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ORIGINAL ARTICLE

The lizard assemblage from Seasonally Dry Tropical Forest enclaves in the Cerrado biome, Brazil, and its association with the Pleistocenic Arc

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ABSTRACT

Aim To determine if the distributions of lizard species from Seasonally Dry Tropical Forest (SDTF) enclaves within the Cerrado biome in central Brazil are associated with the Tropical Seasonal Forests Region, a recently proposed phytogeographic unit of South America, corroborating the existence of a Pleistocenic Arc of SDTFs.

Location SDTF remnants in the Paranã River valley, municipality of São Domingos, Goiás, Brazil.

Methods Lizards were extensively sampled using haphazard sampling, funnel traps, and pitfall traps with drift fences during four expeditions. The composition of the SDTF lizard assemblage was compared with those from other South American phytogeographic regions (Caatinga, Cerrado, Chaco, Llanos, and the dry forests of Colombia and Bolivia), based on the literature and our own unpublished data.

Results The SDTF lizard assemblage contained 20 species, including 11 species with extensive distributions among the regions considered, seven species shared exclusively with Cerrado localities, a single species shared exclusively with other SDTFs, and one endemic species. The presence of *Lygodactylus klugei* (Smith, Martin & Swain, 1977), presumably endemic to the Pleistocenic Arc formed by the Tropical Seasonal Forests Region, considerably extends the known distribution of this species, suggesting historical connections between Caatinga and Cerrado SDTF enclaves.

Main conclusions The composition of the lizard assemblage in Cerrado SDTF enclaves seems to corroborate the recent proposal that the SDTF should be recognized as a phytogeographic unit (or dominium). The presence of disjunct populations and endemic species highlights the urgency of considering the uniqueness of the Paranã River valley SDTFs and the importance of its conservation.

Keywords

Biogeography, Brazil, Caatinga, Cerrado, Chaco, community, lizards, Seasonally Dry Tropical Forests.

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INTRODUCTION

Seasonally Dry Tropical Forests (SDTFs) occur in frost-free areas where the mean annual temperature is higher than 17 °C and the mean annual rainfall is highly seasonal (Murphy & Lugo, 1986). They are restricted to fertile mesotrophic soils derived from basic rocks, with high nutrient levels, low levels of aluminium, and moderate to high pH (Ratter *et al.*, 1978; Ratter, 1992). Usually, SDTFs are not associated with water courses, and the vegetation is semi-deciduous or deciduous during the dry season, when more than 50% of the arboreal cover can be completely lost (Murphy & Lugo, 1986; Felfili & Silva Júnior, 2001). Much confusion exists in the literature owing to the different regional names associated with SDTFs, including: tropical and subtropical dry forest, Caatinga, deciduous and semi-deciduous forest, bosque caducifolio seco,

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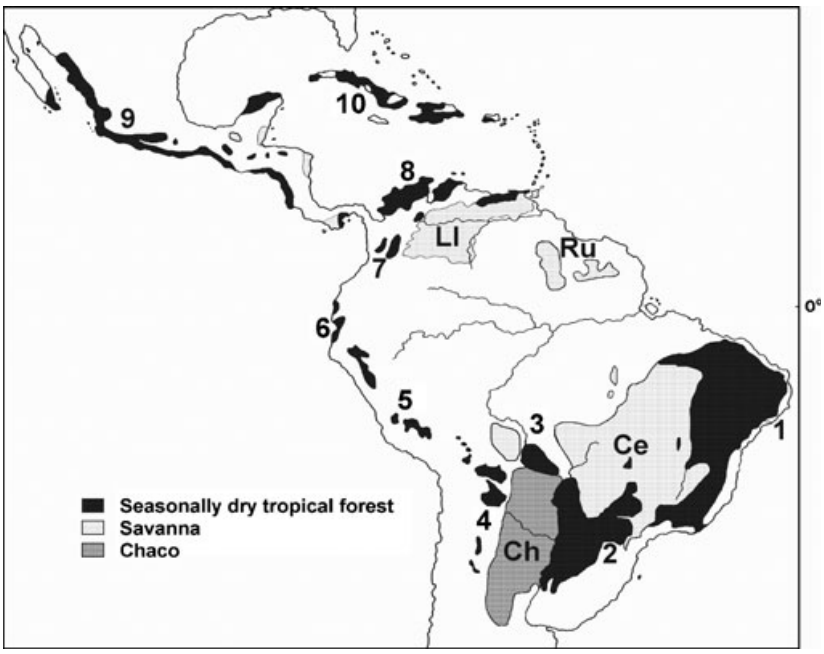

Figure 1 Distribution of Seasonally Dry Tropical Forests (SDTFs) and other dry vegetation types (savannas, including Cerrado [Ce], Chaco [Ch], Llanos [Ll] and Rupununi [Ru]) in the Neotropical region, according to Prado & Gibbs (1993). SDTFs occur in the following areas: 1. Northeast Brazil (Caatingas), 2. Misiones Nucleus, 3. Bolivian Chiquitano region, 4. Piedmont Nucleus, 5. Bolivian and Peruvian Inter Andean valleys, 6. Pacific coastal Ecuador, 7. Colombian Inter Andean valleys, 8. Caribbean coast of Colombia and Venezuela, 9. Central America, and 10. Antilles. From Pennington *et al.* (2000), with permission.

bosque espinoso, and mesotrophic forest (Murphy & Lugo, 1986; Pennington *et al.*, 2004). SDTFs have a discontinuous distribution, from the Caatinga in north-eastern Brazil to the Uruguay River valley (Fig. 1). Some less studied and more isolated remnants of SDTFs occur as enclaves within the Cerrado, a savanna biome that covers the central Brazilian plateau (Oliveira & Marquis, 2002) in areas of favourable edaphic conditions (Ratter *et al.*, 1978; Silva, 1995a; Silva & Bates, 2002). In central Brazil, SDTFs are typically fragmented and once covered more than 15% of the two million hectares of the Cerrado biome, forming a 'seasonal corridor of fragments' (Felfili, 2003).

