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Lizard Assemblages from Natural Cerrado Enclaves in Southwestern Amazonia: The Role of Stochastic Extinctions and Isolation¹

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ABSTRACT

We used null model analyses to investigate the existence of structure in lizard assemblages from open vegetation enclaves in Rondônia, southwestern Amazonia, in relation to species richness, species co-occurrence, diet, and size overlap. These enclaves presumably have been isolated since the Holocene, providing a history of long-term isolation. We assumed that the presence of structure in lizard assemblages from the Rondônia enclaves is consistent with the notion that extinctions are a deterministic process, some species being more prone to extinction than others. We grouped enclaves into four categories: latosol cerrado, sandy cerrado, transitional forest, and rocky field. We collected 14 Cerrado lizard species, consisting of five families in all sampled areas. Analyses of species richness, co-occurrence, diet overlap, and size overlap patterns suggested lack of organization in the assemblages. The assemblages from the rocky fields of Guajará-Mirim and the sandy cerrados in Vilhena were significantly structured in diet overlap, whereas the remaining assemblages lacked structure. This probably resulted from phylogenetic inertia and not from ecological interactions. Our results suggest that extinctions proceeded in a stochastic fashion and that historical factors had a dominant role in shaping lizard assemblages in detriment of present-day ecological factors. In addition, we identified endemic species in the enclaves as well as a tight association between unique ecogeographic features of the landscape and species occurrences. We propose that conservation measures in the region must adequately preserve these features to ensure the survival of the species.

RESUMO

Nós utilizamos análises de modelos nulos para investigar a existência de estrutura em taxocenoses de lagartos de enclaves de vegetação aberta em Rondônia, sudoeste da Amazônia, em relação à riqueza de espécies, co-ocorrência de espécies, dieta e sobreposição de tamanho corporal. Esses enclaves presumivelmente estão isolados desde o Holoceno, proporcionando uma história de prolongado isolamento. Nós assumimos que a presença de estrutura nas taxocenoses de lagartos dos enclaves de Rondônia é consistente com a noção de que extinções são um processo determinístico, algumas espécies sendo mais sujeitas à extinção do que outras. Nós agrupamos os enclaves em quatro categorias: cerrado sobre latossolo, cerrado sobre solo arenoso, floresta de transição e campo rupestre. Nós coletamos 14 espécies de lagartos do Cerrado, consistindo de cinco famílias em todas as áreas amostradas. As análises dos padrões de riqueza de espécies, co-ocorrência, sobreposição de dieta e sobreposição de tamanho do corpo sugeriram ausência de organização nas taxocenoses. As taxocenoses nos campos rupestres de Guajará-Mirim e cerrados arenosos de Vilhena foram significativamente estruturadas na sobreposição da dieta, enquanto que as taxocenoses restantes não foram estruturadas. Isso provavelmente resultou de inércia filogenética e não de interações ecológicas. Nossos resultados sugerem que as extinções ocorreram de maneira estocástica e que fatores históricos tiveram um papel dominante na formação das taxocenoses de lagartos, em detrimento de fatores ecológicos atuais. Ainda, nós identificamos espécies endêmicas nos enclaves, assim como uma forte associação entre feições ecogeográficas únicas da paisagem e a ocorrência de espécies. Nós propomos que medidas de conservação na região devem preservar adequadamente essas feições, para assegurar a sobrevivência das espécies.

Key words: Amazonia; Brazil; Cerrado; community structure; extinction; lizards; long-term isolation; null models.

THE STUDY OF COMMUNITY STRUCTURE HAS BEEN HOTLY DEBATED in the literature by many ecologists studying different taxa and biomes (Cody 1974,

Joern & Lawlor 1980, Case 1983a, Winemiller & Pianka 1990, Jackson *et al.* 1992, Vitt & Zani 1996a, Churchfield *et al.* 1997). Few studies, however, have investigated the effects of long-term isolation on lizard community structure (Case 1983b, Murphy 1983). Isolation promotes colonization and extinctions and one or both will influence spe-

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cies interactions. The longer the time since isolation, the more susceptible the species are to extinction (Case & Cody 1987, Foufopoulos & Ives 1999). These extinctions can occur either in a deterministic or stochastic manner, according to the intensity of species interactions in the studied assemblages.

The development of neutral models has provided powerful tools for investigating community structure (Sale 1974; Caswell 1976; Inger & Colwell 1977; Connor & Simberloff 1979; Pianka *et al.* 1979; Strong *et al.* 1979; Joern & Lawlor 1980; Pianka 1980, 1986; Graves & Gotelli 1983; Colwell & Winkler 1984; Winemiller & Pianka 1990; Jackson *et al.* 1992). Neutral models yield null communities that are generated by randomizing the original matrix, hence generating communities with no biological interaction. If a significant departure from random is observed in species packing, then the community is said to be structured. These models allow observed communities to be tested statistically for structure against generated null communities. In addition, they permit comparisons among communities (Pianka 1980, Winemiller & Pianka 1990).

Lizard community structure has been well documented in several biomes, such as Amazon rain forest (Vitt & Caldwell 1994; Vitt & Zani 1996a, 1998; Vitt *et al.* 1999) and deserts (Pianka 1973, 1980, 1986; Pianka *et al.* 1979; Vitt 1991a). The ecological parameters that have been emphasized as affecting lizard community structure are diet, microhabitat, morphology, and time of activity (Schoener 1974, 1986; Pianka 1986; Losos 1992, 1994; Vitt & Carvalho 1995; Vitt & Zani 1996a, 1998; Vitt *et al.* 1999). We used null models to investigate the existence of structure in lizard assemblages from open vegetation enclaves in southwestern Amazonia. These areas are floristically very similar to the Cerrado biome of Central Brazil (Sanaïotti 1996) to which they were most likely connected during glacial (dry) periods of the Pleistocene and Holocene (Van der Hammen 1974, Absy & Van der Hammen 1976, Van der Hammen & Absy 1994). Preliminary studies in Rondônia have indicated that lizard assemblages of open vegetation enclaves are depauperate and consist of a subset of the Cerrado assemblage, with a few additions (Vanzolini 1986, Vitt 1993, Vitt & Caldwell 1993). Presumably, after the expansion of forests during the current interglacial (humid) period, the connection between the open vegetation landscapes in Rondônia and Central Brazil was broken, leading both to extinction (more prominent) and differ-

entiation (less prominent) processes. We assume that the presence of significant structure in lizard assemblages from Rondônia enclaves is consistent with the notion that extinctions are a deterministic process, some species being more prone to extinction than others.

