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Ecology of a Cerrado Lizard Assemblage in the Jalapão Region of Brazil

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We examined the relative roles of contemporary (species interactions) and historical factors (phylogeny) in structuring a lizard assemblage (14 species) from one of the last remaining large expanses of undisturbed Cerrado in Brazil. Niche breadth for microhabitat was low for all species in the assemblage, and microhabitat niche overlaps varied from none to almost complete and appeared associated with phylogenetic similarity. Mean microhabitat and diet overlaps among lizard species did not differ statistically from random, based on a pseudocommunity analysis, indicating a negligible role of contemporary factors in assemblage structure. Prey overlaps were highest within Gymnophthalmidae and Teiidae. A cluster analysis of principal component scores of morphometric variables revealed groups corresponding to lizard families, suggesting a strong association between morphology and phylogeny. Similarities among closely related species in microhabitat use, diel activity, and diet breadth, based on cladogram inspection, suggested that phylogeny might affect assemblage structure. However, a Canonical Phylogenetic Ordination (CPO) analysis revealed no significant phylogenetic effects on lizard microhabitat use or diet composition. We suggest that under-representation of species in major clades (low taxon sampling) renders it difficult to detect potential historical and ecological effects on assemblage structure.

THE structure (or organization) of animal assemblages can be defined in a number of ways, but often incorporates the geographic area where species live, their ecological interactions, resource use patterns, and evolutionary relationships among species (Ricklefs and Miller, 1999). In a more restricted way (the one we use in this study), structure can be defined as non-random patterns of resource use among coexisting species (Winemiller and Pianka, 1990). Ecological factors (competition and predation in particular) were deemed the primary determinants of assemblage structure until recently (Wiens, 1977; Diamond, 1978; Semlitsch, 1987). Although community-level processes may influence structure of some assemblages (e.g., Spiller and Schoener, 1989, 1990; Case and Bolger, 1991), ecological differences among syntopic species may have their origins deep in the evolutionary history of clades comprising present-day assemblages (Losos, 1994, 1996; Vitt et al., 2003). One difficulty in assessing phylogenetic effects on assemblage structure is that taxon sampling in low diversity assemblages may not allow robust statistical tests. Using combined data from Neotropical rainforests and world deserts, Vitt and Pianka (2005) showed that nearly 80% of dietary variation of 184 lizard species in 12 families from four continents could be tied to six major divergence points deep in squamate evolutionary history.

Several recent studies have demonstrated structure in Neotropical lizard assemblages. In a lizard assemblage of a Restinga area in the Brazilian state of Rio de Janeiro, morphometric data distinguished two groups: one of bromeliad lizards and another of ''sandy runners'' (Araújo, 1991). In a Caatinga lizard assemblage, similarities among closely related species suggested that phylogeny contributed to observed structure (Vitt, 1995). Vitt and Zani (1998a) reached the same conclusion in describing the structure of a lizard assemblage in a transitional forest in Amazonia. Gainsbury and Colli (2003) used null model analyses to assess structure in lizard assemblages from open vegetation enclaves in the Brazilian state of Rondônia and suggested lack of organization in the assemblages. In a lizard assemblage in Amazon Savanna (in Roraima), eight species sorted into three foraging guilds: herbivores, active foragers, and sit-and-wait foragers (Vitt and Carvalho, 1995). A Cerrado lizard assemblage near Alto Araguaia, in Mato Grosso State with only nine species contained some species that diverged in microhabitat use (Tropiduridae and Polychrotidae) and others that appeared to converge in microhabitat use (Teiidae and Gymnophthalmidae; Vitt, 1991). However, in Cerrado and Amazon Savanna lizard assemblage studies, historical factors were not considered.

The Cerrado harbors a diverse herpetofauna with numerous endemic species (Colli et al., 2002) and covers about 2,000,000 km^2, 25% of Brazil (Oliveira and Marquis, 2002). It is considered among the most threatened biomes in the world as the result of anthropogenic activities (Alho and Martins, 1995). Monthly temperatures average 20 to 22 C and 1500–2000 mm of highly predictable and strongly seasonal precipitation falls annually, mostly from October to April (Nimer, 1989). The biome includes forests, where arboreal plant species predominate, savannas, with trees and shrubs dispersed in an herbaceous stratum, and grasslands, with herbaceous plant species and some shrubs. Tree trunks are tortuous, with thick corky barks and hard, coriaceous leaves (Ribeiro and Walter, 1998).

Even though the Cerrado covers 25% of Brazil, the largest country in South America, only a few studies have focused on lizard assemblages. Lizards have been shown to be model organisms for ecological research, particularly studies aimed at understanding patterns of community structure (Huey et al., 1983; Vitt and Pianka, 1994). The most relevant study on lizard assemblages from the Cerrado was carried out in Alto Araguaia, Mato Grosso State, and the lizard assemblage was considered depauperate compared with those of other Neotropical biomes (Vitt, 1991). More recent studies have shown that many Cerrado lizard assemblages are nearly as diverse as Amazonian lizard assemblages (Colli et al., 2002).

Herein, we describe the lizard assemblage from the Jalapão region, one of the last remaining large expanses of undisturbed Cerrado. To examine structure of this assemblage, we combine ecological and morphometric data with phylogenetic data to examine the relative role of history (e.g., Brooks and McLennan, 1991; Losos, 1996) and analyze niche overlaps to examine the relative role of species interactions. Because the Cerrado is one of the most threatened biomes in world, these data should also be useful in developing conservation and management strategies for the Cerrado.

MATERIALS AND METHODS

Study site.—Field work was conducted from 13 February to 10 March 2002 in a Cerrado area in the Jalapão region near the city of Mateiros (10°32′46.69″S, 46°25′13.20″W) in eastern Tocantins State, Brazil. The Jalapão covers approximately 53,341 km^2. The region is characterized by an open and low Cerrado on sandy soils with strong influence of the Caatinga biome from northeastern Brazil. It has one of the lowest human densities in Brazil, with only 1.21 inhabitants per km^2, but anthropic pressures are increasing mainly due to tourism.

Microhabitat and temperatures.—We captured lizards with drift fences, by hand, or using a shotgun. In the lab, we killed live lizards with an injection of Tiopental®, in accordance with approved protocols, and fixed them with 10% formalin. When we captured lizards by hand or shotgun, we immediately took cloacal, substrate, and air temperatures to the nearest 0.2 C, with a Miller and Weber® cloacal thermometer. We also recorded microhabitat and hour of capture. We recorded microhabitats in which lizards were first observed, using the following microhabitat categories: grass, open ground, termite nests, tree trunks, and rocks. We computed microhabitat niche breadths (B) using the inverse of Simpson's diversity index (Simpson, 1949):

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

where p is the proportion of microhabitat category i, and n is the number of categories. Values vary from 1.0 (exclusive use of a single microhabitat) to 5.0 (equal use of all five microhabitats). We also calculated microhabitat use overlap with the equation:

$$\phi_{ij} = \frac{\sum_{i=1}^{n} p_{ij} p_{ik}}{\sqrt{\sum_{i=1}^{n} p_{ij}^2 \sum_{i=1}^{n} p_{ik}^2}},$$

where p represents the proportion of microhabitat category i, n is the number of categories, and j and k represent the species being compared (Pianka, 1973). Overlap $\emptyset_{ij}$ varies from 0 (no overlap) to 1 (complete overlap). To investigate presence of non-random patterns in microhabitat niche overlap, we used the Niche Overlap Module of EcoSim (Gotelli and Entsminger, 2003). Data for such an analysis consists of a matrix in which each species is a row and each microhabitat category is a column. The matrix is reshuffled to produce random patterns that would be expected in the absence of underlying structure. We used the options ''Pianka's niche overlap index'' and ''randomization algorithm two'' in EcoSim. Randomization algorithm two substitutes the microhabitat category in the original matrix with a random uniform number between zero and one, but retains the zero structure in the matrix (Winemiller and Pianka, 1990).