Present-day SDTFs may represent relics of a formerly more extensive and contiguous formation, which presumably reached its maximum extension during the last glacial maximum of the late Pleistocene, the so-called Pleistocenic Arc (Prado, 1991; Prado & Gibbs, 1993). Based on floristic data and patterns of endemism of plant taxa, Prado (2000) regarded the region covered by the Pleistocenic Arc as a new phytogeographic unit (or dominium) of South America, the Tropical Seasonal Forests Region. This region has three nuclei: (1) the Caatingas nucleus in north-eastern Brazil, (2) the Misiones nucleus along the Paraguay-Paraná river, and (3) the 'Subandean Piedmont nucleus' in south-western Bolivia and north-western Argentina [for a fuller discussion see Prado & Gibbs (1993), Prado (2000) and Pennington *et al.* (2000)] (Fig. 1). Using molecular data from some plant groups, Pennington *et al.* (2004) found that many SDTF species are primarily pre-Pleistocenic, leading them to reject the hypothesis that endemics were produced allopatrically by Pleistocene vicariance. However, they argued that evidence from widespread species distributions is still suggestive that SDTFs were historically more extensive and contiguous.

The importance of considering SDTFs as being distinct from savannas in biogeographical analyses and conservation strategies has been emphasized in previous work (Pennington *et al.*, 2000). However, these studies were primarily based on plant distributions (Pennington *et al.*, 2000; Felfili, 2003), with a few including bird distributions (Silva, 1995a,b; Porzecanski & Cracraft, 2005). The SDTF fauna could have followed vegetation cycles and had contiguous, widespread populations during the existence of the Pleistocenic Arc. If this really was the case, some components of Caatinga may have colonized the Cerrado region, where populations would have been maintained at present-day levels in SDTF enclaves (Silva & Bates, 2002).

Early studies indicated that Caatinga and Cerrado lack a characteristic lizard fauna (Vanzolini, 1974, 1976, 1988; Vitt, 1991), both biomes being part of a 'diagonal of open formations' (Vanzolini, 1963) or a 'savanna corridor' (Schmidt & Inger, 1951) that extends from south-western to north-eastern South America. Caatinga and Cerrado have diverse lizard faunas with many endemics (Rodrigues, 1996; Colli *et al.*, 2002; Rodrigues, 2003), and the great diagonal includes areas that presumably do not share the same history (Colli, 2005). However, the composition and historical relationships of lizard assemblages from Cerrado STDF enclaves are still unknown.

Their occurrence on fertile soils, highly favourable for agriculture, the presence of timber species with commercial importance, and the low attention to conservation efforts give SDTFs the status of the most threatened tropical ecosystem (Janzen, 1988; Scariot & Sevilha, 2000, 2003; Sánchez-Azofeifa *et al.*, 2005; Prance, 2006; Vieira & Scariot, 2006). Among tropical forests, SDTFs have the greatest annual destruction rate, 0.96% (Whitmore, 1997), and, on a global basis, SDTFs of Latin America experienced the greatest deforestation rates between 1980 and 2000, estimated at 12% (Miles *et al.*, 2006).

Furthermore, 97% of the remaining areas of tropical dry forests are at risk of extinction (Miles *et al.*, 2006), rendering the associated fauna highly susceptible to extinction (Ceballos & Garcia, 1995). These points highlight the importance and urgency of investigating the species composition of SDTFs and their relationships with the surrounding vegetation types. Herein, we describe the lizard fauna of SDTF remnants in the Paranã River valley, within the Cerrado biome. Our main goals are: (1) to describe the composition of the lizard assemblage of a highly threatened area of SDTFs, (2) to evaluate the contribution of surrounding faunas (Caatinga and Cerrado) to the composition of the local lizard assemblage, and (3) to identify patterns of endemism and vicariance, to determine if lizard distributions are associated with the Tropical Seasonal Forests Region, a new phytogeographic unit of South America proposed by Prado (2000).

MATERIAL AND METHODS

Study site

The Paranã River basin covers 5,940,382 ha in central Brazil, between the Divisor São Francisco-Tocantins Plateau and the Central Goiano Plateau (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. The climate in the region falls into Köppen's Aw category, with a mean annual temperature of 24 °C, mean annual rainfall of 1500 mm year^{-1}, at least 5–6 months receiving less than 200 mm, and altitudes ranging from 400 to 600 m (IBGE, 1995). The main woody plant species from SDTF enclaves of São Domingos, Goiás are listed in Table 1. The intense human occupation during the 1980s restricted SDTFs to small fragments in flat, lowland areas or on limestone outcrops (Scariot & Sevilha, 2000, 2003). The region is considered to be of extremely high ecological relevance for conservation (MMA, 1999).

