

Structure of a Lizard Assemblage in a Semiarid Habitat of the Brazilian Caatinga

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ABSTRACT: We investigated the importance of ecological and historical effects in structuring a lizard assemblage in a semiarid area of Caatinga habitat. We collected lizards using pitfall traps and active searching; we also collected data concerning microhabitat and diet composition for the lizard species examined. We used null models to test whether or not the community was structured following microhabitat or trophic niches. We also tested whether or not such structure had a historical or ecological origin using canonical phylogenetic ordination and phylogenetic principal component analysis. *Gymnodactylus geckoides* and *Tropidurus hispidus* were most generalized in their microhabitat use. *Hemidactylus brasiliensis* and *Phyllorpezus pollicaris* had the greatest numeric niche breadth, whereas *P. pollicaris* and *T. hispidus* had the greatest volumetric niche breadth. In contrast, *Brasiliscincus heathi* and *Ameiva ameiva* had the smallest numeric and volumetric niche breadths, respectively. The lizard assemblage examined had structure in both microhabitat and trophic niches. We detected phylogenetic conservatism on the basis of spatial niches in the clades Teoidea, Teiidae, and Tropiduridae. In contrast to the predictions of the niche complementarity hypothesis, we found high trophic overlap coupled with low microhabitat overlap for tropidurids. Moreover, spatial niche structure was mainly attributable to historical factors (phylogenetic), whereas ecological factors were more important determinants of trophic niche structure.

Key words: Brazil; Canonical phylogenetic ordination; Diet; Ecological factors; Historical factors; Microhabitat use; Niche overlap; Phylogenetic principal component analysis

STUDIES of assemblage structure evaluate the presence of nonrandom patterns in the use of resources by co-occurring species (e.g., Winemiller and Pianka 1990; Mesquita et al. 2006a, 2007; Werneck et al. 2009). Competition has traditionally been considered the main determinant of structure in natural communities (Schoener 1974; Ricklefs and Schluter 1993), but ecological factors also influence assemblage structure. For example, temperature might negatively affect assemblage diversity (Buckley and Jetz 2010); diversity and habitat heterogeneity are not always positively correlated (Tews et al. 2004); and biotic interactions (such as predation or symbioses) might affect reproductive activities, foraging mode, thermoregulation, and refuge selection for each species in an assemblage (e.g., Pianka 1973; Chesson 2000; Afonso and Eterovick 2007; Goodman et al. 2008). In particular, assemblages of lizards, especially those having rare or specialist species, can be negatively affected by invasive woody plants (Bateman and Ostoja 2012).

Historical factors, such as the evolutionary history and phylogenetic inertia of a species, might explain existing ecological patterns more adequately than current ecological processes (Pearson and Juliano 1993; Losos 1994, 1996). For example, assemblages of emydid turtles in southeastern North America tend to have a greater proportion of aquatic species than those in the northeast because of phylogenetic conservatism in two basal clades (thereby limiting convergence in assemblage structure between regions; Stephens and Wiens 2004). Other historical factors that contribute to assemblage structure might include species composition and richness, spatial distribution, ecological or phenotypic traits of species, and evolutionary relationships among the species

representing the community (Brooks and McLennan 1993; Losos 1996).

Several studies of lizard assemblages have been conducted across a range of habitat types (e.g., Pianka 1973; Ricklefs et al. 1981; Winemiller and Pianka 1990; Bell and Donnelly 2006). These studies revealed that variation in available resources among areas (i.e., ecological factors) and species evolutionary history (i.e., historical factors) can, singly or in combination, influence the structure of the particular assemblage. For example, ecological factors responsible for the structure of lizard assemblages in the Kalahari Desert include the niche dimensions of space and time, whereas lizard assemblages in North American deserts and in dry forests in the Brazilian Cerrado are structured by the trophic niche dimension (Pianka 1973; Werneck et al. 2009).

Although studies on lizard assemblages in the Neotropical region have increased considerably in recent years (e.g., Gainsbury and Colli 2003; Mesquita et al. 2006a,b, 2015; Winck et al. 2016), studies in the semiarid Caatinga, an environment restricted to the Brazilian northeast, are still scarce (but see Vitt 1995; Andrade et al. 2013; Passos et al. 2016). Only Vitt (1995) provided information about lizard assemblage structure in the Caatinga region and tested its relationship to historical factors. He concluded that the community structure has its basis in historical trophic patterns, with foraging mode as the primary determining factor. The Caatinga covers 750,000 km² of Brazilian territory, and contains 79 lizard species that likely present variation in ecological aspects and biogeography, including endemism (Andrade et al. 2013; Mesquita et al. 2017). Further study is warranted in this region to test for general patterns among its lizard assemblages, especially for the species therein for which basic life-history data are lacking.

We analyzed patterns of microhabitat use and the trophic niches of a lizard assemblage in a Caatinga habitat of Brazil. We aimed to determine whether or not assemblages have

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nonrandom patterns of resource use and, if so, to evaluate if that structure has an ecological or historical origin. Specifically, we (1) identified and quantified species abundance in the assemblage; (2) measured spatial and trophic niche breadths for each species and niche overlap between pairs of species; (3) tested the niche complementarity hypothesis between each pair of species; (4) used null models to quantify the degree of structure within the assemblage; and (5) tested whether structure, if present, had an ecological or historical origin.

MATERIALS AND METHODS

Study Site

Our study was conducted on the 305-ha Angico farm (08°07'S, 40°05'W; datum = SAD69) located in the rural zone of the municipality of Ouricuri, in the State of Pernambuco, Brazil. The farm is located in a Neotropical semiarid region, with vegetation characterized mainly by deciduous forest and by hypoxerophytic Caatinga. The local climate is hot and semiarid with an average annual temperature of 24.7°C, and monthly average temperatures varying from 22.7°C in the coldest month to 26.2°C in the hottest month (Climate-Data.org 2017). There are distinct rainy and dry seasons, with the rainy season occurring from December to April and the dry season from May to November. The mean annual precipitation is approximately 550 mm (APAC 2013), but with great unpredictability and irregularity in the amount of rainfall (Velloso et al. 2002).

Data Collection

We conducted field activities during five sampling expeditions of 6 d each in December 2011 and in February, April, June, and August of 2012. Two pairs of collectors, in turn, performed active searches from 0800 to 2200 h along trails within the habitat. Sighted lizards were stunned with rubber bands and collected, and the time of capture and the microhabitat where each lizard was first observed were recorded. Our active-searching sampling effort totaled 28 h per day (7 h per person), 168 h per field expedition, and 840 h for all five expeditions combined.

In addition to active searching, we deployed 12 arrays of pitfall traps with drift fences. Each pitfall array was composed of four 20-L buckets configured in a “Y” formation (Cechin and Martins 2000). We opened the pitfall traps on the first of the 6-d sampling period, before the beginning of active searching, and closed them on the last day of each expedition, resulting in a total of 144 h of open traps per expedition, and 720 h for the entire study. We checked pitfall traps twice a day, once in the morning and once in the evening. We euthanized all collected lizards using a lethal dose of lidocaine chlorohydrate 2% (following Resolution #714 of Conselho Federal de Medicina Veterinária 2002), fixed them in 10% formaldehyde, preserved them in 70% ethanol, and deposited voucher specimens in Coleção Herpetológica da Universidade Regional do Cariri.

Spatial Niche

To evaluate the spatial niche of each species, we recorded the microhabitat used by each lizard according to the following categories: tree trunk, tree branch, under tree bark, bromeliads, burrow in the ground, termite nest, leaf

litter, piles of small woody debris, fallen trunk, rock outcrops, bare soil, and soil between vegetation. To measure the spatial niche breadth of each species (B_{spatial}), we calculated the inverse of Simpson's diversity index:

$$B = \frac{1}{\sum_{i=1}^n P_i^2}$$

where i is the category of microhabitat, P is the proportion of microhabitat i , and n is the number of categories. The values can range from 1 (exclusive use of a single category of microhabitat) to n (equal use of all microhabitat categories by each species).