Diet.—We analyzed stomach contents under a stereomicroscope, identifying prey items to level of order, with the exception of ants (Formicidae), which were considered as a separate prey category. We recorded the length and width (0.01 mm) of intact prey with Mitutoyo® electronic calipers and estimated prey volume (V) as an ellipsoid:

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

where w is prey width and l is prey length. We calculated numeric and volumetric percentages of each prey category for pooled stomachs. From these percentages, we computed niche breadths (B) using the inverse of Simpson's diversity index (Simpson, 1949), as described above except that values for diet niche breadth can vary from 1.0 to 30 (30 prey categories were recognized). Throughout the text we used the average between numeric and volumetric niche breadths, referred to as diet niche breadth. We also calculated the percentage of occurrence of each prey category (number of stomachs containing prey category i, divided by the total number of stomachs). We excluded from the volumetric analyses prey items that were too fragmented to allow reliable estimates of their volumes. To determine the relative contribution of each prey category, we calculated the importance index for pooled stomachs using the following equation:

$$I = \frac{F\% + N\% + V\%}{3},$$

where $F\%$ is the percentage of occurrence, $N\%$ is the numeric percentage, and $V\%$ is the volumetric percentage.

We calculated dietary overlap using the overlap equation as described above for microhabitat (Pianka, 1973). To investigate presence of nonrandom patterns in microhabitat niche overlap, we used ''Niche Overlap Module'' of EcoSim (Gotelli and Entsminger, 2003) as described above for microhabitat.

Morphometry.—Using Mitutoyo® electronic calipers, were recorded the following morphometric variables to the nearest 0.01 mm: snout-vent length (SVL), body width (at its broadest point), body height (at its highest point), head width (at its broadest point), head height (at its highest point), head length (from the tip of the snout to the commissure of the mouth), hindlimb length, forelimb length, and tail length (from the cloaca to the tip of the tail). To maximize availability of data, we estimated intact tail length of lizards with broken or regenerated tails using a regression equation relating tail length to SVL, calculated from lizards with intact tails, separately for populations and sexes. We log-transformed (base 10) all morphometric variables prior to analyses to meet requirements of normality (Zar, 1998). To partition total morphometric variation between size and shape variation, we defined body size as an isometric size variable (Rohlf and Bookstein, 1987) following the procedure described by Somers (1986). We calculated an isometric eigenvector, defined *a priori* with values equal to $p^{-0.5}$, where p is the number of variables (Jolicoeur, 1963). Next, we obtained scores from this eigenvector, hereafter called body size, by post-multiplying the n by p matrix of log-transformed data, where n is the number of observations, by the p by 1 isometric eigenvector. To remove the effects of body size from the log-transformed variables, we used residuals of regression between body size and each variable. The resultant residuals were used in a principal component analysis to examine size-free morphological variation and to identify the taxonomic level at which ecological variation among species occurred.

Statistical analysis.—We used SYSTAT 11.0 and SAS 8.1 for Windows, with a significance level of 5% to reject null hypotheses for statistical hypothesis testing. Throughout the text, means appear ±1 SD.

To assess the role of history in structuring the assemblage, we used Canonical Phylogenetic Ordination–CPO (Giannini, 2003). Canonical Phylogenetic Ordination is a modification of Canonical Correspondence Analysis–CCA (Ter Braak, 1986), a constrained ordination method that promotes the ordination of a set of variables in such a way that its association with a second set of variables is maximized. The significance of the association is tested via randomizations of one or both of the data sets. In our CPO, one of the matrices (Y) contained data (diet composition or microhabitat use) measured over the lizard species in the assemblage, whereas the second matrix (X) consisted of a tree matrix that contained all the monophyletic groups in the assemblage, each coded separately as a binary variable. The analysis thus consisted of finding the subset of groups (columns of X) that best explained the variation in Y, using CCA coupled with Monte Carlo permutations. We performed CPO in CANOCO 4.5 for Windows, using the following parameters: symmetric scaling, biplot scaling, downweighting of rare species, manual selection of environmental variables (monophyletic groups), 9,999 permutations, and unrestricted permutations. Because of differences in completeness of data for microhabitat use and diet composition, we used two different trees, defined in Figure 1.

RESULTS

Species composition and activity.—The lizard assemblage in Jalapão contains 14 species; one iguanid (*Iguana iguana*), two polychrotids (*Anolis nitens* and *Polychrus acutirostris*), one tropidurid (*Tropidurus ''oreadicus''*), two gekkonids (*Briba brasiliana* and *Gymnodactylus carvalhoi*), three teiids

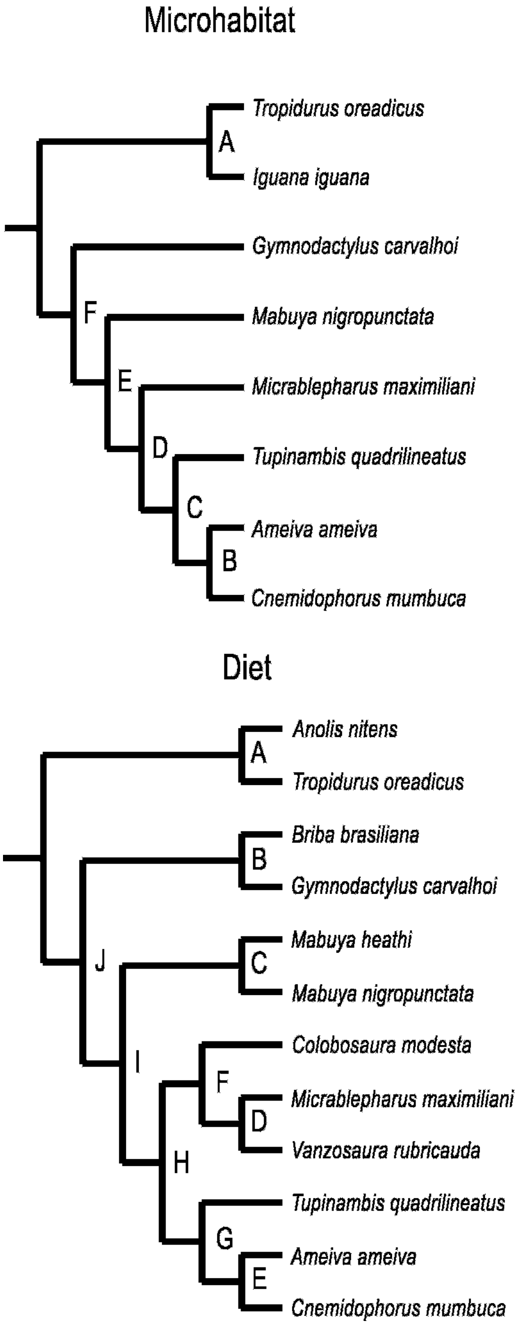


Fig. 1. Individual groups used in canonical phylogenetic ordination for microhabitat and diet data. Phylogeny based on Estes et al. (1988).

