BREVIORA

Museum of Comparative Zoology
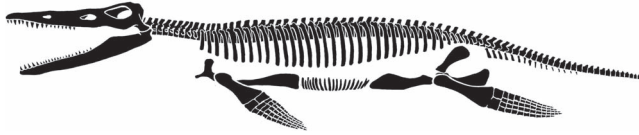
THE ANOLES OF LA SELVA: NICHE PARTITIONING AND ECOLOGICAL MORPHOLOGY IN A MAINLAND COMMUNITY OF *ANOLIS* LIZARDS

Christian A. Perez-Martinez,[1,2] Ambika Kamath,[3] Anthony Herrel,[4] and Jonathan B. Losos[5]

Abstract. Describing the relationships among morphology, behavior, and ecology is central to understanding the processes of evolutionary diversification. *Anolis* lizards are an excellent group for studying such ecomorphological relationships. Extensive research on anole ecological morphology has been conducted in the Caribbean, where sympatric species have repeatedly and convergently evolved to partition habitat through differential perch use. Six ecomorphs have been described, each with particular behavioral, morphological, and ecological characteristics well-suited for the microhabitat it occupies. However, little research has been conducted in mainland Central or South America, and a few case studies suggest that mainland anoles may not conform to the ecomorph classes recognized for Greater Antillean anoles. In this study, we examine the ecological morphology of sympatric mainland species of *Anolis* in a tropical lowland rainforest in Costa Rica and compare these species to the Caribbean ecomorphs. Our results show overlapping niches and substantial variability in habitat use across many species. Moreover, the relationship between relative hindlimb morphology and habitat use in *Anolis humilis* and *Anolis limifrons* does not conform to that of Caribbean species. Predation and fluctuating environmental conditions likely structure morphological variation differently in the mainland, leading the independent radiation of mainland anoles to produce divergent ecomorphological relationships compared with the Caribbean islands.

Key words: ecomorphology; *Anolis*; community structure; niche partitioning; microhabitat; ecology; mainland; adaptive radiation

[1] Division of Biological Sciences, University of Missouri, Columbia, Missouri 65211, USA; e-mail: perez.christian.alessandro@gmail.com.

[2] Museum of Comparative Zoology, 26 Oxford Street, Harvard University, Cambridge, Massachusetts 02138, USA.

[3] Miller Institute for Basic Research in Science and Department of Environmental Science, Policy, and Management, University of California Berkeley, Berkeley, California 94720, USA; e-mail: ambikamath@gmail.com

[4] UMR 7179 C.N.R.S/M.N.H.N., Département Adaptations du Vivant, Bâtiment d'Anatomie Comparée, 55 rue Buffon, 75005 Paris, France; e-mail: anthony.herrel@mnhn.fr

[5] Department of Biology and Living Earth Collaborative, Campus Box 1137, Washington University, St. Louis, Missouri 63130, USA; e-mail: losos@wustl.edu

INTRODUCTION

Studies of ecological morphology draw comparisons between an organism's use of the environment and its morphological traits (Norton et al., 1995). They are built on the premise that morphological differences contribute to differences in an organism's performance in the environment, thereby conferring a fitness advantage to individuals that can outperform others in ecologically relevant tasks (Losos, 1990c; Winemiller et al., 1995). Moreover, the relationship between ecology and morphology is not unidirectional—changes in an organism's behavior and ecological niche can in turn alter the functional significance of morphological traits (Wainwright, 1991). The interplay between ecology and morphology has been explored in many taxa, often within a phylogenetic framework, to examine rates of trait evolution and their adaptive significance in radiations (Galewski et al., 2005; Østbye et al., 2006; Kozak et al., 2007; Streelman et al., 2007; Maestri et al., 2016; Evans et al., 2019). Investigating ecomorphological relationships, particularly in comparative contexts, can therefore lend insight into the adaptive forces shaping an organism's biology.

Anolis lizards in the Caribbean have well-documented relationships between ecology and morphology, mediated by their locomotor behaviors (Losos, 2009). For instance, terrestrial anoles that use broad perches benefit from having longer limbs in quadrupedal running and jumping (Moermond, 1979; Pounds, 1988; Losos and Sinervo, 1989; Losos, 1990a, 1990b; Irschick et al., 1996, 1997; Losos and Irschick, 1996). Conversely, arboreal anoles that use narrow supports have short limbs for walking (Pounds, 1988; Losos, 1990a, 1990b). On the basis of these relationships, six distinct ecomorphs have been described, each with particular behavioral, morphological, and ecological characteristics adapted for the microhabitat it occupies (Rand and Williams, 1969; Williams, 1972, 1983; Rodríguez-Schettino et al., 2010; see Mahler et al., 2016, for a proposed seventh ecomorph). Anoles have largely radiated independently on each of the four islands of the Greater Antilles, convergently producing analogous sets of ecomorphs on each island (Williams, 1983; Losos, 2009).

Compared with the West Indies, mainland Central and South America have approximately 30% more species of *Anolis*, with more than 210 recognized species (Poe et al., 2017). However, the adaptive radiation and extent of convergent evolution of mainland anoles have received substantially less attention. Behavioral and ecological studies are much more difficult to conduct on mainland anoles, because they are far less abundant (Andrews, 1979) and tend to have more cryptic behaviors (Irschick et al., 1997; Losos et al., 2012), making them less commonly found (Losos, 2009). Divergent selective pressures in mainland and island habitats because of environmental variation contribute to differences in population densities, locomotor patterns such as prey capture and escape behavior, and microhabitat selection (Irschick et al., 1997). Thus, the ecological characteristics that make mainland anoles difficult to study are precisely the aspects that beg the question of how *Anolis* diversification has been shaped on the mainland. It is unlikely that mainland anoles have undergone selection to conform to the ecomorph classes found in Caribbean anoles (Irschick et al., 1997; Velasco and Herrel, 2007); in a comprehensive study examining 123 mainland anole species through morphospace analyses, only 15 corresponded to a Caribbean ecomorph group (Schaad and Poe, 2010).

Patterns of ecomorphological relationships differ between mainland and island anoles. For example, perch height is positively correlated with lamella number and negatively correlated with forelimb length in mainland anoles, whereas on islands it is negatively correlated with tail length and hindlimb length (Irschick et al., 1997; Schluter, 2000). Perch diameter is negatively correlated with tail length in mainland anoles, but it is positively correlated with limb length and body mass in island anoles (Irschick et al., 1997; Losos, 2009). The slope of the relationship between forelimb length and perch diameter, as well as body mass and perch diameter, is also greater in the Caribbean, whereas the slope of perch height versus tail length is greater on the mainland (Irschick et al., 1997). Lastly, toepad width, area, and lamella number are greater in islands (Macrini et al., 2003).

The mounting evidence against mainland anoles conforming to the island ecomorph classes may be either the result of insufficient sampling in the mainland or indicative of divergent ecomorphological patterns. Considering the latter possibility, we must ask how selective pressures differ between mainland and island habitats and how they explain variation in mainland anole morphology. On the mainland, ratios of predator-to-prey biomass are significantly higher (Fig. 1), anole population densities are lower, and the abundance of arthropod prey is high (Andrews, 1979). In contrast, Caribbean anoles are food limited, and intraspecific competition is thought to be the primary barrier to high reproductive fitness (Rand, 1967; Andrews, 1971). If interspecific competition is low in the mainland, there may be a decreased selective pressure for niche partitioning through competition. Alternatively, predation may lead to apparent competition and likewise result in changes

Figure 1. Predation on a mainland anole; brown vine snake (*Oxybelis aeneus*) consuming slender anole (*Anolis limifrons*) at La Selva Biological Station, Costa Rica. Photographed on 6 June 2016 by C.A.P.-M.

in niche structure (Bonsall and Hassell, 1997; Falk et al., 2015).

To examine the roles of competition and predation in the diversification of mainland anoles, baseline data are needed. The present study partly addresses this gap by examining habitat use of eight sympatric species of *Anolis* and ecological morphology of the three most abundant species in a Costa Rican tropical rainforest. We hypothesize that mainland anoles exhibit:

1. low habitat differentiation and a high degree of niche overlap,
2. morphological relationships that deviate from the patterns observed in the Caribbean ecomorphs, and
3. if competition plays a non-negligible role in structuring habitat use, variation in local habitat use dependent on the abundance of other co-occurring species.

For example, in areas with high abundances of species with arboreal tendencies, more terrestrial-oriented anoles may modify their habitat use by occupying lower perches. Finally, we supplement our examination of ecomorphology with data on these species' escape behavior as a baseline for future
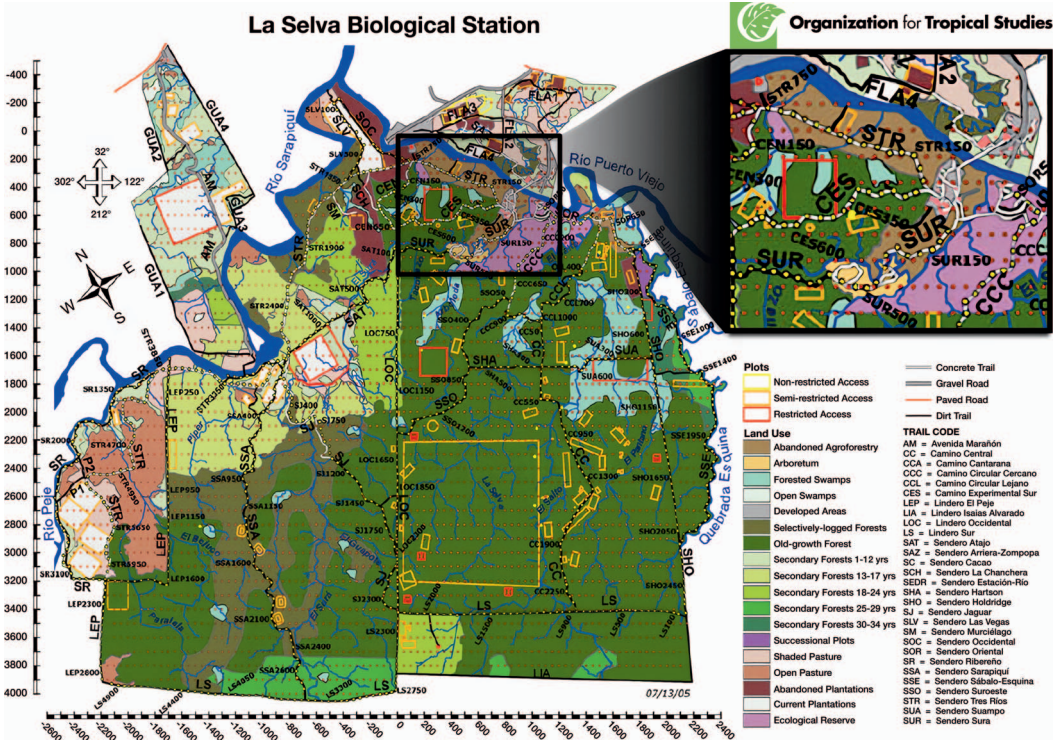
Figure 2.   Map of habitat types at La Selva Biological Station, near Sarapiquí, Heredia Province, Costa Rica. Adapted from Clark and Clark (2006).

investigation of the adaptive diversification of mainland *Anolis*. We predict that mainland anoles employ variable escape tactics, reducing the predictability of escape behavior in an environment with high predation pressure and enabling maneuverability and evasion on a variety of substrates.