We calculated microhabitat overlap between all pairs of species in Ecosim software v7.0 (Gotelli and Entsminger 2001) using Pianka's (1973) overlap index:

$$\phi_{jk} = \frac{\sum_{i=1}^n P_{ij}P_{ik}}{\sqrt{\sum_{i=1}^n (P_{ij}^2)(P_{ik}^2)}}$$

where P_{ij} and P_{ik} are the proportions of microhabitat use of the category i , and j and k represent the pairs of compared species. The values of overlap range from 0 (without overlap) to 1 (total overlap).

Trophic Niche

We removed the stomach contents of all collected lizards and analyzed them under a stereomicroscope to identify prey items to the lowest taxonomic level possible (usually Order, except for Formicidae). We measured length and width of intact prey items with digital calipers (± 0.01 mm). Assuming a roughly equal width and depth of each prey item, we estimated its volume using the ellipsoid formula:

$$V = \frac{4}{3}\pi\left(\frac{l}{2}\right)\left(\frac{w}{2}\right)^2$$

where V = volume, l = length and w = width. We calculated the numeric and volumetric percentages of each prey category by species. From these percentages, we obtained numeric and volumetric niche breadths (B_{num} and B_{vol} , respectively) using the inverse of Simpson's diversity index. Then, we used Pianka's niche overlap index with the sum of the volume of each prey category for each lizard species to evaluate trophic overlap between each pair of species. To determine the relative contribution of each prey category to the diet of each species, we calculated the index of relative importance (IRI) for each species using the formula (Powell et al. 1990):

$$\text{IRI} = \frac{F\% + N\% + V\%}{3}$$

where $F\%$, $N\%$, and $V\%$ are the percentages of frequency, number, and volume, respectively.

Statistical Analysis

We obtained null models by randomizing the data from the original matrix of niche overlap for the studied

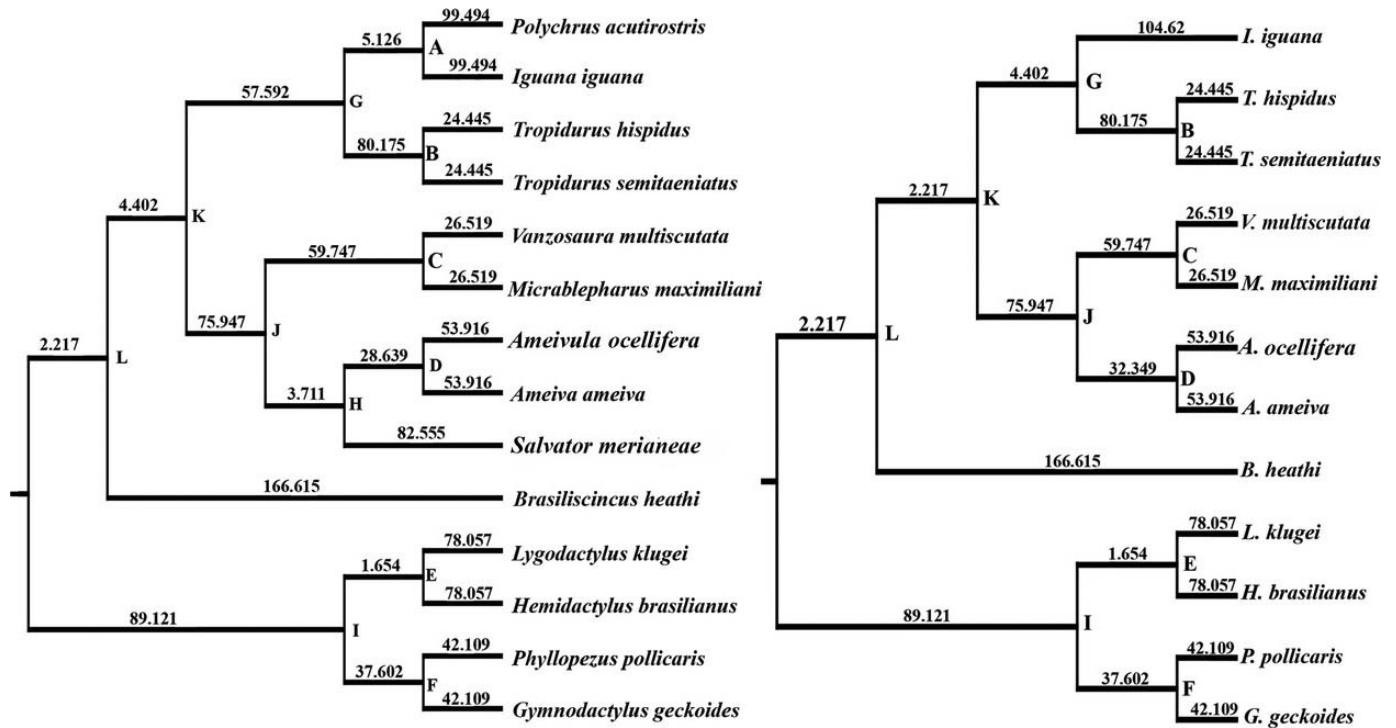


FIG. 1.—Phylogenetic trees (adapted from Pyron et al. 2013) for species of lizards collected in a Caatinga habitat in Brazil. Individual groups were used in canonical phylogenetic ordination for microhabitat (left panel) and diet (right panel). Letters at each node designate the taxa in each clade: A = Polychrotidae and Iguanidae, B = Tropiduridae, C = Gymnophthalmidae, D = Teiinae, E = Gekkonidae, F = Phyllodactylidae, G = Iguania, H = Teiidae, I = Gekkota, J = Teoidea, K = Episcquamata, L = Unidentata.

assemblage to determine if mean overlap in spatial and trophic niche dimensions were lower than expected by chance (Gotelli and Graves 1996; Gotelli and Entsminger 2001). The presence or absence of structure in the assemblage was established by comparing means of observed and simulated overlap. We used the niche overlap module of EcoSim (Gotelli and Entsminger 2001) to test for the presence of nonrandom patterns in niche overlap based on microhabitat use and diet between each pair of species. Data for this analysis consisted of a matrix in which each row represented a lizard species and each column represented category (microhabitat or diet), with the values of each cell corresponding to the proportion of microhabitat use or volume of each prey category. We executed the niche overlap module of EcoSim using each of the following options: Pianka's overlap index, randomization algorithm II (RA2), and 1000 randomizations of the original matrix.

For trophic niche, we added the sum of total volume of each prey category in all species of the assemblage to define the state of resources and, in this way, gave different weights to each category. The RA2 algorithm replaces microhabitat and diet values in the original matrix with a uniform randomization of values between 0.0 and 1.0, but retains the zero structure in the matrix (Winemiller and Pianka 1990). We performed the same procedure for the analysis of diet overlap, running the analysis under three sets of parameters: (1) including all species examined that had food items in stomachs and all categories of prey found, (2) excluding species with $n < 5$ prey categories (excluded: *Iguana iguana* [$n = 4$] and *Micrablepharus maximiliani* [$n =$

1]), and (3) excluding species with $n < 15$ prey categories (excluded: *Ameiva ameiva* [$n = 6$], *Brasiliscincus heathi* [$n = 8$], and *Vanzosaura multiscutata* [$n = 12$]). Because the results were similar, we presented only those from the most complete matrices, but see Appendix I for results of spatial and trophic niche structure analysis with each parameter used. We used canonical phylogenetic ordination (CPO; Giannini 2003) to evaluate whether or not there is phylogenetic influence on the ecology of the lizard assemblage. To execute the CPO, we created two matrices based on the lizard species sampled: matrix X consisting of phylogenetic data and matrix Y consisting of life-history data (proportional use of microhabitat and IRI for diet). To generate these matrices, we used a phylogenetic tree with only the species from the assemblage by pruning the Squamata phylogeny of Pyron et al. (2013; see Fig. 1). Because *Tropidurus semitaeniatus* and *Gymnodactylus geckoides* were absent in this phylogeny, and assuming that this would bias our interpretation, we used these taxa in place of *Tropidurus hygomi* and *Phyllopezus periosus*, respectively, which were the most closely related species present in the phylogeny. We used the CPO to identify those groupings within matrix X that explain variation in matrix Y by using a canonical correspondence analysis with 9999 Monte Carlo permutations (Giannini 2003). We executed the CPO using CANOCO v4.5 (Ter Braak and Smilauer 2002), following the procedure described in Mesquita et al. (2006a).