MATERIALS AND METHODS

STUDY AREA.—The study areas were located in the state of Rondônia, Brazil, in southwestern Amazonia (Fig. 1). The region is at the transition between the Cerrado, an open biome that covers the Central Brazilian highlands (Eiten 1972, Oliveira & Marquis 2002), and the lowlands of the Amazon River basin, covered by rain forest (Pires & Prance 1985). Mean air temperatures vary from 24° to 26°C and rainfall is between 2000 and 2500 mm per year, with well-defined dry and wet seasons (Nimer 1989). Fires are frequent during the dry season. The open vegetation enclaves we studied in Rondônia can be grouped in four categories: latosol cerrado, sandy cerrado, transitional forest (“carasco”), and rocky fields (“campo rupestre”). The latosol cerrado enclaves (2) are located in Pimenta Bueno (11°90’S, 60°49’W) and Vilhena (12°43’S, 60°07’W), consisting of a layer of scleromorphic, woody vegetation and another formed by grasses on top of oligotrophic, well drained soils (Fig. 2). The sandy cerrado enclaves, in Guajará-Mirim (10°48’S, 65 22’W;1), Pimenta Bueno (1) and Vilhena (1), are formed by sparse trees and a ground layer where sedges often predominate (Fig. 2). We sampled only one transitional forest enclave, in Pimenta Bueno, which is covered with a tall, thorny, semi-deciduous forest on top of latosols (Fig. 2). The rocky field enclaves (3) in Guajará-Mirim are part of the Pacaás-Novos range, and consist of sparse clusters of woody and herbaceous plants on top of sandstones (Fig. 2). The three rocky field enclaves were joined to form one assemblage and the two sandy cerrados in Vilhena were joined to form another assemblage due to the proximity of sites as well as similar lizard composition. We conducted fieldwork in Vilhena from 20 August 1999 to 22 September 1999, during the dry season; in Pimenta Bueno from 1 July 2000 to 24 August 2000, during the dry season; and in Guajará-Mirim from 20 December 2000 to 29 January 2001, during the wet season.

Global climate fluctuations have promoted extreme changes in the vegetation cover of tropical regions: during glacial periods (dry climate), savannas expanded at the expense of forests, whereas

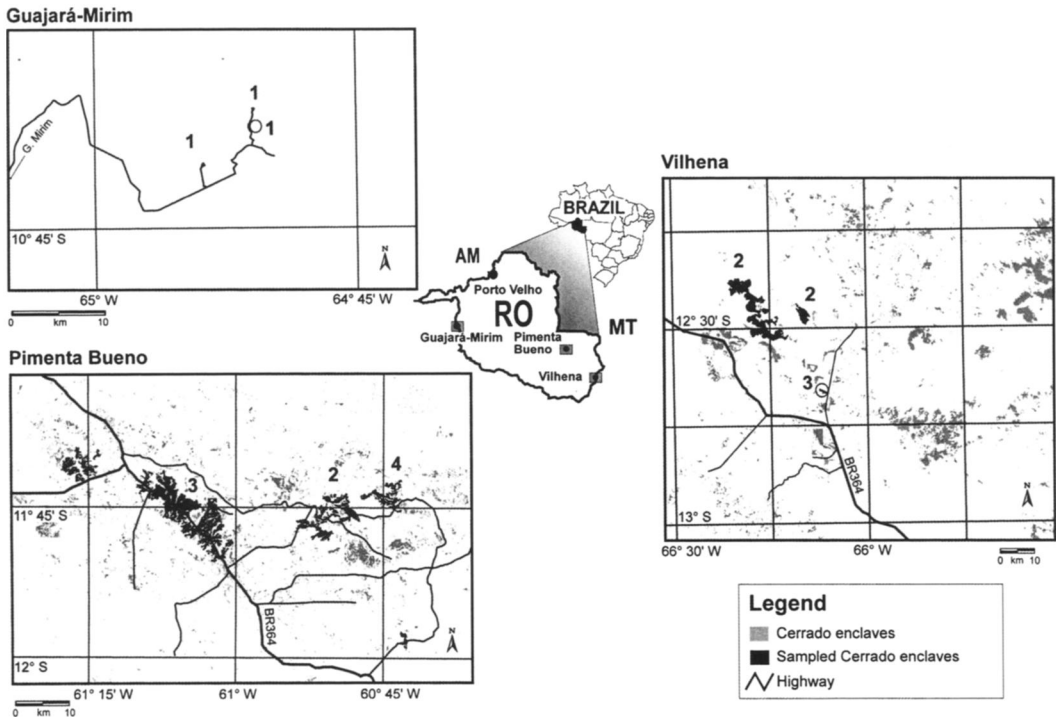


FIGURE 1. Study area in the state of Rondônia, southwestern Amazonia.

during interglacial periods (humid climate), savannas retreated as forests expanded (Haffer 1969, Van der Hammen & Absy 1994). Rondônia lies at the forest–savanna boundary and experiences pronounced dry seasons; therefore, small changes in precipitation could lead to savanna replacement of forest. A number of palynological and sedimentary studies indicate that in Rondônia, open vegetation replaced the forest in the recent past. At the border of the states of Amazonas and Rondônia, soil organic matter analyzed via C isotopes indicated that savannas expanded *ca* 9000 to 3000 years B.P. during a dry spell, after which forest expansion took place during a more humid climate to form present-day isolated enclaves of savanna (Freitas *et al.* 2001). During drier periods, fires probably assisted in altering the forest–savanna boundaries. Since fires tend to occur only during drier climates, a study in Eastern Amazonia with organic sediments from charcoal found in core sediments documented the existence of savannas *ca* 3800 years B.P. (Sifedine *et al.* 2001). Hence, the open vegetation enclaves we studied in Rondônia apparently have been isolated for at least 3000 years.

SAMPLING.—We captured lizards using a shotgun and pitfall traps with drift fences. In each enclave,

with the exception of rocky field enclaves, we placed 25 arrays of pitfalls and drift fences, *ca* 10 m apart of each other. Each array consisted of four buckets (20 l), arranged in a “Y,” with three buckets at the extremities connected to a central bucket by a 5 m long drift fence. In each study site, we checked traps daily during the entire duration of the expedition. We humanely killed captured lizards with a lethal injection of Tiopental®, recorded the snout–vent length (SVL) with a steel ruler to the nearest 0.1 mm, fixed animals with 10 percent formalin, preserved them in 70 percent alcohol, and deposited them in the Coleção Herpetológica da Universidade de Brasília (CHUNB). In the laboratory, we dissected lizards to obtain sex and reproductive condition. We checked the completeness of our species lists by constructing species accumulation curves with the software EstimateS v. 6b1 (Colwell 1997). All curves examined indicated a clear tendency for stabilization toward the end of the field collection.