METHODS

Study site and lizard sampling

Data in this study were collected in March 2005 (J.B.L.), June–July 2008 (A.H.), June–July 2016 (C.A.P.-M.), and January 2017 (C.A.P.-M.) at La Selva Biological Station, a tropical wet forest preserve operated by the Organization for Tropical Studies (10°26′N, 83°59′W; Fig. 2). La Selva is located in the

Heredia Province of Costa Rica near Puerto Viejo de Sarapiquí and consists of both primary and secondary tropical lowland wet forest (Holdridge, 1947). The preserve resides in the Caribbean lowlands on the northern Atlantic slope and connects to Parque Nacional Braulio Carillo (Kelm et al., 2008). The climate is humid throughout the year with seasonal fluctuations and an annual precipitation of approximately 400 cm (Tschapka, 2005). For all years, only adult *Anolis* lizards were considered, and sampling was conducted throughout the Sendero Tres Ríos, Sendero Sura, Sendero Oriental, Sendero Holdridge, Sendero Arriora-Zompopa, Sendero Atajo, Camino Circular Cercano, and Camino Circular Lejano trails and surrounding habitat (Fig.

TABLE 1. DESCRIPTIVE STATISTICS OF PERCH USE BY EIGHT SYMPATRIC SPECIES OF *ANOLIS* AND *POLYCHRUS GUTTUROSUS* AT LA SELVA. GROUND PERCHES EXCLUDED FROM DIAMETER MEASUREMENTS, RESULTING IN THE DIFFERENCES IN SAMPLE SIZE. SPECIES ORDERED IN TERMS OF INCREASING MEAN PERCH HEIGHT.

Species	n	Mean	SD	SE	Minimum	Median	Maximum
			Perch Height (cm)				
A. humilis	308	36.5	42.9	2.4	0.0	24.6	240.0
A. capito	15	46.0	82.7	21.3	0.0	0.0	230.0
A. oxylophus	50	62.4	60.7	8.6	0.0	45.7	250.0
A. limifrons	429	76.2	58.9	2.8	0.0	68.6	400.0
A. carpenteri	9	115.7	92.3	30.8	0.4	100.0	300.0
A. lemurinus	100	118.9	97.6	9.8	0.0	100.8	500.0
A. biporcatus	20	419.7	452.9	101.3	20.0	200.0	1,800.0
A. pentaprion	1	2,500.0	—	—	—	2,500.0	—
Polychrus gutturosus	2	185.0	21.2	15.0	170.0	185.0	200.0
			Perch Diameter (cm)				
A. humilis	214	24.3	47.4	3.2	0.5	10.0	405.0
A. capito	4	69.2	104.0	52.0	12.0	19.9	225.0
A. oxylophus	42	39.1	78.2	12.1	0.5	11.5	350.0
A. limifrons	386	26.4	48.5	2.5	0.5	9.4	418.0
A. carpenteri	7	22.1	27.9	10.5	1.3	7.6	75.0
A. lemurinus	92	55.6	81.0	8.4	0.6	23.3	405.0
A. biporcatus	18	32.6	41.8	9.9	0.5	15.0	157.0
A. pentaprion	1	7.0	—	—	—	7.0	—
Polychrus gutturosus	2	4.5	4.9	3.5	1.0	4.5	8.0

2). In 2005, 2008, and 2017, the entirety of sampling was done through transects, in which the observer walked along trail systems searching for anoles. In 2016, we sampled both along transects and in plots (described below). *Anolis* species under study include *A. humilis*, *A. limifrons*, *A. lemurinus*, *A. oxylophus*, *A. capito*, *A. carpenteri*, *A. biporcatus*, and *A. pentaprion*. Of these species, *A. humilis*, *A. limifrons*, and *A. lemurinus* co-occur in primary and secondary forest habitats, and the former two have the greatest population densities of understory anoles sampled at La Selva (Tables 1, 2). *Polychrus gutturosus* is a large arboreal lizard sympatric with the eight *Anolis* species, and we choose to devote a brief section to this species to supplement the treatment of the *Anolis* community at La Selva. During all years of study, we recorded perch height,

perch diameter (excluding lizards on the ground), and perch type by category (ground, root/buttress, trunk, leaf, stem, vine, branch, man-made). We report frequencies of substrate use for each species and descriptive statistics of perch height and diameter (Tables 1, 2). Because of the scarcity of *A. lemurinus* in both secondary and primary forest habitat, we collected the majority of this species from a managed habitat within Finca La Selva called the Holdridge Arboretum. The Arboretum is a 3.5-ha tract of land consisting of very little understory and canopy vegetation density, with about 1,200 trees planted by 1994 belonging to more than 250 native species (McDade et al., 1994). The soil is mostly composed of alluvium, and before 1968 it was maintained as a cacao plantation (McDade et al., 1994). Remnants of under-

TABLE 2. FREQUENCIES OF SUBSTRATE USE BY EIGHT SYMPATRIC SPECIES OF *ANOLIS* LIZARDS AND *POLYCHRUS GUTTUROSUS* AT LA SELVA. ROOTS AND BUTTRESSES ARE CONSIDERED UNDER THE SINGLE PERCH CATEGORY "ROOT."

Species	n	Relative Proportion							
		Ground	Root	Trunk	Leaf	Stem	Vine	Branch	Man-made
A. humilis	303	0.34	0.05	0.22	0.21	0.06	0.03	0.08	—
A. capito	15	0.73	—	0.20	—	—	—	0.07	—
A. oxylophus	51	0.14	0.08	0.25	0.20	0.04	0.04	0.18	0.08
A. limifrons	409	0.09	0.07	0.29	0.28	0.13	0.03	0.07	0.04
A. carpenteri	8	—	0.13	0.50	0.13	0.13	0.13	—	—
A. lemurinus	96	0.09	0.10	0.57	0.09	0.05	0.04	—	0.04
A. biporcatus	19	—	—	0.42	0.26	0.11	0.11	0.11	—
A. pentaprion	1	—	—	—	—	—	—	—	1.00
Polychrus gutturosus	2	—	—	—	0.50	—	—	0.50	—

story vegetation typical of surrounding secondary forest are scarce, and trails permeate the area. Additionally, a single observation of *A. pentaprion* by Oberbauer et al. (2013) was incorporated to present data on all *Anolis* species at La Selva.

In June and July 2016, we conducted sampling of lizards in 20 × 20-m plots in secondary forest habitat along the 350–750-m markers on the Sendero Tres Ríos trail. This region was used as an agroforestry plot by Leslie Holdridge for approximately one decade starting in the late 1950s. Maintenance involved undergrowth clearing, although no trees were cut down. In 1996, an invasive plant management program removed all cacao trees from the site, estimated at around 3,000, and the secondary forest continued its growth uninterrupted for the next 20 years (C. de la Rosa, personal communication, 3 February 2017). Few light gaps occur in this habitat because of a dense canopy composed mostly of *Cecropia* spp., *Goethalsia meiantha*, *Laetia procera*, and *Rollinia microsepala* (McDade et al., 1994), and the most abundant plants in the understory were palms, including *Welfia georgii*, *Asterogyne martiana*, *Geonoma congesta*, and *Socratea exorrhiza* (Joyal, 1994). Each plot was separated from adjacent plots by an average of 40 ± 23 m (and a minimum

of 10 m) to minimize the chance of resampling the same individual. The diameter of the home range of *A. humilis* is less than 10 m (Guyer, 1988) and for *A. limifrons* is less than 15 m (Andrews and Rand, 1983), so the distance between plots was effective for minimizing resampling. These plots were spatially arranged adjacent to the trail on both sides with boundaries at least 5 m away from the trail. Plot locations were chosen in an attempt to select homogeneous habitat with respect to understory vegetation type, understory vegetation density, canopy cover, and evenness, quality, and moisture of terrain. In our analyses, "plot" designates the eight plots of equal areas, whereas "site" represents categories of broader geolocation data that are nonequal in area.

From the hours of 0900 to 1700 hours, we collected as many anoles as possible in a single plot and recorded the same measures of habitat use as in transect sampling. Almost all individuals sampled in plots were *A. humilis* ($n = 69$) or *A. limifrons* ($n = 94$), compared with only eight total individuals of the other six species combined. Lizards were caught with a loop attached to a fishing pole or by hand. The following day, we withheld these lizards and sampled within the same plot in an attempt to sample exhaustively all lizards whose home range was inside the

plot. After morphological data were taken, as described below, all lizards were released back into the plot, and we began sampling in an adjacent plot. We marked lizards on the underside with a permanent marker that stays visible until the lizards shed their skin. Because adjacent plots were completely sampled within a time span of less than a week, recaptured individuals were likely to have been noted. When rain or other environmental conditions decreased lizard activity, we devoted an additional day to sampling in a single plot. Although different amounts of time were spent in each plot, the likelihood of encountering each species remained constant, so only proportional densities within each plot are addressed.

In January 2017, one of the authors (C.A.P.-M.) induced escape behavior by simulating a predatory approach. Escape behaviors are defined as behaviors elicited after direct pursuit by a predator (Schall and Pianka, 1980). Data were collected from the same segment of secondary forest surrounding the Sendero Tres Ríos trail as in the plot sampling. After spotting each lizard, the observer approached to a distance of 2 m from the lizard and paused for 5 seconds. Next, the observer continued approaching until the lizard made a movement, at which point the observer immediately ceased moving and proceeded to take observational data, which consisted of the type of movement (run or jump) and the direction and distance of each movement until the lizard stopped moving for 5 seconds. If a distance of 30 cm was reached without eliciting movement from the lizard, the observer stopped walking and reached a hand forward at a constant speed parallel to the ground. A constant walking speed was maintained while traversing habitat in search of lizards, and to minimize the effect of color as a stimulus, the observer wore dark colored clothing (i.e., a green/blue shirt and gray pants) (Fondren et al., 2019). Similar methodology has been adopted in other studies quantifying escape behavior of anoles (Irschick, 2000; Cooper, 2006; Vanhooydonck et al., 2007; Moon and Kamath, 2019).

Morphology

For all anoles sampled in 2016, we took the following morphological measurements in the laboratory with digital calipers with ± 0.01 mm resolution (Fig. 3): 1) snout-vent length (SVL)—between the cloaca and the tip of the snout, 2) head height—between the parietal eye and the lower jaw in a plane orthogonal to the orientation of the body axis of the lizard, 3) head width—between the two sides of the lower jaw at the widest part of the head, 4) head length—between the quadrate-articular jaw joint on the right side to the tip of the snout, 5) forelimb length—between the radiocarpal joint to the glenohumeral joint on the right side, 6) hindlimb length—between the talocrural joint and the acetabulofemoral joint on the right side, 7) tail length—between the cloaca and the tail tip, and 8) tail regeneration—the length of the portion of the tail that has been regenerated after autotomy (Fig. 3). Because of sample size limitations, we only consider three species (*A. humilis*, *A. limifrons*, and *A. lemurinus*) in our morphological analyses.

