Oecologia
DOI 10.1007/s00442-007-0725-z

COMMUNITY ECOLOGY

Ecological release in lizard assemblages of neotropical savannas

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Received: 11 November 2005 / Accepted: 8 March 2007

Abstract We compare lizard assemblages of Cerrado and Amazonian savannas to test the ecological release hypothesis, which predicts that niche dimensions and abundance should be greater in species inhabiting isolated habitat patches with low species richness (Amazonian savannas and isolated Cerrado patches) when compared with nonisolated areas in central Cerrado with greater species richness. We calculated microhabitat and diet niche breadths with data from 14 isolated Cerrado patches and Amazon savanna areas and six central Cerrado populations. Morphological data were compared using average Euclidean distances, and lizard abundance was estimated using the number of lizards captured in pitfall traps over an extended time period. We found no evidence of ecological release with respect to microhabitat use, suggesting that historical factors are better microhabitat predictors than ecological factors. However, data from individual stomachs indicate that ecological release occurs in these areas for one species (*Tropidurus*) but not others (*Ameiva ameiva*, *Anolis*, *Cnemidophorus*, and *Micrablepharus*), suggesting that evolutionary lineages respond differently to environmental pressures, with tropidurids being more affected by ecological factors than polychrotids, teiids, and gymnophthalmids. We found no evidence that ecological release occurs in these areas using morphological data. Based on abundance data, our results indicate that the ecological release (density compensation) hypothesis is not supported: lizard species are not more abundant in isolated areas than in nonisolated areas. The ecology of species is highly conservative, varying little from assemblage to assemblage. Nevertheless, increases in niche breadth for some species indicate that ecological release occurs as well.

Keywords Community ecology · Cerrado · Amazonian savannas · Historical factors · Ecological factors

Introduction

Communities are usually defined as associations among populations that coexist in an easily defined place. Many community studies focus on assemblages, groups of phylogenetically related species that coexist in a specific geographic area (Ricklefs and Miller 1999). Primary determinants of assemblage structure are species interactions, resource use patterns, and historical relationships among taxa comprising the assemblage (Begon et al. 1990; Pianka 1994; Ricklefs and Miller 1999). Historically, ecological factors have received the most attention from ecologists who argued that competition and predation were the main causes of assemblage organization (Dunham 1983; Mitchell 1979; Wiens 1977). More recently, historical factors have received special attention (Losos 1994, 1996; Vitt et al. 1999; Webb et al. 2002). Historical factors can be defined as ‘‘the integration of events over a long period that result in the accumulation of inherited species

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Communicated by Thomas Miller.

Electronic supplementary material The online version of this article (doi:10.1007/s00442-007-0725-z) contains supplementary material, which is available to authorized users.

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traits that affect co-occurrence and diversity'' (Pearson and Juliano 1993; Ricklefs and Schluter 1993). Repeatedly, ecological factors alone (competition, predation, or environmental pressure) have not been sufficient to explain observed patterns of organization in species assemblages (Brooks and McLennan 1993; Pearson and Juliano 1993; Ricklefs and Schluter 1993). What we observe today may not result only from recent ecological factors, but from ecological factors impacting species or their ancestors in the distant past (the ghost of competition past) (Connell 1980; Losos 1994; Pearson and Juliano 1993; Webb et al. 2002). Evidence of historical factors includes lack of divergence in ecological traits (e.g., microhabitat use, diet) among closely related species independent of the assemblage in which they reside. Divergence in ecological traits among closely related species is viewed as evidence of the importance of ecological factors (Brooks and McLennan 1991; Losos 1996). Clearly, both historical and ecological factors contribute to structure in present-day animal assemblages (Cadle and Greene 1993; Losos 1994, 1996; Vitt and Pianka 2005).

Islands generally contain fewer species compared with continental areas, but species are often more abundant on islands. This phenomenon was described initially for bird assemblages and called ''density compensation'' (Crowell 1962; Pianka 1994; Ricklefs and Miller 1999). In addition, island species often expand their habitat niche breadth in response to a lower number of competitors, occupying habitats that are occupied by other species in continental areas, a phenomenon known as ''niche expansion'' (MacArthur et al. 1972; Pianka 1994; Ricklefs and Miller 1999). In combination, both processes (density compensation and niche expansion) are referred to as ''ecological release'' (Pianka 1994; Ricklefs and Miller 1999). For example, Rodda and Dean-Bradley (2002) found strong evidence that amphibians and reptiles (mainly lizards) have higher biomass and density in small islands than in continental areas. Conversely, a study correlating island size with density of animal populations suggested that density compensation might be less common than previously thought (Connor et al. 2000). A study on *Anolis* lizards in the Antilles tested the hypothesis that lizards from small islands (few species) should exhibit a generalized morphology and greater microhabitat niche breadth compared with lizards from large islands (more species). However, lizards on small islands did not have a generalized morphology and did not have greater microhabitat niche breadth (Losos and de Queiroz 1997).

We test the ecological release hypothesis using lizard assemblages from the Cerrados of Brazil. Cerrado lizard assemblages are ideal for testing this hypothesis because the Cerrado contains a vast core area (the ''mainland'') and numerous variously sized enclaves (''islands'') embedded in Amazon rainforest. Based on the ecological release hypothesis, we predict that niche dimensions (e.g., microhabitat, diet, and morphology) should be greater and abundance higher in species of Cerrado enclaves isolated in the Amazon when compared with species in nonisolated areas in the central Cerrado.

