ECOLOGY LETTERS

Ecology Letters, (2019) doi: 10.1111/ele.13246

LETTER

Ecomorphological convergence in *Eleutherodactylus* frogs: a case of replicate radiations in the Caribbean

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Abstract

Replicate radiations, the repeated multiplication of species associated with ecological divergence, have attracted much attention and generated as much debate. Due to the few well-studied cases, it remains unclear whether replicate radiations are an exceptional result of evolution or a relatively common example of the power of adaptation by natural selection. We examined the case of *Eleutherodactylus* frogs, which radiated in the Caribbean islands resulting in more than 160 species that occupy very diverse habitats. A time-calibrated phylogeny revealed that these frogs independently diversified on all larger islands producing species that occupy a broad range of microhabitats in different islands. Using phylogenetic comparative methods, we found an association between morphological traits and particular microhabitats, and for most microhabitats detected significant morphological convergence. Our results indicate Caribbean *Eleutherodactylus* are a novel example of replicate radiations, and highlight the predictability of evolutionary processes, as similar ecological opportunities can lead to similar outcomes.

Keywords

Adaptive radiation, convergence, ecological speciation, ecomorph, *Eleutherodactylus*, replicate radiations.

Ecology Letters (2019)

INTRODUCTION

One of the main aims in evolutionary biology is to identify the mechanisms responsible for the spectacular diversity of life on Earth. Because speciation is the end result of divergence between evolutionarily distinct lineages, much research effort has focused on the mechanisms generating isolation, be they natural barriers, adaptation to ecologically distinct niches or sexual selection (Coyne & Orr 2004). Ecological divergence is thought to play a key role in speciation. Adaptive radiation is a particular case of speciation by ecological divergence, in which lineages exhibit exceptional adaptive diversification to exploit distinct ecological niches (Schluter 2000; Gavrilets & Losos 2009). As such, adaptive radiation is a primary representation of Darwin's 'principle of divergence' (Glor 2010) and has long captured the interest of evolutionary biologists. Indeed, it is considered by some of foremost importance and potentially responsible for most of the ecological and phenotypic diversity of life (Gavrilets & Losos 2009). Nonetheless, the importance of adaptive radiation in explaining current diversity has long been debated, and given there are but a few well-studied cases, it is still unclear how far these can be generalised (Schluter 2000; Futuyma 2003).

Some of the most iconic examples of adaptive radiation are the so called replicate radiations, such as Greater Antillean anoles (Losos 2009), postglacial lakes fishes (Snorrason & Skúlason 2004) and African rift-lake cichlids (Salzburger 2009). These rare examples of adaptive radiation have attracted much interest because of their replicated nature, with convergence in species that have independently invaded similar niches resulting in similar phenotypes. Replicate radiations offer what is arguably the strongest evidence that Darwinian natural selection acting on organisms exposed to similar selection pressures can sometimes overwhelm historical and ecological contingencies (Losos 2009; Glor 2010). Nonetheless, as elegantly pointed out by Futuyma (2003): 'the cases of parallel radiation are as exquisitely appealing as great works of art, but whether or not they are equally exceptional remains to be seen'. The exceptionality of these radiations calls into question the role they may play in explaining diversity patterns worldwide. Therefore, comparisons across different taxa are much needed to determine whether similar ecological opportunities, within a given geographical setting, can lead to equivalent outcomes.

We focus our study on frogs of the genus *Eleutherodactylus*, which currently includes 199 species (Frost 2018) distributed from southern North America (south of the United States and Mexico) to northern Central America (Belize and Guatemala), although the vast majority of the diversity (84% of all species) is found in the Caribbean (the Antilles biogeographic region). The extraordinary species richness of the Caribbean *Eleutherodactylus* was suggested in previous works to be the result of an adaptive radiation (Hedges 1989a,b; Hass & Hedges 1991; Hedges *et al.* 2008; Ricklefs & Bermingham 2008), although this has never been formally tested (but see Kaiser 2002 for Lesser Antillean *Eleutherodactylus*), which is surprising given the large body of work dedicated to the Caribbean *Anolis* lizard radiation (e.g. Williams 1983; Pinto *et al.* 2008; Losos 2009; Mahler *et al.* 2010, 2013). *Eleutherodactylus* frogs are an excellent study system to test whether the multiplication of species was the result of an adaptive process to different niches with accompanying convergent evolution across the different islands. The adaptive radiation of the Caribbean *Anolis* unfolded in the same geographic region and we may ask

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whether the ecological and paleogeographical setting of the Caribbean has set the stage for replicate radiations in distinct lineages.

To test whether the diversification of the Caribbean *Eleutherodactylus* resulted from replicate radiations, we constructed the most complete time-calibrated phylogeny for the genus. We then performed a historical biogeography analysis to describe the sequence of island colonisation and *in-situ* radiations. We collected ecological information from the literature and our own field experience for all species to determine their microhabitat use. To describe a species' morphology, we used 26 linear measurements and then tested for associations between particular morphological traits and microhabitats. Finally, we tested for morphological convergence for each microhabitat between the different islands and quantified its strength using recently developed phylogenetic comparative analyses.

MATERIAL AND METHODS

Genetic and morphological data

We collected nuclear and mitochondrial sequences from published data sets (e.g. Hedges *et al.* 2008; Padial *et al.* 2014) for the *Eleutherodactylidae* family. Our molecular data set comprised four mitochondrial genes and three nuclear genes belonging to 151 Caribbean *Eleutherodactylus* taxa (three of them corresponding to species awaiting formal description), four continental *Eleutherodactylus* and eight taxa of the three other genera included in the same family (*Adelophryne*, *Diasporus* and *Phyzelaphryne*). We also included 19 *Brachycephalidae* species and two hylids (*Agalychnis callidryas* [Cope, 1862] and *Litoria caerulea* [White, 1790]) as outgroups. A complete list of genes used per species with their GenBank accession numbers is available in Table S1.

We examined 1876 adult specimens from 162 species of Caribbean *Eleutherodactylus* belonging to 19 zoological collections from four different countries (see Appendix S1 for complete list). Sex was determined by the presence of secondary sexual characters (vocal sac and slits) and/or direct examination of gonads by making a small posterolateral incision. When available, at least six adult males and six adult females from each species were measured.

To characterse the body shape and size of the specimens, we recorded 26 linear measurements for each individual, some of which were combined to create comprehensive variables (Fig. S1) resulting in 10 morphological traits: snout-vent length (SVL, from the tip of the snout to the cloaca), head width (HW, at the widest point of the head), tympanum length (TyL, maximum diameter), forearm length (FaL, from elbow to the proximal edge of thenar tubercle), hand length (HaL, from the proximal edge of thenar tubercle to the proximal edge of the first subarticular tubercle on the third finger), total finger length (TF, sum of all the finger lengths), total finger pad (TFP, sum of all the finger pad widths), total limb length (TLL, sum of thigh, tibia and foot length), total toe length (TT, sum of all the toe lengths) and total toe pad (TTP, sum of all the toe pad widths). These morphological variables were chosen based on their putatively adaptive potential, since they have been associated with important biological functions as jumping, swimming, climbing, burrowing, clinging or foraging (Emerson 1976, 1978, 1985, 1991; Emerson & Diehl 1980; Lutz & Rome 1994; Nauwelaerts *et al.* 2005; Manzano *et al.* 2008), and thus could contribute to adaptation to specific microhabitats. All measurements were taken by ADC to ensure consistency using a Mitutoyo digital caliper to the nearest 0.01 mm.

