



Vicariance and endemism in a Neotropical savanna hotspot: distribution patterns of Cerrado squamate reptiles

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ABSTRACT

Aim To test predictions of the vicariance model, to define basic biogeographical units for Cerrado squamates, and to discuss previous biogeographical hypotheses.

Location Cerrado; South American savannas south of the Amazon, extending across central Brazil, with marginal areas in Bolivia and Paraguay and isolated relictual enclaves in adjacent regions.

Methods We compiled species occurrence records via field sampling and revision of museum specimens and taxonomic literature. All species were mapped according to georeferenced locality records, and classified as (1) endemic or non-endemic, (2) typical of plateaus or depressions, and (3) typical of open or forested habitats. We tested predictions of the vicariance model using biotic element analysis, searching for non-random clusters of species ranges. Spatial congruence of biotic elements was compared with putative areas of endemism revealed by sympatric restricted-range species. Effects of topographical and vegetational mosaics on distribution patterns were studied according to species composition in biotic elements and areas of endemism.

Results We recorded 267 Cerrado squamates, of which 103 (39%) are endemics, including 20 amphisbaenians (61% endemism), 32 lizards (42%) and 51 snakes (32%). Distribution patterns corroborated predictions of the vicariance model, revealing groups of species with significantly clustered ranges. An analysis of endemic species recovered seven biotic elements, corroborating results including non-endemics. Sympatric restricted-range taxa delimited 10 putative areas of endemism, largely coincident with core areas of biotic elements detected with endemic taxa. Distribution patterns were associated with major topographical and vegetational divisions of the Cerrado. Endemism prevailed in open, elevated plateaus, whereas faunal interchange, mostly associated with forest habitats, was more common in peripheral depressions.

Main conclusions Our results indicate that vicariant speciation has strongly shaped Cerrado squamate diversity, in contrast to earlier studies emphasizing faunal interchange and low endemism in the Cerrado vertebrate fauna. Levels of squamate endemism are higher than in any other Cerrado vertebrate group. The high number of recovered endemics revealed previously undetected areas of evolutionary relevance, indicating that biogeographical patterns in the Cerrado were poorly represented in previous analyses. Although still largely undocumented, effects of vicariant speciation may be prevalent in a large fraction of Cerrado and Neotropical biodiversity.

Keywords

Biodiversity, biogeography, biotic elements, conservation biogeography, distribution patterns, open areas, reptiles, South American savanna.

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INTRODUCTION

Detailed distribution data and well delimited biogeographical units provide the first step for uncovering the origin and history of biotas, the ultimate goal of biogeography (Croizat *et al.*, 1974; Nelson, 1978; Rosen, 1978). Biogeographical units also provide the most valuable source of information on what spatial portions of biodiversity should be conserved (Crisci, 2000; Whittaker *et al.*, 2005). However, one of the major obstacles within biogeography is the lack of objective and replicable methods for detecting and delineating the units of biogeographical analysis (Harold & Mooi, 1994). Delineation of biogeographical units has been hampered by the pervasive occurrence of dispersal across barriers, erasing signs of historical vicariant speciation (Nelson & Platnick, 1981; Harold & Mooi, 1994). Other major obstacles are the lack of formal tests on statistical significance of co-occurrences, and the lack of objective thresholds between random and non-random distribution patterns (Hausdorf, 2002; Mast & Nyffeler, 2003).

Due to the confounding effects of dispersal and the lack of observed strict sympatry among co-distributed species, the analysis of raw distribution data alone is insufficient for proposing and clearly delineating fundamental biogeographical units based solely on endemism patterns (Hausdorf, 2002). Hence, biotic element analysis has emerged as an alternative method for detecting biogeographical units, testing vicariant patterns without requiring strict allopatry of species ranges (Hausdorf, 2002; Hausdorf & Hennig, 2003). Biotic element analysis is based on the central assumption that, if vicariant processes fragmented ancestral ranges, groups of significantly clustered (but not strictly allopatric) and non-random species ranges should emerge and be detectable (Hausdorf, 2002; Hausdorf & Hennig, 2003). The concept of biotic elements is thus a powerful descriptive tool that summarizes all generalities of the geographical distributions of organisms and, in contrast to areas of endemism, can be studied based on distribution data alone (Hausdorf, 2002).

The apparently trivial and largely descriptive task of detecting spatial units is a critical phase of biogeographical analyses (Harold & Mooi, 1994; Mast & Nyffeler, 2003). This task becomes even more challenging in rich and relatively poorly studied Neotropical biotas, whose basic distribution patterns have been a matter of scientific inquiry since the early stages of biogeography (Wallace, 1852; Nelson, 1978), but remain elusive due to combined high biological diversity and lack of basic distributional and taxonomic data (da Silva & Bates, 2002), known as the Wallacean and Linnean shortfalls (Whittaker *et al.*, 2005). Lack of basic data in the Neotropical region is especially problematic because biogeographical syntheses are supposed to seek and explain general patterns, based on careful examination of distributional data from a wide array of taxa (Croizat *et al.*, 1974; Crisci, 2000). However, available distributional data on Neotropical species are largely incomplete, as most studies have focused on forest environments and

biotas (Haffer, 1969; Vanzolini & Williams, 1970, 1981; da Silva & Oren, 1996; da Silva *et al.*, 2004).

One of the largest, least studied (Heyer, 1988; da Silva & Bates, 2002), and most threatened global regions is the Cerrado (Myers *et al.*, 2000; Mittermeier *et al.*, 2004), the largest block of Neotropical savannas. Studies on avian raw distributions, taxonomy and natural history in the Cerrado indicate high influence of faunal interchange with adjacent forested regions and low endemism, concentrated in three areas (da Silva, 1997; da Silva & Bates, 2002). These studies also indicate that savannas and grasslands are the ancient habitat type in central Brazil (Cole, 1986), as older, well differentiated Cerrado avian endemics are often associated with open habitats, whereas more recent endemics are usually found in gallery forest habitats (da Silva, 1997; da Silva & Bates, 2002). Similar analyses for non-avian vertebrate groups are lacking, but would provide the basis for more general interpretations of diversity and distribution patterns in the Neotropics (da Silva & Bates, 2002).

Cerrado savannas are dominated by an ancient, fire-adapted flora, which defines a relictual, disjunct ecosystem, formerly widespread in central South America (Cole, 1986; Ratter *et al.*, 1997). Cerrado savannas develop mostly on ancient, stable plateaus forming the end products of old tectonic cycles of uplift, erosion and soil impoverishment, being slowly degraded by recent dissection and expansion of peripheral depressions (Cole, 1986), where more recent forest biotas expand and predominate (Cole, 1986; Ratter *et al.*, 1997; da Silva, 1997; da Silva & Bates, 2002). Thus, the Cerrado region develops on two major geomorphological units: gently rolling or level headwater plateaus, mostly between 500 and 1700 m a.s.l.; and peripheral depressions, generally below 500 m a.s.l., eroded by major drainage systems (da Silva, 1997; Silva *et al.*, 2006).