Materials and methods

Study sites

The Cerrado covers about 2,000,000 km^2, nearly 25% of Brazil, and is located in the central region, with some isolated patches in northern Brazil (Oliveira and Marquis 2002). The region receives annually 1,500–2,000 mm of highly predictable and strongly seasonal precipitation, from October to April. Monthly temperatures average 20–22 °C (Nimer 1989). The Cerrado biome harbors forests where arboreal species predominate; savannas, with trees and shrubs dispersed in an herbaceous stratum; and grasslands, with herbaceous species and some shrubs. Tree trunks are tortuous, with thick corky barks and hard, coriaceous leaves (Ribeiro and Walter 1998). During a six-year period from 1998 to 2004, we sampled eight isolated Cerrado sites, six nonisolated (core) Cerrado areas, and seven (reduced to six) Amazonian savanna sites representing six habitat types: dry forest, latosoil, rocky field, sandy soil, and transitional forest (see Appendix 1 in the ''Electronic supplementary material'').

One explanation for the formation of the Amazonian savannas is the ''Pleistocene refuge hypothesis,'' which posits that during glacial periods, with reduced precipitation, large portions of the Amazon were covered with savannas, restricting forest to isolated patches (Ab'Sáber 1982; Bigarella and Andrade-Lima 1982; Eden 1974; Huber 1982). Such periods were followed by forest expansion, isolating patches of Amazonian savanna and Cerrado in the Amazon, and leaving vestiges of a large savanna that extended from central Brazil to the Guianas (Prance 1978). The Amazonian savannas isolated in Amazon Forest now cover about 150,000 km^2, or 2% of Brazil (Pires 1973). The climate is highly seasonal and annual precipitation averages 1,700 mm (Eidt 1968). Vegetation is dominated by typical species of the Cerrado, but diversity is usually lower (Eiten 1978). The distinction between Amazonian savannas and isolated Cerrado areas was proposed by Eiten (1978) based mainly on differences in numbers of plant species. Usually, Amazonian savannas are poorest when compared with various Cerrado areas (isolated and nonisolated) (Eiten 1972, 1978). Here, we consider all enclaves as islands to test the ecological release hypothesis. Even though it is well known that

Amazonian savannas and isolated patches are islands for open-formation lizard populations (i.e., Colli 1996; França et al. 2006), we sampled in the forested matrix associated with all isolated patches, using similar sampling efforts with pitfall traps and/or by hand. No open-area lizard species were found in adjacent forest, with the exception of widespread generalist species, such as *Ameiva ameiva*, which are known to occur in most habitat types in tropical Brazil (see Sartorius et al. 1999; Vitt and Colli 1994). This confirms that open areas in the Amazon function as ''islands'' for open formation lizard species.

All specimens examined were deposited in the Coleção Herpetológica da Universidade de Brasília (CHUNB). Collecting sites are indicated in Appendix 2 in the ''Electronic supplementary material.''

Species composition and microhabitat

We captured lizards with drift fences, by hand, or using a shotgun. In the lab, we humanely killed live lizards with an injection of Tiopental® and fixed them with 10% formalin. We recorded the microhabitat for each lizard collected. We used the following microhabitat categories: clear ground, grass, hole, inside termite nest, leaf, leaf litter, log, rock, shrub, stick, tree trunk, under leaf, under leaf litter, under log, under manure, under rock, tree bark, under tree bark, and wall. We computed microhabitat niche breadths (*B*) using the inverse of Simpson's (1949) diversity index:

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

where p is the proportion of microhabitat category i and n is the number of categories.

We made comparisons among assemblages using differences among isolated and nonisolated areas as a model to test the ecological release hypothesis. We compared average microhabitat niche breadth of species among assemblages. If ecological release occurs in isolated areas, we expect average niche breadth to be higher than in nonisolated areas.

Diet composition

We analyzed stomach contents under a stereoscopic microscope, identifying prey items to ordinal level. We recorded length and width (0.01 mm) of intact items with Mitutoyo® (Aurora , IL, USA) 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 and individual stomachs. From these percentages, we computed niche breadths (*B*) for pooled and individual stomachs, using the inverse of Simpson's diversity index (Simpson 1949), as described above. We excluded from the volumetric analyses prey items that were too fragmented to allow a reliable estimation of their volumes. Average niche breadths of all species from each assemblage were compared between isolated and nonisolated areas, as a test of the ecological release hypothesis. We also made comparisons with just closely related species, to minimize historical effects. Because analyses with pooled stomachs provided only a single diet niche breadth value for each species, we made comparisons among closely related species of different assemblages with data generated for individual stomach means. We used averages of numeric and volumetric niche breadths for both individual and pooled stomachs. This balances the cost of acquiring prey (energy expended capturing each prey item) with energy gains associated with individual prey types. Throughout the text, this average is referred to as the diet niche breadth.

Morphometry

Using Mitutoyo® electronic calipers, we recorded morphometric variables to the nearest 0.01 mm, including: 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 species. When the regression was not statistically significant, we used the average of intact tails. We log-transformed (base 10) all morphometric variables prior to analyses to meet requirements of normality (Zar 1998).

To compare the assemblages using morphometry, we calculated a matrix of Euclidean distance among all pairs of species at each locality using the following formula:

$$D_{ij} = \left[\sum_{k=1}^{9} (X_{ik} - X_{jk})^2\right]^{1/2}$$

where D_{ij} is the Euclidean distance between species i and j, and X_{ik} and X_{jk} are averages of log-transformed morphometric variables k for species i and j. From the distance matrix for each assemblage, we calculated the average neighbor distance and compared them between isolated and nonisolated areas. Based on the ecological release hypothesis, we expected average neighbor distance to be lower in isolated than in nonisolated areas.

