ORIGINAL RESEARCH

Hierarchical partitioning of multiple niche dimensions among ecomorphs, species and sexes in Puerto Rican anoles

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Abstract

Assemblages of co-occurring closely related species tend to vary in one or more niche dimensions, but niche partitioning also occurs at levels of biological organization above and below the species level. Niche space occupied by a community may involve variation among groups of species, such as guilds or ecomorphs, and among sexes or individuals within species. We examined variation in structural microhabitat, thermal habitat, and prey size and composition in an assemblage of six anole lizards belonging to three habitat specialist ecomorph categories in a Puerto Rican rainforest. As predicted, ecomorphs were most distinct in structural microhabitat, while species within ecomorphs varied mainly in thermal habitat. Ecological sex dimorphism was limited, and considerable variation in all dimensions was unexplained or potentially related to individual-level niche variation. Our analysis largely corroborates the view of anole adaptive radiation and community assembly as involving structural habitat divergence among ecomorphs and secondary divergence among species using different climatic niches. A hierarchical approach to niche variation presents opportunities for taking a comparative approach to understanding how ecological diversity is partitioned within communities.

Introduction

Stable coexistence of species at the local scale is generally understood to require a degree of niche difference, without extreme inequalities in fitness (Chesson, 2000). Niche differences may arise through a combination of evolutionary processes, such as character displacement driven by competition, and ecological processes, such as dispersal and species sorting into stable combinations. The inherent multidimensionality of the niche means that species differences may occur along one or more niche dimensions including multiple aspects of habitat and diet (Hutchinson, 1957). Regardless of the process driving it, differentiation on one or more niche dimension can permit diverse assemblages of even closely related species to co-occur in the same space (Schoener, 1968).

While differences among species receive the most attention, ecological diversity is intrinsically hierarchical and important niche partitioning can occur at multiple levels of biological organization. Thus, species assemblages may be viewed as a hierarchical set of levels of diversity, each of which may or may not show significant variation in a given niche dimension. At higher levels of organization, taxonomic or functional groups of species may be grouped into discrete guilds or ecotypes that use particular food types or structural or climatic microhabitats (Simberloff & Dayan, 1991). At lower levels of organization, intraspecific diversity can lead to still finer filling of niche space within communities (Cloyed & Eason, 2017). Subgroups within populations can show as much ecological difference as some species, for example, through ecological sex dimorphism (Giery & Layman, 2019; Shine, 1989). Finally, even within these subgroups, individuals can show considerable repeatable variation in resource use (Bolnick et al., 2003). While the importance of each of these levels of niche diversity has been well-demonstrated, few if any studies have simultaneously assessed how multiple niche dimensions can be partitioned among levels in the hierarchy.

Because they exhibit ecologically relevant diversity at multiple levels of biological organization, Greater Antillean *Anolis* lizards (anoles) present an ideal study system in which to investigate the hierarchical partitioning of niche dimensions. Anoles have famously evolved similar sets of ecomorphs on different islands (Losos, 2009). Anole ecomorphs are defined as species having similar morphological and behavioral adaptations to use particular structural niches (e.g. vegetation microhabitats, such as grasses, tree trunks, branches or twigs), whether or not they are close relatives (Williams, 1972).

Speciation within ecomorph classes has led to considerable species diversity on some islands, with species in the same ecomorph often differentiated along climatic gradients (Huey & Webster, 1976; Ruibal, 1961). Sexual dimorphism increases the degree of packing in morphospace and likely in niche space as well (Butler et al., 2007; Schoener, 1967). Finally, consistency in microhabitat use (Kamath & Losos, 2017) and diet (Giery & Stroud, 2019) has recently been demonstrated at the individual level in anoles. Studies of introduced anoles consistently reveal the key role that competition can play in driving character displacement that increases the niche divergence between newly interacting species (Stroud et al., 2019; Stuart et al., 2014). The organization of anole assemblages, therefore, depends on the partitioning of multiple niche dimensions across biological levels.

