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Biogeography of anurans and squamates in the Cerrado hotspot: coincident endemism patterns in the richest and most impacted savanna on the globe

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ABSTRACT

Aim To analyse ranges of endemic squamates and anurans in the Cerrado hotspot, searching for coincident distributional patterns in two ecologically distinct clades, and proposing a testable and comprehensive regionalization scheme for the richest and most threatened savanna on the planet.

Location Cerrado region, central South America.

Methods We updated previous point-locality compilations for endemic species of the Cerrado herpetofauna, gathering 4588 unique occurrence records. Using a 1° grid cell, we compared regionalization results of biotic element (BE) and endemism analyses. To search for a unified regionalization pattern, we compared analyses with a combined dataset (anurans + squamates) with those obtained in single-group analyses.

Results The analysis with the combined dataset recovered more complete results than those in taxon-specific analyses. We found 13 main biogeographical units formed by anurans and squamates that were recovered in both analyses with the combined dataset, and formed our general regionalization scheme. In general, biogeographical units defined by BEs correspond to those recovered by endemism analysis with the combined dataset. Most recovered biogeographical units were formed both by anurans and squamates, with fewer areas determined solely by one group.

Main conclusions Common regionalization processes operated on both anurans and squamates, shaping general biogeographical patterns for the Cerrado. The general regionalization pattern recovered with anurans and squamates may be valid for other taxa, and should be tested in future studies. As in previous results, most biogeographical units are found over ancient plateaus, separated by peripheral depressions. These major topographical barriers may explain major coincident patterns, linking the evolution of Cerrado biotas to the geomorphological history of the Brazilian shield.

Keywords

amphibians, areas of endemism, biodiversity, biotic elements, distributional patterns, Neotropical region, open areas, regionalization, reptiles

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INTRODUCTION

The global biota is divided into many different regions formed by taxa that share common patterns of endemism (Sclater, 1858; Wallace, 1876; Holt *et al.*, 2013). The search for these general patterns is a major goal of biogeography

and a necessary first step for all subsequent analysis (Morrone, 2009; Ebach & Parenti, 2015). The search for coincident regionalization patterns among organisms with different traits and evolutionary histories increases the reliability of the regionalization hypothesis, because common patterns for very distinct groups may indicate general, common processes

(Croizat *et al.*, 1974; Vargas *et al.*, 1998). Therefore, many studies have analysed different taxa to search for co-incident patterns of regionalization, especially at continental scales (Linder *et al.*, 2012; Procheş & Ramdhani, 2012; Rueda *et al.*, 2013). Thus, different features of different organisms are not an obstacle to biogeography, and pattern analysis may provide clues into the impact of those differences on the origin of distributions (Craw *et al.*, 1999).

Although large-scale global patterns are relatively well established (Holt *et al.*, 2013), finer scale, intracontinental regionalization patterns are more difficult to detect, representing a major challenge to biogeographers (Szumik *et al.*, 2012; Ebach & Parenti, 2015). At this level, biogeographical patterns provide valuable information on what spatial portions of biodiversity should be conserved (Crisci, 2001; Whittaker *et al.*, 2005), especially if coincident among diverse sets of organisms. Thus, the use of multi-taxon data matrices, following a total evidence approach analogous to that applied in phylogenetic studies, should provide better results than any *a posteriori* inference or consensus of independent results from different taxa (García-Barros *et al.*, 2002; Szumik *et al.*, 2012).

Squamate reptiles and anurans are very distinct in terms of biology and natural history (Huey, 1982; Duellman & Trueb, 1994), and common distributional patterns between these two groups may be interpreted as a signal of shared historical processes, regardless of ecological or ecophysiological differences. Both squamates and anurans are low dispersal groups and show high endemism levels in the Cerrado region (Nogueira *et al.*, 2011; Valdujo *et al.*, 2012a), the largest block of Neotropical savannas (Silva & Bates, 2002). Major biogeographical patterns in the Cerrado have only recently been described, and many new species have been described in recent years (Costa *et al.*, 2007; Nogueira *et al.*, 2011; Valdujo *et al.*, 2012a). Ranges of Cerrado endemic squamates are clustered over different areas, especially on plateaus, forming seven groups of significantly co-distributed species (Nogueira *et al.*, 2011). Unlike squamates, major distributional patterns of anurans are related to proximity to forested domains, but some species with more restricted distributions are located in different higher areas of the Cerrado (Valdujo *et al.*, 2012a). However, many new restricted range species were described for both anurans and squamates in the last few years, and despite intensive data accumulation, no comparative biogeographical studies were made between these very distinctive and highly endemic groups at the Cerrado region.

Therefore, we used the most comprehensive and largest database of endemic species ever compiled in the Cerrado, including more than 200 endemic species of anurans and squamates, to search for coincident biogeographical patterns between two important and highly endemic components of Neotropical faunas. The recovery of coincident range patterns in very distinctive groups may indicate general biogeographical processes acting over entire biotas, being more useful than patterns based on unique groups, both for

evolutionary interpretations and conservation goals. The aims of our study are: (1) to detect and delineate non-random, coincident biogeographical units for anurans and squamates endemic to the Cerrado, minimizing the influence of the method choice; (2) to compare results found for each group to those found in a combined dataset (anurans + squamates), in order to detect a general regionalization hypothesis for the Cerrado herpetofauna; (3) to provide a hypothesis about the origins of biogeographical patterns in the Cerrado.