Abundance

We used pitfall traps with drift fences to estimate abundance of lizards. Each trap array consists of four buckets, with one in the center and the others in the extremities, connected with plastic, at angles of 120° from each other. In most areas, 100 buckets were used in each sampled area. When more than 100 buckets were used in an area, we corrected abundance data by dividing the original data by one plus the additional proportion of buckets.

Our density estimates consisted of the average number of lizards per species per day collected in the buckets. We compared abundances among assemblages, ignoring species. We then used data from the four most widely distributed genera (*Ameiva*, *Cnemidophorus*, *Anolis*, and *Micrablepharus*) to make comparisons among sampled areas. Next, we performed regressions, on a species-by species basis, to determine the relationship between lizard abundance and number of species in the assemblages. The ecological release hypothesis predicts that in isolated areas, where diversity is lower, species should occur at higher densities (density compensation). We expect that, if ecological release occurs in these areas, species in isolated areas should be more abundant than in nonisolated areas, having expanded their niches to include microhabitats used by lizard species that are missing.

Statistical analysis

We carried out statistical analyses using SYSTAT 11.0 and SAS 8.1 for Windows, with a significance level of 5% to reject null hypotheses. Throughout the text, means appear ± 1 SD.

Results

Species composition and microhabitat

We collected 51 lizard species in the 20 study sites (Appendix 3 in the ‘‘Electronic supplementary material’’). Lizard fauna in nonisolated areas was significantly richer than in isolated areas (Table 1). Isolated area richness varied from 11 species in Vilhena to two species in the rock field at Guajará-Mirim (Appendix 3). Among nonisolated areas, richness was greatest in dry forest at São Domingos and in latosoil cerrado in Paracatu-MG, with 16 lizard species. The lowest richness was in the sandy cerrado and rocky field in Alvorada do Norte, with eight species (Appendix 3). The most diverse lizard clade was Teiidae, with 11 open vegetation species and three typical forest species, followed by Gymnophthalmidae (8/4), Tropiduridae (7/0), Gekkonidae (6/1), Polychrotidae (5/1), and Scincidae (5/0) (Appendix 3).

Microhabitat niche breadths were generally low, ranging from 1.00 in several species to 5.04 in *Gymnodactylus geckoides* from São Domingos (Appendix 4 in the ‘‘Electronic supplementary material’’). Average niche breadth among species in each assemblage varied from 1.32 in the sand Cerrado in Jalapão to 2.74 in the rock field of Guajará-Mirim-RO (Appendix 4). No differences were detected in average niche breadths between isolated vs. nonisolated areas (Table 1). Further, no significant association existed between average niche breadth and number of species in each assemblage ($R = 0.311$, $F_{(1,11)} = 0.178$, $P = 0.301$) (Fig. 1). To minimize historical effects, we conducted separate analyses on populations of closely related species of the four most widely widespread genera (*Ameiva*, *Cnemidophorus*, *Anolis* and *Tropidurus*). No differences were detected in average microhabitat niche breadths of isolated vs. nonisolated areas considering only these four genera (Table 1). Likewise, no significant relationships were detected between microhabitat niche breadths and number of species in each assemblage for these genera, except for *Ameiva ameiva* (Fig. 1). Even with significant results for *Ameiva*, the comparisons between average microhabitat niche breadths of isolated vs. nonisolated are not significant, leading us to conclude that ecological release does not occur. These results indicate that ecological release in microhabitat use does not occur in the studied assemblages.

Diet composition

We analyzed the contents of 3,583 lizard stomachs and recognized 38 prey categories. Based on pooled stomachs, *Mabuya nigropunctata* from the transitional forest in Pimenta Bueno-RO and *Kentropyx paulensis* from the latosoil Cerrado in Paracatu had the lowest diet niche breadth, and *Kentropyx striata* from Roraima had the greatest niche breadth (Appendix 5 in the ‘‘Electronic supplementary material’’). Based on individual stomachs, the lowest diet niche breadth was observed in *Mabuya nigropunctata* from the transitional forest in Pimenta Bueno-RO and in *Kentropyx paulensis* from the latosoil Cerrado in Paracatu-MG; and the greatest niche breadth was observed in *Ameiva ameiva* from the sandy Cerrado in Vilhena-RO (Appendix 5).

Based on pooled stomachs, no difference in average niche breadths existed between isolated vs. nonisolated areas (Table 1), and the relationship between dietary niche

Table 1 Summary of ecological traits of lizard assemblages from 20 isolated and nonisolated open vegetation areas from Brazil