Here, we investigate how ecological diversity is distributed across multiple niche dimensions for six species of anole that are broadly sympatric in a Puerto Rican rainforest. These species belong to a monophyletic group that radiated within Puerto Rico (Losos, 1992; Williams, 1972) and represent three ecomorphs: Trunk-Crown (*A. evermanni* Stejneger, 1904 and *A. stratulus* Cope, 1861), Trunk-Ground (*A. gundlachi* Peters, 1877 and *A. cristatellus* Duméril and Bibron, 1837), and Grass-Bush (*A. krugi* Peters, 1877 and *A. pulchellus* Duméril and Bibron, 1837). One species per ecomorph (*A. evermanni*, *A. gundlachi* and *A. krugi*) is generally associated with cooler interior forest habitats, while the other (*A. stratulus*, *A. cristatellus* and *A. pulchellus*) occurs more often in open and sun-exposed habitats (Rand, 1964). We collected structural microhabitat (perch height and diameter/curvature), body temperature, and diet (size and composition) data from each species in an area of sympatry. To explore how ecological diversity was partitioned within this community, we decomposed the total variance in each niche dimension to calculate the proportion explained by differences among ecomorphs, between species within ecomorphs, and between sexes within species. For diet variables, we repeated this analysis including individual as the lowest level in the hierarchy. We predicted that structural microhabitat would vary most between ecomorphs and that body temperature as a proxy for thermal niche would vary most between species within ecomorphs. We also predicted that interspecific differentiation in diet would be limited but that sexual dimorphism would be present in most dimensions due to size and habitat differences between males and females.

Materials and methods

Lizard sampling

Between 3 June and 14 July 2012, we collected the six anole species from areas near the El Verde Field Station (EVFS), within the Caribbean National Forest in northeastern Puerto Rico. We sampled each of the six species within two elevation ranges. Approximately half of the individuals of each species was collected between 300 and 380 m elevation in the area immediately surrounding the EVFS (on trails through the

tabonuco (*Dacryodes excelsa*) forest, and in a nearby roadside clearing). The remaining individuals of each species were sampled at a second site: a secondary growth forest adjacent to an abandoned and overgrown government work facility located at 180-200 m elevation.

We haphazardly searched for adult anoles and captured them by lasso or by hand, after first taking note of their perch location prior to capture. Immediately upon catching the anole, we measured its body temperature (T_b) using a copper-constantan thermocouple (0.1°C resolution) inserted into its cloaca. We then measured the height above ground and the diameter of its perch. We later converted perch diameter to perch curvature, the reciprocal of the radius (assuming a cylindrical perch), which allowed anoles captured on the ground (defined as curvature = 0) to be included in analysis of this niche dimension. We marked the location where each lizard was collected with flagging tape, then returned them to the El Verde Field Station for further processing the same day. All animal use was approved by the Harvard University Standing Committee on the Use of Animals in Research and Teaching (Protocol No. 26-11).

We measured the snout-vent length (SVL) of each anole to the nearest mm and determined sex by inspection of the postanal scales. We then took a 1–2 cm distal section of the tail for potential genetic analysis, ensuring that it broke along a fracture plane to permit regeneration. To sample stomach contents, we induced the anole to bite down upon a small plastic ring that held its mouth open. We then inserted a stainless steel feeding needle (20 gauge for individuals less than ~50 mm SVL, 15 gauge for larger individuals) with a soft tip down its throat and into its stomach. With the lizard's head angled downward, we used a syringe to flush the stomach with water and induce stomach contents to be regurgitated into a fine mesh filter. Lizards were then returned to the precise site of capture, marked with a permanent felt-tipped marker pen to avoid recaptures, and released. The presence of the distal break in the tail was also used to ensure any previously sampled individual was not recaptured at a later date after molting.

Stomach contents were preserved in 95% ethanol for later inspection. Stomach contents were counted under a dissecting microscope and identified to taxonomic categories. These largely corresponded to orders, but in some cases were aggregated at higher taxonomic categories (Plantae, Annelida, Diplopoda, Gastropoda, Aves [bird feathers]) and Hymenoptera were divided into ants (Formicidae) and non-ants (a paraphyletic grouping of bees and wasps). Where individual prey items were intact, they were measured for maximum length (L) and width (W) in mm. These were converted to a coarse biovolume by calculating the volume of an ellipsoid $V = (4/3) * \pi * (L/2) * (W/2) * (W/2)$ following Magnusson et al. (2003). Volume estimates in mm^3 were averaged for each individual as a measure of prey size, and log-transformed to approximate normality.

Data analysis

For univariate characters – perch height, perch curvature, body temperature, and mean log prey volume – we visualized

variation with beanplots (Kampstra, 2008) and then carried out a nested analysis of variance with sex nested within species nested within ecomorph as predictors. We included site nested within sex to account for any differences between the two sampling areas at different elevations. We tested the significance of each level at $\alpha = 0.05$, then extracted the variance components associated with ecomorph, species, sex, site, and residual variation using the function 'anovaVCA' in the 'VCA' R package (Schuetzenmeister & Dufey, 2020). Any negative variance components were set to zero for the purpose of calculating percent variation explained. For log prey volume which had multiple measures for many individuals, we repeated the nested ANOVA and variance component extraction with the prey item as the replicate, with individual ID as the lowest level of nesting (Ecomorph/Species/Sex/Site/ID).