Phylogenetic and biogeographical reconstructions

Sequences were aligned using MAFFT (Katoh & Standley 2013). We then removed poorly aligned positions in our matrices using the Gblocks (v0.91b) (Talavera & Castresana 2007) web server, and concatenated them into a super-matrix using Mesquite (v3.03) (Maddison & Maddison 2015). We identified a two-partition scheme as best for our data using PartitionFinder (v1.1.1) (Lanfear *et al.* 2012): one partition for mitochondrial genes and the other for the nuclear genes, and a GTR+I+G model of substitution for both partitions, allowing for independent estimates of model parameters for each partition. We generated a time-calibrated phylogenetic reconstruction from the collected genetic data using BEAST v.1.8.2 (Drummond *et al.* 2012). We performed two independent runs, each for 30 000 000 generations, sampling every 3000 generations. We calibrated the phylogeny using three calibration points following Heinicke *et al.* (2007) (see Figure S2 for details). The convergence of both independent runs was verified with Tracer v1.5. Both runs were combined with LogCombiner v1.8 and we obtained a consensus tree from the combined runs, which was used for all subsequent comparative analyses.

To infer the origin and the pattern of colonisation and inter-island dispersal, and thus determine whether species richness on each island was the result of a single or multiple separate radiations, we performed a historical biogeography analysis using the R (R Core Team 2015) package BioGEOBEARS (Matzke 2013). The method compares across a number of models (DIVALIKE, DEC and BAYAREA) of how biogeography evolves along a phylogeny and estimates ancestral geographical ranges, accounting for founder-event speciation (+J), a potentially important process in island clades (Matzke 2014). We used AIC to assess model fit. We implemented a time-stratified analysis, based on Caribbean geological history (Iturralde-Vinent 2006), with four different time periods starting at 34 Mya. For each period, we defined a dispersal rate matrix between regions, which ranged from 0 when one of the two regions was not emerged, making colonisation impossible, to 0.75 for contiguous land-connected regions (see Table S2 for details). Analyses without time-stratification gave qualitatively similar results (not shown). Due to difficulties in identifying the origin of some species present on more than one island, the Lesser Antilles were considered a single entity. The Virgin Islands were included with Puerto Rico (hereafter, Puerto Rico Bank) since they formed a single emerged landmass during the last glacial maximum. Geological intra-island histories were not considered since our interest here was to describe the pattern of island colonisation. Thus, nine regions were defined: *North/Central America*, *South America*, *Cuba*,

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Bahamas, *Jamaica*, *Hispaniola*, *Mona*, *Puerto Rico Bank* and *Lesser Antilles* (see map in Fig. 1). The maximum range size for one species was set to two regions, since only a single species (*Diasporus quidditus* [Lynch, 2001]) from the entire family *Eleutherodactylidae* currently inhabits two regions.

Microhabitats

We categorised species based on their microhabitat use and behaviour (when available), as reported in the literature and our own (AR) fieldwork experience. We included 10 microhabitat categories: *bromelicolous*, *arboreal*, *semiarboreal*, *terrestrial*, *leaf-litter*, *petricolous*, *cave-dwelling*, *stream-dwelling*, *fossorial and riparian* (see Box 1 for a description of each microhabitat). Such categorisation is obviously a rough rendering of the habitat use and behaviour of these frogs and might be inaccurate for those species that have been poorly studied in the field. Thus, we also conducted an additional set of analyses using a low-resolution classification, including only five microhabitats, which allowed us to account for uncertainty in microhabitat classification. We combined *arboreal* and *bromelicolous*, *petricolous* and *cave-dwelling*, *terrestrial* and *leaf-litter*, and *stream-dwelling* and *riparian* species into the *tree*-, *rock*-, *ground*- and *water*-related microhabitats respectively. We also re-assigned semiarboreal species mainly occurring on herbaceous vegetation to the ground and those found in bushes or trees to the *tree* microhabitat (microhabitat classifications and sources are listed in Table S3). All microhabitats have been previously used in published works to classify Caribbean *Eleutherodactylus* (e.g. Hedges 1989a,b; Díaz & Cádiz 2008).

To estimate the ancestral microhabitat use and determine whether the observed distribution of microhabitats across the different islands in Caribbean *Eleutherodactylus* was the result of independent colonisation events, we performed a microhabitat ancestral state reconstruction with all the species of the family *Eleutherodactylidae* included in our phylogeny using the function rerootingMethod in *phytools* (Revell 2012) under a model with symmetric transition rates among ecotypes, as it was the best-fitting model.

Morphological analyses

Morphological variables were log transformed to approach normality after restricting the data matrix to the 148 named Caribbean *Eleutherodactylus* species represented in the phylogenetic reconstruction. In addition, to control for the allometric relationship of all measures with body size, we size-corrected species mean values performing phylogenetic linear regression of each trait on body size (lnSVL) to obtain residual values (Revell 2009; Mahler *et al.* 2013). As principal component analysis (PCA) might result in undesirable statistical artefacts during evolutionary model fitting (Uyeda *et al.* 2015), we used body size and size-corrected values of the phenotypic traits for all subsequent analyses. To estimate the phylogenetic signal