(*Ameiva ameiva, Cnemidophorus mumbuca*, and *Tupinambis quadrilineatus*), three gymnophthalmids (*Colobosaura modesta, Micrablepharus maximiliani*, and *Vanzosaura rubricauda*) and two scincids (*Mabuya heathi* and *Mabuya nigropunctata*). Almost all species are diurnal, with exception of the gekkonids *B. brasiliana*, which is strictly nocturnal, and *G. carvalhoi*, which is active both during the day and at night. Although we did not find *G. carvalhoi* during searches at night, they were abundant in drift fences that were monitored early in the morning, suggesting that they were active outside of termite nests early in the evening the night before, at night, or early in the morning.

Lizard activity occurred from 0700 h to 2200 h or later and varied among species. Usually, sit-and-wait lizards tended to be active earlier than active foragers. For example, the first active *T.* ``*oreadicus*'' was observed near 0800 h, whereas the first active *A. ameiva* and *C. mumbuca* were not observed until nearly 1000 h. Activity of diurnal lizards ended around 1800 h, and nocturnal lizards initiated activity around 1800 h. The latest record was 2200 h for the gecko *B. brasiliana.* Because we did not search for lizards after 2200 h, their activity period may be longer. The diurnal lizard *M. maximiliani* was common in pitfall traps indicating that most activity was during the day. Several found between 1800 h and 2000 h were inside termite nests and probably not active.

Microhabitat use and body temperatures.—A majority of the lizard fauna occurs in open areas, but a small portion was restricted to gallery forest (*Anolis nitens, Colobosaura modesta*, and *Tupinambis quadrilineatus*). The teiids, gymnophthalmids, and scincids are primarily terrestrial, the iguanid and polychrotids are both terrestrial and arboreal, and the tropidurid is ubiquitous (Fig. 2).

Ameiva ameiva occurred primarily in open ground and grass microhabitats (Fig. 2), similar to the other teiids *Cnemidophorus mumbuca* and *Tupinambis quadrilineatus*, but these species live only inside gallery forests. *Briba brasiliana* was observed active at night. A few individuals were found inactive during the day under loose bark on tree trunks. *Gymnodactylus carvalhoi* was found almost exclusively inside of termite nests (Fig. 2). *Iguana iguana* occurred on the ground and in trees (Fig. 2), in open and forested habitats, closely associated with watercourses. *Mabuya nigropunctata* was observed in open and forested areas, occurring in the open ground microhabitat (Fig. 2). *Micrablepharus maximiliani* was collected inside termite nests (Fig. 2) and in drift fences, indicating that termite nests are important to these lizards. Individuals moved on open ground, especially in areas with leaf litter. *Tropidurus "oreadicus"* was found in most microhabitats (Fig. 2). *Anolis nitens* was associated with forested habitats, where it used the ground and low perches on trees. *Polychrus acutirostris* lives

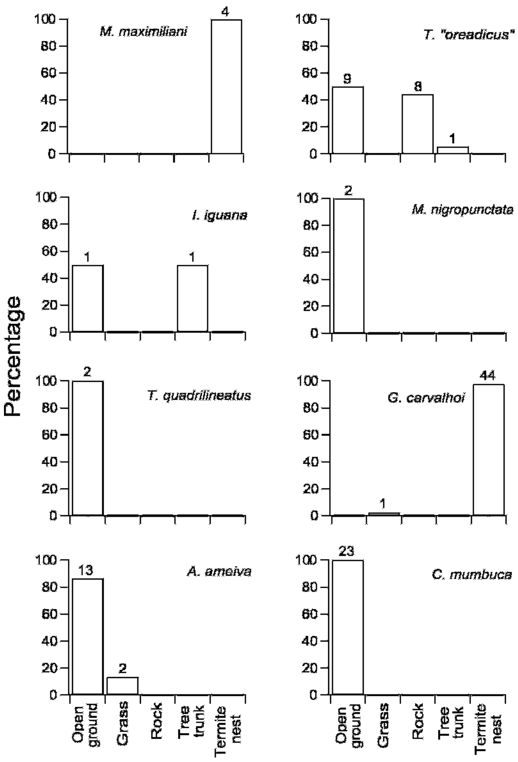


Fig. 2. Frequency distribution of individuals according to microhabitat categories for Jalapão lizards. Sample sizes are indicated at the top of the bars.

in trees in open habitats but descends to the ground to disperse. Because of their cryptic coloration and behavior, they were difficult to observe. *Colobosaura modesta* was associated with forested habitats, but also occurred in open areas on the ground. *Vanzosaura rubricauda* and *M. heathi* were observed in open ground in open areas of Cerrado.

Niche breadth for microhabitat was low for all species in the assemblage. *Tropidurus "oreadicus"* had the largest (2.22) and *C. mumbuca, T. quadrilineatus, M. maximiliani,* and *M. nigropunctata* had the smallest (1.00) niche breath values. Microhabitat niche overlap varied from none to almost complete (Table 1). The lowest results for niche overlap were found between species most distant phylogenetically. *Iguana iguana* had intermediate values for niche overlap with most other species, but probably does not interact with other species because it is more often found in gallery forests whereas other species are usually found in open Cerrado. The sit-and-wait forager *T. "oreadicus"* also had intermediate values of overlap with most other species, but not with *M. maximiliani* and *G. carvalhoi,* which were found nearly exclusively inside termite nests. However, both of these were also common in drift fences, suggesting that they frequently move about outside termite nests. Microhabitat overlaps among active foragers tended to be high for all species combinations.

Mean body temperatures ranged from 29.1 C in *M. maximiliani* to 40.0 C in *I. iguana.* Because of a high association between body and air temperature (R^2 = 0.66, $F_{3,102}$ =66.04, $P <$ 0.0001), we removed the effect of air temperature by calculating an ANCOVA, with air temperatures as a covariate followed by a *post hoc* Tukey test. The ANCOVA detected significant differences among species ($F_{4,1,98}$ = 38.05, $P <$ 0.0001), and a *post hoc* Tukey test identified one statistically homogeneous group containing the teiids *A. ameiva* and *C. mumbuca.* Mean niche overlap in microhabitat use was 0.48, and the

TABLE 1. OVERLAP IN MICROHABITAT (BOLDFACE) AND DIET FOR JALAPÃO LIZARDS.

	I. i.	*A. n.*	*T. o.*	*B. b.*	*G. c.*	*A. a.*	*C. m.*	*T. q.*	*C. mo.*	*M. m.*	*V. r.*	*M. h.*	*M. n.*
I. i.		—	—	—	—	—	—	—	—	—	—	—	—
A. n.	—		0.282	0.000	0.208	0.277	0.559	0.097	0.611	0.754	0.646	0.856	0.168
T. o.	**0.585**	—		0.106	0.468	0.337	0.469	0.049	0.292	0.319	0.300	0.361	0.262
B. b.	—	—	—		0.393	0.448	0.302	0.000	0.000	0.081	0.000	0.034	0.348
G. c.	**0.000**	—	**0.000**	—		0.928	0.874	0.019	0.216	0.401	0.217	0.298	0.881
A. a.	**0.699**	—	**0.736**	—	**0.003**		0.883	0.144	0.263	0.427	0.263	0.431	0.872
C. m.	**0.707**	—	**0.745**	—	**0.000**	**0.989**		0.068	0.611	0.719	0.610	0.667	0.801
T. q.	**0.707**	—	**0.745**	—	**0.000**	**0.988**	**1.000**		0.081	0.077	0.090	0.129	0.058
C. mo.	—	—	—	—	—	—	—	—		0.889	0.991	0.71	0.344
M. m.	**0.000**	—	**0.000**	—	**0.999**	**0.000**	**0.000**	**0.000**	—		0.902	0.784	0.552
V. r.	—	—	—	—	—	—	—	—	—	—		0.72	0.352
M. h.	—	—	—	—	—	—	—	—	—	—	—		0.323
M. n.	**0.707**	—	**0.745**	—	**0.000**	**0.988**	**1.000**	**1.000**	—	**0.000**	—	—	

Note: *I. i–Iguana iguana, A. n.– Anolis nitens, T. o.–Tropidurus "oreadicus," B. b.–Briba brasiliana, G. c.–Gymnodactylus carvalhoi, A. a.–Ameiva ameiva, C. m.–Cnemidophorus mumbuca, T. q.–Tupinambis quadrilineatus, C. mo.–Colobosaura modesta, M. m.–Micrablepharus maximiliani, V. r.–Vanzosaura rubricauda, M. h.–Mabuya heathi, M. n.–Mabuya nigropunctata.*

TABLE 2. IMPORTANCE INDEX OF PREY CATEGORIES IN THE DIET OF 12 LIZARD SPECIES FROM JALAPÃO.