For prey composition analysis, we excluded prey taxa with fewer than four individual items recorded (Annelida, Aves [feathers], Opiliones, and Pseudoscorpionida). We used the function *adipart* in the R *vegan* package (Oksanen et al., 2020) to partition the Shannon diversity of diet items into a nested series of α-diversities corresponding to the diversity within each level and β-diversities corresponding to the variance between groups at each level. As above, we constructed the hierarchy as site within sex within species within ecomorph. We extracted the analogous diversity components to match the variance components for the univariate characters, dividing by γ-diversity to calculate percentage variation explained, and using 9999 permutations of the data set to obtain significance. As with prey size, we repeated this analysis with individual specified as the lowest level of nesting to incorporate between-individual variation.

Results

We collected niche data for a total of 200 anoles in the area around El Verde Field Station, with 31–40 individuals per species. Males were overrepresented in all species but *A. stratulus*. At least 21 individuals of each species had non-empty stomachs allowing collection of identifiable diet data, including at least 5 of each sex in each species. Males consistently had higher body size (SVL) than females, especially in the larger species *A. gundlachi*, *A. cristatellus* and *A. evermanni* (Fig. 1a).

Structural microhabitat variables distinguished Grass-Bush species from the rest but did little to differentiate Trunk-Ground and Trunk-Crown species (Fig. 1b,c). *A. pulchellus* had the highest body temperature and *A. gundlachi* the lowest (Fig. 1d). The three largest species (*A. gundlachi*, *A. cristatellus* and *A. evermanni*) had the highest average prey size, although there was an extensive overlap (Fig. 1e). The species had broadly similar diet composition with some variation (Fig. 1f), and across all anoles, diets were numerically dominated by Formicidae (44%), Coleoptera (21%), plant matter (9%) and Hemiptera (8%).

Niche dimensions differed considerably in the variance explained at each level of the hierarchical analysis (Table 1; Fig. 2). Ecomorph explained significant variation in each variable, though it explained the most variation only for perch

height (23.1%) and curvature (29.4%) and for prey volume when individual variation was not considered (9.6%). Species nested within ecomorph explained the most variation in body temperature (58.5%), while sex explained relatively little of any variable (<10%). Considerable among-individual variation was inferred for prey size (27.8%) and prey composition (49.6%) when individual was included as a level in the variance partitioning, assuming that multiple diet items represented replicates. There was appreciable variation in body temperature and prey composition among the two sampling areas that differed in elevational range.

Discussion

Our study provides a quantitative picture of how multiple niche dimensions are partitioned hierarchically within a tropical lizard assemblage. Overall, the patterns were consistent with our predictions, derived from longstanding ideas about anole community organization, namely that ecomorphs partition structural habitat while species partition thermal habitat and partitioning of diet is limited.

Our analysis of hierarchical niche partitioning corroborated the general view of anole ecomorphs as primarily microhabitat specialists. By far the most variation in perch height and curvature was explained by ecomorph, although more than 60% of the variation in each measure was unexplained. The Grass-Bush anoles *A. krugi* and especially *A. pulchellus* were clearly characterized by low perch heights and high perch curvatures (i.e. narrow perch diameters). Somewhat surprisingly, there was little separation between the Trunk-Crown and Trunk-Ground species, and in fact perches of the Trunk-Ground species were very slightly higher on average, likely because our sampling was restricted to within a few meters of ground level. Ecomorph also explained significant variation in body temperature, though species nested within ecomorph explained much more, driven by higher T_b in *A. cristatellus* than *A. gundlachi* and much higher T_b in *A. pulchellus* than *A. krugi*. Overall, these results match our expectation and are consistent with the interpretation of climatic niche as a secondary axis along which anole species within ecomorphs undergo divergence. We did find significant diet variation among ecomorphs, though the variation explained was small. Ecomorphs differed more in prey size than composition, with larger prey generally consumed by larger ecomorphs. This, plus the finding that diet composition was more closely related to site than to ecomorph or species, is consistent with the general view that diet differentiation among anole species is largely incidental.

