

Local richness and distribution of the lizard fauna in natural habitat mosaics of the Brazilian Cerrado

CRISTIANO NOGUEIRA,^{1*} GUARINO R. COLLI² AND MARCIO MARTINS³

¹*Programa de Pós-graduação em Ecologia,* ³*Departamento de Ecologia, Instituto de Biociências, Universidade de São Paulo, São Paulo,* ²*Departamento de Zoologia, Universidade de Brasília, Brasília, Brazil*

Abstract We investigate local lizard richness and distribution in central Brazilian Cerrado, harbouring one of the least studied herpetofaunas in the Neotropical region. Our results are based on standardized samplings at 10 localities, involving 2917 captures of 57 lizard species in 10 families. Local richness values exceeded most presented in earlier studies and varied from 13 to 28 species, with modal values between 19 and 28 species. Most of the Cerrado lizard fauna is composed of habitat-specialists with patchy distributions in the mosaic of grasslands, savannas and forests, resulting in habitat-structured lizard assemblages. Faunal overlap between open and forested habitats is limited, and forested and open areas may act as mutual barriers to lizard distribution. Habitat use is influenced by niche conservatism in deep lineages, with iguanians and gekkotans showing higher use of forested habitats, whereas autarchoglossans are richer and more abundant in open habitats. Contrary to trends observed in Cerrado birds and large mammals, lizard richness is significantly higher in open, interfluvial habitats that dominate the Cerrado landscape. Between-localities variation in lizard richness seems tied to geographical distance, landscape history and phylogenetic constraints, factors operating in other well-studied lizard faunas in open environments. Higher richness in dominant, open interfluvial habitats may be recurrent in Squamata and other small-bodied vertebrates, posing a threat to conservation as these habitats are most vulnerable to the fast, widespread and ongoing process of habitat destruction in central Brazil.

Key words: biodiversity, Cerrado, lizards, habitat use, squamate reptiles.

INTRODUCTION

Open habitats, including savannas, deserts and semi-arid regions, are recognized for their rich lizard faunas, favoured by the ability of ectotherms to reduce activity and metabolic costs during stress periods in unpredictable or highly seasonal environments (Pianka 1986; Morton & James 1988). Lizard richness peaks in Australian arid regions, where a single locality may harbour more than 50 species (Pianka 1996). Variations in richness among independently evolved lizard faunas in tropical open areas are well-documented around the globe, but remain far from completely understood (Morton & James 1988; Pianka 1989). Such patterns, in ecologically comparable independent sites, have provided a fertile debate on the determinants of diversity, and the many proposed hypotheses rely on variables acting at different temporal and spatial scales (see Pianka 1989), including habitat horizontal stratification and habitat specificity

(Pianka 1966, 1969), differences in composition of potential competitors and predators, or the 'niche usurpation' hypothesis (Pianka 1969, 1973), and biogeographical and phylogenetic factors related to the history of landscapes and species pools (Pianka 1989; Vitt & Pianka 2005).

The central Brazilian Cerrado region, originally covering at least 12% of South America (Oliveira-Filho & Ratter 2002) is the second largest Neotropical biome and a unique savanna hotspot (Myers *et al.* 2000; Mittermeier *et al.* 2004). Although clearly not a desert or semi-arid region, the Cerrado shares general ecological similarities with open areas in Australia, Africa and North America (see broad comparisons in Colli *et al.* 2002), including the dominance of an open, mostly savanna-like vegetation, impoverished soils, frequent action of natural wildfires and prominently horizontal (instead of vertical) stratification. Although lizard faunas from Australian, African and North American open areas are relatively well studied (see Morton & James 1988; Pianka 1989), conflicting interpretations still permeate the literature on even the most basic aspects of richness and composition of lizard assemblages in the Cerrado (Colli *et al.* 2002).

As indicated by Colli *et al.* (2002), most previous studies on Cerrado lizard diversity have described

*Corresponding author. Present address: Conservation International, Cerrado Program, SAUS Qd. 3 Lt. 2 Bl. C Ed. Business Point Sala 715-722. CEP 70070-934 Brasília, DF, Brazil (Email c.nogueira@conservation.org.br)

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poor assemblages (Vanzolini 1948, 1976, 1988; Vitt 1991; Vitt & Caldwell, 1993) dominated by habitat-generalist species, shared with the semi-arid Caatinga (Vanzolini 1963, 1976, 1988). Nevertheless, new data and interpretations describe the Cerrado lizard fauna as formed by complex, rich and characteristic assemblages, dominated by species tightly associated to specific microhabitats (Gainsbury & Colli 2003; Mesquita *et al.* 2006) unevenly distributed in habitat mosaics (Colli *et al.* 2002; Nogueira *et al.* 2005). Regardless of recorded lizard richness, habitat diversity probably plays a major role in determining local diversity in Cerrado (Colli *et al.* 2002; Nogueira *et al.* 2005), as already documented for birds (Silva 1997; Silva & Bates 2002) and mammals (Redford & Fonseca 1986; Mares & Ernest 1995; Johnson *et al.* 1999).

Herein we present results of standardized surveys of the lizard fauna in 10 localities throughout the Cerrado region (Fig. 1), to provide comparable data on local richness, distribution and diversity. The main goal of our study was to provide rigorous comparisons of species richness and abundance patterns among different Cerrado localities, as baseline data for analyzing the effects of local habitat heterogeneity, large scale environmental variables and phylogenetic effects on lizard richness and composition. Central questions in our study were: (i) How many lizard species are sympatric in Cerrado localities and how many are syntopic in the major habitat types? (ii) Are habitat-generalist species dominant in Cerrado lizard faunas, as proposed in earlier studies? (iii) Are forested habitats richer than open habitats throughout the Cerrado, as documented for birds and mammals? (iv) Is faunal overlap between forested and open areas significant or can these two habitat types be considered as local barriers for lizards? (v) Are habitat requirements uniform among lizards in major squamate clades in the Cerrado? (vi) What are the effects of local and large-scale environmental variables on lizard richness, abundance and local distribution? (vii) How richness and local distribution patterns of Cerrado lizards compare with those in other open regions of the globe, and how can these local Cerrado patterns help in explaining richness variation across tropical open areas?

METHODS

Field sampling

The limits of the Cerrado region were defined according to IBGE (1993), as in previous studies (Silva 1995). We sampled 10 localities (Fig. 1; Table 1), including poorly sampled regions and localities. Sampling methods were standardized in all localities, restricted to a maximum 50-km radius (785.000 ha), originating from a central collecting point (generally the main

lodge). Except for two long-term samplings, (AACR (Área Alfa Cerrado reserve), six field trips from October 1999 to February 2002, Nogueira *et al.* 2005); ENP (Emas National Park), September 2001 to February 2002), all fieldwork took place during intensive field samplings, concentrated from October to May, in the rainy season (Uruçuí-una Ecological Station (UUES) February-March 2000; Grande Sertão Veredas National Park (GSVNP) October-November 2001; SBO (Serra da Bodoquena region) April to May 2002; URT (Upper Rio Taquari) April to May 2002; Serra das Araras Ecological Station (SAES) October 2002; Águas de Santa Bárbara Ecological Station (ASBES) January-February 2003; Serra Geral do Tocantins Ecological Station (SGTES) March-April 2003; Serra da Canastra National Park (SCNP) November-December 2004).