The dominant and typical vegetation on plateaus is open grassy savanna and grassland, ranging from *campo limpo* (open grasslands) to typical cerrado (cerrado *sensu stricto*), crossed by strips of wetlands and gallery forests along riparian areas, in relatively sparse drainage systems (Eiten, 1972; Oliveira-Filho & Ratter, 2002). Habitat composition on depressions is more complex, with a matrix of savannas crossed by widespread tracts of gallery forests along the denser drainage networks, with scattered dry forests on richer soils and semi-deciduous forests on eroded escarpments and hillsides (Eiten, 1972; Cole, 1986; Oliveira-Filho & Ratter, 2002). Detailed data on Cerrado ecology and natural history can be found in Oliveira & Marquis (2002).

Basic questions on the composition and distribution of Cerrado fauna and flora remain poorly investigated and represent major knowledge gaps in Neotropical biogeography (Vanzolini, 1976, 1988; Heyer, 1988; da Silva, 1995, 1997; da Silva & Bates, 2002). Percentages of Cerrado endemics are highly variable across taxonomic groups (Myers *et al.*, 2000; da Silva & Bates, 2002; Klink & Machado, 2005). Contrasting with high endemism levels in vascular plants (Myers *et al.*, 2000; Klink & Machado, 2005), current knowledge points to

low levels of vertebrate endemism in the Cerrado, ranging from 28–30% in amphibians (Myers *et al.*, 2000; Colli *et al.*, 2002), 17–20% in reptiles (Myers *et al.*, 2000; Colli *et al.*, 2002) through 9–12% in mammals (Myers *et al.*, 2000; Marinho-Filho *et al.*, 2002) to as low as 1–4% in birds (da Silva, 1995; Macedo, 2002).

Recent studies indicate that Cerrado harbours a rich, complex and characteristic reptilian fauna, highly influenced by horizontal habitat variation and historical constraints on ecological traits (Colli *et al.*, 2002; Nogueira *et al.*, 2005, 2009, 2010b). However, patterns of species distribution and endemism remain poorly understood for the Cerrado herpetofauna (Colli *et al.*, 2002). Given the ‘problem of dispersal’ (Nelson & Platnick, 1981), organisms with smaller ranges are classical candidates for biogeographical studies (Croizat *et al.*, 1974; Rosen, 1978). Hence, the analysis of distribution patterns of squamate reptiles, dominated by species with relatively low dispersal ability and small ranges (Gaston, 1996), high habitat and microhabitat fidelity, and extensive variation in life-history parameters (Greene, 1997; Pianka & Vitt, 2003), may provide detailed data on distribution patterns, information critical to conservation strategies based on evolutionary and biogeographical interpretations (Crisci, 2000).

Here we use biotic element analysis to provide a first detailed and comprehensive biogeographical assessment of the Cerrado squamate reptile fauna. Our main goals are: (1) to describe biogeographical patterns and endemism levels of Cerrado squamates; (2) to test predictions of the vicariant model of speciation on distribution and endemism patterns in the Cerrado; (3) to test the congruence between regional clusters of co-occurring species and putative areas of endemism identified by sympatric restricted-range species; and (4) to evaluate the effects of major topographical and vegetational divisions on distribution patterns in Cerrado squamates. In addition to generating a timely and objective delineation of biogeographical units in a highly threatened region, we aim to provide the first rigorous test on the role of vicariance on Cerrado biodiversity, generating important clues on the effects of geographical isolation on the formation of rich and complex tropical biotas.

MATERIALS AND METHODS

Data sources

We used the Brazilian vegetation map (IBGE, 1993) to define the approximate limits of the Cerrado region. We use the name Cerrado in reference to the largest South American block of savannas, covering most of the Brazilian Shield plateaus and adjacent peripheral depressions south of the Amazon River (da Silva & Bates, 2002). We obtained data from the revision of voucher specimens in zoological collections and compilation of literature records, complemented by standardized fieldwork to fill former sampling gaps (Nogueira *et al.*, 2009). Partial results of these studies are available elsewhere (Nogueira, 2001, 2006; Valdujo & Nogueira, 2001; Nogueira *et al.*, 2005;

Nogueira & Rodrigues, 2006; Recoder & Nogueira, 2007; Rodrigues *et al.*, 2008; Ribeiro *et al.*, 2009; Valdujo *et al.*, 2009). The data we present complement and update recently published results on Cerrado squamate diversity (Costa *et al.*, 2007; Nogueira *et al.*, 2010b).

Field-collected specimens were determined after comparison with museum vouchers and taxonomic literature, and were deposited at Museu de Zoologia da Universidade de São Paulo (MZUSP), Coleção Herpetológica da Universidade de Brasília (CHUNB), and Instituto Butantan (IB), three of the largest Brazilian herpetological collections, which were the source of voucher specimens analysed during this study. We included in our analyses every species with at least one vouchered record in the Cerrado region (IBGE, 1993). Species recorded in faunal lists without reference to voucher specimens were not included in our database. Moreover, records in electronic databases, including unchecked, error-prone raw museum data, were not used in our analyses and compilations. Higher-level squamate systematics follows Vidal & Hedges (2009), and snake systematics follows Zaher *et al.* (2009). Taxonomy at the family, genus and species level follows the Brazilian List of Reptile species (Bérnils, 2010), except for the taxonomy of *Liophis*, *Lygophis* and *Erythrolamprus*, which follows Curcio *et al.* (2009), and of *Amphisbaenia*, which follows traditional taxonomy (Gans, 2005) despite recent proposed changes (Mott & Vieites, 2009).

Analyses

We mapped point-locality records for each species based on available and verified locality records, using standard GIS procedures. We classified each species according to the two most general geomorphological units of the Cerrado, namely plateaus and depressions (see da Silva & Bates, 2002), by comparing elevational records with a set of 200 random elevational values for the Cerrado, using a Kruskal–Wallis test. Species with elevational records higher than random were classified as typical of plateaus, while species with values lower than random were classified as typical of depressions. Species with fewer than three records were classified according to visual inspection of available locality records against digital elevation layers: species found above 500 m were classified as typical of plateaus, and those found below this threshold as typical of depressions (da Silva & Bates, 2002). We also classified species as typical of forested or open habitats based on field data and literature accounts (Ávila-Pires, 1995; Colli *et al.*, 2002; França *et al.*, 2008; Nogueira *et al.*, 2009; Valdujo *et al.*, 2009). Species classified as riparian, found mostly in swamps or water bodies regardless of surrounding major vegetation type, were excluded from previous comparisons, as were habitat generalists.

We classified each species as endemic or non-endemic to the Cerrado. As in da Silva (1997), we considered as endemic those species with locality records fully or largely coincident with the approximate limits of Cerrado vegetation (IBGE, 1993), which includes most of the Pantanal region (largely influenced by

upland Cerrado savannas) and transition areas with neighbouring morphoclimatic domains (Ab'Sáber, 1977). Neotropical regions outside the Cerrado were defined as in Redford & da Fonseca (1986) and complemented by the terrestrial map of global ecoregions (Olson *et al.*, 2001).