Intraspecific niche diversity has been relatively understudied in anoles compared to variation at the species and ecomorph levels. Sexual dimorphism has previously been documented in size and ecomorphology of many Greater Antillean anoles (Butler & Losos, 2002; Butler et al., 2007), and males are larger than females in all species in this study, especially in the Trunk-Ground species (Butler et al., 2000). Even so, sex explained at most small amounts of the variation in any niche dimension. Sex did explain significant variation in perch height, with males perching higher than females in five of the six species (Butler & Losos, 2002). While sex differences in
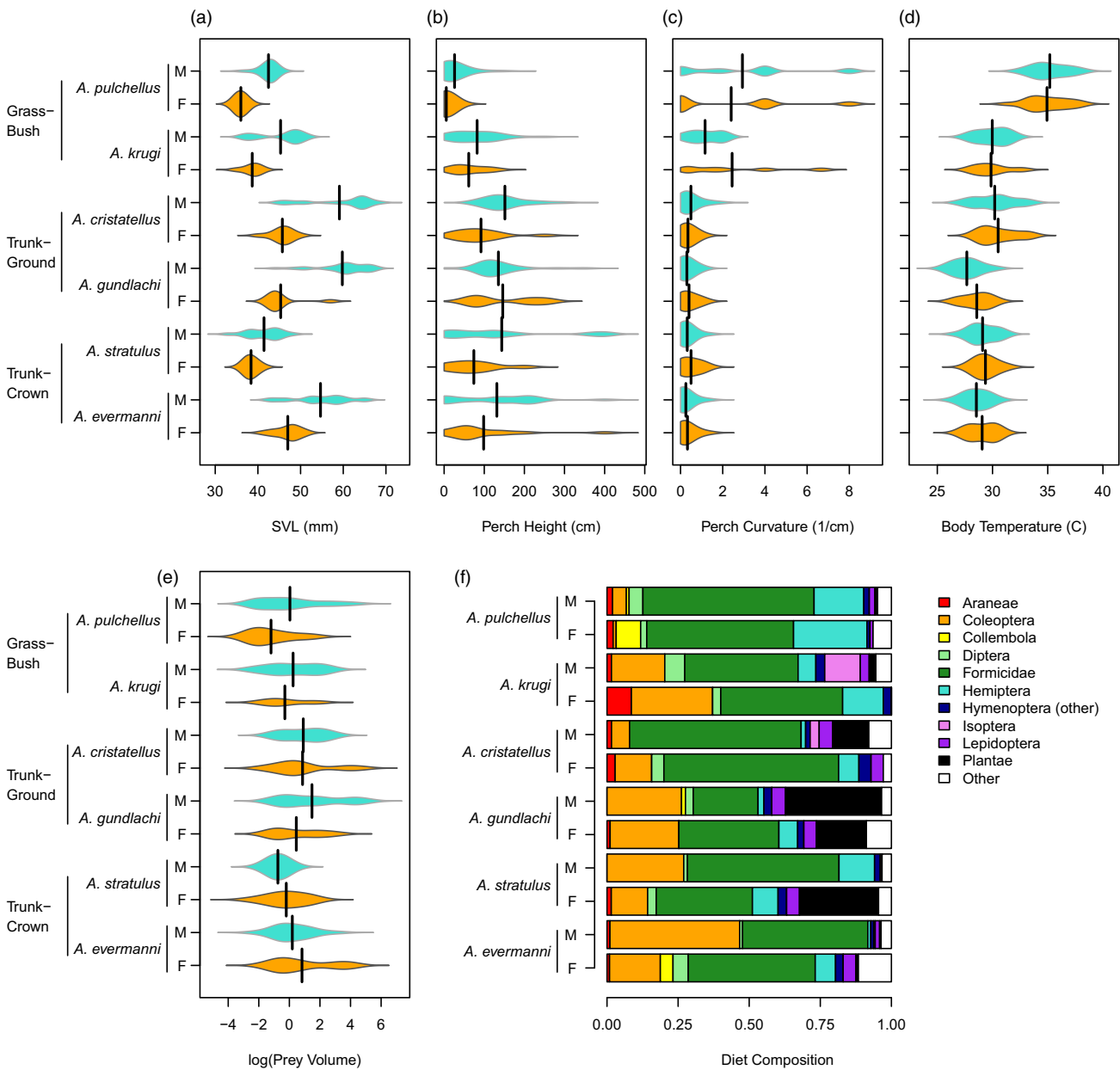
Figure 1 Distribution of body size (SVL) and five niche dimensions for males and females of six Puerto Rican anole species from three ecomorph classes. Beanplots show the median and kernel density estimated for (a) SVL, (b) perch height, (c) perch curvature, the reciprocal of perch diameter, (d) body temperature and (e) log-transformed estimated mean prey volume. (f) Barplot showing the diet composition for males and females of each species (nine rare prey types are grouped as "Other" to improve readability).