In each locality we surveyed lizards in at least one patch of cerrado grasslands, cerrado savannas and forests, the three main Cerrado habitat types (see Oliveira-Filho & Ratter 2002; Nogueira *et al.* 2005). The only exception was SBO, where no native grassland area was accessible. Briefly described, natural Cerrado habitats include completely open grasslands with few or no trees and shrubs (*campo limpo*), open grasslands with scattered shrubs (*campo sujo*), open grasslands with scattered shrubs and trees (*campo cerrado*), semi-closed savannas with shrubs and trees (*cerrado sensu stricto*, in a three-layered savanna) and woodlands dominated by a layer of trees and few or no grasses and shrubs (*cerradão* and *carrasco*). The denser habitat types include gallery and mesophytic forests, with a closed canopy and shaded, relatively sparse understory. Sampled grassland habitats included *campo limpo*, *campo sujo* and *campo cerrado*, whereas sampled cerrado savannas included *cerrado sensu stricto*, *carrasco* and *cerrado rupestre* (cerrados on rocky outcrops). Finally, sampled forested habitats included *cerradão*, gallery forest and mesophytic forest.

We collected lizards using haphazard searches and pitfall traps with drift fences (PTDFs, see Nogueira *et al.* 2005). We used a variety of methods for capturing lizards in haphazard searches, including noosing, shooting with an air-compressed rifle, inspecting shelters under fallen logs and termite mounds and opportunistic encounters. Haphazard sampling took place mostly in the morning (9–12 h), in the same habitat patches sampled with PTDFs. Each PTDF consisted of an array of four 35 l buckets buried at ground level, one at the centre and three radiating from, and connected to, the central bucket by a 5 m long \times 0.5 m high plastic fence, forming 120° angles (see Nogueira *et al.* 2005). In each habitat patch, we placed 5 to 10 PTDFs, 15 m apart from each other, along linear transects through homogeneous, undisturbed areas. In each locality, we installed 30–70 PTDFs, which were checked daily. The number of PTDFs per habitat patch was the same for a

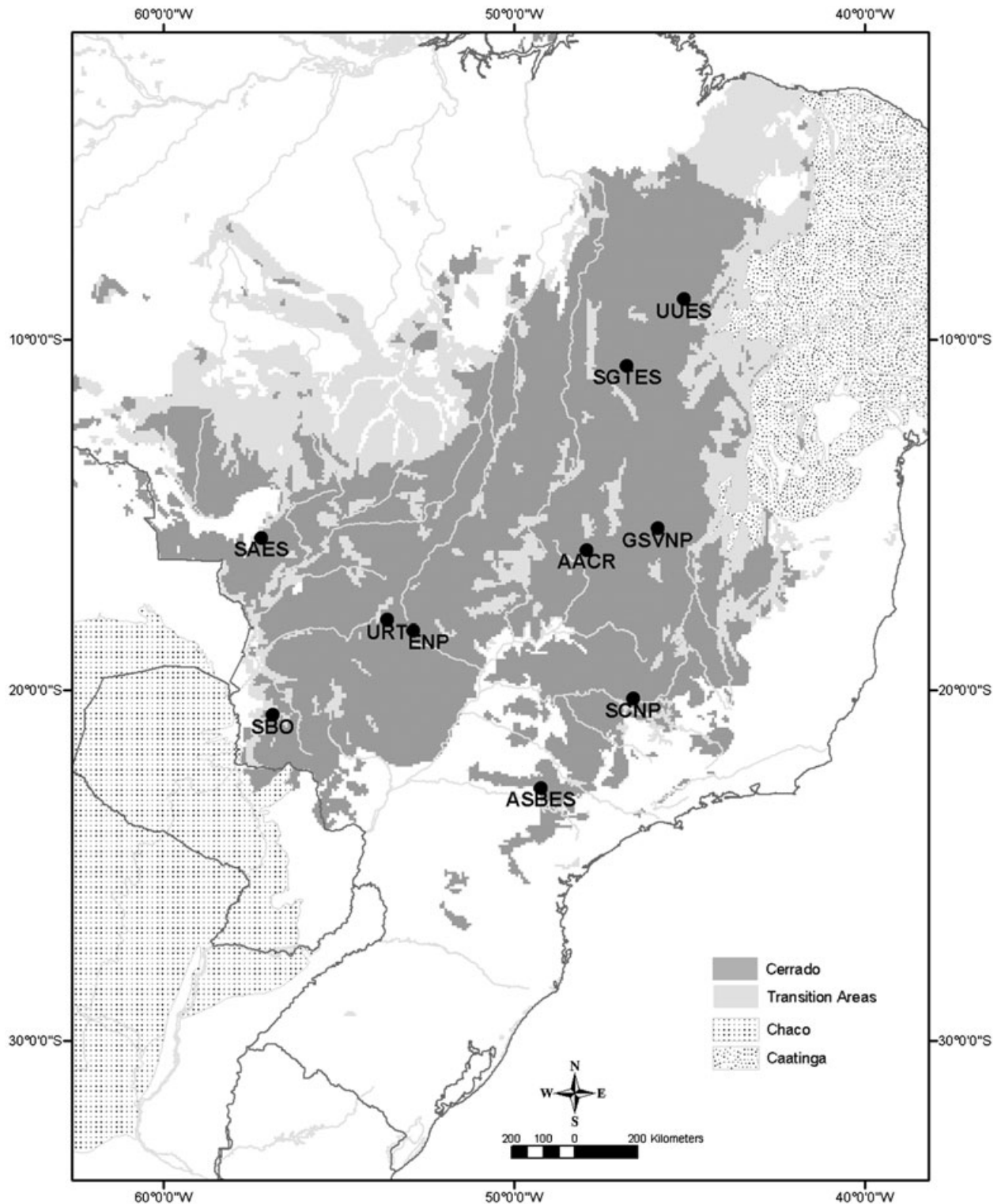


Fig. 1. Sampled localities within the Cerrado. AACR, Área Alfa Cerrado reserve; ASBES, Águas de Santa Bárbara Ecological Station; ENP, Emas National Park; GSVNP, Grande Sertão Veredas National Park; SAES, Serra das Araras Ecological Station; SBO, Serra da Bodoquena region; SCNP, Serra da Canastra National Park; SGTES, Serra Geral do Tocantins Ecological Station; URT, Upper Rio Taquari; UUES, Uruçuí-una Ecological Station. Cerrado region adapted from IBGE (1993).