We performed a phylogenetic principal component analysis (pPCA; Jombart et al. 2010) to identify the main phylogenetic influences in the life-history data. We used a

TABLE 1.—Lizard species observed in a semiarid Caatinga habitat in Brazil. Nmu = number of microhabitat use records; Ncol= number of collected specimens; $B_{spatial}$ = spatial niche breadth; B_{num} = numeric trophic niche breadth; B_{vol} = volumetric trophic niche breadth.

Species	Nmu (n = 468)	Ncol (n = 425)	$B_{spatial}$	B_{num}	B_{vol}
<i>Ameiva ameiva</i>	8	6	2.13	1.88	1.30
<i>Ameivula ocellifera</i>	91	97	2.87	1.39	2.59
<i>Brasiliscincus heathi</i>	10	8	1.92	1.02	2.19
<i>Gymnodactylus geckoides</i>	32	44	5.17	1.39	4.41
<i>Hemidactylus brasilianus</i>	27	42	2.33	6.86	4.89
<i>Iguana iguana</i>	4	2	1.60	1	1
<i>Lygodactylus klugei</i>	77	71	3.86	4.32	5.32
<i>Micrablepharus maximiliani</i>	1	1	1	2.57	2.35
<i>Phyllopezus pollicaris</i>	40	65	3.94	5.75	7.44
<i>Polychrus acutirostris</i>	2	2	1	—	—
<i>Salvator merianae</i>	7	0	1.96	—	—
<i>Tropidurus hispidus</i>	97	49	6.49	2.30	6.25
<i>Tropidurus semitaeniatus</i>	55	26	1.16	4.6	1.64
<i>Vanzosaura multiscutata</i>	13	12	1.98	1.40	3.36

matrix with branch lengths from the phylogenetic tree of Pyron et al. (2013), and a matrix with quantitative life-history data of species of the assemblage (i.e., the same matrix used for the CPO). We used this analysis to detect the presence of: (1) global phylogenetic structure as indicated by the global phylogenetic component axis (Global PC) generated by the pPCA, where large positive eigenvalues indicate strong phylogenetic inertia in the conservation of ecological features; or (2) local structure (ecological), indicated by the local phylogenetic axis (Local PC), where large negative eigenvalues indicate ecological convergence, resulting in variation of niche traits close to the terminal branches (Jombart et al. 2010). We performed this analysis using the Adephylo package (Jombart and Dray 2013) of R software (v3.6.1; R Core Team 2016).

Finally, we performed a Mantel test based on 999 Monte Carlo permutations to determine whether or not the diet and microhabitat overlap matrices were inversely correlated. If so, we could identify those species having high overlap in one niche dimension, but low overlap in the other. We performed this test using the Picante package (Kembel et al. 2010) in R (R Core Team 2016).

TABLE 2.—Spatial (above the diagonal) and trophic (below the diagonal) niche overlap indices between pairs of lizard species observed in a Caatinga habitat in Brazil. Aa = *Ameiva ameiva*; Bh = *Brasiliscincus heathi*; Ao = *Ameivula ocellifera*; Gg = *Gymnodactylus geckoides*; Hb = *Hemidactylus brasilianus*; Ii = *Iguana iguana*; Lk = *Lygodactylus klugei*; Mm = *Micrablepharus maximiliani*; Pp = *Phyllopezus pollicaris*; Pa = *Polychrus acutirostris*; Th = *Tropidurus hispidus*; Sm = *Salvator merianae*; Ts = *Tropidurus semitaeniatus*; Vm = *Vanzosaura multiscutata*.

Species	Aa	Bh	Ao	Gg	Hb	Ii	Lk	Mm	Pa	Pp	Th	Sm	Ts	Vm
Aa	—	0.18	0.97	0.32	0.07	0.12	0.09	0.00	0.00	0.00	0.59	0.95	0.05	0.28
Bh	0.03	—	0.12	0.14	0.02	0.00	0.16	0.00	0.00	0.08	0.31	0.00	0.00	0.09
Ao	0.23	0.70	—	0.39	0.08	0.12	0.10	0.00	0.00	0.03	0.59	0.94	0.05	0.38
Gg	0.10	0.85	0.89	—	0.28	0.16	0.26	0.07	0.00	0.30	0.59	0.41	0.08	0.66
Hb	0.60	0.51	0.30	0.36	—	0.23	0.44	0.00	0.23	0.29	0.24	0.08	0.01	0.08
Ii	0.01	0.00	0.00	0.00	0.00	—	0.57	0.00	0.95	0.19	0.34	0.19	0.01	0.24
Lk	0.17	0.46	0.40	0.55	0.53	0.00	—	0.00	0.56	0.50	0.75	0.10	0.01	0.11
Mm	0.02	0.54	0.04	0.29	0.49	0.00	0.30	—	0.00	0.00	0.00	0.00	0.00	0.00
Pa	—	—	—	—	—	—	—	—	—	0.20	0.29	0.00	0.02	0.00
Pp	0.35	0.17	0.14	0.33	0.50	0.00	0.82	0.30	—	—	0.49	0.00	0.85	0.06
Th	0.70	0.58	0.81	0.72	0.62	0.15	0.41	0.14	—	0.33	—	0.55	0.14	0.24
Sm	—	—	—	—	—	—	—	—	—	—	—	—	0.05	0.46
Ts	0.04	0.07	0.10	0.09	0.07	0.99	0.09	0.01	—	0.06	0.23	—	—	0.00
Vm	0.49	0.81	0.70	0.80	0.67	0.00	0.71	0.41	—	0.53	0.80	—	0.08	—

RESULTS

Species Composition

We observed 14 lizard species in the assemblage occurring on the Angico farm during the five expeditions. Of these, we collected 425 specimens of 13 lizard species (no individual of *Salvator merianae* was collected) and recorded the microhabitat used by 464 individuals. The most abundant species was *Tropidurus hispidus* (n = 97), followed by *Ameivula ocellifera* (n = 91) and *Lygodactylus klugei* (n = 77). *Micrablepharus maximiliani* (n = 1) and *Polychrus acutirostris* (n = 2) were the least abundant species (Table 1).

Spatial Niche

Spatial niche breadth ranged from 1.16 to 6.49 when *M. maximiliani* and *P. acutirostris* (both with low n) were excluded (Table 1; Fig. 2). The frequent use of rock outcrops by the tropidurid *T. semitaeniatus* made it the most specialized species, followed by *S. merianae* and *V. multiscutata* (mainly associated with bare soil and leaf litter, respectively). The teiids *Ameiva ameiva* and *Ameivula ocellifera* also had low niche breadths and were usually associated with bare soil and leaf litter as well. The most generalist species was the tropidurid *T. hispidus*, followed by the geckonids *G. geckoides*, *Phyllopezus pollicaris*, and *L. klugei* (Table 1). The greatest degrees of spatial niche overlap were among species of Teiidae, mainly because of their association with bare soil. The lowest values for spatial niche overlap were not constrained to a single lizard family (Table 2).

Trophic Niche

Lizard diet was mainly composed of arthropods, but also included plant material, lizards, young birds, and eggs of vertebrates (lizards or birds; Table 3). Numeric and volumetric breadths of dietary niche ranged from 1.00 to 6.86 and 1.00 to 7.44, respectively (frequencies, abundances, and volumes of prey categories for each lizard species are presented in Appendix II). *Iguana iguana* had relatively small values for both numeric and volumetric trophic niche breadths. Higher values for numeric and volumetric niche breadths were present in the geckonids *Hemidactylus*