Variable	Isolated	Nonisolated	Comparisons
All species richness	5.786 ± 2.778 (6)	12.000 ± 3.847 (14)	$F_{(1,18)} = 16.744$, $P = 0.001$
Microhabitat niche breadth	1.959 ± 0.428 (9)	1.879 ± 0.463 (4)	$F_{(1,11)} = 0.093$, $P = 0.766$
Diet niche breadth (pooled)	3.386 ± 1.057 (14)	2.722 ± 0.561 (6)	$F_{(1,18)} = 2.072$, $P = 0.167$
Diet niche breadth (individual)	1.503 ± 0.267 (14)	1.233 ± 0.135 (6)	$F_{(1,18)} = 5.422$, $P = 0.032$
Nearest neighbor Euclidean distance	1.151 ± 0.395 (14)	1.119 ± 0.224 (6)	$F_{(1,18)} = 0.032$, $P = 0.859$
Abundance of shared species	4.744 ± 5.328 (7)	7.905 ± 3.083 (5)	$F_{(1,10)} = 1.399$, $P = 0.264$
Ameiva ameiva			
Microhabitat niche breadth	2.194 ± 0.626 (9)	1.643 ± 0.593 (4)	$F_{(1,11)} = 2.206$, $P = 0.166$
Abundance	1.406 ± 1.699 (7)	0.541 ± 0.398 (4)	$F_{(1,10)} = 1.215$, $P = 0.296$
Cnemidophorus			
Microhabitat niche breadth	1.974 ± 0.367 (5)	1.442 ± 0.565 (4)	$F_{(1,7)} = 2.949$, $P = 0.130$
Abundance	3.130 ± 3.492 (2)	2.525 ± 2.583 (5)	$F_{(1,5)} = 0.067$, $P = 0.806$
Anolis			
Microhabitat niche breadth	2.286 ± 1.818 (2)	1.823 ± 1.164 (2)	$F_{(1,2)} = 0.092$, $P = 0.790$
Abundance	1.568 ± 1.820 (3)	1.374 ± 1.693 (2)	$F_{(1,3)} = 0.014$, $P = 0.913$
Tropidurus			
Microhabitat niche breadth	2.446 ± 0.823 (5)	2.812 ± 0.862 (4)	$F_{(1,7)} = 0.422$, $P = 0.537$
Micrablepharus			
Abundance	1.610 ± 0.787 (2)	1.054 ± 0.839 (4)	$F_{(1,4)} = 0.605$, $P = 0.480$

Sample sizes are in parentheses

breadths and number of species in the assemblage was not significant (Fig. 2). Considering only the five most widespread genera (*Ameiva*, *Cnemidophorus*, *Micrablepharus*, *Anolis* and *Tropidurus*), we found no evidence of ecological release (Table 2), and no relationship between diet niche breadths and number of species of each assemblage for these five genera (Fig. 2).These results indicate that, based on pooled stomachs, ecological release does not occur in these areas.

Based on individual stomachs, niche breadths were higher in isolated relative to nonisolated areas (Table 1), and a significant relationship exists between dietary niche breadths and number of species in the assemblage (R = 0.471, $F_{(1,18)} = 5.128$, $P = 0.036$) (Fig. 3). Considering the five most widely widespread genera (*Ameiva*, *Cnemidophorus*, *Micrablepharus*, *Anolis* and *Tropidurus*), we found no statistical differences in diet niche breadths on isolated vs. nonisolated areas, except for *Tropidurus* (Table 2). Linear regression analyses failed to detected significant relationships between diet niche breadths and number of species of each assemblage for these four genera (Fig. 3). These results indicate that, based on individual stomachs of all species, ecological release should occur, and that among the four most widely widespread genera, it occurs only in *Tropidurus*.

Morphometry

We found significant differences in average nearest neighbor Euclidean distance among populations (ANOVA

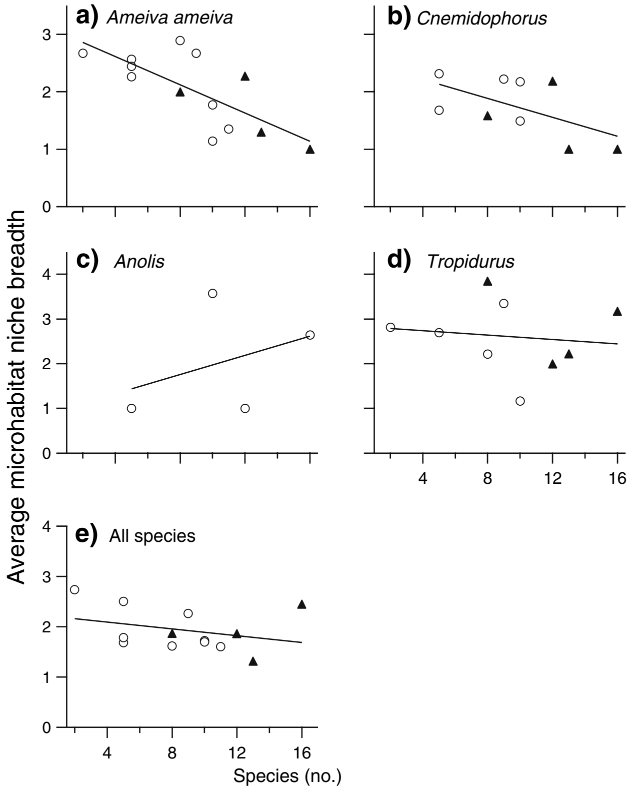

Fig. 1a–e Relationship between average microhabitat niche breadths (variance of organism resource use) and number of lizard species from isolated (*circles*) and nonisolated (*filled triangles*) Cerrado-like open vegetation habitats in Brazil for **a** *Ameiva ameiva* (P = 0.005, r = 0.730), **b** *Cnemidophorus* (P = 0.107, r = 0.572), **c** *Anolis* (P = 0.616, r = 0.384), **d** *Tropidurus* (P = 0.744, r = 0.127) and **e** all species (P = 0.301, r = 0.311)

