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ECOLOGY OF AN AMAZONIAN SAVANNA LIZARD ASSEMBLAGE IN MONTE ALEGRE, PARÁ STATE, BRAZIL

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Abstract: We describe the lizard assemblage from an Amazonian savanna in the region of Monte Alegre, Pará, Brazil, using ecological, morphological, and life history data, and examining the role of history in the assemblage. The lizard assemblage in Monte Alegre contained seven species. Microhabitat niche breadth was low for all species in the assemblage and niche overlap varied from none to almost complete. The least overlap in microhabitat occurred among more distantly related species and the greatest overlap occurred among teiids. Lizards were active between 9:00 and 17:00 h. Active foragers tended to be active during the hottest hours of day, whereas sit and wait foragers were more commonly observed later in the day, when temperatures were lower. Analysis of body temperatures identified two statistically homogeneous groups, one with teiids and another with the remaining species. Dietary overlap was highest among teiids. Pseudocommunity analyses showed that neither mean dietary overlap nor mean microhabitat overlap differed statistically from random, indicating lack of structure. Factor scores of morphological variables per species revealed clusters corresponding to lizard families. An examination of ecological traits mapped onto a tree depicting phylogenetic relationships among species and comparisons with related species from other biomes clearly indicated the role of history in the Monte Alegre lizard assemblage. This result was corroborated by Canonical Phylogenetic Ordination analysis.

Key words: assemblage structure, historical factors, ecological factors, Amazonian Savannas, lizards.

Introduction

An assemblage is a group of closely related species that coexist in a defined area and assemblage organization (structure) may be the result of several factors (Strong Jr. *et al.,* 1984; Diamond and Case, 1986). Ecologists have traditionally considered that ecological relationships among taxa were the primary factors in structuring assemblages (Roughgarden and Diamond, 1986; Werner, 1986; Yodzis, 1986); recently, however, more attention has been given to the importance of historical factors, since ignoring the role of phylogenetic history may result in equivocal conclusions about the determinants of assemblage structure (Losos, 1994; Losos, 1996; Webb *et al.,* 2002).

Differences along niche axes (*e.g.,* food, time, or microhabitats) among closely related species are usually viewed as evidence of ecological factors prevailing over historical factors (*e.g.,* Pianka, 1973). On the other hand, lack of divergence among closely related species suggests that historical factors prevail over ecological factors (Brooks and McLennan, 1991; Vitt, 1995; Losos, 1996). Likewise, similar patterns of structure in different assemblages suggest that historical factors predominate, whereas variation in patterns among assemblages indicates the prevalence of ecological factors (Brooks and McLennan, 1991; Cadle and Greene, 1993).

Recently, several studies were performed in Neotropical open formations. In Caatinga, the lizard assemblage was described with regard to activity, body temperatures, habitat, microhabitat, and diet data; and phylogeny influenced lizard assemblage structure more than present-day ecological relationships among species (Vitt, 1995). In a Cerrado site, the lizard assemblage showed microhabitat divergence between tropidurids and polychrotids and overlap between teiids and gymnophytalmids, but differences in body size promoted divergence in diet (Vitt, 1991). In a northern Amazonian Savanna site, eight species were grouped into three alimentary guilds: herbivores, active, and sit-and-wait foragers, and the main determinant of guilds was not diet composition, but prey acquisition mode (Vitt and Carvalho, 1995). However, in both the Cerrado and Amazonian Savanna studies, authors failed to consider the influence of historical factors.

During Pleistocene glacial periods, great expanses of the Amazon basin were covered by savannas, with forest restricted to isolated patches (Eden, 1974; Ab'Sáber, 1982; Bigarella and Andrade-Lima, 1982; Huber, 1982). Presumably, Amazonian savannas represent vestiges of a large savanna that once extended from central Brazil through the Guianas (Prance, 1978) and now persist as islands embedded in the Amazon forest (Pires, 1973). In addition, Amazonian savannas are still poorly known; have high endemism; are highly threatened by agricultural expansion, mining, cattle ranching, and fire (Ávila-Pires, 1995; Vitt and Carvalho, 1995; Colli, 1996; Mesquita, 2003; Machado *et al.,* 2004); and are under-represented in conservation units (Cavalcanti, 1995).

Herein, we describe the lizard assemblage of an Amazonian savanna from Monte Alegre region, Pará State, using ecological, morphological, and life history data, and we examine the role of phylogenetic history in assemblage structure (e. g., Brooks and McLennan, 1991; Losos, 1996; Giannini, 2003). Our hope is to increase the database of South American studied assemblages and contribute to elucidate the issue of the importance of history of species in assemblage structure.

