Determinants of assemblage structure in Neotropical dry forest lizards

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Abstract We investigated the structure of a lizard assemblage from Seasonally Dry Tropical Forest enclaves in the Brazilian Cerrado biome, by testing the roles of ecological and historical components. We analysed data from 469 individuals, belonging to 18 lizard species, sampled by a combination of pitfall, funnel and glue traps, as well as by haphazard sampling. Null model analyses and Canonical Phylogenetic Ordination analysis, coupled with Monte Carlo simulations, revealed lack of both ecological and phylogenetic structure in microhabitat use. Conversely, these analyses revealed a mean overlap in diet composition significantly smaller than expected by chance and significant historical structure. Structure in diet composition was due to phylogenetic effects corresponding to the most basal divergence of the squamate phylogeny (Iguania/Scleroglossa) and the clades Teiidae and Gymnophthalmidae. Among lizards, evolutionary constraints on microhabitat use appear less than on prey use, suggesting that the availability of historically preferred prey types moderates microhabitat selection. The lack of structure in microhabitat use suggests absence of competitive interactions on the spatial component. On the other hand, food preferences have a deep historical basis and do not reflect current competitive interactions.

Key words: Canonical Phylogenetic Ordination, Cerrado, community ecology, lizard, phylogenetic constraint, Seasonally Dry Tropical Forest.

INTRODUCTION

During community assembly, different species may invade, persist and become extinct, sometimes repeatedly (Hang-Kwang & Pimm 1993). Throughout this process, the time interval and the particular sequence of species invasions may influence the observed final structure (Drake 1991; Putman 1996). Both stochastic (Connor & Simberloff 1979, 1983; Bell 2001; Gainsbury & Colli 2003) and deterministic (historical or ecological, Diamond & Gilpin 1982; Roughgarden 1983; Gotelli & McCabe 2002) events can influence community structure and assembly. Considering deterministic events, studies on the structure of biological communities should investigate both causal levels: proximate, related to ecological or current processes, and ultimate, related to historical or evolutionary processes (Brooks & McLennan 1991; Losos 1996; Webb *et al.* 2002).

At the ecological level, competition is often viewed as most important in structuring communities (Diamond & Gilpin 1982; Roughgarden 1983; Gotelli & McCabe 2002). Nevertheless, predation, mutualism, environmental heterogeneity, temporal variation of conditions and resource partitioning (temporal, spatial or dietary) may also influence communities (Pianka 1973; Brooks & McLennan 1993; Brown 1995). Because current ecological patterns may reflect phylogenetic inertia instead of adaptation, neither should be used as the sole hypothesis to investigate community structure (Losos 1994). Hence, related species should not be treated as independent units in conventional statistical analyses that investigate community structure (Brooks & McLennan 1991, 1993; Miles & Dunham 1993). The historical approach recognizes that community composition results from a combination of vicariant (association by descent), dispersing (association by colonization) and *in situ* evolutionary (speciation) events, the resultant community being a mosaic of historical and ecological influences (Brooks & McLennan 1991, 1993; Webb *et al.* 2002).

In Cerrado, a vast, predominantly open-vegetation biome that covers the central Brazilian Plateau (Oliveira & Marquis 2002) and one of the 25 global biodiversity hotspots (Myers *et al.* 2000), local lizard richness is comparable to that of Neotropical forests, in some cases reaching 25 species (Colli *et al.* 2002). This is partially due to a rich mosaic of vegetation types, including grasslands, woodlands and forests (e.g. Eiten 1972, 1979; Oliveira & Marquis 2002), among which different lizard species are distributed (Colli *et al.* 2002; Nogueira *et al.* 2005; Vitt *et al.* 2007a). Thus, forest ecosystems in Cerrado, such as

'cerradão', gallery forest and Seasonally Dry Tropical Forest (SDTF) enclaves, are important to the maintenance of viable populations of forest species, contributing to the regional diversity and to community dynamics (Silva 1995a,b; Brandão & Araujo 2001; Silva & Bates 2002; Werneck & Colli 2006).

Seasonally Dry Tropical Forests are tree-dominated ecosystems that occur on fertile soils under strongly seasonal climates (Murphy & Lugo 1986; Bullock *et al.* 1995; Pennington *et al.* 2006). SDTFs have a discontinuous distribution in the Caribbean and Central and South America, from Mexico to Argentina, with three recognized nuclei: the 'Caatingas nucleus' of northeastern Brazil, the 'Misiones nucleus' on the Paraguay-Paraná River and the 'Subandean Piedmont nucleus' of south-western Bolivia and north-western Argentina (Prado & Gibbs 1993; Pennington *et al.* 2000; Prado 2000; Pennington *et al.* 2006). Because of their fertile soils, SDTFs are highly suitable for cultivation and are under drastic conversion into agricultural lands. This, combined with a reduced attention from conservation agencies, makes SDTFs one of the most threatened tropical ecosystems (Janzen 1988; Scariot & Sevilha 2003; Sánchez-Azofeifa *et al.* 2005; Scariot & Sevilha 2005; Miles *et al.* 2006; Pennington *et al.* 2006; Prance 2006; Vieira & Scariot 2006). Several less-studied and more-isolated SDTF remnants occur as enclaves within Cerrado, in areas of favourable edaphic conditions derived from basic rocks (Ratter *et al.* 1978; Silva 1995a; Silva & Bates 2002). Some of the largest remnants occur in northeastern Goiás state, in the municipality of São Domingos (Scariot & Sevilha 2000, 2003, 2005; Felfili 2003). A biogeographical analysis of lizard assemblages from São Domingos SDTF enclaves (Werneck & Colli 2006) revealed the combined influences of dispersal (from neighbour Cerrado assemblages), history/vicariance (from Caatinga) and *in situ* evolution (e.g. *Mabuya* sp.). Herein we investigate the role of species interactions (mainly competition) and historical constraints in the formation of the lizard assemblage in São Domingos SDTF enclaves. More specifically, we test for the presence of assemblage structure, in terms of microhabitat use and diet composition, using null models (Gotelli & Graves 1996; Gotelli 2000) and Canonical Phylogenetic Ordination analysis (Giannini 2003).

METHODS

Study site

The Paranã River basin is a depression in central Brazil, between the Divisor São Francisco-Tocantins and the Central Goiano plateaux (IBGE 1995). The headwaters of the Paranã River are in Serra Geral de Goiás, whereas in the city of Paranã, southern Tocantins state, the Paranã River merges with the Tocantins River, a major tributary of the Amazonas River. SDTFs are the dominant native vegetation in the Paranã River valley. Altitude in the region ranges from 400 to 600 m (IBGE 1995), and the climate falls into Köppen's Aw category (Nimer 1989), with a mean annual temperature of 24°C, mean annual rainfall of 1500 mm/year, and at least 5–6 months receiving less than 200 mm. During the 1980s, intense human occupation in the Paranã River valley reduced SDTFs to small fragments in flat, lowland areas or on limestone outcrops (Scariot & Sevilha 2000, 2003; Felfili 2003). Cattle ranching (70%), farming, forestry and charcoal production are the main uses of the modified matrix among fragments (Scariot & Sevilha 2005). Because of its high biodiversity and conservation threats, the region was recently considered as of extremely high ecological relevance for conservation (MMA 1999).

Lizard sampling

We conducted four expeditions spanning wet and dry periods, to account for seasonal effects (30 August–11 September 2003, 19 November–15 December 2003, 14–22 March 2004, and 22 November–1 December 2004), totalling 59 days of field work. We sampled lizards in both disturbed and undisturbed SDTF fragments, on flat lowlands and limestone outcrops in the municipality of São Domingos, Goiás, Brazil (13°23′54″S, 46°16′06″W) (Fig. 1). We installed 25 arrays of pitfall traps with drift fences, 30 m apart from each other, along a trail in an undisturbed 250 ha SDTF fragment at Fazenda Flor do Ermo (13°39′26″S, 46°45′09″W). Each array consisted of four 30-L plastic buckets arranged in a 'Y', with a central bucket connected to each of three peripheral buckets by a 5 m long and 0.5 m high plastic drift fence, forming three 120° angles (Fig. 1E). We buried the base of the plastic fences in the soil (ca. 10 cm) to prevent lizards from passing underneath. We checked arrays daily and closed the buckets between expeditions to prevent unwarranted captures. We also collected additional specimens in neighbouring SDTF fragments using funnel traps (Fig. 1F), glue traps and haphazard sampling (by hand, noose or using a shotgun).