Table 1. Elevation, dominant habitat patches and sampled habitat patches in each of the 10 localities studied in the Cerrado

| Locality | Mean Altitude (m) | Altitudinal Gradient (m) | Number of habitat patches/SUs | Main habitat type and sampled habitat patches |
|----------|-------------------|--------------------------|-------------------------------|---|
| AACR | 1114 | 5 | 3/6 | GR: csu (2); CE: cer (2); FO: gfo (2) |
| ASBES | 634 | 18 | 4/5 | GR: cli, csu; CE: cer; FO: gfo (2) |
| ENP | 805 | 48 | 5/6 | GR: cli, csu (2); CE: cer; FO: cao, gfo |
| GSVNP | 774 | 77 | 5/5 | GR: csu (2), cli; CE: cer, car; FO: gfo |
| SAES | 288 | 3 | 4/5 | GR: cli (2); CE: cer; FO: cao; mfo |
| SBO | 614 | 302 | 4/6 | CE: cer (2); FO: cao, mfo, gfo (2) |
| SCNP | 1339 | 75 | 4/6 | GR: cli (3), cce; CE: cer; FO: gfo |
| SGTES | 487 | 82 | 6/6 | GR: cli (2), cce; CE: cer, cru; FO: gfo |
| URT | 336 | 17 | 4/6 | GR: csu; CE: cer (3); FO: cao, gfo |
| UUES | 433 | 222 | 5/6 | GR: csu (2); CE: cer, car; FO: mfo, gfo |

Main habitat types are referred as GR, grasslands; CE, cerrado; FO, Forests. Habitat patches abbreviations: cao, *cerradão*; car, *carrasco*; cce, *campo cerrado*; cer, *cerrado sensu strictu*; cli, *campo limpo*; cru, *cerrado rupestre*; csu, *campo sujo*; gfo, gallery forest; mfo, mesophytic forests. Numbers in parentheses refer to the number of independent sampling units placed per habitat patch. AACR, Área Alfa Cerrado reserve; ASBES, Águas de Santa Bárbara Ecological Station; ENP, Emas National Park; GSVNP, Grande Sertão Veredas National Park; SAES, Serra das Araras Ecological Station; SBO, Serra da Bodoquena region; SCNP, Serra da Canastra National Park; SGTES, Serra Geral do Tocantins Ecological Station; SU, sampling units; URT, Upper Rio Taquari; UUES, Urucuí-una Ecological Station.

given locality, but we varied this number across localities (Table 1) according to the number of available and accessible natural habitat patches, sampling the largest possible amount of habitat variation.

In each locality, each sampling day included 30–70 PTDFs and 10 min of haphazard search for each 10 PTDFs (e.g. 30 min of daily search for 30 PTDFs). We standardized sampling effort by adopting 10 PTDFs coupled with 10 min of visual search as the basic field effort unit. We calculated the number of field effort units in each locality by multiplying the total number of PTDFs by the total number of days and dividing this total by 10. After a series of specimens (approximately 10) was collected, individuals of abundant species were marked by toe clipping and released at the capture site. Recaptured lizards were not included in analyses. Lizard specimens were deposited at Museu de Zoologia da Universidade de São Paulo (MZUSP), with some additional specimens housed at Coleção Herpetológica da Universidade de Brasília (CHUNB).

We included in each species list all records within the 50-km radius study area, previously deposited in herpetological collections, and hereafter we refer to the pooled number of species in each locality as ‘total richness’. All species identities of museum specimens used in this study were checked and confirmed, via direct analysis of voucher specimens housed at MZUSP and CHUNB. To properly decide which records to include in each locality, we mapped lizard distributions (according to MZUSP, CHUNB and literature data) and selected those recorded within 50-km buffer zones around each central collecting point, using standard GIS procedures.

Analyses

To evaluate sampling effort, compare sampling results, and estimate species richness, we produced individual-based rarefaction curves (Gotelli & Colwell 2001) for each locality, based on combined PTDF and haphazard samplings, using the Species Diversity module of EcoSim v. 7.58 (Gotelli & Entsminger 2005). We estimated richness, including species not recorded in any sample, mostly with non-parametric estimators (Colwell & Coddington 1994), often more accurate than the alternative curve-fitting methods (Brose *et al.* 2003; Walther & Moore 2005), based on rarefaction curves derived from 1000 randomizations of the original sampling order, without replacement, using EstimateS 7.5 (Colwell 2005). We evaluated estimator performance by regressing mean estimated values with total richness (adapted from Brose *et al.* 2003). We measured estimator precision as the r^2 value of regressions (Brose *et al.* 2003), with estimator bias measured as Scaled Mean Error (SME, see Walther & Moore 2005). All between-localities comparisons were made using data obtained in standardized field samplings, with non-standardized museum data used for evaluating estimator performance and for adding data on rare and patchily distributed species.

To describe patterns of local abundance, we calculated capture rates for each species in each major habitat type (Habitat Capture Rates (HCR)) as the number of PTDF captures divided by the total PTDF sampling effort in each habitat type (grassland, savanna, or forest), considering only localities where the species was captured. We also calculated

percentage of habitat capture rates (%HCR) for each species in each habitat type, dividing HCR by the sum of the three HCR values for that species. We also calculated %HCR for each of the three main lizard clades (Iguania, Gekkota and Autarchoglossa, cf. Estes *et al.* 1988), as the sum of %HCRs for all members of a clade in a given habitat type divided by the sum of all %HCRs in that clade. To test for non-random differences in habitat use among major lizard clades, we performed MANOVA on %HCR results per species (arcsin transformed, see Losos *et al.* 1998), with lizard clade as the independent variable. For this analysis, we excluded species with less than five captures.

We studied lizard co-occurrence patterns in different habitats with null model analysis of 5000 randomizations of original samples (presence/absence matrix for different sampling units, PTDF plus haphazard sampling) within each locality, using the *C*-score index and EcoSim v. 7.58 (Gotelli & Entsminger 2005). The *C*-score index is a measure of the number of mutually exclusive species in any two given sampling units and, if this index is higher than expected by chance, we consider the local community significantly (non-randomly) structured in relation to habitat use, with mutual exclusion either determined by ecological interactions (e.g. competitive exclusion) or historical differences in habitat requirements (Gotelli *et al.* 1997; Gainsbury & Colli 2003; Nogueira *et al.* 2005).

We investigated the effects of 11 environmental variables (latitude, longitude, soil type, vegetation type, altitude, length of dry season, mean annual temperature, annual rainfall, number of habitats, topography and distance from water bodies) on lizard abundances in each habitat type in each locality (total of 51 habitat samples, SCNP (Serra da Canas-

tra National Park) samples excluded because of unusual low capture rates), using canonical correspondence analysis (CCA). We implemented CCA on CANOCO for Windows v. 4.51 (ter Braak & Smilauer 2002), with manual selection of environmental variables, tested under 9999 permutations in Monte Carlo test, inter-species distance and biplot scaling and downweighting of rare species (similar procedures in Vitt & Pianka 2005). Environmental variables form a sub-sample of those used in a similar analysis of lepidopteran diversity in the Cerrado and were coded accordingly (Brown & Gifford 2002), except for vegetation type (coded as 1 – grasslands, 2 – cerrado savannas, 3 – forests). We also included a new variable, distance to water (1 – interflaves, 2 – riparian habitats). Data for all sample units were obtained in the field, with information on length of the dry season, mean annual temperature and annual rainfall obtained in RADAMBRASIL (1982–1983).

RESULTS

After 504 field days and a total sampling of 1971 field effort units, corresponding to 19 530 PTDF-days plus 325.5 h of visual search, we captured 2917 individuals of 51 lizard species. Six additional species were only recorded in herpetological collections, totaling 57 lizard species (Table 2, Online Appendix, <http://www.ecolsoc.org.au/What%20we%20do/Publications/Austral%20Ecology/AE.html>) in the 10 studied localities. Out of the 39 species recorded in PTDFs, 28 (49% of total richness) were also captured with haphazard sampling, with the remaining 11 (19%) obtained only in PTDFs. Twelve other species (21% of total richness) were obtained only with haphazard sampling.