Material and Methods

Study site

We conducted field work from 27 November to 18 December 2002 in an Amazonian savanna near Monte Alegre, northern Pará, Brazil (2°00'S, 44°20'W). The region is characterized by open and low Cerrado-like vegetation (Amazonian savanna) on sandy soil with rocky areas. Amazonian savannas occur as scattered islands within the Amazon Forest and cover about 150,000 km^2, or 2% of Brazil (Pires, 1973). The climate (Aw type of Köppen classification system) is highly seasonal and annual precipitation averages 1700 mm (Eidt, 1968). The vegetation is dominated by species typical of the Cerrado, but diversity is lower (Eiten, 1978).

Microhabitat and activity, and temperature

We captured lizards using drift fences with pitfall traps, by hand, or using a shotgun. In the lab, we killed live lizards with an injection of Thiopental® in accordance with approved protocols and preserved them in 10% formalin. When we captured lizards by hand or gun, we took cloacal, substrate, and air temperatures at the time of capture to the nearest 0.2 C with a Miller & Weber® cloacal thermometer. We also recorded microhabitat where the lizard was first observed (grass, open ground, termite nests, tree trunks, or rocks) and the time of capture. We computed microhabitat niche breadths *(B)* using the inverse of Simpson's diversity index (Simpson, 1949). 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 Pianka's overlap index (Pianka, 1973). Overlap index varies from 0 (no overlap) to 1 (complete overlap). To investigate the presence of non-random patterns in microhabitat niche overlap, we used the Niche Overlap Module of EcoSim (Gotelli and Entsminger, 2003). Data for such analyses consist 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 composition

We analyzed stomach contents under a stereoscope, identifying prey items to the level of order, with the exception that ants (Formicidae) were considered a separate category. We recorded the length and width (to the nearest 0.01 mm) of intact items 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 the 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 25 (25 prey categories were recognized). Throughout the text, we refer to diet niche breadth, which is the average between numeric and volumetric niche breadths. We also calculated the percent occurrence of each prey category (number of stomachs containing prey category i divided by the total number of stomachs). We excluded prey items that were too fragmented to allow a reliable estimate of their volumes from volumetric analyses. To determine the relative contribution of each prey category, we calculated an importance index for pooled and individual stomachs using the average of percentage of prey occurrence *(F%),* numeric percentage *(N%),* and volumetric percentage *(V%).*

We calculated dietary overlap using the equation for microhabitat overlap above (Pianka, 1973). To investigate the presence of non-random patterns in diet niche overlap, we used "Niche Overlap Module" of EcoSim (Gotelli and Entsminger, 2003) in the same manner described for microhabitat above.

Morphometry

Using Mitutoyo® electronic calipers, we recorded the following morphometric variables: 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), hind limb length, forelimb length, and tail length (from the cloaca to the tip of the tail). To maximize availability of data, we estimated tail length of lizards with broken or regenerated tails using a regression equation relating tail length to SVL, calculated from lizards with intact tails. We calculated separate regression equations for sexes. Prior to analysis, we $\log_{10}$-transformed all morphometric variables to meet requirements of normality (Zar, 1998). The transformed morphometric variables were used in a principal components analysis, based on a correlation matrix, to examine the morphological variation and to identify the taxonomic level at which ecological variation among species occurred.

To conduct statistical analyses we used SYSTAT 11.0 and SAS 8.1 for Windows, with a significance level of 0.05 to reject null hypotheses. Throughout the text, means appear ± 1 SD. To assess the role of history in assemblage structure, we used Canonical Phylogenetic Ordination (Giannini, 2003) coupled with Monte Carlo permutations (9,999) in CANOCO 4.5 for Windows. Two basic matrices were created: one with the comparative data (ecological data) measured over taxa and another with a tree matrix that contains all the phylogenetic groups, each coded separately as a binary indicator variable (*e.g.,* "0" and "1") of the phylogenetic tree available for those taxa. The analysis consists of canonical ordination to identify divergence points within the reduced tree matrix that best explains ecological patterns (Giannini, 2003).

Because of differences in completeness of data for microhabitat use and diets, we used two different trees (Figure 1). For microhabitat, we used frequencies of microhabitat use, and for diet, we used the average of the importance index based on individual stomach means and pooled data.

RESULTS

Species composition, microhabitat, activity, and body temperature

The lizard assemblage in Monte Alegre contains seven species: one polychrotid *(Anolis auratus),* one tropidurid *(Tropidurus hispidus),* three teiids *(Ameiva ameiva, Cnemidophorus cryptus* and *Kentropyx striata),* one gymnophthalmid *(Gymnophthalmus underwoodi),* and one scincid *(Mabuya nigropunctata).* In the study region, we documented additional lizard species such as the forest-dweller gekkonids *Gonatodes humeralis* and *Thecadactylus rapicauda* (pers. comm. Josseham Frota), the teiid *Tupinambis teguixin,* and the iguanid *Iguana iguana;* however, in this paper, we consider only the species that occur in the area of the pitfall traps.