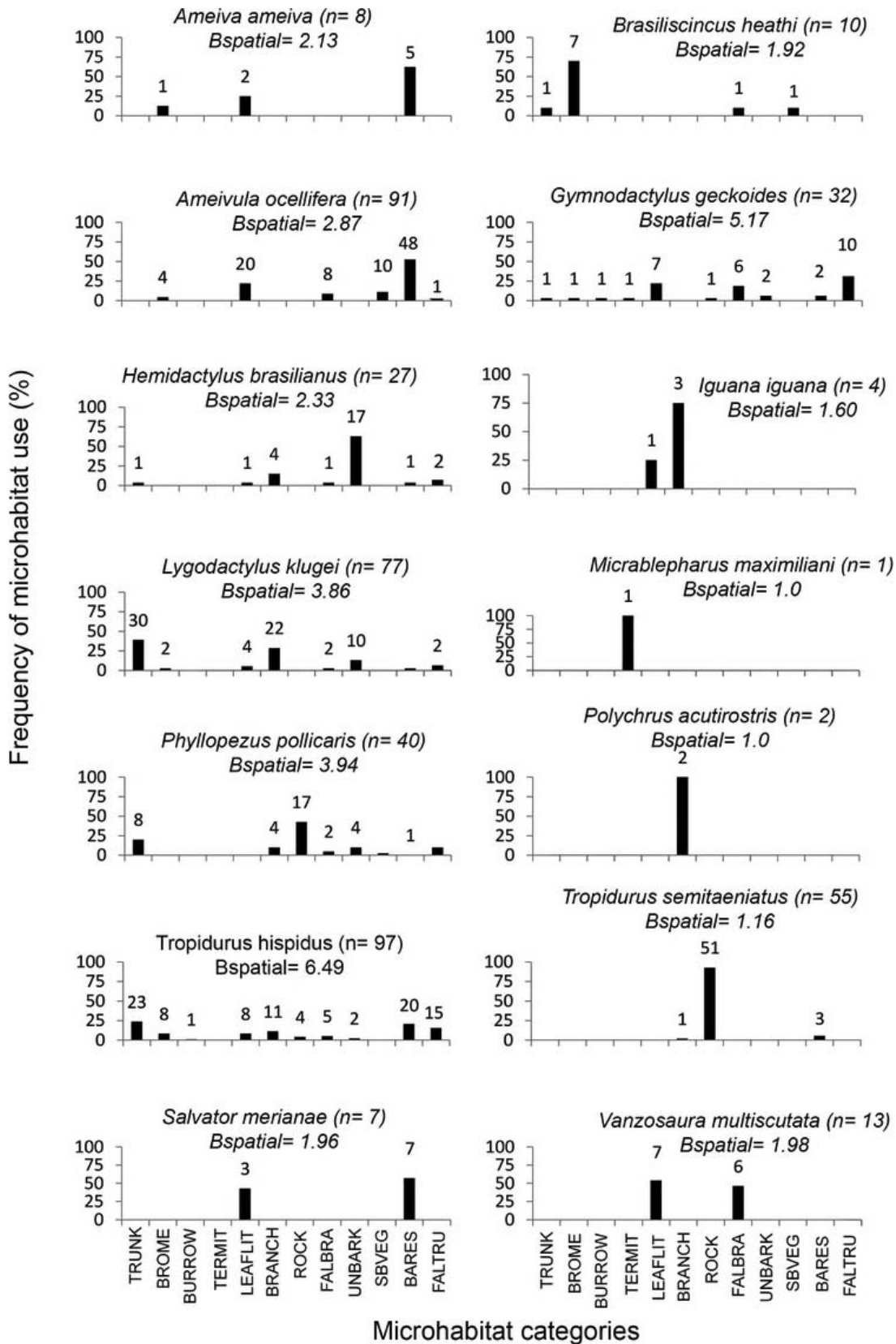


FIG. 2.—Niche breadth and frequency of microhabitat use by an assemblage of 14 lizard species observed in a Caatinga habitat in Brazil. BARES = bare soil; BRANCH = tree branch; BROME = bromeliads; BURROW = burrow in the ground; FALBRA = piles of woody debris; FALTRU = fallen trunk; LEAFLIT = leaf litter; ROCK = rock; SBVEG = soil between vegetation; TERMIT = termite nest; TRUNK = tree trunk; UNBARK = under tree bark.

TABLE 3.—Diet composition of 13 of the 14 lizard species observed in a Caatinga habitat in Brazil. Values represent the index of relative importance of each prey category. See Table 2 for definition of species abbreviations.

Prey categories	Species												
	Aa	Ao	Bh	Gg	Hb	Ii	Lk	Mm	Pa	Pp	Th	Ts	Vm
Invertebrates													
Araneae	4.64	4.99	21.20	10.60	19.27	—	14.17	43.66	—	5.78	6.52	5.67	15.00
Blattodea	—	0.46	6.50	0.87	6.71	—	0.89	19.55	—	4.16	0.44	0.57	—
Chilopoda	2.12	—	—	1.63	—	—	—	—	—	0.49	—	0.53	—
Coleoptera	61.37	14.76	—	6.01	26.08	—	24.27	—	—	24.08	17.05	7.62	27.46
Dermoptera	—	0.47	—	—	—	—	—	—	—	—	—	0.52	—
Diplopoda	—	0.20	—	—	—	—	—	—	—	—	—	—	—
Diptera	—	0.20	—	1.46	6.64	—	5.64	—	—	5.21	0.73	1.50	—
Formicidae	—	3.81	—	5.92	2.00	—	4.67	—	—	12.31	19.22	12.70	—
Hemiptera	3.04	1.13	—	—	1.95	—	0.52	—	—	5.87	0.68	2.27	—
Hymenoptera	4.24	3.07	—	3.40	8.83	—	9.60	—	—	5.92	3.77	3.78	—
Isoptera	10.82	54.33	72.31	53.80	8.60	—	11.36	—	—	3.13	31.40	15.64	50.28
Insect larvae	—	0.47	—	—	—	—	—	—	—	—	0.83	1.92	—
Lepidoptera	2.18	4.55	—	1.75	3.67	—	1.14	—	—	0.98	1.42	0.54	—
Mantodea	—	0.19	—	—	—	—	—	—	—	—	0.23	—	—
Neuroptera	—	1.15	—	—	—	—	—	—	—	1.34	3.53	0.54	—
Odonata	1.92	0.28	—	—	—	—	—	—	—	—	—	—	—
Oligochaeta	—	0.20	—	—	—	—	—	—	—	—	—	—	—
Orthoptera	3.56	5.78	—	1.53	13.90	—	8.13	—	—	7.34	3.68	4.84	—
Phasmatodea	1.92	—	—	—	—	—	—	—	—	—	—	—	—
Pseudoescorpiones	—	0.19	—	—	—	—	0.55	—	—	1.49	0.24	1.66	—
Scolopendromorpha	—	0.89	—	—	—	—	2.78	—	—	0.49	1.66	1.63	—
Scorpiones	—	—	—	1.65	—	—	1.19	36.79	—	2.65	0.25	—	—
Unidentified taxa	—	1.92	—	4.58	2.36	—	13.39	—	—	14.54	0.54	2.94	7.26
Vertebrates													
Birds	—	—	—	—	—	—	—	—	—	—	1.13	—	—
Eggshell	—	—	—	—	—	—	—	—	—	—	0.26	—	—
Lizard shed skin	—	—	—	5.41	—	—	0.61	—	—	4.20	—	—	—
Sauria	—	0.95	—	—	—	—	—	—	—	—	1.61	—	—
Undentified taxa	—	—	—	—	—	—	—	—	—	—	1.29	—	—
Plants													
Plant material	4.19	—	—	1.38	—	100	1.08	—	—	—	3.50	35.13	—
Numeric niche	2.00	1.39	1.02	1.39	6.86	1.0	4.32	2.57	—	5.75	2.30	4.60	1.40
Volumetric niche	1.31	2.59	2.19	4.41	4.89	1.0	5.32	2.35	—	7.44	6.25	1.64	3.36
Empty stomachs	0	13	2	8	2	1	10	0	2	5	2	0	4

brasiliensis and *P. pollicaris*, respectively (Table 1). The IRI varied from 0.20% (Mantodea and Pseudoescorpionida for *A. ocellifera*) to 72.31% (Isoptera for *B. heathi*) and 100% (plant material for *I. iguana*). Considering all species collectively, the more important items were Araneae (*M. maximiliani*), Coleoptera (*Ameiva ameiva*, *H. brasiliensis*, *L. klugei*, and *P. pollicaris*), Isoptera (*Ameivula ocellifera*, *G. geckoides*, *B. heathi*, *T. hispidus*, and *V. multiscutata*), and plant material (*I. iguana* and *T. semitaeniatus*). Vertebrates were also ingested: two adult *A. ocellifera* each ingested one adult *H. brasiliensis* and one juvenile *T. hispidus*, whereas one adult *T. hispidus* ingested one adult *H. brasiliensis* and two other *T. hispidus* ingested young birds (Table 3). Trophic niche overlap, calculated from the volumes of prey categories used by each pair of species, varied from 0.03 (*Ameiva ameiva* vs. *B. heathi*) to 0.89 (*Ameivula ocellifera* vs. *G. geckoides*; Table 2). Except for *I. iguana* (herbivorous) and *M. maximiliani* ($n = 1$), *B. heathi* and *A. ocellifera* were numerically the most specialized in the assemblage, with a diet mainly composed of termites. In contrast, the geckos *H. brasiliensis* and *P. pollicaris* were the most generalized species in terms of diet. Volumetrically, *Ameiva ameiva* (Coleoptera) and *T. semitaeniatus* (plant material) were the most specialized species, whereas *P. pollicaris* and *T. hispidus* were the most generalized (Table 3).