MATERIALS AND METHODS

Study area

The Cerrado region occupies at least 1.8 million square kilometres at the centre of South America, and is characterized by an ancient, fire-adapted flora (Ratter *et al.*, 1997; Silva & Bates, 2002). With a highly endemic and threatened biota, the Cerrado is the only tropical savanna listed as a biodiversity hotspot (Myers *et al.*, 2000; Myers, 2003). This region is characterized and dominated by seasonal interfluvial savannas, crossed by corridors of evergreen gallery forests along drainage systems (Eiten, 1972, 1994). Ancient tectonic cycles of uplift, erosion and soil impoverishment, and recent dissection and expansion of peripheral depressions, formed the two major geomorphological units of the Cerrado: ancient headwater plateaus, generally above 500 m, and younger depressions, eroded by major drainage systems (Silva, 1997; Ab'Saber, 1998; Silva *et al.*, 2006).

Data sources

We used the list of Cerrado endemic species and the distributional data compiled by Nogueira *et al.* (2011) for squamates and Valdujo *et al.* (2012a) for anurans. We updated the taxonomy according to the List of Brazilian Reptiles (Bérnils & Costa, 2012) and the List of Brazilian Amphibians (Segalla *et al.*, 2012). We complemented this source by literature review, including new records and recently described endemic species (up to December 2013). Endemic anurans of difficult determination, such as all species of *Pseudopaludicola* and some species of *Leptodactylus* (*Leptodactylus furnarius* and *L. pustulatus*) or *Physalaemus* (*Physalaemus centralis*, *P. marmoratus*), were not included in the analysis. As in earlier studies (Nogueira *et al.*, 2011), we used the Brazilian vegetation map (IBGE, 1993) to define approximate limits of the Cerrado region. We follow Silva (1997) and Nogueira *et al.* (2011) and considered as endemic those species with records largely coincident with the approximate limits of Cerrado vegetation, including part of the Pantanal region and adjacent transition areas (Ab'Saber, 1977).

Delineating biogeographical units

To perform all analyses, we produced presence–absence matrices from point-locality records of anurans, squamates

(taxon-specific datasets) and from a combined dataset (anurans + squamates) by intersecting the records with a $1 \times 1^\circ$ cell grid coincident with the core area of the Cerrado. We eliminated cells with fewer than two species to avoid misleading signals (Kreft & Jetz, 2010). First, we analysed distributional patterns in each group separately. Then, to search for a unified biogeographical regionalization for both anurans and squamates, we repeated the analyses using the combined dataset. We checked the results of the taxon-specific dataset against the combined dataset to test for possible loss of biogeographical signal using a total evidence approach. As our dataset consisted of similar numbers of anurans and squamates, we avoided any bias resulting from unequal numbers of endemics in each group (see Linder *et al.*, 2012).

To search for a unified regionalization hypothesis, we compared the results of biotic element (BE) analysis and endemism analysis – NDM (Szumik *et al.*, 2002; Hausdorf & Hennig, 2003). By doing so, we verified the influence of method choice in detecting regionalization patterns in the Cerrado. As these two analyses operate differently, similar biogeographical units detected in both methods should be a result of a shared biogeographical signal, independent of analytical procedures. We used the name ‘biogeographical unit’ to refer to common results obtained in both areas of endemism (AOE) and BE analyses, forming our general regionalization hypothesis.

Analyses

Biotic element analysis was implemented in ‘prabclus’ (Hausdorf & Hennig, 2003, 2004), an add-on package for the statistical software R (available at <http://cran.r-project.org>). This analysis provides a test for non-random congruence of species distributions, and detects groups of taxa whose ranges are more similar to one another than to those of other such groups (Hausdorf, 2002). They can be detected even if some species dispersed from the AOE where they originated and/or when there is no strict distributional coincidence among species (Hausdorf & Hennig, 2003) and was already tested with reptiles in other regions of the world (Chen, 2013). We first constructed a dissimilarity matrix using the *geco* coefficient from the presence–absence matrix (Hennig & Hausdorf, 2006). This coefficient is a generalization of the Kulczynski dissimilarity, and takes into account the geographical distances between species occurrences, allowing the use of smaller grid cells and being more robust against incomplete sampling (Hennig & Hausdorf, 2006; Wronski & Hausdorf, 2008). For the required *geco* tuning constant, we used $f = 0.2$. Hennig & Hausdorf (2006) tested values zero, 0.1 and 0.2 for this constant in the explanation about the *geco* coefficient and indicated the choice of higher F -values (> 0.1) when the grid is coarse in relation to the species presences. We considered the $1 \times 1^\circ$ grid as relatively coarse in relation to our point-locality dataset, containing more than 200 species and resulting in very few empty cells. Moreover, even our most uncertain localities, georeferenced based

on municipalities, were more detailed than the $1 \times 1^\circ$ grid, as we previously calculated the average radius size of Cerrado municipalities as *c.* 20% of one degree. The use of higher F -values increases the importance of geographical proximity between grid cells, and balances the choice of a coarse grid when constructing the dissimilarity matrix (see Hennig & Hausdorf, 2006).