Data analyses

Statistical tests were performed in R 3.6.2 (R Core Team, 2019). We ran eight linear mixed-effects models in a Bayesian framework by the Markov chain Monte Carlo (MCMC) method (R package *MCMCglmm*; Hadfield, 2010) to determine whether species was a significant predictor of morphological variables (forelimb length, hindlimb length, tail length, SVL) and habitat use variables (perch height, perch diameter, perch type, and ground perch type). All morphological
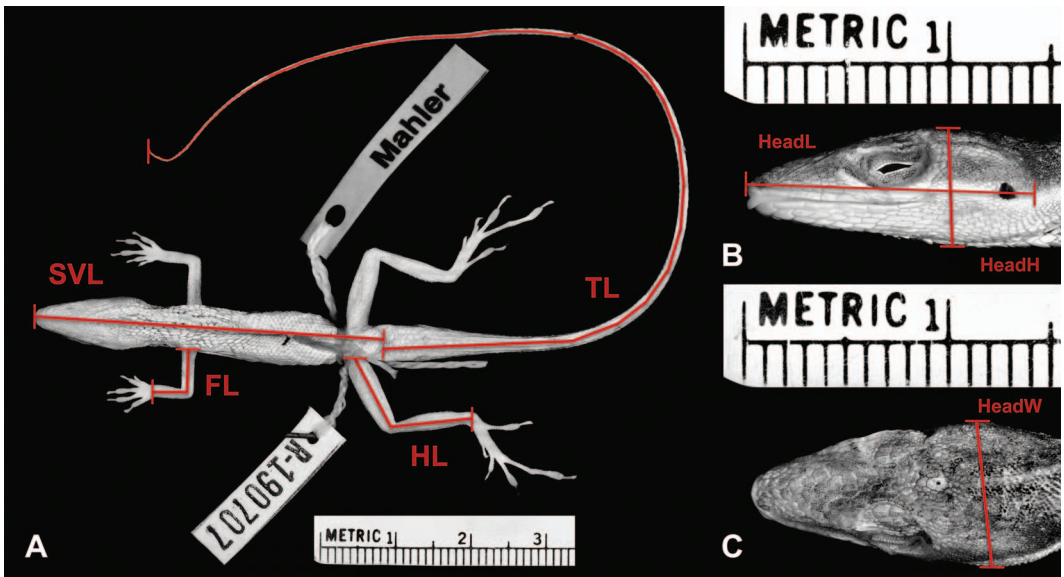
Figure 3. Morphological measurements. (1) Snout–vent length; *SVL*. (2) Head height, *HeadH*. (3) Head width, *HeadW*. (4) Head length, *HeadL*. (5) Forelimb length, *FL*. (6) Hindlimb length, *HL*. (7) Tail length, *TL*. Specimen pictured—*Anolis olssoni* from the herpetological collection of the Museum of Comparative Zoology at Harvard University. Three scanned images (A, B, C) produced by Joseph Martinez.

data were collected (by C.A.P.-M.) in 2016, and ecological data incorporated observations from multiple authors over several years (C.A.P.-M., A.H., and J.B.L.). Only adult males and females of the three most abundant species (*A. humilis*, *A. limifrons*, and *A. lemurinus*) were considered because of low sample sizes for other species, and lizards with regenerated tails were excluded from the model of tail length. Models with morphological response variables, except for SVL, included species, sex, and log-transformed SVL as fixed effects, and a random effect of site. Similarly, models of habitat use variables were run with species and sex as fixed effects, and because habitat use was recorded by three of the authors, we included a random effect of observer in addition to site. Lizards that perched on the ground were removed from the model with perch height as a response because of the log transformation and from the model of perch diameter

because ground perches cannot be assigned a diameter measurement. In addition to analyses for perch type, a categorical variable of eight substrate categories, we created the binary variable "ground perch type" to denote whether lizards perched on the ground. All six continuous response variables were log transformed to satisfy assumptions of normality, and we used generalized linear mixed effects models of the binomial family for perch type and ground perch type. Models were run with 155,000 iterations, a thinning rate of 100, and an initial 5,000 burn-in iterations. Uninformative diffuse normal priors centered at zero were used for the fixed effects, and uninformative inverse-Wishart priors were specified for the random effects and residual variance structure ($V = 1$, $v = 0.01$). We also incorporated a variance–covariance matrix generated by a pruned and inverted *Anolis* tree (Poe et al., 2017) to account for

phylogenetic nonindependence between species. For all Bayesian models, we first ran them with an interaction between species and sex, and if nonsignificant ($P > 0.05$), the interaction was removed. For interpretation of the results, we used posterior sample means, their 95% credible intervals, and MCMC P values. Model convergence was checked for fixed and random effects, autocorrelation was low, and all model residuals were relatively normally distributed. To examine pairwise differences, we reran models with different species as reference levels.

Following the Bayesian models, for each of the three species we ran a post hoc linear mixed effects model with restricted maximum likelihood to evaluate sex as a predictor of SVL, and a generalized linear model with maximum likelihood to test differences in ground perch type attributed to sex. Again, continuous variables were log transformed, a binomial distribution family was used for binary variables, and assumptions of normality for the response variables and residuals were checked. A random effect of site was used in models of SVL but was not included in models of ground perch type because of a lack of variance within sites that resulted in a singular fit.

We performed two principal components analyses (PCAs) for head and body shape across the three species. To characterize body shape we used forelimb length, hindlimb length, tail length, and SVL, and for head shape we used head height, head width, head length, and SVL. All variables were log transformed. A reduced dataset was used for the body shape PCA because lizards with incomplete or regenerated tails were excluded. We ran Bayesian MCMC linear mixed effects models to determine whether species was a significant predictor of the first two principal components in each PCA. Species and sex were fixed effects, and site was a random effect. As in the previous Bayesian models, we used identical methodologies to choose priors, incorporate interactions, verify assumptions of normality and model convergence, and take into account phylogenetic nonindependence.

In the following tests, we solely used data collected from the eight sampling plots to examine intraspecific variation and interspecific effects on habitat use. Only two species (A. humilis and A. limifrons) were considered because they comprised over 95% of the lizards sampled in plots. To test the effect of plot and species on habitat use (perch height and perch diameter, log transformed), we ran two multivariate linear regression models with analysis of variance Type III sum of squares, each with species and plot as predictors. We also performed a likelihood ratio chi-square test for ground perch type with the same predictors. To measure the strength of association between perch height of one species and relative density of the other, we calculated Spearman's rank correlations, and we used a Pearson's product-moment correlation to test the association of mean perch heights by plot between A. humilis and A. limifrons.

We tested for differences in escape behavior (flight distance and movement distance, log transformed) between A. humilis and A. limifrons with linear regression models. Flight distance was defined as the distance between the experimenter as the predatory stimulus and the lizard when the latter makes its first movement, and movement distance was defined as the total distance the lizard moves until it stops for 5 seconds. Two likelihood ratio chi-square tests were used to examine differences in activity type and movement direction between the two species. Activity type was designated as either jumping or running, and movement direction was categorized as upward, downward, or
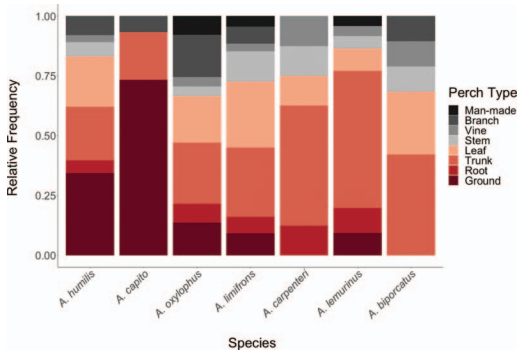
Figure 4. Structural habitat use of seven species of *Anolis* lizards: *A. humilis* ($n = 301$), *A. capito* ($n = 15$), *A. oxylophus* ($n = 51$), *A. limifrons* ($n = 409$), *A. carpenteri* ($n = 8$), *A. lemurinus* ($n = 96$), and *A. biporcatus* ($n = 19$) at La Selva, represented by relative frequency of perch type by species. Canopy species *A. pentaprion* and *Polychrus gutturosus* excluded because of exceedingly low sample sizes.

horizontal movement. Model assumptions were checked as previously stated.

NATURAL HISTORY SYNTHESIS OF LA SELVA ANOLES

The eight species of anoles at La Selva vary greatly in habitat use (Tables 1, 2; Fig. 4) and can be broadly categorized into understory, canopy, and multihabitat species. Understory species—*A. humilis*, *A. capito*, *A. oxylophus*, and *A. limifrons*—have a mean perch height of less than 1 m. *Anolis humilis* and *A. limifrons* in particular make up the greatest species abundances of understory anoles and likely of the entire La Selva anole community (Tables 1, 2). Our data suggest that *A. carpenteri* and *A. lemurinus* occupy understory, subcanopy, and canopy stratifications, which we refer to as a multihabitat lifestyle. The remaining two species, *A. biporcatus* and *A. pentaprion*, are canopy species with mean perch heights greater than 4 m. However, our measures of habitat use likely underestimate perch height, particularly for subcanopy and canopy species,

Figure 5. *Anolis humilis*, La Selva Biological Station, Costa Rica. Photographed on 17 January 2017 by C.A.P.-M.

because spotting was mostly done from the lower understory.

Here, we summarize ecological information and natural history observations to characterize the La Selva *Anolis* community, synthesizing past literature and our results. All data presented were collected in our study unless otherwise stated. We begin by describing the four most common anoles, *A. humilis*, *A. limifrons*, *A. lemurinus*, and *A. oxylophus*, followed by four less frequently observed anoles in order of mean perch height and, lastly, a co-occurring species of the genus *Polychrus*.

Anolis humilis

Of the small *Anolis* species at La Selva, *A. humilis* is the stockiest, having short SVL (mean 33.4 mm), limbs, and tail (Guyer and Donnelly, 2005; Fig. 5). *Anolis humilis* is primarily terrestrial with a mean perch height of 36.5 cm (Table 1; Fig. 6). This anole perches on the ground more frequently than *A. limifrons* and is second only to *A. capito* in selecting ground perches (Table 2; Fig. 4). Mean perch height tends to be lower for females than males, and females occupy a greater proportion of ground perches (Fig. 6;
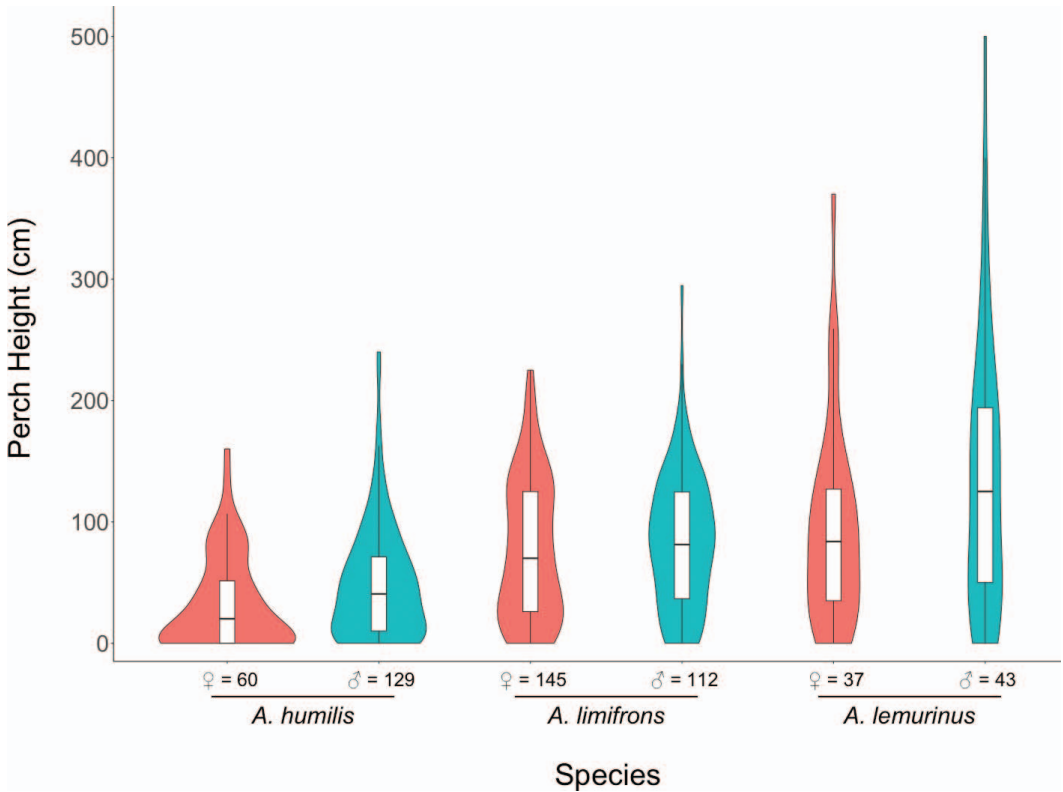
Figure 6. Distribution of perch height across the three most abundant species of *Anolis* lizards by sex. Violin plots were generated by Gaussian kernels with tails trimmed and bandwidth adjustment of 1 (function *geom_violin* in the R package *ggplot2*; Wickham, 2016).