SPECIES RICHNESS.—We compared lizard assemblages from different vegetative physiognomies in a pairwise fashion to test for significant differences in species richness. We used the rarefaction ap-

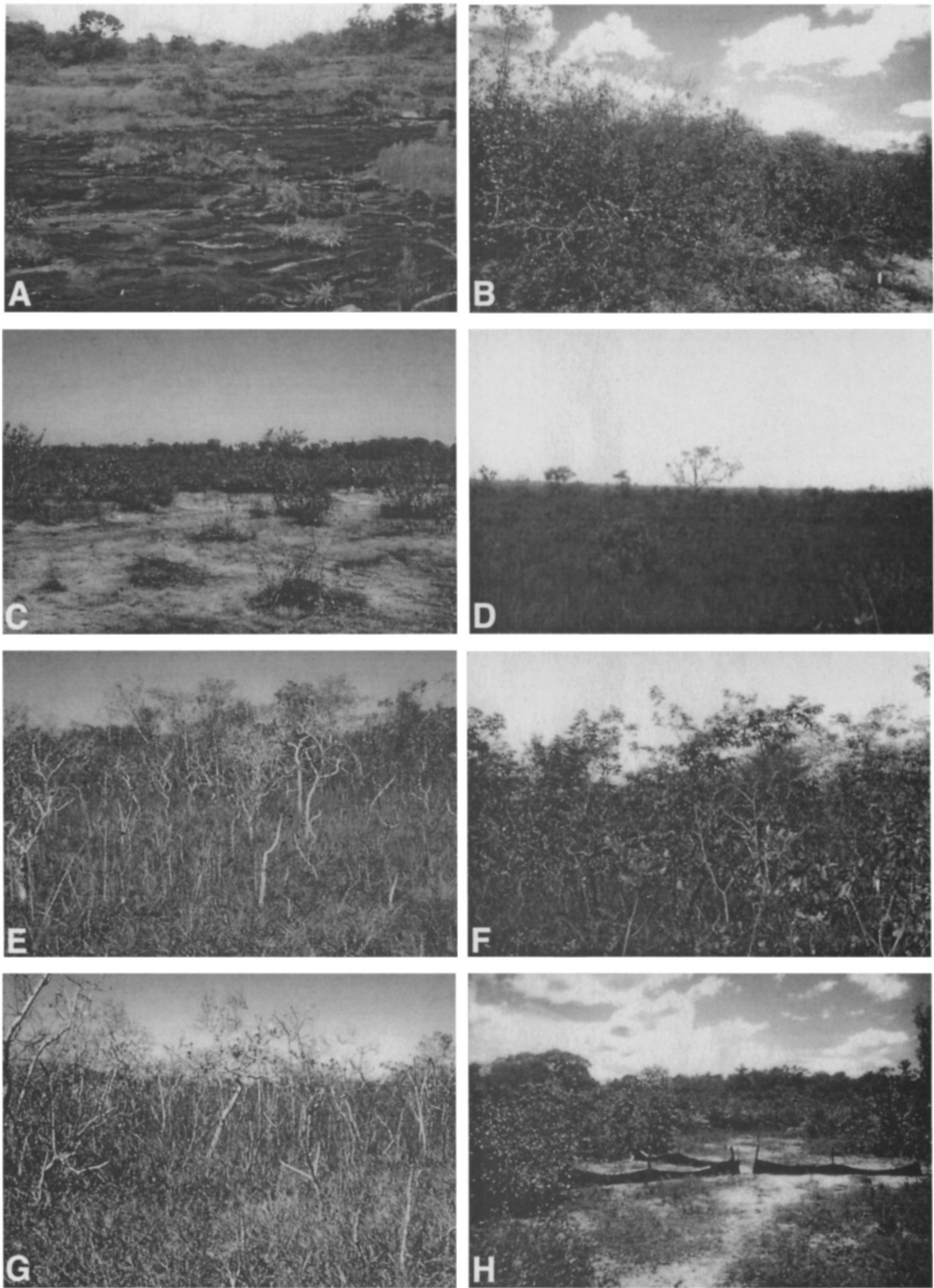


FIGURE 2. Open vegetation enclaves studied in Rondônia, southwestern Amazonia, and details of pitfall traps. a = rocky fields in Guajará-Mirim, b = sandy cerrado in Guajará-Mirim, c = sandy cerrado in Vilhena, d = sandy cerrado in Pimenta Bueno, e = latosol cerrado in Pimenta Bueno, f = latosol cerrado in Vilhena, g = transitional forest in Pimenta Bueno, and h = pitfall trap.

proach proposed by Sanders (1968) and implemented by the Species Diversity Module of EcoSim (Gotelli & Entsminger 2001). When comparing two assemblages with different abundances (*e.g.*, (A) higher abundance, (B) lower abundance), rarefaction determines the expected number of species to be found in “rarefied” samples of abundance B, randomly drawn from assemblage A. We derived the expectation and variance of species richness based on 1000 randomized samples using the following options of EcoSim: independent sampling, species richness index, and abundance level used in sampling equal to the assemblage with the lowest abundance. Next, we used a *Z*-test (Zar 1998) for hypotheses testing. Because the lizard assemblages in Guajar a–Mirim had only two species, rarefying any of these assemblages would result in a variance of 0. Therefore, whenever a pairwise comparison would imply in rarefying one of the Guajar a–Mirim assemblages (because of higher abundance of individuals), we rarefied the assemblage with lower abundance of individuals (*n*), specifying an abundance level of *n* – 2. We then determined the probability of obtaining two species from the resulting simulation curve using a *Z*-test. Since the Guajar a–Mirim were the most species-poor assemblages studied, this approach resulted in a very conservative test.

CO-OCCURRENCE.—To test for nonrandom patterns of species co-occurrence, we used the Co-occurrence Module of EcoSim (Gotelli & Entsminger 2001). The data for such analysis consist of a matrix in which each species is a row and each site is a column. Entries in the matrix indicate presence (1) or absence (0) of a species in each site. The presence–absence matrix is reshuffled to produce random patterns that would be expected in the absence of competitive interactions. We used the following options of EcoSim: *C*-score index, fixed sum row and column constraints, and “Sequential Swap” algorithm for randomizing matrices. For each unique pair of species, the *C*-score index (Stone & Roberts 1990) measures the average number of “checkerboard units” of the form:

$$\begin{array}{cc} 01 & 10 \\ \text{or} & \\ 10 & 01. \end{array}$$

The number of checkerboard units (CU) for any species pair is calculated as: $CU = (r_i - S)(r_j - S)$, where r_i and r_j are row totals, and *S* is the number of sites occupied by both species. The *C*-

score is the average CU for all unique pairs of species and in a structured community should be significantly larger than expected by chance. Using fixed sum row and column constraints produces null matrices with the same number of site occurrences per species (row totals) and the same number of species per site (column totals) as observed in the original data set. The sequential swap algorithm reshuffles the original matrix by repeatedly swapping submatrices that preserve row and column totals and is not overly prone to Type I or Type II errors (Gotelli & Entsminger 2001).

DIET OVERLAP.—We removed and dissected stomachs in the laboratory, identifying prey items with a stereomicroscope. We used Pianka’s (1986) prey categories, with the exception that our data separated mantids–phasmids and homopterans–hemipterans. In addition, we augmented the data with the following categories: Acarina, Annelida, spider egg sacs, Dermaptera, Diplopoda, Gastropoda, Odonata, Opiliones, vertebrate eggs, pseudoscorpions, seeds, and shed skin. We obtained dietary data of *Cnemidophorus parecis* from Mesquita and Colli (2003), of *Polychrus acutirostris* from Vitt and Lacher (1981), and of *T. merianae* from Colli *et al.* (1998). We measured length and width (0.01 mm) of intact prey with Mitutoyo® digital calipers and estimated prey volume with the following formula: $\text{Volume} = 4/3 [\pi (1/2 \text{ prey length}) (1/2 \text{ prey width})^2]$.

