Based on their shared ecological and morphological traits, most Greater Antillean anole species have been assigned to one of six classes termed “ecomorphs”, named (mostly) after the structural microhabitats characteristically used by their members: crown-giant, grass-bush, trunk, trunk-crown, trunk-ground and twig (Rand & Williams, 1969; Williams, 1972, 1983; Losos, 2009; Fig. 1). Although many investigations have studied the evolution and pervasiveness of the Caribbean ecomorphs (Irschick *et al.*, 1997; Losos & de Queiroz, 1997; Losos *et al.*, 1998; Velasco & Herrel, 2007; Schaad & Poe, 2010), the six ecomorphs do not describe the full range of ecological diversity exhibited by anoles, even in the West Indies (Mahler *et al.*, 2013). For instance, there are ground-dwelling, rock-dwelling and semi-aquatic anoles in both island and mainland settings (Losos, 2009). The semi-aquatic species have not converged on similar morphologies (Leal *et al.*, 2002; Muñoz *et al.*, 2015); however, other habitat specialists might constitute undescribed ecomorphs that have been overlooked by studies that used only the six Caribbean ecomorphs to investigate convergent patterns of adaptive radiation (Mahler *et al.*, 2013; Moreno-Arias & Calderón-Espinosa, 2016; Poe & Anderson, 2019; Moreno-Arias *et al.*, 2020).

Of the 430 described species of anoles (Uetz *et al.*, 2020), the majority occur in Central and South

America, yet the ecological and morphological evolution of mainland anoles remains understudied (Nicholson *et al.*, 2005; Losos, 2009). There are two clades of mainland anoles; one of which, the *Draconura* clade, is derived from a Caribbean ancestor that recolonized the mainland (Nicholson *et al.*, 2005; Poe, 2017). The *Draconura* clade exhibits comparable species richness, rates of morphological evolution and physiological diversity to the Caribbean anoles, suggesting that this clade underwent adaptive radiation on the mainland (Pinto *et al.*, 2008; Nicholson *et al.*, 2012; Poe *et al.*, 2018; Salazar *et al.*, 2019; Poe & Anderson, 2019). Relatively little is known about their ecology, but natural history data suggest that many *Draconura* species are associated with similar structural habitats to those of the Caribbean ecomorphs (Savage, 2002; Köhler *et al.*, 2014; McCranie & Köhler, 2015). Additionally, several *Draconura* species are most often found on the ground, a habitat preference found in only a few Caribbean anoles (Vitt *et al.*, 2001, 2002, 2003; Henderson & Powell, 2009; Fig. 2). These ecological similarities and differences set the stage to investigate whether mainland *Draconura* species have converged on similar morphological adaptations as their island counterparts.

Previous attempts to classify mainland anoles into the Caribbean ecomorphs have found a low number of mainland ecomorph species, suggesting that island and mainland anoles are on separate evolutionary trajectories (Irschick *et al.*, 1997; Velasco & Herrel, 2007; Schaad & Poe, 2010). These studies relied on the well-established links between ecology and morphology in Caribbean anoles to assign mainland species to the same ecomorphs based on morphological similarities to the Caribbean anoles (Irschick *et al.*, 1997; Velasco & Herrel, 2007; Schaad & Poe, 2010). This approach may be too restrictive if the assignment criteria are unrealistic or the Caribbean species used to delimit the ecomorphs do not encompass the full extent of morphological diversity associated with a given ecomorph. As a result, mainland species may have remained unclassified despite potentially being ecologically and morphologically similar to one of the ecomorphs. However, recent studies using cluster methods have objectively detected similar island and mainland anole morphotypes (Moreno-Arias *et al.*, 2016; Poe & Anderson, 2019). Recognizing species with less extreme ecomorphological adaptations and distinguishing them from those that do not conform to any ecomorph (ecologically or morphologically) may provide more insights into whether species in distinct geographic regions have evolved similar traits in response to similar selective pressures.

Here, we reassess patterns of ecomorph convergence between Caribbean anoles and the mainland *Draconura* clade of anoles using an extensive morphological data set. We propose a framework to

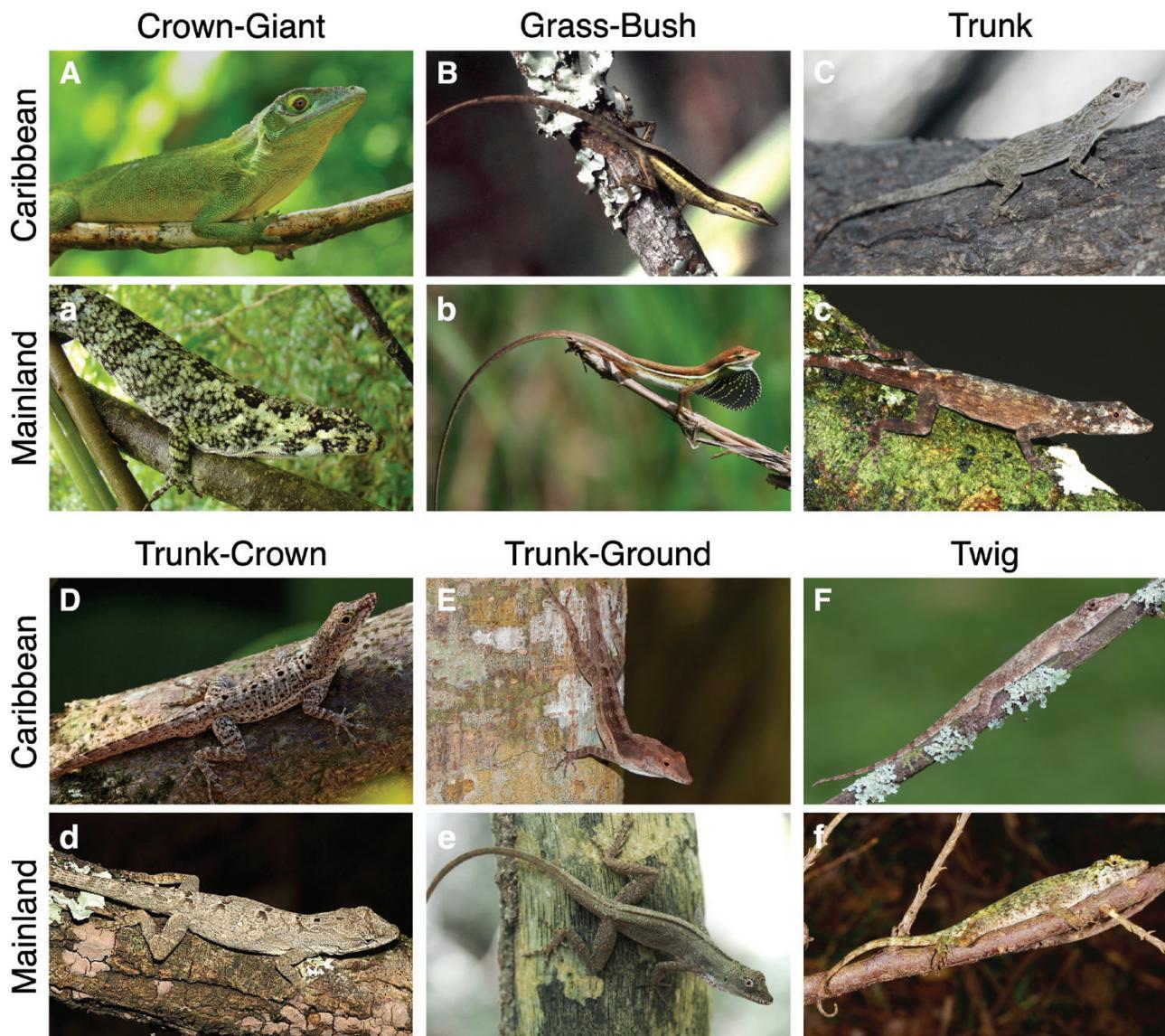


Figure 1. West Indian *Anolis* lizards representing the six Caribbean ecomorphs (A-F) and the morphologically similar mainland *Draconura*-clade species (a-f). (A) *Anolis cuvieri*, photo courtesy of Matt McElroy; (B) *Anolis pulchellus*, photo courtesy of Kristiina Ovaska; (C) *Anolis distichus*, photo courtesy of Pierson Hill; (D) *Anolis stratulus*, photo courtesy of Alberto López; (E) *Anolis lineatopus*, photo courtesy of D. Luke Mahler; (F) *Anolis occultus*, photo courtesy of D. Luke Mahler; (a) *Anolis petersii*, photo courtesy of Carlos R. Beutelspacher; (b) *Anolis auratus*, photo courtesy of Kenro Kusumi; (c) *Anolis ortonii*, photo by Ivan Prates; (d) *Anolis omiltemanus*, photo courtesy of Gunther Köhler; (e) *Anolis bicaorum*, photo courtesy of Sofia Prado-Irwin; (f) *Anolis salvini*, photo courtesy of Sebastian Lotzkat.

assign mainland species to the Caribbean ecomorphs with different levels of morphological support. We also investigate whether island and mainland ground-dwelling anoles share morphological traits that are distinct from those of the six Caribbean ecomorphs. We regard our ecomorph assignments as hypotheses of habitat use and evaluate our assignments based on currently available ecological data. We then use phylogenetic comparative methods to investigate whether the ecomorphs have evolved repeatedly

on the mainland and test the strength of their convergence. Lastly, we test whether the mainland *Draconura* clade and Caribbean radiations are convergent without a priori ecomorph assignments. To assess convergent evolutionary outcomes within and between island and mainland anoles, we specifically ask: (1) Are mainland *Draconura* species assignable to the Caribbean ecomorphs based on morphology? (2) Do island and mainland ground-dwelling anoles constitute a previously unrecognized ecomorph



Figure 2. Four species of ground-dwelling *Anolis* lizards. (A) *A. humilis* (mainland), photo courtesy of Sebastian Lotzkat; (B) *A. trachyderma* (mainland), photo by Ivan Prates; (C) *A. tandai* (mainland), photo by Ivan Prates; (D) *A. barbouri* (Caribbean), photo by Kevin de Queiroz.

class? (3) Have the six Caribbean ecomorphs and potential ground ecomorph evolved on the mainland independently from the Caribbean, and if so, did they evolve repeatedly? (4) To what extent do the Greater Antillean and mainland *Draconura* radiations exhibit morphological similarity?

MATERIAL AND METHODS

We approached our investigation of morphological convergence between Caribbean and mainland *Draconura*-clade anoles with two complementary approaches. We first assessed whether mainland *Draconura* and previously unclassified Caribbean species can be assigned to ecomorph classes based on their morphological similarity to Caribbean ecomorph species. We also assessed their degree of convergence. However, these results may be biased by subjective a priori assignments of reference ecomorph species, so we also used more objective methods (e.g. cluster analyses, tests for species-for-species matching and the detection of morphological shifts across the

adaptive evolutionary landscape) to identify instances of convergence without a priori ecomorph assignments. Congruent results across approaches would support the robustness of our conclusions.

SPECIMEN SAMPLING AND MORPHOLOGICAL MEASUREMENTS

We collected morphological data for 205 *Anolis* species (including 99 *Draconura*-clade species) using preserved specimens deposited in natural history collections. We examined 347 adult male lizards, with an average of 1.69 (range 1–4) specimens per species. Armstead & Poe (2015) demonstrated that a single specimen per species is sufficient to capture ecologically relevant interspecific morphological variation in anoles. Specimens were identified as male based on the presence of hemipenes or enlarged post-anal scales. Of the 99 *Draconura*-clade species, 91 were found in mainland Central and South America, and eight species were endemic to Caribbean or Pacific islands. Together they represent roughly 67% of the total known *Draconura* species (Nicholson, 2012; Poe *et al.*, 2017). Of the remaining 106

species that we sampled, 71 were Caribbean species that have sufficient ecological and morphological data to support previous ecomorph assignments (hereafter referred to as “Caribbean ecomorph” species), and 35 were Greater and Lesser Antillean species not assigned to an ecomorph (hereafter referred to as “previously unclassified Caribbean” species). The [Supporting Information \(Table S1\)](#) contains a full species list with ecomorph assignments.