Supplementary Table S1; Pounds, 1988). Other studies also describe this species as dwelling in the leaf litter and on low perches less than 60 cm high, and it is active in deep-shaded habitats in both primary and secondary forests (Talbot, 1976, 1979; Corn, 1981; Pounds, 1988; Vitt and Sani, 1998; Tulli, 2012).

Anolis limifrons

Anolis limifrons is thin and small-bodied (mean SVL 37.2 mm) with a long tail; it tends to occupy both shaded and open microhabitats (Guyer and Donnelly, 2005; Fig. 7). This species exhibits mostly arboreal habitat use in the understory; mean perch

Figure 7. *Anolis limifrons*, La Selva Biological Station, Costa Rica. Photographed on 19 April 2016 by C.A.P.-M.

Figure 8. *Anolis lemurinus*, La Selva Biological Station, Costa Rica. Photographed on 17 April 2016 by C.A.P.-M.

Figure 9. *Anolis oxylophus*, La Selva Biological Station, Costa Rica. Photographed on 4 July 2016 by C.A.P.-M.

height was less than 1 m, but highly variable, ranging from the ground to 400 cm high (76.2 cm; Table 1). Previous studies reported higher average perch heights in vegetation 1–2 m above the ground (Talbot, 1976, 1979). Mean perch diameter is broad (26.4 cm; Table 1) because some lizards perched on very large trees, but median perch diameter is also relatively broad (9.4 cm; Table 1), and choice of substrate is highly variable (Table 2; Fig. 4). The formation of stable male–female pairing has been documented in *A. limifrons*, and in the field, 45–75% of lizards can be found in pairs (Talbot, 1979; Harrison, 2013). This life history trait may be unique among *Anolis* lizards (but see Gorman, 1980); more data are needed to see how intraspecific competition may promote this behavior. In contrast, we did not encounter pairs of *A. limifrons* at high frequencies.

Anolis lemurinus

Anolis lemurinus has a medium build (mean SVL 52.0 mm), with a body size larger than *A. humilis* and *A. limifrons* (Savage, 2002; Fig. 8). *Anolis lemurinus* has the greatest variability in perch height of all understory species, occupies trunk perches most often, and is second to *A. capito* in having the greatest average perch diameter when perching on the ground is excluded (55.6 cm; Tables 1, 2; Fig. 4). The long forelimbs and hindlimbs of *A. lemurinus* may hinder movement through arboreal habitats on thin branches, which may be counteracted by a preference for wide perches. By occupying large perch diameters, *A. lemurinus* is likely able to cross between understory and canopy stratifications. The abundance of large and tall trees in the arboretum may explain why *A. lemurinus* was relatively common there, and in secondary forest, *A. lemurinus* consistently used trunks thicker than 20 cm. Corn (1981) encountered *A. lemurinus* on large tree trunks and observed them to flee upwards in response to a disturbance.

Anolis oxylophus

Anolis oxylophus is a medium-sized anole (mean SVL 64.8 mm; Irschick et al., 1997) with long hindlimbs and a long tail (Fig. 9). This anole is the only semiaquatic species at La Selva (Guyer and Donnelly, 2005). It is restricted to riparian microhabitats, often found perching on broad leaves and trunks

Figure 10. *Anolis capito*, La Selva Biological Station, Costa Rica. Photographed on 22 June 2016 by C.A.P.-M.

near slow-moving streams. In contrast to another aquatic Costa Rican anole (*Anolis aquaticus*), *A. oxylophus* generally does not use rocks as perches, although this may simply reflect a difference in substrate availability (Leal et al., 2002; Muñoz et al., 2015; Herrmann, 2017). Our data describe a varied choice of substrate by *A. oxylophus* (Table 2; Fig. 4), and all individuals collected by C.A.P.-M. were found within 8 m of a body of water. We observed *A. oxylophus* escape a perceived threat (the observer) by diving underwater. Savage (2002) states that lizards can remain submerged under water for prolonged periods of time. Additionally, remarkable observations have been made of *A. oxylophus* breathing underwater through a recycled air bubble above its head (Swierk, 2019). Future studies examining other behaviors, including underwater foraging and locomotion, will help reveal how this species has developed adaptations to aquatic environments.

Anolis capito

Anolis capito is a large terrestrial anole (mean SVL 78.3 mm; Köhler et al., 2005) with long limbs and a robust body (Savage, 2002; Fig. 10). Its head shape is the most morphologically distinct of sympatric anoles; the skull is wide and tall, though shorter in length, with prominent ridges along the eyes and a short snout (Guyer and Donnelly, 2005). Most *A. capito* encountered in this study, a mixture of adults and juveniles, were found on the ground (73% of observations; Table 2; Fig. 4), and when startled they hopped several times before freezing again. Few ecological data have been published for this species, but it is almost always found on or near the forest floor (Andrews, 1979; Corn, 1981), and when off the ground, *A. capito* perches on low, thick trees (Vitt and Zani, 2005). Ameivas (*Holcosus festivus* and *Holcosus quadrilineatus*) dominate the forest floor through active foraging and very high abundances, and *A. capito* might choose to forage when ameivas are less active (C.A.P.-M., personal observation). This temporal shift may also require that *A. capito* be able to sustain activity in darker, cloudier environmental conditions when the heliophilic ameivas are almost entirely inactive (Vitt and Zani, 1996). We also observed this species exhibit prolonged death feigning in response to direct contact.

Anolis carpenteri

Anolis carpenteri is a small-bodied anole (mean SVL 40 mm) with a similar morphology to *A. limifrons*, although with a slightly shorter hindlimb and tail (Savage, 2002; Fig. 11). This species is among the rarest species of anole at La Selva, preferring shaded microhabitats (Fitch, 1976; Guyer and Donnelly, 2005), and its small body size and less distinct morphology make it difficult to detect relative to other upper understory or canopy species. Half of the time *A. carpenteri* were found on tree trunks, although 39% of observations were on thin leaves, stems, and vines. The low sample size of *A. carpenteri* (*n*

Figure 11. *Anolis carpenteri*, La Selva Biological Station, Costa Rica. Photographed on 16 July 2016 by C.A.P.-M.

Figure 12. *Anolis biporcatus*, La Selva Biological Station, Costa Rica. Photographed on 29 April 2016 by C.A.P.-M.

= 8) allows two observations of broad perches to skew the mean perch diameter to a value of 22.1 cm, although *A. carpenteri* has a median perch diameter of 7.6 cm, similar to those of *A. humilis* and *A. limifrons* (Table 1). We suggest that *A. carpenteri* may primarily utilize thin perches high in the forest canopy (Corn, 1981), with the caveat that it may occasionally use broad perches such as tree trunks to traverse between canopy and understory levels. Corn (1981) argued that observations of *A. carpenteri* in the understory and on the forest floor may be due to the "drop-and-freeze" escape behavior in this species, and he recorded *A. carpenteri* among recently felled trees. At La Selva, 10 individuals of *A. carpenteri* have been collected on lichen-covered rocks on the forest floor, and additional sampling yielded seven at ground level and three at the bases of trees (Echelle et al., 1971; Fitch, 1976).

Anolis biporcatus

Anolis biporcatus is the largest species of anole at La Selva (mean SVL 86.7 mm; Guyer and Donnelly, 2005; Armstead et al., 2017; Fig. 12). Body coloration is bright green with rings of light blue dots along the body, but these lizards can rapidly change to dark brown. This species had a mean perch height greater than 4.0 m and a maximum of more than 18 m (Table 1). Its habitat use likely extends into the highest layers of the canopy, and we document a varied substrate use (Table 2). These data are in agreement with previous studies (e.g., Villareal-Benítez, 1997) that document *A. biporcatus* as a canopy specialist, although Villareal-Benítez (1997) additionally describes a strong tendency for this species to occupy large branches. We observed one individual change color from uniform green to thick lateral stripes of strongly contrasted dark green and yellow-green while feeding on a tuxedo grasshopper (*Copiocera specularis*).

Anolis pentaprion

Anolis pentaprion is a moderate-sized anole (mean SVL 59.7 mm; Köhler et al. 2005) with relatively short limbs that dwells on large tree trunks (Savage, 2002; Fig. 13). We did not encounter this species in our study, although we incorporate one observation by Oberbauer et al. (2013) of *A. pentaprion* found at a height of 25 m on a canopy tower at La Selva. Subsequent

Figure 13. *Anolis pentaprion*, Gandoca, Costa Rica. Photographed on 23 June 2017 by C.A.P.-M.

Figure 14. *Polychrus gutturosus*, La Selva Biological Station, Costa Rica. Photographed on 16 July 2016 by C.A.P.-M.

observations by the same authors recorded individuals up to the top of the canopy tower at 42 m high. Oberbauer et al. (2013) documented several instances of parachuting behavior by *A. pentaprion*, in which the lizard jumped off the tower and appeared to glide and direct its descent to land back on the canopy tower. Its relatively flat body shape may aid in this antipredator behavior. Corn (1981) claims *A. pentaprion* is an open-habitat species, basking on exposed tree trunks in the crowns of forest trees and adept at moving across thin twigs and branches. Along the edges of disturbed forest habitat in Gandoca, which lies within the Atlantic versant of Costa Rica, one individual of *A. pentaprion* was found two meters high, facing downwards near the lower end of a thin branch (Figure 13; C.A.P.-M., personal observation). In Panama, the species has been observed high in trees on relatively narrow branches (A.H., personal observation; J.B.L., personal observation).