Due to inadequacies of scale in continental vegetation maps, which are not intended to provide detailed descriptions of complex limits between adjacent vegetation types (see discussion in Lopes, 2008), species with most records within the Cerrado but with marginal records in neighbouring regions and transition areas were considered as endemics. Although many Cerrado enclaves are known in neighbouring regions (Ratter *et al.*, 1997; Oliveira-Filho & Ratter, 2002; Lopes, 2008), most isolated areas are too small to be mapped using continental-scale vegetation maps, resulting in a poor resolution of enclaves and contact areas (Ab'Sáber, 1977; Lopes, 2008). Thus, the adherence to a strict definition of endemism, following artificial, linear regional boundaries, could lead to the omission of species whose evolutionary and biogeographical affinities are closely tied to the Cerrado region, despite occurring marginally outside the uncertain limits of a continuous Cerrado area. Species confined to low-lying floodlands of the Paraguay River, typical of the Pantanal region of western Brazil, and with few or no records in adjacent interfluvial plateaus, were not considered as Cerrado endemics.

The predictions of the vicariance model on distribution patterns were tested using biotic element analysis (Hausdorf, 2002; Hausdorf & Hennig, 2003), based on a presence-absence matrix resulting from species records mapped in a $2^\circ \times 2^\circ$ -cell grid, covering the core area of the Cerrado. Biotic element analysis was implemented in *prabclus* (Hausdorf & Hennig, 2003), an add-on package for the statistical software R, available at <http://cran.r-project.org>. We analysed two datasets: the first included 254 grid-mapped species in the Cerrado region; the second was a subset of 101 Cerrado endemics (hereafter called the endemic dataset). Clusters of species ranges found with the endemic dataset were termed endemic biotic elements.

We excluded 13 species from the biotic element datasets: species with very poorly documented or unknown ranges in the Cerrado, species recorded only outside the core Cerrado area (not covered by the $2^\circ \times 2^\circ$ grid), and *Hemidactylus mabouia* (Moreau de Jonnés, 1818), a perianthropoc, introduced species. Two endemic Cerrado species were listed but also not included in biotic element datasets: *Amphisbaena ibijara* Rodrigues, Andrade & Lima, 2003, found at marginal Cerrado areas outside the grid-mapped area; and *Apostolepis tertulianoibeui* Lema, 2004, described from an uncertain Cerrado locality.

Biotic element analysis is based on two major predictions of the vicariance model (Hausdorf, 2002; Hausdorf & Hennig, 2003). The first prediction posits that the division of ancestral biotas by vicariance events should produce regionalized groups of taxa (biotic elements) whose ranges are more similar to each other than to those of taxa of other such groups (Hausdorf, 2002; Hausdorf & Hennig, 2003). A second

prediction dictates that closely related species resulting from vicariance (after allopatric speciation in different areas of endemism) should be found in different biotic elements (Hausdorf & Hennig, 2003), that is, should pertain to different clusters of significantly co-occurring species. The first prediction (clustering of species ranges) investigated in *prabclus* is based on the test of the hypothesis that the observed degree of range clustering can be explained by varying range sizes, by varying numbers of taxa per geographical unit, and by the spatial autocorrelation of the occurrences of a taxon alone (Hausdorf & Hennig, 2003). To test this hypothesis, three specifications must be made: a distance measure between species ranges, a test statistic, and a null model for the generation of random sets of ranges. As distance measure we used the Kulczynski distance, which does not overestimate values of range distances between sympatric taxa with differing range sizes (see Hausdorf & Hennig, 2003), as the vicariance model does not require similar range sizes in taxa belonging to the same biota after the emergence of a dispersal barrier (Hennig & Hausdorf, 2004). The specified test statistic *T* (Hausdorf & Hennig, 2003) is based on the assumption that, given a significant clustering of ranges, distances are small between ranges of the same cluster and large between ranges of different clusters (Hausdorf & Hennig, 2003; Hennig & Hausdorf, 2004). This statistic is measured as the ratio between a fixed proportion of the smallest and largest distances, and is expected to be small for clustered data and larger for homogeneous data (Hausdorf & Hennig, 2003). The distribution of test statistics under the null hypothesis is approximated by Monte Carlo simulation, in which artificial ranges are produced so that their cell number distribution approximates the actual distribution of the number of cells per range, richness distribution of cells approximates the actual richness distribution of cells, and the tendency to form disjunct areas is governed by a parameter that is estimated from the real data set (Hausdorf & Hennig, 2003).

Clusters of species ranges, delimiting regionalized biotic elements, were defined with model-based Gaussian clustering as implemented in the software *MCLUST*, as proposed by Hausdorf & Hennig (2003). This method provides a decision about the number of meaningful clusters, and detects ranges that cannot be adequately assigned to any biotic elements (noise component: Hausdorf & Hennig, 2003; Hennig & Hausdorf, 2004). Model-based Gaussian clustering operates on a dataset where cases are defined by variables of metric scale. Therefore, we performed non-metric multidimensional scaling (NMDS) on the matrix of Kulczynski distances and four NMDS dimensions. As suggested by Hausdorf & Hennig (2003), we used constant $k = \text{number of species}/40$, rounded up to the next integer (three for the endemic dataset, seven for the larger dataset) for detecting the noise component. The second prediction of the vicariance model (closely related species in different biotic elements, Hausdorf, 2002; Hausdorf & Hennig, 2003) was tested in *prabclus* with a χ^2 test on the distribution of congeneric species among biotic elements (Hausdorf & Hennig, 2003), using the endemic species dataset.

We detected restricted-range endemic species as those with known ranges smaller than 60,000 km², following previous analyses for Cerrado birds (da Silva & Bates, 2002). Areas harbouring sympatric restricted-range species were delimited as continuous watershed boundaries (6th order Ottobasins), encompassing all species records within polygons of the Brazilian map of catchment areas (see similar site delineation for restricted-range species in Nogueira *et al.*, 2010a). These continuous areas harbouring sympatric restricted-range endemics were here considered as areas of endemism (AOEs). The congruence between the composition of biotic elements and AOEs was tested following the procedure for testing the presence of closely related species in different biotic elements, using the χ^2 test in *prabclus* (Hausdorf & Hennig, 2003), and biotic elements of the endemic species dataset. This same test was used to investigate if species typical of plateaus or depressions occur randomly across endemic biotic elements. The prevalence of endemism and faunal interchange in plateaus versus depressions, and forests versus open areas, was tested using Fisher's exact test.

RESULTS

Species richness

We recorded 267 Cerrado squamate species comprising 76 lizards, 158 snakes and 33 amphisbaenians (see Appendix S1 in Supporting Information). These results were obtained after revising, georeferencing and mapping more than 25,000 vouchered records, including at least 8500 non-redundant records (unique species \times locality combinations from the Cerrado and adjacent Neotropical domains). These records included at least 1769 voucher specimens collected in the field in the 10 localities studied via standardized samplings (Nogueira *et al.*, 2009), plus non-standardized additional collections throughout the Cerrado.

Of the 267 recorded species, 158 were already detected in the first synthesis of Cerrado herpetofaunal diversity (Colli *et al.*, 2002). Another 66 species were previously recorded in the taxonomic literature or as vouchers in MZUSP and IB collections (Appendix S1). Finally, 43 species were added as a result of recent taxonomic studies published after the 2002 synthesis (Colli *et al.*, 2002). Of the 267 recorded species, 140 were present in field samples during data collection (Appendix S1).