We euthanized captured lizards with a lethal injection of Tiopental and fixed them in 10% formalin. We deposited all specimens in Coleção Herpetológica da Universidade de Brasília. During manual captures, we recorded the time of capture and microhabitat where lizards were first sighted. We investigated assemblage structure in microhabitat use (spatial niche) and
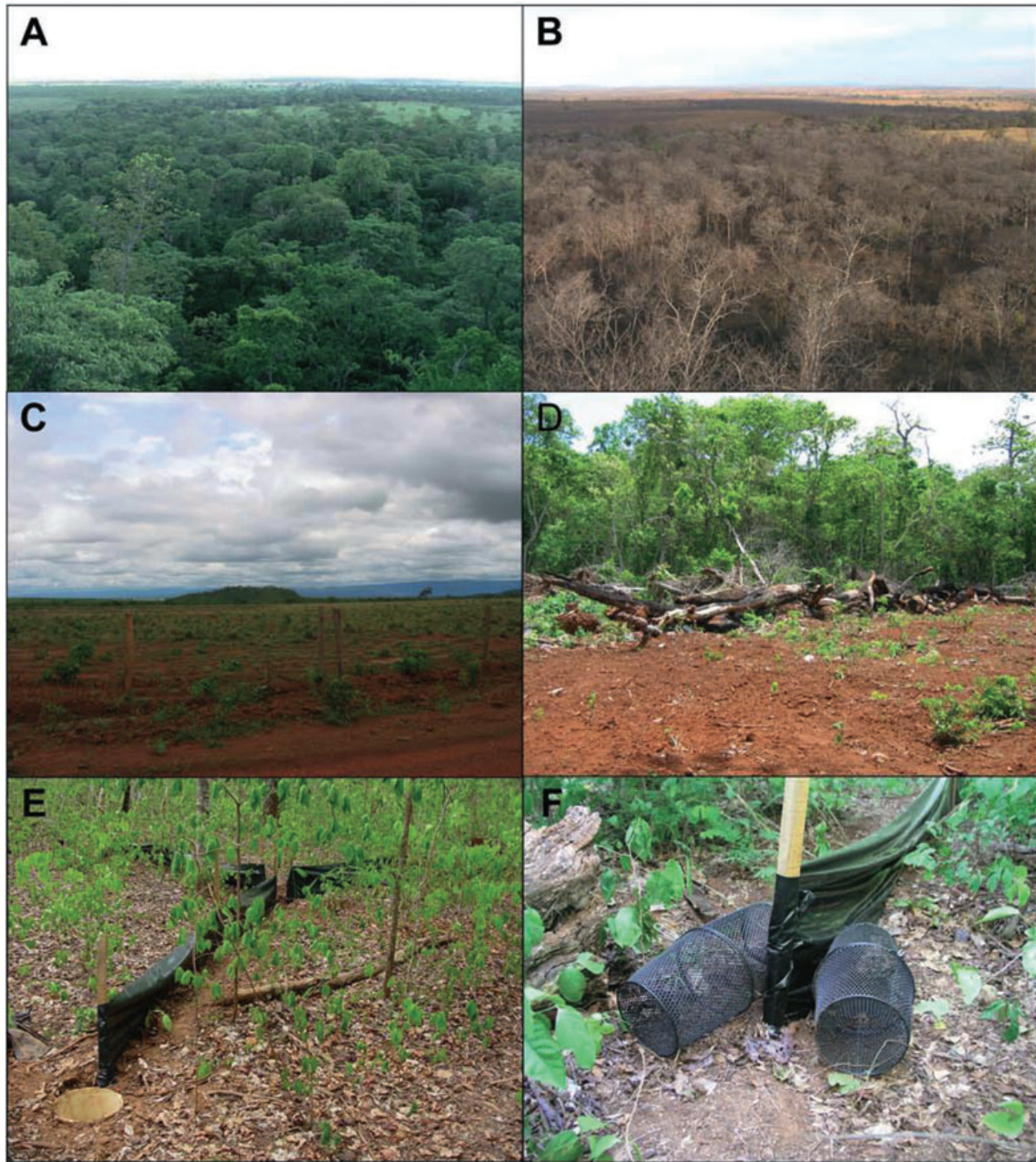
Fig. 1. Seasonally Dry Tropical Forests in the region of São Domingos, Goiás and details of pitfall and funnel traps. (A) Wet season, September 2003 (RN Leite). (B) Dry season, December 2003 (RN Leite). (C) Landscape fragmentation in the region (FP Werneck). (D) Intense habitat deforestation and fragmentation (FP Werneck). (E) Pitfall traps at SDTF fragment at Fazenda Flor do Ermo (AB Gamble). (F) Funnel traps at SDTF fragment at Fazenda Flor do Ermo (RN Leite).

diet composition (alimentary niche). Even though fine-scale temporal differences may enable species coexistence (Goodman 2007), the temporal niche is less important in this lizard assemblage, because most species are diurnal, except *Gymnodactylus carvalhoi*

(Colli *et al*. 2003) and *Phyllopezus pollicaris* (Vitt 1995), which are primarily nocturnal. Additionally, general lack of finer time partitioning has been previously reported in other tropical lizard communities (Vitt & Zani 1996).

Data analyses

Sampling efficiency

To determine the efficiency of our sampling effort, we produced a sample-based rarefaction curve (*sensu* Gotelli & Colwell 2001), using 10 000 random samples of the original data, without replacement, with EstimateS v. 7.5 (Colwell 2005). The data used in this analysis consist of a matrix in which each species is a row and each sampling day is a column. Entries in the matrix are the number of lizards collected for each species on each day. Additionally, we estimated expected richness in the assemblage using the 'Abundance-based Coverage Estimator (ACE)', which accounts for species not captured (Colwell & Coddington 1994; Colwell 2005).

Microhabitat use

We used the following categories of microhabitats used by lizards when first sighted: branch, building (walls), burrow, leaf litter, log, open ground, rock, rock crevice, trunk, under leaf litter, under log and under tree bark. Individuals collected in pitfall trap arrays were not included in this analysis. For each species, we computed the microhabitat niche breadth using the inverse of Simpson's diversity index (Simpson 1949):

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

where i is the microhabitat category, n is the number of categories, and p is the proportion of microhabitat category i. Simpson's diversity index varies from 1 (a single microhabitat category is used) to n (equal use of the n microhabitat categories). We also calculated the overlap in microhabitat use among all species pairs using Pianka's overlap index (Pianka 1973):

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

where P represents the proportion of microhabitat category i, while j and k represent the species pair being compared. Pianka's overlap index varies from zero (no overlap) to one (complete overlap).

Diet composition

In the laboratory, we removed stomachs from all collected lizards and analysed stomach contents under a stereoscope, identifying prey items following Pianka (1986), with the exception of ants (Formicidae), which we considered a separate category. We recorded the length and width of intact prey to the nearest 0.01 mm, with Mitutoyo electronic calipers and estimated prey volume (*V*) as an ellipsoid:

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

where w is prey width and l is prey length. This approximation has been criticized (Magnusson *et al.* 2003). However, it is broadly used in works on lizard ecology and widely regarded as the best estimate of the volume of most prey consumed by lizards (e.g. Vitt & Zani 1996, 1998b; Colli & Zamboni 1999; Vitt *et al.* 1999; Colli *et al.* 2003; Mesquita *et al.* 2006b). In addition, use of this measure allows comparison with other data sets.

For each species, we calculated the numeric and volumetric percentage of each prey category based on the pooled stomachs (all individuals considered as a single stomach). From these percentages, we computed niche breadths and overlaps as explained above. Values of diet niche breadth refer to the average between numeric and volumetric niche breadths.

To determine the relative importance of each prey category for each lizard species, we calculated an importance index (*I*) for pooled stomachs, which considers the numeric percentage (*N%*), volumetric percentage (*V%*) and percentage of occurrence (*F%*, number of stomachs with prey category i, divided by the total number of stomachs) of each prey category,

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

Null model analyses

To determine if mean overlap in microhabitat use and diet composition among all pairs of lizard species is smaller than expected by chance, we obtained null models by randomizing the original assemblage data (Gotelli & Graves 1996; Gotelli 2001). Null models were used to build a null hypothesis, simulating assemblage organization in the absence of biological interactions, such as interspecific competition. We investigated the presence of non-random patterns in microhabitat use and diet overlap using the Niche Overlap Module of EcoSim v.7 (Gotelli & Entsminger 2004). Data in this analysis consist of a matrix, in which lizard species are rows and microhabitat or prey categories are columns. Cell values are utilization frequencies for each microhabitat category or I values for each prey category. We used the following options of EcoSim: Pianka's niche overlap index, randomization algorithm two (RA2), and 10 000 randomizations of the original matrix. RA2 replaces the microhabitat or

prey category in the original matrix with a random uniform number between zero and one, but retains the zero structure of the matrix (Winemiller & Pianka 1990). In this manner, RA2 assumes that, even in the absence of biological interactions among species, some microhabitats or prey categories are unavailable to some species. The result of the analysis is a null distribution of niche overlap values against which the observed (mean) value of niche overlap in the assemblage is checked with a one-tailed Z-test. We considered the significance level of 0.05 to reject the null hypothesis.