To compare the ecomorphology of mainland *Draconura* and Caribbean species, we measured 13 external morphological traits previously associated with ecology and locomotor performance ([Losos, 1990](#); [Beuttell & Losos, 1999](#); [Macrini et al., 2003](#); [Elstrott & Irschick, 2004](#)). Measurements were taken as defined by [Köhler \(2014\)](#) and included: snout-vent length (SVL), tail length, head length, snout length, head width, humerus length, radius length, hand length, femur length, tibia length, foot length and the width of the subdigital pads on the fourth finger and fourth toe. For tail length, we only measured individuals that possessed a complete, non-regenerated tail, and obtained at least one tail measurement per species. We were unable to obtain any specimens with complete tails for 11 species, so we used the body proportions from [Poe & Anderson \(2019\)](#) to estimate tail length. In the single species where subdigital pads are absent (*Anolis onca*), we measured the width of the digit in the corresponding region (antepenultimate phalanx). All measurements were taken to the nearest 0.1 mm with digital calipers or to the nearest 0.5 mm with a ruler by a single author (J.M.H.).

Prior to all analyses, the raw data were natural log transformed and averaged by species to produce mean trait values. To remove the effects of size and account for phylogenetic non-independence among species, the “phyl.resid” function from the *phytools* R package was used to phylogenetically regress each trait against SVL ([Revell, 2012](#)). When size-correcting tail length, we regressed the data separately using the average SVL values calculated from only the specimens with tail data, including the specimens for which we estimated tail data. The residuals from each regression were treated as our size-corrected data. For this and subsequent phylogenetic analyses, we used the maximum clade credibility (MCC) tree from [Poe et al. \(2017\)](#), which was estimated from both morphological and molecular data, and pruned it to include only our sampled taxa ([Supporting Information, Materials and methods S1](#)). However, we also repeated all of our analyses using a time-calibrated phylogeny from [Poe et al. \(2017\)](#), which was estimated from genetic data only (referred to as the maximum clade credibility time, or MRCT, by the original authors). We qualitatively compared the results inferred using the MCC and time-calibrated phylogenies and report notable deviations below.

ASSESSING SUPPORT FOR THE ECOMORPHS

To investigate morphological variation of the mainland *Draconura* and Caribbean anoles, we plotted their positions in a multidimensional trait space. We used the “phyl.pca” function in the *phytools* package ([Revell, 2012](#)) to perform a phylogenetically informed principal component analysis (pPCA) with a covariance matrix that incorporated the phylogenetically size-corrected traits and SVL as a proxy for body size. Based on a visual scree test, we retained the first five pPC axes for subsequent analyses. These axes accounted for 85.9% of the total trait variation and exhibited clear correlations with specific body traits.

To test whether the Caribbean ecomorphs occupied distinct areas of the morphospace, we performed a series of randomization tests to assess the significance of the Euclidean distances between their centroids. Using the pPC scores for the a priori Caribbean ecomorph species (from the retained pPC axes), we calculated the Euclidean distances between the centroids of each pairwise ecomorph combination. To determine whether the distance between two ecomorph centroids was greater than expected under a null model, we combined the members of those ecomorphs into a single set and then randomly assigned them to two groups, each with the same number of species originally assigned to each ecomorph. Then, using the pPC scores for the randomly assigned species, we calculated the centroids for each group and the Euclidean distance between them. This process was repeated 1000 times per ecomorph pair and the proportion of randomly sampled values less than the observed value was used as a p-value (alpha level = 0.05 with a Bonferroni correction for multiple comparisons).

We also assessed support for the ecomorphs using a hierarchical cluster analysis to group species based on morphological similarity. First, we calculated a Euclidean distance matrix using the size-corrected trait values and SVL for all a priori Caribbean ecomorph species. This matrix was the input for a hierarchical cluster analysis using the Ward method ([Murtagh & Legendre, 2014](#)), implemented with the “hclust” R function.

As a third method for assessing support for the ecomorphs, we used a discriminant function analysis (DFA). We performed a DFA and a MANOVA to test for significant differences among the Caribbean ecomorph classes with the size-corrected trait values and SVL using the *MASS* package in R ([Venables & Ripley, 2002](#)). We then assessed the DFA’s ability to correctly assign species to their respective ecomorphs using re-substitution and cross-validation.

CLASSIFICATION OF MAINLAND ANOLES TO THE CARIBBEAN ECOMORPHS BASED ON MORPHOLOGY

To assess whether any mainland *Draconura* species can be assigned to a Caribbean ecomorph based on morphology, we used the DFA trained with Caribbean ecomorph species data to classify *Draconura* species and the previously unclassified Caribbean species into ecomorph classes. A caveat with the DFA method is that it classifies all species, even those that are a poor fit to any of the possible classifications. Therefore, we also developed a set of criteria to assign species to ecomorphs based on their relative positions in the morphospace. Using the retained pPC scores for the Caribbean ecomorph species, we calculated three measures to capture the morphospacial relationships between species in the same ecomorph (Supporting Information, Table S3). First, we calculated the Euclidean distance between each Caribbean ecomorph species and the centroid (centroid distance, CD) of its respective ecomorph. Then we calculated the mean pairwise distance (MPD) between each ecomorph species and all of the members of its ecomorph. Lastly, we calculated the distance between each ecomorph species and its nearest neighbour (NND) from the same ecomorph. To classify the *Draconura* and previously unclassified Caribbean species based on whether they exhibit similar morphospatial relationships as the Caribbean ecomorph species, we calculated CD, MPD and NND for each *Draconura* and unclassified Caribbean species, relative to each ecomorph.

Based on the Euclidean distances, a species was assigned to an ecomorph if: (1) its distance to that ecomorph's centroid was \leq the CD of the furthest member of that class; (2) its average distance to all the members of that ecomorph was \leq the largest MPD among members of that ecomorph; and (3) its distance to the nearest member of that ecomorph was \leq the largest NND among the members of that ecomorph. We assessed every *Draconura* and previously unclassified Caribbean species for each criterion independently so that each species could satisfy one or more of the three criteria. We also allowed species to be classified into multiple ecomorphs using the same criterion to assess uncertainty in ecomorph assignments and support for alternative assignments.

We consolidated the results of the DFA and Euclidean distance classifications into a final ecomorph assignment using two composite criteria. A species was confidently assigned to a single ecomorph if the DFA assigned it with a posterior probability ≥ 0.90 , and it also satisfied any combination of at least two Euclidean distance criteria for the same ecomorph as the DFA assignment. Alternatively, a species was confidently assigned to an ecomorph if the DFA assigned it with a posterior probability ≥ 0.95 , and it also satisfied any

one of the Euclidean distance criteria for the same ecomorph as the DFA assignment. With this approach, species that did not meet both the DFA and Euclidean distance criteria were considered unclassified even if they were assigned to an ecomorph with a high DFA posterior probability. However, several species with a DFA posterior probability < 0.9 for a single ecomorph exhibited strong DFA and Euclidean distance support for two ecomorphs and likely represent intermediate or less specialized ecomorph species. These species were given two potential ecomorph assignments if the DFA assigned them to two ecomorphs with a total posterior probability ≥ 0.90 , they were closest to the centroids of those ecomorphs, and their nearest ecomorph neighbour was a member of one of those ecomorphs. The final ecomorph assignments inferred from morphology were evaluated using available ecological and natural history data in the literature (Supporting Information, Table S9).

ASSESSING A NOVEL GROUND ECOMORPH

To assess the existence of a previously unrecognized ground ecomorph, we conducted a literature review to identify Caribbean and mainland *Draconura* species that are predominantly ground-dwelling. Based on observations of perch use and other natural history data, we designated ten mainland *Draconura* species (*Anolis bombiceps*, *Anolis brasiliensis*, *Anolis chrysolepis*, *Anolis humilis*, *Anolis planiceps*, *Anolis quaggulus*, *Anolis scypheus*, *Anolis tandai*, *Anolis trachyderma*, *Anolis uniformis*), and one unclassified Caribbean species (*Anolis barbouri*) as exemplars of a hypothesized ground ecomorph (Avila-Pires, 1995; Howard *et al.*, 1999; Vitt *et al.*, 2001, 2002, 2003; Savage, 2002; McCranie & Köhler, 2015; Fig. 2). We then performed randomization tests and a cluster analysis as described above to assess whether the putative ground ecomorph occupied an area of the morphospace and formed a morphological cluster distinct from the six Caribbean ecomorphs, respectively.

To determine whether other mainland *Draconura* or unclassified Caribbean anoles might belong to the putative ground ecomorph, we repeated our ecomorph classification analyses with the addition of the ground ecomorph. In cases where previously classified mainland species were assigned to different ecomorphs in the analyses with and without the ground ecomorph, we incorporated their latter assignment into the final classification. However, some species were classified into a Caribbean ecomorph without the ground ecomorph but were not classified when it was included. This generally occurred because the DFA support for those species' original assignments fell below the 0.90 threshold, causing them to be unclassified. Because these species

were assigned to a Caribbean ecomorph before the addition of the ground ecomorph class, it is likely they still belong to an ecomorph (either their original ecomorph or the ground ecomorph). Therefore, we assessed the newly unclassified species based on their DFA posterior probabilities and their ecomorph centroid distances. If a newly unclassified species had a DFA posterior probability ≥ 0.75 for its original ecomorph assignment and was closest to the centroid of that ecomorph, it retained its original assignment. Conversely, if a species had a DFA posterior probability ≥ 0.75 for the ground ecomorph and was closest to the centroid of the ground ecomorph, it was reassigned to it.

RECONSTRUCTING THE EVOLUTION OF MAINLAND ECOMORPHS AND THEIR CONVERGENCE

We reconstructed ecomorph evolution across the Caribbean and mainland *Draconura*-clade anoles to investigate how many times each ecomorph has evolved on the mainland. To estimate the frequency of ecomorph transitions, we used discrete stochastic character mapping via SIMMAP (Bollback, 2006). Two separate SIMMAP analyses were performed: one with just the six Caribbean ecomorphs, and another with the addition of the ground ecomorph. Both analyses included all species in our morphometric data set. We scored the Caribbean ecomorph species with their respective assignments in both analyses and scored the a priori ground ecomorph species as such in the second SIMMAP analysis. The *Draconura* species and the previously unclassified Caribbean species were scored with their final morphology-based ecomorph classifications (when applicable). Species we considered to be intermediate between ecomorphs were assigned prior probabilities equivalent to their DFA posterior probabilities for each ecomorph to which they were assigned. All species not assigned to an ecomorph were treated as non-ecomorph species.

We conducted our SIMMAP analyses using the *phytools* package (Revell, 2012), with the symmetrical-rates model of character state transitions. We determined that this model fitted our data better than the equal-rates and all-rates-different models using likelihood-ratio tests. To account for uncertainty in the estimation of branch lengths and topology, we performed the SIMMAP analyses on a set of 100 randomly sampled post-burn-in trees from Poe *et al.* (2017), with 1000 simulations per tree. To estimate the number of independent ecomorph transitions among only the mainland species, we pruned the SIMMAP results to include only the mainland members of the *Draconura* clade using *phytools* (Revell, 2012). We considered a posterior probability > 0.95 for at least one transition and for more than one transition as strong support for a separate mainland origin and

multiple independent mainland origins of a given ecomorph, respectively.

To evaluate the degree of morphological convergence among species belonging to the same ecomorph, we used a distance-based measure, C_1 , described by Stayton (2015). The C_1 metric measures the degree of convergence between two taxa as how similar they are in the morphospace relative to the largest reconstructed distance between their ancestors. C_1 values range from zero to one, where values closer to one indicate stronger convergence. We calculated C_1 values using the scores from the five retained pPC axes for multiple sets of putatively convergent taxa, each representing a different ecomorph. To assess the significance of the detected convergence, the calculated C_1 values were compared against a null distribution of C_1 values calculated from 1000 sets of trait values simulated across the tree under Brownian Motion (BM).