From the pooled stomachs, we calculated the frequency (percentage of stomachs containing prey category), numeric percentage, and volumetric percentage of each prey category. We obtained a single importance index of each prey category by taking the average of the frequency and the numeric and volumetric percentages. In the few cases that volumetric data were missing, we calculated the importance index from the frequency and numeric percentages only.

To investigate the presence of nonrandom patterns in dietary niche overlap, we used the Niche Overlap Module of EcoSim (Gotelli & Entsminger 2001). The data for such analysis consist of a matrix in which each species is a row and each prey category is a column. Entries in the matrix represent the importance index of a prey category in each species. The matrix is reshuffled to produce random patterns that would be expected in the absence of competitive interactions. We used the following options of EcoSim: Pianka’s niche overlap index and randomization algorithm two (RA2). Pianka’s (1973) niche overlap index is obtained by:

$$O_{jk} = \frac{\sum_{i=1}^n p_{ij}p_{ik}}{\sqrt{\sum_{i=1}^n (p_{ij}^2)(p_{ik}^2)}},$$

where O_{jk} is niche overlap between species j and species k , p_{ij} is the proportion of resource i used by species j , p_{ik} is the proportion resource i used by species k , and n is the total number of resource items. Niche overlap varies from 0 (no overlap) to 1 (complete overlap). We calculated a separate index for each species pair within each lizard assemblage. Randomization algorithm two (RA2) substitutes the importance index in the original matrix with a random uniform number between 0 and 1, but retaining the zero structure in the matrix (Winemiller & Pianka 1990). This assumes that in the absence of species interactions, certain dietary items are unavailable for each species. We excluded from the analysis prey categories with an importance index less than 5 percent for all lizard species.

SIZE OVERLAP.—We used the mean SVL of adult individuals of each species in this analysis. To determine minimum size for adulthood in each sex, we used the smallest male with enlarged testes and epididymides and the smallest female with eggs, vitellogenic follicles, or corpora lutea. Because of the small number of individuals collected, we augmented sample sizes of the species that follow with data from the literature or from specimens deposited at CHUNB: *Bachia cacerensis* (Castrillon & Strüssmann 1998), *Mabuya frenata*, and *Ma. nigropunctata* (Pinto 1999).

To investigate the presence of nonrandom patterns in size overlap, we used the Size Overlap Module of EcoSim (Gotelli & Entsminger 2001). The data for such analysis consists of a matrix in which each species is a row and each site is a column. Entries in the matrix represent the SVL of each species. The original matrix is then reshuffled to produce random patterns that would be expected in the absence of competitive interactions. We used the following options of EcoSim: variance in segment length as size overlap metric, logarithmic transformation, no rounding, and all species in the matrix included in the source pool, with colonization weights set to 1. Because the rocky field and sandy cerrado enclaves in Guajar -Mirim harbored only two species, we used the minimum segment length metric because the variance in segment length would be equal to 0.

Segment length is calculated by ordering the

analyzed assemblage's adult mean SVL from smallest to largest. The "segment" represents the difference in body size between two consecutive species. Using the variance in segment length as the size overlap metric, the overall tendency for the observations to be evenly spaced is measured; thus, a structured assemblage would have an observed variance significantly smaller than in random assemblages. When the minimum segment length metric is selected, the smallest segment for the assemblage is calculated by measuring the spacing between the closest pair of species. This measure determines whether a minimum spacing between species is necessary for coexistence to occur in an assemblage. In a structured assemblage, the minimum segment length should be larger than expected by chance.

Transforming the body size data to logarithms prior to the analysis leads to an analysis of size ratios, which may be adequate whenever there are large differences in body size among species. The no-rounding option treats the simulated data as continuous measures; thus, there is virtually no chance of a tie, which would generate a segment of length 0. Including all species of the original matrix in the source pool tells EcoSim to construct each random assemblage by sampling randomly, without replacement, n species from the source pool. We set n equal to the observed number of species in each assemblage being tested. Finally, setting the colonization weight of each species to one gives all species an equal chance of being drawn.

RESULTS

SPECIES RICHNESS.—We collected a total of 20 lizard species in the open vegetation enclaves of Rond nia (Table 1). Among them, we recorded 6 Amazonian forest species collected primarily along the Cerrado-forest ecotones. By far, Gymnophthalmidae was the most diverse family (8 spp. in total/4 Cerrado spp.), followed by Teiidae (5/4), Polychrotidae (3/2), Scincidae (2/2), and Tropiduridae (2/2). The open vegetation enclaves in Vilhena had both the greatest total species richness (15) and the greatest richness of Cerrado species (11), followed by Pimenta Bueno (11/6), and Guajar -Mirim (5/3). Differences in species richness between physiognomies within localities were negligible (Table 1).

The rarefaction analyses indicated that Vilhena enclaves had a significantly greater richness than all other open vegetation enclaves (Table 2). In addition, in two-thirds of the comparisons, the Pimenta Bueno enclaves had greater species richness than the Guajar -Mirim enclaves. There were no sig-

TABLE 1. Composition of lizard assemblages in open vegetation enclaves from Rondônia, southwestern Amazonia. LC = latosol cerrado, RF = rocky field, SC = sandy cerrado, and TF = transitional forest.

Lizard species	Guajar�-Mirim		Pimenta Bueno			Vilhena	
	RF	SC	LC	TF	SC	LC	SC
Gymnophthalmidae							
<i>Bachia cacerensis</i>	—	—	—	—	—	—	2
<i>B. dorbigny</i> ^b	—	1	—	—	—	—	—
<i>Cercosaura ocellata</i>	—	—	23	77	2	13	—
Gymnophthalmidae sp. ^a	—	—	1	—	1	—	—
<i>Iphisa elegans</i> ^a	—	—	—	1	—	3	—
<i>Micrablepharus atticolus</i>	—	—	—	—	112	—	65
<i>M. maximiliani</i>	—	6	—	—	—	—	—
<i>Prionodactylus eigenmanni</i> ^a	—	—	—	9	—	2	—
Polychrotidae							
<i>Anolis meridionalis</i>	—	—	—	—	—	12	49
<i>A. ortoni</i> ^b	—	—	—	1	—	—	—
<i>Polychrus acutirostris</i>	—	—	—	—	—	1	1
Scincidae							
<i>Mabuya frenata</i>	—	—	—	—	—	21	1
<i>M. nigropunctata</i>	—	—	—	1	—	1	—
Teiidae							
<i>Ameiva ameiva</i>	94	48	86	12	75	64	61
<i>Cnemidophorus parecis</i>	—	—	—	—	—	—	51
<i>Kentropyx altamazonica</i> ^a	—	2	9	45	—	45	7
<i>K. vanzoi</i>	—	—	—	—	—	—	68
<i>Tupinambis merianae</i>	—	—	1 ^b	1	1 ^b	1 ^b	1
Tropiduridae							
<i>Stenocercus</i> sp.	—	—	9	—	—	2	—
<i>Tropidurus</i> sp.	124	—	—	—	—	—	—
Total species richness	2	4	6	8	5	11	10
Cerrado species richness	2	2	4	4	4	8	9
Total no.	218	57	129	147	191	165	306

^a Forest species.