All species in the assemblage are diurnal and typical of open areas, except *M. nigropunctata* and *Ameiva ameiva* that also occur in the forest. In the open areas sampled in this study, the teiid *Ameiva ameiva* occurs mainly in open ground and grass microhabitats, like the other teiids *Cnemidophorus cryptus* and *Kentropyx striata,* and the scincid *Mabuya nigropunctata. Tropidurus hispidus* was found almost exclusively in saxicolous microhabitats. *Anolis auratus* occurs on the ground and low perches on trees (Fig. 2).

Niche breadth for microhabitat was low for all species in the assemblage. *Anolis auratus* had the largest (2.27) and *A. ameiva* and *T. hispidus* had the smallest (1.14 and 1.16, respectively) niche breath values

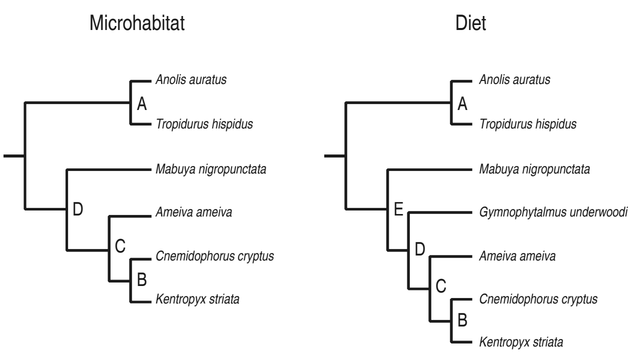

Figure 1: Individual groups used in canonical phylogenetic ordination for microhabitat and diet data. Phylogeny based on Estes *et al.* (1988) and Reeder *et al.* (2002).

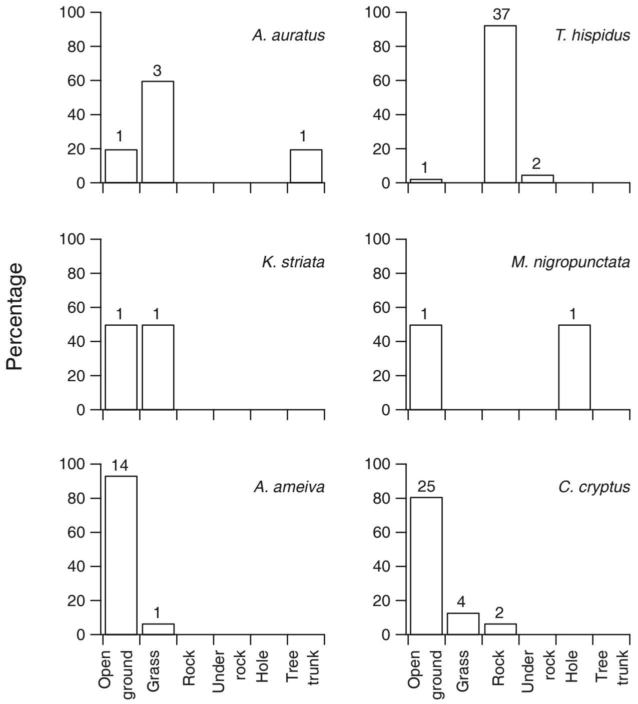

Figure 2: Frequency distribution of individuals according to microhabitat categories for Monte Alegre lizards. Sample sizes are indicated at the top of bars.

(Fig. 3). Microhabitat niche overlap varied from none to almost complete (Table 1). The lowest results for niche overlap were found between species most distant phylogenetically (*e.g.,* between *T. hispidus* and *A. ameiva* and between *M. nigropunctata* and *A. auratus*) whereas the greatest overlap occurred among teiids (Table 1). The pseudocommunity analysis showed that mean microhabitat overlap among lizard species did not differ from random (P = 0.31), indicating lack of assemblage structure with respect to microhabitat (*i.e.,* absence of competition).

Lizards were active from 9:00 to 17:00 h, but activity times varied among species. Usually, active foragers tended to be active during the hottest hours of day. For example, most teiids and scincids were active between 9:30 and 13:30 h, whereas the sit and wait forager *T. hispidus* was active from 10:30 until 17:00 h.