Table 2. Sampling effort in trap-search days (10 min search for each 40 traps × days), number of captures, capture rates and richness values for all localities studied

| Locality | Field effort units | Traps × days | Search hours | Captures (PTDF + hand) | Capture rates PTDF (%) | Field richness (PTDF + hand) | Total richness (field + museum) |
|----------|--------------------|--------------|--------------|------------------------|------------------------|------------------------------|---------------------------------|
| AACR | 777 | 30 × 259 | 129.5 | 232 (223 + 9) | 0.72 | 18 (16 + 2) | 28 (18 + 10) |
| ASBES | 85 | 50 × 17 | 14.2 | 73 (71 + 2) | 2.09 | 09 (8 + 1) | 15 (9 + 6) |
| ENP | 360 | 36 × 100 | 60.0 | 574 (544 + 30) | 3.78 | 18 (14 + 6) | 24 (18 + 6) |
| GSVNP | 85 | 50 × 17 | 14.2 | 186 (180 + 6) | 5.29 | 19 (15 + 4) | 25 (19 + 6) |
| SAES | 100 | 50 × 20 | 16.7 | 249 (230 + 19) | 5.75 | 16 (13 + 3) | 25 (16 + 9) |
| SBO | 144 | 60 × 24 | 24.0 | 144 (135 + 9) | 2.34 | 13 (10 + 3) | 19 (13 + 6) |
| SCNP | 102 | 60 × 17 | 17.0 | 52 (7 + 45) | 0.17 | 12 (4 + 8) | 13 (12 + 1) |
| SGTES | 90 | 60 × 15 | 15.0 | 490 (470 + 20) | 13.06 | 14 (9 + 5) | 22 (14 + 8) |
| URT | 102 | 60 × 17 | 17.0 | 450 (438 + 12) | 10.74 | 20 (17 + 3) | 20 (20 + 0) |
| UUES | 108 | 70 × 18 | 21.0 | 467 (406 + 61) | 9.40 | 18 (8 + 10) | 19 (18 + 1) |
| Totals | 1953 | 19 530 | 325.5 | 2917 (2704 + 213) | 3.46 | 51 (39 + 12) | 57 (51 + 6) |

Field richness refers to species collected in the field, either in pitfall with drift fences or hand captures. Total richness includes field samplings + museum and literature records. PTDF, pitfall traps with drift fence.

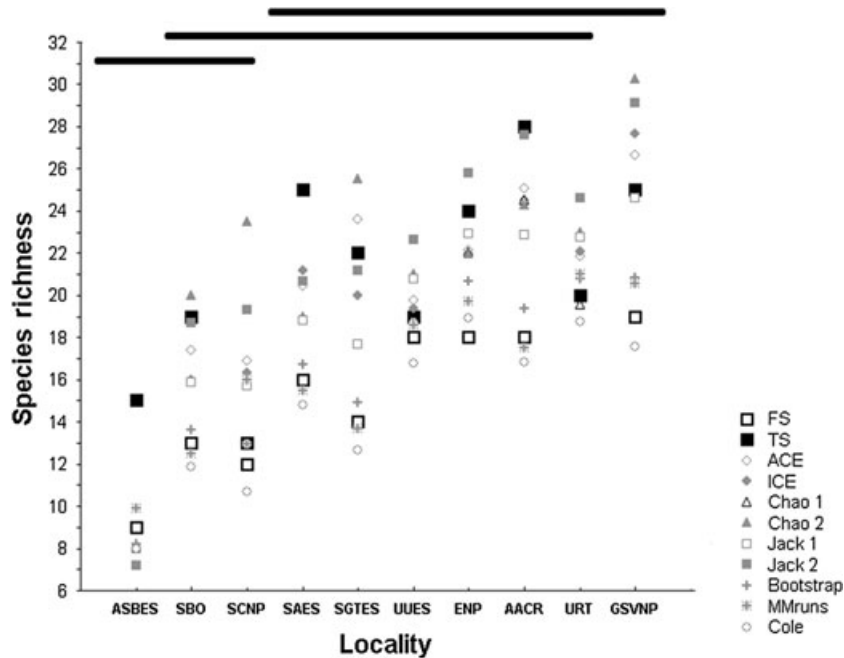


Fig. 2. Comparison of richness values among the ten studied localities, based on empirical data (FS, field richness and TS, total richness; see text for details) and estimated richness values (ACE, ICE, Chao 1, Chao 2, Jackknife 1, Jackknife 2, Bootstrap, MM runs and Coleman) obtained by rarefaction in 1000 randomizations of the original samples in EstimateS (Colwell 2005). Richness differences among localities were significant (Kruskal–Wallis ANOVA: $H_9 = 56.80$; $P < 0.001$), with statistically similar values linked by horizontal bars.

Lizard richness in Cerrado localities

Total richness values (TS, including literature and museum records) ranged from 13 to 28 species, being similar (Kruskal–Wallis, $H_1 = 0.7$; $P = 0.39$, $n = 39$) to those presented for 25 Neotropical forest sites with variable areas and sampling methods (Silva & Sites 1995; Vitt 1996), and additional Cerrado sites obtained in Colli *et al.* (2002). Three different levels of richness could be detected as the result of richness comparisons among localities (Fig. 2). An intermediary level grouped most localities, with richness ranging from 19 to 28 species. A single locality stood out as the poorest site (TS = 15, Águas de Santa Bárbara Ecological Station (ASBES)) in the peripheral, southernmost part of the Cerrado, and another single locality, Grande Sertão Veredas National Park (GSVNP), stood out as the richest site (TS = 25, estimated richness up to 30 species).

In most localities, rarefaction curves were past the inflection point after 100–150 individuals captured (Fig. 3). However, the shape and extension of curves varied among localities and depended heavily on number of captures, regardless of sampling effort, as we found no significant relationship between sampling effort and number of captures ($r = 0.10$; $t_8 = 0.28$; $P = 0.78$), field richness (FS) ($r = 0.33$; $t_8 = 1.01$; $P = 0.34$) or TS ($r = 0.40$; $t_8 = 1.24$; $P = 0.24$).

However, significant positive relationships were found between TS and estimated richness values (Table 3), that ranged from 7 to 30 species (Fig. 2). Most richness estimators returned values between FS and TS (Fig. 2). We found significant differences in richness values (including FS, TS and estimated values) among localities (Kruskal–Wallis: $H_9 = 56.80$; $P < 0.001$; $n = 110$), grouped in three main richness levels, according to significant richness differences (see Fig. 2).

Habitat specialization and lizard richness patterns

According to capture rates in PTDFs, most species were more abundant in open habitats, with 12 species restricted to open areas and five restricted to forests (Fig. 4). Richness values in sampling units located in both types of open habitats (cerrado grasslands + cerrado savannas) were significantly higher than those in forested habitats (Kruskal–Wallis, $H_2 = 15.5$; $P < 0.001$; $n = 52$; Tukey *post hoc* test: $P < 0.01$ for both $GR \times FO$ and $CE \times FO$, GR, grasslands; CE, cerrado; FO, Forests; Fig. 5). Lizard local distribution (among different habitats) was significantly structured, non-random, in 6 out of 10 localities (Table 4).