^b Species sighted but not captured.

nificant differences in lizard richness among different physiognomies within localities. These results indicate that species richness is more influenced by regional than by local factors.

CO-OCCURRENCE.—Only *Ameiva ameiva* formed no checkerboard unit in the presence–absence matrix, whereas the largest number of checkerboard units (5) was observed between *Tupinambis merianae* and *Tropidurus* sp. and between *T. merianae* and *Micrablepharus maximiliani*. In addition, there were only four site-specific species: *Cnemidophorus parecis* and *Kentropyx vanzoi* (sandy cerrado, Vilhena), *Mi. maximiliani* (sandy cerrado, Guajar -Mirim), and *Tropidurus* sp. (rocky field, Guajar -Mirim), comprising 29 percent of the total number of species. The observed *C*-score index was not greater than expected ($P = 0.23$, Fig. 3). This pattern is consistent with the hypothesis that local coexis-

tence of lizard species in Rond nia enclaves is not constrained by limiting resources.

DIET OVERLAP.—We analyzed the contents of 1248 lizard stomachs, identifying 35 prey categories in total (34 numeric, 33 volumetric). The proportion of empty stomachs was 27 percent. Taking all localities together, termites were the most numerous prey category in the lizard stomachs, followed by ants, beetles, spiders, seeds, and crickets/grasshoppers. Likewise, termites were the most numerous prey in each locality. Volumetrically, beetles were the most important prey category, followed by crickets/grasshoppers and spiders. Differences among localities in volumetric composition were more pronounced: larvae were most important in Guajar -Mirim, crickets/grasshoppers were most important in Pimenta Bueno, and beetles were most important in Vilhena.

TABLE 2. Results of rarefaction analysis comparing lizard species richness from seven open vegetation enclaves in Rondônia, southwestern Amazonia. Values indicate species richness (main diagonal), Z-scores (upper half), and probability values (lower diagonal). Probabilities lower than 0.05 indicate significant differences in species richness between localities. GM = Guajará-Mirim, PB = Pimenta Bueno, and VI = Vilhena. LC = latosoil cerrado, RF = rocky field, SC = sandy cerrado, and TF = transitional forest.

	GM-RF	GM-SC	PB-LC	PB-SC	PB-TF	VI-LC	VI-SC
GM-RF	2	—	-19.900	-19.900	-9.800	-26.610	-6.400
GM-SC	—	2	-2.960	-1.131	-1.774	-4.237	-4.775
PB-LC	0.001	0.004	4	0.850	0.534	23.325	-2.603
PB-SC	0.001	0.258	0.396	4	1.189	7.567	-3.699
PB-TF	0.001	0.076	0.596	0.234	4	-4.574	-2.451
VI-LC	0.001	0.001	0.001	0.001	0.001	8	1.567
VI-SC	0.001	0.001	0.010	0.001	0.014	0.116	9

In only two assemblages, the mean diet overlap among lizard species was significantly smaller than random: the rocky field assemblage in Guajará-Mirim ($P = 0.04$) and the sandy cerrado assemblage in Vilhena ($P = 0.01$; Fig. 4). Since we captured only one individual of *Ma. frenata* and only one individual of *B. cacerensis* contained stomach contents, we reanalyzed the diet overlap data for the sandy cerrado assemblage in Vilhena after the removal of *Ma. frenata* and *B. cacerensis*. This resulted in an observed mean overlap not significantly smaller than random, indicating lack of structure.

Niche overlap between the only two species inhabiting the rocky field was 0.56, with *Tropidurus* sp. consuming predominantly ants, wasps, and cockroaches; *Am. ameiva* consumed mostly termites, larvae, and crickets/grasshoppers (Fig. 5). In the sandy cerrado, niche overlap ranged from 0 to 0.95 (Table 3). *Ameiva ameiva* and *K. vanzoi* had the largest overlap, with the former consuming predominantly beetles, termites, crickets/grasshoppers, and spiders, and the latter consuming mostly beetles and spiders. The lowest overlap was between *Ma. frenata*/*Po. acutirostris* and *T. merianae*/*B. cacerensis* (Table 3). *Mabuya frenata* consumed only cockroaches, whereas *Po. acutirostris* consumed mainly crickets/grasshoppers and plants (Fig. 6). *Tupinambis merianae* consumed mostly plants, ants, and vertebrates, whereas *B. cacerensis* consumed predominantly larvae (Fig. 6). The most important dietary items for the remaining species were as follows: ants and beetles for *Anolis meriodionalis*, spiders and cockroaches for *Micrablepharus atticolus*, and termites for *Cn. parecis* (Fig. 6).

SIZE OVERLAP.—The largest lizard we sampled in Rondônia was *T. merianae*, whereas the smallest was *Mi. maximiliani* (Table 4). Mean segment length was smallest in the transitional forest in Pi-

menta Bueno and the latosoil cerrado in Vilhena, and the largest was in the sandy cerrado in Guajará-Mirim (Fig. 7). The size overlap analysis based on the minimum segment length indicated that in no lizard assemblage was the observed mean overlap significantly larger than expected (Fig. 7). The smallest variance in SVL was observed in the sandy cerrado assemblage in Vilhena and the largest variance occurred in the transitional forest in Pimenta Bueno. The size overlap analysis based on the variance in segment length showed that in no lizard assemblage was the observed variance significantly smaller than random (Fig. 7). Therefore, both analyses indicated a lack of structure in the lizard assemblages from Rondônia.

