



Ecological specialization and morphological diversification in Greater Antillean boas

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Colonization of islands can dramatically influence the evolutionary trajectories of organisms, with both deterministic and stochastic processes driving adaptation and diversification. Some island colonists evolve extremely large or small body sizes, presumably in response to unique ecological circumstances present on islands. One example of this phenomenon, the Greater Antillean boas, includes both small (<90 cm) and large (4 m) species occurring on the Greater Antilles and Bahamas, with some islands supporting pairs or trios of body-size divergent species. These boas have been shown to comprise a monophyletic radiation arising from a Miocene dispersal event to the Greater Antilles, though it is not known whether co-occurrence of small and large species is a result of dispersal or in situ evolution. Here, we provide the first comprehensive species phylogeny for this clade combined with morphometric and ecological data to show that small body size evolved repeatedly on separate islands in association with specialization in substrate use. Our results further suggest that microhabitat specialization is linked to increased rates of head shape diversification among specialists. Our findings show that ecological specialization following island colonization promotes morphological diversity through deterministic body size evolution and cranial morphological diversification that is contingent on island- and species-specific factors.

KEY WORDS: Boidae, Caribbean, *Chilabothrus*, ecomorphology, morphometrics, multilocus, phylogenetics.

Islands have played a major role in the origin of organismal diversity. Because they support a novel collection of species and are geographically isolated, islands provide opportunities for the species that colonize them to adapt and diversify in ways that are often unavailable to their mainland relatives. Islands are known to give rise to highly derived forms in some lineages, such as flightless birds, as well as elevated morphological and species

diversity in so-called adaptive radiations, such as the Caribbean anoles (Losos 2009) or Hawaiian honeycreepers (Amadon 1950). The study of island organisms has thus played a key role in understanding mechanisms of evolution (Losos et al. 1998; Losos and Ricklefs 2009), and studies of island biogeography provide critical insight into the processes of adaptation and diversification (MacArthur and Wilson 1967; Losos 2010).

Body size evolution on islands is a particularly well-studied phenomenon. Island colonists of several mammalian and squamate lineages, among others, have evolved extreme body sizes—the familiar “Island Rule,” which states that relatively large species will evolve smaller body size, and that relatively small species will evolve larger body size, after colonizing an island habitat (Foster 1964). Island gigantism or dwarfism is thought to be a product of both general and idiosyncratic selective forces acting on individual island populations (Diamond 1973; Lomolino 2005; Raia et al. 2010). For instance, predatory animals must strike a balance between changes in body size related to prey availability and the ability to navigate habitat to find and capture their prey (Case 1978). At the same time, ecological specialization is expected when island colonization results in an expansion into novel ecological contexts (Schluter 2000; Losos and Ricklefs 2009), and such specialization might carry concomitant changes in body size or other phenotypic attributes (Losos 2009; Mahler et al. 2010).

Snakes have figured prominently in investigations into the role of islands in generating biodiversity. Snakes exploit diverse island habitats and prey resources (Rodríguez-Robles and Greene 1996; Boback 2006; Boback and Carpenter 2007) and exhibit a wide variety of morphological and behavioral adaptations to them, even resulting in substantial differentiation among closely related species (Vitt and Vangilder 1983; Guyer and Donnelly 1990; Cadle and Greene 1993; Lillywhite and Henderson 1993; França et al. 2008). Head shape and body size in snakes are thought to contribute to a greater degree of trophic specialization than is typical of other reptilian groups (Savitzky 1983; Voris and Voris 1983; Henderson et al. 1988; Martins et al. 2002; Vincent et al. 2004; Hampton 2011), and both aspects of morphology can evolve rapidly on islands in response to divergent substrate preference and prey size (Arnold 1993; Madsen and Shine 1993; Rodríguez-Robles and Greene 1996; Forsman and Shine 1997; Vincent et al. 2004; Keogh et al. 2005; Boback 2006; Natusch and Lyons 2012; Aubret 2015), though some plasticity in these characteristics is also likely (Queral-Regil and King 1998; Madsen and Shine 2000; but see Schuett et al. 2005).

Some boid snakes are known to conform to the Island Rule. The large-bodied *Boa constrictor* has repeatedly evolved dwarfism on continental islands (Boback 2006; Card et al. 2016), a pattern that, at least in some snakes, is thought to be related to adaptation toward a dietary optimum (Shine 1991; Boback and Guyer 2003; Keogh et al. 2005). However, the closely related West Indian species (*B. orophias* and *B. nebulosa*), found on the larger Lesser Antillean islands of St. Lucia and Dominica, respectively, do not show a pattern of dwarfism relative to their continental congener (Schwartz and Henderson 1991), suggesting that different island populations might experience idiosyncratic selective

pressures or reflect an inverse relationship between island area and rates of body size change (Filin and Ziv 2004; Millien 2011).

West Indian boid snakes in the genus *Chilabothrus* are an exclusively insular squamate radiation exhibiting significant ecological and morphological variation. The 11 species of this nocturnal clade occupy habitats ranging from xeric scrub to montane rainforest and have maximum adult body sizes spanning a range from <1 m to nearly 4 m (Tolson and Henderson 1993; Fig. 1). Two main morphotypes have been recognized in this genus based on ecological, morphometric, and meristic analyses (Sheplan and Schwartz 1974; Tolson 1987; Kluge 1989): large-bodied generalists (five species) and small-bodied specialists (six species; Table 1). Adults of large-bodied species are ecological generalists in that they use both terrestrial and arboreal substrates and prefer a wide variety of prey (euryphagous), such as birds, mammals, and large ectotherms (Henderson et al. 1987; Tolson and Henderson 1993; Henderson and Powell 2009, and references therein). Small-bodied species are either terrestrial or arboreal (never both) and are nearly exclusively saurophagous, feeding largely on *Anolis* lizards (Table 1). Both large and small species are distributed across the West Indies, though no single island has more than one large species, and small species always co-occur with large species (with the exception of the Bahamas banks; Table 1).