Endemism

We detected 103 species as Cerrado endemics, representing 39% of regional richness, and including 20 amphisbaenians (61% endemism), 32 lizards (42%) and 51 snakes (32%) (Appendix S1). Endemism levels varied widely among lineages, from 0 (e.g. Iguanidae, Anguinae, Hydropsini) to 47% in Tropiduridae, 57% in Gymnophthalmidae, 61% in Amphisbaenidae, 67% in Phyllodactylidae and Leptotyphlopidae, 80% in Elapomorhini, and 100% in Hoplocercidae (Appendix S1).

For proper comparisons, after the inclusion of 10 species of Chelonia and five Crocodylia recorded for the Cerrado (Colli *et al.*, 2002), overall reptilian richness (282) and endemism level (36%) greatly surpassed values presented in recent syntheses on Cerrado herpetofauna (Myers *et al.*, 2000; Colli *et al.*, 2002). The level of endemism was also considerably higher than that found in other vertebrate groups (Myers *et al.*, 2000; Colli *et al.*, 2002; Macedo, 2002; Marinho-Filho *et al.*, 2002; Lopes, 2008).

Test of vicariant distribution patterns

Biotic element analyses on a dataset of 254 grid-mapped species (including endemics and non-endemics; Appendix S2) corroborated major predictions of the vicariance model: ranges were significantly clustered, forming distinguishable, localized biotas across the Cerrado region. The *T* statistic (Hausdorf & Hennig, 2003) was 0.423, significantly smaller ($P = 0.0009$) than expected by chance (for 1000 artificial populations, *T* varied between 0.429 and 0.498, mean = 0.461). To test if results were not a direct effect of species interchange with adjacent regions, we repeated the analysis with the endemic dataset (101 species). For this dataset the *T* statistic was 0.459, also significantly smaller ($P = 0.027$) than expected under the null model (for 1000 artificial populations, *T* varied between 0.447 and 0.568, mean = 0.494).

Determination of biotic elements

As previous tests indicated that Cerrado squamates are divided into species groups with significantly regionalized ranges, a next step was to determine biotic elements according to species clusters in the first two dimensions of the NMDS analysis, using *MCLUST*. In the analysis with non-endemics, 235 species (88%) contributed to the detection of eight biotic elements, while 19 species (12%) were included in the noise component (Fig. 1; Appendix S1).

Biotic element 1 (BE1) was formed by 53 species and, despite being widespread, was centred at the core portion of the Brazilian Shield, the central part of the Cerrado region (Fig. 2). BE2 grouped 51 species and ranged mostly along the southern portion of the Cerrado, at the headwaters of the La Plata River system. BE3 was formed by 49 species and was also widespread, with disjunct centres in the central and western portions of the Cerrado (Fig. 2). BE4 was formed by 39 species and was also widespread in the Cerrado, but with two distinct cores in the north-western and north-eastern portions of the Cerrado. BE5 was formed by 17 species restricted to the north-eastern portion of the Cerrado. BE6 was formed by nine species restricted to the south-western portion of the Cerrado. BE7 was formed by nine species restricted to the Espinhaço range, at the south-eastern limits of the Cerrado. Finally, BE8 was formed by eight species restricted to the central-northern portion of the Cerrado, mostly along the Araguaia river basin and with a core range at the Chapada dos Guimarães plateau and headwaters.

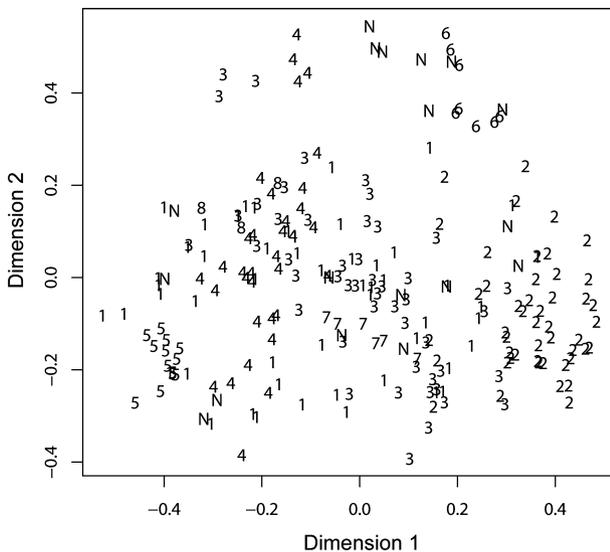


Figure 1 Species clusters in the first two dimensions of a non-metric multidimensional scaling analysis, obtained according to the ranges of all 254 grid-mapped Cerrado squamates (endemic + non-endemic) analysed in MCLUST (Hausdorf & Hennig, 2003). Characters indicate model-based clustering with noise (N).

In the analysis with the endemic dataset, seven endemic biotic elements were detected, based on 51 (50%) species in significant range clusters, while 50 species were included in the noise component (Fig. 3; Appendix S1). Endemic biotic elements were mostly coincident with biotic elements detected with species shared with adjacent regions (Table 1). All 11 species of endemic element 1 (EE1) belonged to the fifth element (BE5) of the larger dataset (Table 1), also largely restricted to the north-eastern portion of the Cerrado (Fig. 4). Due to its location, EE1 is here defined as the Tocantins–Serra Geral element. All nine species of EE2 belonged to BE4 (Table 1), coinciding with the western core of the larger biotic element, on the Paraguay–Guaporé headwaters and watershed plateaus (Fig. 4); EE2 is thus named Paraguay–Guaporé element. All eight species of EE3 belonged to BE2 (Table 1), located mostly on the southern portion of the Cerrado (Fig. 4); EE3 is here named the Paraná–Paraguay headwaters endemic element. Most (57%) of the seven species of EE4 belonged to BE8 (Table 1), largely associated with the Guimarães and Roncador plateaus (Fig. 4); EE4 is thus named the Guimarães–Roncador endemic element. All seven species of EE5 belonged to BE7 (Table 1), and were also largely restricted to the Espinhaço range (Fig. 4); EE5 is here named the Espinhaço endemic element. Most (75%) of the four species of EE7 belonged to BE1 (Table 1), and coincide with its core range at the central portion of the Cerrado (Fig. 4); EE7 is here named the Central Plateau element. A single endemic element, EE6, shared its species equally between two larger biotic elements: BE3 and BE8 (Table 1). This endemic element was, however, composed mainly of species found in the Araguaia–Xingu drainages (Fig. 4), being here named the Araguaia endemic element.

Congeneric taxa and biotic elements

Eight genera contained at least two species defining endemic biotic elements (i.e. not included in the noise category of the analysis with the endemic dataset), and were used to test the prediction that closely related species were segregated by vicariance. These genera included *Amphisbaena* (seven species), *Bronia* and *Cercolophia* (three species each); the elapomorphine snake genera *Apostolepis* (11 species) and *Phalotris* (two species); and the lizard genera *Tropidurus* (four species) and *Bachia* (three species). A χ^2 test failed to reject the null hypothesis that closely related species were homogeneously distributed across different biotic elements ($P = 0.524$). The same test adopting the taxonomy proposed in recent molecular studies (Mott & Vieites, 2009), considering all Neotropical amphisbaenid genera as synonyms of *Amphisbaena*, recovered similar results ($P = 0.647$).