DISCUSSION

SPECIES RICHNESS.—The open vegetation enclaves in southwestern Amazonia present a reduced number of species relative to other regions in tropical South America. We recorded only 14 open vegetation lizard species in total, with local richness ranging from 2 to 9 species. Lizard richness in Amazonian Savannas range from 4 species in Alter do Chão, Pará, to 8 in the Lavrado of Roraima (Magnusson & Silva 1993, Vitt & Carvalho 1995). Local richness in Amazonia is larger: 33 lizard species were recorded in eastern Rondônia and 27 lizard species at the Rio Xingu, Pará (Vitt 1995). Other localities in Amazonia have presented similar numbers of species (Duellman 1990). In the Caatinga biome, local richness ranges from 10 to 18 species, depending on the locality (Vanzolini 1974, 1976; Vitt 1995), and the sand dunes in Bahia harbor an even higher diversity with an extraordinary amount of endemic species (Rodrigues 1991). The Cerrado biome has been reported in the past as presenting low richness of lizards, but further investigations

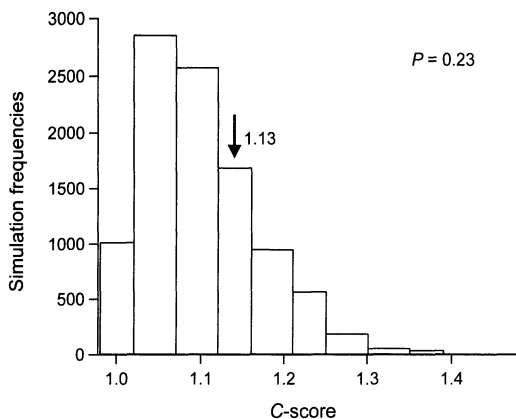


FIGURE 3. Frequency distribution of checkerboard C -scores, obtained from 10,000 simulations producing random lizard assemblages from open vegetation enclaves in Rondônia, southwestern Amazonia. Arrow indicates observed mean; P -value is probability that observed mean is larger than expected mean.

have concluded that local richness in the Cerrado is as high as in Amazonia (Colli *et al.* 2002).

Lizard richness differed significantly among localities, but there were no differences among physiognomies within localities. The southernmost locality Vilhena presented the highest species richness followed by Pimenta Bueno and Guajará-Mirim, the northernmost locality. Therefore, local variations in ecological parameters seem to have little influence upon species richness. Furthermore, the greater the distance from the core of the Cerrado biome in Central Brazil, the lower the species richness.

Geographical differences in species richness are often attributed to variations in local factors such as area (MacArthur & Wilson 1967, MacArthur 1972, Williamson 1981) and habitat heterogeneity (Case 1975, Ricklefs & Lovette 1999). In Australian open landscapes, unpredictable precipitation, abundance and diversity of termites, and fire cycles are local factors that seem to affect lizard richness (Pianka 1986, 1989; Morton & James 1988). In Rondônia's open vegetation enclaves, however, major differences in habitat heterogeneity among physiognomies within localities are not paralleled by differences in species richness. This suggests the prevalence of historical or regional determinants of species richness over local factors (Cornell & Lawton 1992). Likewise, recent studies in Australian deserts have indicated that lizard richness is "determined more by continental biogeography rather than by ecological interactions" (James & Shine 2000).

The open vegetation enclaves in Rondônia were formed during the last 3000 years as the Cerrado retreated south, whereas the Amazon Forest expanded from the north (Freitas *et al.* 2001). In this scenario, differentiation, extinction, and immigration may all have affected lizard richness in the enclaves. Immigration is influenced by both isolation (matrix permeability) and distance from the source pool (Williamson 1981, Whittaker 1998). The Guajará-Mirim enclaves are highly isolated within the Amazon Forest, being the most distant from the Central Brazilian Cerrado source pool and the most species-poor. The Pimenta Bueno enclaves lie at an intermediate distance from the source pool relative to Guajará-Mirim and Vilhena, harboring an intermediate richness of lizard species. The greatest species richness occurs in the Vilhena enclaves, which are closest to the Cerrado. Therefore, the observed patterns are consistent with the notion that distance from the source pool (= chances of immigration) determine lizard richness; however, with the exception of *Am. ameiva* (Vitt & Colli 1994, Sartorius *et al.* 1999), the tropical rain forest acts as an impenetrable barrier for open vegetation lizard species. For example, we placed 300 buckets in the Guajará-Mirim rain forest and, with the exception of *Am. ameiva*, collected no open vegetation species (G. R. Colli, pers. obs.). Therefore, immigration must have played a secondary role in creating observed differences in species richness among localities.

We suggest that extinction following isolation during the Holocene was the most important process that shaped differences in species richness among Rondônia's open vegetation enclaves. As forests expanded from north to south after the last pleniglacial, Guajará-Mirim was the first area to be isolated, followed by Pimenta Bueno and then by Vilhena. Probability of extinction increases with time since isolation (Case & Cody 1987, Foufopoulos & Ives 1999).

CO-OCCURRENCE.—The co-occurrence analysis indicated that the observed number of checkerboard units is not different from random; *i.e.*, local co-existence of lizard species in Rondônia enclaves is not limited. There is a long lasting debate on whether communities are structured or not via the analysis of co-occurrence patterns (Connor & Simberloff 1979, Gilpin & Diamond 1984). Some mechanisms that cause limited coexistence are the following: interspecific competition, whereby species are aggressive with one another, competition for habitat that occurred in the past, and species