First, we assessed the strength of convergence among just the a priori Caribbean and ground ecomorph members. Then we evaluated the strength of convergence among the a priori members and all species assigned to each ecomorph in our final classifications. For this second set of analyses, C_1 was calculated once including species classified with only the six Caribbean ecomorphs and once with the species classified with the inclusion of the ground ecomorph. All species with intermediate classifications were treated as non-convergent taxa given the uncertainty in their classifications. Finally, we evaluated the strength of convergence among mainland *Draconura*-clade species assigned to the same ecomorph by calculating C_1 for all the ecomorphs for which the SIMMAP analyses indicated strong support for more than one independent transition. Again, we calculated C_1 once for the classifications made with and without the addition of the ground ecomorph and did not include species with intermediate classifications.

INVESTIGATING FAUNAL CONVERGENCE BETWEEN ISLAND AND MAINLAND RADIATIONS

We visualized morphological convergence across the phylogeny between Caribbean and mainland *Draconura*-clade anoles using a tanglegram. First, we performed another hierarchical cluster analysis with all species in our morphological data set. Then we compared the topologies of the MCC phylogeny and a dendrogram showing the morphological clusters using the tanglegram, produced with the ‘‘cophylo’’ function in *phytools* (Revell, 2012). Lines were drawn to show the location of species in both diagrams and indicate cases of convergence across regions.

To investigate whether the radiation of mainland *Draconura* anoles is convergent with the Greater

Antillean radiations, we tested for species-for-species matching between the different regions by adopting the approach by [Mahler et al. \(2013\)](#). For each Greater Antillean and mainland *Draconura* species (excluding any island endemics), we calculated the Euclidean distance between it and its nearest neighbours (NND) in the morphospace from each of the other four regions (using pPC scores from the five retained axes). To quantify the average faunal similarity among regions with a single metric, we first averaged the calculated NND values for all species occurring in the same region, and then averaged those five values together. We compared the resulting mean against a null distribution of mean distances calculated from 1000 simulated morphospaces. To simulate morphospaces, we fitted the first five pPC axes to a BM model of evolution and simulated trait data using empirically-estimated rate parameters (σ^2). For each morphospace, the pPC axes were simulated independently and then combined. We then calculated the mean NND values using the same methods for each morphospace. A significantly lower empirical mean NND value (alpha level = 0.05) would provide evidence that the Greater Antillean and mainland *Draconura* fauna are more similar than expected by chance.

However, strong similarities among the Greater Antillean radiations may confound our results. Thus, we also isolated the average similarity between the mainland *Draconura* clade and the four different Caribbean radiations (by averaging all of the calculated NND values between each mainland species and its Greater Antillean neighbours from each island), as well as the average similarity between the Greater Antillean radiations and the mainland *Draconura* radiation (by averaging all of the calculated NND values between Greater Antillean species and their nearest mainland neighbours). We compared these additional metrics against two null distributions of mean distances calculated from the simulated morphospaces.

We performed a final test of morphological convergence between island and mainland anoles without a priori ecomorph assignments. For this, we used the *l1ou* method and corresponding R package (Khabbazian *et al.*, 2016) to detect the number and location of adaptive evolutionary shifts in morphology. This method uses the Ornstein–Uhlenbeck (OU) process to model changes in multivariate phenotypic data over time and over lineages and selects a shift configuration using the LASSO (least absolute shrinkage and selection operator) method (Khabbazian *et al.*, 2016). The *l1ou* method also uses a non-parametric bootstrap procedure to quantify the support for a given shift as well as determine which regimes are converging towards the same adaptive optima (Khabbazian *et al.*, 2016). We used the Akaike information criterion (AIC)

to evaluate models because AIC performed best in identifying regimes associated with the Caribbean ecomorphs in an empirical study (Khabbazian *et al.*, 2016). Our analyses were performed using the retained pPC scores for all species in our study. If island and mainland anoles are evolving under similar selective pressures, we would expect to find convergent regimes.

DATA AVAILABILITY

The full data set used in this study and the R scripts used to analyse it have been archived in GitHub: <https://github.com/jmhuie/Mainland-Anole-Ecomorphology>.

RESULTS

MAINLAND AND CARIBBEAN ANOLES IN THE MORPHOSPACE

A large part of the morphological space occupied by the mainland *Draconura* clade overlapped with that occupied by the Caribbean ecomorphs ([Fig. 3](#); [Supporting Information, Table S2](#)). However, while some *Draconura* species resembled the large crown-giants and others the short-legged twig anoles, they did not achieve the same extremes in the morphospace as the Caribbean exemplars of those ecomorphs ([Fig. 3A](#)). Likewise, mainland species did not have tails as long as those of the most extreme Caribbean grass-bush anoles ([Fig. 3C](#)). Conversely, several mainland anoles occupied regions of the morphospace not occupied by any Caribbean ecomorph species. For example, many *Draconura* species had longer limbs than those of the Caribbean ecomorph species but resembled several of the previously unclassified Caribbean anoles. Mainland anoles also exhibited a wider range of finger- and toe-pad sizes than Caribbean ecomorph species ([Fig. 3B](#)). They exhibited similar maximum pad widths; however, the pad-less *A. onca* and a few other species had narrower digits/pads than any of the Caribbean ecomorph species. *Draconura* species also did not achieve head lengths as great as those of some Caribbean species, particularly ones representing the crown-giant, grass-bush, trunk-crown and twig ecomorphs ([Fig. 3D](#)).

SUPPORT FOR THE CARIBBEAN ECOMORPHS

The randomization tests indicated that the centroid distances between all Caribbean ecomorph pairs were significant at the $P < 0.001$ level. The hierarchical cluster analysis indicated that most of the ecomorphs formed single clusters, although the trunk-crown species formed two ([Supporting Information, Fig. S2](#)). The discriminant function analysis revealed significant differences among ecomorphs (MANOVA:

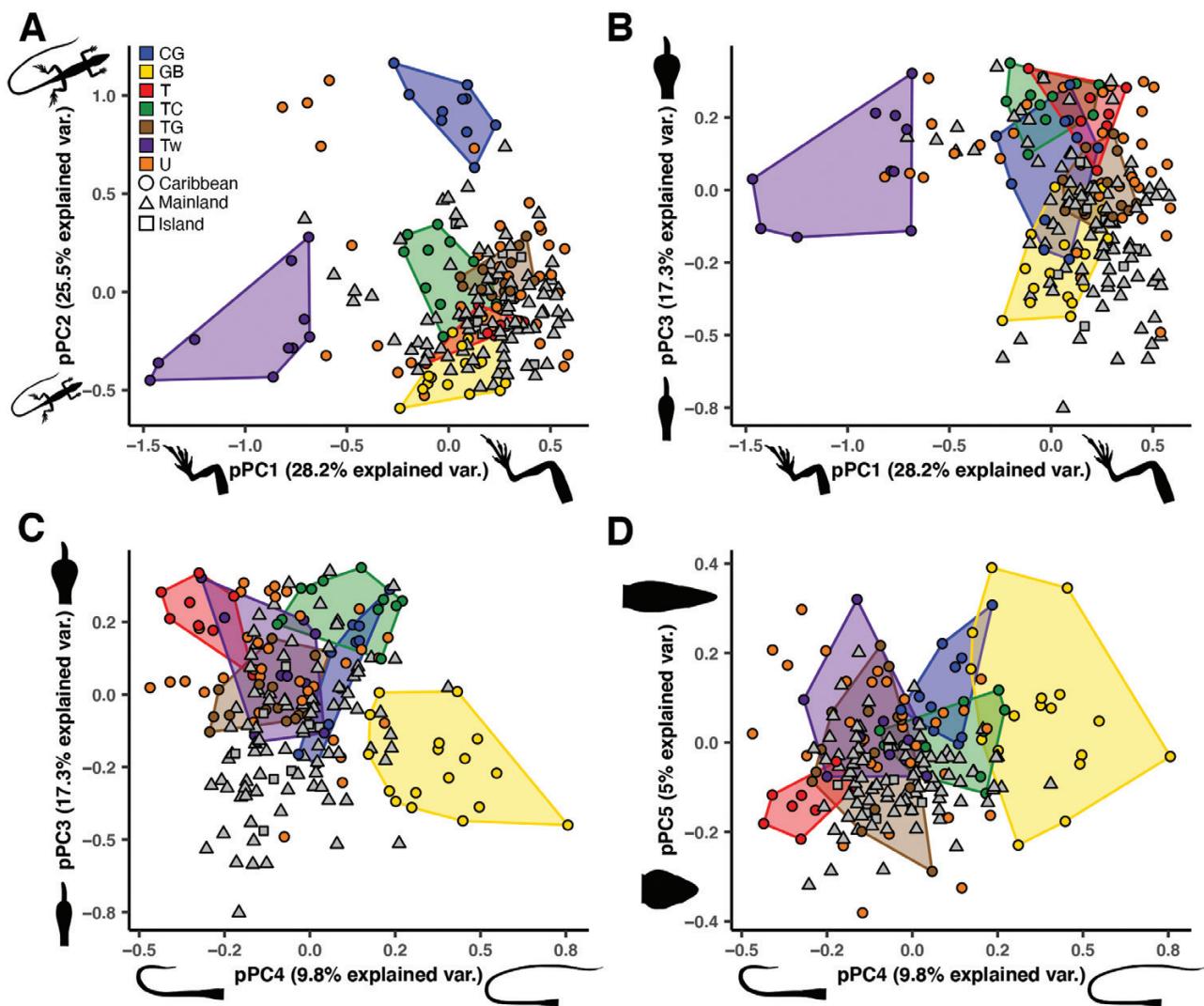


Figure 3. Relative positions of 205 species of Caribbean and *Draconura* anoles in a morphological space. A, pPC2 vs. pPC1; (B) pPC3 vs. pPC1; (C) pPC3 vs. pPC4; (D) pPC5 vs. pPC4. Silhouettes of lizards or their parts represent the predominant trait variation on each pPC axis (body size, limb length, finger- and toe-pad width, tail length and head shape). See Supporting Information (Table S2) for the detailed trait loadings for each pPC axis. Convex hulls were drawn around the Caribbean ecomorphs. Grey triangles indicate mainland *Draconura* species, grey squares indicate island *Draconura* species and coloured circles indicate Caribbean species. CG (blue) = Crown-Giant; GB (yellow) = Grass-Bush; T (red) = Trunk; TC (green) = Trunk-Crown; Tw (purple) = Twig; U (orange) = previously unclassified Caribbean species.

Wilks' $\lambda < 0.001$, $F = 17.160$, $P < 0.001$) and successfully classified 98.6% and 94.4% of the Caribbean ecomorph species to their respective classes when using re-substitution and cross-validation, respectively (Supporting Information, Result S1).

CLASSIFICATION OF MAINLAND ANOLES INTO THE SIX CARIBBEAN ECOMORPHS

Out of the 99 *Draconura* species, the DFA classified 70 mainland and eight island species into ecomorphs with a posterior probability of 0.90 or greater

based on morphological characters (Supporting Information, Table S4). The DFA also classified 28 out of 35 previously unclassified Caribbean species (Supporting Information, Table S4). Ecomorph assignments for *Draconura* species were as follows: eight grass-bush, five trunk-crown, 63 trunk-ground and two twig anoles (Supporting Information, Table S4). The ecomorph assignments for the previously unclassified Caribbean species were as follows: three crown-giant, four grass-bush, two trunk, four trunk-crown, 13 trunk-ground and two twig anoles (Supporting Information, Table S4).