Polychrus gutturosus

The Neotropical chameleon, or monkey lizard, *Polychrus gutturosus* is a large arboreal lizard (mean SVL 128.3 mm; Savage, 2002; Fig. 14). Although historically the genus *Polychrus* was considered to be the sister clade to *Anolis*, recent work suggests it is not as closely related as initially thought (Townsend et al., 2011; Pyron et al., 2013; Poe et al., 2017; Torres-Carvajal et al., 2017a). Similar to *Anolis*, *P. gutturosus* has an extensible gular flap that may be used in male displays, and its body is dorsolaterally compressed. Perhaps the most distinctive feature of lizards in the genus *Polychrus* is the extremely long prehensile tail (Torres-Carvajal et al., 2017b). The tail of *P. gutturosus* is more than three times the length of the body, and although it likely cannot support the lizard's entire body weight, the tail is useful in conferring stability. Locomotion is slow and staggered, as in chameleons. Lizards will rock the body forward and backward rhythmically in forward motion. Hands and feet are used to grasp branches. In particular, the fifth tarsus of the hindfoot faces backwards at about 120° and is highly movable, providing the clawed feet with better grip. The tail is sometimes used in lieu of the hindlimbs to prop the lizard up: while maneuvering forward by the forelimbs, lizards may grasp a branch with the tail, allowing the hindlimbs to be entirely suspended in the air
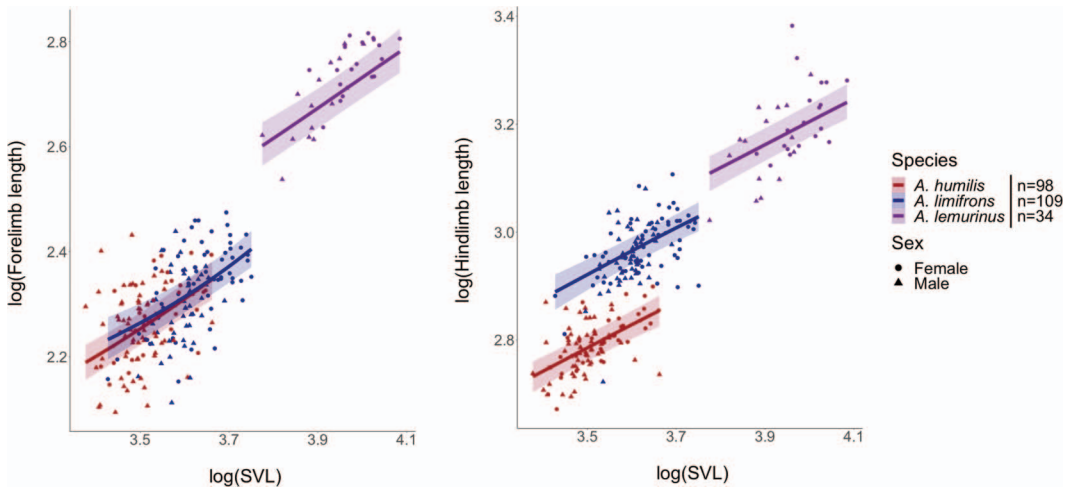
Figure 15. Forelimb length (left) and hindlimb length (right) by SVL across species. Data points are log transformed raw values measured in millimeters. Regression lines are calculated from the distribution of posterior means from Bayesian MCMC models and their 95% credible intervals, smoothed via *LOESS* for visualization.

between branches. We observed gradual color change over the course of 8 minutes from bright green to solidly dark brown and back to bright green. Like some others in the genus, *P. gutturosus* is a denizen of the forest canopy, having been recorded at heights of more than 40 m (Savage, 2002). It is seldom seen at lower perches.

RESULTS

Ecological morphology and behavior of *A. humilis*, *A. limifrons*, and *A. lemurinus*

Anolis humilis perched lower than both *A. limifrons* and *A. lemurinus*, and *A. lemurinus* perched higher than *A. limifrons* (Supplementary Table S1; Fig. 6). Perch diameter was greater in *A. lemurinus* than in both *A. humilis* and *A. limifrons*, but perch diameter did not differ between the latter two species (Supplementary Table S1). *Anolis humilis* occupied different perch types than *A. limifrons* and *A. lemurinus*, but *A. limifrons* and *A. lemurinus* did not differ (Supplementary Table S1; Fig. 4). Specifically, *A.*

lemurinus utilized trunks most often, and *A. limifrons* was more likely to be found on stems than *A. humilis*. However, effective sample sizes were less than 400 for the eight-level categorical variable of perch type, questioning the reliability of interpretations made from the perch type model results. All other Bayesian analyses in this study yielded effective sample sizes ranging from 1,000 to beyond 1,500. Considering solely ground compared with nonground perch types, *A. humilis* perched on the ground significantly more often than *A. limifrons* and *A. lemurinus*, and likewise, *A. limifrons* and *A. lemurinus* did not differ (Supplementary Table S1; Fig. 4). Females of *A. humilis* occupied a greater proportion of ground perches but were not significantly different in perch height or perch diameter (Supplementary Table S1). Males and females of *A. limifrons* and *A. lemurinus* did not differ in any measure of habitat use (Supplementary Table S1).

Anolis lemurinus had a greater forelimb length than *A. humilis* and *A. limifrons*, but there was no difference between *A. humilis*
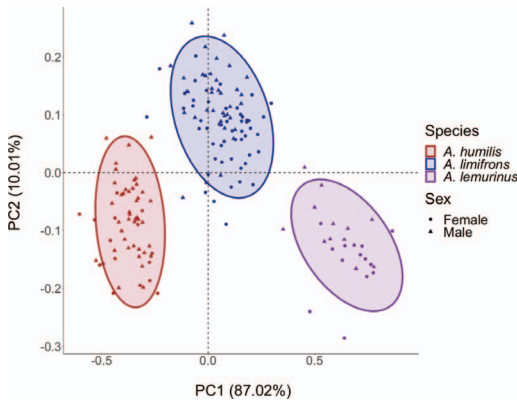
Figure 16. Principal components analysis of body shape across species by sex, with 95% confidence ellipses. Morphological variables incorporated include SVL, forelimb length, hindlimb length, and tail length (mm), all log transformed. Individuals with cut or regenerated tails were excluded. See Supplementary Table S5 for loadings. *A. humilis* ♀, $n = 16$; *A. humilis* ♂, $n = 42$; *A. limifrons* ♀, $n = 53$; *A. limifrons* ♂, $n = 36$; *A. lemurinus* ♀, $n = 14$; *A. lemurinus* ♂, $n = 12$.
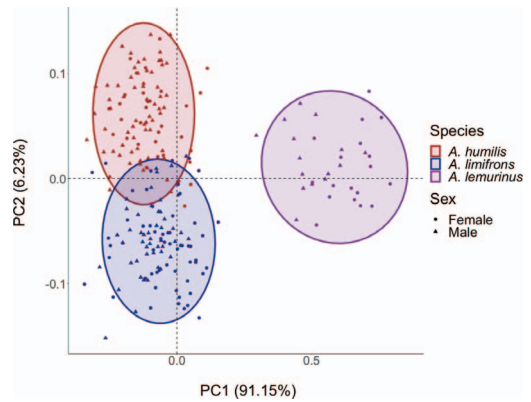

Figure 17. Principal components analysis of head shape across species by sex, with 95% confidence ellipses. Morphological variables incorporated include SVL, head height, head width, and head length (mm), all log transformed. See Supplementary Table S6 for loadings. *A. humilis* ♀, $n = 33$; *A. humilis* ♂, $n = 63$; *A. limifrons* ♀, $n = 59$; *A. limifrons* ♂, $n = 47$; *A. lemurinus* ♀, $n = 18$; *A. lemurinus* ♂, $n = 15$.

and *A. limifrons* (Supplementary Table S2; Fig. 15). *Anolis lemurinus* also had a greater hindlimb length than *A. humilis* and *A. limifrons,* and *A. limifrons* had a greater hindlimb length than *A. humilis* (Supplementary Table S2; Fig. 15). *Anolis humilis* had a shorter tail length than both *A. limifrons* and *A. lemurinus*, but *A. lemurinus* did not differ in tail length from *A. limifrons* (Supplementary Table S2). *Anolis lemurinus* had the largest SVL of the three species, and *A. limifrons* had a larger SVL than *A. humilis* (Supplementary Table S2).

In the morphospace for body shape, principal component 1 (PC1) loaded positively for all variables; we interpret PC1 as an indicator of overall body size. Higher values of PC2 indicated larger tail length, shorter forelimb length, shorter SVL, and a negligible difference in hindlimb length (Supplementary Table S3; Fig. 16). The interaction between *A. limifrons* and sex was a significant predictor of PC1; likewise,

the interaction between *A. humilis* and sex was significant (Supplementary Table S3). Differences in PC1 as a main effect between the species were therefore not interpretable. However, with regard to body size, females of *A. humilis*, *A. limifrons*, and *A. lemurinus* had a greater SVL than males (Supplementary Table S2). In the body shape PCA, *A. limifrons* had greater values of PC2 than *A. humilis* and *A. lemurinus*, but *A. humilis* and *A. lemurinus* did not differ (Supplementary Table S3; Fig. 16). Differences in species clusters in body shape PCA visualizations were generally consistent with morphological comparisons of individual variables between species (Supplementary Tables S2, S3; Fig. 16).

In the head shape morphospace, PC1 loaded positively for all variables and was interpreted as an indicator of overall head size. Higher values of PC2 indicated greater head height and head width, but shorter head length and SVL (Supplementary Table S4; Fig. 17). The interaction between *A.*
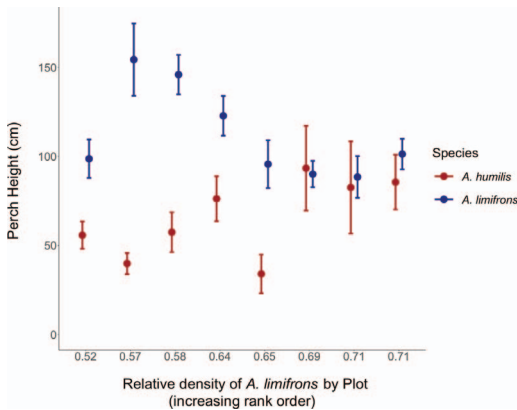
Figure 18. Mean perch heights and standard errors of *A. humilis* and *A. limifrons* by eight plots, rank-ordered by increasing *A. limifrons* relative density. All plots had greater numbers of *A. limifrons* than *A. humilis* (i.e., relative densities greater than 0.5).

lemurinus and sex was a significant predictor of PC1; therefore, differences in PC1 as a main effect between the species were not interpretable. *Anolis humilis* had greater values of PC2 than *A. limifrons* and *A. lemurinus*, and *A. lemurinus* was greater than *A. limifrons* (Supplementary Table S4; Fig. 17).

Perch height and perch diameter varied substantially across plots for both *A. humilis* and *A. limifrons* (Fig. 18). The interaction between species and plot was a significant predictor of perch height, but for perch diameter and ground perch type, neither the interaction nor species were significant predictors (Supplementary Table S5). Among plots, perch height of *A. humilis* had a moderate, marginally significant, positive correlation with relative density of *A. limifrons* (Supplementary Table S5; Fig. 18), and perch height of *A. limifrons* had a nonsignificant positive correlation with relative density of *A. humilis* (Supplementary Table S5). Additionally, a negative correlation between perch heights of *A. humilis* and *A. limifrons*

was not significant (Supplementary Table S5).

We also tested the hypothesis that species differing in habitat use would also differ in escape behavior. *Anolis humilis* and *A. limifrons* did not differ in flight distance or activity type, and the two species had marginally significant differences in movement distance and movement direction (Supplementary Table S6). *Anolis humilis* fled upward in 20% and fled downward in 26% of observations, whereas *A. limifrons* fled upward in 13% and downward in 35% of observations. *Anolis humilis* ran in 42% and jumped in 58% of all movements, and *A. limifrons* ran in 32% and jumped in 68% of movements.