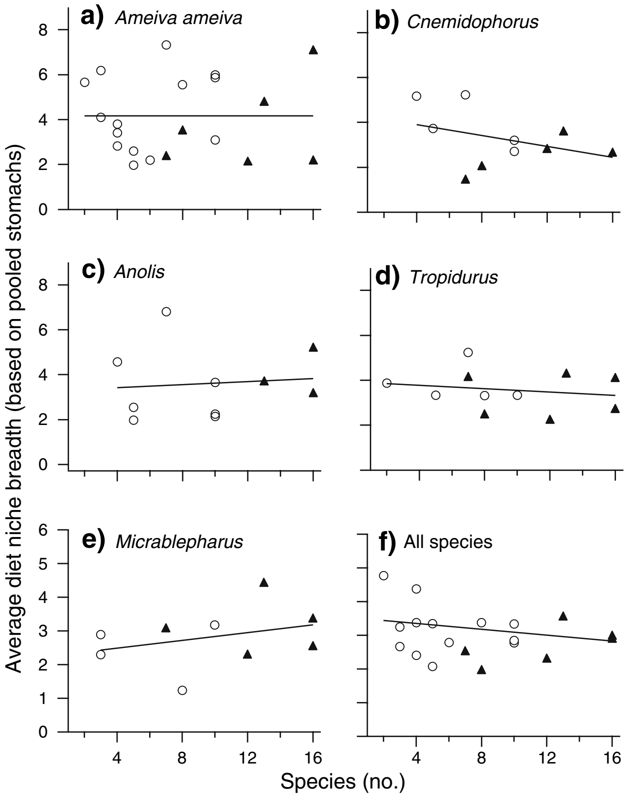

Fig. 2a–f Relationship between average diet niche breadths based on pooled stomachs and number of species from isolated (*circles*) and nonisolated (*filled triangles*) Cerrado-like open vegetation habitats in Brazil for **a** *Ameiva ameiva* ($P = 0.706$, $r = 0.090$), **b** *Cnemidophorus* ($P = 0.291$, $r = 0.371$), **c** *Anolis* ($P = 0.796$, $r = 0.094$), **d** *Tropidurus* ($P = 0.580$, $r = 0.188$), **e** *Micrablepharus* ($P = 0.339$, $r = 0.321$) and **f** all species ($P = 0.431$, $r = 0.186$)

$F_{(19,640)} = 6.877$, $P < 0.0001$). The smallest average distances were those in the rock field assemblage at Guajará Mirim ($\bar{x} = 0.66 \pm 0.000$) and the sandy Cerrado in Amapá ($\bar{x} = 0.66 \pm 0.29$). The largest was that in the lizard assemblage in transitional forest in Pimenta Bueno($\bar{x} = 1.95 \pm 1.15$). We found no significant differences in average nearest neighbor Euclidean distance of lizard assemblages between isolated and nonisolated areas (Table 1), and no significant relationship between nearest neighbor Euclidean distance and number of species in each assemblage ($R = 0.169$, $F_{(1,18)} = 0.526$, $P = 0.447$) (Fig. 4). These results indicate that ecological release does not occur in these areas.

Abundance

Based on all assemblages combined, the rarest lizard species were *Enyalius* cf *bilineatus*, *Kentropyx paulensis*, and *Bachia cacerensis*, and the most abundant species were *Cnemidophorus* cf *ocellifer*, *Tropidurus* cf *oreadicus*, and *Ameiva ameiva*. Based on each assemblage, the rarest lizards were *Enyalius* cf *bilineatus* and *Kentropyx paulensis*, from Paracatu-MG, and *Bachia cacerensis*, from the sandy Cerrado in Vilhena, and the most abundant lizards were *Cnemidophorus cryptus*, from Monte Alegre, and *Cnemidophorus* cf *ocellifer*, from Paranã (Appendix 6 in the ‘‘Electronic supplementary material’’). The assemblage with lowest lizard abundance was Humaitá-AM, and those with the highest abundances were Paranã and Monte Alegre. Based on abundance relative to number of species in each assemblage, lizards were less abundant in Paracatu and Humaitá and more abundant in Alvorada do Norte, the sandy cerrado in Pimenta Bueno, Dianópolis, Paranã, and Monte Alegre (Appendix 6).

Lizard abundances between isolated and nonisolated areas were similar (Table 1). Because richer assemblages have higher probabilities of exhibiting higher lizard abundances than poorer assemblages, we repeated the analyses with number of species in each assemblage as a covariate. Likewise, we found no significant difference in abundance of lizards between isolated and nonisolated areas (ANCOVA $F_{(1,9)} = 0.312$, $P = 0.590$).

To further refine our analyses, we compared the abundances of *Ameiva*, *Anolis*, *Cnemidophorus* and *Micrablepharus*, but we did not find significant differences in lizard abundance between isolated and nonisolated habitats

Table 2 Comparisons of diet niche breadths based on individual stomach means of five lizard genera from Cerrado assemblages