To avoid miscalculation of null models because of the small sample size of some species, we repeated both analyses (overlap in microhabitat use and diet composition) retaining only the most abundant lizard species and using two different cut-offs ($n > 5$ and $n > 15$). As both approaches produced identical results, we only present results for the more complete data set (including all species with $n > 5$). For microhabitat use, we excluded *Ameiva ameiva* ($n = 3$), *Cnemidophorus ocellifer* (1), *Iguana iguana* (3), *Mabuya nigropunctata* (5), *Polychrus acutirostris* (2), *Tropidurus torquatus* (1), *Tupinambis merianae* (3) and *Tu. quadrilineatus* (1). For diet composition, we excluded *Am. ameiva* (5), *Lygodactylus klugei* (4), *Tr. torquatus* (1) and *Tu. merianae* (1). For diet composition, we also repeated the analysis excluding prey categories with an importance index less than 5% for at least one lizard species. Excluded prey categories were Acari, Dermaptera, Diplopoda, Mantodea, plant material, lizard skin, Odonata, Opiliones, insect eggs, Pseudoscorpionida, Scorpionida and Solifuga.

Canonical Phylogenetic Ordination

To assess the role of history in structuring the lizard assemblage from SDTFs enclaves, we combined phylogenetic hypotheses from different studies (Presch 1974; Kluge 1987; Estes *et al.* 1988; Frost & Etheridge 1989; Frost *et al.* 2001; Lee 2005) to build a supertree relating all lizard species in the assemblage (Sanderson *et al.* 1998; Webb *et al.* 2002) (Fig. 2). We also ran a separate analysis considering a recent, molecular phylogeny for Squamata, in which Iguania is nested within, and not forming a basal dichotomy with Scleroglossa, as in the traditional, morphological phylogeny (Townsend *et al.* 2004; Vidal & Hedges 2005; Fry *et al.* 2006). To test the existence of phylogenetic effects, we used Canonical Phylogenetic Ordination (CPO) (Giannini 2003) coupled with Monte Carlo permutations (9999), in CANOCO 4.5 for Windows (Ter Braak & Smilauer 2002). CPO is a multivariate ordination technique that relates the variation in a matrix of dependent variables (microhabitat use or diet composition) with another matrix of independent variables (phylogenetic structure of the supertree), maximizing their correlations (Ter Braak 1986; Giannini 2003; Vitt & Pianka 2005). When more than one clade showed significant effects, we conducted a stepwise, manual selection of variables in CPO. In this analysis, after testing each variable individually to obtain *F*- and *P*-values, we added only significant variables to the model, in decreasing order of importance. Because of differences in completeness of data for microhabitat use and diet composition, we used two different supertrees (Fig. 3). As in the case of null model analyses, we repeated the above-mentioned steps after the exclusion of species
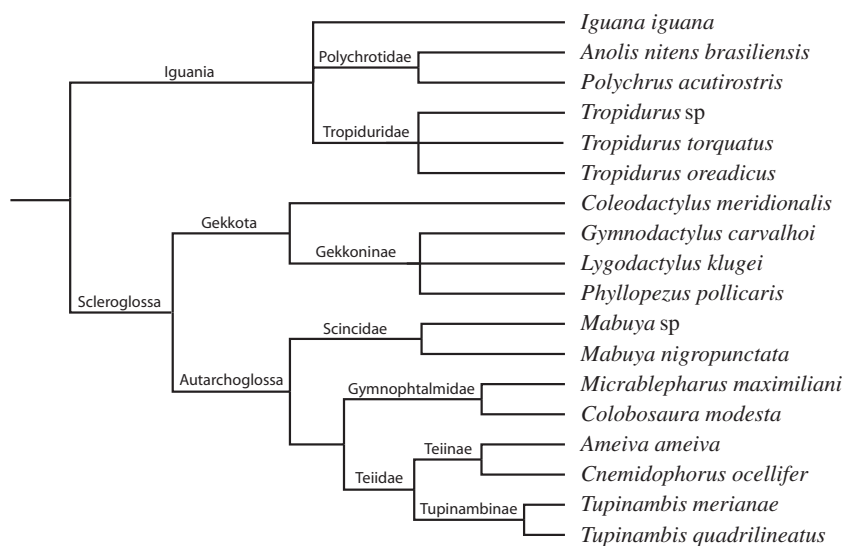

Fig. 2. Supertree of the lizard assemblage from Seasonally Dry Tropical Forest enclaves in São Domingos, Goiás, Brazil. Phylogeny based on several authors (see text for details).
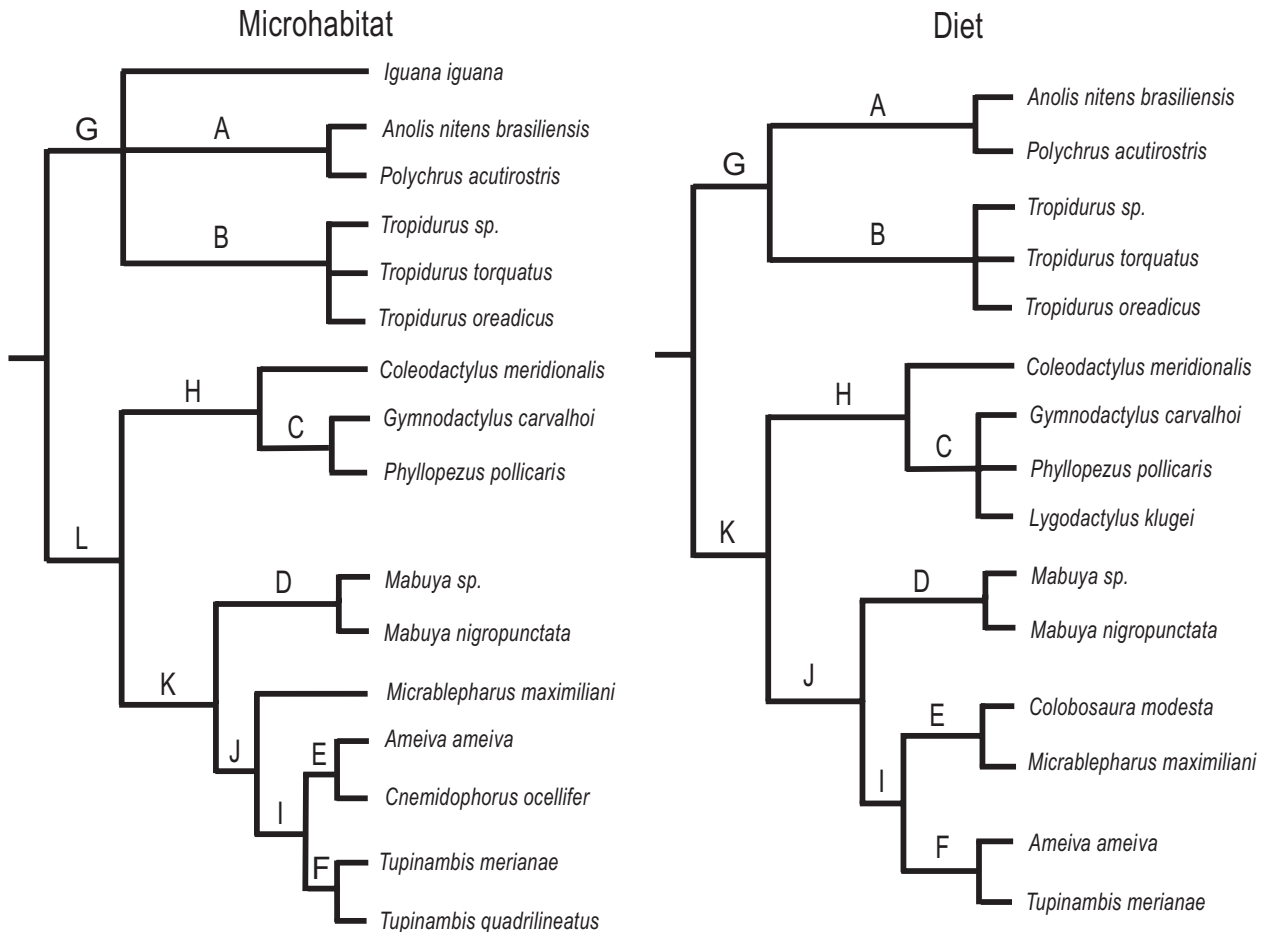
Microhabitat

Diet

Fig. 3.   Individual groups used in Canonical Phylogenetic Ordination for microhabitat and diet data.

with $n \leq 5$ and the exclusion of prey categories with $I \leq 5\%$. The analysis is highly conservative because it uses clade membership relying only on topological information rather than distance values.

Taxonomic note

We identified two undescribed species in SDTF enclaves: *Mabuya* sp. and *Tropidurus* sp. *Mabuya* sp. is likely endemic to the region and is similar to *M. frenata*, whereas *Tropidurus* sp. shows some affinities with *T. itambere* and has been previously recorded by us on rock outcrops in other Cerrado localities (see Werneck & Colli 2006).

RESULTS

Sampling efficiency, species richness and abundance

During 59 days, and considering captures both in traps and in haphazard sampling, we collected

469 individuals belonging to 18 lizard species and seven families (Table 1). From the total abundance, we gathered ecological data of microhabitat use and composition from 240 and 359 individuals, respectively. The most abundant species was *Anolis nitens brasiliensis* ($n = 129$), followed by *G. carvalhoi* (105) and *Mabuya* sp. (55). The most diverse families in the assemblage were Gekkonidae and Teiidae, with five and four species, respectively (Table 1).