The Euclidean distance criteria varied in the number of species they classified, but all assigned at least one mainland *Draconura* species to each Caribbean ecomorph ([Supporting Information, Tables S5–S7](#)). Seventy-seven species (55 mainland *Draconura*, five island *Draconura* and 17 unclassified Caribbean species) were as close or closer to the centroid of at least one ecomorph than was the furthest member of that ecomorph ([Supporting Information, Table S5](#)). Eighty-five species (58 mainland *Draconura*, five island *Draconura* and 22 unclassified Caribbean species) were assigned to at least one ecomorph based on having a mean pairwise distance to the members of an ecomorph that was less than or equal to the largest MPD among members of that ecomorph ([Supporting Information, Table S6](#)). Eighty-two species (56 mainland *Draconura*, five island *Draconura* and 21 unclassified Caribbean species) were assigned to at least one ecomorph based on having a distance to a neighbouring ecomorph species that was less than the largest NND among the members of that ecomorph ([Supporting Information, Table S7](#)).

After evaluating the DFA and Euclidean distance classifications to produce final ecomorph assignments based on morphology, 61 species (39 mainland *Draconura*, five island *Draconura* and 17 unclassified Caribbean species) showed strong morphological support for belonging to a Caribbean ecomorph ([Table 1](#)). An additional 14 mainland *Draconura* species and five previously unclassified Caribbean species were considered to be intermediate between two ecomorphs. Most of these intermediate species were between the grass-bush and trunk-ground ecomorphs, with some between the crown-giant and three other ecomorphs. Among the *Draconura* anoles assigned to a single ecomorph, there were eight grass-bush, three trunk-crown, 31 trunk-ground and two twig anoles. The previously unclassified Caribbean species were assigned as one crown-giant, three grass-bush, one trunk, 11 trunk-ground and one twig anole. Except for the Caribbean species *A. barbouri*, none of our a priori ground anoles was assigned to an ecomorph in this analysis.

EVALUATION OF A NEW GROUND ECOMORPH

The ground anoles exhibited morphologies that distinguished them from each of the Caribbean ecomorphs ([Fig. 4](#)). In general, the ground anoles had longer forelimbs and hindlimbs than the Caribbean ecomorphs, but their limbs were only slightly longer than those of the grass-bush, trunk and trunk-ground anoles ([Fig. 4A; Supporting Information, Fig. S1](#)). They also had narrower subdigital pads than the Caribbean ecomorphs but were only slightly narrower than those of the grass-bush anoles ([Fig.](#)

[4B; Supporting Information, Fig. S1](#)). The ground anoles had comparable body sizes ([Fig. 4A; Supporting Information, Fig. S1](#)) and tail lengths to most Caribbean ecomorph species ([Fig. 4C; Supporting Information, Fig. S1](#)) but were smaller than the crown-giant species and had shorter tails than the grass-bush species. The ground anoles also generally had shorter heads and snouts than most of the Caribbean ecomorph species, although these features were similar to those of the trunk and some of the trunk-ground species ([Fig. 4D; Supporting Information, Fig. S1](#)). The randomization tests indicated that the ground ecomorph was morphologically different from each Caribbean ecomorph ($P < 0.001$ in all cases). However, hierarchical cluster analysis indicated that the *Draconura* ground species formed two clusters and *A. barbouri* clustered with the grass-bush ecomorph ([Supporting Information, Fig. S2](#)).

A DFA that included the putative ground ecomorph class revealed significant differences among ecomorphs (MANOVA: Wilks' $\lambda < 0.001$, $F = 14.84$, $P < 0.001$) and successfully classified 98.8% and 93.9% of the Caribbean and ground ecomorph species to their respective ecomorphs when using re-substitution and cross-validation, respectively ([Supporting Information, Result S1](#)). The DFA classified 78 species (44 mainland *Draconura*, six island *Draconura* and 28 unclassified Caribbean anoles) into ecomorphs with a posterior probability of 0.90 or greater ([Supporting Information, Table S8](#)). The classifications for *Draconura* species were as follows: 22 ground, two grass-bush, one trunk, four trunk-crown, 18 trunk-ground and three twig anoles ([Supporting Information, Table S8](#)). The classifications for previously unclassified Caribbean species were as follows: two ground, three crown-giants, two grass-bush, three trunk, three trunk-crown, 12 trunk-ground and three twig anoles ([Supporting Information, Table S8](#)).

Considering the *Draconura* and unclassified Caribbean species that satisfied Euclidean distance criteria for the ground ecomorph ([Supporting Information, Tables S5–S7](#)), 29 species (25 mainland *Draconura*, two island *Draconura* and two unclassified Caribbean species) were closer to the ground ecomorph centroid than was the furthest member of that ecomorph ([Supporting Information, Table S5](#)). Of the *Draconura* species, 13 satisfied this criterion for only the ground ecomorph; the remaining 14 also satisfied the CD criterion for the grass-bush and/or trunk-ground ecomorphs ([Supporting Information, Table S5](#)). Twenty-four species (20 mainland *Draconura*, two island *Draconura* and two unclassified Caribbean species) had a mean pairwise distance to all of the ground ecomorph species less than the largest MPD among the members of that ecomorph ([Supporting Information, Table S6](#)). Of

Table 1. List of the 80 *Draconura* and previously unclassified Caribbean anole species that were assigned to one or two different ecomorph classes when only using the Caribbean ecomorphs. Also shown are the DFA posterior probabilities and the Euclidean distances for each of the classification criterion that each species satisfied for its predicted ecomorph. For intermediate species, where we adopted different CD and NND (and no MPD) criteria, all relevant Euclidean distances are shown for their predicted ecomorphs. Although intermediate species did not need to satisfy the same CD and NND criteria as those assigned to a single ecomorph, asterisks (*) indicate instances where they did.

Species	Region§	Predicted ecomorph†	DFA	CD	MPD	NND
<i>A. altavelensis</i>	C	T	1.00	0.25	0.32	0.19
<i>A. amplisquamatus</i>	M	GB	0.94	0.45	0.54	-
<i>A. apletophallus</i>	M	TG	1.00	0.37	0.43	-
<i>A. argenteolus</i>	C	T / TG	0.78 / 0.22	0.37* / 0.36*	NA	- / 0.25*
<i>A. armouri</i>	C	TG	0.96	-	-	0.24
<i>A. auratus</i>	M	GB	1.00	0.39	0.50	0.23
<i>A. barbatus</i>	C	Tw / CG	0.56 / 0.44	1.19 / 0.96	NA	0.74 / -
<i>A. barbouri</i>	C	GB	1.00	0.33	0.45	0.19
<i>A. barkeri</i>	M	TG	1.00	0.35	0.41	-
<i>A. benedicti</i>	M	TG	1.00	0.28	0.35	0.19
<i>A. bicaorum</i>	I	TG	1.00	0.31	0.38	0.26
<i>A. biporcatus</i>	M	CG / TG	0.63 / 0.37	0.57 / 0.60	NA	0.44 / -
<i>A. boulengerianus</i>	M	TG	0.98	0.26	0.34	0.19
<i>A. charlesmyersi</i>	M	Tw	0.97	0.50	0.62	0.28
<i>A. concolor</i>	I	TG	1.00	0.24	0.33	0.22
<i>A. conspersus</i>	C	TG	0.99	0.19	0.30	0.20
<i>A. cristifer</i>	M	Tw	1.00	0.65	0.75	0.28
<i>A. cusuco</i>	M	TC	0.99	-	0.49	0.16
<i>A. deschensis</i>	C	TG	0.92	0.36	0.42	0.20
<i>A. dollfusianus</i>	M	TG / GB	0.80 / 0.20	0.51 / 0.47*	NA	- / 0.30*
<i>A. dunnii</i>	M	TG	1.00	0.23	0.31	0.10
<i>A. ernestwilliamsi</i>	C	TG	1.00	0.35	0.42	0.22
<i>A. fuscoauratus</i>	M	GB	0.99	0.37	0.48	0.25
<i>A. gadovii</i>	M	TG	1.00	0.30	0.37	0.26
<i>A. gaigei</i>	M	TG / GB	0.72 / 0.28	0.48 / 0.48*	NA	- / 0.37
<i>A. imias</i>	C	TG	0.98	0.36	0.42	0.25
<i>A. isolepis</i>	C	Tw	1.00	0.49	0.60	0.18
<i>A. johnmeyeri</i>	M	TG	0.98	0.16	0.28	0.17
<i>A. kemptoni</i>	M	TC	1.00	0.35	0.43	0.21
<i>A. lemurinus</i>	M	TG	1.00	-	0.43	-
<i>A. liogaster</i>	M	TG	0.99	-	0.43	0.18
<i>A. longitibialis</i>	C	TG	1.00	-	0.43	-
<i>A. loveridgei</i>	M	CG / TG	0.78 / 0.22	0.35* / 0.70	NA	0.23* / -
<i>A. lucius</i>	C	TG / T	0.79 / 0.15	0.48 / 0.49	NA	0.32* / -
<i>A. lyra</i>	M	TG	1.00	0.36	0.42	0.26
<i>A. macrolepis</i>	M	TG	1.00	0.36	0.42	0.23
<i>A. magnaphallus</i>	M	TG	1.00	0.27	0.35	0.20
<i>A. mariarum</i>	M	TG	0.96	-	-	0.26
<i>A. matudai</i>	M	TG	1.00	0.17	0.28	0.06
<i>A. mccraniei</i>	M	TG	1.00	0.33	0.40	-
<i>A. meridionalis</i>	M	GB	1.00	0.50	0.59	-
<i>A. milleri</i>	M	TG	1.00	-	-	0.26
<i>A. monensis</i>	C	TG / T	0.78 / 0.20	0.24* / 0.33*	NA	0.18* / -
<i>A. morazani</i>	M	GB	1.00	0.47	0.55	0.21
<i>A. muralia</i>	M	GB	0.99	0.44	0.53	0.23
<i>A. nebulosus</i>	M	TG	0.95	0.26	0.34	0.17
<i>A. notopholis</i>	M	TG / GB	0.83 / 0.17	0.49 / 0.69	NA	0.41 / -
<i>A. ortonii</i>	M	T / TC	0.52 / 0.48	0.26* / 0.46	NA	- / 0.19*

Table 1. Continued

Species	Region§	Predicted ecomorph†	DFA	CD	MPD	NN
<i>A. osa</i>	M	TG	1.00	0.34	0.41	0.27
<i>A. petersii</i>	M	TC / CG	0.80 / 0.17	0.61 / 0.55	NA	- / 0.34
<i>A. pijolense</i>	M	TG	1.00	0.23	0.32	0.21
<i>A. pinchoti</i>	I	TG	1.00	0.27	0.35	0.24
<i>A. poecilopus</i>	M	TG	1.00	0.21	0.31	0.17
<i>A. pogus</i>	C	GB	1.00	0.46	0.54	0.29
<i>A. purpurlaris</i>	M	TG	0.99	0.25	0.33	0.23
<i>A. reconditus</i>	C	TG	1.00	-	-	0.21
<i>A. rivalis</i>	M	TG	1.00	0.29	0.36	0.17
<i>A. roatanensis</i>	I	TG	1.00	0.24	0.33	0.16
<i>A. rodriguezii</i>	M	GB / TG	0.78 / 0.22	0.43* / 0.49	NA	0.28* / -
<i>A. rubribarbaris</i>	M	TC	0.98	0.40	0.47	0.25
<i>A. rupinæ</i>	C	GB / TG	0.75 / 0.25	0.79 / 0.59	NA	- / 0.46
<i>A. salvini</i>	M	Tw / TC	0.65 / 0.35	0.54* / 0.54	NA	0.34* / -
<i>A. schwartzi</i>	C	GB	0.96	-	0.64	-
<i>A. scriptus</i>	C	TG	1.00	-	-	0.25
<i>A. serranoi</i>	M	TG / GB	0.78 / 0.22	0.31* / 0.63	NA	0.23* / -
<i>A. shrevei</i>	C	TG	1.00	0.21	0.31	0.15
<i>A. sminthus</i>	M	GB / TG	0.89 / 0.09	0.46* / 0.32*	NA	0.13* / -
<i>A. strahmi</i>	C	TG	1.00	-	0.43	0.24
<i>A. subocularis</i>	M	TG	1.00	0.37	0.43	-
<i>A. taylori</i>	M	TG	1.00	0.25	0.33	0.19
<i>A. tolimensis</i>	M	TG	0.92	0.31	0.38	0.20
<i>A. townsendi</i>	I	TG	1.00	0.27	0.35	0.23
<i>A. tropidolepis</i>	M	TG	0.98	0.36	0.42	-
<i>A. unilobatus</i>	M	GB	0.90	0.33	0.45	0.31
<i>A. vermiculatus</i>	C	CG	1.00	0.38	0.45	0.12
<i>A. vittigerus</i>	M	GB / TG	0.50 / 0.50	0.58 / 0.42	NA	- / 0.31*
<i>A. wattsi</i>	C	TG	1.00	0.26	0.34	0.17
<i>A. wellbornae</i>	M	TG / GB	0.75 / 0.22	0.58 / 0.36*	NA	- / 0.31*
<i>A. wermuthi</i>	M	GB	0.99	0.53	0.60	0.16
<i>A. zeus</i>	M	GB / TG	0.66 / 0.34	0.47* / 0.55	NA	0.34 / -

§C = previously unclassified Caribbean species, M = mainland *Draconura* species, I = island *Draconura* species.