Genera	$\bar{X}$ isolated	$\bar{x}$ nonisolated	Comparisons
Ameiva ameiva	4.324 ± 1.731 (14)	3.707 ± 1.958 (6)	$F_{(1,18)} = 0.496$, $P = 0.490$
	1.632 ± 0.258 (14)	1.605 ± 0.208 (6)	$F_{(1,18)} = 0.049$, $P = 0.827$
Cnemidophorus	4.006 ± 1.149 (5)	2.540 ± 0.808 (5)	$F_{(1,8)} = 5.444$, $\mathbf{P = 0.048}$
	1.606 ± 0.285 (5)	1.226 ± 0.243 (5)	$F_{(1,8)} = 5.141$, $P = 0.053$
Micrablepharus	2.398 ± 0.855 (4)	3.162 ± 0.837 (5)	$F_{(1,7)} = 1.821$, $P = 0.219$
	1.142 ± 0.148 (4)	0.990 ± 0.263 (5)	$F_{(1,7)} = 1.050$, $P = 0.340$
Anolis	3.419 ± 1.765 (7)	4.053 ± 1.053 (3)	$F_{(1,8)} = 0.324$, $P = 0.585$
	1.290 ± 0.364 (7)	1.014 ± 0.194 (3)	$F_{(1,8)} = 1.472$, $P = 0.260$
Tropidurus	3.818 ± 0.829 (5)	3.360 ± 0.949 (6)	$F_{(1,9)} = 0.421$, $P = 0.421$
	1.662 ± 0.278 (5)	1.333 ± 0.107 (6)	$F_{(1,9)} = 7.223$, $\mathbf{P = 0.025}$

Bold face indicates statistically significant differences, upper values are based on pooled means of stomachs and lower values are based on individual stomachs, and sample sizes are in parentheses

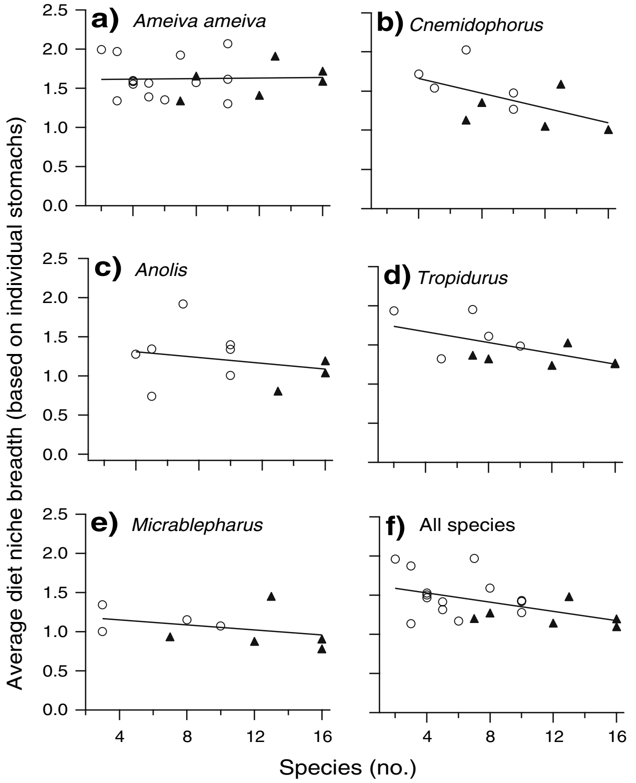

Fig. 3a–f Relationship between average diet niche breadths based on individual stomachs and number of species from isolated (*circles*) and nonisolated (*filled triangles*) Cerrado-like open vegetation habitats in Brazil for **a** *Ameiva ameiva* ($P = 0.878$, $r = 0.037$), **b** *Cnemidophorus* ($P = 0.096$, $r = 0.554$), **c** *Anolis* ($P = 0.504$, $r = 0.240$), **d** *Tropidurus* ($P = 0.053$, $r = 0.285$), **e** *Micrablepharus* ($P = 0.339$, $r = 0.361$) and **f** all species ($P = 0.036$, $r = 0.471$)

in any genus (Table 1). A significant negative correlation was obtained between number of species in assemblages and abundance of *Micrablepharus* ($P = 0.039$, $r = 0.834$) (Fig. 5). Our results indicate that the density compensation hypothesis does not appear to be applicable to Cerrado lizard assemblages, with lizard species being equally abundant in isolated and nonisolated areas.

Discussion

Species composition and microhabitat

The ecological release hypothesis predicts that on islands, where species diversity is lower, species should be more generalized (have wider niche breadths) than in continental areas where diversity is higher (Crowell 1962; MacArthur et al. 1972). The ecological release hypothesis has its roots in competition theory. It posits that, with reduced interspecific competition, species should expand their use of microhabitats in response to fewer competitors (Crowell 1962; Losos and de Queiroz 1997). The ecological release hypothesis was initially developed based on island–continent comparisons. We applied the model to nonisolated Cerrado areas (‘‘mainland’’) vs. isolated enclaves (‘‘islands’’) to test the hypothesis. Our prediction was that, if ecological release occurs in these areas, microhabitat niche breadths of lizards from isolated areas should be higher than in nonisolated areas. However, our results do not support these predictions. We found no difference in average microhabitat niche breadth between isolated vs. nonisolated areas, whether all species or only the most widespread genera (*Ameiva*, *Cnemidophorus*, *Anolis* and *Tropidurus*) are considered. Moreover, no significant correlation existed between microhabitat niche breadth and number of species in assemblages. Our results showed that ecological release in microhabitat niche breadth did not occur in these areas.