The rarefaction curve showed the observed richness approaching the estimated assemblage asymptote (Fig. 4). According to the randomization results, an average of 13 species would be collected with 10 days of sampling (17% of the time), corresponding to 72% of the total observed richness. In addition, an average of 18 species would be collected at the 35th day, after which the rarefaction curve stabilized. Additionally, both observed and expected richness had similar asymptotes, around 18 species, with the difference that the ACE stabilized faster, around the 20th day (Fig. 4).

Table 1. Composition and abundance of 18 lizard species from Seasonally Dry Tropical Forest enclaves of São Domingos, Goiás and respective values of microhabitat use niche breadth (B_m)

Species	Abundance	B_m	Microhabitat
Gekkonidae			
Coleodactylus meridionalis (D)	30	2.57 (11)	LL, OG, RC, UG
Gymnodactylus carvalhoi (D/N)	105	5.34 (45)	LL, LO, OG, RC, RO, TB, TR, UG, UL
Lygodactylus klugei (D)	7	–	–
Phyllopezus pollicaris (N)	34	1.32 (30)	BD, RO, TB, TR
Iguanidae			
Iguana iguana (D)	8	1.00 (3)	BR
Polychrotidae			
Anolis nitens brasiliensis (D)	129	2.72 (37)	BU, LL, OG
Polychrus acutirostris (D)	9	2.00 (2)	BR, OG
Tropiduridae			
Tropidurus oreadicus (D)	17	3.33 (10)	LO, OG, RC, RO
Tropidurus sp. (D)	23	1.71 (20)	LO, OG, RO, TR
Tropidurus torquatus (D)	2	1.00 (1)	TR
Scincidae			
Mabuya nigropunctata (D)	11	3.57 (5)	LL, LO, OG, UL
Mabuya sp. (D)	55	3.02 (52)	BU, LL, LO, OG, RO, TB, TR, UG
Teiidae			
Ameiva ameiva (D)	6	1.00 (3)	OG
Cnemidophorus ocellifer (D)	2	1.00 (1)	UG
Tupinambis merianae (D)	4	1.00 (3)	OG
Tupinambis quadrilineatus (D)	1	1.00 (1)	OG
Gymnophthalmidae			
Colobosaura modesta (D)	8	–	–
Micrablepharus maximiliani (D)	18	5.12 (16)	LL, LO, OG, RC, TB, UL
Total abundance	469		

Values inside parentheses correspond to sample size by species. Activity: D, diurnal; N, nocturnal. Microhabitats: BD, building (walls); BR, branch; BU, burrow; LL, leaf litter; LO, log; OG, open ground; RC, rock crevice; RO, rock; UG, under log; UL, under leaf litter; TB, under tree bark; TR, trunk.
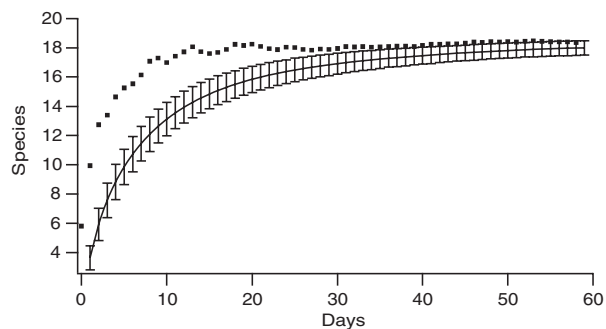

Fig. 4. Sample-based rarefaction curve for lizard species collected during 59 sampling days in SDTFs remnants, São Domingos, Goiás, Brazil. The line represents rarefaction means ± SD and points represent the Abundance-based Coverage Estimator.

Microhabitat use

Niche breadth (B_m) based on microhabitat use ranged from 1.00 to 5.34 in the São Domingos lizard assemblage (Table 1). The teiids *Am. ameiva* (n = 3),

Tu. merianae (3) and *Tu. quadrilineatus* (1), exclusively associated with open ground, and the iguanid *I. iguana* (3), exclusively associated with tree branches, had more restricted use of microhabitats (B = 1). *Tropidurus torquatus* and *C. ocellifer*, represented by a single individual each, were observed on trunk and under log, respectively. On the other hand, *G. carvalhoi* (B = 5.34, n = 45) and *Micrablepharus maximiliani* (5.12, 16) had the largest values of niche breadth (Table 1, Fig. 5).

Niche overlap in microhabitat use varied from none to almost complete (Table 2), the greatest overlap occurring between *Tropidurus* sp. and *Ph. pollicaris* (0.98), two species that primarily used rocks (Fig. 5). *Anolis nitens brasiliensis* and the teiids exclusively associated with open ground (mentioned above) also had high overlaps in microhabitat use. Conversely, niche overlap among the most abundant species (*An. nitens*, *Mabuya* sp., *G. carvalhoi* and *Coleodactylus meridionalis*) was low (however not significantly different from random as shown below). In addition, niche overlap among phylogenetically related species (sister species in the assemblage supertree, Fig. 2) varied from 0.0
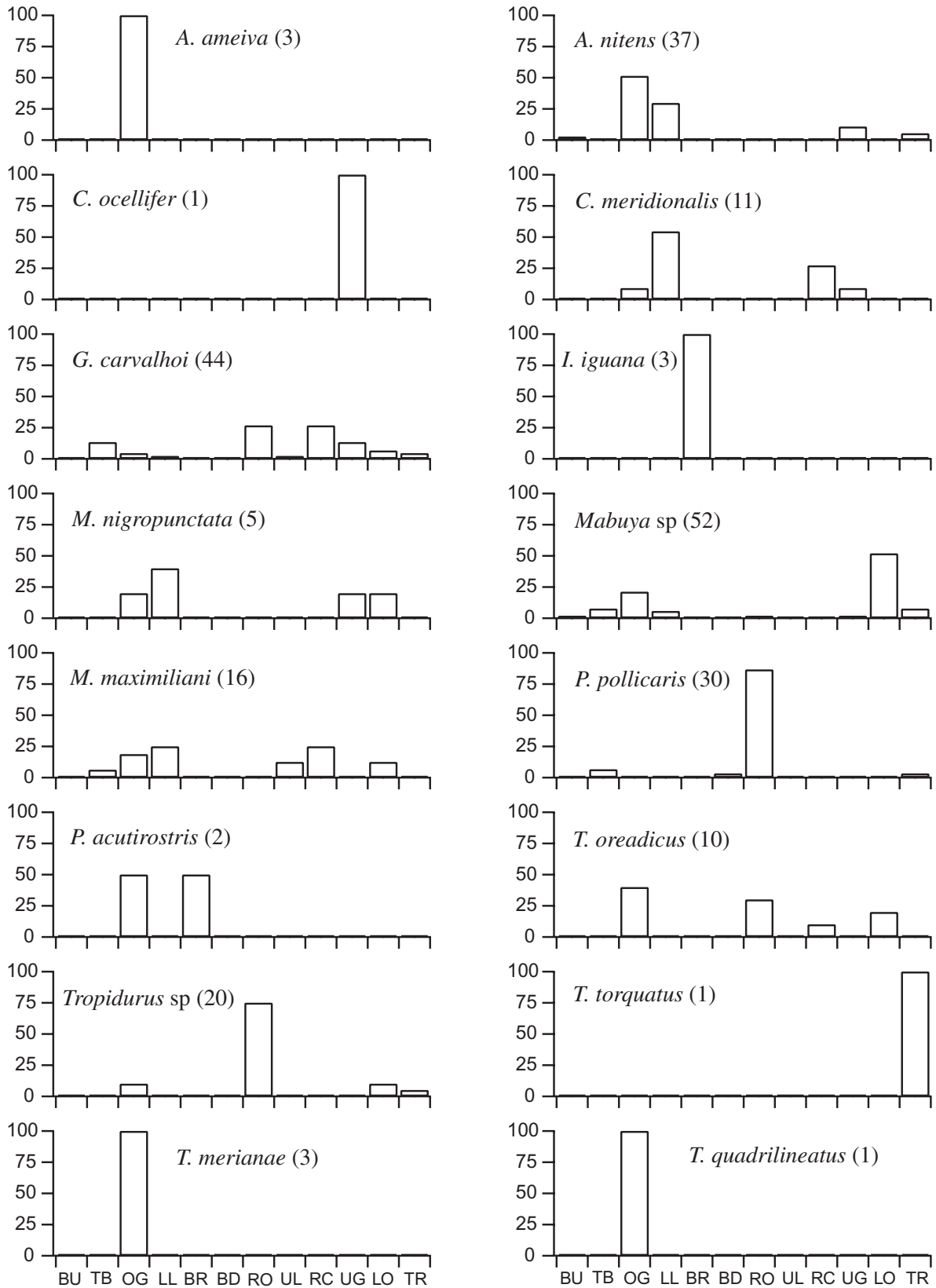
Fig. 5. Frequency distribution of individuals according to microhabitat categories for SDTFs of São Domingos lizards. Microhabitats: BD, building (walls); BR, branch; BU, burrow; LL, leaf litter; LO, log; OG, open ground; RC, rock crevice; RO, rock; UG, under log; UL, under leaf litter; TB, under tree bark; TR, trunk. Sample sizes in parentheses.