Table 1 Main woody plant species from Seasonally Dry Tropical Forest enclaves of São Domingos, Goiás. Adapted from Scariot & Sevilha (2000)

Species	Vernacular name
Anacardiaceae	
Myracrodruon urundeuva	Aroeira
Spondias mombim	Cajá-mirim, tapereba
Apocynaceae	
Aspidosperma pyrifolium	Peroba
Aspidosperma subincanum	Perobinha
Bignoniaceae	
Tabebuia impetiginosa	Ipê rosa
Bombacaceae	
Cavanillesia arborea	Barriguda
Chorisia pubiflora	Barrigudinha
Caesalpiniaceae	
Bauhinia sp.	Pata-de-vaca
Combretaceae	
Combretum duarteanum	Vaqueta
Combretum sp.	
Fabaceae	
Lonchocarpus muehelbergianus	Rabo-de-bugio
Meliaceae	
Cedrella fissilis	Cedro
Mimosaceae	
Anadenanthera macrocarpa	Angico-vermelho

Data collection

Field studies were conducted during four expeditions of 12 days each, from August to September 2003 (dry season), December 2003 (wet season), April 2004 (early dry season), and November 2004 (early wet season). We collected lizards in SDTF remnants, both in undisturbed and disturbed fragments, on flat lowlands and limestone outcrops in the municipality of São Domingos, Goiás, Brazil (13°23′54″ S, 46°16′06″ W) (Fig. 2). We installed an array of 25 pitfall traps in an undisturbed SDTF fragment at Fazenda Flor do Ermo (13°39′26″ S, 46°45′09″ W). Each trap consisted of four buckets (30 L) arranged in a 'Y', with a central bucket connected to three peripheral buckets by a 5-m long and 0.5-m high plastic drift fence, forming three 120° angles. The base of the plastic fence was buried in the soil (*c.* 10 cm), to prevent lizards from passing underneath. Arrays were placed along a transect, 30 m apart from each other, and were checked daily. Additional specimens were collected by haphazard sampling, using a shotgun, sticky traps, or by manual collection in neighbouring SDTF fragments. We killed captured lizards with a lethal injection of Tiopental®, recorded morphometric variables (using Mitutoyo® electronic calipers), and fixed them using 10% formalin. All specimens were deposited in the 'Coleção Herpetológica da Universidade de Brasília' (CHUNB).

Species list

To compare our results with those of other regions, we compiled species lists from the literature and our own unpublished data for Cerrado (Colli *et al.*, 2002; Mesquita *et al.*, 2006a,b), Caatinga (Rodrigues, 2003), Chaco (Gallardo, 1979; Norman, 1994; Gil *et al.*, 1995; Lavilla *et al.*, 1995; Fitzgerald *et al.*, 1999), Llanos (Staton & Dixon, 1977; Rivero-Blanco & Dixon, 1979), and dry forests of Colombia (F. Castro, pers. comm.) and Bolívia (D. Embert, Florida Province, Departmento Santa Cruz, pers. comm.). The species list for SDTF enclaves is based exclusively on our fieldwork, since there are no published accounts on the herpetofauna of the region. We followed the taxonomic arrangement of Frost & Etheridge (1989) and Frost *et al.* (2001).

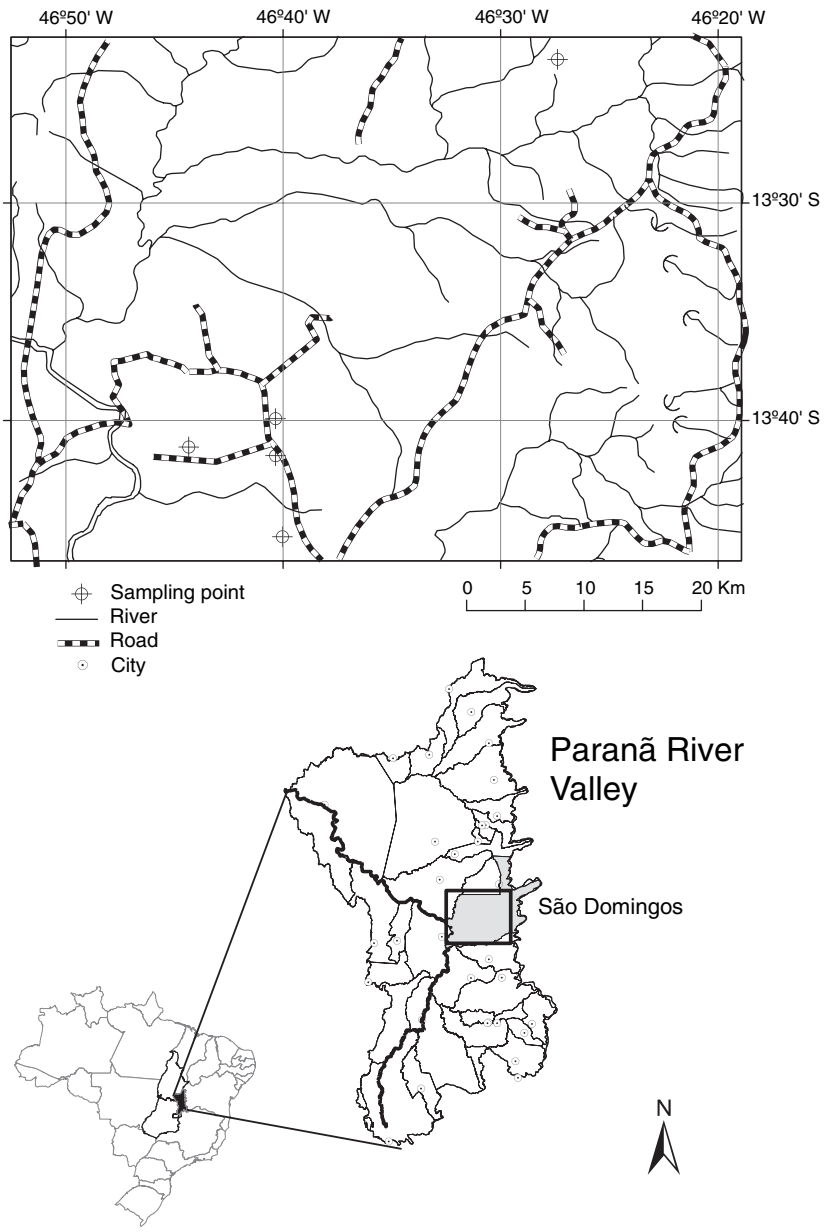

Figure 2 Lower left: location of the Paranã River Valley in Brazil. Middle: location of study area (rectangle) in the Paranã River Valley. Shapes represent municipalities, with São Domingos municipality highlighted in grey. Paranã River indicated by bold path. Top: study area, with indication of sampling points.