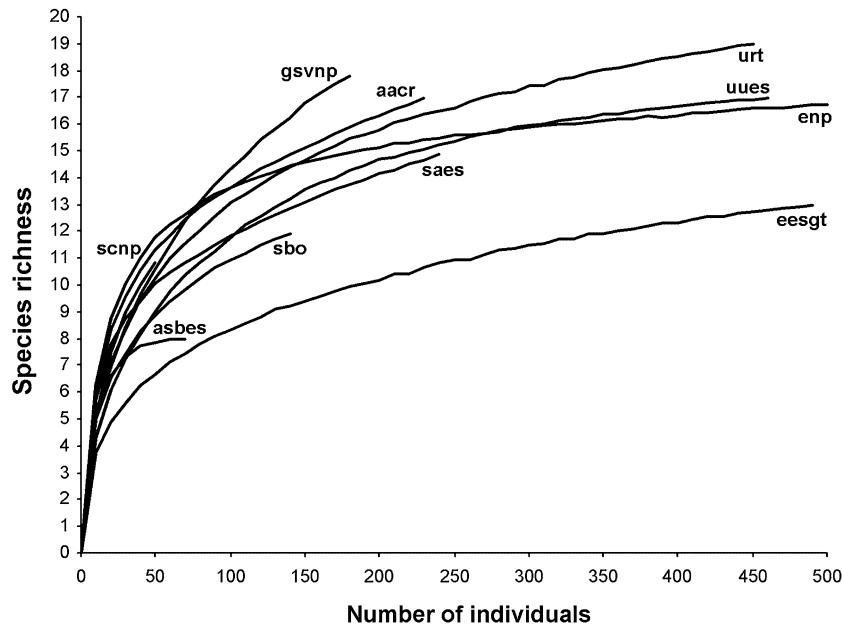


Fig. 3. Individual-based rarefaction curves (Gotelli & Colwell 2001) for each of the 10 sampled localities, obtained in EcoSim (Gotelli & Entsminger 2005), from 1000 randomizations of the original field samples. Locality abbreviations as in Fig. 1.

Table 3. Comparison of richness estimates obtained by number of species in field samples (Field S) and non-parametric richness estimators, based on 1000 randomizations of original field data in EstimateS v.7.5.0 (Colwell 2005)

| Estimator | Precision(r^2) | P | SME |
|-----------|--------------------|--------|--------|
| Field S | 0.794 | <0.001 | -0.242 |
| ACE | 0.839 | <0.001 | -0.035 |
| ICE | 0.842 | <0.001 | -0.059 |
| Chao1 | 0.654 | <0.005 | 0.040 |
| Chao2 | 0.647 | <0.005 | 0.056 |
| Jack 1 | 0.795 | <0.001 | -0.088 |
| Jack 2 | 0.777 | <0.001 | 0.039 |
| Bootstrap | 0.79 | <0.001 | -0.199 |
| MMruns | 0.664 | <0.005 | -0.192 |
| Cole | 0.779 | <0.001 | -0.294 |
| Total S | - | - | - |

Precision values for richness estimates measured by the regression coefficient between estimated values and total richness (Total S, field + museum and literature data), with SME as a measure of bias (see text for details). SME, scaled mean error.

Faunal overlap between different habitat types and natural barriers for dispersion

Mean faunal overlap (Jaccard index) among sampling units located in open habitats was significantly higher than that between open and forested habitats (Fig. 6). Overlap between forested and open habitats is thus relatively low, with few species being shared between these major habitat types. The lowest values of faunal

Table 4. Results of the null-model analysis on habitat use, using C -score index in the 10 studied lizard communities (see text for abbreviations)

| Locality | Observed C -score | Mean simulated C -score | P (observed > simulated) |
|----------|---------------------|---------------------------|----------------------------|
| AACR | 1.80 | 1.54 | <0.0001 |
| ASBES | 0.64 | 0.46 | 0.066 |
| ENP | 1.04 | 0.92 | 0.002 |
| GSVNP | 1.08 | 1.09 | 0.619 |
| SAES | 0.44 | 0.39 | 0.045 |
| SBO | 1.95 | 1.97 | 0.599 |
| SCNP | 1.50 | 1.59 | 1.000 |
| SGTES | 0.72 | 0.44 | 0.036 |
| URT | 1.87 | 1.76 | 0.017 |
| UUES | 1.94 | 1.72 | 0.031 |

Bold values refer to localities where local distribution among sampling units (placed in different habitat types) is significantly structured, non-random.

overlap were found between forests and grasslands, two extremes in terms of habitat structure in the Cerrado.

Habitat use in lizards from three major squamate clades

Capture rates in PTDFs varied according to major squamate clade, with Iguania and Gekkota showing higher percentages of capture rates in forested habitats, whereas capture rates of Autarchoglossa