Despite having been repeatedly cited as an example of island-induced diversification, the evolutionary processes that gave rise to the distribution of body sizes among Greater Antillean boas are still a matter of debate. Whereas some morphological data suggest that small size evolved once and small-bodied species dispersed among islands (Sheplan and Schwartz 1974; Kluge 1988), molecular phylogenetics suggests instead a scenario in which small-body size evolved repeatedly on separate islands (reviewed in Reynolds et al. 2013). Here, we provide the first phylogenetic analysis of a comprehensive multilocus molecular dataset for the clade, and we use the resulting species tree as the basis for testing alternative scenarios of body size evolution in West Indian boas, *Chilabothrus*. Finding evidence of repeated evolution of small body size, we then test the association between size evolution and ecological specialization. In addition, because of the oft-observed strong relationship between ecological and morphological divergence among snakes, we also ask whether specialization influences diversification of cranial morphology independent of its effect on body size.

Methods

FIELD COLLECTION

We sampled boas in the Dominican Republic, Puerto Rico, Bahamas, and Turks and Caicos Islands by nocturnal surveys using headlamps or by opportunistically sampling road kill specimens. We conducted 1–10 separate research trips to each of these

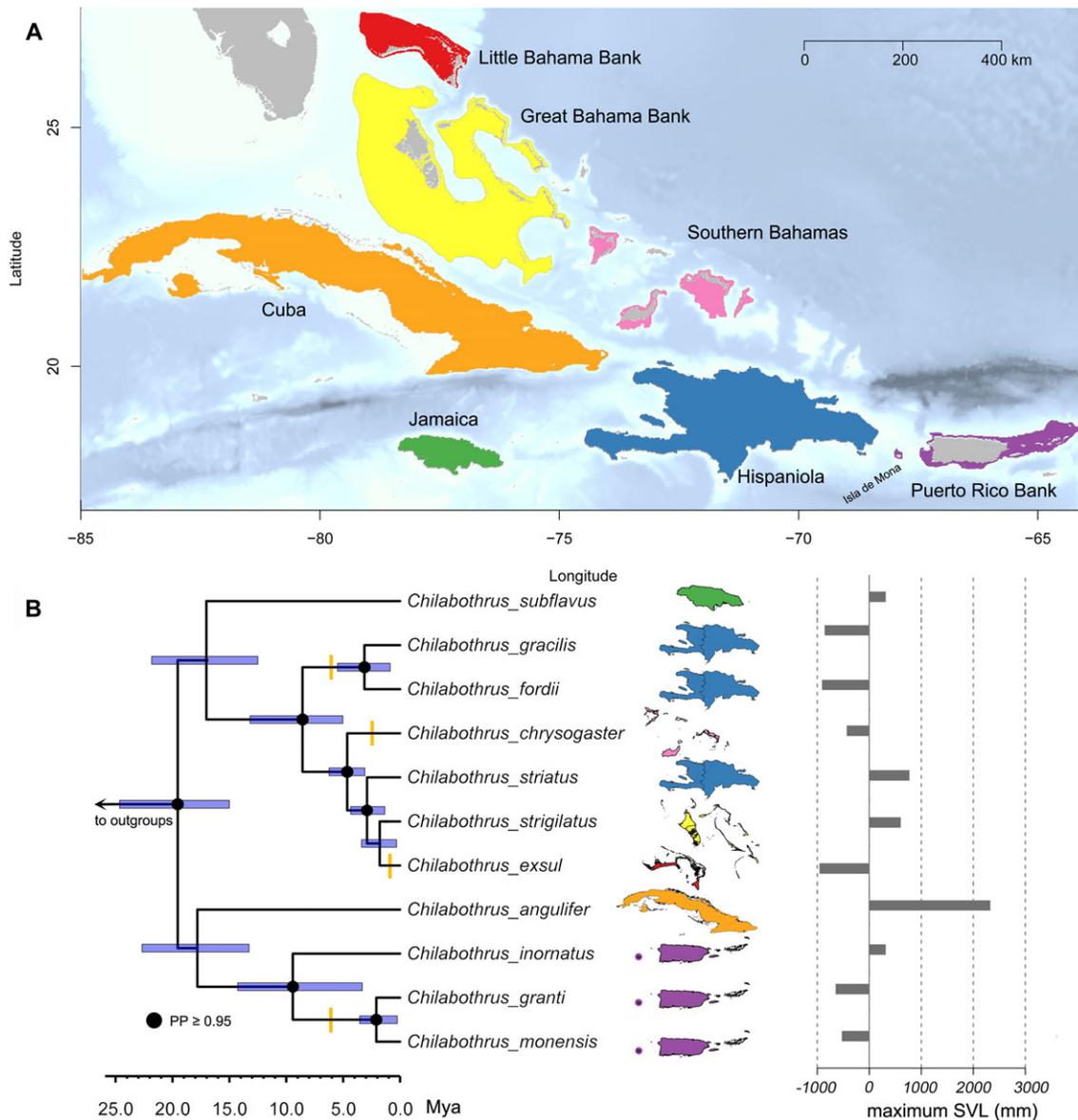


Figure 1. (A) Distribution of boas (genus *Chilabothrus*) in the West Indies. The larger islands are shown using solid colors, while smaller islands are colored by bank with emergent areas given in gray. The shallowest isobath (~250 m bsl) is colored in light blue, while progressively deeper isobaths are colored from light blues to darker slate-grays. (B) Maximum clade credibility tree from the fossil calibrated *BEAST analysis, with tips labeled with biogeographic distribution and body size (centered maximum SVL, in mm). Nodal bars represent 95% highest posterior density (HPD) intervals. Posterior probabilities for nodes ≥ 0.95 are labeled with black dots. Vertical orange hash-marks indicate inferred body-size transitions. See Figures S1 and S2 for complete species tree and posterior trees, respectively. [Color Fig.].

regions between 2007 and 2014. We hand-captured live boas and kept them overnight in a cloth bag for daytime processing, releasing each one at its point of capture the following evening. We took measurements of each boa (see below), as well as tissue samples for genetic analysis, obtaining between two and 225 samples per species (Table S1). Samples consisted of 3–10 mm tail clips preserved in 95% ethanol. We sanitized tails before and after clipping and applied antiseptic dermal adhesive to prevent infection. Any boa found with a clipped or damaged tail tip was not

sampled to prevent repeated sampling. We extracted whole genomic DNA using the Promega Wizard SV DNA purification system according to the manufacturer's protocol and stored the extracts at -20°C .

