Universidade de Brasília
Instituto de Ciências Biológicas
Programa de Pós-Graduação em Zoologia

Endemismo, vicariância e padrões de distribuição da herpetofauna do Cerrado

Josué Anderson Rêgo Azevedo

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Tese apresentada ao Programa de Pós-Graduação em Zoologia, Instituto de Ciências Biológicas, Universidade de Brasília, como parte dos requisitos para a obtenção do título de Mestre em Zoologia.

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Introdução Geral

Mesmo antes das primeiras tentativas de mapeamento da biodiversidade em nível mundial, e especialmente com os trabalhos de Augustin Pyramus de Candolle, Philip Sclater e Alfred Russel Wallace, é reconhecido que, em sua maioria, os organismos estão distribuídos de maneira limitada a diferentes porções dos continentes e em diferentes níveis de endemismo (Candolle, 1820; Sclater, 1858; Wallace, 1876). Nos mais de 150 anos passados desde então, uma enorme quantidade de dados foram acumulados e várias metodologias diferentes foram propostas para a delimitação de unidades biogeográficas (Hausdorf & Hennig, 2004; Morrone, 2013; Rueda *et al.*, 2013). Ainda assim, estudos atuais encontram basicamente o mesmo padrão geral de regionalização que Wallace propôs em sua época (Kreft & Jetz, 2013), mostrando que, em larga escala, tais padrões de distribuição são robustos e similares entre os distintos grupos de animais. Em menor escala, por outro lado, os problemas na delimitação de unidades biogeográficas se tornam mais aparentes devido à falta de simpatria estrita entre espécies co-distribuídas, aos papéis da dispersão e da extinção e ao conhecimento taxonômico e sistemático incompletos – os chamados Déficits Lineliano e Wallaceano (Cracraft, 1994; Morrone, 1994; Hausdorf, 2002; Whittaker *et al.*, 2005).

Encontrar padrões gerais e coincidentes de endemismo entre grupos de organismos com diferentes características gerais e histórias evolutivas distintas é um dos elementos-chave da biogeografia, já que tais padrões gerais requerem explicações gerais para os processos formadores da diversidade (Croizat *et al.*, 1974; Vargas *et al.*, 1998). Um processo geral que pode explicar a distribuição coincidente de vários grupos de organismos é a vicariância, onde o surgimento de uma barreira gera a fragmentação de uma biota ancestral mais amplamente distribuída levando, com o passar do tempo, ao aparecimento de um padrão congruente de distribuição entre as várias espécies formadas de cada lado da barreira (Croizat *et al.*, 1974; Hausdorf, 2002). Outros processos gerais também podem levar à regionalização da biota, tais como a migração conjunta de vários organismos quando uma barreira geográfica desaparece (Lieberman, 2003), ciclos alternados de migração e isolamento geográfico – *taxon-pulse* (Erwin, 1981; Halas *et al*., 2005), e a formação de refúgios climáticos/ecológicos (Haffer & Prance, 2002; Wronski & Hausdorf, 2008). Por outro lado, padrões de endemismo podem representar apenas coincidências geográficas da distribuição de vários organismos geradas por diferentes processos e eventos ao longo do tempo (Nihei, 2008). Para distinguir entre tais eventos e processos, se gerais ou não, é necessária a informação dos relacionamentos filogenéticos entre as espécies que compõe as diferentes unidades biogeográficas e a informação temporal sobre quando ocorreram os eventos de cladogênese para a comparação com as épocas em que diferentes eventos geológicos ou climáticos ocorreram (Platnick & Nelson, 1978; Cracraft, 1982; Humphries & Parenti, 1999; Upchurch & Hunn, 2002).

Entender tais processos geradores de endemismo e diversidade é essencial para decisões sobre como, onde e o que conservar (Avise, 2005; Faith, 2007). Sendo a única savana tropical listada como um *hostspot* global para a conservação (Mittermeier *et al.*, 2004), o Cerrado é o maior bloco contínuo de savanas neotropicais, (Ab’Saber, 1977; Silva & Bates, 2002). Localizado na região central da América do Sul, estende-se por mais de 1.8 milhões de quilômetros quadrados e ocupa, primariamente, uma região dominada por antigos planaltos altamente dissecados e depressões periféricas adjacentes (Ab’Saber, 1983; Silva, 1997).