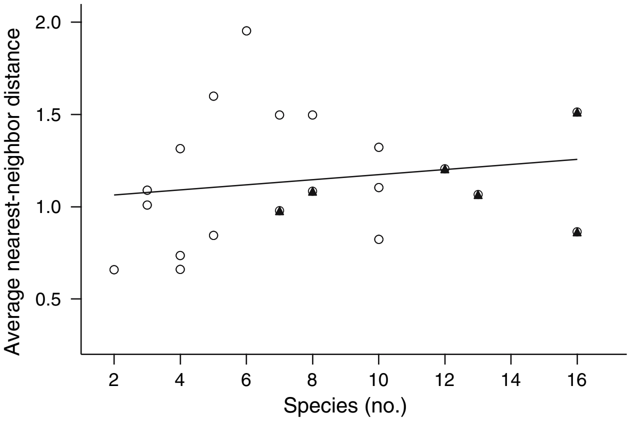

Fig. 4 Relationship ($P = 0.447$, $r = 0.169$) between average nearest neighbor Euclidean distance of log-transformed morphometrical data of lizards from isolated (*circles*) and nonisolated (*filled triangles*) Cerrado-like open vegetation habitats in Brazil and number of species of each assemblage

Ecological factors (e.g., competition and predation) have been considered the most important factors affecting relationships among species in assemblages (Diamond 1978; Dunham 1983; Wiens 1977; Wilbur 1972). More recently, history has been identified as a factor contributing to community structure, and if ignored, erroneous conclusions can result (Brooks and McLennan 1991; Cadle and Greene 1993; Losos 1994, 1996). Although we have no doubt that competition and predation influence assemblage structure (Case and Bolger 1991; Losos et al. 1993; Spiller and Schoener 1989), some ecological differences in assemblages have their roots deep in the evolutionary history of species (the ghost of competition past) (Connell 1980; Losos 1995; Vitt et al. 2003, 1999). The ecological release hypothesis maintains that ecological factors should be more important than history in determining assemblage structure, and this should be detectable as increases in

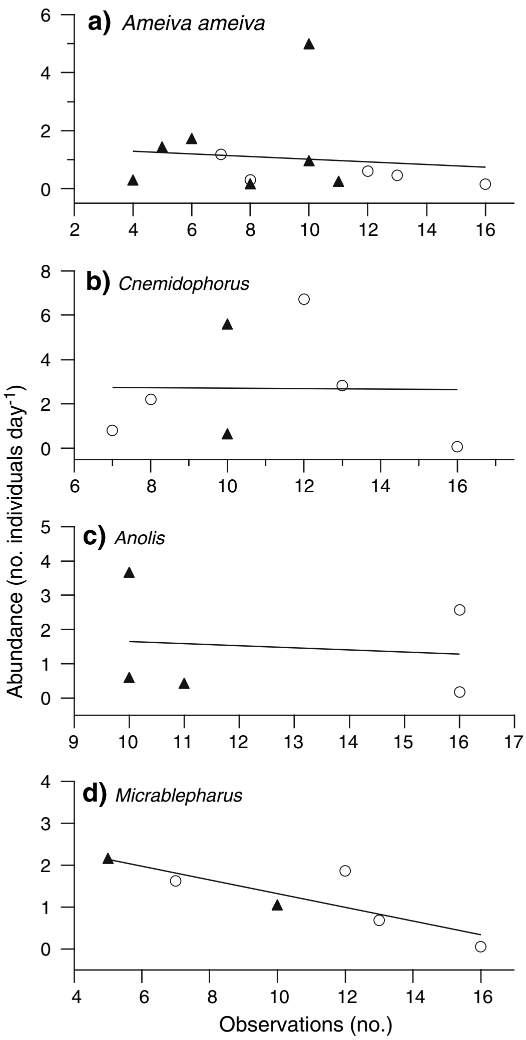

Fig. 5a–d Relationship between abundance (number of individuals per day) for lizards in the genera**:** **a** *Ameiva* ($P = 0.716$, $r = 0.118$), **b** *Cnemidophorus* ($P = 0.975$, $r = 0.015$), **c** *Anolis* ($P = 0.839$, $r = 0.127$) and **d** *Micrablepharus* ($P = 0.039$, $r = 0.834$) and number of species in each assemblage collected in 100 pitfall traps in several Cerrado-like open vegetation habitats in Brazil

density in isolated areas along with niche expansion. We were unable to support this. Lizard species are highly conservative in their ecological traits, and this is reflected in low variation among populations in niche breadth (see Mesquita and Colli 2003; Vitt and Colli 1994; Vitt et al. 1998), emphasizing the importance of the evolutionary history of species in assemblage structure.

Diet composition

Considering the ecological release hypothesis, the low number of species in isolated areas should promote reduced competition and consequently allow the species to eat a larger spectrum of prey, resulting in larger diet niche breadths (Crowell 1962; MacArthur et al. 1972). Our results partially support this hypothesis. The results based on pooled stomachs indicate that ecological release does not occur in these areas. However, based on individual stomachs, the ecological release hypothesis appears to be applicable for *Tropidurus*, but not *Ameiva ameiva*, *Anolis*, *Cnemidophorus*, and *Micrablepharus*.

Environmental pressures appear to promote differential evolutionary responses among different taxa. Our results indicate that *Ameiva ameiva*, *Cnemidophorus* (Teiidae), *Anolis* (Polychrotidae) and *Micrablepharus* (Gymnophthalmidae) are more conservative in diet. Comparisons among several populations from different assemblages, with different numbers of syntopic lizard species and differences in potential competitors and predators, show that the diets of these lizards do not vary considerably. Consequently, historical effects are stronger than ecological factors (e.g., Brooks and McLennan 1991; Losos 1994, 1996; Miles and Dunham 1993). Apparently, teiids, gymnophthalmids, and polychrotids are more conservative in diet than tropidurids. Teiids occur from Argentina up to the USA, gymnophthalmids occur throughout South America, extending north through most of Central America and reaching southern Mexico, and polychrotids occur from southeastern USA down to Central America and most of South America (Pough et al. 1998; Zug et al. 2001). Despite this wide distribution, ecological traits among species are conservative (see Mesquita and Colli 2003; Pianka 1970; Vitt et al. 1997b, 1998, 2001). On the other hand, tropidurids appear much more variable in their ecological traits. Closely related tropidurids from several populations in Brazil differ in diets and morphology in response to the use of different microhabitats (Vitt 1981, 1993; Vitt et al. 1997a). Our results suggest that different lineages show differential responses to environmental pressures; tropidurids were more affected by ecological factors than teiids, polychrotids and gymnophthalmids, corroborating previous results (see Mesquita and Colli 2003; Vitt 1993; Vitt et al. 1997a, 1997b), and they also suggest that both historical and ecological factors are important for maintaining assemblage structure.