Next, a t -test for a departure from a null model of co-occurrence (Monte Carlo simulation) is made, and then, BEs (groups of non-random, co-distributed species) are determined. We used the ‘hprabclus’ command (in ‘prabclus’ package), which clusters the dissimilarity matrix by taking the cut-partition of a hierarchical clustering and declaring all members of too small clusters as ‘noise’ (see description in ‘prabclus’ Package, Hausdorf & Hennig, 2003, 2004). We used UPGMA clustering metric as it is considered an efficient method in a biogeographical framework (Kreft & Jetz, 2010). The software requires two parameters: the ‘cutdist’, that is a value to take the ‘h-cut’ partition, and the ‘nnout’, that is the minimum number of members to form a cluster. To estimate the value to cut the tree (cutdist), we tested values between 0.1 and 0.5 (dissimilarity values within clusters) with the combined dataset, against a value of $nnout = 2$ (more than two species to form a cluster). We adopted the value that maximized dissimilarity while still preserving spatial contiguity of the clusters in the combined dataset. We applied the same value to the taxon-specific analysis for anurans and squamates. The result of BE analysis is a list of species classified into their respective biogeographical units, with species not classified in any of these included in the noise component (Hausdorf & Hennig, 2003). We used non-metric multidimensional scaling ordination of species ranges in *hprabclus*, to visualize the degree of clustering between both groups within each BE (Hausdorf & Hennig, 2003, 2004).

Endemism analysis (NDM/VNDM) searches for areas with groups of taxa with congruent ranges (Szumik *et al.*, 2002). The method uses the presence–absence matrix as a representation of the taxon ranges. Sets of cells are selected to maximize the number of range-restricted taxa in the selected grid cells (more details in Szumik & Goloboff, 2004). Like BE analysis, the method allows areas to overlap. We used the option ‘observed presences’ = 20% to cover possible imprecisions of georeferenced points, some georeferenced based on municipalities, after estimating the average radius size of the municipalities in the Cerrado region to *c.* 20% of one degree. We used the option ‘assumed presences’ = 50% as the maximum distance value from point-localities to consider empty cells as assumed presences. In this case, adjacent cells were considered as assumed presences if located not farther than half the size of a grid cell side (*c.* 50 km, or half degree) from a verified record. These filling options minimize bias due to incomplete sampling without the use of a coarser grid. Searches were conducted saving sets of two or more endemic species, saving scores above 2.0, temporarily saving sets within 0.995 of the current score, and discarding duplicated sets in 100 replicates. Consensus endemic areas were searched using the option

'consense areas', with a cut-off of 50% similarity in species, using the option 'against any of the other areas in the consensus'. We chose a minimum value of the parameter 'keep overlapping subsets' that constrains species to be classified in only one area of endemism (AOE).

Mapping

The endemism analysis viewer (VNDM) automatically draws the consensus AOE as the set of grids with best scores. To compare results of NDM with BE analysis, we drew the biogeographical units resulting from BEs according to the region (set of grid cells) that contained two or more of its component species (in a 20-km radius from point-localities, similar to the NDM fill option). Then, biogeographical units with restricted patterns, that is, those composed by two or more species with congruent clustered ranges, were characterized according to the main geomorphological areas in which they are located. If some patterns were duplicated in the results (i.e. two overlapping AOE at the same geographical region, a common output of these analyses), we merged these areas. If a resulting biogeographical unit fully overlapped more than one restricted biogeographical unit, we opted to consider only the more restricted patterns nested inside that area.

To test if BEs in the combined dataset are uniformly composed by anurans and squamates, we performed a chi-square test for independence of rows and columns of a cross-table, with rows as taxonomic groups (anurans and squamates) and columns as biogeographical units (biotic elements). We also used chi-squared test to verify if species classified in some AOE in the combined dataset analysis (rows) belonged to an equivalent BE (columns). Finally, we tested if species classified in a given BE in the taxa-specific analysis (rows) tended to belong to the same BE in the combined datasets (columns).

RESULTS

Species distributional data

We added 8 squamates and 11 anurans to the list of endemic species of the Cerrado (see Appendix S1 in Supporting Information). In total, 750 new records were added to the original databases. These new records represent recently described species or extensions to the known range of each species. This resulted in 4588 unique point localities of 216 taxa, spread across 213 grid cells (see Appendix S2 in Supporting Information), including 103 endemic anurans (with three undescribed species), and 113 endemic squamates (with eight undescribed species). These 11 undescribed species are easily diagnosable taxa found in surveyed collections during recent syntheses of the Cerrado herpetofauna (Nogueira *et al.*, 2011; Valdujo *et al.*, 2012a).

Clustering of distributions

For all BE analyses (squamates, anurans and combined dataset), the *T* statistics of the tests for a departure from a null

model of co-occurrence were significantly lower than expected by chance (Table 1). This indicates that ranges were significantly clustered, forming localized biotas across the Cerrado in all analyses. The value of 'cutdist' = 0.35 was the maximum value that preserved spatial contiguity of BEs (Table 2). Values larger than 0.35 resulted in a smaller number of clusters, with a less resolved delimitation due to the inclusion of species with very widespread ranges. For NDM, the minimum value of the parameter 'keep overlapping subsets' that constrained species to be classified in no more than one AOE was 60%. Values smaller than 60% allowed some species to be classified in up to three different AOE.

Taxon-specific analyses

Biotic element analysis for anurans recovered 10 main biogeographical units – areas with the occurrence of two or more species that compose a BE – (Fig. 1a, Table 3 – Restricted patterns), whereas endemism analysis found seven biogeographical units (Fig. 1b), including a single region (AOE – 11, *Chapada das Mesas* region) with no corresponding biogeographical unit in BEs analysis (Fig. 1a,b). By contrast, four anuran BEs resulted in biogeographical units (BEs – 2, 3, 6 and 16) not recovered in endemism analysis (Fig. 1a,b).