To evaluate the contribution of other South American open vegetation biomes to the species composition of our study area, we grouped lizard species in the following geographic distribution categories: (1) species with extensive distributions (present in three or more regions, including the study area), (2) species shared exclusively with other SDTFs (Caatinga, Colombian and/or Bolivian dry forests), (3) species shared exclusively with Cerrado, and (4) species endemic to the study area.

RESULTS AND DISCUSSION

Local richness

We recorded 20 lizard species in the study area, distributed in seven families (Table 2; Fig. 3). Gekkonidae and Teiidae were the most species-rich families, with five and four species each, respectively (Table 2). We identified four biogeographical patterns of occurrence for the lizards in our study area, which suggest that the lizard fauna of SDTF enclaves at São Domingos is a mosaic of dispersing (association by colonization) and historical/vicariant (association by descent) elements (Brooks & McLennan, 1991, 1993; Webb *et al.*, 2002).

Widespread species

Eleven species have extensive distributions among the landscapes considered, being found in at least three of them (Table 2). *Ameiva ameiva* (Linnaeus, 1758), *Iguana iguana* (Linnaeus, 1758), and *Tupinambis merianae* (Duméril & Bibron, 1839), besides being widespread in open vegetation landscapes, also occur in forested landscapes. *Phyllopezus*

Table 2 Composition of lizard assemblage from SDTF enclaves at São Domingos, Goiás and in other open-vegetation biomes. Geographic distribution categories: (a) extensive distribution, (b) shared exclusively with other SDTFs (Caatinga, Colombian and/or Bolivian dry forests), (c) shared exclusively with Cerrado, and (d) endemic to the study area. BOL: Bolivian dry forest, CAA: Caatinga, CER: Cerrado, CHA: Chaco, COL: Colombian dry forests, LLA: Llanos. See text for details

Lizard taxa	BOL	CAA	CER	CHA	COL	LLA
Gekkonidae						
Briba brasiliana (a)		X	X			
Coleodactylus meridionalis (a)		X	X			
Gymnodactylus geckoides (a)		X	X			
Lygodactylus klugei (b)		X				
Phyllopezus pollicaris (a)	X	X	X	X		
Iguanidae						
Iguana iguana (a)		X	X		X	X
Polychrotidae						
Anolis nitens brasiliensis (c)			X			
Polychrus acutirostris (a)	X	X	X	X		
Tropiduridae						
Tropidurus oreadicus (c)			X			
Tropidurus sp. (c)			X			
Tropidurus torquatus (c)			X			
Scincidae						
Mabuya nigropunctata (c)	X		X			
Mabuya sp. (d)						
Teiidae						
Ameiva ameiva (a)	X	X	X	X	X	X
Cnemidophorus ocellifer (a)	X	X	X	X		
Tupinambis merianae (a)		X	X	X		
Tupinambis quadrilineatus (c)			X			
Gymnophthalmidae						
Colobosaura modesta (c)			X			
Micrablepharus maximiliani (a)	X	X	X			
Vanzosaura rubricauda (a)	X	X	X	X		
Shared species	7	12	17	6	2	2
Total richness	16	48	50	31	15	12

pollicaris (Spix, 1825), *Polychrus acutirostris* (Spix, 1825), and *Vanzosaura rubricauda* (Boulenger, 1902) are widespread along the 'great diagonal' of open landscapes, from Chaco to Caatinga. The presence of these species in the SDTF enclaves is of little help in understanding their historical connections with other areas. *Cnemidophorus ocellifer* (Spix, 1825), *Coleodactylus meridionalis* (Boulenger, 1888), and *Gymnodactylus geckoides* (Spix, 1825) occur in Caatinga and Cerrado, but clearly represent species complexes and their taxonomy needs to be clarified before any firm conclusions can be drawn from their distributions. *Micrablepharus maximiliani* (Reinhardt & Lütken, 1862) is widespread in Cerrado and penetrates neighbouring biomes, such as Caatinga. Its presence in SDTF enclaves is probably a result of colonization from the surrounding Cerrado. Conversely, *Briba brasiliana* (Amaral, 1935) is widespread in Caatinga and penetrates the Cerrado along the contact zones between the two biomes, where it occurs in isolated populations. The presence of *B. brasiliana* in SDTF enclaves may have resulted from historical connections with Caatinga (vicariance) or from dispersal throughout the intervening Cerrado matrix. Only a detailed phylogeographic analysis could choose between these conflicting hypotheses.

Species shared exclusively with Cerrado

Seven species (*Anolis nitens brasiliensis* (Vanzolini & Williams, 1970), *Tropidurus oreadicus* (Rodrigues, 1987), *Tropidurus* sp., *Tropidurus torquatus* (Wied, 1820), *Mabuya nigropunctata* (Spix, 1825), *Tupinambis quadrilineatus* (Manzani & Abe, 1997), and *Colobosaura modesta* (Reinhardt & Lütken, 1862)) are shared exclusively with Cerrado (Table 2). These occurrences in SDTF enclaves probably represent instances of post-isolation dispersion. Four of these species, *A. n. brasiliensis*, *C. modesta*, *M. nigropunctata*, and *T. quadrilineatus*, are primarily associated with forested habitats of Cerrado (Colli *et al.*, 1998, 2002; Brandão & Araújo, 2001), suggesting an extensive interchange between the latter and STDF enclaves. Therefore, SDTF enclaves, as gallery forests within Cerrado, may be very important in maintaining viable populations of forest species within a matrix of open vegetation (Silva, 1995a; Brandão & Araújo, 2001), reinforcing the importance of dry forest enclaves in the maintenance of regional lizard species richness and the need for conservation attention (Felfili, 2003). Furthermore, the fact that SDTFs in the Paranã River valley are arranged as isolated enclaves, whereas gallery forests form an interconnecting network (Brandão & Araújo, 2001), highlights their endangered status and relevance to conservation.