Ecological \times Historical Effects

We detected an assemblage structure based on microhabitat use (spatial niche; $\bar{X}\Phi_{\text{Mobserved}} = 0.2141$, $\bar{X}\Phi_{\text{Msimulated}} = 0.3026$, $P < 0.001$). Phylogeny had a greater influence on structure than ecology, with higher eigenvalues for the global component (historical) than for the local component (Fig. 3a). The largest positive eigenvalues of the historical component were among teiids, which had positive phylogenetic autocorrelation for spatial niche, corroborating the CPO results for spatial niche (Table 4). Global and local components of microhabitat use were positively influenced by almost the same categories: termite nest and bare soil followed by leaf litter in the global component and rocks in the local component (Fig. 3a). On the other hand, global and local components differed in the categories that negatively influenced the components: tree branches and under tree bark were most important in the global component (X -axis) compared with leaf litter and fallen branches in the local component (Y -axis).

We also detected an assemblage structure based on trophic niche ($\bar{X}\Phi_{\text{Fobserved}} = 0.355$, $\bar{X}\Phi_{\text{Fsimulated}} = 0.458$, $P < 0.0001$). As with microhabitat use, phylogeny influenced the trophic niche, but only for Iguania (Table 4). When we removed species with $n < 5$ individuals and underrepresented prey categories, the CPO revealed phylogenetic effects in the diet for Tropiduridae (Table 4). However,

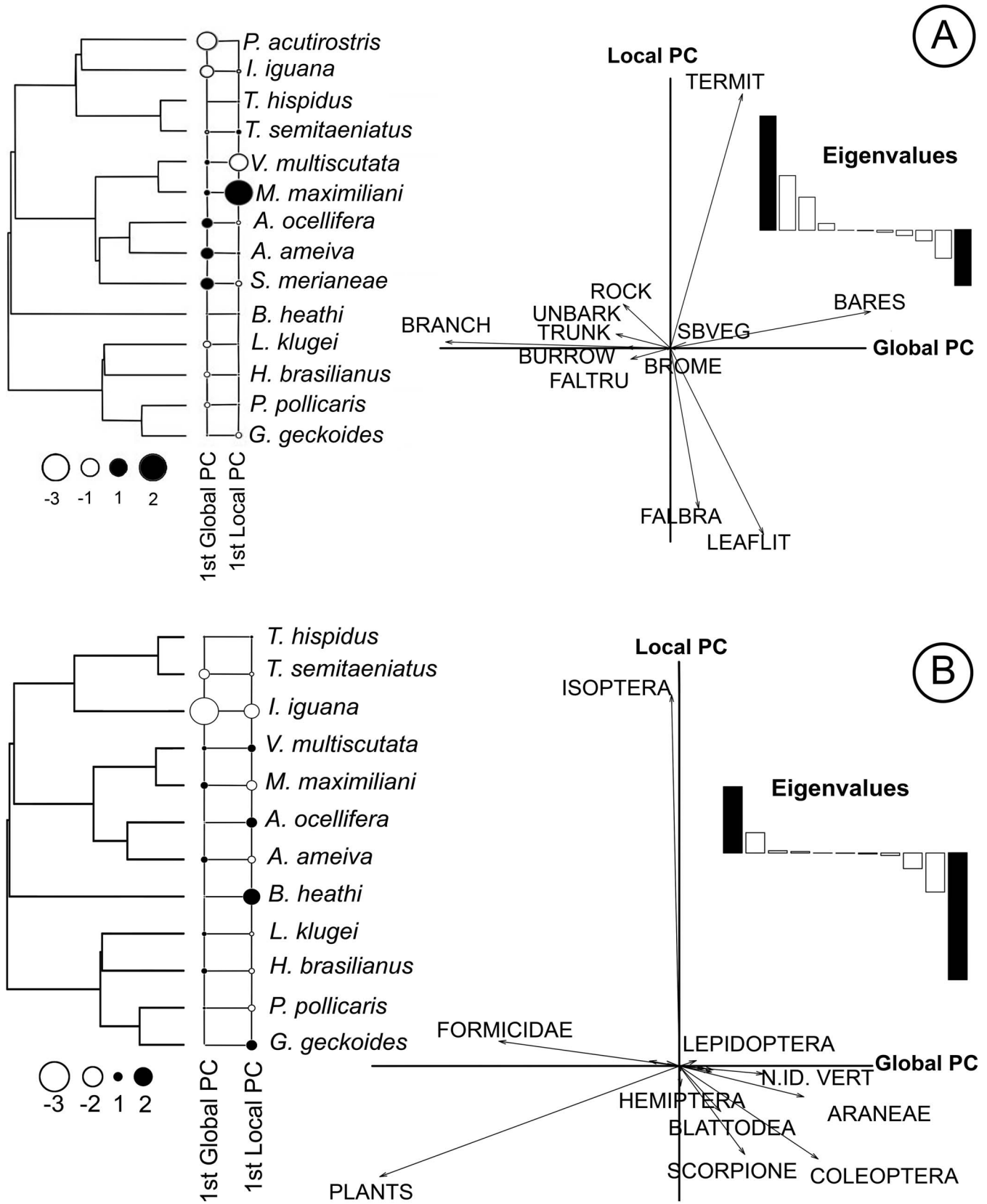


FIG. 3.—Phylogenetic principal component analyses for lizard microhabitat use (A) and diet (B) in a Caatinga habitat in Brazil. The left-hand panels show trees built for the lizard assemblage that incorporate the first global (black circles) and local (white circles) principal components. Circle size is proportional to score value. Eigenvalue bar plots in the right-hand panels correspond to global (left) and to local (right) principal components. Trophic categories close to 0 on both X and Y axes were omitted. Acronyms for microhabitat types are as defined as for Fig. 2.

TABLE 4.—Results of canonical phylogenetic ordination (9999 Monte Carlo permutations) for the matrices of microhabitat and diet of lizard species observed in a Caatinga habitat in Brazil. See Fig. 1 for the clade(s) represented by each of the letters, and see text for those subgroups of prey types that were removed. * = statistically significant *P*-values.

Category/Clade	Variation	Variation %	<i>F</i>	<i>P</i>
Microhabitat				
All species included				
J Teoidea	0.612	18.43	2.13	0.002*
C Gymnophthalmidae	0.604	18.19	2.10	0.07
A Polychrotidae and Iguanidae	0.590	17.77	2.04	0.08
H Teiidae	0.527	15.87	1.79	0.06
G Iguania	0.409	12.32	1.35	0.18
K Episquamata	0.390	11.75	1.28	0.20
I/L Gekkota/Unidentata	0.370	11.27	1.20	0.29
E Gekkonidae	0.364	10.96	1.18	0.30
D Teiinae	0.314	9.46	1.11	0.48
B Tropiciduridae	0.302	9.10	0.97	0.53
F Phyllodactylidae	0.171	5.15	0.53	0.80
Species with <i>n</i> > 5 prey types				
J Teoidea	0.576	30.72	2.53	0.006*
H Teiidae	0.513	27.36	2.19	0.03*
E Gekkonidae	0.460	24.53	1.91	0.05
I/L Gekkota/Unidentata	0.429	22.88	1.76	0.06
K Episquamata	0.409	21.81	1.66	0.07
D Teiinae	0.290	15.47	1.12	0.46
B Tropiciduridae	0.280	14.93	1.08	0.50
F Phyllodactylidae	0.158	8.43	0.58	0.77
Diet				
All species included				
G Iguania	0.447	32.89	2.93	0.01*
C Gymnophthalmidae	0.261	19.21	1.53	0.27
I/L Gekkota/Unidentata	0.187	13.76	1.05	0.39
J Teoidea	0.184	13.54	1.03	0.42
K Episquamata	0.169	12.44	0.94	0.52
E Gekkonidae	0.137	10.08	0.75	0.48
D Teiinae	0.136	10.01	0.74	0.50
B Tropiciduridae	0.121	8.90	0.66	0.56
F Phyllodactylidae	0.100	7.36	0.53	0.71
Species with <i>n</i> > 5, and subgroupings of prey removed				
B Tropiciduridae	0.259	41.77	2.46	0.03*
J Teoidea	0.127	20.48	1.04	0.42
K Episquamata	0.120	19.35	0.97	0.48
I/L Gekkota/Unidentata	0.110	17.74	0.89	0.56
E Gekkonidae	0.101	16.29	0.81	0.63
D Teiinae	0.097	15.65	0.77	0.64
F Phyllodactylidae	0.059	9.52	0.45	0.81