†CG = Crown-Giant, GB = Grass-Bush, T = Trunk, TC = Trunk-Crown, TG = Trunk-Ground, Tw = Twig.

the *Draconura* species, 12 satisfied the MPD criterion for only the ground ecomorph, while the remaining 10 also satisfied it for the grass-bush and/or trunk-ground ecomorph (Supporting Information, Table S6). Twenty-eight species (22 mainland *Draconura*, three island *Draconura* and three unclassified Caribbean species) were closer to a ground ecomorph species than the largest nearest-neighbour distance among the members of that ecomorph (Supporting Information, Table S7). Of the *Draconura* species, 15 satisfied the NND criterion for only the ground ecomorph, while the remaining 10 also satisfied this criterion for the grass-bush and/or trunk-ground ecomorphs (Supporting Information, Table S7).

After evaluating the morphology-based DFA and Euclidean distance ecomorph assignments with

the inclusion of the ground ecomorph, we classified 59 species (36 mainland *Draconura*, five island *Draconura* and 18 unclassified Caribbean anoles) with strong morphological support (Table 2). An additional 13 *Draconura* species (seven of which were previously assigned to an ecomorph before the addition of the ground ecomorph) and two previously unclassified Caribbean species were assigned to two ecomorphs as potential intermediate species. The majority of the intermediate species were between the ground and trunk-ground ecomorphs. Among the mainland species assigned to a single ecomorph, there were 22 ground, two grass-bush, one trunk, four trunk-crown, 18 trunk-ground and three twig anoles. Of the 22 species of *Draconura* ground anoles, 16 were not previously classified into a Caribbean

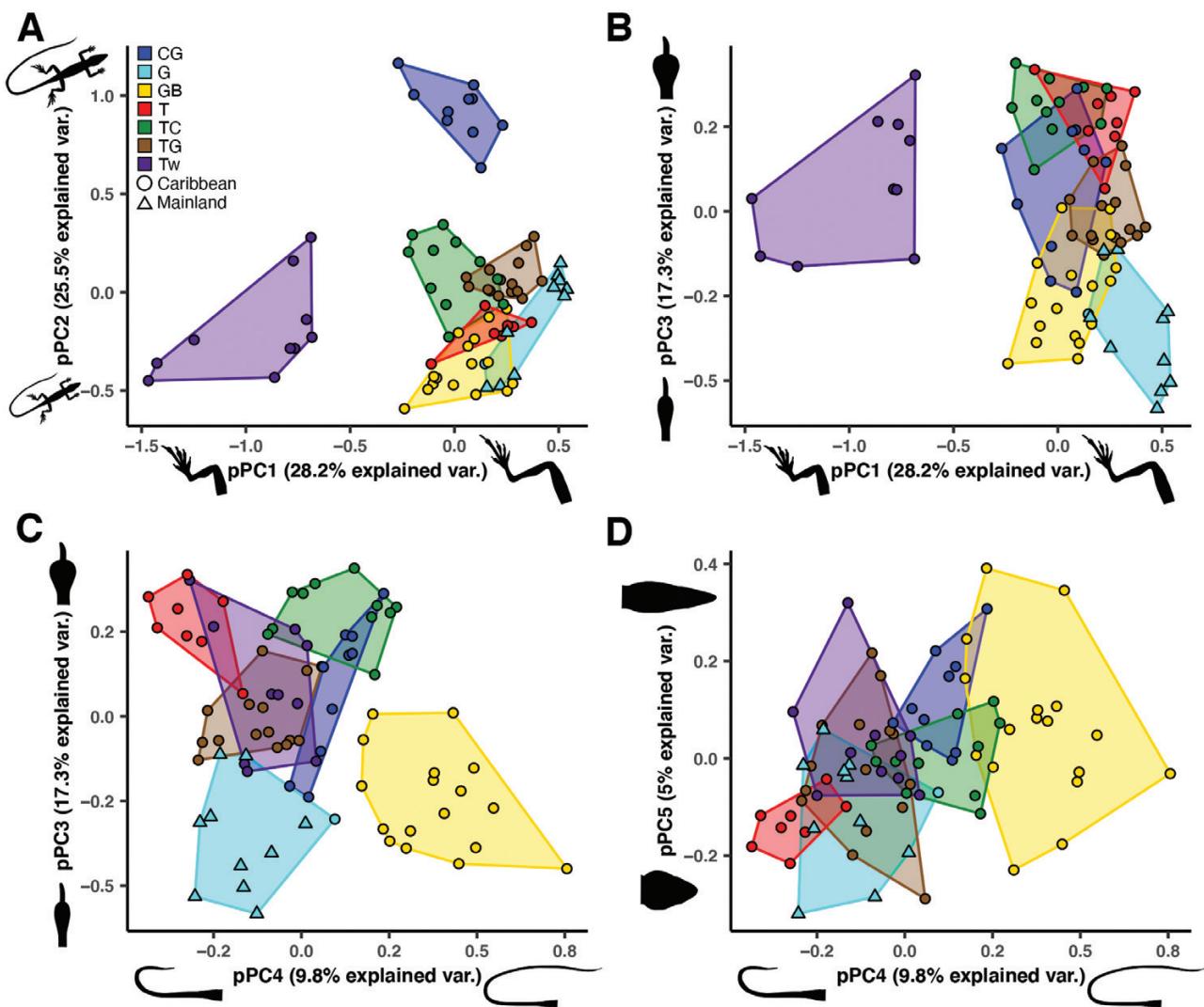


Figure 4. Relative positions of the six Caribbean ecomorphs and the putative ground ecomorph in a morphological space. A, pPC2 vs. pPC1; (B) pPC3 vs. pPC1; (C) pPC3 vs. pPC4; (D) pPC5 vs. pPC4. Silhouettes of lizards or their parts represent the predominant trait variation on each pPC axis (body size, limb length, finger- and toe-pad width, tail length and head shape). See Supporting Information (Table S2) for the detailed trait loadings for each pPC axis. Convex hulls were drawn around each ecomorph. Triangles indicate mainland *Draconura* species and circles indicate Caribbean species. Abbreviations and colours as in Figure 3 (when applicable), but with the addition of G (cyan) = Ground.

ecomorph, while six species were previously classified as trunk-ground anoles and reassigned to the ground ecomorph (*A. lemurinus*, *A. meridionalis*, *A. milleri*, *A. subocularis* and *A. tropidolepis*). Most other ecomorph assignments remained consistent with the previous assignments made without the ground ecomorph, except for the addition of one mainland trunk anole (*Anolis ortonii*) and one mainland twig anole (*Anolis salvini*). Meanwhile, the previously unclassified Caribbean species were classified as two ground (*Anolis rupinae* and *Anolis etheridgei*), one crown-giant, one grass-bush, two trunk, 11 trunk-ground and one twig anole.

REPEATED ECOMORPH EVOLUTION ON THE MAINLAND
The stochastic character mapping analyses indicated that most of the ecomorphs arose within the *Draconura* clade in Central and South America independently from the Caribbean (Greater Antillean) anoles with a posterior probability greater than 0.98 (Table 3). The exceptions were the crown-giant and trunk ecomorphs, which showed weak support for a mainland origin because no mainland *Draconura* species were classified to those ecomorphs unambiguously (intermediate species only). However, the trunk ecomorph showed strong support for a mainland origin with the inclusion of the ground

Table 2. List of the 76 *Draconura* and previously unclassified Caribbean anole species that were assigned to one or two different ecomorph classes with the inclusion of the ground ecomorph. Also shown are the DFA posterior probabilities and the Euclidean distances for each of the classification criterion that each species satisfied for its predicted ecomorph. For intermediate species, where we adopted different CD and NND (and no MPD) criteria, all relevant Euclidean distances are shown for their predicted ecomorphs. Although intermediate species did not need to satisfy the same CD and NND criteria as those assigned to a single ecomorph, asterisks (*) indicate instances where they did.

Species	Region	Predicted ecomorph [†]	DFA	CD	MPD	NND
<i>A. altavelensis</i>	C	T	1.00	0.25	0.32	0.19
<i>A. aquaticus</i>	M	G / TG	0.63 / 0.37	0.36* / 0.41	NA	- / 0.29*
<i>A. argenteolus</i>	C	T	0.91	0.37	0.40	0.27
<i>A. armouri</i>	C	TG	0.99	-	-	0.24
<i>A. auratus</i>	M	GB	0.99	0.39	0.50	0.23
<i>A. barkeri</i>	M	TG / G	0.60 / 0.40	0.35* / 0.43*	NA	0.28* / -
<i>A. benedicti</i>	M	TG	0.92	0.28	0.35	0.19
<i>A. bicaorum</i>	M	G / TG	0.73 / 0.27	0.36* / 0.31*	NA	0.24* / -
<i>A. biporcatus</i>	M	TG / CG	0.84 / 0.16	0.60 / 0.57	NA	- / 0.44
<i>A. boulengerianus</i>	M	G / TG	0.87 / 0.12	0.33* / 0.26*	NA	- / 0.19*
<i>A. charlesmyersi</i>	M	Tw	1.00	0.50	0.62	0.28
<i>A. christophei</i>	C	G / TG	0.56 / 0.38	0.27* / 0.26*	NA	- / 0.21*
<i>A. cobanensis</i>	M	G / TG	0.82 / 0.10	0.43* / 0.41	NA	- / 0.32*
<i>A. concolor</i>	I	TG	0.99	0.24	0.33	0.22
<i>A. conspersus</i>	C	TG	0.97	0.19	0.30	0.20
<i>A. cristifer</i>	M	Tw	1.00	0.65	0.75	0.28
<i>A. cryptolimifrons</i>	M	G	0.99	0.31	0.45	0.18
<i>A. cupreus</i>	M	G	0.98	0.39	0.50	0.13
<i>A. cusuco</i>	M	TC / T	0.57 / 0.43	0.44 / 0.40	NA	0.16* / -
<i>A. desechensis</i>	C	TG	0.94	0.36	0.42	0.20
<i>A. dollfusianus</i>	M	G	0.99	0.40	0.50	0.15
<i>A. dunnii</i>	M	TG	0.99	0.23	0.31	0.10
<i>A. ernestwilliamsi</i>	C	TG	0.99	0.35	0.42	0.22
<i>A. etheridgei</i>	C	G	1.00	0.42	0.54	0.33
<i>A. fuscoauratus</i>	M	GB / G	0.57 / 0.42	0.37* / 0.57	NA	0.25* / -
<i>A. gaigei</i>	M	G	1.00	0.23	0.41	0.27
<i>A. gracilipes</i>	M	G	1.00	0.28	0.42	0.16
<i>A. granuliceps</i>	M	G	1.00	0.29	0.45	0.30
<i>A. imias</i>	C	TG	0.98	0.36	0.42	0.25
<i>A. isolepis</i>	C	Tw	1.00	0.49	0.60	0.18
<i>A. johnmeyeri</i>	M	TG	0.97	0.16	0.28	0.17
<i>A. kemptoni</i>	M	TC	0.99	0.35	0.43	0.21
<i>A. lemurinus</i>	M	G	0.99	0.22	0.41	0.22
<i>A. liogaster</i>	M	TG	1.00	-	0.43	0.18
<i>A. longitibialis</i>	C	TG	1.00	-	0.43	-
<i>A. loveridgei</i>	M	CG / TG	0.51 / 0.49	0.35* / 0.70	NA	0.23* / -
<i>A. lynchi</i>	M	G	0.93	0.38	0.52	-
<i>A. lyra</i>	M	TG	0.98	0.36	0.42	0.26
<i>A. maculiventris</i>	M	G / TG	0.64 / 0.36	0.42* / 0.57	NA	0.25* / -
<i>A. mariarum</i>	M	TG	0.97	-	-	0.26
<i>A. matudai</i>	M	TG	0.99	0.17	0.28	0.06
<i>A. medemi</i>	I	G	1.00	0.25	0.43	0.18
<i>A. milleri</i>	M	G	0.97	0.35	0.49	-
<i>A. monensis</i>	C	TG / T	0.88 / 0.10	0.24* / 0.33*	NA	0.18* / -
<i>A. nebulosus</i>	M	TG	0.94	0.26	0.34	0.17
<i>A. notopholis</i>	M	G	1.00	0.22	0.41	0.27
<i>A. ortonii</i>	M	T	0.98	0.26	0.33	0.24
<i>A. osa</i>	M	G	0.97	0.18	0.39	0.23