Table 2. Pianka's niche overlap index based on diet composition (upper diagonal) and microhabitat use (lower diagonal) of lizards from Seasonally Dry Tropical Forest enclaves in São Domingos, Goiás, Brazil

	Aam	Ani	Coc	Cme	Cmo	Gca	Iig	Lkl	Mni	Msp	Mma	Ppo	Pac	Tor	Tsp	Tto	Tqu	Tme
Aam		0.73	–	0.58	0.00	0.29	–	0.04	0.54	0.26	0.37	0.70	0.20	0.52	0.34	0.65	–	0.66
Ani	0.85		0.18	0.75	0.33	0.50	–	0.37	0.84	0.51	0.76	0.92	0.21	0.49	0.34	0.73	–	0.78
Coc	0.00	0.18		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Cme	0.15	0.58	0.15		0.19	0.86	–	0.17	0.68	0.91	0.38	0.87	0.09	0.64	0.22	0.47	–	0.54
Cmo	–	–	–	0.19		0.19	–	0.84	0.13	0.14	0.37	0.14	0.00	0.25	0.00	0.00	–	0.00
Gca	0.10	0.18	0.31	0.38	0.19		0.00	0.22	0.51	0.94	0.25	0.60	0.12	0.80	0.41	0.33	–	0.12
Iig	0.00	0.00	0.00	0.00	–	0.00		–	–	–	–	–	–	–	–	–	–	–
Lkl	–	–	–	–	–	–	0.00		0.15	0.13	0.56	0.20	0.42	0.28	0.12	0.23	–	0.00
Mni	0.38	0.76	0.38	0.77	–	0.25	0.00	–		0.55	0.69	0.76	0.22	0.37	0.15	0.52	–	0.58
Msp	0.37	0.38	0.03	0.15	–	0.27	0.00	–	0.57		0.20	0.68	0.07	0.61	0.16	0.28	–	0.28
Mma	0.43	0.64	0.00	0.80	–	0.52	0.00	–	0.70	0.49		0.55	0.20	0.19	0.20	0.42	–	0.38
Ppo	0.00	0.00	0.00	0.00	–	0.64	0.71	–	0.00	0.05	0.01		0.25	0.50	0.30	0.77	–	0.84
Pac	0.71	0.60	0.00	0.10	–	0.07	0.00	–	0.27	0.26	0.30	0.55		0.24	0.20	0.60	–	0.17
Tor	0.73	0.62	0.00	0.19	–	0.58	0.00	–	0.41	0.62	0.52	0.98	0.52		0.75	0.52	–	0.10
Tsp	0.13	0.12	0.00	0.02	–	0.65	0.00	–	0.10	0.21	0.09	0.04	0.09	0.68		0.63	–	0.10
Tto	0.00	0.09	0.00	0.00	–	0.10	0.00	–	0.00	0.13	0.00	0.00	0.00	0.00	0.07		0.00	0.73
Tqu	1.00	0.85	0.00	0.15	–	0.10	0.00	–	0.38	0.37	0.43	0.00	0.71	0.73	0.13	0.00		–
Tme	1.00	0.85	0.00	0.15	–	0.10	0.00	–	0.38	0.37	0.43	0.00	0.71	0.73	0.13	0.00	1.00	

Aam, *Ameiva ameiva*; Ani, *Anolis nitens brasiliensis*; Coc, *Cnemidophorus ocellifer*; Cme, *Coleodactylus meridionalis*; Cmo, *Colobosaura modesta*; Gca, *Gymnodactylus carvalhoi*; Iig, *Iguana iguana*; Lkl, *Lygodactylus klugei*; Mni, *Mabuya nigropunctata*; Msp, *Mabuya* sp; Mma, *Micrablepharus maximiliani*; Ppo, *Phyllopezus pollicaris*; Pac, *Polychrus acutirostris*; Tor, *Tropidurus oreadicus*; Tsp, *Tropidurus* sp; Tto, *Tr. torquatus*; Tqu, *Tupinambis quadrilineatus*; Tme, *Tu. merianae*.
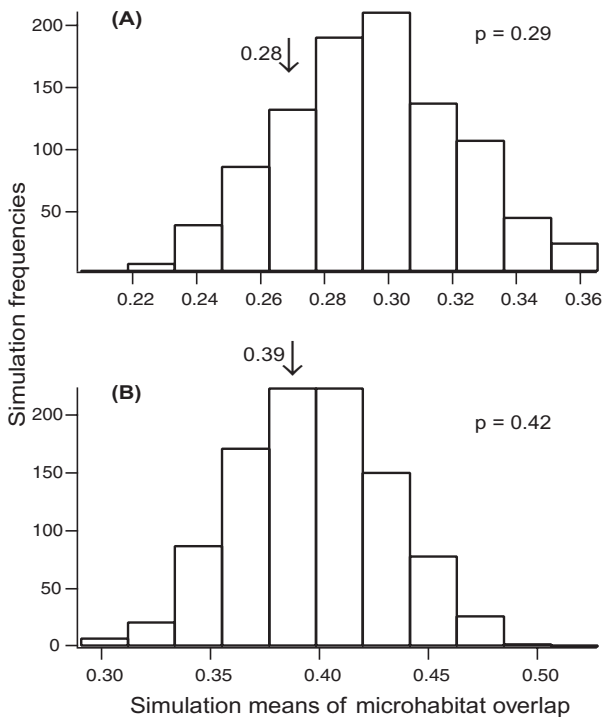
Fig. 6. Observed and expected mean microhabitat niche overlap among lizards from SDTFs of São Domingos, considered all species (A) and only the most abundant species (B). Arrows indicate observed means, *P*-values are probabilities that observed means are smaller than expected random means (10 000 simulations).

(*Am. ameiva vs. C. ocellifer* and *Tr. torquatus vs. Tr. oreadicus*) to 1.0 (*Tu. merianae vs. Tu. quadrilineatus*). However, in most cases these values were low or moderate (Table 2, see pairs of sister species).

Mean overlap in microhabitat use was not significantly different from random (Fig. 6), taking either all species ($\bar{x}_\phi = 0.28$; $P = 0.29$) or only the most abundant species ($\bar{x}_\phi = 0.39$; $P = 0.42$), indicating lack of assemblage structure with respect to microhabitat use. The CPO, coupled with Monte Carlo simulations, revealed no significant phylogenetic effects upon patterns of microhabitat use, taking either all lizard species or only the most abundant (Table 3) and also considering the molecular phylogenetic hypothesis (results not shown).

Diet composition

We analysed 359 stomachs belonging to 15 of the 18 collected species (*C. ocellifer, I. iguana* and *Tu. quadrilineatus* had empty stomachs). We identified 24 prey categories (Table 4), whose importance indices varied from 0.45 (Opiliones for *An. n. brasiliensis*) to 70.99 (Formicidae for *Tropidurus* sp.). Taking all lizard species together, the most important prey categories were spiders (*Ma. nigropunctata* and *Mi. maximiliani*), roaches (*Colobosaura modesta* and *L. klugei*), termites (*Cole. meridionalis, G. carvalhoi* and *Mabuya* sp.), ants (*Tropidurus* sp.), orthopterans (*An. n. brasiliensis, Ph. pollicaris, Tu. merianae* and *Tr. torquatus*) and insect larvae (*Am. ameiva* and *Tr. oreadicus*) (Table 4).

Niche breadth based on diet composition varied from 1.00 (*Tu. merianae* and *Tr. torquatus*) to 5.51 (*An. n. brasiliensis*) (Table 4). However, excluding *Tu. merianae* and *Tr. torquatus*, each with a single analysed stomach, the lowest values of diet breadth were of *Colo. modesta* (1.35) and *Am. ameiva* (2.20). Overlaps in diet composition ranged from zero (*Am. ameiva vs. Colo. modesta, Colo. modesta vs. Po. acutirostris, Colo. modesta vs. Tropidurus* sp., *Colo. modesta vs. Tr. torquatus, Colo. modesta vs. Tu. merianae* and *L. klugei vs. Tu. merianae*) to 0.94 (*G. carvalhoi vs. Mabuya* sp.) (Table 2). The highest overlaps in diet composition occurred among species that feed preferentially on termites (*Cole. meridionalis, G. carvalhoi* and *Mabuya* sp.). Like observed patterns of microhabitat use, sister species in the assemblage supertree (Fig. 2) showed low to moderate overlaps in diet composition, from a minimum of 0.200 (*L. klugei vs. Ph. pollicaris*) to a maximum of 0.748 (*Tropidurus* sp. *vs. Tr. oreadicus*) (for all pairs see Table 2). *Mabuya* sp. and *Ma. nigropunctata* presented high overlaps with almost all species, but only a moderate value between themselves (0.546).