Morphometry

The ecological release hypothesis predicts that in isolated areas, due to habitat expansion (see Crowell 1962; MacArthur et al. 1972), morphology of lizards should be more generalized than in nonisolated areas, and this should be reflected in a lower average neighbor Euclidean distance in isolated areas than in nonisolated areas (see Losos and de Queiroz 1997). However, in spite of differences in average neighbor Euclidean distance among assemblages, we detected no differences between isolated and nonisolated areas. Morphological data do not support the ecological release hypothesis. These conclusions are consistent with conclusions based on studies of *Anolis* lizards on Caribbean Islands (Losos and de Queiroz 1997). Our results suggest that morphology of lizards is very conservative among assemblages, and is barely affected by ecological factors, emphasizing the importance of the history of the species.

Abundance

Density compensation was described initially for birds (Case et al. 1079; Crowell 1962; MacArthur et al. 1972), but was also described for other taxa, like lizards (Case 1975; Rodda and Dean-Bradley 2002; Wright 1979), small mammals (Webb 1965), bats (Stevens and Willig 2000), and invertebrates (Dean and Ricklefs 1979; Faeth 1984; Faeth and Simberloff 1981; Janzen 1973).

The density compensation hypothesis is derived from competition theory and most explanations rest on the premise that, in simple assemblages, resources are more abundant, resulting in less competition when compared with mainland areas, thus permitting species to occur at higher densities (Crowell 1962; MacArthur et al. 1972). Several explanations not based on competition theory have been provided to explain the occurrence of density compensation in islands. The increase in animal populations could be related to predation and parasitism, which may be reduced in islands (Case 1975; Grant 1966; MacArthur et al. 1972; Rodda and Dean-Bradley 2002). Gene flow, which is restricted between islands and the mainland, could promote high levels of local adaptations, and consequently higher densities (Emlem 1978; Emlem 1979). The climate tends to be more moderate on islands too, affecting population size by increasing survivorship (Case 1975). Another explanation proposed to explain density compensation is the ‘‘fence’’ effect. Population density may be higher on islands because isolating mechanisms obstruct the escape of individuals that would otherwise emigrate (Emlem 1979; Krebs et al. 1969; MacArthur et al. 1972).

Our density data do not support the density compensation hypothesis. Species are not more abundant in isolated areas than in nonisolated areas. The density compensation hypothesis maintains that ecological factors should be more important than history, and this should be detectable as increases in density in isolated areas. However, lizard abundance was similar in isolated and nonisolated areas, showing that the low number of competitors and predators on islands do not promote density compensation, emphasizing the importance of the evolutionary history of species in assemblage structure.

Our results suggest that both historical and ecological factors are important for the maintenance of assemblage structure, and that different clades respond differently to environmental pressures, with tropidurids being more affected by ecological factors than teiids, polychrotids and gymnophthalmids. In the past, global changes in climate promoted the expansion of forest from north to south, and consequently the isolation of populations of open areas in Amazonia (Colli 1996, 2005). The lizard fauna entrapped in enclaves experienced stochastic extinctions, producing nonstructured assemblages with different species richnesses (usually low when compared with Cerrado mainland) (Gainsbury and Colli 2003). The low richness and the absence of closely related species promotes a low probability of competition, which is probably reflected in the failure to detect significant ecological release patterns. In addition, it is prudent to conclude that differential isolation times among areas could also influence extinction rates, thereby affecting competition levels and patterns of ecological release.

Acknowledgments We thank Alison Gainsbury, Adrian Garda, Ayrton Péres Jr., Cristiane Batista, Daniel Diniz, Frederico França, Gabriel Costa, Gustavo Vieira, Helga Wiederhecker, Janalee Caldwell, Kátia Colli, Mariana Zatz, and S. Balbino for help with the fieldwork. This work was supported by a doctorate fellowship from Coordenação de Aperfeiçoamento de Pessoal de Nível Superior-CAPES to DOM, a research fellowship from Conselho Nacional de Desenvolvimento Científico e Tecnológico-CNPq to GRC (# 302343/88-1). Programa Nacional de Diversidade Biológica-PRONABIO (project ‘‘Estrutura e dinâmica de isolados naturais e antrópicos de Cerrado: lições para biologia da conservação’’), Fundação o Boticário de Proteção à Natureza (project ‘‘Herpetofauna das savanas amazônicas: subsídios para sua preservação’’), and Conservation International do Brasil (project ‘‘Proposta de levantamento da herpetofauna da micro-região do Jalapão’’) funded the research. Portions of the project were conducted under the auspices of a National Science Foundation (USA) grant DEB-0415430. Any opinions, findings, and conclusions or recommendations expressed in this material are those of the author(s), and do not necessarily reflect the views of the National Science Foundation. We declare that the research performed in the present manuscript comply with the current laws of Brazil.

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