pPCA revealed greater influence of ecology vs. history in trophic niche breadths. Araneae and Coleoptera were the prey categories that most positively influenced the historical component (Global PC), whereas plant material and Formicidae had the greatest negative influence. The ecological component (Local PC) was positively influenced by Isoptera and negatively influenced by plant material, Coleoptera, and Scorpiones (Fig. 3b). The trophic and microhabitat overlap matrices were not inversely correlated (Mantel test, $R = 0.24$, $P = 0.07$), indicating no niche complementarity among species.

DISCUSSION

Approximately 18% of the lizard species reported from the Caatinga domain were found in the present study. Richness was lower than that reported by Miranda and Miranda (1982) for the same municipality (16 spp.), and by Vitt (1995) in the municipality Exu (18 spp.), which is ~50 km from our study site. Among the lizards reported from the Ouricuri municipality, we did not record *Hemidactylus*

mabouia and *Notobachia ablephara*. The former of these is a nonnative species of African origin (Carranza and Arnold 2006) with a nearly cosmopolitan distribution (Rocha et al. 2011). In contrast, *N. ablephara* is endemic to the Caatinga, with secretive habits that make its detection difficult. *Notobachia ablephara* was previously described from paleoquaternary dunes of the São Francisco River (Rodrigues 1984), with a single record outside these dunes (Miranda and Miranda 1982).

Gymnodactylus geckoides and *T. hispidus* were the most generalist species at our study site. The generalist habit of *G. geckoides* differs from that described by Vitt (1995) and Andrade et al. (2013) in other Caatinga areas, where *G. geckoides* presented specialized microhabitat preferences for rock piles and inside decomposing logs or branches. The niche breadth for *G. geckoides* is similar to that of its congener *Gymnodactylus amarali (carvalhoi)* in a Cerrado area (Werneck et al. 2009), indicating a tendency toward habitat generalism among members of this genus. On the other hand, *T. semitaeniatus*, the most specialized species, was almost exclusively associated with rock outcrops of isolated metamorphic rocks within vegetation (inselbergs), corroborating Vitt (1995). Sit-and-wait foragers usually have smaller spatial niche breadths than active foragers (Vitt 1995). However, some members of Tropiciduridae are generalists, such as *Tropicidurus torquatus*, which occupies rock outcrops, cities, and restingas (Bergallo and Rocha 1994; Sena et al. 2008), and *T. hispidus* in areas of Caatinga and in an ecotone between Amazon forest and savanna (Vitt 1995; Vitt and Zani 1998).

According to the niche complementarity hypothesis, ecologically similar species tend to avoid competition by segregating niche dimensions (e.g., temporal, spatial, or trophic), allowing their coexistence (Rosenzweig and Winakur 1969; MacArthur 1984). The results of our Mantel test between microhabitat and trophic niche overlap matrices did not corroborate this hypothesis. Teiids had the largest niche overlaps in microhabitat use (*Ameiva ameiva* vs. *Ameivula ocellifera*; *Ameiva ameiva* vs. *S. merianae*; and *Ameivula ocellifera* vs. *S. merianae*). This high overlap is related to phylogenetic conservatism among teiids (Vitt et al. 1999), and corroborated by our CPO and pPCA results. There was also high spatial niche overlap between *T. semitaeniatus* and *P. pollicaris*; however, it is unlikely that these species compete directly for space as *T. semitaeniatus* is diurnal and *P. pollicaris* is nocturnal (Vitt 1995).

Overlap in microhabitat use between pairs of species was lower than expected by chance, indicating that species segregate microhabitat use within the studied assemblage. There are at least two hypotheses that can explain this pattern: (1) available microhabitats are a limiting resource and interspecific competition plays an important role in structuring the assemblage (Pianka 1973; Schoener 1974; Connell 1980); and (2) the structure observed might have a phylogenetic origin (Brooks and McLennan 1993) wherein the microhabitats used by species are related to their morphology and physiology as reflected by their ancestral taxa (Losos 1996; Goodman et al. 2008). In fact, the CPO revealed phylogenetic conservation of spatial niches in Teoidea (Teiidae + Gymnophthalmidae), and the pPCA of the spatial niches revealed greater global eigenvalues than local. Taken together, these results indicate that evolutionary

history can be more influential than ecological pressures in some lineages.

Whereas we did not detect support for the niche complementarity hypothesis across all sampled species of this lizard community, an analysis of overlap values provided some evidence that this pattern might be occurring with some of these species. The geckos *P. pollicaris* and *L. klugei* presented high numeric (5.75 and 4.32, respectively) and volumetric (7.44 and 5.32) trophic niche breadths. These species also had high trophic (0.89) and relatively high microhabitat (0.50) overlap, coupled with temporal segregation. *Gymnodactylus geckoides* had the second most generalized trophic niche, and also had high trophic niche overlap with *B. heathi* (0.85), *Ameivula ocellifera* (0.89), and *V. multiscutata* (0.80), primarily because of a high rate of termite ingestion (Table 3). There was low microhabitat overlap among these species (Table 2), however, in part because the habit of *G. geckoides* is crepuscular/nocturnal.

Of interest, plant material (mainly leaves) was the most important item in the diet of *T. semitaeniatus*. The consumption of plant material has been described as occurring accidentally while these animals are foraging (cf. Ribeiro and Freire 2011; Siqueira et al. 2011). The large amount of plant material found in the stomachs of *T. semitaeniatus*, however, suggests that its ingestion might not be accidental. Furthermore, the consumption of plant material can facilitate the elimination of intestinal parasites and trituration of arthropod exoskeletons (Evans and Lampo 1996). It also represents an important source of nutrients (if digestible) and water for lizards, especially in the dry season when arthropod availability is lower (Kolodiuk et al. 2010). Additionally, *T. semitaeniatus* is a pollinator and seed disperser of the cactus *Melocactus ernestii*, and a seed disperser for *Commiphora leptophloeos* (Imburana) in other areas of the Caatinga (Ribeiro et al. 2008).

The overlap in diet composition between pairs of species was lower than expected by chance, indicating that species segregate along this niche dimension (assemblage structure). The pPCA based on the trophic niche dimension indicates that structure is caused by current ecological effects. This result is at least partially corroborated by the CPO, which revealed phylogenetic conservatism in Tropiciduridae. Whereas both *T. hispidus* and *T. semitaeniatus* showed generalist dietary habits, ingesting similar prey items, they differed in both numeric and volumetric trophic niche breadths. These tropidurids were segregated almost completely along the spatial niche dimension. *Tropidurus semitaeniatus* was the most specialized species, occurring almost exclusively on rock outcrops (92% of specimens), whereas *T. hispidus* was the most generalist species, occurring in 10 of the 13 identified microhabitat categories. The abundance of *T. hispidus* was lower in rock outcrops, however, with a proportion of about five *T. semitaeniatus* to each *T. hispidus* (personal observation). A possible explanation for the greater volumetric niche breadth for *T. hispidus* is that its generalist habits in microhabitat use and its larger body size might result in a preference for larger prey (Costa et al. 2008).