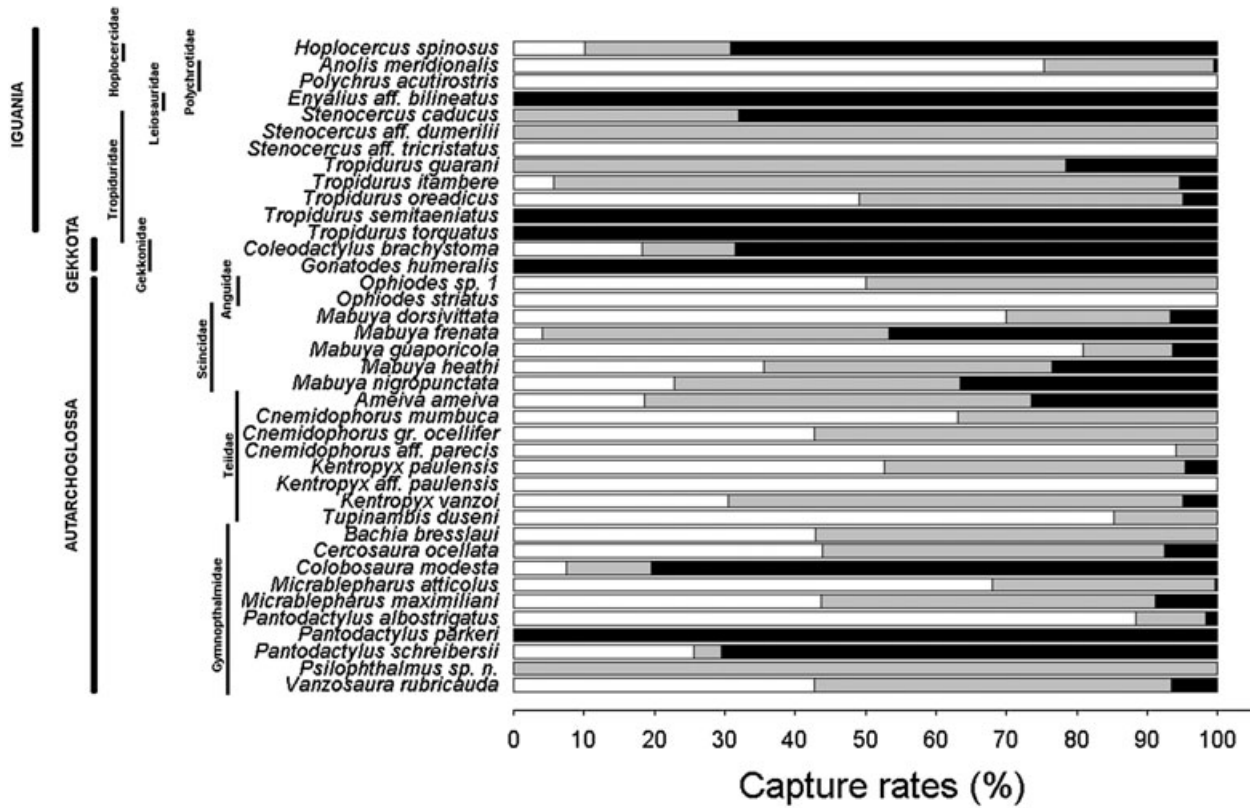


Fig. 4. Percentage of capture rates in each habitat type, in pitfall with drift fences samplings in 10 Cerrado localities. White bars = grasslands; grey = cerrado; black = forests. The three main lizard clades are indicated by vertical bars.

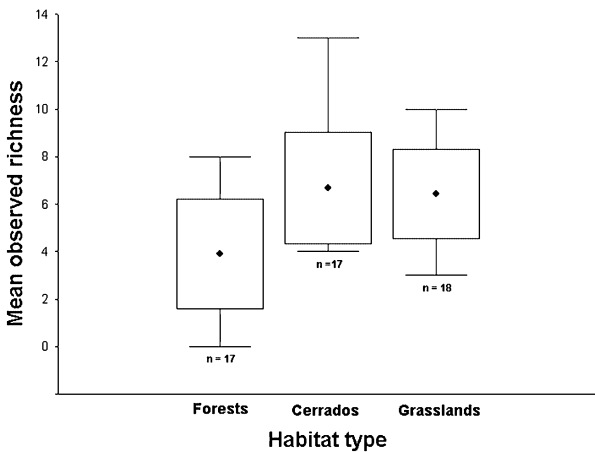


Fig. 5. Mean lizard richness in 52 sampling units in 10 Cerrado localities. Mean richness in open habitat patches (grasslands and typical cerrado) is similar, and higher than that found in forested habitat patches (Kruskal–Wallis, $H_2 = 15.5$; $P < 0.001$; Tukey *post hoc* test: $P < 0.01$ for both GR \times FO and CE \times FO). Point = mean, box = SD, lines = range. GR, grasslands; CE, cerrado; FO, Forests.

were higher in grasslands (Fig. 7). A MANOVA on percentages of habitat capture rates revealed significant abundance differences between Autarchoglossa and remaining clades (Gekkota represent-

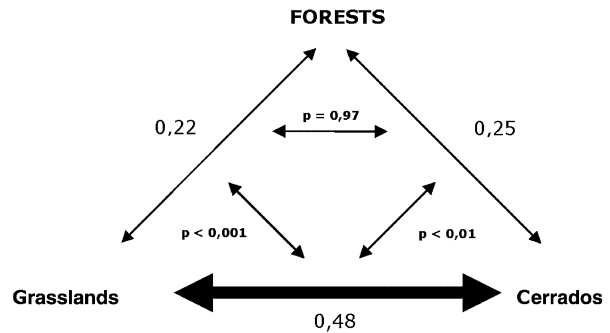


Fig. 6. Comparison of faunal overlap values (Jaccard index) among 52 sample units in three main habitat types in 10 Cerrado localities. Mean overlap values are significantly different (ANOVA, $F_{2,93} = 11.28$; $P < 0.01$), with mean overlap values between grassland and cerrado (0.48) significantly higher than that between cerrado and forest (0.25; Tukey HSD (honestly significant difference); $P < 0.01$) and between grasslands and forests (0.22; Tukey HSD; $P < 0.001$).

ed by a single species with more than five captures in PTDF) in the three main habitat types of Cerrado (Wilks’s Lambda = 0.65; $P = 0.01$). Moreover, the number of species more abundant in open habitats (see Fig. 5) was significantly higher in Autarchoglossa, as compared with combined Gekkota and Iguania (Fisher exact test, $P = 0.02$).

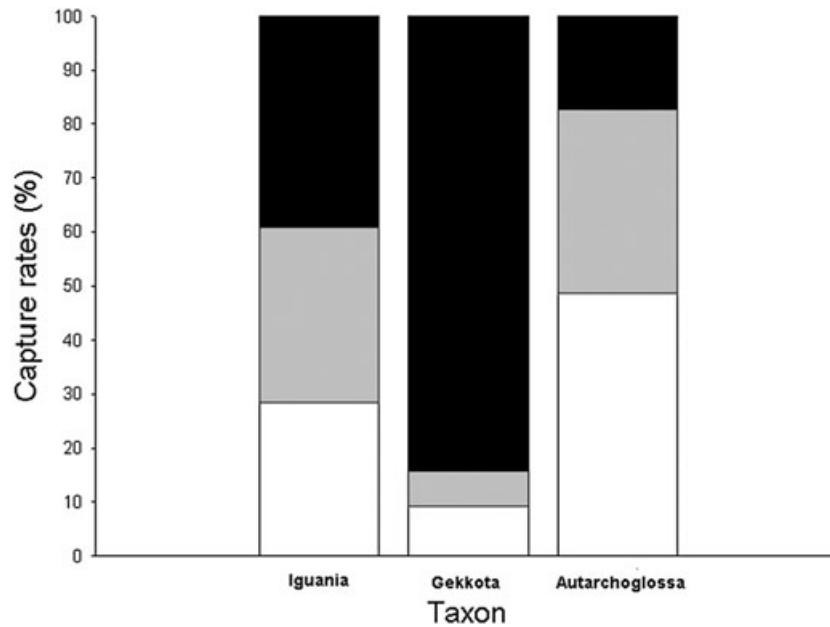


Fig. 7. Percentage of capture rates in each of the three main lizard clades, according to pitfall with drift fences capture rates per species, in 10 Cerrado localities. White bars = grasslands; grey = cerrado; black = forests.

Table 5. Results of the Canonical Correspondence Analysis (CCA) on environmental variables and capture rates per species, in 51 pitfall traps with drift fences sampling units in 10 Cerrado localities. ni = not included in the model ($P > 0.05$)

| | Cumulative Variation | Cumulative Variation (%) | <i>F</i> | <i>P</i> | Axis 1 | Axis 2 |
|----------------------------------|----------------------|--------------------------|----------|--------------|---------|---------|
| Latitude (lat) | 0.63 | 22% | 5.49 | 0.001 | 0.9044 | -0.0832 |
| Soil type (sol) | 0.97 | 35% | 3.15 | 0.001 | 0.5004 | -0.3572 |
| Vegetation type (veg) | 1.28 | 46% | 2.91 | 0.001 | 0.1989 | 0.5923 |
| Longitude (long) | 1.55 | 55% | 2.66 | 0.001 | 0.8317 | 0.0534 |
| Altitude (alt) | 1.77 | 63% | 2.24 | 0.003 | 0.1135 | 0.0525 |
| Length of dry season (dry) | 2.01 | 72% | 2.59 | 0.002 | -0.7751 | 0.1437 |
| Temperature (temp) | 2.21 | 79% | 2.12 | 0.012 | -0.7532 | 0.3699 |
| Rainfall (plu) | 2.43 | 87% | 2.39 | 0.004 | 0.8751 | -0.2065 |
| Number of habitats (vegmos) | ni | ni | ni | >0.05 | ni | ni |
| Topography | ni | ni | ni | >0.05 | ni | ni |
| Distance from water bodies | ni | ni | ni | >0.05 | ni | ni |
| Total variation | 2.79 | 87% | | | | |
| Eigenvalues | | | | | 0.669 | 0.477 |
| Species-environment correlations | | | | | 0.963 | 0.843 |

Bold values indicate statistically significant results, $P < 0.05$.