Restricted-range species, areas of endemism and biotic elements

Ten putative local areas of endemism (AOEs A–J, Fig. 5; see also Appendix S1) harbouring at least two sympatric restricted-range species (known ranges smaller than 60,000 km²) were delimited: Tietê–Rio Grande headwaters (AOE A, *Amphisbaena sanctaeritae*, *Liotyphlops schubarti*); Miranda depression (AOE B, *Apostolepis intermedia*, *Bronia bedai*); Huanchaca plateau (AOE C, *Tropidurus callathelys*, *Tropidurus chromatops*); northern portion of the Parecis plateau (AOE D, *Apostolepis striata*, *Bachia didactyla*, *Cnemidophorus parecis*); Serra das Araras range (AOE E, *Apostolepis christineae*, *Cercolophia absaberi*); Chapada dos Guimarães plateau (AOE F, *Amphisbaena brevis*, *Amphisbaena neglecta*, *Apostolepis lineata*, *Cercolophia cuiabana*); Tocantins depression (AOE G, *Bachia psamophila*, *Bronia saxosa*, *Hydrodynastes melanogigas*); Jalapão and Serra Geral plateau (AOE H, *Anops acrobeles*, *Bachia oxyrhina*, *Cnemidophorus mumbuca*, *Cnemidophorus jalapensis*); Upper Tocantins plateaus (AOE I, *Apostolepis cerradoensis*, *Atractus edioi*); Espinhaço range (AOE J, *Eurolophosaurus nanuzae*, *Gymnodactylus guttulatus*, *Placosoma cipoense*, *Rhachisaurus brachylepis*, *Tantilla boipiranga*).

Of the 29 restricted-range species defining areas of endemism (i.e. found in sympatry with at least another restricted-range species), 25 (86%) defined endemic elements (Table 2). All 10 proposed areas of endemism are roughly coincident with grid cells harbouring core areas of endemic biotic elements (i.e. cells harbouring more than 30% of the species in each endemic biotic element, Fig. 5). All species defining AOE B (Miranda depression) and one of the two species from AOE A (Tietê–Rio Grande headwaters) form the core of Paraná–Paraguay headwaters endemic element (EE3, Fig. 5; Table 2). All species from AOE C (Huanchaca plateau), AOE D (northern portion of the Parecis plateau) and AOE E (Serra das Araras range) form the core of Paraguay–Guaporé endemic element 2 (EE2, Fig. 5; Table 2).

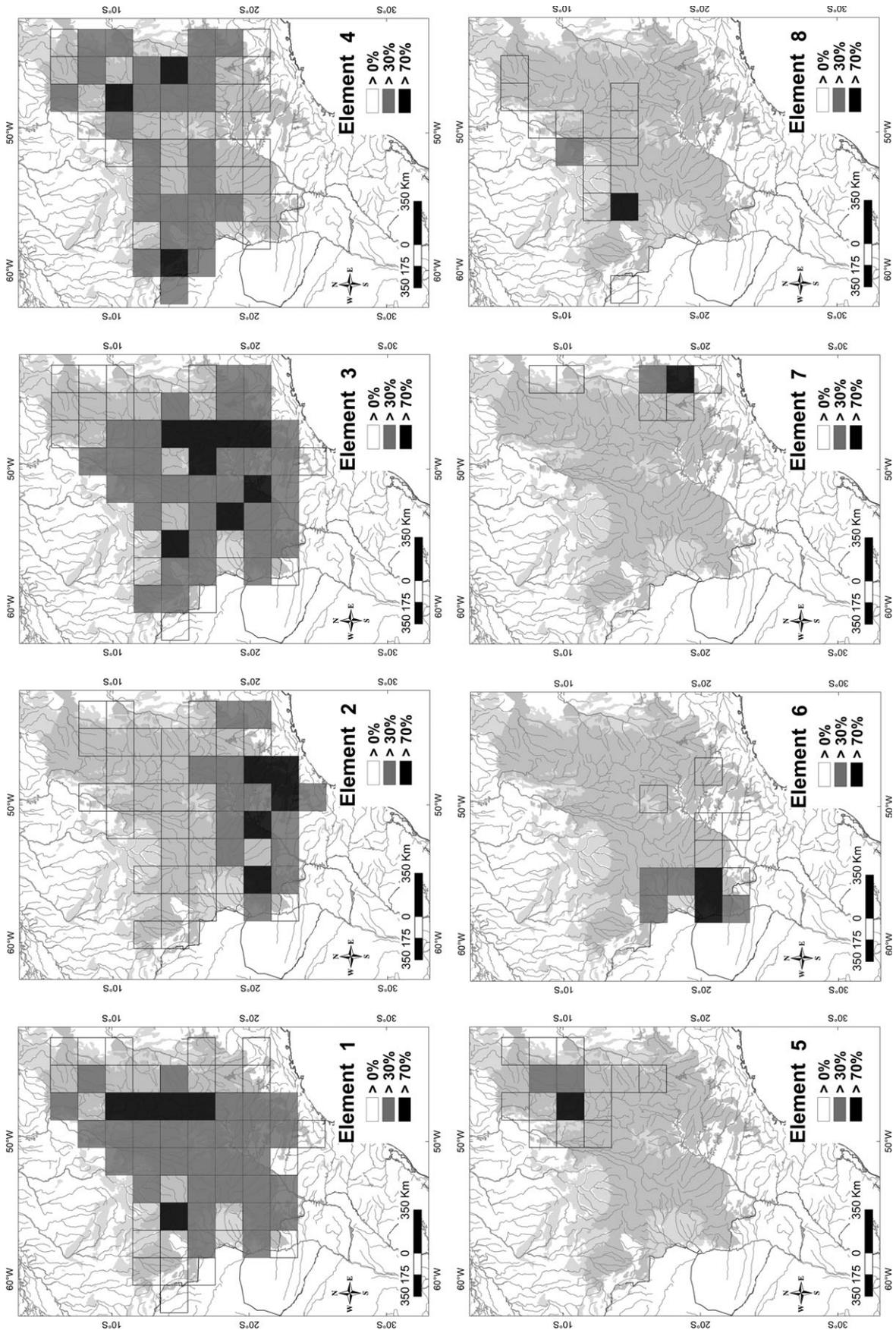


Figure 2 Distribution of biotic elements (BE1–8) recovered according to the range of 254 Cerrado squamates. Shadings indicate the areas where $> 70\%$, $> 30\%$ and $> 0\%$ of the species of an element are present.