Mean body temperatures ranged from 28.2°C in *Anolis auratus* to 41.8°C in *Ameiva ameiva.* Because of a high association between body and substrate temperature ($R^2 = 0.53$, $F_{1,93} = 102.45$, $P < 0.0001$), we removed the effect of substrate temperature by calculating residuals of a regression between body and substrate temperatures and then performed an ANOVA on the residuals followed by post-hoc Tukey tests. The ANOVA detected significant differences among species ($F_{5,88} = 7.642$, $P < 0.0001$) and post-hoc Tukey tests identified two statistically homogeneous groups, one containing the teiids and another consisting of the other species *(A. auratus, M. nigropunctata,* and *T. hispidus).*

Diet composition

We analyzed the contents of 245 stomachs of seven lizard species and recognized 25 prey categories. The percentage of empty stomachs was 6.9% (n = 17). Based on all lizard species, termites were the most important prey type followed by orthopterans and spiders. The results based on data from individual and pooled stomachs were similar. The most important prey for *A. ameiva* and *C. cryptus* were termites and spiders; for *K. striata,* spiders and orthopterans; for *T. hispidus,* mainly ants; for *M. nigropunctata,* orthopterans and beetles; for *G. underwoodi,* spiders; and for *A. auratus,* termites (Table 2).

Diet niche breadths calculated from the average between numeric and volumetric percentages of prey were usually low, with lowest values for *G. underwoodi* and *A. auratus* and the largest values for *A. ameiva* and *C. cryptus* (Table 2). Prey overlap varied from 0.125 *(G. underwoodi* vs. *T. hispidus)* to 0.951 *(A. ameiva* vs. *C. cryptus)* (Table 1). *Tropidurus hispidus* had low overlap with all other species, with the greatest overlap with *C. cryptus* (0.422) (Table 1). Overlaps were high among teiids, with the lowest between *K. striata* and *A. ameiva* (0.686) (Table 1). A

Table 1: Overlap in microhabitat (lower half of matrix) and diet (upper half) for Monte Alegre lizards.

	A. ameiva	*C. cryptus*	*K. striata*	*T. hispidus*	*M. nigropunctata*	*G. underwoodi*	*A. auratus*
A. ameiva		0.951	0.686	0.226	0.579	0.683	0.748
C. cryptus	0.993		0.709	0.422	0.513	0.716	0.799
K. striata	0.756	0.807		0.132	0.512	0.730	0.193
T. hispidus	0.027	0.105	0.019		0.312	0.125	0.487
M. nigropunctata	0.705	0.696	0.500	0.019		0.187	0.312
G. underwoodi	–	–	–	–	–		0.286
A. auratus	0.365	0.439	0.853	0.008	0.213	–	