Biotic element analysis for squamates also resulted in 10 biogeographical units (Fig. 1c), while endemism analysis found seven biogeographical units (Fig. 1d), including one with no corresponding BE (AOE – 17 – *Serranía de Huanchaca*). Four squamate BEs showed no corresponding AOE (BEs – 1, 2, 6 and 18) (Fig. 1c,d).

Table 1 *T* statistics from the test for the clustering of the ranges of anurans and squamates in the Brazilian Cerrado. *P*-values smaller than 0.05 indicate significantly clustered distributions. Minimum, maximum and mean values of *T*, for 1000 artificial populations are shown (details in Hennig & Hausdorf, 2004).

Dataset	<i>T</i> statistic	<i>T</i> minimum	<i>T</i> maximum	<i>T</i> mean	<i>P</i> -value
Anurans	0.360	0.379	0.521	0.444	< 0.001
Squamates	0.374	0.372	0.478	0.425	0.002
Combined	0.378	0.408	0.489	0.443	0.001

Table 2 Values of *cutdist* (0.1–0.5), resulting number of species not classified in any biotic element (noise), and the number of restricted range biotic elements in the analysis with the combined dataset for endemic anurans and squamates in the Brazilian Cerrado. The maximum number of biotic elements was reached with *cutdist* = 0.35 (bold values).

<i>Cutdist</i> value	0.1	0.15	0.2	0.25	0.3	0.35	0.4	0.45	0.5
Noise	160	124	93	71	47	37	21	11	9
Restricted BEs	8	12	14	14	15	16	14	11	9

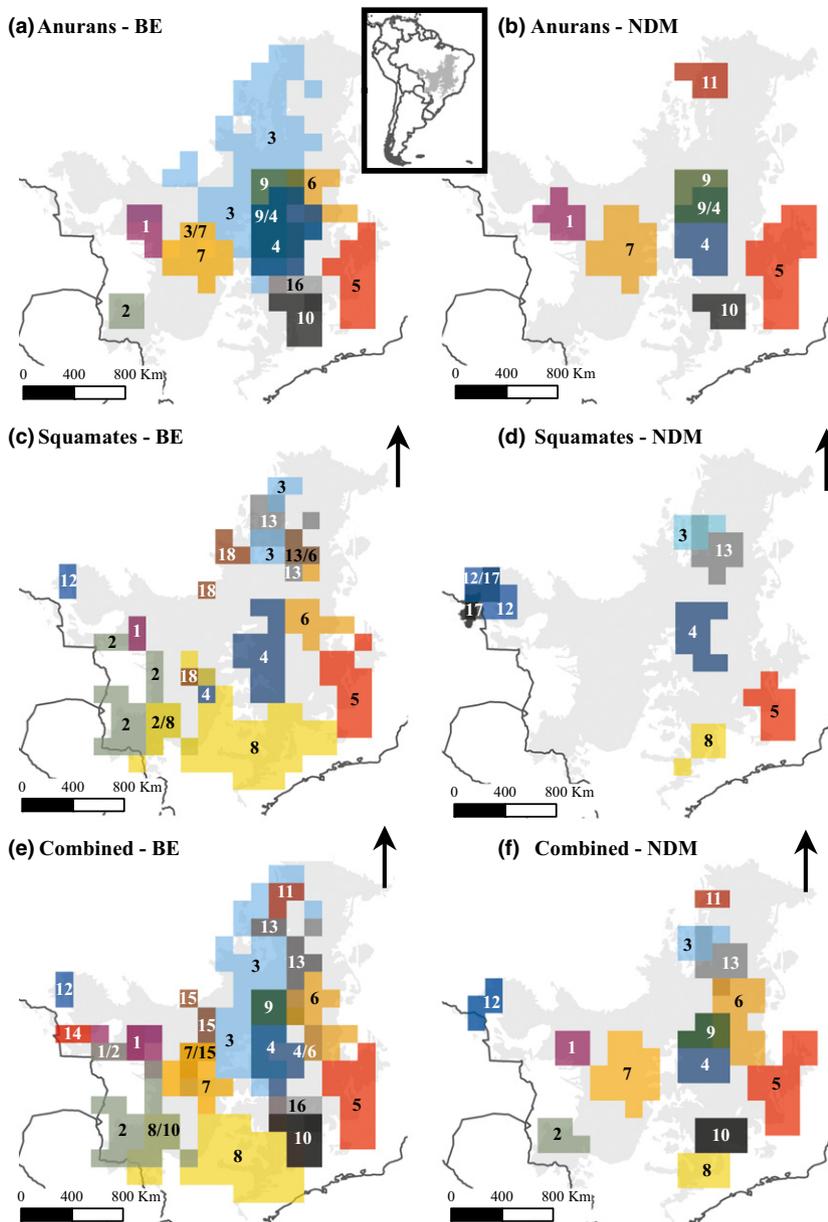


Figure 1 Biogeographical units detected for the Cerrado herpetofauna, with taxon-specific and combined datasets (below) resulted of biotic element (BE) and endemism (NDM) analyses, in cells containing at least two sympatric species. Grey colour indicates Cerrado limits. Biogeographical units named according to corresponding major geomorphological units: 1 – Guimarães plateau. 2 – Pantanal and Bodoquena. 3 – Tocantins–Araguaia basin. 4 – Central Brazilian plateau. 5 – Espinhaço mountain range. 6 – Serra Geral plateau. 7 – Caiapônia plateau. 8 – Central Paraná basin plateau. 9 – Veadeiros plateau. 10 – Canastra plateau. 11 – ‘Chapada’ das Mesas. 12 – Parecis plateau. 13 – Jalapão. 14 – Serra da Borda. 15 – Roncador plateau. 16 – Upper Parnaíba region. 17 – Huanchaca plateau. 18 – Without a main core area. See Fig. 3 for more details of geomorphological units.