Prey Type	*A. a.*	*C. m.*	*T. q.*	*T. o.*	*B. b.*	*G. c.*	*C. mo.*	*M. m.*	*V. r.*	*M. h.*	*M. n.*	*A. n.*
Annelida	—	—	—	—	—	0.55	—	—	—	—	—	—
Aranae	7.00	9.07	8.57	2.47	—	3.16	33.34	21.65	34.73	9.49	24.69	—
Blattaria	5.73	2.86	—	1.30	—	2.22	4.63	4.71	—	4.76	5.75	—
Chilopoda	0.93	0.55	—	0.21	—	0.84	—	—	—	—	—	—
Coleoptera	6.49	4.54	—	11.05	—	3.78	—	—	—	10.25	—	—
Dermaptera	0.47	—	—	—	—	—	—	—	—	—	—	—
Diplopoda	0.92	0.49	—	1.27	42.15	1.07	—	—	—	—	—	—
Diptera	—	0.28	—	—	—	—	—	3.77	—	—	—	—
Egg	0.95	—	—	0.16	—	—	—	—	—	—	—	—
Formicidae	0.45	4.45	—	42.29	—	11.76	3.67	0.91	3.79	—	—	—
Gastropoda	0.45	—	—	—	—	0.38	—	—	—	—	—	—
Gryllidae	0.84	1.87	—	—	—	1.40	—	—	—	—	—	—
Gryllotalpidae	5.78	—	—	—	34.09	—	—	—	—	—	—	—
Hemiptera	5.11	1.36	—	2.45	—	—	—	—	—	—	—	—
Homoptera	—	2.89	—	5.47	—	3.06	4.08	20.71	7.13	11.19	13.15	26.20
Hymenoptera (non ants)	—	0.14	—	—	—	—	—	—	—	—	—	—
Insect larvae	11.02	8.69	11.61	6.03	—	3.73	—	2.99	2.38	18.53	—	30.73
Isoptera	38.78	30.96	—	10.29	23.75	55.80	—	9.25	—	3.20	50.93	—
Lepidoptera	0.52	—	—	—	—	—	—	—	—	—	—	—
Mantoidea	—	1.81	—	0.44	—	—	4.34	1.85	—	7.27	—	—
Neuroptera	0.57	0.63	—	0.15	—	—	—	—	—	6.83	—	—
Odonata	0.58	0.86	—	—	—	—	—	—	—	—	—	—
Opilionida	—	0.30	—	—	—	—	—	—	—	—	—	—
Orthoptera	8.69	24.51	—	11.07	—	12.25	45.27	32.68	45.52	23.42	5.49	43.07
Phasmida	—	0.48	—	0.18	—	—	—	—	—	—	—	—
Plant material	3.36	—	60.42	0.87	—	—	—	—	—	—	—	—
Pseudoscorpionida	—	0.13	—	0.43	—	—	—	—	—	—	—	—
Scorpionida	—	—	—	0.15	—	—	—	—	—	—	—	—
Solifuga	—	3.13	—	3.70	—	—	4.68	1.49	6.46	5.06	—	—
Vertebrate	1.34	—	19.39	—	—	—	—	—	—	—	—	—
n	37	167	2	142	3	73	13	33	23	12	4	2
Numeric niche breadth	1.47	2.28	1.18	2.21	3.00	1.66	3.13	4.34	2.95	7.86	1.30	3.00
Volumetric niche breadth	8.14	5.48	2.60	6.84	2.06	2.98	2.55	4.58	2.74	4.96	2.68	2.12

Note: Species abbreviations are the same as in Table 1.

pseudocommunity analysis indicated that the probability of observing, by chance, a mean niche overlap of 0.48 or less is 0.91, revealing a lack of community structure.

Diet composition.—We analyzed contents of 557 stomachs and recognized 30 prey categories. The percentage of empty stomachs was 8.26%. Based on all lizard species, orthopterans were the most important prey type followed by termites and spiders (Table 2). Based on the dietary importance index, the most important prey for *A. ameiva* were termites and insect larvae; for *C. mumbuca*, termites and orthopterans; for *T. quadrilineatus*, plant material, mainly fruits, and vertebrates, a single individual of the toad, *Bufo granulosus*; for *T. "oreadicus,"* mainly ants; for *B. brasiliana*, millipedes and mole crickets; for *G. carvalhoi*, termites; for *C. modesta*, spiders; for *M. maximiliani*, spiders and homopterans; for *V. rubricauda*, grasshoppers and spiders; for *M. heathi*, grasshoppers and insect larvae; for *M. nigropunctata*, termites and spiders; and for *A. nitens*, grasshoppers and insect larvae (Table 2). Diet niche breadths calculated from the average between numeric and volumetric percentages of prey were usually low, with lowest values for *T. quadrilineatus* and *M. nigropunctata* and the largest values for *M. heathi*, *A. ameiva*, *T. "oreadicus,"* and *M. maximiliani*.

Prey overlap varied from zero (*B. brasiliana* vs. *A. nitens*, *C. modesta*, *T. quadrilineatus* and *V. rubricauda*) to 0.991 (*V. rubricauda* vs. *C. modesta*; Table 1). *Tupinambis quadrilineatus* had low overlaps with all species, the greatest of which was with *A. ameiva* (Table 1). Overlaps were high among the gymnophthalmids, the lowest of which was between *M. maximiliani* and *C. modesta* and the greatest between *C. modesta* and *V. rubricauda* (Table 1). With the exception of *T.*

TABLE 3. PRINCIPAL COMPONENT ANALYSIS OF SIZE-FREE MORPHOLOGICAL DATA FROM JALAPÃO LIZARDS.

	Factor I	Factor II	Factor III
Adjusted-SVL	0.837	−0.080	0.226
Adjusted-TL	0.195	−0.700	0.140
Adjusted-HW	0.025	0.897	0.191
Adjusted-HL	0.024	0.136	0.948
Adjusted-HH	−0.607	0.511	0.247
Adjusted-BW	0.456	0.617	−0.197
Adjusted-BH	0.678	0.303	−0.309
Adjusted-LL	−0.810	−0.311	0.008
Adjusted-FL	−0.757	0.331	−0.280
Eigenvalues	3.005	2.260	1.278
Percent of variance explained	33.393	25.108	14.198

Note: SVL–snout-vent length, TL–tail length, HW–head width, HL–head length, HH–head height, BW–body width, BH–body height, LL–leg length, and FL–forelimb length.

quadrilineatus, teiid lizards had high overlaps (Table 1). Mean niche overlap in diet composition was 0.40, and the pseudocommunity analysis indicated that the probability of observing, by chance, a mean niche overlap of 0.40 or less is 0.94, indicating a lack of community structure.