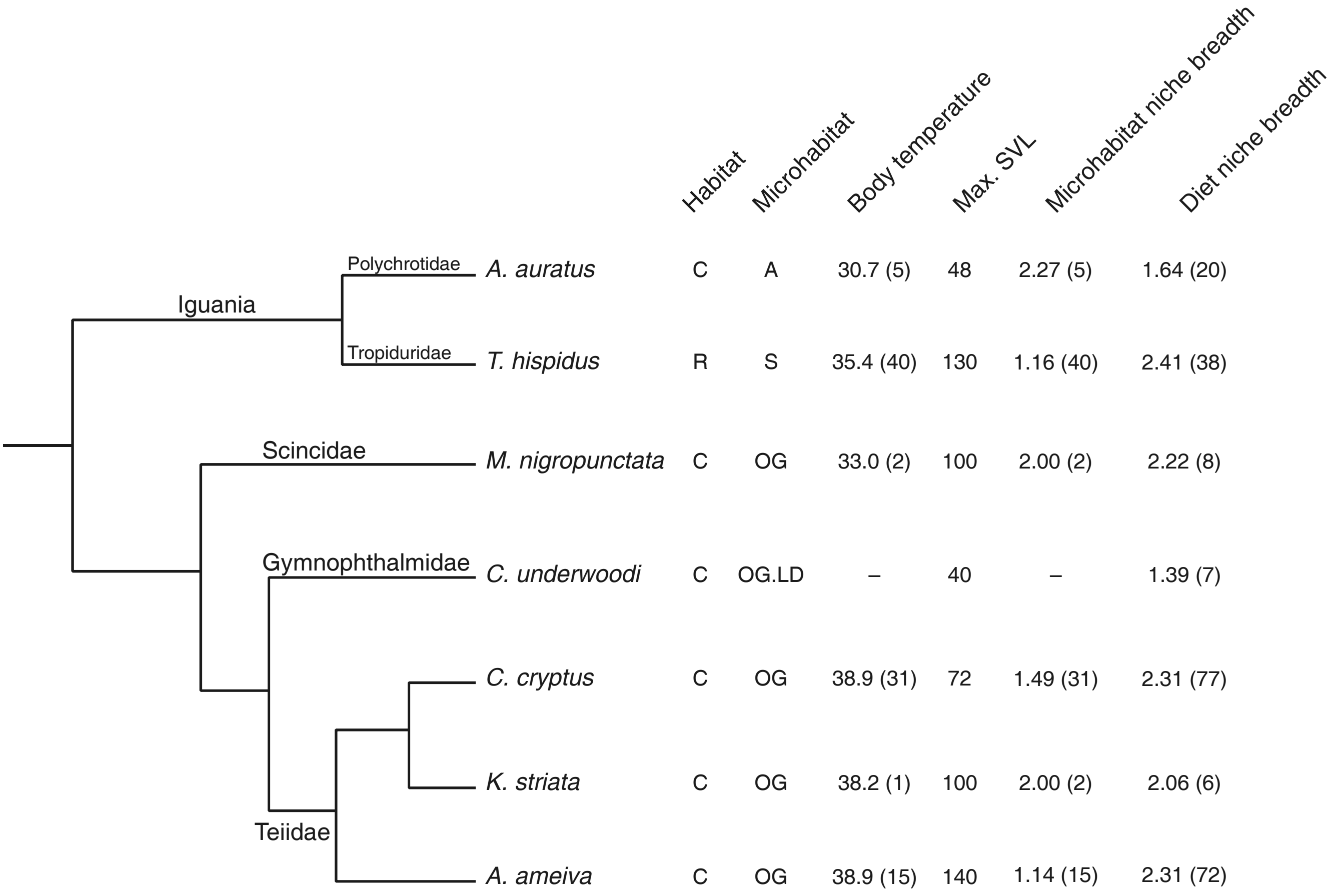

Figure 3: Phylogeny of Monte Alegre lizards showing the mapping of ecological characteristics. Abbreviations for habitat are: C = cerrado, R = rocky field. Abbreviations for microhabitat are: A = arboreal, OG = open ground, LD = litter-dwelling, S = saxicolous. Note: general microhabitat categories are 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).

pseudocommunity analysis with all original prey categories showed that mean diet overlap among lizard species did not differ from random (P = 0.98), indicating lack of structure.

Morphometry

The first two factors of the principal component analysis (PCA) of morphological variables accounted for 97.5% of the variation (Table 3). The first factor (56.1%) describes a gradient of increasing hind limb length, forelimb length and tail length, and decreasing head height and head length (Table 3). The second factor (41.4%) describes a gradient of increasing body height and body width (Table 3). A plot of the average of factor scores by species for the first two principal components revealed clusters corresponding to lizard families, specifically within the bigger teiids of the assemblage, *Ameiva ameiva* and *Kentropyx striata,* which were grouped together (Fig. 4). The teiid *Cnemidophorus cryptus* occupies similar morphological space regarding the second factor of PCA, but not as well regarding the the first factor, which may be due differences in body size.

Historical effects

A detailed inspection of the cladogram (Fig. 3) revealed several patterns indicating a role of history in the Monte Alegre lizard assemblage, mainly among teiioid lizards. Microhabitats, body temperatures, and diet niche breadths of teiids and gymnophthalmids were similar, suggesting that history plays an important role in determining the observed pattern. Some differences occurred in niche breadth (diet and microhabitat), microhabitat use, and body temperature of *A. auratus* and *T. hispidus;* however, these species are not closely related even though they were placed together in the cladogram, which suggests that differences are not promoted by ecological factors.

Table 2: Importance index, based on individual stomach means and pooled data (in parentheses), of prey categories in the diet of seven lizard species from Monte Alegre.