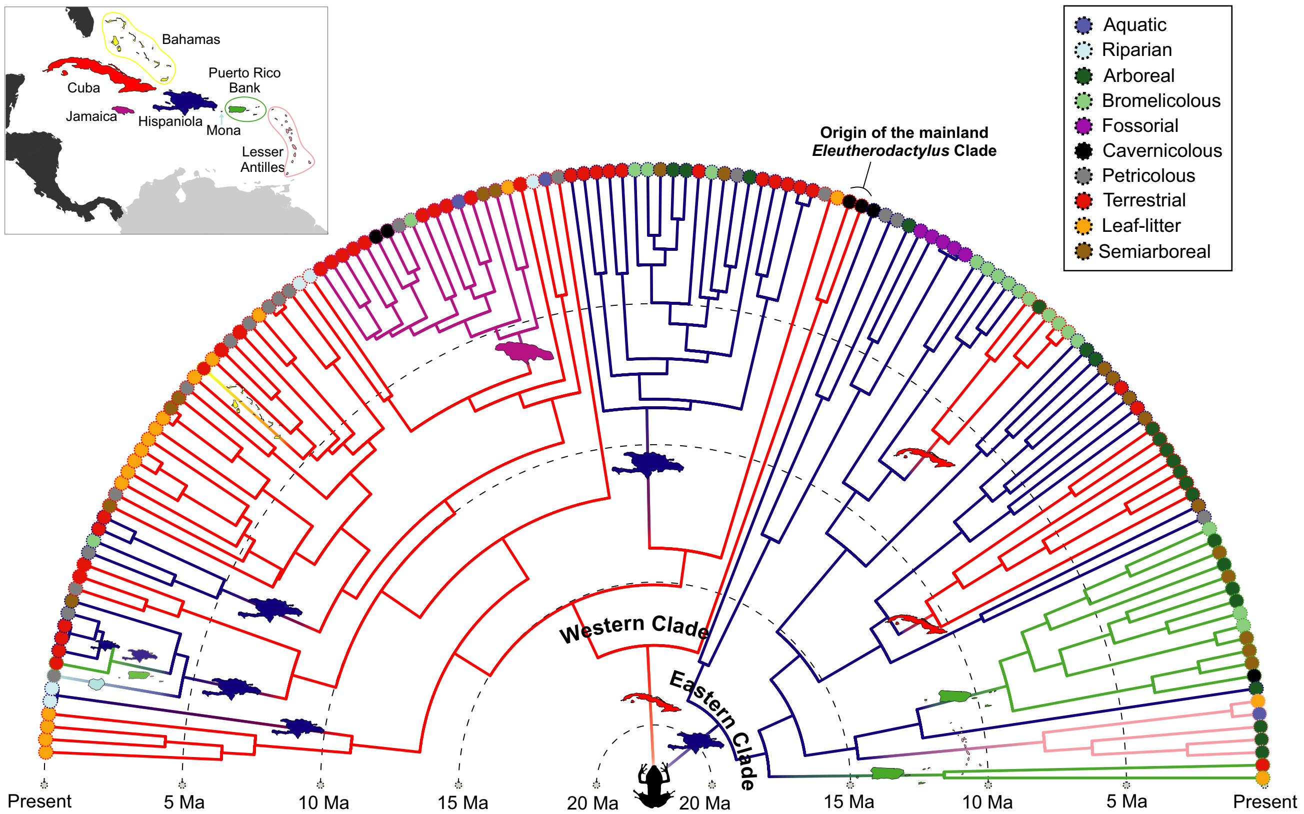

Figure 1 Summary of the time-calibrated phylogeny and biogeographical history of the Caribbean *Eleutherodactylus*. The colours of the circles at the tips of the tree represent the microhabitat occupied by each species. Branch colours represent the island inhabited by the lineage based on ancestral range estimations, and islands above nodes represent inferred colonisation events.

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Box 1

Description of microhabitat classifications and ecomorphs for Caribbean *Eleutherodactylus*. The classification is based on the most frequent microhabitats where species have been observed and, when available, their behaviour. The ecomorphs are defined based on the results of the comparative analyses of associations between microhabitats and morphology as well as the convergence analyses.

Microhabitat	Description	Ecomorph
Arboreal	Usually active in vegetation (0–6 m) during the night, with diurnal retreat sites in vegetation or on the ground	Species are medium in size, have a wide head, a small tympanum, long fingers, and large pads
Bromelicolous	Develop most of their nocturnal activity in the forest canopy diurnally retreating in bromeliads	Species are medium in size, have a wide head, a small tympanum, long fingers, and large pads
Cave-dwelling	Usually active and with reproductive behaviour (calls, egg deposition, clutch attendance) and retreat sites inside, and frequently deep into caves.	Species are large, have a large tympanum, and elongated forearms.
Fossorial	Commonly found in underground chambers or burrows used for calling, breeding and retreat	Species are large, with a large tympanum, and elongated forearms, and large hands
Leaf-litter	Ground species that are found active and with retreat sites in the leaf-litter, including species frequently found under moss	Species are small to very small in size, with a large tympanum, short fingers and small pads
Petricolous	Commonly found active in rocky outcrops, boulders, or karstic habitats and with retreat sites in crevices or caves	Species are medium to large, with a large tympanum, elongated forearms, and long fingers with large pads
Riparian	Commonly found along water bodies with retreat sites in the ground	Species are medium to large, have large hands, long hind limbs, long toes, and reduced pads
Semiarboreal	Frequently found active in low vegetation (< 1.5 m) but also on the ground, retreating diurnally to the ground	Species are small to medium in size, with a small tympanum, long fingers, and large pads
Stream-dwelling	Commonly found in mountain streams often immersed in water	Species are medium to large in size, with large hands, large pads, and long toes and fingers
Terrestrial	Frequently found active and retreating in the ground	Species are small to medium in size, with a large tympanum, and small pad

of the continuous traits used in the analyses, we calculated Pagel's λ (Pagel 1999), the best-fitting model of trait evolution for all morphological traits (see Table S4). We estimated the maximum likelihood value of λ and compared the log-likelihood with that of a model where λ was fixed at 0, no phylogenetic signal, using a log-likelihood ratio test.

To evaluate whether microhabitats were associated with differences in morphological traits, we conducted univariate and multivariate ANOVAs using the novel RRPP method (Collyer & Adams 2018), a refined method of residual randomisation using permutations which shows higher statistical power than phylogenetic ANOVA in highly aggregated groups across the phylogeny (Adams & Collyer 2018b). We performed 1000 permutations for each analysis using the R package *RRPP* (Collyer & Adams 2018). We created a projection of the phylogeny in morphospace (phylomorphospace) for combinations of body size and other size-corrected traits. Finally, we also ran a discriminant function analysis (DFA) including all size-corrected traits and body size (SVL). Estimates of λ and phylomorphospace analyses were done in the package *phytools* (Revell 2012) and DFA in the package *MASS* (Venables & Ripley 2002) in R.

Convergence analyses

To analyse the convergence, we used a distance-based method implemented in the R package *convevol*, based on the idea that convergence results in two taxa evolving to become more similar to each other than their ancestors were (Stayton 2015). The method quantifies the amount of convergence by comparing the current phenotypic distance between two lineages (D_{tip}), measured as Euclidean distances, to the maximum distance between them in the past (D_{max}), based on ancestral state estimates. An index of convergence (C_1) is produced ($C_1 = 1 - (D_{tip}/D_{max})$), scaled to permit comparisons among different taxa. The observed degree of convergence was compared to a null model (no convergence), based on 1000 simulations under a Brownian motion model of trait evolution. We did not use the alternative *SURFACE* method as it can suffer from model over-fitting (see Khabbazian *et al.* 2016; Adams & Collyer 2018a). Following the method's guidelines, clades of species in the same microhabitat were collapsed and

Table 1 Morphological and genetic data collected for Caribbean *Eleutherodactylus* for each region

Region	Morphological data Species (% from total)	Specimens (range, mean/species)	Genetic data Species (% from total)
Hispaniola	64 (96)	695 (1–20, 10.9)	57 (85)
Cuba*	57 (97)	683 (3–26, 12)	52 (88)
Puerto Rico Bank†	19 (100)	223 (1–21, 11.7)	17 (89)
Jamaica	17 (100)	215 (10–18, 12.6)	17 (100)
Lesser Antilles	5 (100)	60 (10–13, 12)	5 (100)
Total	162 (97)	1876 (1–26, 11.6)	148 (89)

*Includes the only Bahamian species (*E. rogersi*).

†Includes the only species from Mona (*E. monensis*).

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represented by the group average as it makes little sense to estimate convergence for clades where terminals and ancestors occupy the same microhabitat. The fossorial microhabitat appeared only once in the phylogeny so its morphological convergence could not be tested.