PHYLOGENETIC ANALYSIS

Two samples are generally minimally sufficient for multilocus coalescent analysis (Heled and Drummond 2010), and most species in the *Chilabothrus* clade have been previously delimited and

Table 1. Maximum SVL, neonate SVL (at parturition), and diet of large and small-bodied West Indian *Chilabothrus* from published accounts.

Island	Species	Body type	Substrate preference	Maximum SVL (mm)	Neonate SVL	Adult diet	Juvenile diet
Greater Antilles							
Cuba	<i>angulifer</i>	Large	Generalist	4000	540 ^a –618 ^b	Bats, birds, mammals, snakes, eggs, turtles, lizards	Mammals
Jamaica	<i>subflavus</i>	Large	Generalist	2050	360–530	Bats, birds, mammals, lizards (<i>Anolis</i> , <i>Cyclura</i>)	<i>Anolis</i> , frogs
Hispaniola	<i>striatus</i>	Large	Generalist	2489 ^c (1905 ^d)	370–508	Birds, rodents, <i>Solenodon</i> , <i>Cyclura</i>	<i>Anolis</i>
	<i>fordii</i>	Small	Terrestrial	860	250	<i>Anolis</i> , <i>Mus</i> , <i>Rattus</i>	<i>Anolis</i>
Puerto Rico	<i>gracilis</i>	Small	Arboreal	905	300	<i>Anolis</i>	<i>Anolis</i>
	<i>granti</i>	Small	Arboreal	1112	206–280	<i>Anolis</i> , occasional <i>Ameiva</i> and small birds	<i>Anolis</i>
(incl. Isla de Mona)	<i>inornatus</i>	Large	Generalist	2050	332–367	<i>Rattus</i> , bats, crabs, birds	<i>Anolis</i> , <i>Eleutherodactylus</i>
	<i>monensis</i>	Small	Arboreal	1230	206–280	<i>Anolis</i> , some <i>Rattus</i>	<i>Anolis</i>
Bahamas							
Great Bahamas Bank	<i>strigilatus</i>	Large	Generalist	2330	318 ^e –500	Lizards (<i>Cyclura</i>), birds, mammals, frogs (<i>Osteopilus</i>)	<i>Anolis</i>
Little Bahamas Bank	<i>exsul</i>	Small	Terrestrial	810	231–280	Lizards, birds, rodents	<i>Anolis</i>
Southern Bahamas banks	<i>chrysogaster</i>	Small	Terrestrial	1321 ^f	290 ^g	Lizards (<i>Cyclura</i> , <i>Spondylurus</i> , <i>Leiocephalus</i>), birds, eggs, rodents (<i>Mus</i> , <i>Rattus</i>)	<i>Anolis</i>

^aP. Tolson (unpubl. data).

^bAmerican Museum of Natural History R-64689.

^cOttenwalder (1985). This size record is not reported in any subsequent literature on this species; however, we have examined this document and found the record to be compelling. Nevertheless, we also report a confirmed size record for this species based on our own work.

^dRGR and SAP 2014 (unpubl. data). This is a larger size record than that reported in most recent literature on the species.

^eMuseum of Comparative Zoology R-7091.

^fReynolds et al. (2011).

^gReynolds and Deal (2010).

Note that maximum SVL is for wild individuals and does not include size records from captivity. Data are drawn largely from Sheplan and Schwartz (1974), Henderson et al. (1987), Schwartz and Henderson (1991), Tolson and Henderson (1993), Henderson and Powell (2009), and references therein. Data from other sources are indicated with superscripts.

are considered well-defined (Reynolds et al. 2013). Therefore, we used a subset of two individuals from each species from the 10-gene alignment in Reynolds et al. (2013) combined with newly generated sequence data for additional taxa to cover all 11 species of *Chilabothrus* (Table S1). We also included outgroup taxa in the alignments (Fig. S1) as in Reynolds et al. (2013). We used the polymerase chain reaction (PCR) to amplify each of these 10 genes (two mtDNA loci and eight nuclear loci) using primers and conditions in Reynolds et al. (2013). We purified and sequenced products in both directions on an automated sequencer (ABI 3730XL) at Massachusetts General Hospital DNA Core Facility, Cambridge, Massachusetts, USA. We assembled contigs and manually verified ambiguous base calls using GENEIOUS 7.1.2 (Biomatters, Auckland, New Zealand). We resolved heterozygous sequences for nuclear loci using PHASE 2.1 (Stephens et al. 2001; Stephens and Donnelly 2003) implemented in DnaSP v5.10.1 (Librado and Rozas 2009) using default parameters for 100 iterations with a burnin of 100. We then aligned sequences using the CLUSTALW 2.1 (Larkin et al. 2007) algorithm implemented in GENEIOUS using reference sequences and default parameters. We deposited all alignments in Dryad (doi:10.5061/dryad.94768).