size and habitat did not translate to consistent differences in prey size, sex did explain a comparable percentage of diet compositional diversity to ecomorph or species. The differences between male and female diet composition appears idiosyncratic and variable across species – for example, males tended to consume more beetles than females in Trunk-Crown species but not the other species – so may reflect differential habitat use rather than consistent behavioral differences.

Individual specialization has not often been studied in *Anolis*, though early work by Roughgarden (1974) found that

individual variation accounted for between 1 and 33% of the population variation in prey size in different species. We measured comparable or higher amounts of variance explained at the individual level for prey size and composition, although there is a significant caveat that this was based on a single stomach flushing per individual, spread over a few weeks. Cross-sectional diet data are highly vulnerable to effects of temporal or spatial aggregation of prey, and multiple prey individuals may not constitute independent foraging decisions (Bolnick et al., 2002). We, therefore, anticipate that our results

Table 1 Percent variance explained by each hierarchical level for each niche measure, as well as statistical results from nested analysis of variance for continuous variables, and hierarchical diversity partition for diet composition

Niche measure	Statistic	Ecomorph	Species	Sex	Site	Individual	Residual
Perch height	P.V.E.	23.1	2.5	5.2	1.9	–	67.3
	d.f.	2	3	6	12	–	174
	F	26.5	3.93	2.34	1.22	–	–
	P	<0.00001	0.0096	0.034	0.27	–	–
Perch curvature	P.V.E.	29.4	8.1	0.2	0*	–	62.2
	d.f.	2	3	6	12	–	174
	F	36.4	5.18	0.93	0.87	–	–
	P	<0.00001	0.0019	0.48	0.58	–	–
Body temperature	P.V.E.	18.7	56.2	0*	7.9	–	17.1
	d.f.	2	3	6	12	–	175
	F	182.2	109.3	0.84	4.66	–	–
	P	<0.00001	0.00001	0.54	<0.00001	–	–
Log Prey volume	P.V.E.	9.6	2.6	0*	4.5	–	83.3
	d.f.	2	3	6	12	–	110
	F	7.15	2.01	1.25	1.29	–	–
	P	0.0012	0.12	0.29	0.24	–	–
Log Prey volume + indiv. level	P.V.E.	2.8	8.4	1.4	0*	28.6	58.9
	d.f.	2	3	6	12	110	1119
	F	56.9	36.8	7.95	4.58	4.97	–
	P	<0.00001	<0.00001	<0.00001	<0.00001	<0.00001	–
Diet composition	P.V.E.	4.0	6.0	5.6	7.8	–	76.7
	H	0.07	0.11	0.10	0.14	–	1.41
	P	<0.0001	<0.0001	0.0009	0.028	–	–
Diet composition + indiv. level	P.V.E.	4.0	6.0	5.6	7.8	41.7	34.9
	H	0.07	0.11	0.10	0.14	0.77	0.64
	P	<0.00001	<0.00001	0.0005	0.025	<0.00001	-

0* indicates a negative value that was set to zero for the purposes of calculating variance explained. H represents the appropriate alpha or beta terms in Shannon diversity.
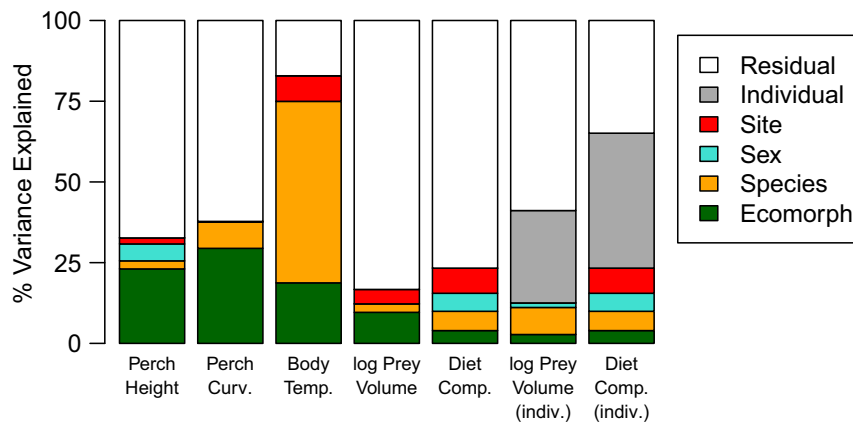