Effects of local × large-scale variables on lizard diversity

We found a significant negative relationship between elevation and capture rates in PTDFs ($r = 0.73$; $t_8 = -3.03$; $P = 0.01$), but no significant relationship between elevation and local richness ($r = 0.19$; $t_8 = -0.55$; $P = 0.59$). We also failed to find any significant relationship between local richness and altitudinal range ($r = 0.31$; $t_8 = -0.91$; $P = 0.38$) or number of habitat patches ($r = 0.15$; $t_8 = 2.54$; $P = 0.66$).

Geographical distance explained about one-fourth of the variation in faunal overlap (Jaccard index) among localities ($r = 0.51$; $t_{43} = -3.95$; $P < 0.01$). A CCA (Fig. 8) on capture rates per species and environmental variables in 51 PTDF transects revealed that the abundance of lizard species was significantly associated with eight of the 11 studied environmental variables (Table 5). A combination of the five most significant variables, including positional variables (latitude, longitude), local environmental variables (soil and vegetation types) and elevation, explained 63% of the variation. The main environmen-

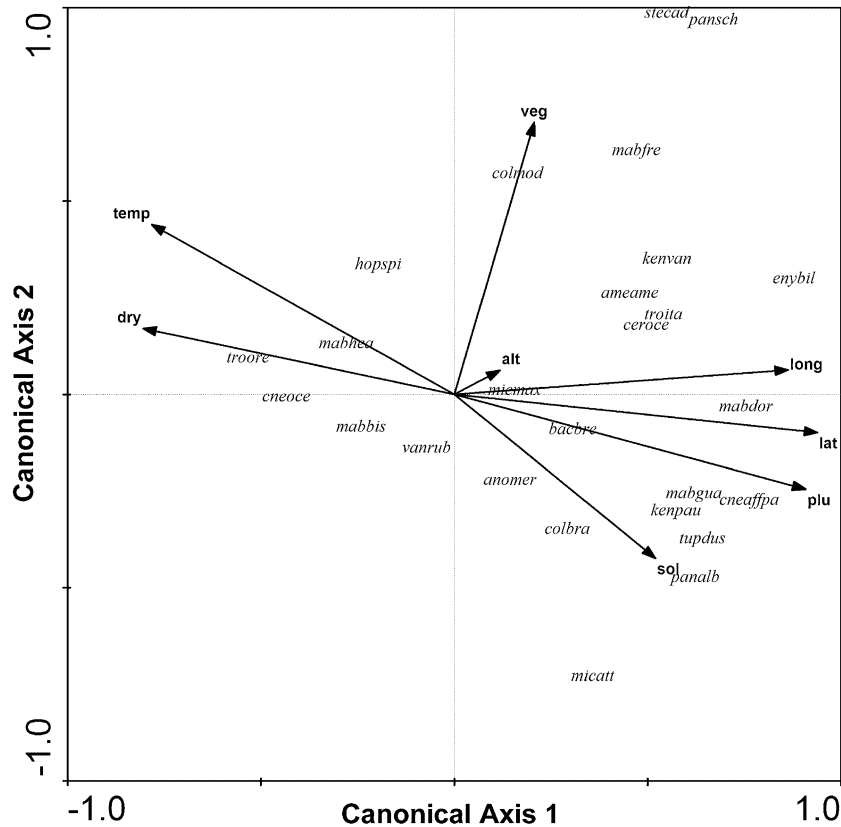


Fig. 8. Biplot of species \times environmental variables from Canonical Correspondence Analysis of pitfall with drift fences capture rates in 51 sampling units in 10 Cerrado localities.

tal variables represented along the first canonical axis (Fig. 8) were latitude, rainfall and longitude, in order of importance. Along the second axis (Fig. 8), the following environmental variables were represented: vegetation type, temperature and soil type.

Along the first axis, species were segregated mostly by continental scale variables, such as latitude, with lizards abundant in southern sites in the upper Paraná basin, such as *Mabuya dorsivittata* and *Enyalius* aff. *bilineatus* segregated from those common in northern localities, as *Tropidurus oreadicus* and *Cnemidophorus* gr. *ocellifer* in the Amazonian and Parnaíba basins. Along axis 2, species were segregated mostly according to local variables of soil and vegetation type, with *Mabuya heathi*, *T. oreadicus* and *Cnemidophorus* gr. *ocellifer*, all abundant in sandy soil cerrado, segregated from *Tupinambis duseni*, *Cnemidophorus* aff. *parecis* and *Pantodactylus albostrigatus*, common in clay-rich soils. Finally, species common in forested habitats, such as *Stenocercus caducus*, *Enyalius* aff. *bilineatus* and *Pantodactylus schreibersii* were segregated from species from open, grassy habitats, such as *Anolis meridionalis*, *T. duseni* and *Micrablepharus atticolus*. Species abundant in typical (semi-open) cerrado, such as *Vanzosaura rubricauda*

and *Micrablepharus maximiliani* were placed at intermediate positions along the diagram.

DISCUSSION

Lizard richness in Cerrado localities

Total lizard richness ranging from 19 to 28 species may be interpreted as modal for Cerrado, as the largest group of localities showed values within this range. These richness values, although much lower than in Australian deserts, are comparable with adjacent rainforest sites with comparable sizes (see Colli *et al.* 2002), and higher than North American and Kalahari deserts (see Pianka 1989).

Differences in lizard richness between the first available studies for Cerrado localities (Warming 1892; Vanzolini 1948, 1976; Vitt 1991; Vitt & Caldwell 1993) and our results may stem from differences in sampling intensity, sampling methods (haphazard *vs.* haphazard + museum records + PTDFs) and sampling coverage (single *vs.* multiple habitats). Most lizard samplings in former studies (Vanzolini 1976;

Vitt 1991) seem to have taken place within homogeneous habitat patches.

Exceptionally high lizard richness levels found in GSVNP are still poorly understood, but may be explained by site location (contact areas between Upper Paraná and São Francisco basins, in the core of Cerrado), high habitat heterogeneity and presence of restricted-range species (*Stenocercus quinarius*, Tropiduridae; *Psilophthalmus* sp., Gymnophthalmidae) associated with scattered habitat patches and found in no other Cerrado region (Nogueira & Rodrigues 2006). On the other side of the spectrum, a single locality (ASBES) stood out as the poorest site, probably due to the isolated nature of the southernmost Cerrado sites in São Paulo state (see discussions on the effects of historical isolation of Cerrado patches in Gainsbury & Colli 2003). In agreement, peripheral areas tended to show lower richness values in recent results of modelled squamate distribution patterns in the Cerrado region (Costa *et al.* 2007).