Endemic species and species shared with other SDTFs

Among the 19 species we recorded in the study area, only two have not previously been recorded in Cerrado: *Lygodactylus klugei*, considered a Caatinga-restricted species (Vanzolini, 1974, 1976; Smith *et al.*, 1977), and *Mabuya* sp., apparently endemic to SDTF enclaves in São Domingos. In terms of the uniqueness of the lizard fauna of SDTF enclaves, these two species not shared with the surrounding Cerrado matrix are key elements.

Lygodactylus is represented in South America by two species with disjunct distributions, separated by the Pantanal and Cerrado biomes: *L. wetzeli* (Smith, Martin & Swain, 1977), restricted to Chaco, and *L. klugei*, restricted to Caatinga (Vanzolini, 1974, 1976; Smith *et al.*, 1977). The presence of *L. klugei* in SDTF enclaves, isolated from Caatinga populations, and its absence from the surrounding Cerrado may be considered a new geographic distribution record and evidence for historical connections between Caatinga and SDTF enclaves in Cerrado. Note that the possibility of jump dispersal cannot be totally dismissed, but this is a less likely process than

Figure 3 Study site and lizard species occurring in seasonally dry tropical forests (SDTFs) remnants in the Paranã River Valley. (a) Pitfall traps in an undisturbed SDTF fragment (photo by A. B. Gamble), (b) *Briba brasiliana* (photo by L. J. Vitt), (c) *Coleodactylus meridionalis* (ABG), (d) *Gymnodactylus geckoides* (ABG), (e) *Lygodactylus klugei* (photo by D. O. Mesquita), (f) *Phyllopezus pollicaris* (ABG), (g) *Iguana iguana* (LJV), (h) *Anolis nitens* (LJV), (i) *Polychrus acutirostris* (photo by F. P. Werneck), (j) *Tropidurus oreadicus* (DOM), (k) *Tropidurus* sp. (ABG), (l) *Mabuya nigropunctata* (photo by G. R. Colli), (m) *Mabuya* sp. (FPW), (n) *Ameiva ameiva* (GRC), (o) *Cnemidophorus ocellifer* (DOM), (p) *Tupinambis merianae* (GRC), (q) *Tupinambis quadrilineatus* (GRC), (r) *Colobosaura modesta* (LJV), (s) *Micrablepharus maximiliani* (FPW), (t) *Vanzosaura rubricauda* (LJV).