Some BEs resulted in biogeographical units that were found only for one group in taxon-specific analyses (BEs – 12, 13, 18 for squamates and BEs – 7, 9, 10, 16 for anurans). Although anurans presented a larger proportion of species classified in BEs (79%) in relation to squamates (57%), the same number of BEs were found for both groups (Fig. 1a,c, Table 3), indicating that ranges of anuran species are more clustered than squamate species. In the case of endemism analysis, only units 4 and 5 were found for both groups.

Taxon-specific versus combined analyses

A comparison between BEs in taxon-specific and combined datasets (Fig. 1a,c,e) reveals that, with the exception of a single BE composed by squamate species with poorly overlapping ranges (BE – 18, Fig. 1c), all other biogeographical units found with taxon-specific datasets were also recovered

in the combined dataset (Fig. 1e). We recovered three additional BEs using the combined dataset (BEs 14, 15 and 16, Fig. 1e). Species forming a given BE in the taxon-specific analyses were generally found in the same BE in the combined analysis ($\chi^2 = 1849, P < 0.001$).

The endemism analysis with the combined dataset yields a more complete result than taxon-specific datasets (Fig. 1b, d,f), recovering two additional biogeographical units composed by both anurans and squamates (AOE 2 and 6) absent in the taxon-specific analysis. Only AOE – 17, found with the squamate dataset, was lost in the combined dataset.

Combined dataset

Contrary to taxon-specific analyses, all biogeographical units found by endemism analysis with the combined dataset had a corresponding biogeographical unit defined by a BE.

Endemicity analysis failed to locate a corresponding BE only in cases where taxa forming a given BE had very poorly overlapping ranges (e.g. BEs 14, 15, 16). For the final

Table 3 Biogeographical units found with endemic Cerrado anurans, endemic Cerrado squamates and combined dataset. Units classified as restricted (bold values) represent the patterns of interest, without widespread and repeated patterns.

Dataset	Biotic element analysis		
	Anurans	Squamates	Combined
Total number	10	14	19
Duplicated	0	1	0
Widespread	0	3	3
Restricted	10	10	16
Restricted n° spp.	79 (76%)	64 (57%)	154 (71%)
Unclassified n° spp.	25 (24%)	49 (43%)	60 (29%)
Dataset	Endemicity analysis (NDM)		
	Anurans	Squamates	Combined
Total number	9	7	17
Duplicated	2	0	4
Widespread	0	0	0
Restricted	7	7	13
Restricted n° spp.	50 (48%)	23 (20%)	87 (41%)
Unclassified n° spp.	54 (52%)	90 (80%)	127 (59%)

regionalization hypothesis, we considered these poorly defined biogeographical units as less robust than the remaining. Species that composed a given biogeographical unit in endemicity analysis were generally classified into the geographically correspondent BE (combined dataset; $\chi^2 = 879$, $P < 0.001$), indicating overall congruence in the location of biogeographical areas.

Unified regionalization hypothesis – BE analysis, combined dataset

Biogeographical units 1–13, were recovered in both methods in the combined dataset (Fig. 1e,f), and comprise our consensual, final regionalization hypothesis (Fig. 2). Of these, in the results of BE analysis, units 1–6 were found with all datasets, that is, they were found both for anurans and squamates and recovered as shared areas with the combined dataset (Fig. 1a,c,e; Coincident patterns – Table 4). A chi-square test indicates that anuran and squamate species are uniformly arranged in these six BEs ($\chi^2 = 6.1067$, $P = 0.1919$). In some of these BEs, the ranges of anuran species tended to be more clustered than ranges of squamate species (e.g. Central plateau, Tocantins-Araguaia and Serra Geral BEs), whereas at Guimarães and Espinhaço BEs, all species of anurans and squamates are very clustered together