Table 2. Continued

Species	Region	Predicted ecomorph [†]	DFA	CD	MPD	NND
<i>A. oxylophus</i>	M	TG / G	0.90 / 0.10	0.45 / 0.47	NA	0.34* / -
<i>A. pijolense</i>	M	TG	0.99	0.23	0.32	0.21
<i>A. pinchoti</i>	I	TG	0.99	0.27	0.35	0.24
<i>A. poecilopus</i>	M	TG	0.96	0.21	0.31	0.17
<i>A. pogus</i>	C	GB	1.00	0.46	0.54	0.29
<i>A. reconditus</i>	C	TG	1.00	-	-	0.21
<i>A. roatanensis</i>	M	TG / G	0.64 / 0.36	0.24* / 0.34*	NA	0.16* / -
<i>A. rodriguezii</i>	M	G	1.00	0.36	0.47	0.19
<i>A. rubribarbaris</i>	M	TC	1.00	0.40	0.47	0.25
<i>A. rupinæ</i>	C	G	0.98	0.36	0.48	0.20
<i>A. salvini</i>	M	Tw	0.91	0.54	0.64	0.34
<i>A. scriptus</i>	C	TG	1.00	-	-	0.25
<i>A. shrevei</i>	C	TG	0.98	0.21	0.31	0.15
<i>A. strahmi</i>	C	TG	1.00	-	0.43	0.24
<i>A. subocularis</i>	M	G	0.96	0.29	0.44	0.24
<i>A. taylori</i>	M	TG	0.99	0.25	0.33	0.19
<i>A. tolimensis</i>	M	G / TG	0.51 / 0.48	0.45 / 0.31*	NA	- / 0.20*
<i>A. townsendi</i>	I	TG	0.93	0.27	0.35	0.23
<i>A. tropidolepis</i>	M	G	0.99	0.19	0.40	0.31
<i>A. vermiculatus</i>	C	CG	0.99	0.38	0.45	0.12
<i>A. villai</i>	I	G	1.00	0.28	0.44	0.23
<i>A. vittigerus</i>	M	G / TG	0.68 / 0.23	0.49 / 0.42	NA	- / 0.31*
<i>A. wampuensis</i>	M	G	0.99	0.15	0.38	0.27
<i>A. wattsi</i>	C	TG	0.97	0.26	0.34	0.17
<i>A. wermuthi</i>	M	GB	0.91	0.53	0.60	0.16
<i>A. woodi</i>	M	G / TG	0.56 / 0.44	0.49 / 0.41	NA	- / 0.29*
<i>A. yoroensis</i>	M	G	0.94	0.39	0.50	0.24
<i>A. zeus</i>	M	G	0.95	0.37	0.49	0.26

[†]Abbreviations as in [Table 1](#), but with the addition of G = Ground.

Table 3. Posterior probabilities of a mainland origin and multiple independent transitions for each ecomorph within the *Draconura* clade based on two separate stochastic character mapping analyses performed on 100 post-burn-in trees with 1000 simulations per tree. Bold values indicate posterior probabilities that show strong support (≥ 0.95).

Ecomorph	Caribbean ecomorphs only			With ground ecomorph		
	Probability of a mainland origin	Probability of > 1 independent transitions	Best-supported number of transitions (probability)	Probability of a mainland origin	Probability of > 1 independent transitions	Best-supported number of transitions (probability)
Crown-Giant	0.463	0.119	0 (0.537)	0.173	0.016	0 (0.827)
Grass-Bush	1.000	1.000	8 (0.204)	1.000	1.000	4 (0.295)
Trunk	0.152	0.003	0 (0.848)	1.000	0.376	1 (0.623)
Trunk-Crown	1.000	1.000	6 (0.345)	1.000	1.000	3 (0.509)
Trunk-Ground	0.986	0.939	4 (0.113)	1.000	1.000	13 (0.178)
Twig	1.000	0.810	2 (0.378)	1.000	0.993	3 (0.396)
Ground	-	-	-	1.000	1.000	7 (0.170)

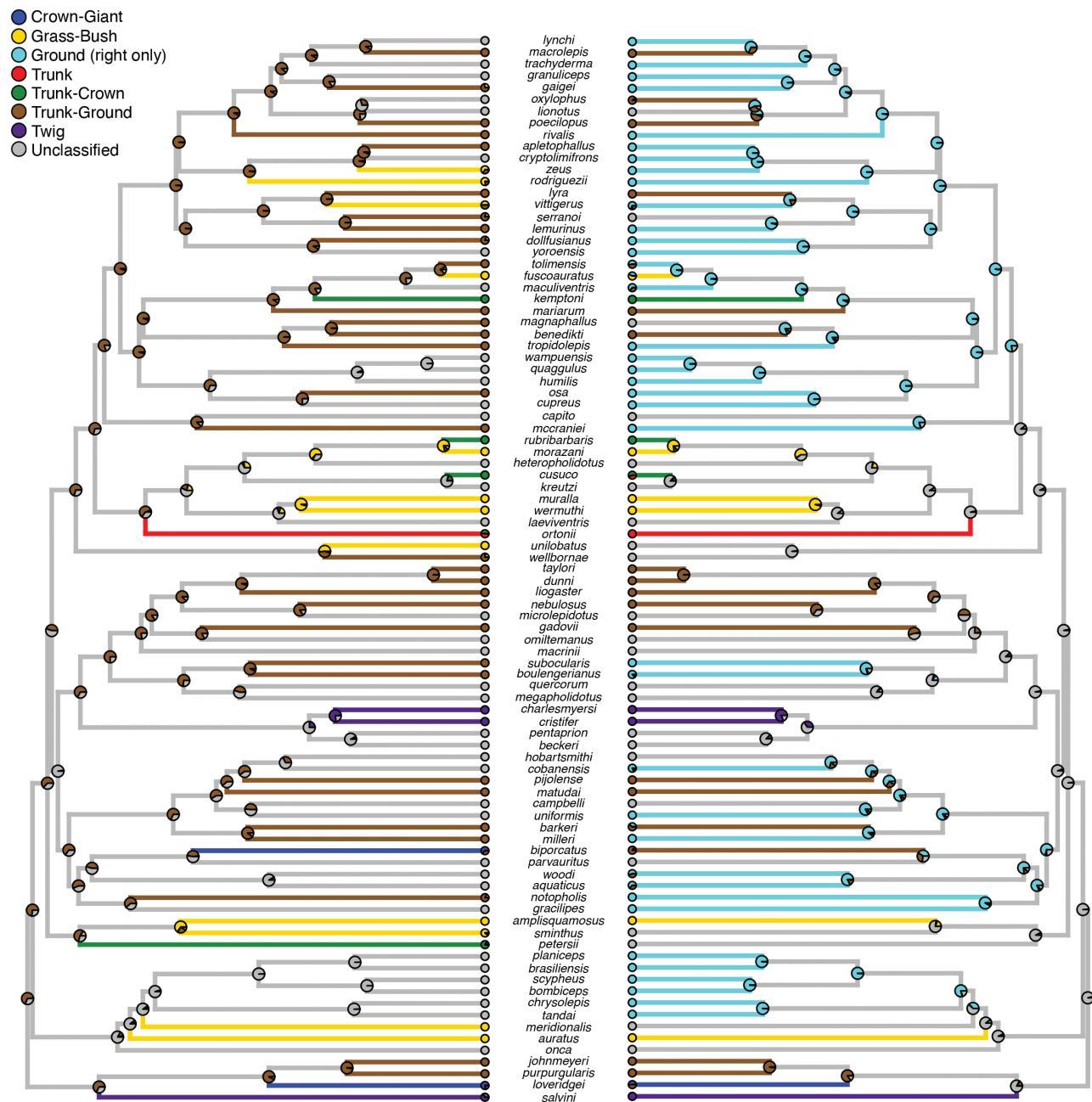


Figure 5. The MCC phylogeny showing the ancestral state reconstructions of ecomorph evolution among mainland *Draconura*-clade anoles based on the final classifications (including intermediates) made with only the six Caribbean ecomorphs (left) and with the addition of the ground ecomorph (right). Tip circles show the final ecomorph classifications or (as pies) the DFA probabilities for the intermediate ecomorph species. Node pies reflect the posterior probabilities of each ecomorph summarized from the two stochastic character mapping analyses performed on 100 post-burn-in trees. Terminal branches are coloured by the ecomorph with the highest tip probability.

ecomorph, when *A. ortonii* was confidently assigned to the trunk ecomorph. For all other ecomorphs that did evolve independently on the mainland, both SIMMAP analyses performed both with and without the ground ecomorph found strong support for multiple origins of those ecomorphs on the mainland (Fig. 5; Table 3).

The C₁ convergence analyses indicated that the Caribbean and ground ecomorphs varied between 0.139 and 0.09 in their degree of morphological convergence (Table 4). All of the a priori ecomorphs exhibited significantly stronger morphological convergence than expected compared to a null distribution of C₁.

Table 4. C_1 values showing the estimated degrees of convergence for each ecomorph with different sets of putatively convergent taxa. There were no mainland *Draconura* species assigned unambiguously to the crown-giant ecomorph (either with or without the inclusion of the ground ecomorph) and only one mainland species assigned to the trunk ecomorph, thus C_1 was not calculated for these ecomorphs when assessing convergence among only the classified mainland *Draconura* species. Bold values represent statistically significant amounts of morphological convergence ($P < 0.05$).

Ecomorph	A priori ecomorphs species	A priori species and final classifications		Final mainland classifications only	
		Caribbean ecomorphs only	With ground ecomorph	Caribbean ecomorphs only	With ground ecomorph
Crown-Giant	0.409	0.425	0.425	-	-
Grass-Bush	0.334	0.272	0.307	0.164	0.072
Trunk	0.156	0.140	0.215	-	-
Trunk-Crown	0.248	0.256	0.259	0.222	0.213
Trunk-Ground	0.180	0.173	0.191	0.153	0.200
Twig	0.381	0.389	0.395	0.043	0.437
Ground	0.139	-	0.205	-	0.160

values (Table 4). Convergence was also found among the *Draconura* and previously unclassified Caribbean species that were assigned to an ecomorph in our final morphology-based classifications, both with and without the ground ecomorph (Table 4). Within the mainland *Draconura* clade, species classified as grass-bush and trunk-ground before the inclusion of the ground ecomorph exhibited significant morphological convergence (Table 4). With the addition of the ground ecomorph, mainland species assigned to the ground, trunk-ground and twig ecomorphs exhibited significant morphological convergence (Table 4).