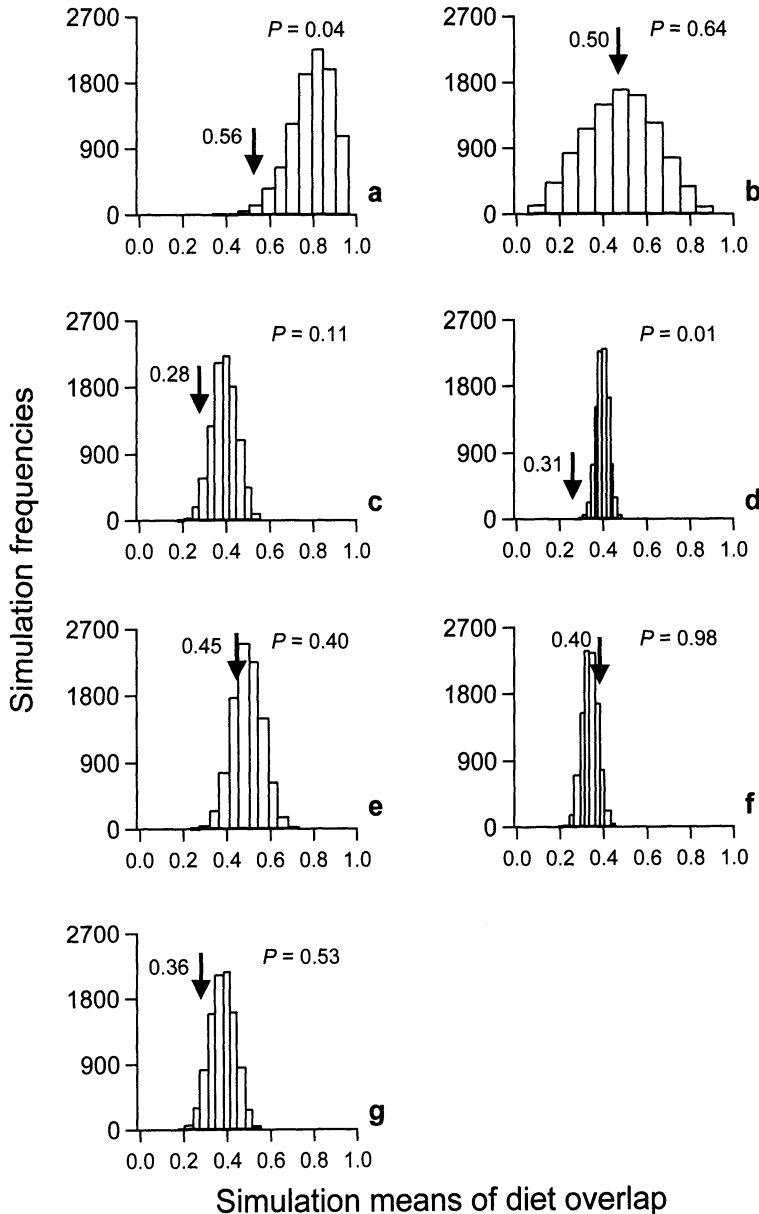


FIGURE 4. Observed and expected mean diet niche overlap among lizards in seven assemblages from open vegetation enclaves in Rondônia, southwestern Amazônia. Arrows indicate observed means, P -values are probabilities that observed means are smaller than expected means (10,000 simulations). a-rocky field in Guajará-Mirim, b-sandy cerrado in Guajará-Mirim, c-sandy cerrado in Pimenta Bueno, d-sandy cerrado in Vilhena, e-latosol cerrado in Pimenta Bueno, f-latosol cerrado in Vilhena, g-transitional forest in Pimenta Bueno.

that evolved distinct habitat preferences on a geographic scale (Gotelli *et al.* 1997). The lack of structure in the Rondônia assemblages suggests that competition does not play a prominent role in co-occurrence patterns.

Given that species densities may be below the necessary levels for competition, nonrandom pat-

terns of species co-occurrence have also been attributed to predator-prey relationships (Case 1983a, Jackson *et al.* 1992). Even though bearing a high diversity of birds and snakes (Duellman 1990, Karr *et al.* 1990), there is a lack of information on the role of predation upon the structure of Neotropical lizard assemblages. Other studies have suggested

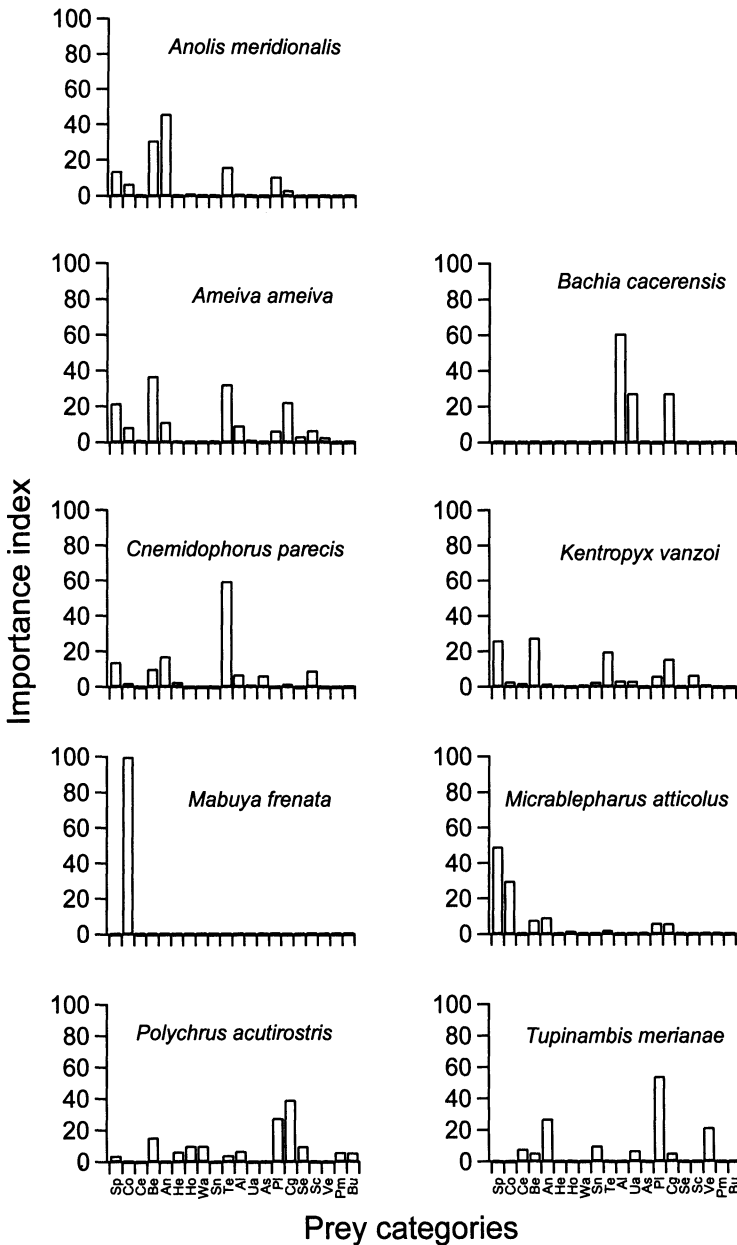


FIGURE 6. Importance index of prey categories used by lizards in the sandy cerrado assemblage from Vilhena. Abbreviations are as follows: As = ants, Sp = spiders, Co = cockroaches, Ce = centipedes, Be = beetles, He = hemipterans, Ho = homopterans, Wa = wasps, Sn = snails, Te = termites, Al = all larvae, Ua = unidentified arthropods, Pl = plants, Cg = cricket/grasshoppers, Se = seeds, Sc = scorpions, Ve = vertebrates, Pm = praying mantids, and Bu = butterflies. Diet data for *Polychrus acutirostris* are from Vitt and Lacher (1981) and data for *Tupinambis merianae* are from Colli *et al.* (1998).

with high overlap, whereas five species show preference for certain items: *An. meridionalis* (ants), *B. cacerensis* (larvae), *Cn. parecis* (termites), *Ma. frenata* (cockroaches), and *Mi. atticolus* (spiders). The low overlap between *Ma. frenata* and other species

may be due to its small sample size. In the latosoil cerrado of Vilhena, a larger sample of *Ma. frenata* indicates that the species is a generalist. The same should apply to *B. cacerensis*. Curiously, *An. chrysolepis*, a close relative of *An. meridionalis*, apparently

TABLE 4. Size statistics of lizards from open vegetation enclaves in Rondônia, southwestern Amazônia. N = sample size, SVL = mean snout-vent length, SE = standard error, and range = minimum and maximum snout-vent length from sample.