To simultaneously estimate the species-tree topology as well as divergence times, we analyzed the dataset using the MCMC method *BEAST (Heled and Drummond 2010) implemented in BEAST v1.8. This method jointly estimates species tree topology, divergence times, and genetic effective population sizes from multiple embedded gene trees under the multispecies coalescent model, which assumes that incongruence among gene trees owes entirely to incomplete lineage sorting (rather than horizontal gene transfer or other factors). We partitioned sequence data by locus and assigned a locus-specific model of nucleotide substitution chosen using BIC in jMODELTEST2 (Guindon and Gascuel 2003; Durraba et al. 2012; Table S2). We unlinked nucleotide substitution models, clock models, and gene trees in all analyses. We employed an uncorrelated lognormal (UCLN) relaxed molecular clock model of rate variation for each locus, and we used a Yule process speciation prior for the branching rates. We assigned calibrations to the nodes as in Reynolds et al. (2013), relying on fossil material (*Titanoboa*†) representing the ancestor of extant Boidae (sensu Pyron et al. 2014) and an extinct *Eunectes* species (*E. stirtoni*), as well as hard and soft minima for the split of Booidae (sensu Pyron et al. 2014), while excluding a *Coralus* calibration (see Reynolds et al. 2013). We ran the MCMC for 400 million generations and repeated the analyses three times with different starting numbers, sampling every 10,000 generations and discarding the first 20% of generations as burn-in. We assured adequate mixing of the chains by calculating the effective sample size (ESS) values for each model parameter, with ESS values greater than 200 indicating adequate sampling of the posterior

distribution (Drummond et al. 2006). We assessed convergence of the independent runs by identifying the number of MCMC generations required for model parameter estimates to reach a stationary distribution by a comparison of likelihood scores and traceplot visualization in TRACER v1.5 (Rambaut et al. 2013). We combined the results from the three analyses using LOGCOMBINER v1.8 and generated a maximum clade credibility (MCC) tree using TREEANNOTATOR v 1.8. We reconstructed the MCC tree in FigTree v1.4, and visualized the sample of trees from the posterior distribution relative to the MCC tree using DensiTree v2.0 (Bouckaert 2010).

MORPHOMETRIC DATA

In addition to generating morphological measurements from the live-captured animals obtained during this study, we also examined and measured all sufficiently intact individuals in the collections of the Harvard Museum of Comparative Zoology (Cambridge, Massachusetts, USA) and the American Museum of Natural History (New York, New York, USA), with supplemental loans of less represented species from the University of Texas Arlington, The National Museum of Natural History, and the University of Kansas Biodiversity Institute (Table S1).

Trophic specialization in snakes is likely to occur as a function of both head shape and body size (Savitzky 1983; Voris and Voris 1983; Henderson et al. 1988; Martins et al. 2002; Vincent et al. 2004; Hampton 2011). Therefore we obtained the following standard measurements from *Chilabothrus* specimens: head width (HW; widest head width); head length (HL; anterior of the rostral scale to the posterior of the mandible); labial length (LL; posterior most labial scale to the anterior tip of the rostral scale); interocular length (IO; narrowest distance between orbits); ocular length (OL; horizontal diameter of ocular scale); nares-ocular length (NO; anterior edge of ocular to posterior edge of nares); rostral-ocular length (RO; anterior edge of ocular to anterior edge of rostral scale); and internares length (IN; narrowest internarial distance). We used digital calipers (Mitutoyo) for all measurements, rounding to the nearest 0.1 mm. We did not record additional body size measurements for preserved specimens, such as snout-vent length, as many museum specimens are damaged and larger specimens frequently consist of just the individual's head and tail. We checked all log-transformed data for normality and outliers by examining residual plots from a multiple regression on head length (HL). We conducted these and all subsequent analyses in the scientific computing software R 3.1.0 (R Core Team 2015).

PHYLOGENETIC COMPARATIVE METHODS

Tests for phylogenetic signal in body size

We obtained maximum SVLs from the literature and our own data (Table 1). We note that characterizing species using

maximum SVL for organisms with indeterminate growth is potentially misleading if sexual dimorphism or limited sampling for a particular species is present in the dataset. Nonetheless, log transformation relativizes the absolute magnitude of among species differences, and, in our dataset, among-species differences in size are (generally speaking) much greater in magnitude than the minor revisions to a species' maximum SVL based on increased sampling. Consequently, we believe that maximum SVL best captures the substantial differences in body size among species. Henceforward, we refer to log-transformed maximum SVL simply as body size.

To assess the strength of evidence that small-bodied island species tend to be closely related to other small-bodied species, and large-bodied species closely related to other large-bodied species (as would be expected if small Greater Antillean boas are descended from a single common ancestor that was small), we measured phylogenetic signal in species maximum body size using Pagel's (1997, 1999) λ , which we estimated using the function *phylosig* of the R package *phytools* (Revell 2012). The logic of this test is that if small body size has evolved only once in the diversification of *Chilabothrus*, small-bodied species will be closely related and phylogenetic signal in body size will be high (i.e., λ approaching 1). Conversely, if small body size has evolved repeatedly in different parts of the phylogeny, then we would find that closely related species will exhibit greater than expected divergence in body size, and thus measured phylogenetic signal will be low (i.e., λ approaching 0). We also used a parsimony analysis to calculate the minimum number of transitions between large and small body size, or vice versa, across the tree. To do this, we first discretized body size as either large (five species) or small (six species) along a natural break point between species that are generally shorter than 1.5 m SVL, and those that are longer than 1.5 m SVL (Fig. 1; Table 1). We computed the minimum number of changes in body size using the function *minCharChange* in the *paleotree* package (Schliep 2011; Bapst 2012).

Ecological specialization and body size evolution

In addition to asking if body size is phylogenetically correlated in Greater Antillean boas, we also examined the relationship between body size evolution and transitions in ecology for the group. We first constructed an ecological classification for each species based on diet and substrate use. Specifically, we categorized each species' adult diet as either specialized saurophagous versus generalist euryphagous (Tolson and Henderson 1993). We also categorized each species on the basis of substrate preference (specialist arboreal or terrestrial versus generalist). These diet and substrate preference data were obtained based on an examination of natural history and ecological literature (Table 1). For example, Hispaniolan *C. gracilis* is a diet and substrate specialist (saurophagous and arboreal), while sympatric *C. striatus*

is a generalist in both regards, being euryphagous and readily occupying both terrestrial and arboreal substrates (Tolson and Henderson 1993). For species with ambiguous natural history information, we opted for a conservative approach and coded them as generalists, such as for the third Hispaniolan species *C. fordii*, which is largely saurophagous but is recorded to also consume endothermic prey (*Mus* sp.; Tolson and Henderson 1993).