Dois dos grupos de vertebrados mais diversos do Cerrado são os répteis da Ordem Squamata e os anfíbios da Ordem Anura (Colli, 2005). Os dois grupos apresentam uma alta taxa de endemismo no Cerrado, com mais de 100 espécies endêmicas cada um (Nogueira *et al*., 2011; Valdujo *et al*., 2012a). A distribuição dos Squamata endêmicos do Cerrado parece delimitada especialmente pelos grandes platôs e planaltos, enquanto os anuros apresentam uma distribuição altamente estruturada em relação à proximidade com os domínios fitogeográficos adjacentes (Nogueira *et al*., 2011; Valdujo *et al*., 2012b). As espécies destes dois grupos apresentam uma enorme diversidade no uso de habitats e microhabitats, e estes se distribuem de maneira heterogênea ao longo do Cerrado. Além de diferenças em uma escala local (entre espécies da mesma Ordem e entre as duas Ordens), anfíbios e répteis são separados por mais de 300 milhões de anos de história evolutiva, sendo dois grupos de organismos altamente distintos em seus requerimentos ecofisiológicos (Vitt & Caldwell, 2009).

Tomando proveito das diferenças gerais entre as duas Ordens e da grande quantidade de dados acumulados em sínteses recentes sobre o Cerrado, tenho como objetivos principais buscar padrões de distribuição coincidentes entre esses dois grupos da herpetofauna, destacando também eventuais padrões únicos de cada linhagem, e por fim, inferir se tais padrões foram originados pelos mesmos eventos e processos.

No capítulo 1, para verificar se é possível delimitar um padrão único de regionalização para os dois grupos, eu complementei as bases de dados de registros de localidades provenientes das sínteses recentes para herpetofauna endêmica do Cerrado (Nogueira *et al*., 2011; Valdujo *et al*., 2012a). Para isso, a partir de buscas bibliográficas, eu adicionei novos registros que ampliassem as distribuições conhecidas e espécies adicionais recentemente descritas. As análises para determinação das unidades biogeográficas foram realizadas com os dados de distribuição de cada grupo em separado (somente Anura ou somente Squamata) e comparadas com uma análise com os dados conjuntos dos dois grupos.

No capítulo 2, a partir das unidades biogeográficas delimitadas, eu busco resolver a relação entre essas áreas ao longo do tempo. Para isso, utilizo filogenias datadas de táxons que possuam registros em, ao menos, três unidades biogeográficas distintas para a produção de um cladograma geral de áreas. A partir deste cladograma de áreas, eu discuto os possíveis eventos envolvidos na diversificação das faunas de anuros e répteis Squamata, verificando se há padrões congruentes de diversificação entre os dois grupos.

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CAPÍTULO 1

Endemismo e padrões biogeográficos de Anura e Squamata do Cerrado

Article type: Original Article

Endemism and biogeographical patterns of anurans and squamates of the Cerrado hotspot

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Running Header: Biogeography of Cerrado herpetofauna

ABSTRACT

Aim. To analyse the ranges of endemic squamates and anurans in the Cerrado hotspot, testing for coincident distribution patterns in these two evolutionarily and ecologically distinct groups of organisms.

Location. Cerrado region, central South America.

Methods. We updated previous point-locality compilations for endemic species of the Cerrado herpetofauna, using 4,588 unique occurrence records. Using a 1° grid cell, we compared the regionalization results using biotic element and endemicity analyses. To search for a unified regionalization pattern, we performed an analysis with a combined dataset (anurans + squamates) and checked these results against those obtained in single group analyses.

Results. We found 12 main biotic elements composed by species of anurans and squamates. The analysis with the combined dataset recovered more complete results than those in group-specific analysis. Except for some biotic elements composed by poorly overlapping ranges, the distribution of most biotic elements corresponded to areas of endemism recovered by endemicity analysis with the combined dataset. The Cerrado region harbours a combination of congruent distributional patterns between these very distinctive groups, with few unique patterns for each group. Species in poorly sampled areas in the northern portion of Cerrado also showed restricted endemism patterns, although resulting in less resolved regionalization.

Main conclusions. Similar overall biogeographical units were recovered with different methods and these may reflect a common regionalization pattern for anurans and squamates. As in previous results, most biogeographical units are found over ancient plateaus, separated from one another by peripheral depressions. These major topographical barriers may explain major coincident patterns.