Null model analyses showed that mean overlap in diet composition was not significantly different from random, taking either all lizard species ($\bar{x}_\phi = 0.41$; $P = 0.62$) or only the most abundant ($\bar{x}_\phi = 0.42$; $P = 0.32$). However, after the exclusion of under-represented prey categories, mean overlap in diet composition was significantly smaller than expected by chance, both for all lizard species ($P = 0.03$) or only the most abundant ($P < 0.001$; Fig. 7), indicating assemblage structure along the food niche axis.

With all prey categories and all lizard species included in the analysis, the CPO coupled with Monte Carlo simulations revealed significant phylogenetic effects only for Iguania/Scleroglossa (Table 5). After the exclusion of infrequent lizard species, the two clades Iguania/Scleroglossa and Gymnophthalmidae accounted for significant fractions of the total variation in diet composition (Table 5). Including only the most important prey categories and all lizard species, we identified two historical dietary divergences (Iguania/Scleroglossa and Teiidae) that, in combination, accounted for 58.4% of the total variation (Table 6). After the exclusion of infrequent lizard species, dietary divergences were only evident in Gymnophthalmidae and Iguania/Scleroglossa, explaining 68.1 % of the total variation (Table 6). Iguania and Scleroglossa, the most basal clades of Squamata according to the traditional, morphological phylogeny,

Table 3. Phylogenetic effects upon patterns of microhabitat use by lizards from Seasonally Dry Tropical Forest enclaves in São Domingos, Goiás, Brazil

Label	Clade	Variation	% of variation	F	P
All lizard species included					
I	Teiidae	0.380	18.217	1.828	0.0639
G/L	Iguania/Scleroglossa	0.300	14.382	1.401	0.1656
B	Tropiduridae	0.296	14.190	1.383	0.1991
K	Autarchoglossa	0.288	13.806	1.342	0.1838
J	Teiioidea	0.282	13.519	1.311	0.2031
F	Tupinambinae	0.266	12.752	1.231	0.3465
C	Gekkoninae	0.260	12.464	1.202	0.3346
E	Teiinae	0.256	12.272	1.178	0.3904
H	Gekkonidae	0.230	11.026	1.051	0.4012
D	Scincidae	0.149	7.143	0.664	0.5989
A	Polychrotidae	0.108	5.177	0.474	0.8281
Only lizard species with $n > 5$ included					
C	Gekkoninae	0.199	27.793	1.345	0.1773
B	Tropiduridae	0.180	25.140	1.192	0.2424
H	Gekkonidae	0.151	21.089	0.970	0.4503
K	Autarchoglossa	0.148	20.670	0.942	0.4740
G/L	Iguania/Scleroglossa	0.130	18.156	0.815	0.5915

Values represent variation and percentage of variation in the microhabitat use matrix explained by individual clades, obtained from a Canonical Phylogenetic Analysis, as well as F and P values based on 9999 Monte Carlo permutations. Clade labels according to Figure 3.

were diametrically opposite in diet composition (Fig. 8). Iguanians fed mainly on coleopterans, ants and other hymenopterans, whereas scleroglossans fed more on termites, orthopterans and spiders (Fig. 8). Teiidae and Gymnophthalmidae had similar diets, with dominance of the same prey categories as other scleroglossans, in addition to insect larvae and roaches (Fig. 8). In agreement with these results, the CPO based on the recent, molecular phylogeny and using all combinations of data sets (varying both number of lizard species and prey categories included) revealed significant phylogenetic effects for the clade Iguania and for at least one of the following clades, Teiidae and Gymnophthalmidae.

DISCUSSION

Sampling efficiency, species richness and abundance

The lizard assemblage of São Domingos SDTF enclaves was phylogenetically diverse, including representatives of the major clades of Neotropical squamates. As in other parts of the globe, Scleroglossa (12 species, snakes excluded) was more species-rich than Iguania (six species), reflecting the adaptive success of this lineage, presumably a result of an ancient competitive superiority in terrestrial microhabitats (Vitt *et al*. 2003). Despite the substantial isolation of Cerrado SDTF enclaves relative to other

SDTFs in South America (Prado & Gibbs 1993; Prado 2000), local lizard richness in São Domingos was high compared with other open-vegetation sites in the Neotropical realm (e.g. Vitt 1995; Colli *et al*. 2002; Nogueira *et al*. 2005; Mesquita *et al*. 2006a,b), highlighting its importance for conservation.

Our sampling effort was adequate to represent local lizard richness, given the shape of the rarefaction curve and the similarity between the observed and estimated richness. Nevertheless, this does not imply assemblage saturation, which seems to be only rarely observed (Cornell & Lawton 1992; Cornell 1993; Westoby 1993). Therefore, the lizard assemblage of São Domingos SDTFs may still be colonized by new species from the regional pool. For instance, among the 20 species known to occur in the São Domingos region (Werneck & Colli 2006), the gekkonid *Briba brasiliana* and the gymnophthalmid *Vanzosaura rubricauda* were not recorded in SDTF enclaves. These potential invaders are apparently more associated with open Cerrado habitats in the region.

The large number of gekkonids in São Domingos SDTFs, relative to other sampled sites within the Cerrado biome (Vitt 1991; Colli *et al*. 2002, 2003; Nogueira *et al*. 2005), reflects the affinities of SDTF enclaves with the Caatinga of northeastern Brazil (Vitt 1995; Werneck & Colli 2006). Nocturnal habits of most gekkonids (but not *Cole. meridionalis* and *L. klugei*) allow them to inhabit rich assemblages with little temporal overlap with other lizard species (Pianka 1986; Morton & James 1988; Morton 1993).

Table 4. Importance index of each prey category and values of diet niche breadth in the diet of lizard species from SDTFs enclaves of São Domingos, Goiás

Prey category	Aam	Ani	Cme	Cmo	Gca	Lkl	Mni	Msp	Mma	Pac	Ppo	Tme	Tor	Tsp	Tto
Acari	–	–	3.09	–	–	–	–	–	–	–	–	–	–	–	–
Aranae	17.76	17.63	6.40	–	8.20	–	**41.31**	4.62	**29.71**	–	7.63	–	8.03	6.08	2.03
Non-identified	–	6.53	8.38	19.05	6.17	16.67	–	4.04	13.47	–	8.64	–	3.43	–	–
Blattaria	–	14.66	7.56	**80.95**	8.98	**43.01**	7.79	8.36	15.80	–	5.19	–	17.52	–	–
Coleoptera	8.96	0.91	–	–	4.78	18.90	7.79	0.81	–	**61.00**	3.74	–	14.54	8.43	23.15
Isoptera	–	10.22	**36.87**	–	**48.79**	–	19.36	**61.52**	–	–	21.22	–	36.05	6.33	2.11
Scorpionida	–	–	–	–	0.49	–	–	1.99	–	–	–	–	–	–	–
Formicidae	–	5.64	–	–	12.85	–	–	0.81	–	–	4.58	–	36.31	**70.99**	23.66
Orthoptera	57.58	**37.21**	26.92	–	6.61	–	33.28	18.01	19.22	10.94	**43.03**	**100**	6.92	8.11	**39.68**
Hymenoptera	–	1.72	–	–	1.49	–	–	3.95	–	14.67	5.09	–	8.17	9.82	8.17
Insect larvae	**62.36**	8.89	13.35	–	12.56	–	–	5.64	–	–	7.46	–	**41.21**	27.46	9.15
Odonata	–	0.48	–	–	–	–	–	–	–	–	–	–	–	–	–
Mantodea	–	0.48	–	–	–	–	–	–	–	–	–	–	–	–	–
Gastropoda	–	2.77	–	–	0.51	–	–	0.84	–	5.56	–	–	7.82	2.24	2.60
Opiliones	–	0.45	–	–	–	–	–	–	–	–	–	–	–	–	–
Lizard eggs	–	–	–	–	–	–	–	–	–	–	1.73	–	–	–	–
Phasmida	–	0.53	–	–	–	–	–	–	–	5.39	–	–	–	–	1.80
Hemiptera/Homoptera	–	8.84	–	–	3.49	21.42	–	–	29.22	16.09	5.45	–	–	16.60	10.90
Diplopoda	–	1.73	–	–	–	–	–	1.03	–	–	–	–	–	–	–
Pseudoscorpiones	–	–	–	–	1.00	–	–	–	–	–	–	–	–	–	–
Dermaptera	–	–	3.23	–	–	–	–	–	–	–	–	–	–	–	–
Plant parts	–	–	–	–	–	–	–	0.81	–	4.85	–	–	–	1.84	2.23
Solifuga	–	–	–	–	–	–	–	0.92	–	–	–	–	–	–	–
Shed skin	–	0.74	3.99	–	–	–	–	–	–	–	1.73	–	–	–	–
N	5	115	17	7	82	4	7	45	9	9	28	1	10	19	1
B_{dn}	1.98	7.57	3.54	1.69	2.36	4.00	3.90	1.20	4.17	3.10	5.18	1.00	2.57	1.48	1.00
B_{dv}	2.42	3.44	4.18	1.00	3.02	1.54	2.07	3.54	2.66	1.68	2.70	1.00	2.96	3.69	1.00
B_{dieta}	2.20	5.51	3.86	1.35	2.69	2.77	2.99	2.37	3.42	2.39	3.94	1.00	2.77	2.59	1.00