Studies of community structure focus on processes related to ecological and historical factors (Losos 1996; Webb et al. 2002; Werneck et al. 2009). Although several studies of vertebrate communities have identified structure related to spatial and trophic niches, there are few general patterns to

suggest that ecological or historical influences play greater roles in determining this structure (cf. Cooper et al. 2008; França et al. 2008; Luiselli 2008; Rabosky et al. 2011). The lizard assemblage studied at our Caatinga site was structured in both microhabitat and trophic niche dimensions. In a Cerrado habitat, however, Mesquita et al. (2007) reported that, when compared with ecological factors, historical factors exerted greater influence on the spatial niches of lizards, which contrasts with what was found for other lizard assemblages (Werneck et al. 2009; Rabosky et al. 2011). Whereas we did not detect phylogenetic signals in the prey consumed, such patterns have been reported previously for other lizard assemblages (e.g., Vitt and Pianka 2005; Werneck et al. 2009). Both historical and ecological factors are known to structure communities of amphibians and lizards occurring in Caatinga habitats (e.g., Vitt 1995; Protázio et al. 2015). Analyzing a gradient from open to forested environments, Luiselli (2008) showed that most (~80%) lizard assemblages were randomly organized considering trophic niche dimensions, and usually do not segregate along the trophic niche dimension. At least where diet composition is concerned, this finding provides evidence of ecological factors having predominance over historical factors. Because structuring processes appear to operate at different spatial, temporal, or phylogenetic scales (Cavender-Bares et al. 2009), broader geographic coverage with standardized comparable analyses and inclusion of data from different taxa will likely facilitate the formulation of theories and comparisons among different lizard communities across the globe.

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APPENDIX I

Mean values of spatial (microhabitat) and trophic (diet) niche overlap from all analyses, tested using null models of pseudocommunities based on 9999 Monte Carlo permutations. See text for those subgroups of prey types that were removed. ObsM = observed mean; SimuM = mean overlap of simulated niches.

	Value		P-value
	ObsM	SimuM	
Microhabitat use			
All species	0.2141	0.3026	<0.0001
Species with ≥5 prey types	0.2729	0.3895	<0.0001
Species with ≥15 prey types	0.3072	0.4460	0.001
Diet			
All prey categories			
All species	0.3548	0.4591	0.0006
Species with ≥5 prey types	0.4476	0.5693	0.0011
Species with ≥15 prey types	0.4222	0.6920	0.0014
Subgroups of prey categories removed			
All species	0.3548	0.4583	0.0006
Species with ≥5 prey types	0.4476	0.5679	0.001
Species with ≥15 prey types	0.4222	0.6921	0.0014

APPENDIX II

Detailed diet composition of 12 lizard species of an area of Caatinga in a Neotropical semiarid region of Brazil. *F* = frequency; *N* = abundance; *V* = volume; *IRI* = index of relative importance.

Categories	<i>Ameiva ameiva</i> (n = 6)						
	<i>F</i>	<i>F%</i>	<i>N</i>	<i>N%</i>	<i>V</i>	<i>V%</i>	<i>IRI</i>
Araneae	2	11.11	2	1.55	924.63	2.91	5.19
Coleoptera	6	33.33	91	70.54	27,823.15	87.66	63.84
Hemiptera	1	5.56	3	2.33	673.79	2.12	3.33
Hymenoptera	2	11.11	3	2.33	299.63	0.94	4.79
Isoptera	3	16.67	23	17.83	276.85	0.87	11.79
Lepidoptera	1	5.56	2	1.55	83.04	0.26	2.46
Plant material	2	11.11	3	2.33	251.89	0.79	4.74
Orthoptera	1	5.56	2	1.55	1407.38	4.43	3.85
Total	18	100	129	100	31,740.36	100	100
Niche breadth			1.8806		1.2955		
Empty stomachs	0						
Categories	<i>Brasiliscincus heathi</i> (n = 8)						
<i>F</i>	<i>F%</i>	<i>N</i>	<i>N%</i>	<i>V</i>	<i>V%</i>	<i>IRI</i>	
Araneae	1	14.29	1	0.57	515.80	48.73	21.20
Blattodea	1	14.29	1	0.57	49.03	4.63	6.50
Isoptera	5	71.43	173	98.86	493.56	46.63	72.31
Total	7	100	175	100	1058.39	100	100
Niche breadth			1.0232		2.1876		
Empty stomachs	2						

APPENDIX II
Continued.

<i>Ameivula ocellifera</i> (n = 97)							
Categories	F	F%	N	N%	V	V%	IRI
Araneae	19	10.22	27	1.17	1076.65	3.58	4.99
Blattodea	2	1.08	2	0.09	67.04	0.22	0.46
Coleoptera	46	24.73	150	6.52	3912.38	13.02	14.76
Dermaptera	2	1.08	2	0.09	77.05	0.26	0.47
Diplopoda	1	0.54	1	0.04	3.62	0.01	0.20
Diptera	1	0.54	1	0.04	3.64	0.01	0.20
Formicidae	14	7.53	46	2.00	574.97	1.91	3.81
Hemiptera	5	2.69	6	0.26	134.63	0.45	1.13
Hymenoptera	11	5.91	42	1.82	438.62	1.46	3.07
Isoptera	35	18.82	1947	84.58	17,910.47	59.60	54.33
Lizard	2	1.08	2	0.09	508.61	1.69	0.95
Insect larvae	2	1.08	2	0.09	70.24	0.23	0.47
Lepidoptera	13	6.53	34	1.46	1558.02	4.93	4.31
Mantodea	1	0.54	1	0.04	0.86	0.00	0.19
Unidentified arthropod	8	4.30	8	0.35	334.22	1.11	1.92
Neuroptera	5	2.69	5	0.22	163.70	0.54	1.15
Odonata	1	0.54	1	0.04	81.48	0.27	0.28
Oligochaeta	1	0.54	1	0.04	10.11	0.03	0.20
Orthoptera	12	6.45	14	0.61	3088.99	10.28	5.78
Pseudoscorpiones	1	0.54	1	0.04	0.99	0.00	0.19
Scolopendromorpha	4	2.15	9	0.39	36.84	0.12	0.89
Total	186	100	2302	100	30,053.13	100	100
Niche breadth			1.3875		2.5874		
Empty stomachs	13						
<i>Gymnodactylus geckoides</i> (n = 44)							
Categories	F	F%	N	N%	V	V%	IRI
Araneae	8	14.04	8	1.69	535.57	16.08	10.60
Blattodea	1	1.75	1	0.21	21.43	0.64	0.87
Chilopoda	2	3.51	2	0.42	32.05	0.96	1.63
Coleoptera	6	10.53	18	3.80	123.68	3.71	6.01
Diptera	2	3.51	2	0.42	14.95	0.45	1.46
Lizard shed skin	3	5.26	3	0.63	344.47	10.34	5.41
Formicidae	4	7.02	27	5.70	168.34	5.05	5.92
Hymenoptera	2	3.51	3	0.63	201.73	6.05	3.40
Isoptera	20	35.09	401	84.60	1390.15	41.72	53.80
Lepidoptera	1	1.75	1	0.21	109.80	3.30	1.75
Plant material	2	3.51	2	0.42	6.81	0.20	1.38
Unidentified arthropod	3	5.26	3	0.63	261.17	7.84	4.58
Orthoptera	2	3.51	2	0.42	22.10	0.66	1.53
Scorpiones	1	1.75	1	0.21	99.43	2.98	1.65
Total	57	100	474	100	3331.70	100	100
Niche breadth			1.3872		4.4140		
Empty stomachs	8						
<i>Hemidactylus brasiliensis</i> (n = 42)							
Categories	F	F%	N	N%	V	V%	IRI
Araneae	10	16.39	10	12.20	1149.82	29.22	19.27
Blattodea	5	8.20	5	6.10	229.21	5.83	6.71
Coleoptera	16	26.23	22	26.83	990.82	25.18	26.08
Diptera	3	4.92	11	13.41	62.08	1.58	6.64
Formicidae	2	3.28	2	2.44	10.68	0.27	2.00
Hemiptera	2	3.28	2	2.44	5.66	0.14	1.95
Hymenoptera	6	9.84	7	8.54	319.65	8.12	8.83
Isoptera	6	9.84	11	13.41	100.16	2.55	8.60
Lepidoptera	2	3.28	2	2.44	207.76	5.28	3.67
Unidentified arthropod	2	3.28	2	2.44	53.74	1.37	2.36
Orthoptera	7	11.48	8	9.76	805.06	20.46	13.90
Total	61		82	100	3934.65	100	100
Niche breadth			6.8612		4.8888		
Empty stomachs	2						

APPENDIX II
Continued.