Keywords. Areas of endemism, Biodiversity, Biotic elements, Distribution patterns, Neotropical region, Open areas, Regionalization.

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). Such regionalization pattern is hierarchically organized, with more restricted areas nested within larger ones (Cracraft, 1991, 1994; Morrone, 2014). The search for these patterns is a major goal of biogeography and a necessary first step for all subsequent analysis (Morrone, 2009). Although large scale global patterns are relatively well established, finer scale, intracontinental regionalization patterns are more difficult to delimit (Szumik *et al*., 2012), and at this level, regionalization patterns provide valuable information on what spatial portions of biodiversity should be conserved (Crisci, 2001; Whittaker *et al*., 2005), especially if coincident between diverse sets of organisms.

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 very different taxa to search for coincident patterns of regionalization, especially at continental scales (Linder *et al*., 2012; Ramdhani, 2012; Holt *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). Following a total evidence approach (analogous to that applied in phylogenetic studies), the use of large data matrices from diverse taxa 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).

Both squamates and anurans show high endemism levels in the Cerrado region (Nogueira *et al*., 2011; Valdujo *et al*., 2012), 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*., 2012). 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). 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*., 2012). Squamate reptiles and anurans are very distinct in terms of biology and natural history (Huey, 1976; Duellman & Trueb, 1994), and common distribution patterns between these two groups may be interpreted as a signal of shared historical processes, regardless of ecological or ecophysiological differences.

Herein we use the most comprehensive species presence database of anurans and squamates to search for a general biogeographical regionalization in the Cerrado. The aims of our study are: (1) to detect and delineate non-random, coincident biogeographic units for anurans and squamates endemic to the Cerrado, minimizing the influence of method choice, and testing major predictions of the vicariant model (Hausdorf & Hennig, 2004); (2) to discriminate shared biogeographical patterns from patterns that are unique to each lineage, comparing the results found for each group to those in a total evidence dataset (anurans + squamates); (3) to provide a hypothesis about the origins of shared and unique patterns.

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 single tropical savanna listed as a biodiversity *hotspot* (Myers *et al*., 2000; Myers, 2003). This region is characterized and dominated by seasonal intefluvial 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'Sáber, 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*. (2012) for anurans. We updated the taxonomy according to the List of Brazilian Reptiles: (Bérnils & Costa, 2012) and to the List of Brazilian Amphibians (Segalla *et al*., 2012). We complemented this source by literature review, including new locations and recently described endemic species (up to December 2013). 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 da 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° × 1° cell grid coincident with the core area of the Cerrado. We eliminated cells with less than two species to avoid misleading signals (Kreft & Jetz, 2010). First, we analysed distribution patterns in each group separately. Then, to search for a unified biogeographical regionalization for both anurans and squamate species, we repeated the analyses using the combined dataset. This is analogous to a total evidence approach. We checked the results of the taxon-specific dataset against the combined dataset to test for possible loss of patterns by 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 the search for a unified regionalization hypothesis, we used biotic element analysis. This analysis provides a test for non-random congruence of species distributions, and their resulting biotic elements: 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 areas of endemism where they originated and/or when there is no strict distributional coincidence among species (Hausdorf & Hennig, 2003). Additionally, we checked the results of Biotic element analysis against areas of endemism identified by endemicity analysis - NDM (Szumik *et al.*, 2002). In that way, we verified the influence of different methods 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 recovered biogeographical signal, independent of choice method. We used the name "biogeographic unit" to refer to both areas of endemism (AOE) and biotic elements (BE).

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.). 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.

Next, a *T* test for a departure from a null model of co-occurrence (Monte Carlo simulation) is made, and then, biogeographic units (defined by their biotic elements) are determined. We used the *hprabclust* 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 this value to the group-specific analysis for anurans and squamates. The result of biotic element analysis is a list of species classified into their respective biogeographic units, and the species not classified in any of these was included in the noise component (Hausdorf & Hennig, 2003).

Endemicity analysis (NDM/VNDM) - To compare the results of biotic element analysis with possible outcomes from alternative methods, we used endemicity analysis (NDM). Endemicity analysis 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 taxon the ranges. Sets of cells are selected to maximize the number of range-restricted taxa in the selected grid cells (more details in Szumzik & Goloboff, 2004). Like biotic element analysis, the method allows areas to overlap. We used the option "observed presences" = 20% and "assumed presences" = 50% to avoid bias of non-overlapped records due to incomplete sampling. Searches were conducted saving sets that had two or more endemic species, and scores above 2.0. We chose to temporarily save sets within 0.995 of the current score and, keeping overlapping subsets if 60% of species were unique, in 100 replicates and discarding duplicated sets. Consensus endemic areas were then 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.