FAUNAL CONVERGENCE BETWEEN ISLAND AND MAINLAND ANOLE RADIATIONS

The tanglegram indicated several instances of morphological convergence between Caribbean and mainland *Draconura*-clade anoles (Fig. 6). Morphological clusters generally corresponded to the different Caribbean ecomorphs and several mainland *Draconura* species clustered with each of them. However, the tanglegram also revealed a large cluster of mostly *Draconura* species with only a few instances of previously unclassified Caribbean species converging on those morphologies. Many *Draconura* species within this cluster also exhibited a mismatch between phylogeny and morphology, suggesting convergence within the *Draconura* clade. All a priori ground ecomorph species, except for *A. barbouri*, fell within this predominantly mainland *Draconura* cluster.

The tests for morphological similarity among the mainland *Draconura* radiation and each of the Greater Antillean radiations found moderate to strong support for species-for-species matching

across regions. Analyses performed with the MCC phylogeny did not find significant faunal similarity across regions (mean NND = 0.37, $p = 0.09$). However, analyses performed with the time-calibrated tree did (mean NND = 0.37, $p = 0.014$). Moreover, the isolated island vs. mainland comparisons showed that mainland *Draconura* species were, on average, more similar to species on each of the Greater Antillean islands than expected by chance (mean NND = 0.376; $p = 0.044$). However, the Greater Antillean fauna was not more similar to the mainland *Draconura* species than expected by chance (mean NND = 0.312, $p = 0.669$).

Adaptive shifts were common across the Caribbean and within the *Draconura* clade (Supporting Information, Fig. S3). The *l1ou* analyses using the MCC phylogeny detected 31 independent shifts, all with moderate to strong bootstrap support (> 55%). Of the 16 adaptive peaks, 11 were occupied by convergent lineages, of which three were shared between the Caribbean and the mainland. One of the convergent peaks corresponded to Caribbean twig anoles of the *Anolis angusticeps* group and the mainland *Anolis pentaprion* group (Supporting Information, Fig. S3, Regime 7). Another peak was occupied by Caribbean grass-bush anoles from the *Anolis olssoni* clade and the mainland species *Anolis auratus* and *Anolis meridionalis* (Supporting Information, Fig. S3, Regime 11). The third shared peak between the Caribbean and the mainland was occupied by the previously unclassified Caribbean anole *Anolis etheridgei* and several *Draconura*-clade anoles that we assigned to the ground or trunk-ground ecomorphs (Supporting Information, Fig. S3, Regime 15). The remaining peaks in the Caribbean broadly corresponded to the Caribbean ecomorphs,

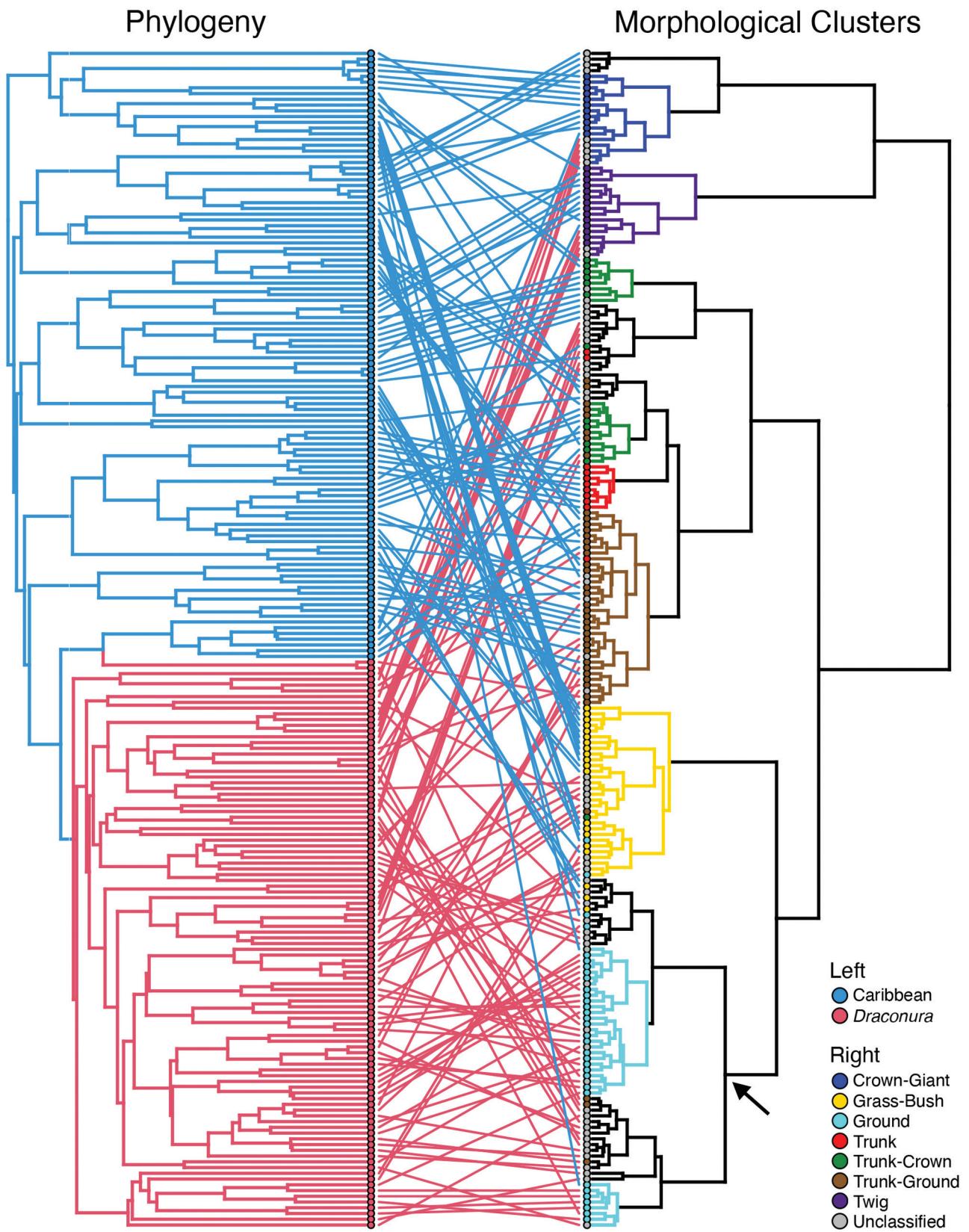


Figure 6. A tanglegram with the MCC phylogeny (left) and a dendrogram showing morphological clusters inferred from a hierarchical cluster analysis (right). Lines are drawn to indicate the location of each species in both diagrams. Lines that

and one exclusively mainland peak (Regime 14) was occupied by species assigned to the ground ecomorph both a priori and a posteriori. The analyses using the time-calibrated tree found fewer shifts and only some of the same regimes detected using the MCC tree. However, the time-calibrated tree analyses still found evidence for convergent regimes between the Caribbean and the mainland (Supporting Information, Fig. S4).

DISCUSSION

We found multiple lines of evidence suggesting that the mainland *Draconura* and Caribbean anole radiations exhibit convergent patterns of phenotypic diversification. Our morphological classifications provided strong evidence for several representatives of all six Caribbean ecomorphs on the mainland (Tables 1, 2; Fig. 1). Many of these species also occupy similar structural microhabitats as the Caribbean members of their corresponding ecomorphs (Supporting Information, Table S9; see below). These findings differ from previous studies that suggested the Caribbean ecomorphs are either absent or uncommon in Central and South America (Irschick *et al.*, 1997; Schaad & Poe, 2010), which led to the idea that different environmental factors are driving distinct evolutionary outcomes in island and mainland anoles (Irschick *et al.*, 1997; Velasco & Herrell, 2007; Pinto *et al.*, 2008; Schaad & Poe, 2010). By contrast, our results indicate that the mainland *Draconura* radiation generally resembles the Greater Antillean fauna, with species from both regions converging on similar morphologies and adaptive peaks (Fig. 6; Supporting Information, Fig. S3). Furthermore, many of the ecomorphs evolved more than once within the *Draconura* clade (also see Poe & Anderson, 2019), signifying that selection related to microhabitat specialization has led to convergent morphologies in separate mainland anole lineages.

Many mainland *Draconura* species resembled one or two ecomorphs but not closely enough to be classified by our methods, suggesting that they may be less specialized or intermediate ecomorph species. Likewise, Caribbean ecomorph species also vary in their degree of ecological and morphological specializations. Because ecomorphological specialization is generally

continuous, it is difficult to categorize intermediate species (Grizante *et al.*, 2010; Arbuckle *et al.*, 2014; Huie *et al.*, 2020), as the misclassifications of a few Caribbean ecomorph species by the DFA and cluster analysis demonstrate (Fig. 6; Supporting Information, Fig. S2). Recent studies, as well as this one, have suggested there is a mix of similar and distinct ecotypes and morphotypes on the mainland relative to the Caribbean (Poe & Anderson, 2019; Moreno-Arias *et al.*, 2020). Although some intermediate species might represent less specialized members of the currently recognized ecomorphs, or transitional species between ecomorphs, others may have morphologies that reflect distinct patterns of habitat specialization relative to the Caribbean ecomorphs. Alternatively, these species might belong to a more inclusive ecomorph, such as a bush-trunk-ground ecomorph. Future studies that examine the relationships between habitat use and morphology in these intermediate species will help refine our understanding of anole ecomorphology.

TESTABLE ECOMORPH CLASSIFICATIONS BASED ON MORPHOLOGY

Our analytical framework, which provides an explicit test for morphological differences between ecomorphs and predicts ecomorph classifications based on morphology assigned a greater relative proportion of mainland *Draconura* species to ecomorph classes compared to the morphology-based methods employed by previous studies (Irschick *et al.*, 1997; Schaad & Poe, 2010). Some differences are likely explained by our more permissive, yet still conservative criteria, which assign species based on the observed variation among a priori members of a given ecomorph. However, we also examined more and slightly different traits compared to previous studies (e.g. head dimensions and toepad width rather than lamella count). Schaad & Poe (2010) used scale counts and sexual size dimorphism (among other traits similar to ours) to classify mainland species into ecomorphs; however, these traits are not directly tied to structural habitat use. As such, they may be poor predictors of habitat use on the mainland and could explain differences in our results. Furthermore, our classification approach quantifies the similarities between less specialized species and the different ecomorphs to propose alternative ecomorph assignments. That said, our morphological

originate from areas of the phylogeny corresponding to Caribbean and mainland anoles but terminate in the same cluster in the dendrogram indicate convergence between the two geographic regions. The branches and tips of the phylogeny are coloured to indicate whether a species is from the Caribbean (blue) or the mainland *Draconura* clade (red). Some dendrogram branches are coloured to indicate which clusters generally correspond to clusters of a priori ecomorph species (black represents a neutral branch colour) and the tips are coloured to indicate our final classifications made with the inclusion of the ground ecomorph. The arrow indicates a morphological cluster composed of mostly *Draconura* species.

classifications are presented as hypotheses to be tested as additional microhabitat use data become available.

For several better-known *Draconura* species, the available natural history data support our hypothesized ecomorph assignments. For example, some mainland species from the *A. pentaprion* clade plus *A. salvini* were classified as twig anoles (Fig. 1). These species are all highly arboreal relative to other *Draconura* species (Savage, 2002; McCranie & Köhler, 2015), and at least *A. pentaprion* is often found on narrow perches, similar to Caribbean twig anoles (J. Losos, pers. comm.). We also classified the mainland *Draconura* species *A. auratus* as a grass-bush anole, a long-recognized assignment based on both ecology and morphology (Avila-Pires, 1995; Irschick *et al.*, 1997; Schaad & Poe, 2010; Fig. 1). Lastly, several *Draconura* species assigned to the trunk-ground ecomorph (*Anolis cryptolimifrons*, *Anolis mccraniei*, *Anolis osa*, *Anolis serranoi* and *Anolis subocularis*) often perch head-down low on tree trunks and regularly descend to the ground (Andrews, 1971; Jackson, 1973; Savage, 2002; Köhler & Acevado, 2004; Köhler *et al.*, 2014; Fig. 1), behaviours that are characteristic of Caribbean trunk-ground anoles. Other well-supported examples of ecomorph assignments are outlined in Supporting Information (Table S9). These corroborated ecomorph classifications highlight the usefulness and potential of our method to generate testable hypotheses based on the relationships between form and function as seen in, but not limited to, fish pharyngeal jaws, bat cranial morphologies, grass leaf shapes and the limb proportions of several frog clades (Santana & Cheung, 2016; Burress *et al.*, 2018; Gallaher *et al.*, 2019; Moen, 2019).