We tested for correlated evolution between species' body size and diet or habitat specialization using a method in which the discrete character evolves under the threshold model. According to this model, which is based on a quantitative genetic model with the same name (Wright 1934), a discrete character evolves as a function of an underlying continuously varying (but unmeasured) attribute called "liability." Once liability crosses a particular value, the state of the observed discrete character changes in value (Felsenstein 2012; Revell 2014). This model is useful for modeling complex or polygenic traits, such as those related to an organism's ecology (Revell 2014), and can be used to test for correlated evolution between continuous and discrete traits.

Fitting the threshold model on phylogenies using univariate and multivariate data has been implemented in a few different software packages or functions (Felsenstein 2012; Revell 2012, 2014). We elected to use the *phytools* function *ancThresh* to generate separate posterior samples of 1000 species habitat and diet liabilities using Bayesian MCMC. We then took each posterior sample and used the package *phylolm* (Ho and Ané 2014) to fit multivariate regressions using phylogenetic generalized least squares under a λ model, which simultaneously fits the regression model coefficients and phylogenetic signal in the model residuals. We next calculated the partial correlations between body size and habitat and diet specialization liabilities, summarized results across the posterior sample of liabilities as the mean correlation, and tested the null hypothesis that the correlation equals zero using a *t*-test, in which the variance of the correlation is computed by summing the variance among posterior samples and the mean variance in the correlation estimate for each sample. This approach merely assumes that the uncertainty in the correlation due to phylogenetic error, and the uncertainty due to the data given any particular tree, are uncorrelated with each other. (If they are negatively correlated the variance will tend to be overestimated, but conversely if they are positively correlated this approach will tend to underestimate the variance of *r*.) In addition, we report the proportion of significant *P* values across *t*-tests for the posterior sample of liabilities.

Ecological specialization and head shape evolution

We examined evolutionary relationships between boa head shape and ecological specialization (diet and substrate). We first estimated species means and variances for each of the eight head measurements and then summarized species head shape as their

scores on the first three principal components (PCs) of a phylogenetically controlled principal component analysis (pPCA) implemented in the function *phyl.pca* of phytools (Revell 2009, 2012). All morphological variables were size corrected prior to pPCA using a phylogenetic regression of each trait on head length—an empirically validated proxy for overall head size in snakes (King 2002; Boback 2006; Skinner 2009; Vincent et al., 2006a,b, 2009)—using the phytools function *phyl.resid* (Revell 2009, 2012).

We hypothesized that ecological specialization could affect rates of cranial evolution. We therefore tested dependence between rates of head shape evolution and ancestral habitat liability across the boa phylogeny. To carry out this test, we estimated rates of cranial shape evolution and ancestral habitat or diet liability for each node of the boa phylogeny and tested the correlation between rates of morphological evolution and liability states (referred to hereafter as the rate-by-state method). We reconstructed ancestral liabilities using *ancThresh* as described above, estimated rates of head shape evolution as squared standardized contrasts, and evaluated the Pearson correlation between ancestral liability and rate of cranial evolution. We obtained *P* values through comparison to a null distribution generated by a simulated Brownian motion process modeling the independent evolution of the two characters. We repeated this analysis across the posterior sample of ancestral liabilities and summarized results as described in the previous section.

Results

We obtained a well-resolved species tree for the Greater Antillean and Bahamian boa clade, with the majority of nodes (7 of 10) showing high (>0.95) posterior probability (Figs. 1B, S1; Table S3) and the majority of posterior trees supporting the MCC topology (Fig. S2). Importantly, we resolve the placement of the highly specialized *C. gracilis*, finding it to be the sister taxon to the terrestrial *C. fordii*. Both small-bodied species appear to have evolved in situ on Hispaniola, with one species becoming exclusively arboreal and the other terrestrial. Some nodes, such as the placement of *C. angulifer*, continue to be problematic (see Reynolds et al. 2013); however our results are consistent with the most recent phylogenetic hypothesis for the superfamily Booidae (Reynolds et al. 2014).

We generated morphometric data (Table S4) for 439 individuals (range 2–225 per species, median = 26) from adults of all 11 species of *Chilabothrus* in the West Indies (Table S1). The only species for which we had fewer than 11 individuals (Table S1) were *C. exsul* (*n* = 8), *C. subflavus* (*n* = 6), and *C. monensis* (*n* = 2). The former two species are poorly represented in collections and *C. subflavus* is extremely difficult to find in the wild (encounter rate of 0.0038 snakes per person hour in prime habitat; S. Koenig, pers. comm.), while the lattermost species is only found on a

remote island bank, is poorly represented in collections, and is only recently diverged from (and morphologically similar to) *C. granti* (Reynolds et al. 2015; Rodríguez-Robles et al. 2015).

Ecological specialization and morphological evolution

We found effectively no phylogenetic signal in the evolution of body size (log maximum SVL; $\lambda = 0.001$), thus rejecting the hypothesis of conservative evolution (such as a single origin of small body size) in favor of the scenario in which small body size evolved multiple times in different parts of the phylogeny of Greater Antillean boas. Moreover reconstruction using maximum parsimony showed a minimum of four independent transitions between large and small body size or vice versa. Furthermore, transitions to small body size are consistently associated with an increase in habitat specialization. We found a significant negative correlation between body size and substrate specialization liability ($r = -0.68 \pm 0.25$, $t = 2.7$, $P = 0.01$, proportion $P < 0.05 = 0.86$; Fig. 2), in which lower values for liability indicate less specialized species. The correlation between body size and diet liability was moderate but statistically nonsignificant ($r = -0.44 \pm 0.32$, $t = 1.39$, $P = 0.12$, proportion $P < 0.05 = 0.34$; Fig. 2), suggesting that body size is more tightly associated with habitat than diet specialization. However, we note substantial overlap in habitat and diet specialists: the latter is a subset of the former with only two habitat specialists categorized as diet generalists (Table 1).