Mapping

The endemicity analysis viewer (VNDM) automatically draws the consensus area of endemism as the set of grids with best scores. To compare results of NDM with BE analysis, we drew biotic elements 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 as in 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 biogeographic unit fully overlapped more than one restricted biogeographical units, we opted to consider only the more restricted patterns nested inside that area.

To represent the ranges of each species that composed a biotic element, we also used the Brazilian map of catchment areas (ANA, 2006). We drew ranges according to 5th order Ottobasins (Pfafstetter Coding) that are inside the species distribution extent or in a 20 km buffer of the point locality (for species with less than 3 point-localities). See a similar site delineation for restricted-range species in Nogueira *et al*. (2010). Catchment areas are correlated with the geomorphology of a region, and provide a better delimitation of biogeographical units than grid cells, used only for methodological purposes in NDM and BE analyses. Biotic element results were drawn as a richness map, highlighting core areas with more than 25% of the species that compose a biotic element (Hausdorf & Hennig, 2004).

To test if biotic elements 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 biotic element (columns). Finally, we tested if species classified in some biotic element in the taxa-specific analysis (rows) generally belonged to the same biotic element in the combined datasets (columns).

RESULTS

Species distribution data

We included eight species to the list of endemic squamates, and 11 species for the list of endemic anurans of the Cerrado (Table 1, supplementary material - SI). In total, 750 new records were added to the original databases. These new records represent new species and records extend in the known range of each species. This resulted in 4,588 unique point localities of 216 taxa, including 103 endemic anurans (with three undescribed species), and 113 squamates (with eight undescribed species). These 11 undescribed species are easily diagnosable taxa found in surveyed collections during the recent mentioned synthesis of the Cerrado herpetofauna (Nogueira *et al*., 2011; Valdujo *et al*., 2012). Endemic anurans of difficult determination, like some species of *Pseudopaludicola, Leptodactylus,* or taxa with taxonomic problems, were not included in the analysis.

Clustering of distributions

For all biotic element analyses (squamates, anurans and combined dataset), the *T* statistics of the tests for a departure from a null model of co-occurrence were significantly smaller 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 biotic elements (Table 2). Values larger than 0.35 resulted in smaller numbers of clusters, with a less resolved delimitation due the inclusion of species with very widespread ranges.

Taxon-specific analyses

Biogeographical map for anurans resulted from BE-analysis show 10 biotic elements mainly distributed over plateaus areas, except for BE 9, at the Middle Tocantins-Araguaia depression (Figure 1). Endemicity analysis found seven AOE for anurans, including a single region (AOE – 17, *Chapada das Mesas* region) with no correspondent in biotic elements (Figure 1). By contrast, three anuran biotic elements (BEs – 9, 5 and 16) were not recovered in AOE results.

Biogeographical map for squamates also resulted in 10 biotic elements (Figure 1). Biotic elements 1, 2, 6, 11 and 12 are located over plateau areas (Fig 2 – for details of the main geomorphological surfaces), and at least three included both plateaus and peripheral depressions (BEs 5, 7, 10). Endemicity analysis for squamates found seven AOE (Figure 1), including one with no corresponding biotic element (AOE – 13 – *Serranía de Huanchaca*). Four squamate biotic elements had no corresponding AOE (BEs – 2, 5, 18 and 11). Although anurans presented a larger number of species classified in biotic elements (79%) in relation to squamates (57%), the same number of biotic elements was found for both groups (Table 3), indicating that ranges of anurans species are more clustered than squamates species.

Comparisons

A comparison between biotic elements in taxa-specific datasets and combined datasets reveals both congruence and differences (Figure 1). With exception of a biotic element composed by squamate species with poor overlapping ranges (BE – 18, figure 1), all other biotic elements found with taxon-specific datasets presented a counterpart in the analysis with the combined datasets. We recovered three additional biotic elements using the combined dataset (BEs 13, 14 and 15, figure 1). Species forming a given BE in the taxa-specific analyses were generally found in the same biotic element in the combined analysis (chi-squared = 1849, *P* < 0.001).