Lizard species	N	SVL	SE	Range
Gymnophthalmidae				
<i>Bachia cacerensis</i>	5	71.34	4.56	60.0–82.3
<i>Cercosaura ocellata</i>	96	40.73	0.45	33.0–53.0
<i>Micrablepharus atticolus</i>	170	35.48	0.16	30.0–40.0
<i>M. maximiliani</i>	6	32.83	1.29	30.0–39.0
Polychrotidae				
<i>Anolis meridionalis</i>	52	46.83	0.34	42.0–51.0
<i>Polychrus acutirostris</i>	3	92.00	20.50	57.0–128.0
Scincidae				
<i>Mabuya frenata</i>	264	60.06	0.22	—
<i>M. nigropunctata</i>	338	80.40	0.66	—
Teiidae				
<i>Ameiva ameiva</i>	391	81.22	1.56	39.5–186.0
<i>Cnemidophorus parecis</i>	58	74.21	1.06	57.0–90.0
<i>Kentropyx vanzoi</i>	59	50.20	0.82	43.0–85.0
<i>Tupinambis merianae</i>	39	284.23	14.56	90.0–448.0
Tropiduridae				
<i>Stenocercus</i> sp.	3	77.33	2.33	75.0–82.0
<i>Tropidurus</i> sp.	124	73.36	1.09	33.5–94.5

avoids ants (Vitt & Zani 1996b). The preference for termites in *Cn. parecis* is a conservative character of the genus (Vitt 1991b, Vitt & Caldwell 1993, Bergallo & Rocha 1994, Vitt & Carvalho 1995, Mesquita 2001). Thus, to some extent, the low niche overlap observed among lizard species in the sandy cerrado of Vilhena may be associated with small sample sizes and phylogenetic inertia.

Five out of seven lizard assemblages we studied presented no significant structure in diet composition. This may be a consequence of lack of competition; *i.e.*, prey items are not limited in these environments, which would cause species to compete for food (Connor & Simberloff 1979). Furthermore, diet overlap may be enhanced by lack of species that specialize on few prey items (Wine-miller & Pianka 1990). Other researchers have suggested that structure is not affected by prey type but by prey size, with large lizards eating larger prey (Vitt & Zani 1998). Apparently, all of the aforementioned factors may apply to lizard assemblages in Rondônia enclaves, resulting in high diet overlap.

SIZE OVERLAP.—Nonrandom patterns of size overlap on different organisms, including Galapagos finches (Abott *et al.* 1977) and desert rodents (Bowers & Brown 1982), have been attributed to

limited food supplies and interspecific competition. Nevertheless, none of the lizard assemblages from Rondônia enclaves presented structure in size overlap patterns. Therefore, seemingly no minimum difference in body size is necessary for coexistence in the studied assemblages and prey are not in short supply. Other studies using null-model analyses have also encountered random size distribution patterns (Strong *et al.* 1979, Simberloff & Boecklen 1981). Explanations for random patterns of size overlap include chance invasions, local extinctions, idiosyncratic co-colonizations, small population sizes, and genetic drift (Strong *et al.* 1979). As mentioned above, invasions and colonizations are remote possibilities due to the isolation of Rondônia enclaves by large tracts of forested areas. Conversely, small population sizes, drift, and local extinctions may be important due to the long isolation of Rondônia enclaves.

CONCLUSION.—In the recent past, the open vegetation areas in Rondônia were contiguous with those in Central Brazil. Global changes in climate promoted the expansion of forests from north to south, breaking the connection between the two regions and leading to the formation of open vegetation enclaves in Rondônia (Freitas *et al.* 2001, Sifeddine *et al.* 2001). The lizard fauna that be-

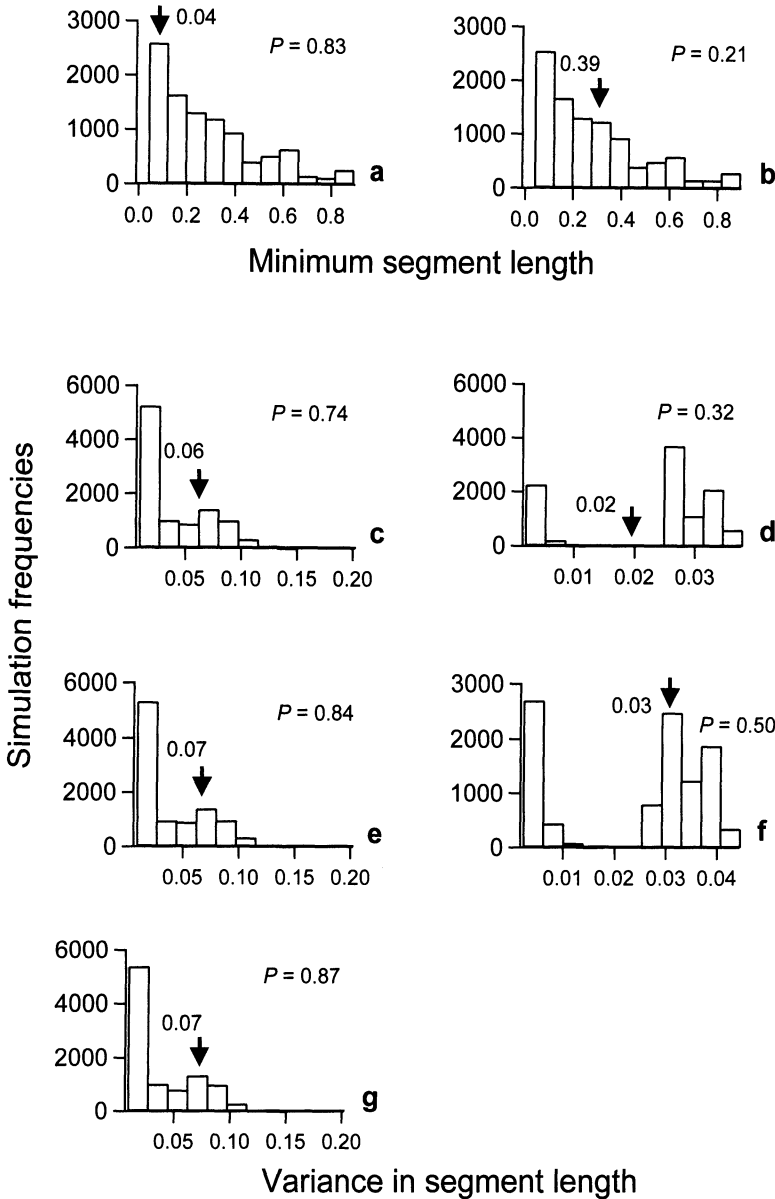


FIGURE 7. Observed and expected size overlap for lizards in the seven studied assemblages from southwestern Amazonia. Metrics used are minimum segment length and variance in segment length, with log transformed values. Arrows indicate observed values and P -values indicate probabilities that observed values are larger than expected by chance (10,000 simulations). a-rocky field in Guajara-Mirim, b-sandy cerrado in Guajara-Mirim, c-sandy cerrado in Pimenta Bueno, d-sandy cerrado in Vilhena, e-latosoil cerrado in Pimenta Bueno, f-latosoil cerrado in Vilhena, and g-transitional forest in Pimenta Bueno.

came entrapped in enclaves experienced stochastic extinctions, producing differences in species richness among localities and nonstructured assemblages in terms of species co-occurrences, diet overlap, and size overlap. Speciation also took place in the enclaves. At least two endemic species presumably evolved this way: *Tropidurus* sp. and *Cn. parecis*.

Finally, several lizard species are tightly associated with unique ecogeographic features of the landscape, such as *Tropidurus* sp., found only in rock outcrops, and *Cn. parecis* and *K. vanzoi*, which occur in sandy areas. Hence, conservation measures in the region must adequately preserve these features to ensure survival of the species.

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