Finally, we applied the *Wheatsheaf index* (Arbuckle *et al.* 2014) to evaluate the strength of morphological convergence for taxa assigned to the same microhabitat. This method provides a simple index to quantify the strength of convergent evolution incorporating both phenotypic similarity and shared ancestry. The *Wheatsheaf index* estimates the strength of convergence as the ratio of the average pairwise distance between all taxa, to the average pairwise distance between 'focal' species (i.e. those in a given microhabitat) accounting for phylogenetic relatedness (Arbuckle *et al.* 2014). We calculated this index for each trait in each microhabitat using the R package *windex (Arbuckle & Minte 2015)*. To assess the statistically significance of the results, we performed 1000 bootstrap replicates.

RESULTS

Genetic and morphological data

Our morphologic data set included 162 Caribbean *Eleutherodactylus* species, representing 97% of the species in the region. For 148 of them, genetic information was also available. All biogeographic regions (islands or island groups) were well-represented in our data set and in all cases 85% or more of the species identified in each region were included in the analyses (Table 1).

Phylogenetic and biogeographical reconstructions

The BioGeoBEARS analyses suggest that the best-fit model for ancestral range estimation was DIVALIKE+J (AICc weight = 0.69) followed by DEC+J (AICc weight = 0.30), while the remaining models had negligible support (see Table S5). Both preferred models propose almost identical ancestral range estimations (see Fig. S3), we therefore present a consensus biogeographical history (summarised in Fig. 1), with dates obtained from our time-calibrated phylogeny (see Fig. S2). Our results suggest that *Eleutherodactylus* diverged from their sister genus *Diasporus* about 25 Mya (95% CI $\approx$ 20–30 Mya). Although the Antillean geographical origin of *Eleutherodactylus* is uncertain, the most likely ancestral ranges are Cuba or Hispaniola. The Caribbean *Eleutherodactylus* diversification began around 22 Mya (95% CI $\approx$ 18–26 Mya), when the group split into two major clades, most likely inhabiting Hispaniola and Cuba. The Western Clade (subgenera *Euhyas* and *Syrrhophus*) presumably originated and mostly diversified in Cuba, and colonised Hispaniola at least four times. One of these Hispaniola subclades later reached the Puerto Rico Bank and Mona. The monophyletic Jamaican radiation also appears to have derived from this Cuban clade. Similarly, our results suggest a Cuban origin for the mainland *Eleutherodactylus* included in this study (see Fig. 1), although this result must be taken with caution as few mainland species were included. However, we expect that the addition of more mainland species would not alter this result, since these species have a common origin, based on taxonomic criteria. Meanwhile, the Eastern Clade (subgenera *Eleutherodactylus*, *Pelorius* and *Schwartzius*) presumably originated and mostly diversified in Hispaniola, dispersed twice to Cuba and the Puerto Rico Bank, and also colonised the Lesser Antilles. The estimated dates for the transitions between islands suggest that they took place when islands were likely no longer interconnected, and thus we can assume that the events were more likely the result of dispersal rather than vicariance. The only case that could be compatible with vicariance is the separation of the Western and Eastern clades, as the land connection between eastern Cuba and northern Hispaniola was interrupted by the expansion of the Windward Passage, during the Lower Miocene (Iturralde-Vinent 2006).

Microhabitats

The total number of Caribbean *Eleutherodactylus* belonging to each microhabitat varied from 37 species for the *terrestrial* microhabitat to just five species for the *stream-dwelling* one (Table S6, which includes all Caribbean *Eleutherodactylus*, not only those represented in the phylogeny). Most microhabitats can be found on almost all islands or island groups, except for the *fossorial* one, which only occurs in a single clade in Hispaniola. The proportion of species in each microhabitat is variable across regions, and the microhabitats are not evenly distributed along the phylogeny (Fig. 1). For example, the Eastern Clade included most of the *tree*-dwelling species (*arboreal*, *bromelicolous* and *semiarboreal*), and all the *fossorial* species. The Western Clade, on the other hand, is less homogeneous, including all *riparian* and most of the *ground*-dwelling (*terrestrial* and *leaf-litter*) and *petricolous* species. Accordingly, the common ancestor of the Eastern and the Western Clades were *tree*-dwelling and *terrestrial* species respectively, as suggested by Hedges (1989a). The different islands in each clade were most probably colonised by species of these microhabitats (Fig. S4). Finally, across the different islands species have independently colonised the diverse microhabitats, and on the larger islands, often more than once (Fig S4). The minimum number of evolutionary transitions (as estimated under maximum parsimony) between microhabitats along the phylogeny is 64, much higher than the number of transitions among regions (16) estimated by our biogeographical reconstruction.

Morphological analyses

All of the morphological variables presented significant phylogenetic signal (i.e. $\lambda > 0$). Maximum likelihood estimates of λ ranged from 0.67 to 0.89, except for hand length and total toe length which showed a weaker phylogenetic signal, although still significantly different from 0 ($\lambda = 0.49$, $P < 0.001$ and $\lambda = 0.39$, $P = 0.05$ respectively) (see Table S7 for the complete results).

The phylomorphospace and the scores of the first two discriminant functions (Fig. 2, see Fig. S5 for other trait combinations in the phylomorphospace) showed that most species found in the same microhabitat tended to group together,

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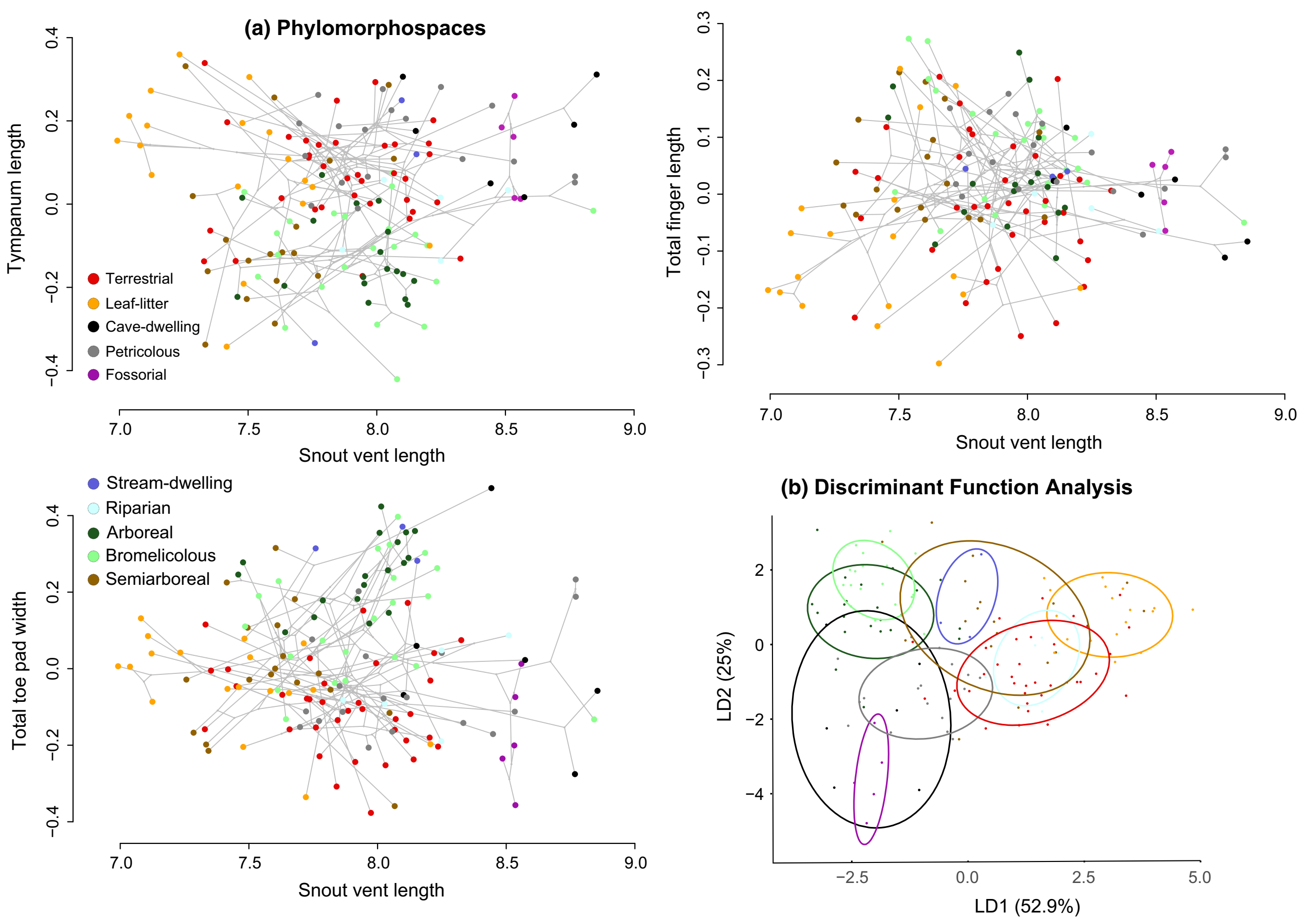