Prey Type	*A. ameiva*	*C. cryptus*	*K. striata*	*T. hispidus*	*M. nigropunctata*	*G. underwoodi*	*A. auratus*
Annelida	–	0.52 (0.52)	–	–	–	–	–
Aranae	21.19 (13.99)	22.68 (21.37)	38.83 (41.37)	5.17 (4.85)	8.53 (8.40)	38.10 (20.68)	5.67 (5.48)
Blattaria	8.67 (8.66)	3.77 (4.41)	2.78 (3.03)	4.82 (5.44)	8.33 (4.17)	14.29 (8.87)	–
Coleoptera	6.18 (4.50)	5.62 (4.03)	–	18.53 (15.12)	12.50 (6.41)	–	9.00 (15.12)
Diplopoda	–	0.43 (0.07)	–	1.59 (1.14)	–	–	–
Diptera	–	–	–	3.62 (3.16)	–	–	–
Formicidae	1.61 (0.81)	9.71 (9.14)	–	64.82 (65.86)	8.01 (12.42)	–	18.58 (13.70)
Gastropoda	–	–	–	1.09 (1.02)	–	–	–
Hemiptera/ Homoptera	3.44 (2.43)	2.96 (2.69)	–	5.84 (5.16)	–	14.29 (6.88)	–
Hymenoptera (non ants)	–	2.02 (1.83)	–	6.68 (7.16)	–	–	–
Insect larvae	4.50 (3.37)	3.73 (2.74)	16.67 (12.27)	5.41 (9.51)	–	–	–
Isoptera	25.27 (42.42)	21.86 (34.23)	–	3.27 (1.40)	–	9.38 (48.45)	40.61 (60.69)
Isopoda	0.45 (0.46)	–	–	–	–	–	–
Lizard skin	–	–	–	–	–	–	0.83 (0.31)
Mantodea	–	0.69 (0.67)	–	–	–	–	5.00 (4.95)
Neuroptera	1.92 (1.62)	1.03 (0.76)	–	–	–	–	–
Non identified	2.09 (0.13)	3.70 (0.91)	5.56 (3.03)	–	–	0.14 (0.83)	2.64 (0.94)
Orthoptera	18.03 (20.62)	13.33 (17.74)	19.51 (34.74)	6.04 (8.28)	48.40 (59.58)	–	10.00 (9.17)
Ooteca	0.65 (0.67)	–	–	–	–	–	–
Plant material	2.16 (2.21)	–	4.50 (3.94)	1.76 (1.75)	–	–	–
Pseudoscorpionida	–	–	–	–	5.91 (6.65)	–	–
Quilopoda	4.44 (4.29)	1.93 (2.32)	–	1.98 (1.96)	–	–	–
Scorpionida	2.44 (2.03)	–	–	2.63 (2.29)	12.48 (14.88)	–	–
Solifuga	0.85 (0.49)	1.97 (1.28)	–	–	–	–	–
Vertebrate	1.13 (6.08)	–	–	0.07 (0.11)	–	–	–
N	72	77	6	38	8	7	20
Numeric niche breadth	1.52 (1.29)	1.54 (2.15)	1.30 (3.46)	1.44 (1.53)	1.53 (4.00)	1.01 (1.53)	1.20 (1.88)
Volumetric niche breadth	1.54 (4.89)	1.32 (4.25)	1.09 (2.40)	1.57 (5.12)	1.54 (1.82)	1.00 (2.03)	1.08 (2.39)

Table 3: Principal component analysis of log transformed morphological data from Monte Alegre lizards.

	Factor I	Factor II	Factor III
Snout-vent length	0.373	0.263	0.434
Tail length	0.419	0.160	0.367
Head width	-0.226	0.441	-0.039
Head length	-0.352	0.307	-0.151
Head height	-0.354	0.307	0.012
Body width	0.087	0.494	0.353
Body height	0.048	0.510	0.193
Leg length	0.434	0.089	-0.126
Forelimb length	0.432	0.105	-0.213
Eigenvalues	5.045	3.726	0.0896
Percent of variance explained	56.059	41.405	0.991

Table 4: Historical effects on the ecology of Cerrado lizards. Results of Monte Carlo permutation tests of individual groups (defined in Fig. 1) for diet and microhabitat matrices. Percentage of 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.

Group(s)	Variation	Variation %	*F*	*P*
		Diet		
D	0.223	33.635	1.458	0.0426
A/E	0.190	28.658	1.187	0.1899
C	0.162	24.434	0.979	0.4961
B	0.114	17.195	0.650	0.9626
		Microhabitat		
A/D	0.427	47.870	1.509	0.2031
C	0.301	33.744	0.956	0.6549
B	0.136	15.247	0.382	0.9803

Monte Carlo permutations (based on 9,999 permutations) revealed a significant phylogenetic effect on dietary composition of Teiioidea, which account for 33.6% of the dietary variation (Table 4). No significant phylogenetic effects on microhabitat use or dietary composition were detected in any other clades (Table 4).

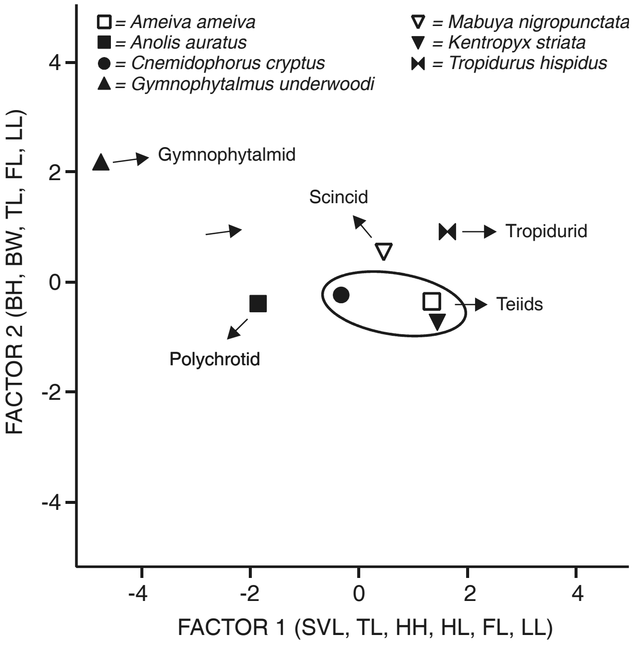

Figure 4: Plot of species means on first two principal components derived from log-transformed morphological data for Monte Alegre lizards. Note: SVL – snout-vent length, TL – tail length, HW – head width, HL – head length, HH – head height, BW – body width, BH – body height, LL – leg length, and FL – forelimb length.