Morphometry.—The principal component analyses of size-free morphological variables revealed two factors accounting for 58.5% of the variation (Table 3). The first factor described a gradient of increasing SVL, as leg length, forelimb length, and head height decrease (Table 3). The second factor describes a gradient of increasing head width and body width as tail length decreases. The third factor describes increasing head length with decreasing forelimb length (Table 3). A plot of the average of factor scores per species for the first two principal components reveals clusters corresponding to lizard families (Fig. 3).

Historical effects.—A detailed inspection of the cladogram (Fig. 4) reveals several patterns suggesting the role of history in the Jalapão lizard assemblage. Microhabitats used by teiids, gymnophthalmids, and scincids were similar, suggesting that at least a portion of microhabitat use patterns reflect general traits of scleroglossan lizards. The same occurs within the polychrotids, with species using similar microhabitats. Activity is very similar among all species except the gekkonids, one of which is nocturnal and the other crepuscular/nocturnal. Body temperature data indicate that teiid lizards are active at very similar body temperatures. The teiids also have similar microhabitat niche breadth values. The two scincids differ in diet niche breadth values.

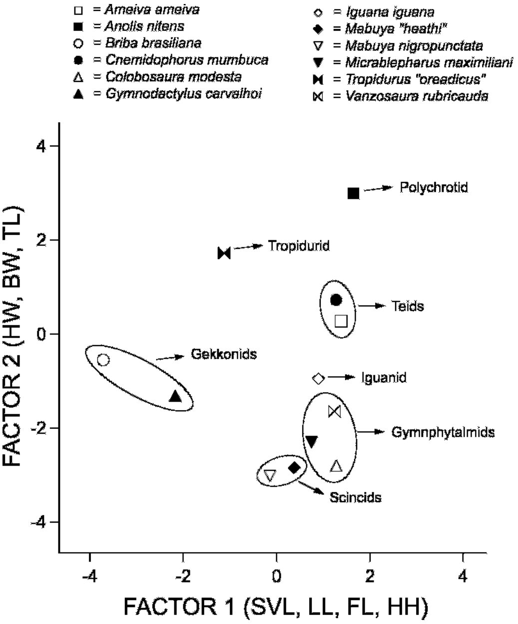
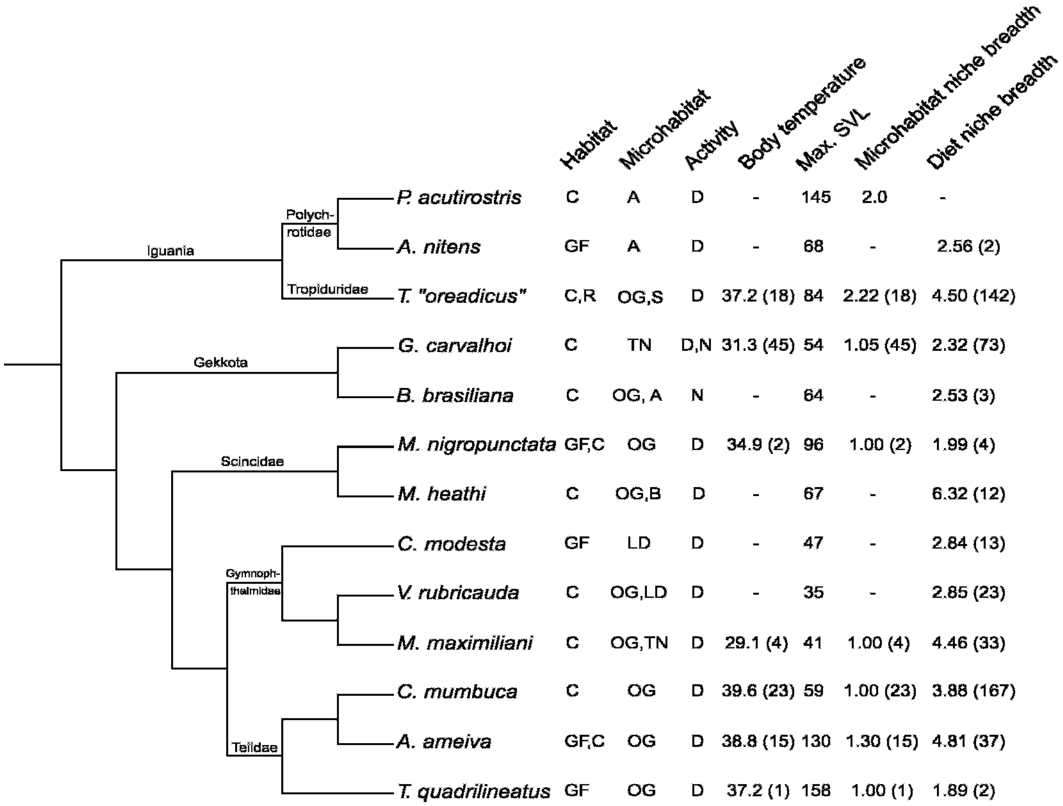


Fig. 3. Plot of the average per species of the first two principal components derived from size-free morphological data for Jalapão lizards.

Monte Carlo permutations (based on 9,999 permutations) from the canonical ordination revealed no significant phylogenetic effect on microhabitats used or dietary composition of the lizards (Table 4). Gekkonids and teiids contributed most to dietary variation (Fig. 1), but even their contributions were not significant ($P = 0.199$ and 0.240, respectively). For microhabitat, taxonomic groups that best explained variation were the basal separation between *Iguania* and *Scleroglossa* (Table 4), accounting for 32.65% of the total variation, and teiids, but none of these was significant ($P = 0.054$ and $P = 0.213$, respectively).

DISCUSSION

A major challenge in understanding determinants of assemblage structure is separating contemporary (species interactions) from historical (phylogenetic) effects (Losos, 1996; Webb et al., 2002). Species assemblages with low diversity may not provide the taxon sampling necessary to detect statistically historical effects even though they may be present and quite strong. Major ecological shifts have already been identified deep in the evolutionary history of squamate reptiles, including shifts in microhabitat use and diets using very large data sets (Vitt et al., 2003; Vitt and Pianka, 2005). We discuss our results in this context, stressing the difficulties imposed



	Habitat	Microhabitat	Activity	Body temperature	Max. SVL	Microhabitat niche breadth	Diet niche breadth
P. acutirostris	C	A	D	-	145	2.0	-
A. nitens	GF	A	D	-	68	-	2.56 (2)
T. "oreadicus"	C,R	OG,S	D	37.2 (18)	84	2.22 (18)	4.50 (142)
G. carvalhoi	C	TN	D,N	31.3 (45)	54	1.05 (45)	2.32 (73)
B. brasiliana	C	OG, A	N	-	64	-	2.53 (3)
M. nigropunctata	GF,C	OG	D	34.9 (2)	96	1.00 (2)	1.99 (4)
M. heathi	C	OG,B	D	-	67	-	6.32 (12)
C. modesta	GF	LD	D	-	47	-	2.84 (13)
V. rubricauda	C	OG,LD	D	-	35	-	2.85 (23)
M. maximiliani	C	OG,TN	D	29.1 (4)	41	1.00 (4)	4.46 (33)
C. mumbuca	C	OG	D	39.6 (23)	59	1.00 (23)	3.88 (167)
A. ameiva	GF,C	OG	D	38.8 (15)	130	1.30 (15)	4.81 (37)
T. quadrilineatus	GF	OG	D	37.2 (1)	158	1.00 (1)	1.89 (2)

Fig. 4. Phylogeny of Jalapão lizards showing the topology of ecological characteristics. Abbreviations for habitat are: C = Cerrado, GF = Gallery forest, R = rocky field. Abbreviations for microhabitat are: A = arboreal, OG = open ground, B = bushes, LD = litter-dwelling, S = saxicolous, TN = termite nest. Abbreviations for activity are: D = diurnal, N = nocturnal, CN = crepuscular/nocturnal. Note: general microhabitat categories are based on data from this work and from Vieira et al. (2000), Vitt (1991), Vitt and Caldwell (1993), Vanzolini et al. (1980), and Ávila-Pires (1995).

when taxon sampling is reduced (as in many local assemblages).