Areas of endemism found with the combined dataset in endemicity analysis resulted in a similar biogeographical regionalization pattern in relation to the biotic elements found with the combined dataset (Figure 1). Contrary to taxa-specific analyses, all AOEs found with the combined dataset had a corresponding biotic element (combined dataset). Endemicity analysis failed to locate a corresponding area of endemism only in cases where the species forming a biotic element (combined dataset) had very poorly overlapping ranges (e. g. BEs 13, 14, 15, 16). For the final regionalization hypothesis, we considered these poorly defined biogeographical units as less robust than the remaining. The AOEs seemed to be located especially over the core areas of biotic elements (BEs 1 – 12, Figure 3). The species that composed a given AOE were generally classified into the correspondent biotic element (combined dataset; chi-squared = 879, *P* < 0.001).

Unified Regionalization hypothesis

Biotic elements 1 – 12 (Figure 3) were the result of a recovered biogeographical signal, i. e. were recovered independent of method choice in the combined dataset. Of these, the following biotic elements found both for anurans and squamates in taxon-specific analysis were also recovered as shared areas with the combined dataset (coincident patterns – Table 4): Guimarães Plateau (BE 2), Central Plateau (BE 6), Espinhaço (BE

12), Serra Geral Plateau (BE 11), Pantanal/Bodoquena region (BE 5), and Tocantins-Araguaia basin - BE 9 (Table 4 for the number of species of each group). A chi-square test indicates that anuran and squamates species are uniformly distributed across these six biotic elements (chi-squared = 6.1067, $P = 0.1919$). Within some of these biotic elements, the ranges of anuran species tended to be more clustered than the range of squamate species (e. g. Central Plateau, Tocantins-Araguaia, and Serra Geral BEs), while at Guimarães and Espinhaço BEs, all species of anurans and squamates are very clustered together (Figure 4).

Patterns found for only one of the groups were also recovered with the combined dataset: Parecis plateau (BE 1) with three squamate species and Jalapão region (BE 7) with eight squamate species, remained squamate-exclusive biotic elements in the combined dataset (Table 4). The remaining patterns that were exclusive for one group in the taxa-specific datasets were recovered with additional species of the other group in the combined dataset analysis: Central Paraná basin plateau (BE 10), Veadeiros plateau (BE 4), Canastra plateau (BE 8), and Caiapônia plateau - BE 3 (Table 4).

The majority of the biotic elements are located over plateau areas, above 500 m (Figure 2). Some lower areas also harboured regionalized biotas shared by both groups, especially the Tocantins-Araguaia basin (BE 9). Some squamates and anurans classified in this BE have their point-localities highly correlated with the river channels (i.e. *Adenomera saci, Pseudis tocantins, Hydrodinastes melanogigas*), whereas others were less related to the river areas (i.e. *Gymnodactylus amarali*), and may be wrongly associated with this BE. Paraná basin plateau (BE 10) and Pantanal/Bodoquena region (BE 5) contained a combination of species related to both plateaus and adjacent depressions. This last biotic element 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 13-17, Figure 3) are located mainly over north areas of the Cerrado and represented results not corroborated in comparisons among datasets or analyses. Area of endemism 13, at *Serranía Huanchaca* was found only with NDM for squamates (merged with Parecis AOE). Biotic element 14, at *Serra da Borda* region, was detected only by BE-analysis with the combined dataset and have their limits inside the southern portion of the *Serranía de Huanchaca*. BEs 15 and 16 were recovered by BE-analyses but without equivalent with NDM results. The species ranges in these three last BEs overlap poorly. Finally, area 17, near *Chapada das Mesas*, was found with the total evidence datasets by both analyses (BE, NDM) and with anuran dataset (NDM). This biogeographic unit was composed by two undescribed species (one *Apostolepis* and one *Adenomera*), plus a poorly known, recently described anuran species (*Elachistocleis bumbameuboi*).