DISCUSSION

Until recently, ecological factors (*i.e.,* competition and predation) were deemed the primary determinants of assemblage structure (Wilbur, 1972; Wiens, 1977; Diamond, 1978; Semlitsch, 1987). Although competition and/or predation no doubt influence structure of some assemblages (*e.g.,* Spiller and Schoener, 1988; Spiller and Schoener, 1989; Spiller and Schoener, 1990; Case and Bolger, 1991), it is becoming increasingly clear that most ecological differences among syntopic species have their origins deep in the evolutionary history of clades (Losos, 1994; Losos, 1996; Vitt *et al.,* 1999; Webb *et al.,* 2002; Vitt *et al.,* 2003c; Vitt and Pianka, 2005). Our data suggest that the phylogeny of lizards in the Monte Alegre area influences assemblage structure in several aspects.

Activity times for *T. hispidus* was similar to other species of *Tropidurus* from different areas, which normally avoided the hottest hours of the day and were more active early in the morning and in late afternoon (Rocha and Bergalo, 1990; Bergallo and Rocha, 1993; Vitt *et al.,* 1996). On the other hand, teiid lizards from Monte Alegre concentrated their activity during warmer periods around mid-day and maintained higher body temperatures than all other species of the assemblage, like closely related species from other places (Vitt, 1991; Vitt *et al.,* 1993; Vitt and Colli, 1994; Vitt, 1995; Mesquita and Colli, 2003b); these results suggest that phylogeny plays an important role in the thermal ecology and activity cycles of these lizards. Additionally, in most cases, microhabitat niche overlaps in Monte Alegre lizards were highest among closely related species, especially teiids, which also indicates phylogenetic conservatism. Although structure in microhabitat use was found in several assemblages (e. g., Pianka, 1986; Winemiller and Pianka, 1990; Vitt, 1995; Vitt and Carvalho, 1995), we did not find such structure in Monte Alegre, which indicates a lack of competition for space. Therefore, microhabitat may not be a limiting resource for these lizards (see Connor and Simberloff, 1979). However, since some species were difficult to observe (*e.g.,* gymnophthalmids), microhabitat data for some species were poor, which may have influenced the results. Additional data could reveal different patterns of microhabitat use.

The highest dietary overlaps were found among closely species (mainly within teiids), which suggests the influence of phylogeny (Brooks and McLennan, 1991; Losos, 1996). On the other hand, low dietary overlap among distantly related species, such as *T. hispidus* vs. *K. striata, G. underwoodi* vs. *T. hispidus,* and *A. auratus* vs. *K. striata,* cannot be interpreted as evidence of competition or local scale effects (see Harvey and Pagel, 1991; Brooks and McLennan, 1993; Losos, 1996). Furthermore, the lack of structure found in the pseudocommunity analysis suggests absence of competition among species. Indeed, a previous study on fat storage cycles in Amazonian Savanna and Cerrado lizards showed that most species accumulate fat in their bodies during the dry season when insect availability is lowest, which indicates that food is not a limiting factor (Colli *et al.,* 1997). Additionally, most species from the Monte Alegre lizard assemblage showed similar diet composition when compared to other conspecific populations (see Vitt and Blackburn, 1991; Vitt, 1993; Vitt and Colli, 1994; Vitt and Carvalho, 1995; Mesquita and Colli, 2003a). These results emphasize the importance of history in the diet of Monte Alegre lizards, which, regardless of differences in prey availability among localities, ingested similar prey. One exception to this pattern was *Anolis auratus,* which differed in diet composition compared to other localities (Magnusson *et al.,* 1985; Vitt and Carvalho, 1995). In Monte Alegre, *A. auratus* had a high proportion of termites in the diet, which is unusual among *Anolis* (Vitt *et al.,* 2001; Vitt *et al.,* 2002; Vitt *et al.,* 2003a; Vitt *et al.,* 2003b) and even for iguanian lizards (Vitt *et al.,* 2003c). This result suggests an important role of ecological factors influencing the diet of this species. Several explanations are possible, including local prey availability, inter-specific interactions and/or seasonality effects; however, more work is necessary to elucidate this issue.