Species composition and activity.—The lizard assemblage in our study site at Jalapão contained 14 species. This appears low when compared with other South American biomes like Amazon Forest, which typically has about 25 species (Vitt, 1996; Vitt and Zani, 1996). In relation to other South American open formations, such as Caatinga (18 species, Vitt, 1995) and Amazon Savanna (eight species, Vitt and Carvalho, 1995), lizard richness is similar or greater. Well-sampled localities in Cerrado average 14–25 species (Colli et al., 2002). Lizard richness for the entire Jalapão region is greater than the 14 species we reported, but this serves well as an estimate of lizard species diversity at a single site. Our recent surveys in the region indicate the presence of at least 22 lizard species (Vitt et al., 2002), including undescribed species of *Cnemidophorus* and *Kentropyx*, highlighting the importance of the conservation of the Jalapão region. Additional species with secretive habits will undoubtedly be found with additional surveys.

Microhabitat use and body temperatures.—Differences in time of activity among diurnal species were small. The single tropidurid was active somewhat earlier in the day than teiids, a common pattern in other South American lizard assemblages (Vitt et al., 1997c; Mesquita and Colli, 2003a, 2003b). Body temperature patterns were consistent with differences in activity. Teiids had higher body temperatures than the tropidurid and higher body temperatures than all other species in the assemblage. In all Neotropical lizard assemblages studied, the highly active teiids had the highest body temperatures, suggesting that high body temperatures and high activity levels are coevolved traits.

Lack of structure in microhabitat use among Jalapão lizards, although unusual (e.g., Pianka, 1986; Winemiller and Pianka, 1990; Vitt and

TABLE 4. HISTORICAL EFFECTS ON THE ECOLOGY OF CERRADO LIZARDS. Results of Monte Carlo permutation tests of individual groups (Defined in Fig. 1) for the Y matrices of diet and microhabitat. Percentage of the variation explained (relative to total unconstrained variation), and F and P values for each variable are given (9,999 permutations were used) for each main matrix. Note that no groups used for selection of variables yielded individual $P \leq 0.05$. See text for details.

Group(s)	Variation	Variation %	F	P
Diet				
B	0.268	23.717	1.759	0.1994
G	0.212	18.761	1.345	0.2404
F	0.194	17.168	1.214	0.3043
I	0.170	15.044	1.046	0.4077
H	0.126	11.150	0.753	0.8633
E	0.118	10.442	0.707	0.5250
D	0.116	10.265	0.693	0.5429
A/J	0.101	8.938	0.596	0.6945
C	0.090	7.965	0.530	0.7882
Microhabitat				
A/F	0.461	32.649	1.986	0.0541
C	0.359	25.425	1.441	0.2130
E	0.296	20.963	1.138	0.4991
B	0.218	15.439	0.800	0.5654
D	0.149	10.552	0.525	0.6534

Carvalho, 1995), suggests lack of competition for space, i.e., microhabitats may not be in limited supply (Connor and Simberloff, 1979). Jalapão lizard populations may be maintained well below carrying capacity by predators. Alternatively, failure to detect structure in microhabitat use may result from sampling problems, since sample size for some species was small. Although most lizard species can be easily trapped in Cerrado habitats, they are very difficult to observe while active, making it difficult to accurately quantify microhabitat use. Others, like *Briba brasiliana* and some species of *Mabuya*, are difficult to collect even using traps, biasing dietary data. Finally, the lack of data for some species reflects, to a certain extent, differences in local abundance.

Diet composition.—With the exception of *Vanzosaura rubricauda*, which ate mainly grasshoppers and spiders in Jalapão but thysanurans and dermapterans in Caatinga (Vitt, 1995), most species from Jalapão had diets similar to those of different populations or closely related species from other Neotropical lizard assemblages. These include *Ameiva ameiva* (termites and insect larvae; Vitt and Colli, 1994), *Cnemidophorus mumbuca* (termites and orthopterans; Eifler and Eifler, 1998; Mesquita and Colli, 2003a, b), *Tupinambis quadrilineatus* (plant material and vertebrates; Colli et al., 1998), *Tropidurus "oreadicus"* (ants; Van Sluys, 1993, 1995; Vitt et al., 1997b), *Gymnodactylus carvalhoi* (termites; Colli et al., 2003), *Micrablepharus maximiliani* (spiders and homopterans; Vieira et al., 2000), *Mabuya heathi* (grasshoppers and insect larvae; Vitt, 1995), *Mabuya nigropunctata* (termites and spiders; Vitt and Blackburn, 1991), and *Anolis nitens* (grasshoppers and insect larvae; Vitt et al., 2001). The diet of these species appears conservative with little detectable variation among populations from different places and different times, suggesting a historical basis for patterns of prey use among Jalapão lizards (see Vitt and Pianka, 2005).

The highest dietary overlaps were found within gymnophthalmids and teiids (except *Tupinambis quadrilineatus*) and between *Gymnodactylus carvalhoi* and *Mabuya nigropunctata*. The primary contributor to these high overlaps was the high consumption of termites. These species do not necessarily capture termites in the same places or at the same times. For instance, teiids dig and break into materials containing termites, whereas gymnophthalmids do not, and *Gymnodactylus carvalhoi* likely capture termites within termite nests where they live. Similar differences in temporal or spatial acquisition of similar prey were reported by Pianka (1986). Low overlap between *T. quadrilineatus* and the other teiids may simply reflect the small sample size or even the large body size of the former.

Lack of structure found with the pseudocommunity analysis could indicate a lack of detectable competition among species, suggesting that resources are effectively non-limiting (Connor and Simberloff, 1979). A previous study on fat storage cycles in Amazon Savanna and Cerrado lizards found that most species accumulate fat during the dry season when insect availability is low, suggesting that food is not limiting (Colli et al., 1997). Considering the range of lizard body sizes in Jalapão, structure may be more affected by prey size than prey type (Vitt and Zani, 1998a).

Morphometry.—Our results show closely related species clustered in morphological space. Some of the best evidence for environmental influences on morphology includes habitat shifts among closely related species associated with changes in morphology (Losos et al., 1993; Losos, 1995; Vitt et al., 1997a). Iguanian lizards in Jalapão are not closely related and morphological differences among them likely evolved in distant ancestors under different ecological conditions. *Anolis nitens* and *Tropidurus "oreadicus,"* for example, are quite similar morphologically and ecologically to their close relatives in other habitats, suggesting that pre-existing morphological and ecological traits permit coexistence in Jalapão. Teiids and gymnophthalmids are conservative in body shape but differ considerably in body size, most likely a consequence of intraguild interactions. Even though the bauplan appears to be little affected by ecological interactions, body size may determine to some extent which species can coexist (Vitt and Zani, 1996; Vitt et al., 1998, 2000). Most tropical New World skinks of the genus *Mabuya* are conservative morphologically, suggesting that lineage effects are more important than local interactions in determining morphological variation.