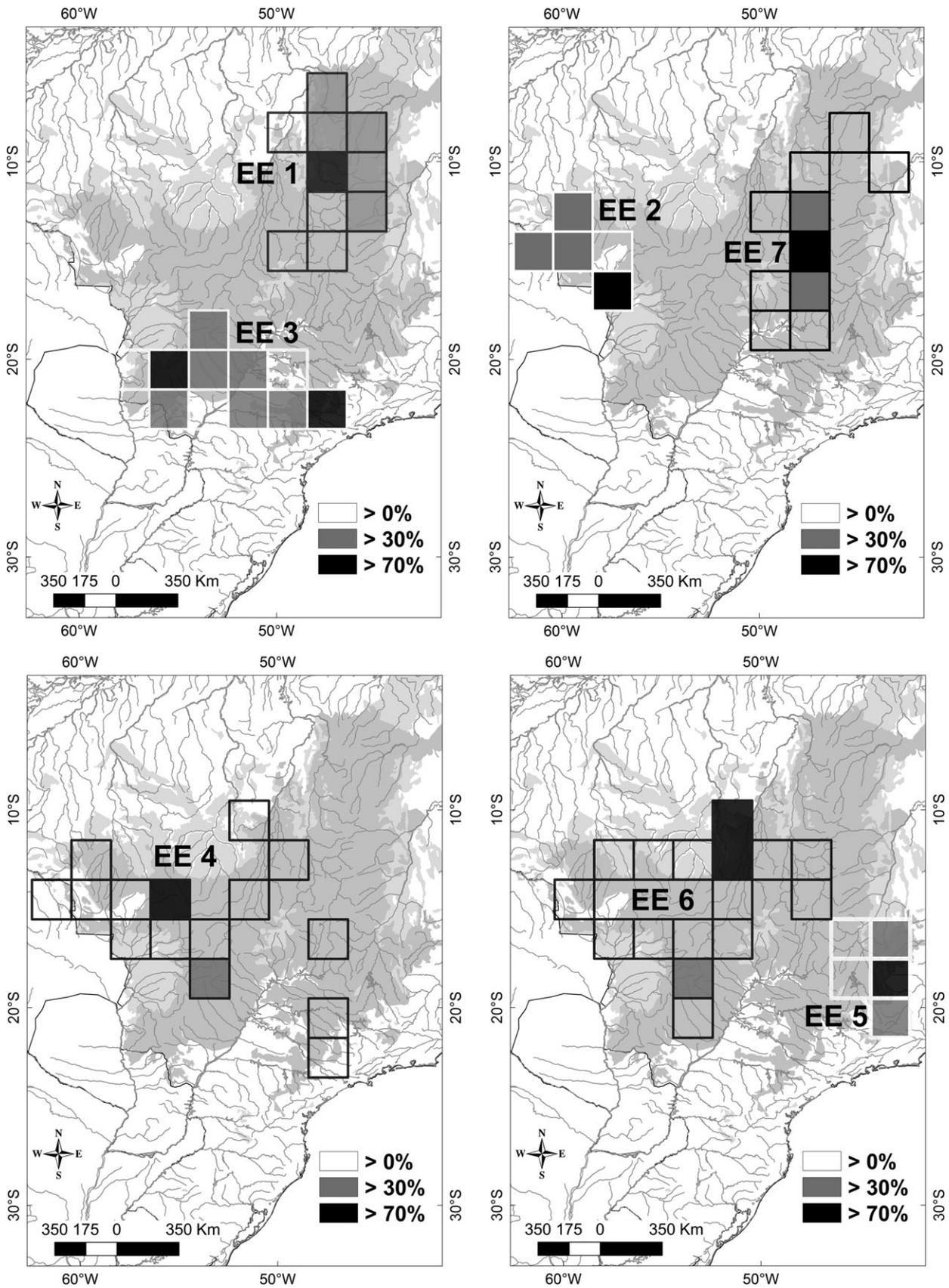


Figure 4 Distribution of endemic biotic elements (EE1–7) recovered according to the range of 101 Cerrado endemic squamates. Shadings indicate the areas where > 70%, > 30% and > 0% of the species of an element are present.

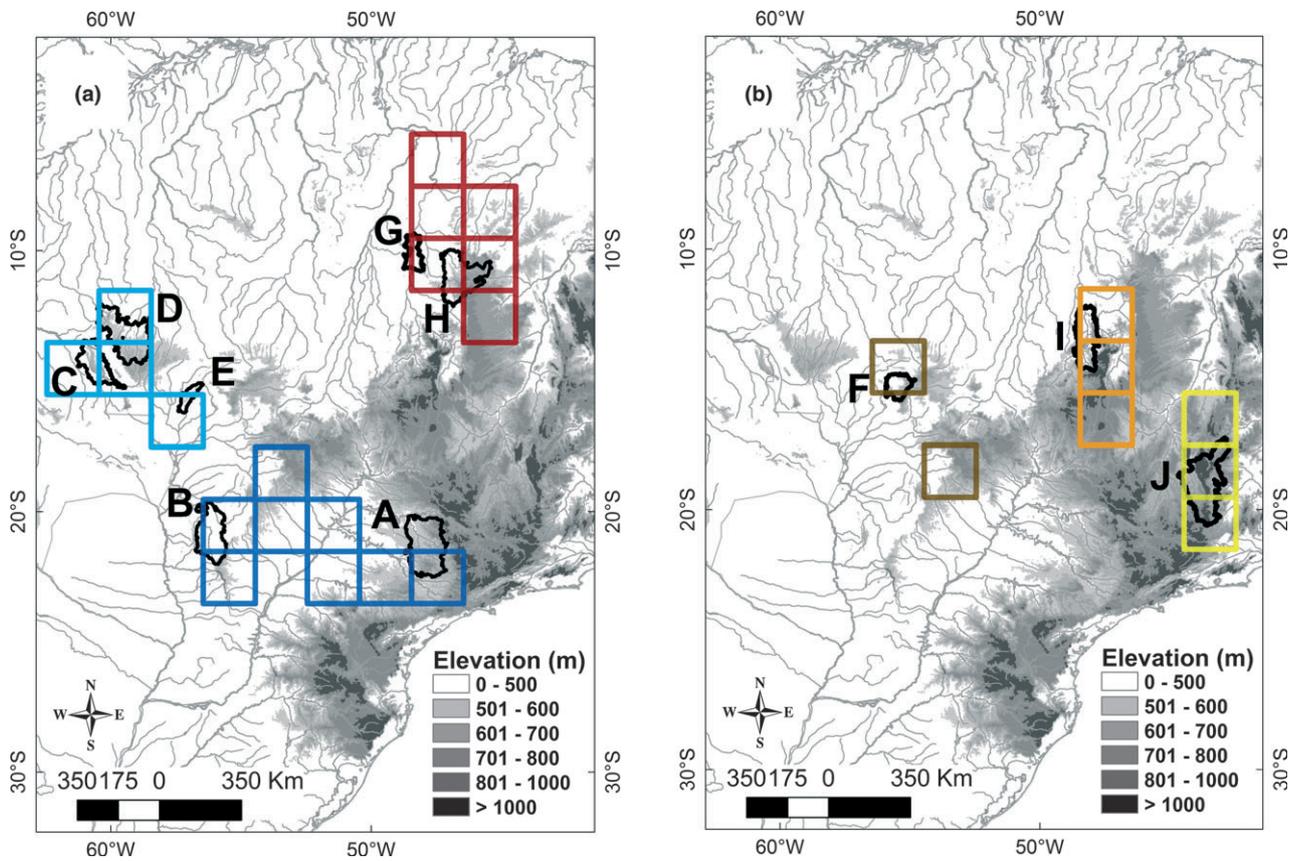


Figure 5 Location of areas of endemism (AOEs A–J) according to elevation and core areas of endemic biotic elements (see also Table 2): AOE A (Tietê–Rio Grande headwaters) and AOE B (Miranda depression) and the core of endemic biotic element 3 (EE3), Paraná–Paraguay headwaters (dark blue); AOE C (Huanchaca plateau), AOE D (northernmost tip of the Parecis plateau) and E (Serra das Araras range) at the core of endemic biotic element 2 (EE2), Paraguay–Guaporé (blue); AOE F (Chapada dos Guimarães plateau) at the core of endemic biotic element 4 (EE4), Guimarães–Roncador (brown); AOE G (Tocantins depression) and AOE H (Jalapão and Serra Geral plateau) and the core of endemic biotic element 1 (EE1), Tocantins–Serra Geral (red); AOE I (Upper Tocantins plateaus) and the core of endemic element 7 (EE7), Central Plateau; AOE J (Espinhaço range) and the core of endemic biotic element 5 (EE5), Espinhaço (yellow).