Categories	<i>Iguana iguana</i> (n = 2)						
	F	F%	N	N%	V	V%	IRI
Plant material	2	100	14	100	9937.84	100	100
Total	2	100	14	100	9937.84	100	100
Niche breadth			1		1		
Empty stomachs	0						
Categories	<i>Lygodactylus klugei</i> (n = 71)						
	F	F%	N	N%	V	V%	IRI
Araneae	16	15.84	21	11.05	395.68	15.62	14.17
Blattodea	1	0.99	1	0.53	28.92	1.14	0.89
Coleoptera	24	23.76	82	43.16	148.97	5.88	24.27
Diptera	9	8.91	13	6.84	29.89	1.18	5.64
Lizard shed skin	1	0.99	1	0.53	8.20	0.32	0.61
Formicidae	8	7.92	10	5.26	20.74	0.82	4.67
Hemiptera	1	0.99	1	0.53	1.27	0.05	0.52
Hymenoptera	12	11.88	16	8.42	215.57	8.51	9.60
Isoptera	9	8.91	24	12.63	317.68	12.54	11.36
Lepidoptera	2	1.98	2	1.05	9.82	0.39	1.14
Plant material	2	1.98	2	1.05	5.18	0.20	1.08
Unidentified arthropod	4	3.96	4	2.11	864.45	34.12	13.39
Orthoptera	7	6.93	7	3.68	349.21	13.78	8.13
Pseudoscorpionida	1	0.99	1	0.53	3.67	0.14	0.55
Scolopendromorpha	3	2.97	4	2.11	82.68	3.26	2.78
Scorpiones	1	0.99	1	0.53	51.73	2.04	1.19
Total	101		190	100	2533.68	100	100
Niche breadth			4.3182		5.3175		
Empty stomachs	10						
Categories	<i>Micrablepharus maximiliani</i> (n = 1)						
	F	F%	N	N%	V	V%	IRI
Araneae	1	33.33	3	50.00	89.07	47.64	43.66
Blattodea	1	33.33	1	16.67	16.18	8.66	19.55
Scorpiones	1	33.33	2	33.33	81.70	43.70	36.79
Total	3	100	6	100	186.95	100	100
Niche breadth			2.5714		2.3505		
Empty stomachs	0						
Categories	<i>Phyllorhynchus pollicaris</i> (n = 65)						
	F	F%	N	N%	V	V%	IRI
Araneae	6	5.77	6	3.06	179,326.10	8.51	5.78
Blattodea	6	5.77	7	3.57	66,032.50	3.14	4.16
Chilopoda	1	0.96	1	0.51	78.65	0.00	0.49
Coleoptera	31	29.81	60	30.61	249,098.38	11.83	24.08
Diptera	7	6.73	7	3.57	112,320.88	5.33	5.21
Lizard shed skin	1	0.96	1	0.51	234,447.79	11.13	4.20
Formicidae	11	10.58	47	23.98	49,759.73	2.36	12.31
Hemiptera	5	4.81	5	2.55	215,954.11	10.25	5.87
Hymenoptera	8	7.69	8	4.08	126,149.84	5.99	5.92
Isoptera	5	4.81	9	4.59	36.28	0.00	3.13
Lepidoptera	2	1.89	2	1.01	29.00	0.00	0.97
Unidentified arthropod	7	6.73	20	10.20	562,091.72	26.69	14.54
Neuroptera	1	0.96	6	3.06	43.66	0.00	1.34
Orthoptera	9	8.65	10	5.10	174,344.62	8.28	7.34
Pseudoscorpionida	2	1.92	5	2.55	11.05	0.00	1.49
Scolopendromorpha	1	0.96	1	0.51	31.44	0.00	0.49
Scorpiones	1	0.96	1	0.51	136,468.28	6.48	2.65
Total	104	100	196	100	2,106,224.02	100	100
Niche breadth			5.7509		7.4415		
Empty stomachs	5						

APPENDIX II
Continued.

<i>Tropidurus hispidus</i> (n = 49)							
Categories	F	F%	N	N%	V	V%	IRI
Araneae	17	11.04	26	1.39	3551.24	7.13	6.52
Bird	2	1.30	2	0.11	988.89	1.98	1.13
Blattodea	1	0.65	3	0.16	255.93	0.51	0.44
Coleoptera	30	19.48	94	5.01	13,287.26	26.66	17.05
Diptera	3	1.95	3	0.16	45.91	0.09	0.73
Formicidae	33	21.43	540	28.80	3698.41	7.42	19.22
Hemiptera	2	1.30	2	0.11	314.34	0.63	0.68
Hymenoptera	11	7.14	22	1.17	1491.64	2.99	3.77
Isoptera	15	9.74	1108	59.09	12,646.31	25.38	31.40
Lizard	1	0.65	1	0.05	2055.27	4.12	1.61
Insect larvae	3	1.95	4	0.21	169.30	0.34	0.83
Lepidoptera	4	2.53	4	0.21	715.80	1.42	1.39
Mantodea	1	0.65	1	0.05	0.96	0.00	0.23
Plant material	6	3.90	16	0.85	2872.02	5.76	3.50
Unidentified arthropod	2	1.30	2	0.11	113.83	0.23	0.54
Unidentified vertebrate	1	0.65	1	0.05	1577.86	3.17	1.29
Neuroptera	5	3.25	29	1.55	2892.79	5.80	3.53
Orthoptera	8	5.19	8	0.43	2707.14	5.43	3.68
Eggshell	1	0.65	1	0.05	38.11	0.08	0.26
Pseudoscorpionida	1	0.65	1	0.05	13.84	0.03	0.24
Scolopendromorpha	6	3.90	6	0.32	376.47	0.76	1.66
Scorpiones	1	0.65	1	0.05	19.55	0.04	0.25
Total	154	100	1875	100	49,832.85	100	100
Niche breadth			2.2970		6.2490		
Empty stomachs	2						
<i>Tropidurus semitaeniatus</i> (n = 26)							
Categories	F	F%	N	N%	V	V%	IRI
Araneae	9	12.00	17	4.06	286.68	0.94	5.67
Blattodea	1	1.33	1	0.24	39.20	0.13	0.57
Chilopoda	1	1.33	1	0.24	4.81	0.02	0.53
Coleoptera	11	14.67	26	6.21	601.44	1.98	7.62
Dermaptera	1	1.33	1	0.24	0.28	0.00	0.52
Diptera	1	1.33	13	3.10	21.06	0.07	1.50
Formicidae	8	10.67	110	26.25	362.11	1.19	12.70
Hemiptera	4	5.33	4	0.95	157.56	0.52	2.27
Hymenoptera	5	6.67	12	2.86	552.10	1.82	3.78
Insect larvae	3	4.00	6	1.43	97.79	0.32	1.92
Isoptera	5	6.67	142	33.89	1933.10	6.37	15.64
Lepidoptera	1	1.33	1	0.24	14.74	0.05	0.54
Plant material	9	12.00	67	15.99	23,505.21	77.41	35.13
Unidentified arthropod	4	5.33	4	0.95	766.18	2.52	2.94
Neuroptera	1	1.33	1	0.24	16.53	0.05	0.54
Orthoptera	5	6.67	6	1.43	1948.34	6.42	4.84
Pseudoscorpionida	3	4.00	4	0.95	9.35	0.03	1.66
Scolopendromorpha	3	4.00	3	0.72	48.86	0.16	1.63
Total	75	100	419	100	30,365.34	100	100
Niche breadth			4.6001		1.6420		
Empty stomachs	0						
<i>Vanzosaura multiscutata</i> (n = 12)							
Categories	F	F%	N	N%	V	V%	IRI
Araneae	1	11.11	1	1.37	22.29	32.53	15.00
Coleoptera	4	44.44	8	10.96	18.48	26.97	27.46
Isoptera	3	33.33	61	83.56	23.26	33.94	50.28
Unidentified arthropod	1	11.11	3	4.11	4.50	6.57	7.26
Total	9	100	73	100	68.53	100	100
Niche breadth			1.4042		3.3556		
Empty stomachs	4						