Figure 2 Percent variance of five niche measures explained by different hierarchical levels. All variables included variation explained by ecomorph, species within ecomorph, and sex within species, as well as site (nested within sex) and residual variation. For log(prey volume) and categorical diet composition, analyses were repeated including individual as a level in the hierarchy, to account for multiple items in each stomach.

overestimate the true degree of individual variation, and we recommend that future studies obtain multiple diet samples per individual to more reliably estimate the variance associated with individual identity. Recent findings of individual consistency in microhabitat preference (Kamath & Losos, 2017) and diet (Giery & Stroud, 2019) of anoles suggest that there is value in revisiting the degree of individual specialization within anole species.

Sampling represented a snapshot of resource use during the wet season (summer). Seasonal changes in resource availability, environmental conditions and reproductive cycles have the potential to alter the degree of niche separation among species and among sexes. Lister (1981) studied seasonal variation in three of the same species (*A. evermanni*, *A. gundlachi*, and *A. stratulus*) at Luquillo and found that in the dry winter season all three species used a narrow range of spatial habitats but a broader range of prey types and sizes, thus shifting the degree of niche overlap in different dimensions. There were also important differences between this study and the present diet data, most notably in that Lister (1981) found orthopterans to be the dominant prey type for *A. gundlachi* in both wet and dry seasons, while they were rarely found in any diets in our sample. This may relate to changes in insect abundances at Luquillo, as Lister & Garcia (2018) showed a decrease in insect and especially orthopteran biomass from 1976–77 to 2011–13 (though this finding has been disputed; Willig et al., 2019).

Our results need to be considered in light of several caveats. While we were able to obtain useful information about several niche dimensions for two hundred individual lizards over a compressed period of time, this necessitated some trade-offs in the quality of each measure. Field body temperature is a useful metric for understanding thermal niche variation (Huey & Webster, 1976). However, it fails to capture key elements of the thermal niche including the effects of thermoregulatory behavior and thermal limits and performance curves (Gunderson et al., 2018). Gastric lavage, while advantageous in permitting nonlethal and potentially serial diet sampling, has the drawback that some stomach contents, especially large items, might not be flushed out as easily and might therefore be missed. This presents another possible explanation for the apparent decline in orthopterans in anole diets, as the earlier study examined whole stomach contents after dissection (Lister, 1981). The measures of structural microhabitat are well-established for anole communities, though we were limited to ground observations and thus may have underestimated perch height of species like *A. evermanni* and *A. stratulus* that are commonly observed during canopy sampling (Reagan, 1992). A more complete hierarchical analysis would also incorporate repeated measures of each of these variables for each individual, allowing greater ability to differentiate consistent individual niche differences from other sources of unexplained variation.

A hierarchical approach to investigating niche variation in communities has the potential to shed light on the historical evolutionary and assembly processes that led to present-day structure. A similar partitioning of trait variances has been proposed in the study of trait-based community assembly (Violle et al., 2012). Applying this approach to measures of resource use will permit more direct inference of niche similarity, as well as inclusion of within-individual niche variation where repeat measures for individuals are available (Ingram et al., 2018). We have demonstrated how investigating diet composition using multiple nested levels of beta-diversity can allow analogous partitioning of categorical data for comparison with continuous ecological variables. Evolutionary assembly of communities has been proposed to proceed in discrete stages involving different niche dimensions (Ackerly et al., 2006; Streelman & Danley, 2003). Anoles on a given island seem to typically diverge first in structural microhabitat as ecomorphs evolve, and later along climatic gradients as species diversify within ecomorphs (Hertz et al., 2013; Williams, 1972). This is consistent with the patterns in Puerto Rico where multiple ecomorphs contain species that are differentiated primarily in their use of different climatic niches (Rand, 1964). By comparing communities of different ages, it may be possible to track how niche partitioning at different levels changes as communities assemble through evolution and colonization.

Considering multiple levels of diversity as well as multiple niche dimensions has the potential to enrich our understanding of the niche structure of communities. Application of this framework to Puerto Rican rainforest anoles confirms and quantifies a number of patterns in this well-studied assemblage. Broader application of this framework may reveal interesting differences between communities in which ecological diversity is primarily partitioned at, above, or below the species level.

Acknowledgements

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