Figure 2 Morphological variation in Caribbean *Eleutherodactylus*. (a) Phylomorphospaces, phylogenetic trees represented within the morphospace defined by log transformed snout-vent length (body size) and tympanum length, total finger length and total toe pad width (see the other traits in Figure S5). (b) Discriminant function analysis plot with 75% confidence ellipses showing partial differentiation in morphology between the frogs using different microhabitats. Dots and ellipses are coloured according to microhabitat of the species.

Table 2 Degree of morphological convergence among Caribbean *Eleutherodactylus* species inhabiting similar microhabitats

Microhabitat (High-resolution)	C_1	*P*-value	Microhabitat (Low-resolution)	C_1	*P*-value
Stream-dwelling	0.401	0.110	*Water*	**0.423**	0.010
Riparian	0.268	0.130			
Arboreal	**0.400**	< 0.001	*Tree*	**0.274**	0.022
Bromelicolous	**0.396**	0.001			
Semiarboreal	**0.475**	< 0.001			
Terrestrial	**0.406**	< 0.001	*Ground*	**0.262**	0.010
Leaf-litter	**0.390**	< 0.001			
Cave-dwelling	**0.433**	0.009	*Rock*	0.165	0.838
Petricolous	**0.413**	< 0.001			

C_1, proportion of the maximum morphological distance between the taxa belonging to a given microhabitat that has been reduced by convergence. Significant results ($P < 0.05$) are shown in bold (see Table S9 for complete results).

although with notable overlap between microhabitats. The observation that species using the same microhabitat had somewhat similar morphology is all the more notable when taking into account that groups are not composed of close relatives. In many cases, species with similar morphologies derive from ancestors that possessed distinct morphologies and lived on different islands, as can be seen for example for the *stream-dwelling* species (Fig. 2, in blue).

The results of the multivariate ANOVA confirmed the existence of significant morphological differences between species living in different microhabitats ($F_{9,138} = 4.23$, $R^2 = 0.22$, Effect size (Z) = 4.78, $P = 0.001$). Furthermore, pairwise comparisons showed significant differences in 17 of the 45 pairwise microhabitat comparisons. Finally, when contrasting mean trait values between microhabitats, we found significant morphological differences in SVL, HW, FaL, HaL, TF, TFP, TTP and only marginally significant for TyL (see Table S8 for complete results).

Convergence analyses

The results of the *convevol* analyses indicate that all microhabitats showed evidence of statistically significant morphological convergence with the exception of the *stream-dwelling* and *riparian* species (Table 2), likely due to the low number of species in those categories, especially the latter. Species from the same microhabitat have an average morphological

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Table 3 Microhabitats' Wheatsheaf indices for each morphological trait

Traits	Stream-dwelling	Riparian	Arboreal	Bromelicolous	Semiarboreal	Terrestrial	Leaf-litter	Petricolous	Cave-dwelling
Snout-vent length	4.012	1.031	**1.319**	**1.920**	**1.729**	**0.976**	0.840	0.974	1.561
Head width	1.397	0.955	**1.233**	1.137	1.219	0.635	0.812	1.039•	1.127
Tympanum length	0.998	1.075	1.080	**1.867**	0.973	**0.929**	0.796	**1.301**	1.705
Forearm length	6.762•	0.977	0.945	1.031	1.364•	0.752	0.535	**1.268**	**3.255**
Hand length	1.123	0.491	0.826	0.910	1.172	**1.015**	0.619	0.943	1.760
Total limb length	1.762	1.160	1.085	**1.337**	**1.548**	0.569	0.590	**1.240**	2.034
Total finger length	**21.364**	1.170	1.095	1.139	1.408•	0.663	0.572	**1.337**	1.638
Total finger pad	2.724	**2.159**	**1.238**	**1.993**	1.158	**1.012**	**1.021**	**1.374**	1.008
Total toe length	3.765	1.176	**1.300**	**1.497**	**1.739**	0.673	0.591	**1.235**	1.730
Total toe pad	3.923	1.097	0.965	**1.616**	1.177	**0.977**	**1.040**	**1.323**	1.014

Statistically significant values ($P < 0.05$) are shown in bold and the results marked with a dot (•) have a P-value < 0.1

distance that is 27 to 48% smaller than that estimated for their putative ancestors, as a result of convergence. Convergence was highest in semiarboreal ($C_1 = 47.5\%$) and lowest among riparian species ($C_1 = 26.8\%$). Results were qualitatively similar when condensing microhabitats to five categories (see Table S9).

The results from the *Wheatsheaf index* analysis indicate that the number of traits with significantly strong convergence differed between microhabitats (Table 3). At one extreme, *petricolous* species showed strong convergence in seven traits (TyL, FaL, TLL, TF, TFP, TT and TTP) while at the other extreme, in *cave-dwelling*, *riparian* and *stream-dwelling* species, only a single trait presented strong convergence (FaL, TFP and TF respectively). Note the very high convergence for TF in *stream-dwelling* species (Table 3).

DISCUSSION

A case of replicate radiations

Several lines of evidence indicate that the extraordinary species richness of Caribbean *Eleutherodactylus* is the result of replicate radiations accompanied by morphological convergence. Across the Caribbean islands, these radiations were accompanied by remarkable ecological divergence, as most include species occupying distinct microhabitats. These ecological diversifications have taken place at least once in each of the Greater Antilles (Cuba, Hispaniola, Jamaica and Puerto Rico) and the Lesser Antilles. Furthermore, species inhabiting the same microhabitats have emerged independently on almost all the islands, with the exception of the *fossorial* species, which are restricted to Hispaniola (Fig. 1). Finally, the independent invasions of the different microhabitats resulted in morphological similarities across distantly related species, as shown by the multivariate ANOVAS (Table S8) and phylomorphospaces (Fig. 2a, Fig. S5). Such morphological similarities are likely due to similar selection pressures acting on particular, putatively adaptive, traits.