DISCUSSION

Taxonomic and distributional knowledge

Only two to three years after the works with distributional data of the Cerrado herpetofauna (Nogueira *et al*., 2011; Valdujo *et al*., 2012), more than fourteen new endemic species were described. The effect of a yet incomplete taxonomy and sampling are probably influencing our results, resulting in some clusters not consistently detected between the analyses, as the biogeographic units found over *Serra da Borda*, *Serranía de Huanchaca* and near Roncador plateau. Another candidate biotic element is in the northeast of the Cerrado, near *Chapada das Mesas*. That region was only recently sampled for the first time, and still requires additional collections and taxonomic studies (Costa *et al*., 2009). Moreover, some reminiscent eroded plateaus in the northeast of the Cerrado, along the *Meio-Norte* sedimentary basin, may harbour another endemic species, like *Amphisbaena maranhensis*, described near *Chapada das Mesas* (Gomes & Maciel, 2012). As these less robust patterns of endemism were generally in the poorly known northern portion of the Cerrado (Bini *et al*., 2006; Costa *et al*., 2007), a lower performance of analyses at these areas were expected. These are priority areas for sampling, as the faunal knowledge about the Cerrado domain has accumulated from south to north areas (Nogueira *et al*., 2010b).

Final Regionalization hypothesis

Our study led to the recovery of regionalized biotas for both anurans and squamates in several regions throughout the Cerrado. These patterns were not lost using the combined dataset and some patterns were recovered only in the total evidence approach. The use of the combined dataset allowed the recovery of shared patterns without the use of subjective visual inspection. A combination of approaches, starting from taxon specific analysis and comparing the results with the combined dataset rendered an opportunity to better differentiate taxa-specific from shared, general patterns. Congruence in the biogeographical regions of different groups at global and continental scales were already reported (Linder, 2001; Lamoreux *et al*., 2006) and are correlated with main phytogeographical domains (Rueda *et al*., 2013). Herein we show that these congruencies between patterns of endemism of different groups may exist even within a phytogeographical domain, allowing for a more refined view of biogeographical regionalization.

The coincident patterns found between anurans and squamates may be related to stable landscapes on isolated plateaus, over the “Campo Cerrado” centre of endemism (Müller, 1973; Werneck *et al*., 2012). One of the most isolated of these areas is the Guimarães plateau, uplifted during Plio-Pleistocene transition (Silva, 1997). By contrast, biotic elements found over the Central Brazilian, Caiapônia, Central-Paraná basin plateaus and the Espinhaço mountain range, are more connected by areas at elevations above 500 m (Figure 2). In fact, a great amount of endemics, have a relatively continuum distribution along these areas. The split between the west and remaining areas coincided with the uplift of the central Brazilian plateau, and may have contributed to old divergences in other Neotropical vertebrates (Prado *et al.,* 2012). Moreover, the formation of plateaus and depressions influences many features of the Cerrado, like the dominant soil composition, vegetation mosaics and the dynamics of the climatic changes (Bush, 1994; Motta *et al*., 2002; Nogueira *et al*., 2011). These geomorphological differences may affect many groups at a time and in a same region, and could be responsible for the congruent distributional patterns between species with very different requirements.

On the other hand, the search for coincidences between both groups highlighted unique, group-specific patterns. Like other sandy areas deposits in the Neotropical region, the Jalapão region (BE 7) harbours a peculiar psammophilous squamate fauna (Rodrigues, 2002; Vitt *et al*., 2002). This area has a complex topography formed mainly by sandy deposits derived from the Serra Geral sandstone plateau (Rodrigues *et al*., 2008), and no anuran species is known (so far) to be restricted to that region. Moreover, the biotic element detected over isolated sandy savanna patches in the Parecis plateau, is also composed by squamates found typically in sandy habitats, like *Ameiva parecis* and

Bachia didactyla (Colli *et al*., 2009; Freitas & Struessmann, 2011), which may corroborate that unique association to sandy soil patterns for squamates.

By contrast, biotic elements over the Veadeiros and Canastra regions (BEs 4 and 8) are composed mainly by anuran species. These areas, typically above 700-1,000 m, contain many small streams in open areas, rock fields, and rocky savannas (Machado & Walter, 2006). Many endemic anurans are dependent of that kind of habitat for reproduction and that may be the cause of the isolation of ancestral populations over these areas. Nevertheless, habitat use alone could not explain all the possible ancestral isolations, as some endemic anurans of these biotic elements are also typical of other habitats, like gallery forests (e. g. *Hypsiboas ericae* or species of *Scinax catharinae* and *Bokermannohyla circumdata* groups; Faivovich, 2002; Faivovich *et al*., 2005) and are also isolated at these biotic elements. In addition, other regions like the Espinhaço and some high areas of the Central Brazilian plateau harbours similar characteristics but also contains many endemic anurans typical of open and forested habitats, not to mention endemic squamates.