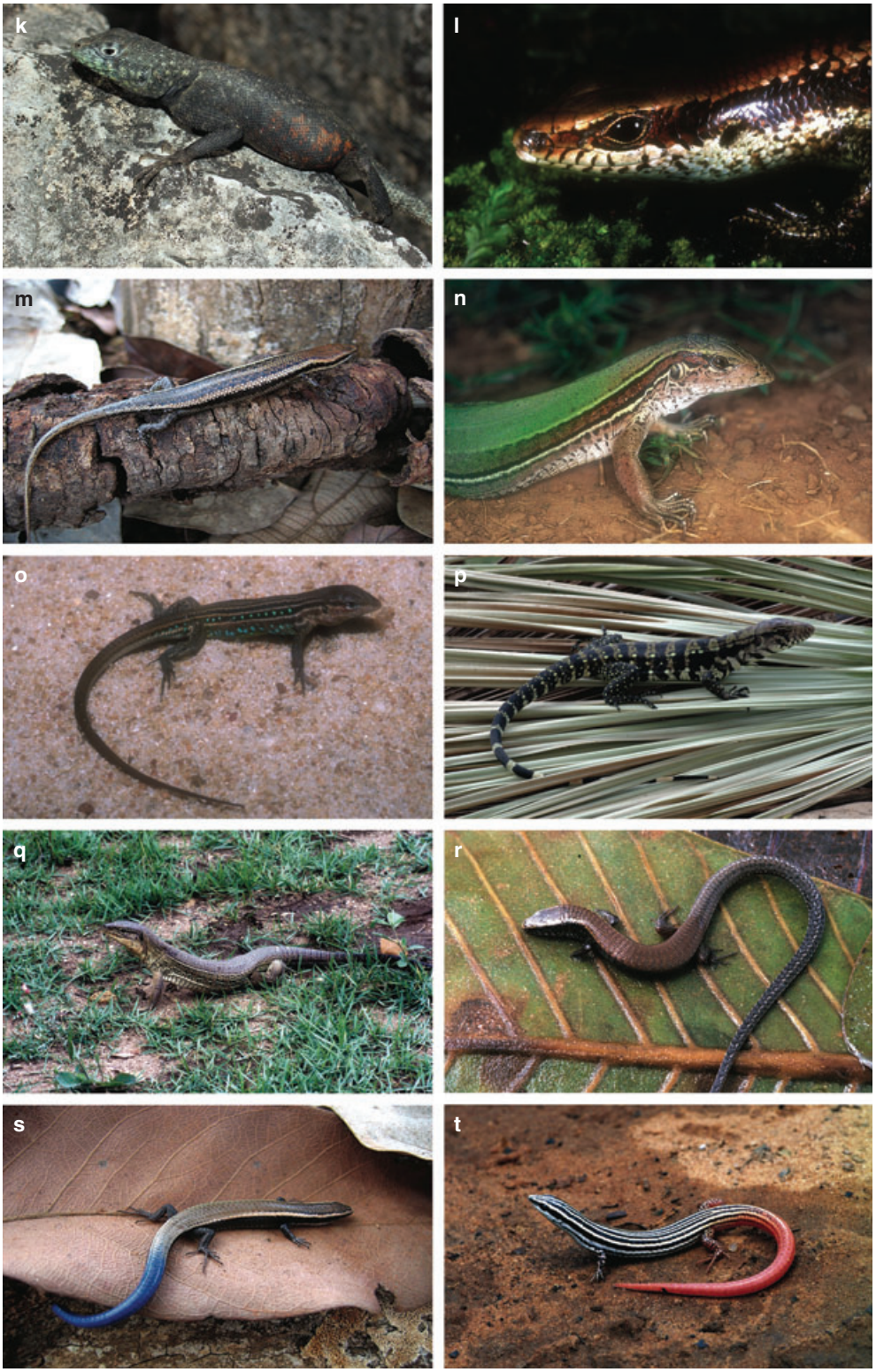

Figure 3 *continued.*

vicariant association (*sensu* Myers & Giller, 1988). Despite its absence from Bolivian and Colombian dry forests, where it may have become extinct, *L. klugei* should be considered an endemic of SDTFs of the Pleistocenic Arc. The presence of endemics was used as evidence to support the establishment of the Tropical Seasonal Forests Region as a new phytogeographical entity by Prado (2000). In comparison with the flora, however, which comprises at least 11 endemic genera and over

300 endemic species, the endemism among lizards is relatively low.

Despite being locally abundant in Caatinga (Vanzolini, 1974, 1976; Vitt, 1995), *L. klugei* was relatively rare in SDTF enclaves at São Domingos, with only seven individuals collected during four expeditions. These populations, isolated by an inhospitable matrix of Cerrado and agriculture, are vulnerable to the detrimental effects of genetic isolation, such as endogamic depression and loss of adaptability in the face of potential environmental changes, increasing the risks of decline and eventual extinction of small and isolated populations (Frankham, 1995, 1998).

The occurrence of a local endemic in our species list, *Mabuya* sp., may be as a result of recent speciation, reinforcing the uniqueness of SDTF enclaves in Cerrado and, consequently, their importance for biodiversity conservation. Because the lizard assemblage of SDTF enclaves is not a subset of the other regions considered, conservation strategies adopted in these other regions would not adequately protect the enclaves.

Relationships with other biomes

When examining the complete list of lizard species for the four regions considered (dry forests, Cerrado, Llanos, and Caatinga), no species are shared exclusively by Chaco and SDTFs. Indeed, Prado (1991) and Colli (2005) indicated that historical connections between Chaco and dry forests (under the regional name of Caatinga in this article) are a fallacy, justifying the exclusion of Chaco from the Pleistocenic Arc. The relationships between the herpetofauna of Cerrado, Caatinga, and Chaco were defined by the uplift of the Central Brazilian Plateau at the closure of the Tertiary (Colli, 2005). This presumably fragmented the range of the common ancestor of *L. klugei* and *L. wetzeli*, which inhabited the 'diagonal of open formations' (Vanzolini, 1963), followed by subsequent extinction of the genus in Cerrado and its differentiation in Caatinga (*L. klugei*) and Chaco (*L. wetzeli*). Alternatively, the range of the common ancestor could first have been fragmented, with *L. wetzeli* originating in Chaco and *L. klugei* associated with the Pleistocenic Arc. Subsequently, *L. klugei* became isolated in SDTF enclaves within Cerrado, when the distribution of SDTFs became vestigial and discontinuous. Clearly, a phylogeographic analysis of *Lygodactylus* is necessary to clarify this issue.

MAIN CONCLUSIONS

The presence of disjunct populations and endemic species highlights, from the point of view of the lizard fauna, the urgency of considering the uniqueness of SDTFs in conservation efforts. The establishment of reserves and corridors to connect large patches of SDTFs (Felfili, 2003), and biodiversity inventories in areas not yet studied should both be considered. The composition of lizard assemblages in SDTF enclaves within Cerrado seems to corroborate the proposal of Prado (2000) of a new phytogeographic unit (or dominium) for South America. The sampling of other faunal groups and additional areas, especially in SDTF remnants of central Brazil and in the Misiones and Subandean Piedmont nuclei, would provide further testing of this biogeographical pattern.

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REFERENCES

Brandão, R.A. & Araújo, A.F.B. (2001) A herpetofauna associada às matas de galeria do Distrito Federal. *Cerrado: Caracterização e Recuperação de Matas de Galeria* (ed. by J.F. Ribeiro, C.E.L. Fonseca and J.C. Sousa-Silva), pp. 561–604. Embrapa Cerrados, Planaltina.

Brooks, D.R. & McLennan, D.A. (1991) *Phylogeny, ecology, and behavior, a research program in comparative biology*. The University of Chicago Press, Chicago.

Brooks, D.R. & McLennan, D.A. (1993) Historical ecology: examining phylogenetic components of community evolution. *Species diversity in ecological communities, historical and geographical perspectives* (ed. by R.E. Ricklefs and D. Schluter), pp. 267–280. The University of Chicago Press, Chicago.

Ceballos, G. & Garcia, A. (1995) Conserving Neotropical biodiversity: the role of dry forests in Western Mexico. *Conservation Biology*, **9,** 1349–1353.

Colli, G.R. (2005) As origens e a diversificação da herpetofauna do Cerrado. *Cerrado: ecologia, biodiversidade e conservação* (ed. by A. Scariot, J.C. Souza-Silva and J.M. Felfili), pp. 249–264. Ministério do Meio Ambiente, Brasília, Distrito Federal.

Colli, G.R., Péres, A.K.J. & da Cunha, H.J. (1998) A new species of *Tupinambis* (Sauria, Teiidae) from central Brazil, with an analysis of morphological and genetic variation in the genus. *Herpetologica*, **54,** 477–492.