elements found with the 254 grid-mapped species dataset. At the continental scale, faunal interchange was similar with adjacent forested regions and open domains (Table 4). However, the effect of adjacent regions was not homogeneous

across biotic elements and geomorphological regions: faunal interchange with the Atlantic Forest and Pampas occurred both in plateaus and depressions and contributed largely to BE2, restricted to the Paraná–Paraguay headwaters. Species

Table 2 Number of squamate species in areas of endemism (A–J) according to endemic biotic elements (EE1–7) and major geomorphological units in the Cerrado region; generalist species occurring randomly in both depressions and plateaus are excluded.

Endemic element	Area of endemism									
	A	B	C	D	E	F	G	H	I	J
EE1 Tocantins–Serra Geral	–	–	–	–	–	–	2	3	–	–
EE2 Paraguay–Guaporé	–	–	2	3	2	–	–	–	–	–
EE3 Paraná–Paraguay	1	2	–	–	–	–	–	–	–	–
EE4 Guimarães–Roncador	–	–	–	–	–	4	–	–	–	–
EE5 Espinhaço	–	–	–	–	–	–	–	–	–	5
EE6 Araguaia	–	–	–	–	–	–	–	–	–	–
EE7 Central Plateau	–	–	–	–	–	–	–	–	1	–
0-Noise	1	–	–	–	–	–	1	1	1	–
Geomorphological unit										
Depressions	–	2	1	–	2	2	3	1	1	0
Plateaus	2	–	1	3	–	2	–	3	1	5

Table 3 Numbers of endemic versus non-endemic Cerrado squamates according to geomorphological units and major habitat types (species lacking habitat data, or species occurring randomly in both plateaus and depressions are excluded).

Unit	Endemic	Non-endemic	Fisher's exact test
Plateaus	44	30	$P < 0.001$
Depressions	31	89	
$n = 194$	75	119	
Forested habitats	10	63	$P < 0.001$
Open habitats	63	65	
$n = 184$	73	128	

shared with Amazonia were found mostly in depressions and contributed mostly to widespread range clusters in BE1, BE3 and BE4. Species shared with Caatinga were also found mainly within depressions and also contributed largely to widespread range clusters (BE1, BE3), but were the most important component of BE5, restricted to north-eastern Cerrado. Species shared with Chaco were also found mostly in depressions and also contributed largely to wide-ranging clusters (BE1, BE3), but formed a large fraction of BE6, restricted to western Cerrado and sharing a large proportion of species with depressions of the Pantanal floodplain.

DISCUSSION

Even considering taxonomic resolution and sampling coverage limitations (Costa *et al.*, 2007), richness and endemism levels recovered for Cerrado squamates largely surpass those detected in recent syntheses (Myers *et al.*, 2000; Colli *et al.*, 2002). These results, showing a rich and complex squamate fauna whose major distribution patterns corroborate central predictions of the vicariance model (Hausdorf & Hennig, 2003), are in clear contrast to earlier interpretations describing an impoverished and homogeneous Cerrado fauna, dominated by wide-ranging generalist species shared along the South American diagonal belt of open formations (Sick, 1965; Vanzolini, 1988).

The endemism level of squamates (39%) is higher than previously recorded in any other vertebrate group in the Cerrado. The number of endemic species (103) documented in the present study is equivalent to 82% of the 126 Cerrado endemic vertebrates analysed by Diniz-Filho *et al.* (2008), and to 86% of the 120 Cerrado endemic vertebrates in the classic hotspot study of Myers *et al.* (2000). The omission of many endemic species in previous studies indicates that endemism levels (and underlying vicariant patterns and processes) were underestimated due to poor compilation of available distributional and taxonomic data, and corroborates previous indications that biogeographical patterns are often neglected in conservation-oriented studies (Crisci, 2000). These results also highlight the crucial importance of detailed point-locality revisions prior to macroecological, biogeographical or conservation planning analyses, so as to make the best use of available biodiversity data (Brooks *et al.*, 2004).

Limited vertebrate endemism in the Cerrado fauna was originally interpreted as the result of extensive faunal interchange with adjacent regions (Sick, 1965; Vanzolini, 1976, 1988), mostly through gallery forest connections and dispersal routes (Redford & da Fonseca, 1986; Marinho-Filho *et al.*, 2002; da Silva & Bates, 2002). However, although faunal interchange with adjacent regions via forested connections seems to be the main factor influencing Cerrado birds and mammals (Redford & da Fonseca, 1986; Marinho-Filho *et al.*, 2002; da Silva & Bates, 2002), our data indicate that isolation in open, elevated savannas played an important role in the history and current diversity of Cerrado faunas. Earlier biogeographical studies emphasized endemism in ancient, stable landscapes on isolated tablelands in central Brazil (Müller, 1973; Brown & Gifford, 2002), forming the core of the 'Campo Cerrado' centre of endemism (Müller, 1973), and are corroborated by data on squamate endemism and distribution.

Our results also corroborate the idea that the homogeneously low endemism levels of Cerrado vertebrate groups may reflect a lack of basic distributional data and taxonomic resolution (da Silva & Bates, 2002). Although we used a broader definition of Cerrado (Lopes, 2008), we interpret the

Table 4 Number of squamate species in major Neotropical regions, according to biotic elements (BE1–8) and major geomorphological units in the Cerrado region.

	Biotic element								Geo-unit		
	1	2	3	4	5	6	7	8	Plateaus	Depressions	P level
Amazonia (63)	29	6	14	10	1	–	1	2	4	56	< 0.001
Atlantic Forest (63)	16	27	17	2	1	–	–	–	24	29	NS
Caatinga (46)	16	6	11	7	4	–	2	–	5	28	< 0.001
Chaco (43)	15	7	12	5	–	4	–	–	10	25	< 0.05
Pampas (17)	3	11	3	–	–	–	–	–	10	4	NS
Pantanal (18)	2	2	2	7	–	5	–	–	–	12	< 0.001

Generalist species occurring randomly in both plateaus and depressions were excluded from comparisons among geomorphological units. Species found in the noise component of biotic element analysis with all 254 grid-mapped taxa were excluded from comparisons among regions. P level refers to results of a χ^2 test on frequencies of occurrence in plateaus and depressions.

increase in endemism levels as a result of increased basic knowledge, incorporated via careful revision of specimens in large herpetological collections and compilation of literature data, complemented by field studies designed to cover previous sampling gaps. The gathering of distributional data in field studies and the comparison with museum specimens has favoured the description of new species (e.g. Colli *et al.*, 2003; Nogueira, 2006; Rodrigues *et al.*, 2008; Ribeiro *et al.*, 2009), and many additional undescribed taxa await formal description, indicating that richness and endemism levels will rise in future syntheses. This rise in knowledge will certainly provide data for further tests of the general patterns described and interpreted here, and will provide a more detailed picture of Cerrado and Neotropical biogeography.