Our data suggest a strong association between morphology and phylogeny, with closely related species grouping together in morphological space, especially the teiid lizards *Ameiva ameiva* and *Kentropyx striata.* The iguanians from Monte Alegre did not cluster together in morphological space and this could be interpreted as evidence of morphological differentiation in response to interactions between these lizards. However, iguanians from Monte Alegre are not closely related and this fact likely explains the morphological differentiation. *Tropidurus hispidus* and *Anolis auratus* are morphologically similar to their close relatives in other habitats (see Magnusson and Silva, 1993; Vitt, 1993; Vitt and Carvalho, 1995), suggesting that differences originated long ago in the history of these species. The morphological similarity between *Ameiva ameiva* and *Kentropyx striata* suggests a major influence of history, whereas the *Cnemidophorus cryptus* plotted not so close to other teiids in morphological space. Teiids are characterized by a strong similarity in body shape, but differ in body size. These morphological differences are most likely a historical consequence of intraguild interactions rather than more recent ecological interactions (Vitt and Zani, 1996; Vitt *et al.,* 1998; Vitt *et al.,* 2000).

An examination of ecological traits mapped on the current phylogenetic hypothesis (Fig. 3) clearly shows the role of history in the Monte Alegre lizard assemblage. This is particularly evident for Teiioidea (teiids and gymnophthalmids), which showed high similarity in most ecological traits examined. Studies with these lizards from drastically different habitats have shown that their ecology is little influenced by local differences, such as environmental and species interactions, further emphasizing the influence of history in their ecology (Vitt and Colli, 1994; Vitt *et al.,* 1997; Vitt *et al.,* 1998; Mesquita and Colli, 2003a). Canonical Phylogenetic Ordination detected significant phylogenetic effects in Teiioidea when considering the diet data. However, we found no phylogenetic effect for any other taxa in the assemblage for diet and no effect in any species when considering microhabitat use.

Some caution should be used when interpreting this result. Microhabitat data may be biased by differences in local abundance. Although most lizard species from Amazonian savannas are abundant and easy to observe, some did not occur in high abundance or were more difficult to capture (*e.g.,* gymnophthalmids). On the other hand, assemblages from Amazonian savannas are depauperate of closely related species. In the Monte Alegre assemblage, additional historical effects could be undetectable because major taxa are under-represented. In more complex assemblages, with greater numbers of closely related species, historical or ecological effects may be more easily detected. In the Amazon forest, a significant phylogenetic effect was detected, primarily in tropidurid lizards, which are represented by two closely related species, *Plica plica* and *P. umbra* (Vitt *et al.,* 1999; Giannini, 2003). In addition, a study with two closely related *Cnemidophorus* species showed strong evidences of both phylogenetic conservatism and microhabitat segregation to facilitate coexistence (Dias and Rocha, 2004). Finally, the lack of a phylogenetic effect may have resulted from a data deficiency in the Canonical Phylogenetic Ordination analysis.

Although there are some analyses of niche structure that can be used to examine the influences of historical factors on species interactions, the use of phylogenetically based analyses is not yet well established and the nature of forces acting on assemblages remains unclear (see Webb *et al.,* 2002). However, studies focusing on ecological characteristics of sympatric, closely related species, as well as comparisons among different assemblages with phylogenetically based analyses are essential to elucidate the relative importance of ecological and historical factors in structuring assemblages.

RESUMO

A taxocenose de lagartos de uma Savana Amazônica na região de Monte Alegre, estado do Pará, é descrita através de dados ecológicos, morfológicos e de história de vida, avaliando a importância da filogenia na taxocenose. A taxocenose amostrada contém sete espécies. A largura de nicho de microhábitat foi baixa para to-

das as espécies e a sobreposição de nicho, baseado no uso de microhábitat, variou de quase nenhuma até quase completa, sendo os menores valores entre espécies mais distantes filogeneticamente e entre os teiídeos. A atividade dos lagartos ocorreu das 9:00 até as 17:00 h e, geralmente, os forrageadores ativos foram mais comumente observados durante as horas mais quentes do dia, enquanto os forrageadores "senta-e-espera" foram mais comuns no entardecer. O teste de Tukey nas temperaturas corporais identificou dois grupos estatisticamente homogêneos, um com os teiídeos e outro com as outras espécies. A análise de pseudocomunidades mostrou que a média de sobreposição de uso de microhábitat pelos lagartos não foi diferente de zero, indicando ausência de estrutura. Os maiores índices de sobreposição de dieta ocorreram entre os teiídeos. A análise de pseudocomunidades mostrou que a média de sobreposição de composição de dieta não foi diferente de zero, indicando ausência de estrutura. O gráfico com as médias dos escores por espécie dos dois primeiros componentes principais mostrou clusters correspondentes às famílias de lagartos. Uma inspeção detalhada das variáveis ecológicas mapeadas na filogenia das espécies e comparações com espécies próximas que ocorrem em outros biomas, indicou que a história das espécies é extremamente importante para a manutenção do padrão encontrado na taxocenose de Monte Alegre, o que foi corroborado pelos resultados da ordenação filogenética canônica.

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