Colli, G.R., Bastos, R.P. & Araújo, A.F.B. (2002) The character and dynamics of the Cerrado herpetofauna. *The Cerrados of Brazil: ecology and natural history of a Neotropical savanna*

(ed. by P.S. Oliveira and R.J. Marquis), pp. 223–241. Columbia University Press, New York.

Felfili, J.M. (2003) Fragmentos de florestas estacionais do Brasil Central: diagnóstico e proposta de corredores ecológicos. *Fragmentação florestal e alternativas de desenvolvimento rural na Região Centro-Oeste* (ed. by R.B. da Costa), pp. 139–160. UCDB, Campo Grande.

Felfili, J.M. & Silva Júnior, M.C. (2001) *Biogeografia do bioma Cerrado: Estudo fitofisionômico da Chapada do Espigão Mestre do São Francisco*. Faculdade de Tecnologia, Universidade de Brasília, Brasília.

Fitzgerald, L.A., Cruz, F.B. & Perotti, G. (1999) Phenology of a lizard assemblage in the dry Chaco of Argentina. *Journal of Herpetology*, **33,** 526–535.

Frankham, R. (1995) Inbreeding and extinction: a threshold effect. *Conservation Biology*, **9,** 792–799.

Frankham, R. (1998) Inbreeding and extinction: island populations. *Conservation Biology*, **12,** 665–675.

Frost, D.R. & Etheridge, R. (1989) A phylogenetic analysis and taxonomy of iguanian lizards (Reptilia: Squamata). *Miscellaneous Publications of the Museum of Natural History, University of Kansas*, **81,** 1–65.

Frost, D.R., Etheridge, R., Janies, D. & Titus, T.A. (2001) Total evidence, sequence alignment, evolution of polychrotid lizards, and a reclassification of the Iguania (Squamata: Iguania). *American Museum Novitates*, **3343,** 1–38.

Gallardo, J.M. (1979) Composición, distribución y origen de la herpetofauna chaqueña. *The South American herpetofauna: its origin, evolution, and dispersal* (ed. by W.E. Duellman), pp. 299–307. The Museum of Natural History, University of Kansas, Lawrence.

Gil, E.M., Moreta, J.C., Perotti, M.G. & Scrocchi, G.J. (1995) Relevamiento preliminar de la herpetofauna del Parque Biológico Sierra de San Javier, Tucumán, Argentina. *XI Reunión de Comunicaciones Herpetológicas* (ed. by G.J. Scrocchi and R. Montero), pp. 15. Asociación Herpetológica Argentina, Tucuman, Argentina.

IBGE (1995) *Zoneamento geoambiental e agroecológico do Estado de Goiás: região nordeste*. IBGE/Divisão de Geociências do Centro-Oeste (Estudos e pesquisas em geociências, n.3), Rio de Janeiro.

Janzen, D.H. (1988) Tropical dry forests: the most endangered major tropical ecosystem. *Biodiversity* (ed. by E.O. Wilson), pp. 130–137. National Academy Press, Washington, DC.

Lavilla, E.O., Cruz, F.B. & Scrocchi, G.J. (1995) Amphibiens et reptiles de la station biologique ''Los Colorados'' dans la province de Salta, Argentine (2e partie). *Revue Française d'Aquariologie et Herpetologie*, **22,** 117–128.

Mesquita, D.O., Colli, G.R., França, F.G.R. & Vitt, L.J. (2006a) Ecology of a Cerrado lizard assemblage in the Jalapão region of Brazil. *Copeia*, **2006,** 459–470.

Mesquita, D.O., Costa, G.C. & Colli, G.R. (2006b) Ecology of an Amazonian savanna lizard assemblage in Monte Alegre Pará State, Brazil. *South American Journal of Herpetology*, **1,** 61–71.

Miles, L., Newton, A.C., DeFries, R.S., Ravilious, C., May, I., Blyth, S., Kapos, V. & Gordon, J.E. (2006) A global overview of the conservation status of tropical dry forests. *Journal of Biogeography*, **33,** 491–505.

MMA (1999) *Ações prioritárias para a conservação da biodiversidade do Cerrado e Pantanal*. MMA, Funatura, Conservation International, Fundação Biodiversitas & Universidade de Brasília, Brasília.

Murphy, F.G. & Lugo, A.E. (1986) Ecology of tropical dry forest. *Annual Review of Ecology and Systematics*, **17,** 67–88.

Myers, A.A. & Giller, P.S. (eds) (1988) *Analytical biogeography: an integrated approach to the study of animal and plant distributions*. Chapman & Hall, London.

Norman, D.R. (1994) *Amphibians and reptiles of the Paraguayan Chaco*, Volume 1. Published by author, San José, Costa Rica.

Oliveira, P.S. & Marquis, R.J. (2002) *The Cerrados of Brazil: ecology and natural history of a Neotropical Savanna*. Columbia University Press, New York.

Pennington, R.T., Prado, D.E. & Pendry, C.A. (2000) Neotropical seasonally dry forests and Quaternary vegetation changes. *Journal of Biogeography*, **27,** 261–273.

Pennington, R.T., Lavin, M., Prado, D.E., Pendry, C.A., Pell, S.K. & Butterworth, C.A. (2004) Historical climate change and speciation: neotropical seasonally dry forest plants show patterns of both Tertiary and Quaternary diversification. *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences*, **359,** 515–538.

Porzecanski, A.L. & Cracraft, J. (2005) Cladistic analysis of distributions and endemism (CADE): using raw distributions of birds to unravel the biogeography of the South American aridlands. *Journal of Biogeography*, **32,** 261–275.

Prado, D.E. (1991) A critical evaluation of the floristic links between Chaco and Caatingas vegetation in South America. PhD thesis, University of St Andrews, St Andrews.