Historical effects.—Comparisons of Jalapão lizards with closely related species in different assemblages suggest that lineage effects played a predominant role in their ecology. However, this is apparently in conflict with our results from CPO analysis, which indicated no significant phylogenetic effects (only a marginally significant P value for the node separating *Iguania* and *Scleroglossa* in the microhabitat analysis). We offer two possible explanations for this apparent inconsistency, one of which may have broad implications.

First, sample size for microhabitat data was either too small or nonexistent for four of the 14 species. Small sample sizes for calculation of niche breadth effectively results in low estimates, potentially creating false specialists (see Pianka, 1986). Because of this, overlap values between these species and others with large sample sizes could be misleading. However, the creation of false specialists would tend to produce significant results in the pseudocommunity and CPO analyses, and this was not the case.

Second, and more important, ecological data sets on species-poor lizard assemblages may suffer from taxon sampling deficiencies, such that real historical effects are undetectable because major taxa are underrepresented. Only a single genus, *Mabuya*, is represented in our study site by more than one species and, in this case, the two species are highly divergent ecologically. *Mabuya nigropunctata* is widespread in Amazon Forest, entering the Cerrado in gallery forests (Vitt and Blackburn, 1991; Vitt, 1996). *Mabuya heathi* is known only from open areas, Caatinga in particular (Vitt, 1995). It should be noted that lack of closely related species may also make it difficult to detect the role of biological interactions. Therefore, the inability to detect both ecological and phylogenetic structure in the Jalapão assemblage may have resulted from a data deficiency in the analysis and will require experimentation in these species-poor communities. Phylogenetic effects detected in an Amazonian lizard assemblage by Vitt et al. (1999) and Giannini (2003) using different analyses were facilitated by a rich lizard fauna that contained several pairs of relatively closely related species. One of the primary phylogenetic effects found was in tropidurid lizards, which included two closely related species (*Plica plica* and *P. umbra*) that were ant specialists. In assemblages with larger numbers of closely related species, differences in ecological traits should be more easily detectable even if a portion of those differences is historical. Studies showing rapid ecological and morphological evolution in closely related *Anolis* species in the Caribbean suggest this (Losos et al., 1993; Losos, 1995).

Application of phylogenetic methods in community ecology studies is still in its infancy (e.g., Webb et al., 2002; Gotelli, 2004). Nevertheless, several analyses at the local (e.g., Vitt and Zani, 1998b; Vitt et al., 2000; Giannini, 2003) and two at the global (Vitt et al., 2003; Vitt and Pianka, 2005) level indicate that portions of lizard community structure have a historical basis. Because some of the ecological differences among lizard clades are deeply rooted in evolutionary history, evolutionary and ecological responses of individual species to changes in assemblage structure and resource abundance and diversity should vary in a manner predictable, to some degree, on how closely related species in different habitats and assemblages respond to such changes. Finally, phylogenetic analyses in which species from different assemblages are combined are essential to understand the relative importance of ecological and historical factors in determining structure in lizard assemblages, because the probability of detecting historical effects may be inversely related to the number of species in each major clade.

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LITERATURE CITED

ALHO, C. J. R., AND E. S. MARTINS. 1995. De Grão em Grão, o Cerrado Perde Espaço. WWF-Fundo Mundial para a Natureza, Brasília.

Araújo, A. F. B. 1991. Structure of a white sand-dune lizard community of coastal Brazil. Rev. Bras. Biol. 51:857–865.

Ávila-Pires, T. C. S. 1995. Lizards of Brazilian Amazonia (Reptilia: Squamata). Zool. Verh., Leiden 1995:3–706.

Brooks, D. R., and D. A. McLennan. 1991. Phylogeny, Ecology, and Behavior, a Research Program in Comparative Biology. The University of Chicago Press, Chicago.

Case, T. J., and D. T. Bolger. 1991. The role of interspecific competition in the biogeography of island lizards. Trends Ecol. Evol. 6:135–139.

Colli, G. R., R. P. Bastos, and A. F. B. Araújo. 2002. The character and dynamics of the Cerrado herpetofauna, p. 223–241. *In*: The Cerrados of Brazil: Ecology and Natural History of a Neotropical Savanna. P. S. Oliveira and R. J. Marquis (eds.). Columbia University Press, New York.

———, D. O. Mesquita, P. V. V. Rodrigues, and K. Kitayama. 2003. The ecology of the gecko *Gymnodactylus geckoides amarali* in a Neotropical savanna. J. Herpetol. 37:694–706.

———, A. K. Péres, Jr., and H. J. Cunha. 1998. A new species of *Tupinambis* (Squamata: Teiidae) from central Brazil, with analysis of morphological and genetic variation in the genus. Herpetologica 54:477–492.

———, ———, and M. G. Zatz. 1997. Foraging mode and reproductive seasonality in tropical lizards. J. Herpetol. 31:490–499.

Connor, E. F., and D. Simberloff. 1979. The assembly of species communities: chance or competition? Ecology 60:1132–1140.

Diamond, J. M. 1978. Niche shifts and the rediscovery of interspecific competition. Am. Sci. 66:322–331.

Eifler, D. A., and M. A. Eifler. 1998. Foraging behavior and spacing patterns of the lizard *Cnemidophorus uniparens*. J. Herpetol. 32:24–33.

Estes, R., K. de Queiroz, and J. Gauthier. 1988. Phylogenetic relationships within Squamata, p. 119–281. *In*: Phylogenetic Relationships of the Lizard Families. Essays Commemorating Charles L. Camp. R. Estes and G. Pregill (eds.). Stanford University Press, Stanford, California.

Gainsbury, A. M., and G. R. Colli. 2003. Lizard assemblages from natural Cerrado enclaves in southwestern Amazonia: the role of stochastic extinctions and isolation. Biotropica 35:503–519.

Giannini, N. P. 2003. Canonical phylogenetic ordination. Syst. Biol. 52:684–695.

Gotelli, N. J. 2004. A taxonomic wish-list for community ecology. Phil. Trans. Roy. Soc. London B 359:585–597.

———, and G. L. Entsminger. 2003. EcoSim: null models software for ecology. Acquired Intelligence Inc. & Kesey-Bear, Jericho, Vermont, http://www.garyentsminger.com/ecosim/index.htm.

Huey, R. B., E. R. Pianka, and A. Schoener. 1983. Lizard Ecology: Studies of a Model Organism. Harvard University Press, Cambridge, Massachusetts.

Jolicoeur, P. 1963. The multivariate generalization of the allometry equation. Biometrics 19:497–499.

Losos, J. B. 1994. Historical contingency and lizard community ecology, p. 319–333. *In*: Lizard Ecology: Historical and Experimental Perspectives. L. J. Vitt and E. R. Pianka (eds.). Princeton University Press, Princeton, New Jersey.

———. 1995. Community evolution in greater antillean *Anolis* lizards: phylogenetic patterns and experimental tests. Phil. Trans. Roy. Soc. London B 349:69–75.

———. 1996. Phylogenetic perspectives on community ecology. Ecology 77:1344–1354.

———, J. C. Marks, and T. W. Schoener. 1993. Habitat use and ecological interactions of an introduced and a native species of *Anolis* lizard on Grand Cayman, with a review of the outcomes of anole introductions. Oecologia 95:525–532.