Although some of our assignment criteria are less strict than those applied in previous investigations, our final classifications may still fail to detect species that belong to an ecomorph. For example, *A. biporcatus* and *A. petersii* are two large, green and highly arboreal species that might represent mainland crown-giants but were not assigned as such (Irschick *et al.*, 1997; Losos, 2009; McCranie & Köhler, 2015), potentially because these “mainland crown-giants” do not attain body sizes as large as their Caribbean counterparts (McCranie & Köhler, 2015; Armstead *et al.*, 2017). Both *A. biporcatus* and *A. petersii* were identified as intermediates between crown-giant and another ecomorph, clustered morphologically with the Caribbean crown-giants, and occupied adaptive peaks close to those occupied by the Caribbean crown-giant species, supporting that they are less specialized (i.e. smaller) crown-giant anoles. These results also highlight how considering only the Caribbean ecomorph species may result in overly narrow morphological (and likely ecological) characterizations

of the ecomorphs. Conversely, our methods may have incorrectly assigned some *Draconura* species to ecomorphs. For instance, *A. kemptoni* was classified as a trunk-crown anole, but it appears to be ecologically more similar to trunk-ground anoles (Savage, 2002), and yet this species showed only weak support for an alternative trunk-ground classification (Supporting Information, Tables S4–S8).

What factors explain these instances where the relationship between morphology and ecology do not correspond to those observed in the ecomorph species? One possibility is that higher or lower diversity in local anole assemblages leads to variable ecomorphological relationships. At some localities on the mainland, as well as in the Caribbean, anole communities are composed of a few or no sympatric anole species (Poe & Anderson, 2019). For example, some *Draconura* species are endemic to islands (Calderón-Espinosa & Barragán Forero, 2011; McCranie & Köhler, 2015; Phillips *et al.*, 2019) or occur in high elevation environments (as is the case for *A. kemptoni*), where they co-exist with few anole species and fewer competitors in general (Savage, 2002; McDiarmid & Donnelly, 2005; Leenders, 2019). Likewise, communities of anoles in the Lesser Antilles, which include many of our previously unclassified Caribbean species, typically include just one or two species per island (Henderson & Powell, 2009; Yuan *et al.*, 2020). There is strong evidence that niche partitioning and morphological specialization are tied to interspecific competition (Losos, 1992; Schlüter, 1998; Pfennig & Pfennig, 2009; Adams, 2010; Yuan *et al.*, 2020). Therefore, the presence of fewer anole competitors in some communities might lead to ecological release or natural selection favouring different patterns of microhabitat use and associated morphological adaptations compared to species-rich assemblages (Carpenter, 1965; Losos & de Queiroz, 1997; Calderón-Espinosa & Barragán Forero, 2011; McCranie & Köhler, 2015). More broadly, community composition is an important factor to consider when assessing the presence (and absence) of convergent evolution.

AN ECOMORPH OF GROUND ANOLES

We found strong evidence for a previously undescribed ecomorph consisting of predominately ground-dwelling mainland and Caribbean anoles. These species exhibit strong morphological convergence (Table 4) and occupy an area of the morphospace that is statistically distinct from all of the other anole ecomorphs. Ground anoles share longer limbs, reduced finger- and toe-pads and shorter heads (Figs 2, 4), traits that are associated with life on the ground in other lizards. For instance, longer limbs allow anoles and other ground-dwelling lizards to sprint more efficiently on broader

surfaces (Losos, 1990; Melville & Swain, 2000; Herrel *et al.*, 2002). Similarly, narrower toepads in ground anoles are consistent with the positive correlation between perch height and toepad size in anoles, and the understanding that toepads are an adaptation for clinging to vertical surfaces (Macrini *et al.*, 2003; Elstrott & Irschick, 2004; Crandell *et al.*, 2014; Collins *et al.*, 2015). A short and stout head, presumably associated with diet, has also evolved more than once in ground-dwelling Australian agamid lizards (Gray *et al.*, 2019). Finally, many of our putative ground ecomorph species have flatter claws than the more arboreal Caribbean ecomorph species, consistent with the inference that flatter claws improve performance while running, whereas highly curved claws are better suited to climbing [Yuan *et al.* (2019) and references therein].

Additional support for the ground ecomorph stems from our ability to classify ecologically similar species to this ecomorph based on morphology. For example, *Anolis cupreus*, *Anolis granuliceps*, *Anolis notopholis* and *Anolis wampuensis* are some of the species commonly found on the ground that remained unclassified both in our study and in past studies prior to the addition of the ground ecomorph (Savage, 2002; Castro-Herrera, 1988; McCranie & Köhler, 2015; Moreno-Arias *et al.*, 2020). *A. notopholis* and three other species classified as either ground or intermediates between ground and trunk-ground also appear to be converging towards the same adaptive peak as the ground anoles from the *A. chrysolepis* complex, assigned a priori to this ecomorph (Supporting Information, Fig. S3, Regime 14). However, ground-dwelling is unlikely to be an ecological monolith. Although the ground species we assigned a priori predominately live among leaf-litter, other terrestrial anoles perch on ground-level structures such as rocks, logs, tree roots and other low vegetation. Moreover, several species we classified as ground anoles may perch on a combination of tree trunks and shrubs at low heights, but potentially less so than typical grass-bush or trunk-ground anoles, in addition to being active on the ground (Savage, 2002; Köhler *et al.*, 2014; McCranie & Köhler, 2015; Muñoz *et al.*, 2015; Supporting Information, Table S9). This variation introduces the possibility of finer partitioning of the broad “ground” category; however, the ecological data needed to tease apart microhabitat preferences for these species are not currently available. Correspondingly, ecomorph classifications near the intersection of the ground, trunk-ground and grass-bush ecomorphs in the morphospace are not always straightforward given the ecological and morphological similarities between those ecomorphs (this study).

The recognition of the ground ecomorph further supports our conclusion that the island and mainland

anole radiations are more similar than previously understood. Under the original anole ecomorph concept, the Caribbean ground anole *A. barbouri* and potential ground species *A. rupinae* (Williams & Webster, 1974) have been regarded as ecological “singletons” that are dissimilar to any of the ecomorph species (Losos, 2009). However, our data reveal that these Caribbean “singletons” resemble some mainland *Draconura* species, specifically the ground-dwelling anoles, suggesting that at least some previously unclassified Caribbean species are not unique when considering the broader radiation of anoles. This finding raises the question of whether there are other undescribed ecomorph classes consisting of both mainland and Caribbean species. For example, there are several island and mainland species that perch on vertical rock walls including those of caves (Glor *et al.*, 2003; Henderson & Powell, 2009; Nicholson *et al.*, 2012; Scarpetta *et al.*, 2015; Muñoz & Losos, 2018), as well as species that commonly perch on top of rock-piles (Birt *et al.*, 2001; Losos, 2009; Muñoz *et al.*, 2015). Most rock-wall species were assigned to the trunk-ground ecomorph in our study, and a few species that perch on top of rocks were intermediate between the ground and trunk-ground ecomorphs; thus, it seems unlikely that rock-dwelling anoles represent a single ecomorph class (Supporting Information, Table S9; Fig. S5). Our classifications are consistent with a difference between vertical and horizontal rock-perching that aligns well with the functional challenges faced by trunk-ground and ground anoles, respectively. This finding illustrates that not all species with distinctive ecologies also have distinct morphologies that warrant a separate ecomorph class, suggesting that some ecomorphs are more inclusive and/or contain subclasses. Along the same vein, it is equally important to recognize that distinct morphologies do not necessarily equate to distinct ecologies as different trait combinations may result in similar performance outcomes (Wainwright *et al.*, 2005). Addressing the possibility of currently unrecognized ecomorphs will require more in-depth ecological and morphological investigations, particularly for mainland taxa.

REPLICATE ADAPTIVE RADIATIONS IN ISLAND AND MAINLAND SETTINGS

Our data provide compelling morphological evidence that the evolution of anole ecomorphs, which has occurred independently multiple times in the Greater Antilles, occurred an additional time when anoles recolonized the mainland. Despite the general similarities, there are subtle differences between the Greater Antillean and mainland *Draconura* radiations. Species representing some of the more arboreal ecomorphs do not appear to be as

ubiquitous in the mainland *Draconura* clade as they are in the Caribbean. In particular, relatively few *Draconura* anoles were assigned to the crown-giant, trunk-crown, trunk and twig ecomorphs. Conversely, there is an abundance of ground-dwelling anole species on the mainland but few in the Caribbean. These patterns may reflect historical contingencies in the evolution of the *Draconura* clade. By the time the ancestor of the *Draconura* clade recolonized the mainland from the Caribbean, Central and South America were already populated by a diverse assemblage of arboreal lizards, including members of the *Dactyloa* clade of anoles (Nicholson *et al.*, 2005, 2012; Lotzkat *et al.*, 2013; Prates *et al.*, 2020). We propose that the limited availability of arboreal niches both restricted the evolution of *Draconura* species into the highly arboreal ecomorphs and facilitated the diversification of ground anoles. In sum, we posit that occupying similar microhabitats in island and mainland settings led to broadscale convergence in the adaptive radiation of anoles; however, regional differences in selective landscapes led to variation in how the details of those radiations unfolded.

The anole system is one of the few recognized examples of replicated radiations that occur outside of just insular and lacustrine environments (Bossuyt & Milinkovich, 2000; Ruedi & Mayer, 2001; Burress *et al.*, 2018; Rincon-Sandoval *et al.*, 2020). Our results are congruent with the idea that continental settings can provide equal or even greater ecological opportunities than island settings (Velasco *et al.*, 2016, 2018; Salazar *et al.*, 2019). This study also suggests that the favourable conditions provided by islands and lakes are not absolutely crucial for replicated radiations to occur. With this in mind, we invite future studies to investigate other lineages that span distinct geographic regions to better understand the factors that facilitate and impede replicated radiations.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Material and Methods S1. Species substitutions in the phylogeny.

Results S1. DFA misclassifications.

Table S1. List of the 205 anole species used in this study and their ecomorph assignments.

Table S2. Loadings for the first five axes of the phylogenetic principal component analysis.

Table S3. Summary of the morphospatial Euclidean distances for a priori ecomorph species.

Table S4. DFA posterior probabilities for the ecomorph classifications made with only the six Caribbean ecomorphs.

Table S5. Centroid distances for the *Draconura* anoles and previously unclassified Caribbean species.

Table S6. Mean pairwise distances for the *Draconura* anoles and previously unclassified Caribbean species.

Table S7. Nearest neighbour distances for the *Draconura* anoles and previously unclassified Caribbean species.

Table S8. DFA posterior probabilities for the ecomorph classifications made with the inclusion of the ground ecomorph.

Table S9. Assessments of the final ecomorph assignments inferred from morphology with ecological data.

Figure S1. Individual trait variation among the a priori Caribbean and ground ecomorph species.

Figure S2. Results from the cluster analyses using the a priori ecomorph species.

Figure S3. $l1ou$ results inferred with the MCC phylogeny.

Figure S4. $l1ou$ results inferred with the time-calibrated phylogeny.

Figure S5. Relative positions of the Caribbean ecomorphs, ground ecomorph and rock anoles in the morphospace.