The main prey category for each species is in boldface. B_{dn}, numeric niche breadth; B_{dv}, volumetric niche breadth; B_{diet}, mean between B_{dn} and B_{dv}. Aam, *Ameiva ameiva*; Ani, *Anolis nitens*; Cme, *Coleodactylus meridionalis*; Cmo, *Colobosaura modesta*; Gca, *Gymnodactylus carvalhoi*; Lkl, *Lygodactylus klugei*; Mni, *Mabuya nigropunctata*; Msp, *Mabuya sp.*; Mma, *Micrablepharus maximiliani*; Pac, *Polychrus acutirostris*; Ppo, *Phyllopezus pollicaris*; Tme, *Tupinambis merianae*; Tor, *Tropidurus oreadicus*; Tsp, *Tropidurus sp.*; Tto, *Tropidurus torquatus*.
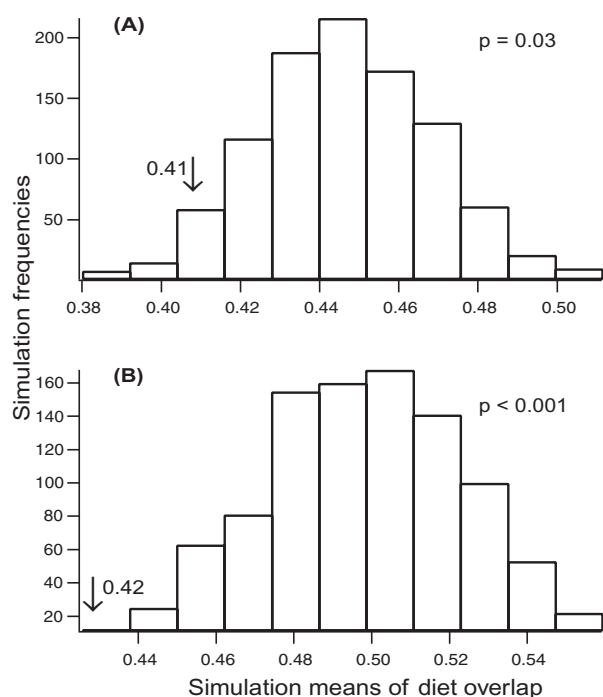
Fig. 7. Observed and expected mean diet niche overlap among lizards from SDTFs of São Domingos, considered most common prey items and all species (A) most common prey items and only the most abundant species (B). Arrows indicate observed means, *P*-values are probabilities that observed means are smaller than expected random means (10 000 simulations).

Microhabitat use

In São Domingos SDTFs, *G. carvalhoi* and *Mi. maximiliani* showed the broadest use of available microhabitats. Previous studies indicated much narrower microhabitat preferences in *G. carvalhoi*, primarily in association with rock outcrops and epigeous termite nests, which provide both shelter and food (Colli *et al*. 2003; Vitt *et al*. 2007b). In São Domingos SDTFs, however, *G. carvalhoi* uses a wider range of microhabitats (Fig. 5), presumably because of a lack of epigeous termite nests and the limited availability of rock outcrops in the study sites (FPW, pers. obs. 2003). Considering the thermal ecology of this species (low body temperatures, Colli *et al*. 2003; Vitt *et al*. 2007b), the dry forest may produce a less thermally extreme environment, resulting in ecological release. Microhabitats under surface objects like dead trees (logs) may not be much different from living in a termite nest or under a rock. In addition, a broader spatial niche may reduce frequency of intraspecific encounters, as in termite nests *G. carvalhoi* often occurs in singles or pairs, or simply be a mechanism to locate their preferred prey (termites). *Micrablepharus atticolus* can occur in association with leaf-cutter ant

nests (Vitt 1991; Vitt & Caldwell 1993), but in São Domingos *Mi. maximiliani* uses primarily the open ground, leaf litter and rock crevices (Fig. 5).

Despite their high overlap in microhabitat use, it is unlikely that *Tropidurus* sp. and *Ph. pollicaris* interact directly, because *Ph. pollicaris* is nocturnal (Vitt 1995) and *Tropidurus* is diurnal. Likewise, the high overlap between *An. n. brasiliensis* and the species of teiids exclusively associated with open ground (*Am. ameiva*, *Tu. merianae* and *Tu. quadrilineatus*) does not reflect direct competition. Teiids are heliothermic and use preferentially forest borders, which receive more direct sunlight (Vitt & Colli 1994; Vitt *et al*. 1997b), whereas *An. n. brasiliensis* uses the leaf litter of the forest floor (Vitt *et al*. 2001) (Fig. 5).

The low overlap in microhabitat use between the sister-species, *Ma. nigropunctata* and *Mabuya* sp., may have permitted the successful establishment of *Mabuya* sp. in São Domingos SDTFs. Neotropical species of *Mabuya* are similar in morphology and ecology, which explains why the genus is usually represented by a single species in local assemblages (Vitt & Zani 1996). When two or more species of *Mabuya* coexist, niche overlap is low, but at this point, we cannot determine whether this is a result of ecological interactions or a more ancient historical divergence (Mesquita *et al*. 2006a). The evolutionary relationship between the two species of *Mabuya* in São Domingos is unknown, therefore the basis for their differences in microhabitat use and diet composition cannot be ascertained (Losos 1996).

Even though overlap in microhabitat use among the most abundant species and between sister-species of the São Domingos lizard assemblage was low, the null model analysis indicated lack of assemblage structure (Table 2 and Fig. 6). Other Neotropical lizard assemblages have similar patterns (e.g. Mesquita *et al*. 2006a,b). Thus, no evidence exists for ongoing competition for microhabitats among lizard species in São Domingos SDTFs. Likewise, we detected no significant phylogenetic effects on patterns of microhabitat use. Among lizards, evolutionary constraints on microhabitat use are less common than on diet composition, that is, within-clade variation in microhabitat use is much higher than variation in diet composition (Vitt *et al*. 1999). Thus, it is likely that the availability of the (historically) preferred prey types moderates microhabitat selection.

Diet composition

Diets of most lizard species in São Domingos SDTFs resemble those of conspecific or congeneric species in other Neotropical assemblages, including *Am. ameiva* (insect larvae and orthopterans, Vitt & Colli 1994), *An. nitens* (orthopterans and spiders, Vitt *et al*. 2001),

Table 5. Phylogenetic effects upon patterns of diet composition by lizards from Seasonally Dry Tropical Forest enclaves in São Domingos, Goiás, Brazil

Label	Clade	Variation	% of variation	F	P
All lizard species included					
G/K	Iguania/Scleroglossa	0.205	24.551	2.118	0.009*
F	Teiidae	0.179	21.437	1.817	0.0524
E	Gymnophthalmidae	0.176	21.078	1.783	0.0570
B	Tropiduridae	0.158	18.922	1.573	0.0812
I	Teiioidea	0.147	17.605	1.456	0.1192
J	Autarchoglossa	0.143	17.126	1.405	0.1422
A	Polychrotidae	0.112	13.413	1.079	0.3844
H	Gekkonidae	0.106	12.695	1.018	0.4148
D	Scincidae	0.097	11.617	0.927	0.4884
C	Gekkoninae	0.067	8.024	0.622	0.8426
Only lizard species with $n > 5$ included					
E	Gymnophthalmidae	0.216	29.711	1.944	0.0388*
G/K	Iguania/Scleroglossa	0.201	27.648	1.787	0.0175*
A	Polychrotidae	0.158	21.733	1.345	0.2074
B	Tropiduridae	0.156	21.458	1.326	0.2276
J	Autarchoglossa	0.156	21.458	1.330	0.1458
H	Gekkonidae	0.112	15.406	0.918	0.5693
D	Scincidae	0.102	14.030	0.822	0.6073
C	Gekkoninae	0.054	7.428	0.420	0.9777

Values represent variation and percentage of variation in the diet composition matrix (all prey categories included) explained by individual clades, obtained from a Canonical Phylogenetic Analysis, as well as F and P values based on 9999 Monte Carlo permutations. Clade labels according to Figure 3. Significant P values are marked with an asterisk.