Additionally, some of these group-specific patterns could be related to differences in the taxonomic and distributional data effort for each group in some of these regions. This is probably the case for isolated biotic elements in the western portion of the Cerrado (i. e. Parecis plateau), where efforts for the study of the reptilian fauna (Harvey & Gutberlet, 1998; Colli *et al*., 2003) may be more extensive than for amphibians, reflecting in the dominance of squamates in these biotic elements. Major differences between the distributional patterns of these two groups, reflecting finer-scale ecological difference and habitat selection, could be more evident in more inclusive scales (within biotic elements). The tendency anuran species for showing more clustered ranges inside biotic elements, and the greater proportion of anurans species classified in different biotic elements than squamates, is probably 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 have some endemics restricted over areas of biotic elements like Espinhaço, Tocantins-Araguaia basin and Central Brazilian plateau (Silva, 1995; Marinho-Filho *et al*., 2002). The majority of species of these two groups are widespread over other South American domains (Macedo, 2002; Marinho-Filho *et al*., 2002). However, if plateaus represent persistent barriers to dispersal, we should expected similar patterns of endemism even between these groups with more dispersal ability and distinctive habitat use in relation to anurans and squamates, at least, taking into account population levels (Avise, 2000). As already demonstrated in other regions of the world, similar regionalization patterns could be found between groups as different as primates and frogs (Evans *et al*., 2003) or with very distinctive dispersal abilities as macropterous and flightless insects (Bouchard & Brooks, 2004). However, to estimate if all congruent patterns are caused by the same events, we need a biogeographical analysis with temporal information, the next step for a comprehension of the Cerrado evolution. The spatial framework discussed herein is thus the necessary first step for understanding the biogeographical events that led to the formation of Cerrado regionalized endemic patterns.

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TABLES

Table 1 - *T* statistics from the test for the clustering of the ranges. *P*-values smaller than 0.05 indicate a significantly clustered distributions. Minimum, maximum and the mean values of *T*, for 1,000 artificial populations were shown (Details in Hennig & Hausdorf, 2004).

Dataset	*T* statistic	*T* minimum	*T* maximum	*T* mean	*P*-value
Anura	0.360	0.379	0.521	0.444	<0.001
Squamata	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 to 0.5) with resulting numbers of species not classified in any biotic element (noise), and the number of restricted range biotic elements in the analysis with combined dataset. Note that the maximum number of biotic elements was reached with *cutdist* = 0.35 (highlighted). Biotic elements were progressively merged with higher values of *cutdist*.

Cutdist value =	0.1	0.15	0.2	0.25	0.3	0.35	0.4	0.45	0.5
Noise n° spp.	160	124	93	71	47	37	21	11	9
Restricted BEs	8	12	14	14	15	16	14	11	9

Table 3 - Biogeographic units found for anuran, squamates and combined datasets. Units classified as restricted represent the patterns of interest, without widespread and repeated patterns.

	Biotic element analysis		
Dataset	Anura	Squamata	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%)
	Endemicity analysis (NDM)		
Total number	9	7	17
Duplicated	2	0	4
Widespread	0	0	0
Restricted	7	7	13
Restricted n° spp.	51 (49%)	22 (19%)	87 (41%)
Unclassified n° spp.	53 (51%)	92 (81%)	127 (59%)

Table 4 – Twelve main biotic elements (BE) composition according to the respective groups (anurans or squamates) in analyses with combined and taxa-specific datasets. First six BEs represent coincident patterns of both groups in taxon-specific analysis and recovered as shared areas with the combined dataset.