For the pPCA analyses (Table S5), we found the majority of the variance in PC1 (46.4%), PC2 (32.7%), and PC3 (12.4%). Positive loading on PC1 indicate a relatively longer jaw and snout, negative loading on PC2 indicate a narrower head and blunter snout (Fig. 3), and negative loading on PC3 indicate a narrower head and snout. Controlling for size, small species do not occupy a morphospace unique from that occupied by large bodied species (Fig. 3). Ecological specialists (dietary or substrate) also are not differentiated from generalist species in morphospace (Fig. 3).

In addition to the results above, we found evidence that ecological specialization influences the rate of cranial evolution. Ancestral substrate specialization is associated with elevated evolutionary rates for head PC2 ($r = 0.64 \pm 0.28$, $t = 2.27$, $P = 0.03$, proportion $P < 0.05 = 0.60$; Table 2) and PC3 ($r = -0.66 \pm 0.27$, $t = 2.42$, $P = 0.02$, proportion $P < 0.05 = 0.65$; Table 2). Cranial PC1 has a moderate but nonsignificant correlation with ancestral substrate liability (Table 2). Relationships between head PCs and diet specialization were qualitatively similar but generally lower and nonsignificant (Table 2).

Discussion

The West Indies is one of the world's biodiversity hotspots (Myers et al. 2000; Smith et al. 2005), and studies of West Indian

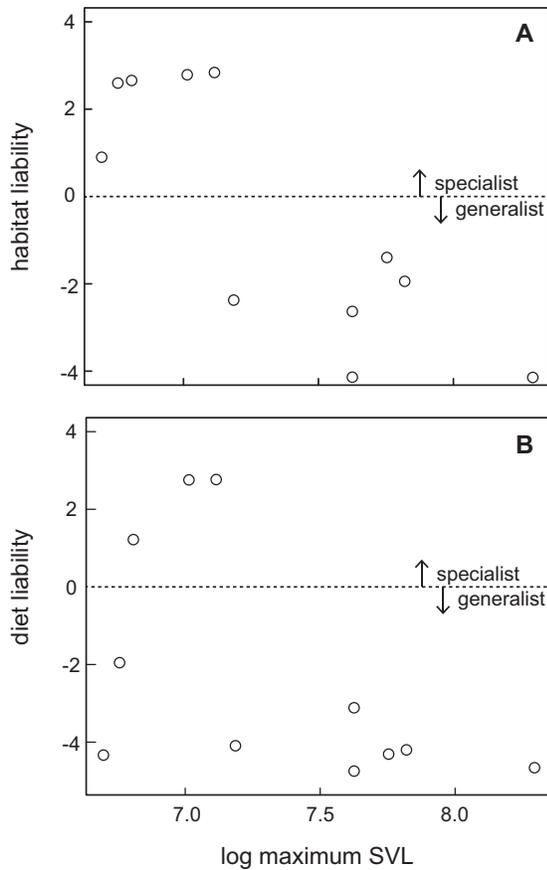


Figure 2. Ecological specialization and body size evolution of boas (genus *Chilabothrus*) in the West Indies under the threshold model. Substrate (habitat, A) and diet (B) are coded as binary characters, and the solid line denotes the threshold between the character states.

herpetofauna have contributed greatly to our understanding of ecology, evolution, and biogeography (e.g., Losos 2009). Forty-one percent of snake species in the family Boidae (13 of 32 species; Pyron et al. 2014) are island or archipelagic endemics, and the West Indian genus *Chilabothrus* represents a diverse and ecologically important radiation comprised of 11 endemic species in the Greater Antilles and Bahamas (Reynolds et al. 2013; Rodríguez-Robles et al. 2015). In resolving a taxonomically complete, dated molecular phylogeny for these West Indian boas, we were able to test hypotheses regarding the substantial morphological evolution seen in this group. We find evidence for repeated evolution of small body size and increased rates of diversification of cranial morphology associated with repeated departures from generalist substrate use to specialized use of terrestrial or arboreal substrate. These findings suggest multifaceted effects of ecological specialization in this genus—both deterministic evolution of small body size from larger ancestors and stochastic (or at least unpredictable) evolutionary divergence in head shape as small body size evolves.

Recent work has suggested that the evolutionary processes of adaptation and speciation on islands or island-like habitats might frequently be deterministic, a view at odds with Gouldian emphasis on contingency in macroevolutionary processes (Gould 2002; Mahler et al. 2013). Some clades, such as the Caribbean *Anolis* lizard radiation, have been shown to conform to a deterministic process of adaptation and speciation driven largely by ecological opportunity coupled with intrinsic diversification potential (Rabosky and Glor 2010; Wagner et al. 2012; Mahler et al. 2013). Although often composed of speciose radiations, extreme morphological, and ecological diversification appears to be rare among other reptile groups on Caribbean islands, such as the lizard genus *Spondylurus* as well as the snake genera *Tropidophis* and *Alsophis* (Hass 1991; Hedges 2002; Losos 2009; Burbrink et al. 2012; Hedges and Conn 2012), though some groups remain understudied (e.g., *Sphaerodactylus*). In fact, it seems clear that relatively few Caribbean squamate clades, even those that are relatively species rich, appear to have undergone classical ecomorphological diversification or convergent evolution despite apparent ecological opportunity (Burbrink et al. 2012; Hedges and Conn 2012). While other studies of Caribbean snakes (e.g., Burbrink et al. 2012) have rejected a pattern of adaptive diversification, studies of Neotropical boids suggest that even clades with few species might show strong evidence for ecomorphological diversification in both body size and dietary (trophic) specialization (Pizzatto et al. 2007a; Henderson et al. 2013).