The suggestion that morphological similarities are a response to similar selection pressures is further supported by the presence of significant morphological convergence across most microhabitats. Virtually all microhabitats involve significant morphological convergence, with the exception of the species-poor *stream-dwelling* and *riparian* ones. Species having colonised similar microhabitats reduced their morphological distance by 39–48% compared to that between the putative ancestors (Table 2). Furthermore, at least one trait (range 1–7) was found to present strong morphological convergence in all microhabitats (Table 3). Perfect convergence was not expected, firstly because we analysed the same putatively adaptive traits across all microhabitats and, as suggested by our results, it is highly that combinations of traits might be involved in adaptation to different microhabitats. Secondly, species may present different morphologies adapted to the same microhabitat (Ridley 1983; Losos 2011), as observed in labrid fishes (Alfaro *et al*. 2004). With respect to *Eleutherodactylus*, it is worth noting that the geographic distribution of microhabitats is not homogeneous and this might result in intra-island variation in the selection pressures. Cuba is a good example of the uneven distribution of the microhabitats; karstic landscapes (providing cave and rock microhabitats) are abundant in the West and Central regions while mountains and streams are concentrated in the East. Such small scale intra-island processes undoubtedly deserve further study.

Caribbean Eleutherodactylus ecomorphs

Our results also indicate that species occupying different microhabitats may be considered ecomorphs, as suggested by Hedges (1989a,b) based on a qualitative morphological study. The ecomorph concept was introduced by Williams (1972, 1983) for *Anolis* lizards to describe species with similar behaviour and morphologies resulting from convergent adaptation to a given niche. Based on the results of our analyses, we present a description of the morphological characters which define species living in the different microhabitats (Box 1).

We note that, in particular cases, the assignment of species to microhabitats must be taken with caution. All species were classified into one of 10 microhabitats (Table S3), which results in conservative analyses as misclassifications would increase noise and reduce the likelihood of detecting an association between morphological traits and microhabitats. Besides possible misclassifications due to equivocal or ambiguous ecological and behavioural data, this classification does not consider potential species singularities, that is species occupying microhabitats not captured precisely by our 10 categories (as is often the case in *Anolis*, Losos 2009), as such the grass-specialist frogs of the *E. varleyi* (Dunn, 1925) complex, the marsh-dwelling *E.*

juanariveroi (Rios-López and Thomas, 2007), the mangrove-specialist *E. caribe* (Hedges and Thomas, 1992), the moss-related *E. unicolor* (Stejneger, 1904) or the terrestrial bromeliad-dweller *E. schwartzi* (Thomas, 1966). Apart from classification-related problems, some species present morphological characteristics that are unique compared to other species in the same microhabitat, for example the giant terrestrial *E. inoptatus* (Barbour, 1914), the large leaf-litter *E. dimidiatus* (Cope, 1862) or the cave-dweller *E. cooki* (Grant, 1932) with large finger and toe pads. Future studies on the ecology and habitat use of *Eleutherodactylus* frogs might result in changes in the microhabitat classification of some species, particularly for some lesser-known Hispaniola species.

The role of ecological opportunity

As previously shown in other adaptive radiations (Losos 2010; Stroud & Losos 2016), our results also suggest that ecological opportunity likely played a key role in the Caribbean *Eleutherodactylus* radiation, by far the most diverse genus of anurans in the Caribbean archipelago. Only six genera of anurans besides *Eleutherodactylus* inhabit the Caribbean, and none comes even close to the species richness or ecological diversity found in *Eleutherodactylus*. For example, *Peltophryne* is represented by only 12 species, *Osteopilus* by eight species, while the rest of the genera include three or fewer species (Frost 2018). The available information suggests that *Peltophryne* possibly colonised Cuba and Hispaniola *c.* 19.7–33.1 Mya (Alonso *et al.* 2012), while *Osteopilus* colonised these islands 21.7–31.9 Mya (Duellman *et al.* 2016). Previous estimates of divergence times pointed to earlier colonisation of the Caribbean by *Eleutherodactylus* (29–47 Mya, Heinicke *et al.* 2007) and the difference with our results (22.1–24.7) is probably due to our increased taxon sampling, including the key sister lineage *Diasporus*. Taken together, these estimated dates place the colonisation of the Caribbean islands by *Osteopilus*, *Peltophryne* and *Eleutherodactylus* in a similar time frame (18–33 Mya), and it is hence possible that *Eleutherodactylus* were not the first anurans to colonise the Caribbean. Nonetheless, they seem to have been particularly successful in their ability to colonise very diverse habitats, which was previously suggested to be associated with high diversity in Terraranans, of which *Eleutherodactylus* is part (Gonzalez-Voyer *et al.* 2011). It is also possible that direct development facilitated the invasion of such a striking diversity of microhabitats by *Eleutherodactylus*, as this reduces their dependence on water for reproduction, potentially allowing for greater dispersion over land and to exploit a greater diversity of habitats (Hedges *et al.* 2008). In sum, *Eleutherodactylus*' ecological opportunity may have come from the colonisation of an almost empty archipelago in conjunction with the potential key innovation of direct development.

Eleutherodactylus and Anolis: similar evolutionary histories

Overall, our results highlight the extraordinary similarity in the evolutionary history of *Eleutherodactylus* and that of its lizard counterpart, *Anolis* (Losos 2009; Mahler *et al.* 2010; Alföldi *et al.* 2011). Both diversifications seem to be the outcome of replicate radiations, which have produced several recognisable ecomorphs. Furthermore, both patterns of colonisation show several similarities. Caribbean *Eleutherodactylus* seem to have originated from a single colonisation of the Antilles, in contrast with the two colonisations inferred for Caribbean *Anolis*, but while one of them was into the southern Lesser Antilles, it is exclusively the second that produced the diverse adaptive radiations throughout the rest of the Caribbean. In both cases the two larger islands of the Caribbean, Hispaniola and Cuba, appear to have played a key role in the diversification, as primary locations of the radiation, and as sources for the colonisation of other Caribbean islands. There were some cross-colonisations between Cuba and Hispaniola, and also a back-colonisation of the mainland where both lineages have also diversified (exemplified by the species-rich *Norops* clade in the case of *Anolis* and most of *Eleutherodactylus* species belonging to subgenus *Syrrhophus*). In both *Anolis* and *Eleutherodactylus*, Jamaica is the only one of the larger islands which was colonised only once, and its diversity is the result of an *in-situ* diversification following a colonisation event from Cuba. It is not surprising that Jamaica is the only large island to have been colonised only once, as paleogeographic evidence suggests it had no connection to the other islands or to the continent, at least during the time the *Eleutherodactylus* radiation took place, also its relatively recent emergence likely made repeated invasions unlikely (Iturralde-Vinent & McPhee 1999; Iturralde-Vinent 2006). Other similarities are a colonisation of the Lesser Antilles, at least two colonisations of Puerto Rico from Hispaniola, and dispersal to Bahamas from Cuba.