Prado, D.E. (2000) Seasonally dry forests of tropical South America: from forgotten ecosystems to a new phytogeographic unit. *Edinburgh Journal of Botany*, **57,** 437–461.

Prado, D.E. & Gibbs, P.E. (1993) Patterns of species distributions in the dry seasonal forests of South America. *Annals of the Missouri Botanical Garden*, **80,** 902–927.

Prance, G.T. (2006) Tropical savannas and seasonally dry forests: an introduction. *Journal of Biogeography*, **33,** 385–386.

Ratter, J.A. (1992) Transitions between Cerrado and forest vegetation in Brazil. *Nature and dynamics of forest-savanna boundaries* (ed. by P.A. Furley, J. Proctor and J.A. Ratter), pp. 417–429. Chapman & Hall, London.

Ratter, J.A., Askew, G.P., Montgomery, R. & Gifford, D.R. (1978) Observations on forests of some mesotrophic soils in central Brazil. *Revista Brasileira de Botânica*, **1,** 47–58.

Rivero-Blanco, C. & Dixon, J.R. (1979) Origin and distribution of the herpetofauna of the dry lowland regions of northern South America. *The South American herpetofauna: its origin,*

evolution, and dispersal (ed. by W.E. Duellman), pp. 281–298. The Museum of Natural History, University of Kansas, Lawrence.

Rodrigues, M.T. (1996) Lizards, snakes, and amphisbaenians from the quaternary sand dunes of the middle Rio São Francisco, Bahia, Brazil. *Journal of Herpetology*, **30,** 513–523.

Rodrigues, M.T. (2003) Herpetofauna da Caatinga. *Ecologia e conservação da Caatinga* (ed. by I.R. Leal, M. Tabarelli and J.M.C. Silva), pp. 181–236. Editora Universitária da UFPE, Recife.

Sánchez-Azofeifa, G.A., Kalacska, M., Quesada, M., Calvo-Alvarado, J.C., Nassar, J.M. & Rodríguez, J.P. (2005) Need for integrated research for a sustainable future in Tropical Dry Forests. *Conservation Biology*, **19,** 285–286.

Scariot, A. & Sevilha, A.C. (2000) Diversidade, estrutura e manejo de florestas deciduais e as estratégias para a conservação. *Tópicos atuais em botânica: palestras convidadas do 51° Congresso Nacional de Botânica* (ed. by T.B. Cavalcanti and B.M.T. Walter), pp. 183–188. Embrapa Recursos Genéticos e Biotecnologia, Brasília.

Scariot, A. & Sevilha, A.C. (2003) Desmatamento e fragmentação do Cerrado: destruição das florestas estacionais e a conservação da biodiversidade. *Ecossitemas Brasileiros: Manejo e Conservação* (ed. by V. Claudino-Sales), pp. 163–169. Expressão Gráfica e Editora, Fortaleza.

Schmidt, K.P. & Inger, R.F. (1951) Amphibians and reptiles of the Hopkins-Branner expedition to Brazil. *Fieldiana (Zool.)*, **31,** 439–465.

Silva, J.M.C. (1995a) Biogeographic analysis of the South American Cerrado avifauna. *Steenstrupia*, **21,** 49–67.

Silva, J.M.C. (1995b) Birds of the Cerrado region, South America. *Steenstrupia*, **21,** 69–92.

Silva, J.M.C. & Bates, J.M. (2002) Biogeographic patterns and conservation in the South American Cerrado: a tropical savanna hotspot. *BioScience*, **52,** 225–233.

Smith, H.M., Martin, R.L. & Swain, T.A. (1977) A new genus and two new species of South American geckos (Reptilia: Lacertilia). *Papéis Avulsos de Zoologia, São Paulo*, **30,** 195–213.

Staton, M.A. & Dixon, J.R. (1977) The herpetofauna of the central llanos of Venezuela: noteworthy records, a tentative checklist and ecological notes. *Journal of Herpetology*, **11,** 17–24.

Vanzolini, P.E. (1963) Problemas faunísticos do Cerrado. *Simpósio sobre o Cerrado* (ed. by M. Ferri), pp. 307–320. Editora da Universidade de São Paulo, São Paulo.

Vanzolini, P.E. (1974) Ecological and geographical distribution of lizards in Pernambuco, Northeastern Brazil (Sauria). *Papéis Avulsos de Zoologia, São Paulo*, **28,** 61–90.

Vanzolini, P.E. (1976) On the lizards of a Cerrado-Caatinga contact, evolutionary and zoogeographical implications (Sauria). *Papéis Avulsos de Zoologia, São Paulo*, **29,** 111–119.

Vanzolini, P.E. (1988) Distributional patterns of South American lizards. *Proceedings of a workshop on Neotropical distribution patterns* (ed. by P.E. Vanzolini and W.R. Heyer), pp. 317–342. Academia Brasileira de Ciências, Rio de Janeiro.

Vieira, D.L.M. & Scariot, A. (2006) Principles of natural regeneration of tropical dry forests for restoration. *Restoration Ecology*, **14,** 11–20.

Vitt, L.J. (1991) An introduction to the ecology of Cerrado lizards. *Journal of Herpetology*, **25,** 79–90.

Vitt, L.J. (1995) The ecology of tropical lizards in the Caatinga of northeast Brazil. *Occasional Papers of the Oklahoma Museum of Natural History*, **1,** 1–29.

Webb, C.O., Ackerly, D.D., McPeek, M.A. & Donoghue, M.J. (2002) Phylogenies and community ecology. *Annual Review of Ecology and Systematics*, **33,** 475–505.

Whitmore, T.C. (1997) Tropical forest disturbance, disappearance and species loss. *Tropical forest remnants: ecology, management and conservation of fragmented communities* (ed. by W.F. Laurance and R.O. Bierregaard), pp. 3–14. The University of Chicago Press, Chicago.

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