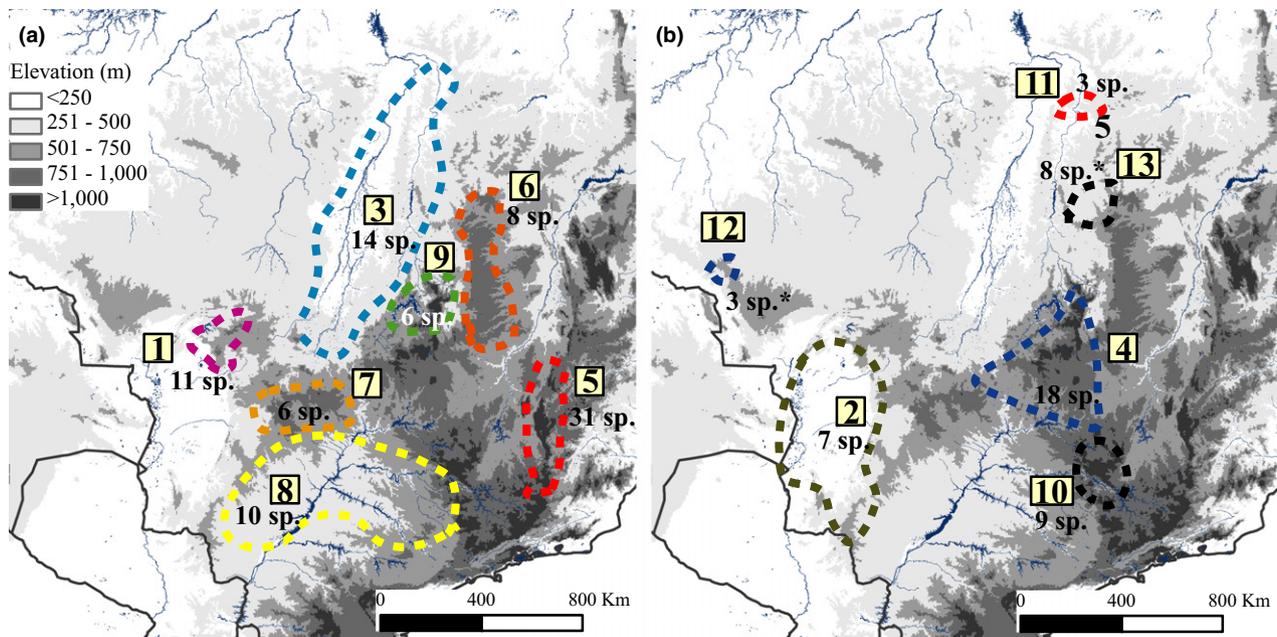


Figure 2 Location of the 13 main Cerrado herpetofaunal biogeographical units according to main geomorphological surfaces of central Brazil, separated in two maps for clarity. (a) 1 – Guimarães plateau ('Chapada dos Guimarães' region). 3 – Tocantins-Araguaia basin (and associated depression). 5 – Espinhaço mountain range (only southern portions along the Cerrado/Atlantic Forest contact areas). 6 – Serra Geral plateau (= 'Chapadão Ocidental do Rio São Francisco'). 7 – Caiapônia plateau (includes also part of Alcantilados, Rio Verde and upper Paraná Basin plateaus). 8 – Central Paraná Basin plateau (and the associated Paraná River Basin depression). 9 – Veadeiros plateau (including associated headwaters). (b) 2 – Pantanal region and Bodoquena plateau (and associated small reminiscent plateaus). 4 – Central Brazilian plateau. 10 – Canastra range (including neighbouring plateaus of southern Minas Gerais including Poços de Caldas, Alto Rio Grande). 11 – Chapada das Mesas region (and neighbouring reminiscent arenitic plateaus). 12 – Parecis plateau. 13 – Jalapão region (including part of the Tocantins depression and reminiscent tabletops of the Serra Geral plateau). Numbers beside each unit indicates total number of species (anurans + squamates), according to the results of biotic element analysis of the combined dataset (see Table 4). Asterisks indicate areas harbouring only squamates.

Table 4 Species composition (anurans and squamates) of areas in our unified regionalization hypothesis, formed by 13 biogeographical units recovered by both methods (biotic element – BE, and endemism analysis – NDM) with the combined dataset of endemic anurans and squamates from the Cerrado. First six biogeographical units were also coincident for both groups in taxon-specific analysis, and were recovered as shared areas with the combined dataset.

Biogeographical units	Combined dataset		Taxon-specific datasets	
	BE/NDM (n° spp.)		BE/NDM (n° spp.)	
	Anurans	Squamates	Anurans	Squamates
1- Guimarães	7/4	4/1	7/4	4/0
2- Pant/Bodoq	1/0	6/2	3/0	6/0
3- Toc/Arag.	8/0	6/3	10/0	3/3
4- Central	13/7	5/3	11/7	7/3
5- Espinhaço	20/18	11/6	20/19	11/4
6- Serra Geral	3/2	5/2	3/0	6/0
7- Caiapônia	4/4	2/1	5/4	None
8- Paraná plt.	1/2	9/1	None	9/3
9- Veadeiros	5/6	1/0	7/6	None
10- Canastra	8/6	1/2	8/7	None
11- Ch. Mesas	1/2	2/1	0/3	None
12- Parecís	None	3/2	None	3/4
13- Jalapão	None	8/7	None	12/6

(Fig. 3). For comparison, in the case of endemism analysis, only the biogeographical units 4 and 5 were recovered with all datasets.

In BE analysis, biogeographical units that were exclusive for one group in the taxon-specific datasets were recovered with additional species in the combined dataset: Caiapônia plateau (BE 7), Central Paraná basin plateau (BE 8), Veadeiros plateau (BE 9) and Canastra plateau (BE 10) (Table 4). Finally, biogeographical units found for a single group were also recovered with the combined dataset: Parecís plateau (BE 12) with three squamate species and the Jalapão region (BE 13) with eight squamate species, remained squamate-exclusive BEs in the combined dataset (Table 4).

The majority of consensual biogeographical units are located over plateau areas, above 500 m (see Fig. 2). Some lower areas also harboured regionalized biotas shared by both groups, especially in the Tocantins-Araguaia basin (BE 3). Based on our point-locality database and natural history data, some squamates and anurans classified in this BE seem to have their occurrences correlated with river channels (i.e. *Pseudis tocantins*, *Hydrodinastes melanogigas*), whereas others are less related to riparian areas (i.e. *Adenomera saci*). Paraná basin plateau (BE 8) and Pantanal/Bodoquena region (BE 2) contained a combination of species related to both plateaus and adjacent depressions. This last BE was composed by species more restricted to the Bodoquena region, as found in the anuran taxa-specific dataset (i.e. *Ameerega picta*) and by species with more widespread distributions over adjacent areas, as found with the combined dataset (i.e. *Phalotris matogrossensis*).