Habitat specialization and lizard richness patterns

When sampling different habitats (typical cerrado savannas, rocky extrusions, forest borders) in Cerrado enclaves in Rondônia, Vitt and Caldwell (1993) noted a clear structure in lizard local distribution, and considered the understanding of patchy distributions as one of the most promising research lines in studies of the Cerrado herpetofauna. Contrary to mammals and birds, where most species use both forested and open habitats (see Johnson *et al.* 1999; Silva & Bates 2002), the Cerrado lizard fauna is dominated by habitat specialists, with predictable abundance differences among habitat types, resulting in low species overlap between open and forested habitats and a structured pattern of local distribution (see similar results in Nogueira *et al.* 2005).

Again in disagreement with patterns described for Cerrado birds (Silva 1997; Silva & Bates 2002) and mammals (Redford & Fonseca 1986; Mares & Ernest 1995), and corroborating recent results on local distribution of the Cerrado herpetofauna (Colli *et al.* 2002; Brasileiro *et al.* 2005; Nogueira *et al.* 2005; Sawaya *et al.* 2008), gallery forests harbour fewer species than open areas in Cerrado. As most forested habitats in Cerrado are scattered within a matrix of open areas, extinction rates of habitat specialists within these forest tracts can be more prominent than in adjacent, dominant and more stable open habitats, an effect that is analogous to the impoverishment of peripheral Cerrado isolates in western Amazonia (see Gainsbury & Colli 2003). This likely results from a combination of the small area covered by forested habitats in Cerrado (a species-area effect, see discus-

sions in Losos & Schluter 2000), a filtering effect along gallery forests, from Amazonia and Atlantic Forests into the core region of Cerrado (Silva 1996) and high extinction rates of habitat specialists (Gainsbury & Colli 2003).

Our results corroborate the 'horizontal habitat stratification' hypothesis, which states that the pronounced horizontal stratification of habitat mosaics promotes lizard richness and compensates the relative vertical simplicity of most habitats found in the Cerrado region (Colli *et al.* 2002). Despite being relatively simple when compared with forested habitats, Cerrado savannas are still complex enough to allow the coexistence of lizards exploring different microhabitats (leaf litter, tree trunks, soil cavities; see Vitt 1991), favouring high richness levels, a trend also detected in the relatively simple 'spinifex' and 'mulga' habitats in Australia (see Pianka 1969), occupied by lizards exploring different levels of habitat space.

Faunal overlap between different habitat types and natural barriers for dispersion

The low faunal overlap between forests and grasslands, two of the most important habitat types in Cerrado, suggests that these two habitat types may act as natural barriers for lizard distribution and dispersal. This may partially explain the relatively poor faunas found in peripheral Cerrado isolates in Amazonia (see Gainsbury & Colli 2003) and in the most species-poor locality, São Paulo, as both are found within a matrix of forest habitats (Amazonian forests in the northwest; Atlantic forest in the southeast). This pattern of local distribution may help to explain speciation processes linked with the isolation of both forest and grasslands within a matrix of unsuitable habitats. Such events of habitat isolation have been identified as one of the key elements for speciation in central Brazilian reptiles (Vanzolini 1997). Habitat specificity and the presence of unsuitable habitat patches are also viewed as major influence on the diversity of Australian desert lizard assemblages (Pianka 1969, 1972).

As postulated by Gainsbury and Colli (2003), the study of peripheral Cerrado isolates may provide important insights on the effects of artificial habitat fragmentation in the Cerrado. At the local scale level, the natural and historical isolation of mesic forest tracts within large areas dominated by grasslands and savannas is congruent with the observed low richness found in forested habitats in the Cerrado, as compared with surrounding, adjacent open habitats.

However, not all forest types are equally unsuitable for open Cerrado species. A recent study in seasonal dry tropical forest enclaves shows that these isolated dry forest areas are dominated by species shared with the Cerrado, with few endemic isolated species (Werneck & Colli 2006).

Habitat use in lizards from three major squamate clades

Open Cerrado habitats seem more suitable than forests for wide-foraging, chemically oriented, terrestrial lizards (the ancestral condition in *Autarchoglossa*), a probable influence of deep historical, phylogenetic effects in shaping extant lizard assemblages (see discussions in Vitt & Pianka 2005). The dominance of *Autarchoglossans*, both in terms of abundance and composition, may also reflect the dominance (historical and recent) of open habitats in the Cerrado landscape (see Ratter *et al.* 1997), with present patterns of habitat use reflecting a coupled history of landscape change and niche conservatism in lizard lineages (see Wiens 2004).

This pattern had already been detected in comparisons between Cerrado and Neotropical rainforest sites in Colli *et al.* (2002), and may be influenced both by the low density of trees in open areas, as most *Iguania* are arboricolous or use higher perches (Vitt *et al.* 2003; Vitt & Pianka 2005), and by higher environmental temperatures in open areas, as most *Scleroglossa* show higher metabolic rates and body temperatures (Vitt *et al.* 2003; Vitt & Pianka 2005).

Effects of local \times large-scale variables on lizard diversity

The importance of large scale environmental variables (such as latitude and longitude) is indicative of the influence of regional evolutionary processes on local faunal composition (see discussions in Ricklefs 2004). Despite the clear importance of habitat type in local distribution (and probably in avoiding extinction, see Colli *et al.* 2002; Gainsbury & Colli 2003), richness variations across the Cerrado seem mostly tied to historical, biogeographical factors (site location, regional species pool, see Ricklefs (2004) than to local factors, such as habitat diversity and topographical variation. As expected, species turnover among localities was highly dependent on geographical distance, indicating the importance of regional species pools in determining local composition, regardless of local habitat mosaics that are relatively similar along the Cerrado.

Contrary to general views that tend to favour tropical forested regions as major sources of biological diversity (see discussions in Mares 1992), tropical open areas around the globe harbour extremely high species richness and diversity. Environmental heterogeneity (both at the local and regional scale), and habitat specialization seem to play a major role in promoting and maintaining high species richness in open environments around the globe. Such environmentally complex and independently evolved ecosystems have provided a

fertile testing ground for hypotheses on speciation and evolution of diversity (Schall & Pianka 1978; Pianka 1989). However, many open environments around the globe are under severe threat, and have traditionally been neglected in terms of legal protection, conservation efforts and funding for scientific research (see discussion for the Cerrado in Marris 2005).

The high lizard richness in open, interfluvial habitats mirrors the patterns found for vascular plants (Ratter *et al.* 1997; Oliveira-Filho & Ratter 2002) and may be the rule in Cerrado biodiversity (but see Redford & Fonseca 1986; Silva & Bates 2002). Unfortunately, open, flatland grasslands are the first habitats cleared for the expansion of mechanized agriculture in the Cerrado (Ratter *et al.* 1997; Klink & Machado 2005), threatening the conservation of the biological diversity and evolutionary legacy of central Brazilian savannas. This non-random pattern of habitat destruction in Cerrado will cause severe and irreversible biodiversity losses if not urgently controlled.

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