The biogeographical patterns found in squamates may be shared with other taxonomic groups with relatively limited ranges and dispersal abilities, where historical processes of vicariant speciation are strong drivers of diversity (Araújo *et al.*, 2001). Although similar patterns of vertebrate endemism have not been properly studied, narrow-endemic amphibians (e.g. *Phyllomedusa* gr. *megacephala*), fishes (e.g. rivulids in the *Simpsonichthys* gr. *boitonei*; the characoid genus *Planaltina* spp.) and mammals (e.g. rodents of the genera *Juscelinomys* and *Microakodontomys*) seem to be associated with central Brazilian plateaus. Isolated plateaus in central Brazil have been interpreted as probable areas of endemism for Cerrado plants in the genus *Mimosa* (Simon & Proença, 2000). However, detailed studies on congruent patterns of endemism on central Brazilian plateaus are lacking and should be considered research priorities.

Although biotic elements are a prediction of the vicariance model, vicariance events may not necessarily be their single explanation (Hausdorf, 2002). Biotic elements can arise after an area is colonized by chance dispersal from different source areas across pre-existing barriers (Hausdorf, 2002). In such cases, biotic elements are geographical but not historical units. However, the significant presence of biotic elements detected with both datasets, and the general coincidence between endemic elements and areas of endemism, indicate that post-speciation dispersal alone cannot explain the recovered clustering of species ranges. The historical relationships among endemic biotic elements, and their validity as historical (and not merely geographical) units, can be tested in future studies with the conversion of taxon cladograms into element cladograms (Hausdorf, 2002; Hausdorf & Hennig, 2003), a test that still depends on phylogenetic hypotheses containing groups of Cerrado endemic congeneric species. Thus, distributional patterns recovered herein should provide important testing grounds for hypotheses based on phylogeographical, phylogenetical or palaeoecological data.

Moreover, recent studies highlight the validity of biotic elements as surrogates for evolutionary processes in conservation planning exercises (Carvalho *et al.*, 2011). Given the widespread paucity of detailed phylogenetic or phylogeographical data (Carvalho *et al.*, 2011), coupled with the urgent need for setting spatial priorities in highly threatened regions,

incorporating biotic elements in conservation biogeographical analyses should be seen as a top research priority to safeguard the evolutionary significance of biodiversity hotspots such as the Cerrado.

The relatively high proportion of endemism in elevated plateaus compared with depressions indicates that ancient elevational gradients clearly affected faunal interchange and speciation in the Cerrado, at least for less vagile organisms. Most Cerrado endemic reptiles may have evolved in isolation after the uplift of Brazilian Shield plateaus during Tertiary tectonic crises (Colli, 2005; Werneck *et al.*, 2009). Geomorphological events in the Tertiary have been identified as important determinants of Cerrado avian diversity (da Silva, 1997; da Silva & Bates, 2002) and are also interpreted as key determinants of Amazonian speciation and biodiversity (Hoorn *et al.*, 2010). Moreover, as forested habitats in the Cerrado region harbour a large proportion of non-endemics, these forests may share a recent history of connections with adjacent Amazonia and seasonally dry tropical forests (Werneck & Colli, 2006; Werneck *et al.*, 2011). The concentration of endemics in isolated tablelands supports an early origin of central Brazilian savannas and associated habitat mosaics, in ancient, stable plateaus of the Brazilian Shield, and disagrees with former interpretations of the Cerrado as a result of recent disturbance, mainly due to anthropogenic changes in fire regimes (see discussions in da Silva & Bates, 2002). As the division of the Cerrado region in plateaus and depressions broadly determines dominant soil composition (Motta *et al.*, 2002) and vegetation mosaics (Oliveira-Filho & Ratter, 2002; da Silva & Bates, 2002), the effects of Pleistocene climatic changes probably depended on pre-existing elevational and topographical conditions and barriers (Bush, 1994).

Although scarce, dated molecular phylogenies, including Cerrado endemics (Giugliano *et al.*, 2007; Torres-Carvajal & de Queiroz, 2009; Werneck *et al.*, 2009), point to ancient origins of Cerrado endemic squamates, indicating Tertiary orogenetic shifts as key determinants of Cerrado herpetofaunal diversity. The split between *Kentropyx vanzoi* and its sister clade is dated around the early Miocene (Werneck *et al.*, 2009), as a probable result of the uplifting of the Parecis plateau (identified as a putative area of endemism), and may be related to the isolation between areas harbouring western Cerrado biotic elements from remaining areas. Although more recent, the divergence between *Kentropyx paulensis* (a widespread Cerrado endemic) and its sister species (an undescribed species apparently restricted to the Jalapão region) dates from the late Miocene to the Plio-Pleistocene transition (Werneck *et al.*, 2009), and may be related to the formation of the complex topography and sandy deposits typical of the fringes of the Serra Geral sandstone plateau (Rodrigues *et al.*, 2008; Ribeiro *et al.*, 2009).

Detailed data on endemism and faunal regionalization are of central importance within conservation biogeography: apart from being intrinsically susceptible to natural or anthropogenic disturbance (Whittaker *et al.*, 2005), localized endemism is often poorly represented in prioritization schemes based on

habitat classes or other coarse-scale biodiversity surrogates (Araújo *et al.*, 2001; Brooks *et al.*, 2004). However, the major importance of detailed biogeographical patterns of endemism comes from their value as indicators of localized evolutionary processes and biological singularity, key components of systematic conservation planning (Margules & Pressey, 2000; Whittaker *et al.*, 2005).

Incomplete knowledge on vertebrate distribution patterns (and their underlying processes) is even more critical when considering the extreme rates of habitat loss in central Brazil (Klink & Machado, 2005; Carvalho *et al.*, 2009). At the local scale, most of this conversion occurs in open, interfluvial savanna habitats, the richest habitats for Cerrado squamates (Nogueira *et al.*, 2009). At the regional, biogeographical scale, habitat loss is concentrated on flatland plateaus, which are the main targets for expansion of mechanized agriculture (Klink & Machado, 2005; Carvalho *et al.*, 2009) and which also harbour most Cerrado endemic squamates.

The coincidence of local richness, endemism and habitat loss in open interfluvial plateau savannas threatens to erase ancient and highly complex evolutionary patterns and processes, posing a serious challenge to the conservation of Neotropical biodiversity. The lack of basic distributional knowledge on the Cerrado fauna not only represents a major gap in Neotropical biogeography, but also favours the wide and ongoing process of destruction of central Brazilian savannas (Cavalcanti & Joly, 2002), still underrated and poorly represented in conservation strategies (Ratter *et al.*, 1997; Marris, 2005). Our study indicates that increased basic knowledge on Cerrado zoogeography provides information on complex historical patterns of species distribution, generating crucial overlooked information for the understanding and conservation of Neotropical biodiversity.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article.

Appendix S1 Species list and distribution patterns of Cerrado squamate reptiles.

Appendix S2 Species–area matrix for 254 Cerrado squamates in 60 2° × 2°-grid cells covering the core of the Cerrado region.

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BIOSKETCH

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