Based on our species tree and quantitative trait analyses for the West Indian genus *Chilabothrus*, we find evidence for the repeated evolution of small body size in this genus on Puerto Rico, Hispaniola, and the Bahamas. These small species are comprised of microhabitat and dietary specialists, derived from generalist ancestors. On Hispaniola and Puerto Rico, we find evidence for in situ speciation resulting in large bodied species and small, arboreal, *Anolis*-eating specialists. Similarly, we find in situ evolution of small terrestrial species on both Hispaniola and the Bahamas. The correlated evolution of body size and substrate use suggests that a reduction in size allows microhabitat specialization and possibly adaptive evolution, as has been found in Neotropical birds (Bravo et al. 2014). In addition, we find increased rates of head PC2 and PC3 evolution with increasing ecological specialization. Taken together, our results indicate that boas have undergone in situ morphological size and shape diversification on Caribbean islands, and that ecological specialization on islands promotes diversity through deterministic evolution of small body size and diversification of cranial morphology guided by species- and island-specific factors.

DETERMINISM AND BODY SIZE EVOLUTION

We found low phylogenetic signal in body size across the Greater Antillean boas, an observation consistent with an evolutionary

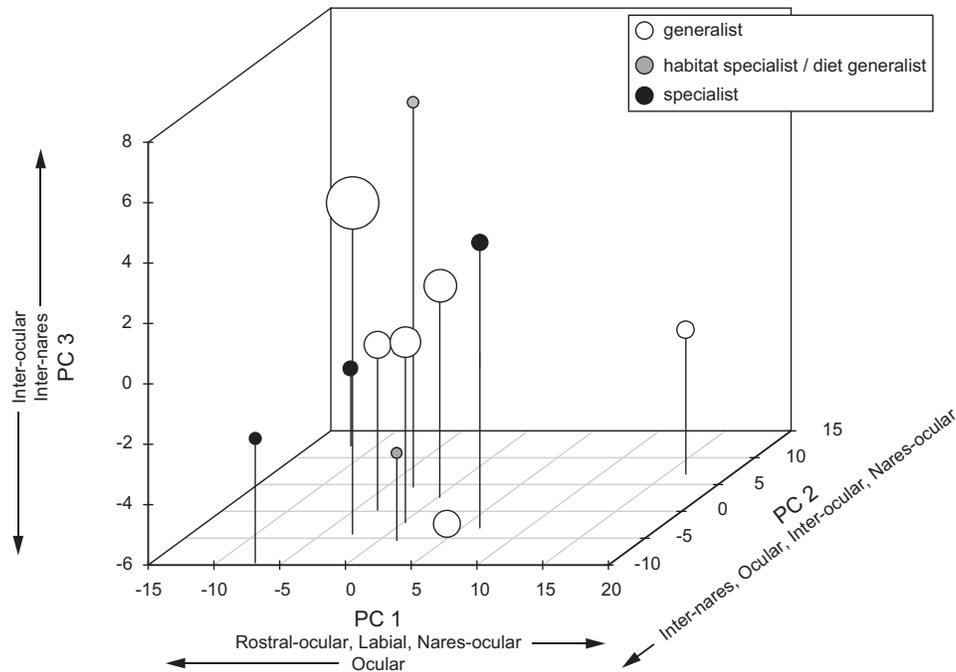


Figure 3. Phylogenetically corrected principal components analysis under a λ model for continuous morphological traits measured from 11 species of boas (genus *Chilabothrus*) in the West Indies. Species are shaded to indicate ecological category, where white is generalist, gray is a substrate specialist, and black is both substrate and dietary specialist. Points are scaled in radius by body size.

Table 2. Results from rate-by-state analyses of morphological evolution by ancestral substrate specialization liability.

State	Rate	$\rho_{\text{rate,state}} \pm \text{se}$	<i>t</i> -statistic	<i>Phylosim P</i>	Prop. <i>phylosim P</i> < 0.05
Substrate liability	Head shape PC1	0.42 ± 0.33	1.25	0.138	0.23
	Head shape PC2	0.64 ± 0.28	2.27	0.032	0.60
	Head shape PC3	0.66 ± 0.27	2.42	0.030	0.65
Diet liability	Head shape PC1	0.56 ± 0.30	1.85	0.074	0.39
	Head shape PC2	0.68 ± 0.27	2.52	0.045	0.63
	Head shape PC3	0.62 ± 0.29	2.17	0.067	0.51

Correlation coefficients (ρ) test the hypothesis that ancestral habitat liabilities from a posterior distribution depend on rates of morphometric evolution (squared contrasts). *Phylosim P* is based on comparison to a null distribution generated under Brownian motion, with Prop. *phylosim P* designating the proportion of simulations in which the estimate of ρ is considered significant. Significance is denoted in bold.

scenario in which small body size has independently evolved in situ multiple times in the clade (Fig. 1). In all vertebrate species, body size is an important character contributing to a variety of organismal attributes. With their simplified body plans, snakes are expected to show a particularly strong association between size and ecomorphology (Vitt 1987; Pyron and Burbrink 2009). Previous work on the evolution of Greater Antillean boas has suggested that small-bodied species are both morphologically and ecologically similar to each other, and were thus hypothesized to be close evolutionary relatives as well (Sheplan and Schwartz 1974; Tolson 1987; Kluge 1988, 1989). Our results contradict this idea but agree with other recent phylogenetic studies indicating that small-bodied species are more closely related to large-bodied species

(Campbell 1997; Burbrink 2004; Rivera et al. 2011; Reynolds et al. 2013, 2014). In addition, instead of ecomorphological similarity among small-bodied boas, we find that repeated origins of small body size are actually associated in many cases with divergence in cranial morphology (Fig. 3, Table 2).