DISCUSSION

In many organisms, morphology, behavior, ecology, and performance are intimately linked and evolve in a coordinated fashion (Losos, 1990b, 1990c). Consequently, behavioral and ecological traits may be inferred from morphology, and similar relationships may appear across a taxonomic group (Williams, 1983; Winemiller et al., 1995; Rüber and Adams, 2001; Wagner and Erwin, 2006; Trontelj et al., 2012; Ellingson et al., 2014; Friedman et al., 2016). Among Caribbean anoles, repeated patterns of ecomorphological diversification have emerged (Rand and Williams, 1969; Williams, 1972, 1983; Losos, 2009). However, a few studies examining whether these relationships hold true in the mainland *Anolis* radiation have revealed that variation is structured differently (Irschick et al., 1997; Velasco and Herrel, 2007; Schaad and Poe, 2010; but see Moreno-Arias and Calderón-Espinosa, 2015).

In line with our predictions, we found substantial variation in habitat use across all species for which we had adequate sample

sizes, namely *A. humilis*, *A. limifrons*, *A. lemurinus*, *A. oxylophus*, *A. capito*, *A. carpenteri*, and *A. biporcatus* (Tables 1, 2; Fig. 4). We argue that these species do not fit the mold of the West Indian ecomorphs and that attempts to classify mainland species into ecomorph classes are not useful in accurately characterizing habitat use and niche partitioning, at least in the La Selva *Anolis* community. For example, *A. lemurinus* has been variably described as a trunk–ground anole perching 0.5–3.0 m above the ground (Costa Rica; Savage, 2002), as an understory anole inhabiting low vegetation and the forest floor (Belize; Stafford and Meyer, 2000), confined to large trees with buttresses and staying 2–3 m above ground (Mexico; Henderson and Fitch, 1975), and even as a canopy anole jumping from branch to branch (Costa Rica; Leenders, 2001). This variability in habitat use by *A. lemurinus* could reflect geographic differences in habitat use of this species or may simply reflect different impressions and data collection methods of various researchers.

Other mainland anoles at La Selva similarly deviate from the ecomorph syndrome of West Indian anoles. *Anolis humilis* has been designated a trunk–ground ecomorph (Andrews, 1979; Huyghe et al., 2007), a class characterized by long hindlimbs, long tails, and the use of low and broad perches (Losos, 2009). Although habitat use by *A. humilis* is on average consistent with trunk–ground ecomorphs, the hindlimbs of this leaf litter inhabitant are relatively short, as opposed to long (Supplementary Table S2; Figs. 15, 16). *Anolis limifrons* has been described as both a grass–bush anole (Andrews, 1979; Huyghe et al., 2007) and a trunk–ground anole (Savage, 2002). Moreover, morphologically, this species is not particularly similar to either trunk–ground anoles, which are stockier and have longer hindlimbs, or grass–bush anoles, which have extremely long tails and

possess long hindlimbs (Supplementary Table S2; Figs. 15, 16). Our observational data of perch height indicates that *A. limifrons* on average occupies higher perches than *A. humilis* (Supplementary Table S1; Talbot, 1976, 1979), ranges from the ground up to 400 cm high, and has a highly variable choice of substrate (Supplementary Tables 1, 2; Figs. 4, 6), which contrasts with the low, narrow supports used by West Indian grass–bush anoles or the low, generally broad surfaces in West Indian trunk–ground ecomorphs. We do not present morphological data of the other six *Anolis* species at La Selva. However, *A. pentaprion* superficially resembles a twig ecomorph, whereas the other species have no clear affinities.

Ecomorphological studies of island anoles have revealed a positive relationship between hindlimb length and perch diameter and a negative relationship between hindlimb length and perch height (Collette, 1961; Irschick et al., 1997; Losos, 1990c). At one extreme, trunk–ground ecomorphs have long hindlimbs and use broader supports; at the other extreme, twig ecomorphs have shorter hindlimbs and use narrow supports (Pounds, 1988; Losos, 1990a, 1990b). We found the opposite relationship when considering the three most abundant species of the La Selva *Anolis* community on the mainland. Relative to their body size, *A. humilis*, a principally terrestrial anole, has proportionally shorter hindlimbs, whereas arboreal *A. limifrons* and *A. lemurinus*, have proportionally longer hindlimbs (Supplementary Tables S1, S2; Figs. 6, 15). Lack of morphological divergence in forelimb length strongly contrasts with the differentiation of hindlimb length in these three species (Supplementary Table S1; Fig. 15). Whether this relationship is maintained in the other six sympatric species at La Selva remains to be determined. However, canopy-dwelling *A. pentaprion* has short hindlimbs, whereas terrestrial *A. capito* has

long hindlimbs (Savage, 2002; Vitt and Zani, 2005), further complicating the relationship.

The entire La Selva *Anolis* community (eight species) for which we provide data was incorporated into a study by Schaad and Poe (2010), which assigned solely *A. carpenteri* to a Caribbean ecomorph class on the basis of morphological data. Because a species' structural microhabitat is one of the two major components of ecomorphological theory (Rand and Williams, 1969; Williams, 1972, 1983), morphological similarity alone cannot be sufficient evidence for pertaining to a particular ecomorph class. In the case of *A. carpenteri*, Schaad and Poe (2010) designate the species as a grass–bush ecomorph, which is at odds with ecological data suggesting that *A. carpenteri* occupies perches high in the forest canopy (Corn, 1981). However, our study remains in accordance with theirs in interpretation; there is little evidence to suggest mainland and Caribbean radiations have produced the same ecomorph syndrome.

Given that tropical rainforest habitats are characterized by high structural complexity of vegetation (Scarano, 2002), La Selva anoles are more likely to encounter and traverse a variety of perches than anoles occupying less heterogeneous environments. It is possible that habitat complexity affords advantages to anoles able to utilize perches of diverse shapes and forms, minimizing differences in habitat use between co-occurring species. By this argument, anoles in structurally complex habitats are less likely to become microhabitat specialists, which may contribute to divergent ecomorphological patterns on account of the environment. Comparisons of whether the availability of perch types differ between mainland and island habitats are needed to test this hypothesis, although existing work indicates habitat complexity may be comparable between the two (Siliceo-Cantero et al.,

2016). Nonetheless, it should be noted that increased habitat complexity has predominantly been theorized to be a driver of niche differentiation, whereby a wider range of microhabitats facilitates specialization to reduce niche space overlap and interspecific competition (Klopfer and MacArthur, 1960; Willis et al., 2004; Loke et al., 2015). Characterization of perch availability and preference assays involving ecologically relevant choices will help unravel the interplay between environment and behavior in explaining variation in habitat use across mainland and island anole populations.

Interspecific effects on habitat use

When two species of the same trophic level overlap in habitat use, the food resources available to each species are reduced, so species should shift to areas with higher food resources, and experimental studies have shown that *A. humilis* will alter its habitat use according to food availability (Guyer, 1988). Direct agonistic interactions between species may likewise contribute to changes in habitat use. Populations of *A. limifrons* that experience high rates of agonistic interactions with congeners exhibit upward shifts in habitat preference, resulting in interpopulation differences between the Pacific and Caribbean versants (Barquero and Bolaños, 2018). Because *A. humilis* and *A. limifrons* are the two most abundant anoles at La Selva, local relative densities of these two species give insight into whether anoles differentiate in habitat use to minimize interspecific competition for space and resources. When both species are abundant, we expect that populations of one species will differ in habitat use depending on the local population density of the other species (i.e., in high abundance of a more arboreal species, a more terrestrial species should use lower perches, and vice versa).

We expected *A. humilis*, the more terrestrial species, to decrease its perch height in plots where *A. limifrons*, the more arboreal species, was abundant. Although local relative density of *A. limifrons* was a marginally significant predictor of *A. humilis* perch height, the relationship between the two variables was contrary to expectations. With increasing relative densities of *A. limifrons*, *A. humilis* was found to occupy higher perches on average (Supplementary Table S5; Fig. 18). Changes in *A. limifrons* perch use according to *A. humilis* density were also found, but they were not statistically significant (Supplementary Table S5). These findings therefore suggest that interspecific competition was not at a high enough level to elicit divergent shifts in habitat use by co-occurring species. Why *A. humilis* actually perches higher, thus spatially overlapping with *A. limifrons* to a greater extent when the latter species is more abundant, is not clear. Our data indicate that the two species do not show parallel increases in perch height across plots (Supplementary Table S5), ruling out the possibility that both are responding to the same factor, such as abundance of ground predators, arboreal prey, or yet another competitor. More research is required to further investigate this finding.

Our unexpected findings of local habitat use patterns among co-occurring *A. humilis* and *A. limifrons* may indicate that low levels of competition between the two species are insufficient in dictating changes in habitat use. However, *A. humilis* and *A. limifrons* may differ in other axes of niche partitioning, such as in thermal and dietary resources. There is evidence for divergence in diet among sympatric *Anolis* species in the mainland (Moreno-Arias et al., 2020), and previous work on the time budgets of *A. humilis* and *A. limifrons* indicates that the two species may allocate particular activities to different subsets of the microhabitats they inhabit (e.g., dissimilar preferences for locations to take refuge and forage) (Talbot, 1979). Another possibility is that because mainland communities comprise a greater diversity of species, anoles experience higher levels of competition with taxa outside of their own genus. La Selva has more than two dozen species of lizards, approximately 50 species of amphibians (McDiarmid and Savage, 2005), a tremendous diversity of insectivorous birds (Sigel et al., 2006), and a high abundance of large carnivorous arthropods (Folt and Lapinski, 2017). Indeed, a lower number of non-anole competitors on islands may promote diversification through exploitation of unfilled niches, whereas on the mainland the presence of non-anole competitors reduces the availability of open niches (Poe and Anderson, 2019). Although recent studies propose similar morphological diversity overall between mainland and island *Anolis* radiations, then, per a given community assemblage, islands tend to be more diverse locally (Anderson and Poe, 2019; Poe and Anderson, 2019). The hypothesis that coexistence patterns with non-anoles may be a major driver of ecomorphological diversity in *Anolis* is promising, although ecological data from populations throughout the mainland are needed to lend further support to this idea.

Escape behavior

Even if two species are sympatric and occupy similar microhabitats, with divergence in morphology one might expect locomotor patterns to differ, such as escape behavior. Previous behavioral data indicate that *A. limifrons* employs cryptic escape behavior by flattening its body against the substrate and moving out of the predator's view (Talbot, 1979; Lattanzio, 2009). When pursued directly, *A. limifrons* runs up to the canopy or jumps, and *A. humilis* drops to the

leaf litter to camouflage against the forest floor (Talbot, 1979). The escape behavior data collected in this study contradict these findings. Movement direction and activity type were highly variable for *A. humilis* and *A. limifrons*, consisting of both running and jumping in every direction (Supplementary Table S6). Cryptic movements were uncommon in *A. limifrons* when directly pursued and probably instead serve as a mechanism to avoid detection from afar by predators. Sympatric species tend to differ in escape response when separated by ecological niche compared with those with overlap in habitat use (Larimer et al., 2006; Lattanzio, 2009). In mainland anoles, a varied substrate choice and high vegetative diversity in the tropical understory may contribute to minimizing behavioral differences. The lack of a regimented escape behavior in *A. humilis* and *A. limifrons* corroborates this idea, although similar variability in escape behavior has also been observed in species occupying different microhabitats (Cooper, 2010), as well as among ecologically similar species that differ in limb proportion (Kahrl et al., 2018). An alternative hypothesis is that varied escape behaviors are advantageous in hindering a predator's ability to learn and predict escape responses, which is most pertinent to mainland environments where predator–prey interactions occur at a high frequency. Conversely, in habitats with fewer predators, uniform evasive tactics should be favored by natural selection to maximize the success of individual escape responses across relatively infrequent agonistic encounters (Schall and Pianka, 1980).