The remaining patterns (areas 14–16, Fig. 1e) represented results not corroborated in comparisons among datasets or analyses. Biotic element 14, at *Serra da Borda* region, was detected only in BE analysis with the combined dataset and has its limits at the southern portion of the *Huanchaca plateau*, a plateau at the border of Brazil and Bolivia (Killeen, 1998). Biotic Elements 15 and 16 were recovered by BE-analyses, but without equivalent in NDM results. Species ranges in these three last BEs overlap poorly. In addition, in the taxon-specific analyses, AOE 17, at *Huanchaca plateau*, was found only with NDM for squamates (merged with Parecís AOE, Fig. 1d).

DISCUSSION

The major result of our analysis is the recovery of shared biogeographical patterns for anurans and squamates, two highly endemic and rich components of Cerrado faunas, using two analytical procedures. Congruence in biogeographical regions for different groups at global and continental scales were already reported (Lamoreux *et al.*, 2006; Linder *et al.*, 2012) and are correlated with main phytogeographical domains (Rueda *et al.*, 2013). Herein, we show that congruent endemism patterns of different groups may exist even within a phytogeographical domain, allowing for a more refined view of biogeographical patterns and reinforcing the importance of endemism as a biodiversity metric (see Lamoreux *et al.*, 2006). As demonstrated in other regions of the world, similar regionalization patterns have already been documented among groups as different as primates and frogs (Evans *et al.*, 2003), or groups with very distinctive dispersal abilities, as macropterous and flightless insects (Bouchard & Brooks, 2004).

The coincident patterns found between anurans and squamates occur mainly over stable landscapes on isolated plateaus, supporting previous hypothesis describing the ‘Campo Cerrado’ centre of endemism, located on plateau areas of the Brazilian shield (Müller, 1973). Furthermore, these patterns partially support climate stability models of Werneck *et al.* (2012), with climate refugia coinciding specially with Serra Geral (BE 6), Central plateau (4) and Jalapão (BE 13), indicating possible influences of climatic oscillations on endemism patterns in the Cerrado. However, despite the importance of climate oscillations, some studies reported older divergences between endemic lineages, reflecting events that pre-date Quaternary climatic changes (Silva, 1997; Prado *et al.*, 2012). One example is the uplift of the Guimarães plateau, during the Plio-Pleistocene transition (Silva, 1997), reflected in isolated populations of the frog *Hysiboas albopunctatus* (Prado *et al.*, 2012). Other ancient western splits are depicted in the phylogenies of the lizard genera *Ameiva* and *Kentropyx*, with isolated western clades dated back to the Miocene (Werneck *et al.*, 2009; Giugliano *et al.*, 2013). Lineages in the eastern part of the Cerrado, like Espinhaço (populations of *Phyllorhynchus polycaris*) and Serra Geral (the frog *Rhinella veredas* and the snake *Bothrops lutzi*) also diverged in the Late Miocene and Early Pliocene (Vallinoto *et al.*, 2010; Gamble *et al.*,

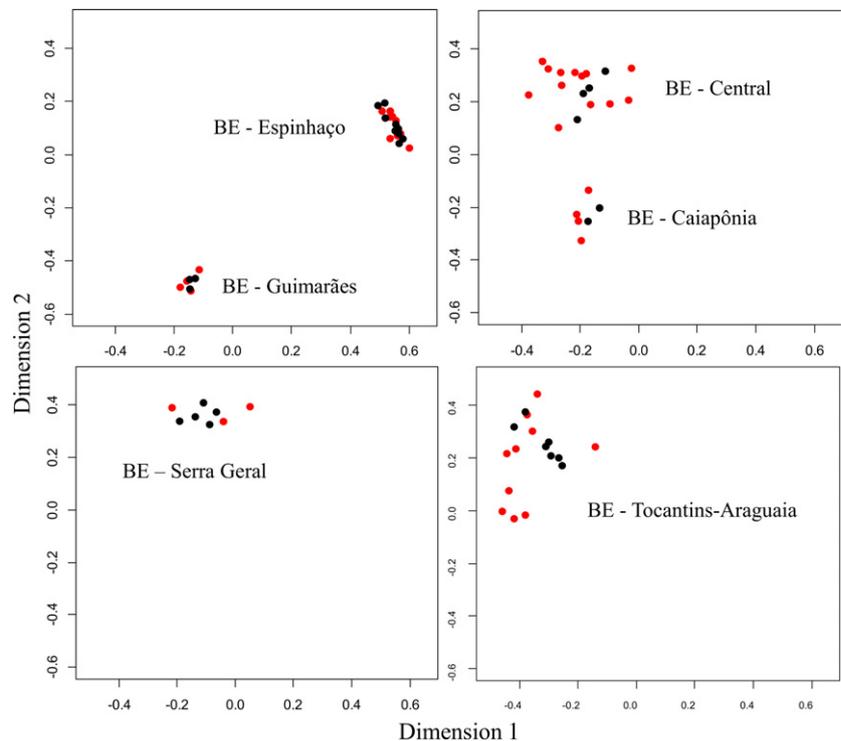


Figure 3 First two dimensions of a non-metric multidimensional scaling ordination of ranges of squamates (red dots) and anurans (black dots) forming biotic elements (BEs) of the Cerrado herpetofauna, in the combined dataset.