Table 6. Phylogenetic effects upon patterns of diet composition by lizards from Seasonally Dry Tropical Forest enclaves in São Domingos, Goiás, Brazil

Label	Clade	Variation	% of variation	F	P
All lizard species included					
G/K	Iguania/Scleroglossa	0.180	29.654	2.545	0.0117*
F	Teiidae	0.174	28.666	2.450	0.0262*
E	Gymnophthalmidae	0.172	28.336	2.405	0.0322
B	Tropiduridae	0.145	23.888	1.977	0.0633
I	Teiioidea	0.136	22.405	1.834	0.0764
J	Autarchoglossa	0.125	20.593	1.667	0.1055
A	Polychrotidae	0.076	12.521	0.959	0.4368
D	Scincidae	0.065	10.708	0.822	0.4991
H	Gekkonidae	0.050	8.237	0.621	0.7680
C	Gekkoninae	0.038	6.260	0.463	0.8764
Only lizard species with $n > 5$ included					
E	Gymnophthalmidae	0.208	41.188	2.860	0.0228*
G/K	Iguania/Scleroglossa	0.173	34.257	2.259	0.0135*
B	Tropiduridae	0.144	28.515	1.796	0.1550
J	Autarchoglossa	0.136	26.931	1.682	0.0909
A	Polychrotidae	0.123	24.356	1.498	0.2517
D	Scincidae	0.070	13.861	0.790	0.5484
H	Gekkonidae	0.045	8.911	0.500	0.8359
C	Gekkoninae	0.016	3.168	0.172	0.9693

Values represent variation and percentage of variation in the diet composition matrix (only most important prey categories included) explained by individual clades, obtained from a Canonical Phylogenetic Analysis, as well as F and P values based on 9999 Monte Carlo permutations. Clade labels according to Figure 3. Significant P values are marked with an asterisk.
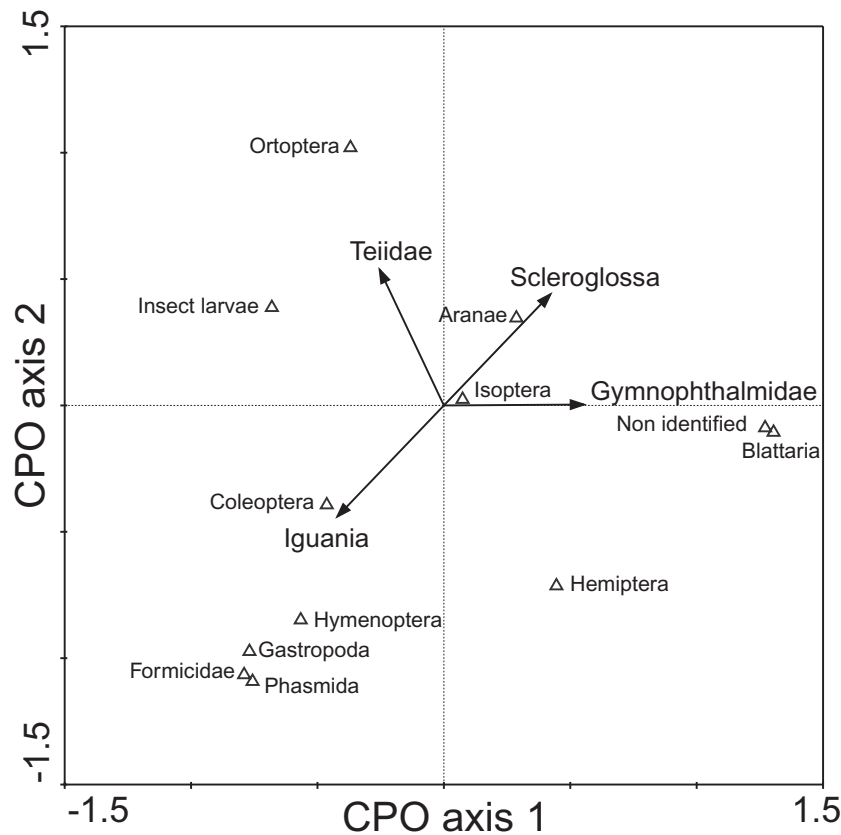
Fig. 8. Biplot showing results of the canonical phylogenetic ordination analysis. This plot shows the position of each prey category (triangles) on the first two axes of dietary niche space. Clades with significant association with prey categories are indicated by arrows. Clades of Squamata that explained significant amounts of the total variation in diet composition are plotted with vectors radiating out from the origin. Length of vectors indicates significance strength, whereas distance of arrow tips to triangles represents relative importance of prey categories in lizard diets for each clade.

G. carvalhoi (termites, Vitt 1995; Colli *et al.* 2003), *Ma. nigropunctata* (spiders, orthopterans, termites, Mesquita *et al.* 2006a,b), *Mi. maximiliani* (spiders, hemipterans/homopterans, orthopterans, Mesquita *et al.* 2006a,b), *Ph. pollicaris* (termites and orthopterans, Vitt 1995), *Tropidurus oreadicus* (ants, termites, insect larvae, Colli *et al.* 1992; Faria & Araujo 2004) and *Tr. torquatus* (orthopterans, ants, coleopterans, Araujo 1987; Bergallo & Rocha 1994). Thus, lizard diets seem to be evolutionarily constrained, with little intra-clade variation.

Individual niche breadth values were relatively low compared with the same species in other assemblages (e.g. Vitt & Carvalho 1995; Dias & Lira-da-Silva 1998; Vitt *et al.* 1999, 2001), suggesting some overall diet partitioning for lizards in São Domingos SDTFs. On the other hand, the relatively high values of diet overlap between some particular species (*Cole. meridionalis*, *G. carvalhoi*, *Mabuya* sp.), relative to other assemblages (e.g. Vitt 1995; Vitt & Carvalho 1995; Vitt & Zani 1996, 1998b), may have arisen from the use of the same prey, particularly termites. As with

microhabitat use, pairs of closely related species showed moderate to low values of diet overlap. This pattern may have resulted from *in situ* divergence, to minimize competitive interactions, or by inheritance from more remote ancestors, thus facilitating coexistence (Brooks & McLennan 1991).

The lizard assemblage of São Domingos SDTFs is structured with respect to diet composition, a pattern found in many lizard assemblages of Neotropical forests (Vitt & Zani 1996, 1998a,b), but uncommon in Neotropical savannas (Gainsbury & Colli 2003; Mesquita *et al.* 2006a,b). Non-random patterns of diet composition may arise by ecological interactions among coexisting species, where low values of diet overlap obviate the need to invoke ongoing competition for food. Conversely, lizard species in the assemblage may coexist because ancestral characters (evolved prior to the formation of the assemblage) promote niche segregation, thus preventing competition. In this case, species are able to enter the assemblage if they bear characteristics not in conflict with the existing assemblage structure (Brooks &

McLennan 1993). The CPO indicated that differences in diet composition among lizards in São Domingos SDTFs have a historical basis, not necessarily reflecting current ecological interactions (Losos 1996).

The first and more dramatic dietary shift in the evolution of Squamata presumably occurred during the late Triassic, when Iguania and Scleroglossa diverged from a pleurodont ancestor (Vitt & Pianka 2005). The historical advent of derived characters for Scleroglossa, such as cranial mesokinesis, chemical prey discrimination, vomeronasal system, jaw prehension and wide foraging, facilitated access to new food sources, and we should expect a detectable divergence in diet composition between Iguania and Scleroglossa, at least on a global scale (Vitt *et al.* 2003). Therefore, some differences in diet composition among lizard species in São Domingos SDTFs, determined by the ability to chemically discriminate prey, were defined long before the formation of the assemblage. In addition to the Iguania/Scleroglossa dichotomy, we identified significant phylogenetic effects in the São Domingos assemblage among teiids and gymnophthalmids. Members of these clades have highly conserved ecologies, with little influence of local environmental conditions, as indicated by geographical variation analyses (e.g. Vitt & Colli 1994; Vitt *et al.* 1997a; Mesquita & Colli 2003). These taxa, prevalent in Neotropical assemblages, often form homogeneous guilds in these assemblages (Mesquita *et al.* 2006a,b). Conversely, other clades represented in the São Domingos assemblage (with no detectable phylogenetic effects) were identified in a global analysis as exerting significant phylogenetic effects on diet composition (Vitt & Pianka 2005). This highlights the fact that taxonomic composition may influence the ability to detect phylogenetic constraints in assemblage structure (Cadle & Greene 1993; Vitt *et al.* 1999; Anderson *et al.* 2004; Mesquita *et al.* 2006a). For instance, because Scleroglossa (12 species) is better represented than Iguania (6) in the São Domingos assemblage, it might be harder to detect significant phylogenetic effects among the latter.

A complex mixture of historical, ecological and stochastic influences, which allow species coexistence, structures-rich and phylogenetically diverse assemblages (Ricklefs & Schluter 1993). The lizard assemblage of São Domingos SDTFs enclaves is historically structured in terms of diet composition, but shows no structure regarding microhabitat use, indicating lack of ongoing interspecific interactions along these niche dimensions. However, other niche dimensions not here considered, such as body size and shape, might also be important in the structure and maintenance of the São Domingos assemblage. The incorporation of additional data, such as evolutionary rates, better resolution of the phylogenetic hypothesis or even the discovery of new species in the assemblage, might corroborate or challenge our conclusions regarding the influence of phylogenetic constraints upon assemblage structure.

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