Mesquita, D. O., and G. R. Colli. 2003a. The ecology of *Cnemidophorus ocellifer* (Squamata, Teiidae) in a Neotropical savanna. J. Herpetol. 37:498–509.

———, and ———. 2003b. Geographical variation in the ecology of populations of some Brazilian species of *Cnemidophorus* (Squamata, Teiidae). Copeia 2003:285–298.

Nimer, E. 1989. Climatologia da região centro-oeste, p. 393–421. *In*: Climatologia do Brasil. Fundação Instituto Brasileiro de Geografia e Estatística-IBGE, Rio de Janeiro, Brazil.

Oliveira, P. S., and R. J. Marquis. 2002. The Cerrados of Brazil: Ecology and Natural History of a Neotropical Savanna. Columbia University Press, New York.

Pianka, E. R. 1973. The structure of lizard communities. An. Rev. Ecol. Sys. 4:53–74.

———. 1986. Ecology and Natural History of Desert Lizards: Analyses of the Ecological Niche and Community Structure. Princeton Univ. Press, Princeton, New Jersey.

Ribeiro, J. F., and B. M. T. Walter. 1998. Fitofisionomias do bioma Cerrado, p. 89–166. *In*: Cerrado: Ambiente e Flora. S. M. Sano and S. P. Almeida (eds.). EMBRAPA-CPAC, Planaltina, DF, Brazil.

Ricklefs, R. E., and G. L. Miller. 1999. Ecology. W. H. Freeman and Company, New York.

Rohlf, F. J., and F. L. Bookstein. 1987. A comment on shearing as a method for ''size correction''. Syst. Zool. 36:356–367.

Semlitsch, R. D. 1987. Relationship of pond drying to the reproductive success of the salamander *Ambystoma talpoideum*. Copeia 1987:61–69.

Simpson, E. H. 1949. Measurement of diversity. Nature 163:688.

Somers, K. M. 1986. Multivariate allometry and removal of size with principal component analysis. Syst. Zool. 35:359–368.

Spiller, D. A., and T. W. Schoener. 1989. Effect of a major predator on grouping of an orb-weaving spider. J. Anim. Ecol. 58:509–523.

———, and ———. 1990. A terrestrial field experiment showing the impact of eliminating top predators on foliage damage. Nature 347:469–472.

Ter Braak, C. J. F. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology 76:1167–1179.

Van Sluys, M. 1993. Food habits of the lizard *Tropidurus itambere* (Tropiduridae) in Southeastern Brazil. J. Herpetol. 27:347–351.

———. 1995. Seasonal variation in prey choice by the lizard *Tropidurus itambere* (Tropiduridae) in Southeastern Brazil. Ciên. Cult. 47:61–65.

Vanzolini, P. E., A. M. M. Ramos-Costa, and L. J. Vitt. 1980. Répteis das Caatingas. Academia Brasileira de Ciências, Rio de Janeiro, Brazil.

Vieira, G. H. C., D. O. Mesquita, A. K. Péres, Jr., K. Kitayama, and G. R. Colli. 2000. Natural history: *Micrablepharus atticolus*. Herp. Rev. 31:241–242.

Vitt, L. J. 1991. An introduction to the ecology of Cerrado lizards. J. Herpetol. 25:79–90.

———. 1995. The ecology of tropical lizards in the Caatinga of northeast Brazil. Occ. Pap. Ok. Mus. Nat. Hist. 1:1–29.

———. 1996. Biodiversity of Amazonian lizards, p. 89–108. *In*: Neotropical Biodiversity and Conservation. A. C. Gibson (ed.). Occasional Publication of the Mildred E. Mathias Botanical Garden 1, Los Angeles.

———, and D. G. Blackburn. 1991. Ecology and life history of the viviparous lizard *Mabuya bistriata* (Scincidae) in the Brazilian Amazon. Copeia 1991: 916–927.

———, and J. P. Caldwell. 1993. Ecological observations on Cerrado lizards in Rondônia, Brazil. J. Herpetol. 27:46–52.

———, ———, G. R. Colli, A. A. Garda, D. O. Mesquita, F. G. R. França, and S. F. Balbino. 2002. Um guia fotográfico dos répteis e anfíbios da região do Jalapão no Cerrado brasileiro. Spec. Pub. Herpetol. 1:1–17.

———, ———, P. A. Zani, and T. A. Titus. 1997a. The role of habitat shift in the evolution of lizard morphology: evidence from tropical *Tropidurus*. Proc. Natl. Acad. Sci. USA 94:3828–3832.

———, and C. M. Carvalho. 1995. Niche partitioning in a tropical wet season: lizards in the Lavrado area of Northern Brazil. Copeia 1995:305–329.

———, and G. R. Colli. 1994. Geographical ecology of a Neotropical lizard: *Ameiva ameiva* (Teiidae) in Brazil. Can. J. Zool. 72:1986–2008.

———, and E. R. Pianka. 1994. Lizard Ecology. Princeton University Press, Princeton, New Jersey.

———, and ———. 2005. Deep history impacts present-day ecology and biodiversity. Proc. Natl. Acad. Sci. USA 102:7877–7881.

———, ———, W. E. Cooper, Jr., and K. Schwenk. 2003. History and the global ecology of squamate reptiles. Am. Nat. 162:44–60.

———, S. S. Sartorius, T. C. S. Ávila-Pires, and M. C. Esposito. 2001. Life on the leaf litter: the ecology of *Anolis nitens tandai* in the Brazilian Amazon. Copeia 2001:401–412.

———, and P. A. Zani. 1996. Organization of a taxonomically diverse lizard assemblage in Amazonian Ecuador. Can. J. Zool. 74:1313–1335.

———, and ———. 1998a. Ecological relationships among sympatric lizards in a transitional forest in the Northern Amazon of Brazil. J. Trop. Ecol. 14:63–86.

———, and ———. 1998b. Prey use among sympatric lizard species in lowland rain forest of Nicaragua. *Ibid.* 14:537–559.

———, ———, and T. C. S. Ávila-Pires. 1997b. Ecology of the arboreal tropidurid lizard *Tropidurus* (= *Plica*) *umbra* in the Amazon region. Can. J. Zool. 75:1876–1882.

———, ———, ———, and M. C. Esposito. 1998. Geographical ecology of the gymnophthalmid lizard *Neusticurus ecpleopus* in the Amazon rainforest. *Ibid.* 76:1671–1680.

———, ———, ———, ———, and D. B. Miles. 2000. Niche segregation among sympatric Amazonian teiid lizards. Oecologia 122:410–420.

———, ———, J. P. Caldwell, M. C. D. Araujo, and W. E. Magnusson. 1997c. Ecology of whiptail lizards (*Cnemidophorus*) in the Amazon region of Brazil. Copeia 1997:745–757.

———, ———, and M. C. Esposito. 1999. Historical ecology of Amazonian lizards: implications for community ecology. Oikos 87:286–294.

Webb, C. O., D. D. Ackerley, M. A. McPeek, and M. J. Donoghue. 2002. Phylogenies and community ecology. Ann. Rev. Ecol. Sys. 33:475–505.

Wiens, J. A. 1977. On competition and variable environments. Am. Sci. 65:590–597.

Winemiller, K. O., and E. R. Pianka. 1990. Organization in natural assemblages of desert lizards and tropical fishes. Ecol. Mon. 60:27–55.

Zar, J. H. 1998. Biostatistical Analysis. Prentice-Hall, Inc., Englewood Cliffs, New Jersey.

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