Concluding remarks

This study aims to uncover ecomorphological characteristics in mainland anoles and compare them with well-documented patterns among island anoles. Our data of eight sympatric anoles in the Costa Rica mainland shows variability in breadth of habitat use and substantial niche overlap. Furthermore, interspecific effects on habitat use by *A. humilis* and *A. limifrons* suggest low levels of competition, which might yield a decreased selective pressure for niche partitioning (although predation can also lead to apparent competition and changes in niche structure; Bonsall and Hassell, 1997; Falk et al., 2015). Why mainland and island radiations of *Anolis* exhibit marked differences in ecological morphology remains unclear. The two clades differ in many aspects of ecology and life history traits (see Andrews, 1979), although further research is needed to corroborate the patterns outlined by Andrews (1979) 40 years ago. Understanding how these factors are interrelated may lead to a better understanding of the different evolutionary trajectories of anoles from these two regions.

ACKNOWLEDGMENTS

SHARED DATA

All data and R scripts from this study can be accessed at doi:10.17605/OSF.IO/ZCQXY.

LITERATURE CITED

Anderson, C. G., and S. Poe. 2019. Phylogeny, biogeography and island effect drive differential evolutionary signals in mainland and island lizard assemblages. *Zoological Journal of the Linnean Society* 185: 301–311.

Andrews, R. M. 1971. Structural habitat and time budget of a tropical *Anolis* lizard. *Ecology* 52: 262–270.

Andrews, R. M. 1979. Evolution of life histories: a comparison of *Anolis* lizards from matched island and mainland habitats. *Breviora* 454: 1–51.

Andrews, R. M., and A. S. Rand. 1983. Limited dispersal of juvenile *Anolis limifrons*. *Copeia* 1983: 429–434.

Armstead, J. V., F. Ayala, O. Torres-Carvajal, M. J. Ryan, and S. Poe. 2017. Systematics and ecology of *Anolis biporcatus* (Squamata: Iguanidae). *Salamandra* 53: 285–293.

Barquero, M. D., and F. Bolaños. 2018. Morphological and ecological variation of a tropical anoline lizard: Are agonistic interactions shaping ecomorphological relationships? *Biological Journal of the Linnean Society* 124: 350–362.

Bonsall, M. B., and M. P. Hassell. 1997. Apparent competition structures ecological assemblages. *Nature* 388: 371–373.

Clark, D. B., and D. A. Clark. 2006. Tree growth, mortality, physical condition, and microsite in an old-growth lowland tropical rain forest. *Ecology* 87: 2132.

Collette, B. B. 1961. Correlations between ecology and morphology in anoline lizards from Havana, Cuba and southern Florida. *Bulletin of The Museum of Comparative Zoology* 125: 137–162.

Cooper, W. E., Jr. 2006. Risk factors affecting escape behaviour by Puerto Rican *Anolis* lizards. *Canadian Journal of Zoology* 84: 495–504.

Cooper, W. E., Jr. 2010. Escape tactics and effects of perch height and habituation on flight initiation distance in two Jamaican anoles (Squamata: Polychrotidae). *Revista de Biología Tropical* 58: 1199–1209.

Corn, M. J. 1981. Ecological separation of *Anolis* lizards in a Costa Rican rainforest. Ph.D. Dissertation. University of Florida: Gainesville, Florida.

Echelle, A. A., A. F. Echelle, and H. S. Fitch. 1971. A new anole from Costa Rica. *Herpetologica* 27: 354–362.

Ellingson, R. A., C. C. Swift, L. T. Findley, and D. K. Jacobs. 2014. Convergent evolution of ecomorphological adaptations in geographically isolated bay gobies (Teleostei: Gobionellidae) of the temperate North Pacific. *Molecular Phylogenetics and Evolution* 70: 464–477.

Evans, K. M., L. Y. Kim, B. A. Schubert, and J. S. Albert. 2019. Ecomorphology of neotropical electric fishes: an integrative approach to testing the relationships between form, function, and trophic ecology. *Integrative Organismal Biology* 1(1): obz015.

Falk, J. J., H. M. ter Hofstede, P. L. Jones, M. M. Dixon, P. A. Faure, E. K. V. Kalko, and R. A. Page. 2015. Sensory-based niche partitioning in a multiple predator–multiple prey community. *Proceedings of the Royal Society B* 282(1808): 20150520

Fitch, H. S. 1976. Sexual size differences in the mainland anoles. *Occasional Papers of the Museum of Natural History, the University of Kansas* 50: 1–21.

Folt, B., and W. Lapinski. 2017. New observations of frog and lizard predation by wandering and orb-weaver spiders in Costa Rica. *Phyllomedusa: Journal of Herpetology* 16(2): 269.

Fondren, A., L. Swierk, and B. J. Putman. 2019. Clothing color mediates lizard responses to humans in a tropical forest. *Biotropica* 52: 172–181.

Friedman, S. T., S. A. Price, A. S. Hoey, and P. C. Wainwright. 2016. *Journal of Evolutionary Biology* 29: 965–978.

Galewski, T., J.-F. Mauffrey, Y. L. R. Leite, J. L. Patton, and E. J. P. Douzery. 2005. Ecomorphological diversification among South American spiny rats (Rodentia: Echimyidae): a phylogenetic and chronological approach. *Molecular Phylogenetics and Evolution* 34: 601–615.

Gorman, G. C. 1980. *Anolis occultus*, a small cryptic canopy lizard: are there pair bonds? *Caribbean Journal of Science* 15: 3–4.

Guyer, C. 1988. Food supplementation in a tropical mainland anole, *Norops humilis*: effects on individuals. *Ecology* 69: 362–369.

Guyer, C., and M. A. Donnelly. 2005. *Amphibians and Reptiles of La Selva, Costa Rica, and the Caribbean*

Slope: A Comprehensive Guide. Berkeley: University of California Press.

Hadfield, J. D. 2010. MCMC Methods for multi-response generalized linear mixed models: the MCMCglmm R package. *Journal of Statistical Software* 33(2): 1–22.

Harrison, A. 2013. Size-assortative pairing and social monogamy in a neotropical lizard, *Anolis limifrons* (Squamata: Polychrotidae). *Breviora* 534: 1–9.

Henderson, R. W., and H. S. Fitch 1975. A comparative study of the structural and climatic habitats of *Anolis sericeus* (Reptilia: Iguanidae) and its syntopic congeners at four localities in southern Mexico. *Herpetologica* 31(4): 459–471.

Herrmann, N. C. 2017. Substrate availability and selectivity contribute to microhabitat specialization in two Central American semiaquatic anoles. *Breviora* 555: 1–13.

Holdridge, L. R. 1947. Determination of world plant formations from simple climatic data. *Science* 105: 367–368.

Huyghe, K., A. Herrel, B. Vanhooydonck, J. J. Meyers, and D. I. Irschick. 2007. Microhabitat use, diet, and performance data on the Hispaniolan twig anole, *Anolis sheplani*: pushing the boundaries of morphospace. *Zoology* 110: 2–8.

Irschick, D. J. 2000. Effects on behavior and ontogeny on the locomotor performance of a West Indian lizard, *Anolis lineatopus. Functional Ecology* 14: 438–444.

Irschick, D. J., C. C. Austin, K. Petren, R. N. Fisher, J. B. Losos, and O. Ellers. 1996. A comparative analysis of clinging ability among pad-bearing lizards. *Biological Journal of the Linnean Society* 59: 21–35.

Irschick, D. J., L. J. Vitt, P. A. Zani, and J. B. Losos. 1997. A comparison of evolutionary radiations in mainland and caribbean *Anolis* lizards. *Ecology* 78: 2191–2203.

Joyal, E. 1994. Palm ethnoecology in the Sarapiqui region of Costa Rica. *Journal of Ethnobiology* 14: 161–172.

Kahrl, A. F., B. M. Ivanov, K. C. W. Valero, and M. A. Johnson. 2018. Ecomorphological variation in three species of Cybotoid anoles. *Herpetologica* 74: 29.

Kelm, D. H., K. R. Wiesner, and O. von Helversen. 2008. Effects of artificial roosts for frugivorous bats on seed dispersal in a neotropical forest pasture mosaic. *Conservation Biology* 22: 733–741.

Klopfer, P. H., and R. MacArthur. 1960. Niche size and faunal diversity. *American Naturalist* 94: 293–300.

Köhler, G., A. Schulze, and M. Vesely. 2005. Morphological variation in *Norops capito* (Peters, 1863), a wide-spread species in southeastern Mexico and Central America. *Salamandra* 41: 129–136.

Kozak, K. H., A. Larson, R. M. Bonett, and L. J. Harmon. 2007. Phylogenetic analysis of ecomorphological divergence, community structure, and diversification rates in dusky salamanders (Plethodontidae: *Desmognathus*). *Evolution* 59: 2000–2016.

Larimer, S. C., R. Powell, and J. S. Parmerlee, Jr. 2006. Effects of structural habitat on the escape behavior of the lizard, *Anolis gingivinus. Amphibia-Reptilia* 27: 569–574.

Lattanzio, M. 2009. Escape tactic plasticity of two sympatric *Norops* (beta *Anolis*) species in northeast Costa Rica. *Amphibia-Reptilia* 30: 1–6.

Leal, M., A. K. Knox, and J. B. Losos. 2002. Lack of convergence in aquatic *Anolis* lizards. *Evolution* 56: 785–791.

Leenders, T. 2001. *A Guide to Amphibians and Reptiles of Costa Rica*. San José, Costa Rica: Distribuidores Zona Tropical.

Loke, L. H. L., R. J. Ladle, T. J. Bouma, and P. A. Todd. 2015. Creating complex habitats for restoration and reconciliation. *Ecological Engineering* 77: 307–313.

Losos, J. B. 1990a. The evolution of form and function: morphology and locomotor performance in West Indian *Anolis* lizards. *Evolution* 44: 1189–1203

Losos, J. B. 1990b. Concordant evolution of locomotor behaviour, display rate and morphology in *Anolis* lizards. *Animal Behaviour* 39: 879–890.

Losos, J. B. 1990c. Ecomorphology, performance capability, and scaling of West Indian *Anolis* lizards: an evolutionary analysis. *Ecological Monographs* 60: 369–388.

Losos, J. B. 2009. Lizards in an evolutionary tree: ecology and adaptive radiation of anoles. Berkeley: University of California Press.

Losos, J. B., and D. J. Irschick. 1996. The effect of perch diameter on escape behaviour of *Anolis* lizards: laboratory predictions and field tests. *Animal Behaviour* 51: 593–602.

Losos, J. B., and B. Sinervo. 1989. The effects of morphology and perch diameter on sprint performance of *Anolis* Lizards. *Journal of Experimental Biology* 145: 23–30.

Losos, J. B., M. L. Woolley, D. L. Mahler, O. Torres-Carvajal, K. E. Crandell, E. W. Schaad, A. E. Narváez, F. Ayala-Varela, and A. Herrel. 2012. Notes on the natural history of the little-known Ecuadorian horned anole, *Anolis proboscis. Breviora* 531: 1–17.