Given the similarities between the *Anolis* and *Eleutherodactylus* radiations in the Caribbean islands, the differences in the estimated timing of the diversifications are striking. Caribbean anole divergence has been recently estimated to have taken place *c.* 38 Mya (Román-Palacios *et al.* 2018), while our results suggest a more recent diversification time for Caribbean *Eleutherodactylus* frogs, similar to that suggested by Losos (2009) for Anoles in view of geological information. This would confer special significance to the morphological convergence of *Eleutherodactylus* since anurans are comparatively less labile in body shape conserving their overall body plan since the early Jurassic (Shubin & Jenkins 1995).

The observation of astonishingly similar evolutionary patterns in two highly different lineages within the same biogeographical stage, leads one to wonder what sets the Caribbean islands apart from other insular systems where no such striking examples of parallel radiations have been reported. The two parallel evolutionary histories also emphasise the idea that evolution can be relatively predictable, even at long timescales (contra Gould 1989). In sum, our results recall Futuyma's elegant statement, but suggest that parallel radiations may not be so exceptional in the right geographic scenario, although undoubtedly they are 'great works of art', and possibly the strongest evidence of Darwinian theory.

FUNDING

This work was supported by the projects CGL2013-47547-P and CGL2016-75227-P from the Spanish Ministry of Economy and Competitiveness and by a PAPIIT-UNAM research grant (IA201716). A.D.-C. was funded by a FPI doctoral fellowship (BES-2011-050123) and three short research stay grants (EEBB-I-13-06648, EEBB-I-14-08498 and EEBB-I-15-09410) from the Spanish Government.

ACKNOWLEDGEMENTS

The members of the Conservation and Evolutionary Genetics group (consevol.org) at the Doñana Biological Station (EBD-CSIC) commented early drafts of the manuscript. Luis Valente and two anonymous referees also provided valuable comments on an earlier version. Sincere thanks to the museums, and their curators and staff for the loan of specimens, and/or the permissions to examine them. Most sincere thanks to José Manuel Padial for his invaluable assistance with access to specimens, numerous discussions at diverse stages of the project and for sharing sequence alignments. This work would not have been possible without the vast and irreplaceable information available in natural history museum collections.

AUTHORSHIP

AGV and CV designed the study, ADC collected the data, AR and ADC classified the species into microhabitats, ADC and AGV analysed the data, ADC wrote the first draft of the manuscript, and all the authors contributed substantially to the interpretation of results and manuscript revisions.

DATA ACCESSIBILITY STATEMENT

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.98414hk.

REFERENCES

Adams, D.C. & Collyer, M.L. (2018a). Multivariate phylogenetic comparative methods: evaluations, comparisons and recommendations. *Syst. Biol.*, 67, 14–31.

Adams, D.C. & Collyer, M.L. (2018b). Phylogenetic ANOVA: group-clade aggregation, biological challenges, and a refined permutation procedure. *Evolution*, 72, 1204–1215.

Alfaro, M.E., Bolnick, D.I. & Wainwright, P.C. (2004). Evolutionary dynamics of complex biomechanical systems: an example using the four-bar mechanism. *Evolution*, 58, 495–503.

Alföldi, J., Di Palma, F., Grabherr, M., Williams, C., Kong, L., Mauceli, E. *et al.* (2011). The genome of the green anole lizard and a comparative analysis with birds and mammals. *Nature*, 477, 587–591.

Alonso, R., Crawford, A.J. & Bermingham, E. (2012). Molecular phylogeny of an endemic radiation of Cuban toads (Bufonidae: Peltophryne) based on mitochondrial and nuclear genes. *J. Biogeogr.*, 39, 434–451.

Arbuckle, K. & Minte, A. (2015). windex: analyzing convergent evolution using the wheatsheaf index in R. *Evol. Bioinforma.*, 11, 11–14.

Arbuckle, K., Bennett, C.M. & Speed, M.P. (2014). A simple measure of the strength of convergent evolution. *Methods Ecol. Evol.*, 5, 685–693.

Collyer, M.L. & Adams, D.C. (2018). RRPP: an R package for fitting linear models to high-dimensional data using residual randomization. *Methods Ecol. Evol.*, 9, 1772–1779.

Coyne, J.A. & Orr, H.A. (2004). *Speciation.* Sinauer Associates, Sunderland: MA.

Díaz, L.M. & Cádiz, A. (2008). *Guía taxonómica de los anfibios de Cuba.* ABC Taxa, ABC Taxa.

Drummond, A.J., Suchard, M.A., Xie, D. & Rambaut, A. (2012). Bayesian phylogenetics with BEAUti and the BEAST 1.7. *Mol. Biol. Evol.*, 29, 1969–1973.

Duellman, W.E., Marion, A.B. & Hedges, S.B. (2016). Phylogenetics, classification, and biogeography of the treefrogs (Amphibia: Anura: Arboranae). *Zootaxa*, 4104, 001–109.

Emerson, S.B. (1976). Burrowing in Frogs. *J. Morphol.*, 149, 437–458.

Emerson, S.B. (1978). Allometry and Jumping in Frogs: helping the Twain to Meet. *Evolution*, 32, 551–564.

Emerson, S.B. (1985). Skull shape in frogs-correlations with diet. *Herpetologica*, 41, 177–188.

Emerson, S.B. (1991). The ecomorphology of Bornean tree frogs (family Rhacophoridae). *Zool. J. Linn. Soc.*, 101, 337–357.

Emerson, S.B. & Diehl, D. (1980). Toe pad morphology and mechanisms of sticking in frogs. *Biol. J. Linn. Soc.*, 13, 199–216.

Frost, D.R. (2018). Amphibian Species of the World: an online reference. *Version 6. Am. Museum Nat. Hist. New York, USA*. Available at: http://research.amnh.org/herpetology/amphibia/index.html. Last accessed 20 November 2018.

Futuyma, D.J. (2003). Accounting for biological diversity. *Evolution*, 57, 1216–1220.

Gavrilets, S. & Losos, J.B. (2009). Adaptive radiation: contrasting theory with data. *Science*, 323, 732–737.

Glor, R.E. (2010). Phylogenetic insights on adaptive radiation. *Annu. Rev. Ecol. Evol. Syst.*, 41, 251–270.

Gonzalez-Voyer, A., Padial, J.M., Castroviejo-Fisher, S., De la Riva, I. & Vilà, C. (2011). Correlates of species richness in the largest Neotropical amphibian radiation. *J. Evol. Biol.*, 24, 931–942.

Gould, S.J. (1989). *Wonderful Life: The Burgess Shale and the Nature of History*. W.W. Norton and Company, New York.

Hass, C.A. & Hedges, S.B. (1991). Albumin Evolution in West-Indian Frogs of the Genus Eleutherodactylus (Leptodactylidae): caribbean biogeography and a calibration of the albumin immunological clock. *J. Zool.*, 225, 413–426.

Hedges, S.B. (1989a). An island radiation: allozyme evolution in Jamaican frogs of the genus Eleutherodactylus (Leptodactylidae). *Caribb. J. Sci.*, 25, 123–147.

Hedges, S.B. (1989b). Evolution and Biogeography of West Indian Frogs of the Genus Eleutherodactylus: Slow-Evolving Loci and the Major Groups. In *Biogeography of the West Indies: Past, Present and Future* (ed Woods, C.). Sandhill Crane Press, Gainesville, Florida, pp. 305–370.