We found that small body size is correlated with substrate specialization. Small species are generally characterized by a completely saurophagus diet and specialized adaptations to terrestrial (*C. exsul* and *C. fordii*) or arboreal (*C. gracilis*, *C. monensis*, and *C. granti*) substrates. Substrate specialization, such as arboreality, influences body proportions (Lillywhite and Henderson 1993; Pizzatto et al. 2007b; Feldman and Meiri 2013), such that arboreal specialist snakes tend to be slender and lightweight, with

longer prehensile tails and different axial skeletal musculature (Jayne 1982; Lillywhite and Henderson 1993; Sheehy et al. 2016 and references therein). In *Chilabothrus*, arboreal specialists are not only smaller bodied than substrate generalists, they tend to have elongate and slender bodies. *Chilabothrus gracilis* is the most slender and specialized boid snake (Henderson and Powell 2002) and more closely resembles Neotropical colubrids of the genus *Imantodes* (Fig. S3), which are likewise slender and arboreal. Arboreal West Indian boas forage nocturnally along terminal branches, shrubs, and grasses for sleeping *Anolis* lizards, and hence substrate structure might impose the strongest selective constraints on body shape and size in this genus (Chandler and Tolson 1990; Rodríguez-Robles and Greene 1996).

ECOLOGICAL SPECIALIZATION AND HEAD SHAPE EVOLUTION

We found that Greater Antillean and Bahamian boa species do not segregate in cranial morphospace either by body size or ecological specialization, but instead small-bodied species occupy a similarly wide range of three-dimensional morphospace (the first three PC axes) as large-bodied species (Fig. 3). Our rate-by-state analyses revealed that ancestral ecological (substrate and diet) specialization might be driving increased rates of head evolution. A similar result has been observed in other terrestrial vertebrates, whereby species of plethodontid salamanders with restricted ranges exhibited higher rates of head-shape evolution (Adams 2014). Reduced ranges in plethodontids might owe to specialization on a particular habitat type. In the case of Greater Antillean boas, the elevated rates of head shape evolution in habitat specialists is not likely driven by morphological divergence associated with different substrate types (i.e., terrestrial and arboreal), as some arboreal species are closer to terrestrial species in morphospace and vice versa.

ECOLOGY AND EVOLUTION IN GREATER ANTILLEAN BOAS

Our results suggest the repeated in situ evolution of small body size and ecological specialization in the Greater Antilles and Bahamas, a possible consequence of similar selective regimes leading to adaptive divergence from generalist competitors and the coupling of dietary shifts and substrate use (Boback 2003). Though we do not find a significant correlation between diet type and body size or diet type and any axes of head size or shape variation (Table 2), there is still an observable pattern of transition to a diet of *Anolis* coupled with a transition to arboreal substrates.

It has been shown that some species respond to similar selective pressures in slightly different phenotypic ways, a situation of ecological convergence with imperfect phenotypic convergence (e.g., Collar et al. 2014). It is hypothesized that this “many-to-one”

mapping of phenotypic traits to ecological outcomes wrought by similar selective pressures might be a far more common outcome than convergence (Hulsey and Wainwright 2002; Alfaro et al. 2004, 2005; Wainwright et al. 2005; Collar et al. 2014). Indeed, we find that substrate specialization is associated with elevated rates of cranial evolution, suggesting extensive morphological divergence between species that use the same habitat or prey types (Fig. 3). Given the many skeletal elements that make up the snake skull, it seems plausible that selection on head dimensions could result in different evolutionary responses in different lineages.

Other selective pressures might also be influencing these repeated evolutionary trends. Different assemblages of potentially competing nonscolecophidian snakes occur on Greater Antillean islands (Schwartz and Henderson 1991). However, Hispaniola has both the highest snake diversity (14 species) and the highest boid species diversity (three species, three ecotypes), and much of the snake diversity likely evolved in situ (Pyron and Burbrink 2014). Interestingly, paedomorphosis, both morphological (Kluge 1989) and ecological (Rodríguez-Robles and Greene 1996), has been proposed as a potential mechanistic underpinning in the evolution of Greater Antillean boa ecotypes. This suggests that small-bodied *Anolis* specialist boas are morphologically and ecologically similar to juvenile boas of all species, and are able to coexist with juvenile congeners owing to the high density of *Anolis* lizards on Greater Antillean islands (as many as two lizards per m²; Reagan 1992). Future research might test this using more extensive osteological, ontogenetic, and ecological data (e.g., Albertson et al. 2010).

CONCLUSIONS

Analyses of morphological traits have significantly increased our understanding of the evolutionary processes underlying divergence and island radiations of reptiles (e.g., Williams 1983; Roughgarden 1995; Losos 2009; Losos and Ricklefs 2009). We have shown that small body size evolved repeatedly in the Greater Antillean and Bahamian boas, associated with a shift toward specialization in substrate use. We also find that a shift toward specialization is associated with increased rates of diversification in head shape, as opposed to convergence toward a single head shape. These results suggest that ecological specialization drives morphological diversification via the effects of both deterministic (repeated) evolution of small body size and stochastic increased rates of cranial evolution. Other Neotropical boid radiations potentially exhibit deterministic ecomorphological evolution (Pizzato et al. 2007a; Henderson et al. 2013; Esquerré and Keogh 2016) and hence an analysis across all Neotropical boids would be a logical next step once taxonomic and evolutionary relationships are more firmly established (Colston et al. 2013; Reynolds et al. 2014).

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DATA ARCHIVING

Data archived: Dryad: 10.5061/dryad.94768

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Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher’s website:

Fig. S1. Full species tree from *BEAST. Node labels correspond to Table S2.

Fig. S2. Visualization of posterior trees from the *BEAST analysis using Densitree (without designating *C. granti*).

Fig. S3. Gross morphological and ecological convergence in a West Indian boid (*Chilabothrus gracilis*, left) and a Neotropical colubrid (*Imantodes cenchoa*, right).

Table S1. Summary of *Chilabothrus* specimens used in this study for genetic and morphometric sampling.

Table S2. Genes and selected best-fit models of evolution.

Table S3. Estimated divergence times (in millions of years) from *BEAST for nodes in Fig. S1.

Table S4. Body and head linear measurements for each of the 11 species of Greater Antillean boas.

Table S5. Results from phylogenetic PCA for species’ means of head measurements.