Macrini, T. E., D. J. Irschick, and J. B. Losos. 2003. Ecomorphological differences in toepad characteristics between mainland and island anoles. *Journal of Herpetology* 37: 52–58.

Maestri, R., L. R. Monteiro, R. Fornel, N. S. Upham, B. D. Patterson, and T. R. O. de Freitas. 2016. The ecology of a continental evolutionary radiation: is the radiation of sigmodontine rodents adaptive? *Evolution* 71: 610–632.

Mahler, L., S. M. Lambert, A. J. Geneva, J. Ng, S. B. Hedges, J. B. Losos, and R. E. Glor. 2016. Discovery of a giant chameleon-like lizard (*Anolis*) on Hispaniola and its significance to understanding replicated adaptive radiations. *The American Naturalist* 188: 357–364.

McDade, L. A., K. S. Bawa, H. A. Hespenheide, and G. S. Hartshorn (eds.). 1994. *La Selva: Ecology and Natural History of a Neotropical Rain Forest*. Chicago: University of Chicago Press.

McDiarmid, R. W., and J. M. Savage. 2005. The herpetofauna of the Rincon area, Peninsula de Osa, Costa Rica, a Central American lowland evergreen forest site. PP. 366–427 IN: M. A. Donnelly, B. I. Crother, C. Guyer, M. H. Wake, and M. E. White, editors. *Ecology and Evolution in the Tropics: A Herpetological Perspective*. Chicago: University of Chicago Press.

Moermond, T. C. 1979. Habitat constraints on the behavior, morphology, and community structure of *Anolis* lizards. *Ecology* 60: 152–164.

Moon, R. M., and A. Kamath. 2019. Re-examining escape behaviour and habitat use as correlates of dorsal pattern variation in female brown anole lizards, *Anolis sagrei* (Squamata: Dactyloidae). *Biological Journal of the Linnean Society* 126: 783–795.

Moreno-Arias, R. A., P. Bloor, and M. L. Calderón-Espinosa. 2020. Evolution of ecological structure of anole communities in tropical rain forests from north-western South America. *Zoological Journal of the Linnean Society* 190: 298–313.

Moreno-Arias, R. A., and M. L. Calderón-Espinosa. 2015. Patterns of morphological diversification of mainland *Anolis* lizards from northwestern South America. *Zoological Journal of the Linnean Society* 176: 632–647.

Muñoz, M. M., K. E. Crandell, S. C. Campbell-Staton, K. Fenstermacher, H. K. Frank, P. van Middlesworth, M. Sasa, J. B. Losos, and A. Herrel. 2015. Multiple paths to aquatic specialization in four species of Central American *Anolis* lizards. *Journal of Natural History* 49: 1717–1730.

Norton, S. F., J. J. Luczkovich, and P. J. Motta. 1995. The role of ecomorphological studies in the comparative biology of fishes. *Environmental Biology of Fishes* 44: 287–304.

Oberbauer, S. F., C. Guyer, V. Paniagua, D. Dierick, and M. A. Donnelly. 2013. *Herpetological Review* 44: 677–678.

Østbye, K., P.-A. Amundsen, L. Bernatchez, A. Klemetsen, R. Knudsen, R. Kristoffersen, T. F. Næsje, and K. Hindar. 2006. Parallel evolution of ecomorphological traits in the European whitefish *Coregonus lavaretus* (L.) species complex during postglacial times. *Molecular Ecology* 15: 3983–4001.

Poe, S., and C. G. Anderson. 2019. The existence and evolution of morphotypes in *Anolis* lizards: coexistence patterns, not adaptive radiations, distinguish mainland and island faunas. *PeerJ: Biodiversity and Conservation* 6: e6040.

Poe, S., A. Nieto-Montes de Oca, O. Torres-Carvajal, K. De Queiroz, J. A. Velasco, B. Truett, L. N. Gray, M. J. Ryan, G. Köhler, F. Ayala-Varela, and I. Latella. 2017. A phylogenetic, biogeographic, and taxonomic study of all extant species of *Anolis* (Squamata; Iguanidae). *Systematic Biology* 66: 663–697.

Pounds, J. A. 1988. Ecomorphology, locomotion, and microhabitat structure: patterns in a tropical mainland *Anolis* community. *Ecological Monographs* 58: 299–320.

Pyron, R. A., F. T. Burbrink, and J. J. Wiens. 2013. A phylogeny and revised classification of Squamata, including 4161 species of lizards and snakes. *BMC Evolutionary Biology* 13: 93.

R Core Team. 2019. *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing.

Rand, A. S. 1967. Ecology and social organization in the iguanid lizard *Anolis lineatopus*. *Proceedings of the United States National Museum* 122: 1–79.

Rand, A. S., and E. E. Williams. 1969. The anoles of La Palma: aspects of their ecological relationships. *Breviora* 327: 1–17.

Rodríguez-Schettino, L., J. B. Losos, P. E. Hertz, K. de Queiroz, A. R. Chamizo, M. Leal, and V. R. González. 2010. The anoles of Soroa: aspects of their ecological relationships. *Breviora* 520: 1–22.

Rüber, L., and D. C. Adams. 2001. Evolutionary convergence of body shape and trophic morphology in cichlids from Lake Tanganyika. *Journal of Evolutionary Biology* 14: 325–332.

Savage, J. M. 2002. *The Amphibians and Reptiles of Costa Rica: A herpetofauna between Two Conti-*

nents, between Two Seas. Chicago: University of Chicago Press.

Scarano, F. R. 2002. Structure, function and floristic relationships of plant communities in stressful habitats marginal to the Brazilian Atlantic rainforest. Annals of Botany 90: 517–524.

Schaad, E. W., and S. Poe. 2010. Patterns of ecomorphological convergence among mainland and island Anolis lizards. Biological Journal of the Linnean Society 101: 852–859.

Schall, J. J., and E. R. Pianka. 1980. Evolution of escape behavior diversity. The American Naturalist 115: 551–566.

Schluter, D. 2000. The Ecology of Adaptive Radiation. Oxford: Oxford University Press.

Sigel, B. J., T. W. Sherry, and B. E. Young. 2006. Avian community response to lowland tropical rainforest isolation: 40 years of change at La Selva Biological Station, Costa Rica. Conservation Biology 20: 111–121.

Siliceo-Cantero, H. H., A. García, R. G. Reynolds, G. Pacheco, and B. C. Lister. 2016. Dimorphism and divergence in island and mainland anoles. Biological Journal of the Linnean Society 118: 852–872.

Stafford, P. J., and J. R. Meyer. 2000. A guide to the reptiles of Belize. San Diego, California: Academic Press.

Streelman, J. T., M. Alfaro, M. W. Westneat, D. R. Bellwood, and S. A. Karl. 2007. Evolutionary history of the parrotfishes: biogeography, ecomorphology, and comparative diversity. Evolution 56: 961–971.

Swierk, L. 2019. Anolis aquaticus (=Norops aquaticus) (water anole). Underwater breathing. Herpetological Review 50: 134–135.

Talbot, J. J. 1976. Ecological and behavioral factors regulating the spatial distribution of Norops humilis and N. limifrons (Sauria: Iguanidae) at a tropical rainforest locality. Ph.D. Dissertation. Los Angeles, University of Southern California.

Talbot, J. J. 1979. Time budget, niche overlap, inter- and intraspecific aggression in Anolis humilis and Anolis limifrons from Costa Rica. Copeia 3: 472–481.

Torres-Carvajal, O., F. P. Ayala-Varela, S. E. Lobos, S. Poe, and A. E. Narváez. 2017b. Two new Andean species of Anolis lizard (Iguania: Dactyloinae) from southern Ecuador. Journal of Natural History 52: 13–16.

Torres-Carvajal, O., C. Koch, P. J. Venegas, and S. Poe. 2017a. Phylogeny and diversity of neotropical monkey lizards (Iguanidae: Polychrus Cuvier, 1817). PLoS ONE 12(6): e0178139.

Townsend, T. M., D. G. Mulcahy, B. P. Noonan, J. W. Sites, Jr., C. A. Kuczynski, and J. J. Wiens. 2011. Phylogeny of iguanian lizards inferred from 29 nuclear loci, and a comparison of concatenated and species-tree approaches for an ancient, rapid radiation. Molecular Phylogenetics and Evolution 61: 363–380.

Trontelj, P., A. Blejec, and C. Fišer. 2012. Ecomorphological convergence of cave communities. Evolution 66: 3852–3865.

Tschapka, M. 2005. Reproduction of the bat Glossophaga commissarisi (Phyllostomidae: Glossophaginae) in the Costa Rican rain forest during frugivorous and nectarivorous periods. Biotropica 37: 409–415.

Tulli, M. J. 2012. Morphometric differences between two sympatric species of Anolis (Reptilia: Squamata: Polychrotidae). North-Western Journal of Zoology 8:132–138.

Vanhooydonck, B., A. Herrel, and D. J. Irschick. 2007. Determinants of sexual differences in escape behavior in lizards of the genus Anolis: a comparative approach. Integrative and Comparative Biology 47: 200–210.

Velasco, J. A., and A. Herrel. 2007. Ecomorphology of Anolis lizards of the Choco region in Colombia and comparisons with Greater Antillean ecomorphs. Biological Journal of the Linnean Society 92: 29–39.

Villareal-Benítez, J. L. 1997. Historia natural del género Anolis. PP. 495–500 IN: E. González-Soriano, E., R. Dirzo, R. C. Vogt, editors. Historia Natural de Los Tuxtlas. Universidad Nacional Autónoma de México, Instituto de Biología.

Vitt, L., and P. Zani. 1996. Ecology of the lizard Ameiva festiva (Teiidae) in southeastern Nicaragua. Journal of Herpetology 30: 110–117.

Vitt, L., and P. Zani. 1998. Prey use among sympatric lizard species in lowland rain forest of Nicaragua. Journal of Tropical Ecology 14: 537–559.

Vitt, L., and P. Zani. 2005. Ecology and reproduction of Anolis capito in rain forest of southeastern Nicaragua. Journal of Herpetology 39: 36–42.

Wagner, P. J., and D. H. Erwin. 2006. Patterns of convergence in general shell form among Paleozoic gastropods. Paleobiology 32: 316–337.

Wainwright, P. C. 1991. Ecomorphology: experimental functional anatomy for ecological problems. American Zoologist 31: 680–693.

Wickham, H. 2016. ggplot2: Elegant Graphics for Data Analysis. New York: Springer-Verlag.

Williams, E. E. 1972. The origin of faunas. Evolution of lizard congeners in a complex island fauna: a trial analysis. Evolutionary Biology 6: 47–89.

Williams, E. E. 1983. Ecomorphs, faunas, island size, and diverse end points in island radiations of *Anolis*. PP. 326–370 IN: R. B. Huey, E. R. Pianka, and T. W. Schoener, editors. *Lizard Ecology: Studies of a Model Organism.* Cambridge, Massachusetts: Harvard University Press.

Willis, S. C., K. O. Winemiller, and H. Lopez-Fernandez. 2004. Habitat structural complexity and morphological diversity of fish assemblages in a Neotropical floodplain river. *Oecologia* 142: 284–295.

Winemiller K. O., L. C. Kelso-Winemiller, and A. L. Brenkert. 1995. Ecomorphological diversification and convergence in fluvial cichlid fishes. *Environmental Biology of Fishes* 44: 235–261.