2012; Machado *et al.*, 2014). These old divergences seem to be related to major geomorphological changes, resulting in the formation of plateaus and depressions that influence many features of the Cerrado, including dominant soil composition, vegetation mosaics (see Brown & Gifford, 2002) and may also have shaped past climate dynamics and stability (Bush, 1994; Motta *et al.*, 2002; Nogueira *et al.*, 2011). Therefore, these geomorphological events may affect many groups simultaneously, and could be responsible for coincident endemism patterns in groups with very different ecological requirements as reported herein.

Despite the overall congruence, our results also highlighted some unique, taxon-specific patterns. The Jalapão region (BE 13) harbours a peculiar psammophilous squamate fauna (Rodrigues, 2002; Vitt *et al.*, 2002), with no endemic anuran species known so far. Other psammophilous endemic Squamates were restricted to the Parecis plateau (BE 12), detected over isolated sandy savanna patches. Both these examples highlight unique psammophilous squamate faunas. In the case of anurans, many narrow endemic species depend upon specific habitats for reproduction, and their presence may be more related to regional topography than to climatic conditions alone, being restricted to small headwater streams in open areas, rocky fields and rocky savannas, found typically above 700–1000 m (Eiten, 1994). These habitats are scattered especially over the Central plateau (BE 4), Espinhaço (BE 5), Guimarães (BE 1) and Canastra ranges (BE 10), and may explain the predominance of anuran species in the last two smaller areas (BE 1 and 10).

Patterns of endemism detected in a single method, or for a single taxon, were generally found in the poorly sampled northern portion of the Cerrado (Costa *et al.*, 2007). These

are priority areas for sampling, as best sampled areas in the Cerrado are found near its southern and southeastern limits (Nogueira *et al.*, 2010). We anticipate that many new endemic species in both groups (and even in other taxonomic groups) may be described in the northern portions of the Cerrado in the near future. Even so, major differences between the distributional patterns of endemic species of these two groups shown in the MDS plots, probably reflect finer-scale ecological differences and habitat selection that could be more evident in more detailed studies, within BEs. The tendency of anuran species to show more clustered ranges inside BEs, and the greater proportion of anuran species classified in BEs than squamates, is likely related to a possible lower dispersal ability of anurans in relation to squamates (Chen *et al.*, 2011).

Even with relative low levels of endemism, other vertebrates like birds and mammals show endemic species whose ranges coincide with some BEs like Espinhaço, Tocantins-Araguaia basin and Central Brazilian plateau (Silva, 1995; Marinho-Filho *et al.*, 2002). Additionally, many species of *Mimosa*, a plant genus with high endemism levels in the Cerrado, support the hypothesis of clustered distributions on major plateau areas (Simon & Proença, 2000). These results indicate that the endemism patterns recovered herein may be general, and not restricted to anurans or reptiles, providing a valid and spatially explicit regionalization hypothesis for Central Brazilian savannas. Examples of non-herpetofaunal Cerrado endemic taxa whose ranges are coincident with biogeographical units recovered herein can be found in Appendix S3.

The biogeographical units found herein are distributed over the entire Cerrado region and are not coincident only

with the richest or more densely sampled areas for squamates (Costa *et al.*, 2007). These areas are also not associated only with proximity to adjacent phytogeographical domains, as suggested by anuran betadiversity patterns (Valdujo *et al.*, 2012b). We interpret these congruent results in endemic patterns of anurans and squamates as the result of the historical interplay between low dispersal ability and major geomorphological changes (which shaped current topography, habitat types and even past climatic oscillations). These two factors resulted in highly regionalized endemism patterns throughout the Cerrado region. Our results, detailing congruent endemism patterns, raise new questions about the history of the globally richest and most imperilled savanna. Are the endemic species of each biogeographical unit more related to species from other areas within the Cerrado region? Alternatively, are the Cerrado endemics more related to species from adjacent phytogeographical domains or biomes? Are species in these biogeographical units of the Cerrado relicts of past general geomorphological events or are these biogeographical units dynamic areas with species originated by independent speciation events over time? Are these endemism patterns historically congruent for both anurans and squamates or are these biogeographical units just a geographical coincidence in the ranges of the species of both groups? Are these patterns really shared with other taxonomical groups with greater dispersal abilities when taking into account population levels?

All these questions require biogeographical inquiries at a continental scale, beyond the Cerrado limits (see Werneck, 2011). Moreover, to assess whether coincident patterns between both groups were caused by the same events, a biogeographical analysis with temporal information is required, generating the next step for understanding the evolution of Cerrado biotas (see Ebach & Parenti, 2015). The spatial framework discussed herein is thus the necessary first step for understanding the biogeographical processes that led to the formation of Cerrado regionalized endemic patterns, providing important insights on the major task of detecting refined biogeographical units in highly endemic tropical faunas across the planet.

ACKNOWLEDGEMENTS

We thank Debora Silvano, Ricardo Sawaya, Reuber Brandão and Thaís Guedes for providing insightful comments on the initial versions of this manuscript. J.A.R.A thanks Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) for providing a graduate fellowship. FAPESP (process # 12/19858-2) and CAPES provided post-doc fellowships to C.C.N.

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SUPPORTING INFORMATION

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

Appendix S1 Cerrado endemic herpetofauna and corresponding biogeographical units.

Appendix S2 Presence–absence matrix for Cerrado endemic herpetofauna.

Appendix S3 Non-herpetofaunal Cerrado endemics and biogeographical units.

BIOSKETCHES

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Editor: Liliana Katinas