Hedges, S.B., Duellman, W.E. & Heinicke, M.P. (2008). New World direct-developing frogs (Anura: Terrarana): molecular phylogeny, classification, biogeography, and conservation. *Zootaxa*, 1737, 1–182.

Heinicke, M.P., Duellman, W.E. & Hedges, S.B. (2007). Major Caribbean and Central American frog faunas originated by ancient oceanic dispersal. *Proc. Natl Acad. Sci. USA*, 104, 10092–10097.

Iturralde-Vinent, M.A. (2006). Meso-cenozoic caribbean paleogeography: implications for the historical biogeography of the region. *Int. Geol. Rev.*, 48, 791–827.

Iturralde-Vinent, M.A. & MacPhee, R.D.E. (1999). Paleogeography of the caribbean region: implications for cenozoic biogeography. *Bull. Am. Museum Nat. Hist.*, 238, 1–95.

Kaiser, H. (2002). Evolution among Lesser Antillean frogs of the genus Eleutherodactylus: ecological adaptation precedes morphological change. *Herpetozoa*, 14, 153–162.

Katoh, K. & Standley, D.M. (2013). MAFFT multiple sequence alignment software version 7: improvements in performance and usability. *Mol. Biol. Evol.*, 30, 772–780.

Khabbazian, M., Kriebel, R., Rohe, K. & Ané, C. (2016). Fast and accurate detection of evolutionary shifts in Ornstein-Uhlenbeck models. *Methods Ecol. Evol.*, 7, 811–824.

Lanfear, R., Calcott, B., Ho, S.Y.W.S.Y.W. & Guindon, S. (2012). PartitionFinder: combined selection of partitioning schemes and substitution models for phylogenetic analyses. *Mol. Biol. Evol.*, 29, 1–22.

Losos, J.B. (2009). *Lizards in an Evolutionary Tree: Ecology and Adaptive Radiation of Anoles*. University of California Press, Berkeley, USA.

Losos, J.B. (2010). Adaptive radiation, ecological opportunity, and evolutionary determinism. *Am. Nat.*, 175, 623–639.

Losos, J.B. (2011). Convergence, adaptation, and constraint. *Evolution*, 65, 1827–1840.

Lutz, G.J. & Rome, L.C. (1994). Built for jumping: the design of the frog muscular system. *Science*, 263, 370–372.

Maddison, W.P. & Maddison, D.R. (2015). Mesquite: a modular system for evolutionary analysis.

Mahler, D.L., Revell, L.J., Glor, R.E. & Losos, J.B. (2010). Ecological opportunity and the rate of morphological evolution in the diversification of Greater Antillean anoles. *Evolution*, 64, 2731–2745.

Mahler, D.L., Ingram, T., Revell, L.J. & Losos, J.B. (2013). Exceptional convergence on the macroevolutionary landscape in island lizard radiations. *Science*, 341, 292–295.

Manzano, A.S., Abdala, V. & Herrel, A. (2008). Morphology and function of the forelimb in arboreal frogs: specializations for grasping ability? *J. Anat.*, 213, 296–307.

Matzke, N.J. (2013). BioGeoBEARS: BioGeography with Bayesian (and Likelihood) Evolutionary Analysis in R Scripts.

Matzke, N.J. (2014). Model selection in historical biogeography reveals that founder-event speciation is a crucial process in island clades. *Syst. Biol.*, 63, 951–970.

Nauwelaerts, S., Stamhuis, E.J. & Aerts, P. (2005). Propulsive force calculations in swimming frogs I. A momentum–impulse approach. *J. Exp. Biol.*, 208, 1435–1443.

Padial, J.M., Grant, T. & Frost, D.R. (2014). Molecular systematics of terraranas (Anura: Brachycephaloidea) with an assessment of the effects of alignment and optimality criteria. *Zootaxa*, 3825, 1–132.

Pagel, M. (1999). Inferring the historical patterns of biological evolution. *Nature*, 401, 877–884.

Pinto, G., Mahler, D.L., Harmon, L.J. & Losos, J.B. (2008). Testing the island effect in adaptive radiation: rates and patterns of morphological diversification in Caribbean and mainland Anolis lizards. *Proc. R. Soc. B Biol. Sci.*, 275, 2749–2757.

R Core Team (2015). *R: A language and Environment for Statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org.

Revell, L.J. (2009). Size-correction and principal components for interspecific comparative studies. *Evolution*, 63, 3258–3268.

Revell, L.J. (2012). phytools: an R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, 3, 217–223.

Ricklefs, R. & Bermingham, E. (2008). The West Indies as a laboratory of biogeography and evolution. *Philos. Trans. R. Soc. B Biol. Sci.*, 363, 2393–2413.

Ridley, M. (1983). *The Explanation of Organic Diversity: The Comparative Method and Adaptations for Mating*. Oxford University Press, Oxford, UK.

Román-Palacios, C., Tavera, J. & Castañeda, M.del.R. (2018). When did anoles diverge? An analysis of multiple dating strategies. *Mol. Phylogenet. Evol.*, 127, 655–668.

Salzburger, W. (2009). The interaction of sexually and naturally selected traits in the adaptive radiations of cichlid fishes. *Mol. Ecol.*, 18, 169–185.

Schluter, D. (2000). *The Ecology of Adaptive Radiation*. Oxford University Press, New York.

Shubin, N.H. & Jenkins, F.A.J. (1995). An Early Jurassic jumping frog. *Nature*, 377, 49–52.

Snorrason, S.S. & Skúlason, S. (2004). Adaptive speciation in northern freshwater fishes. In: *Adaptive Speciation* (eds Dieckman, U., Doebeli, M., Metz, J.A.J. & Tautz, D.). Cambridge University Press, Cambridge, pp. 210–228.

Stayton, C.T. (2015). The definition, recognition, and interpretation of convergent evolution, and two new measures for quantifying and assessing the significance of convergence. *Evolution*, 69, 2140–2153.

Stroud, J.T. & Losos, J.B. (2016). Ecological opportunity and adaptive radiation. *Annu. Rev. Ecol. Evol. Syst.*, 47, 507–532.

Talavera, G. & Castresana, J. (2007). Improvement of phylogenies after removing divergent and ambiguously aligned blocks from protein sequence alignments. *Syst. Biol.*, 56, 564–577.

Uyeda, J.C., Caetano, D.S. & Pennell, M.W. (2015). Comparative analysis of principal components can be misleading. *Syst. Biol.*, 64, 677–689.

Venables, W.N. & Ripley, B.D. (2002). Modern Applied Statistics with S. *Fourth*. Springer, New York.

Williams, E.E. (1972). The origin of faunas. evolution of lizard congeners in a complex island fauna: a trial analysis. *Evol. Biol.*, 6, 47–89.

Williams, E.E. (1983). Ecomorphs, Faunas, Island Size, and Diverse End Points in Island Radiations of Anolis. In: *Lizard ecology: study of a model organism* (eds Huey, R.B., Pianka, E.R. & Schoener, T.W.). Harvard University Press, Cambridge, MA., pp. 326–370.

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Additional supporting information may be found online in the Supporting Information section at the end of the article.

Editor, Kristen Ruegg
Manuscript received 12 June 2018
First decision made 25 July 2018
Second decision made 20 December 2018
Manuscript accepted 16 January 2019

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