Biotic elements	BE analysis - Combined dataset (n° spp.)		BE analysis - Taxa-specific datasets (n° spp.)	
	anurans	squamates	anurans	squamates
Guimarães (BE 2)	7	4	7	4
Central (BE 6)	13	5	11	7
Espinhaço (BE 12)	20	11	20	11
Serra Geral (BE 11)	3	5	3	6
Pant/Bodoq. (BE 5)	1	6	3	6
Toc/Arag. (BE 9)	8	6	10	3
Parecis (BE 1)	none	3	none	3
Jalapão (7)	none	8	none	12
Veadeiros (BE 4)	5	1	7	none
Canastra (BE 8)	8	1	8	none
Paraná plt. (BE 10)	1	9	none	9
Caiapônia (BE 3)	4	2	5	none

FIGURES

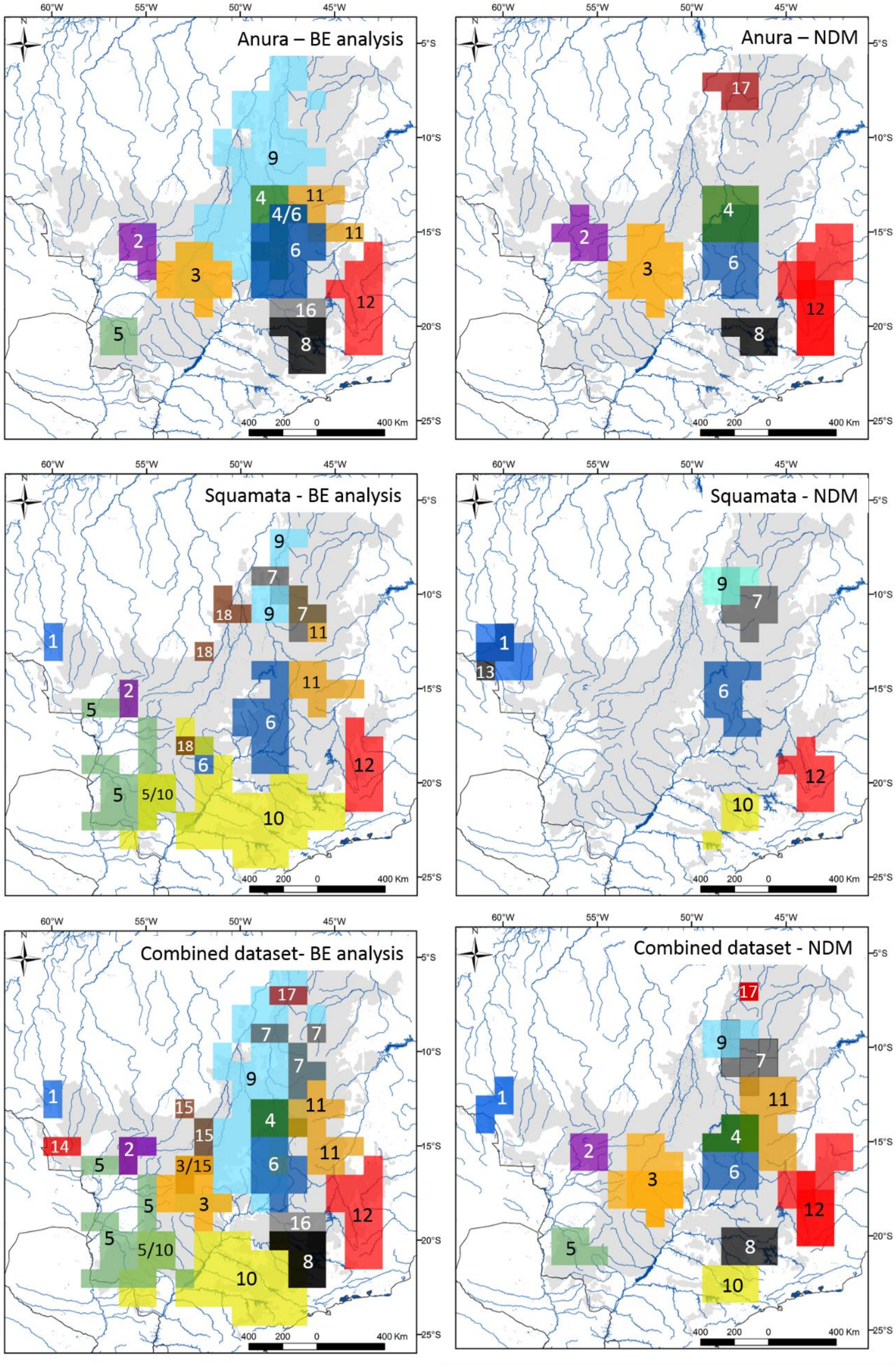
Anura – BE analysis
Anura – NDM
Squamata - BE analysis
Squamata - NDM
Combined dataset- BE analysis
Combined dataset - NDM
60°W
55°W
50°W
45°W
-5°S
-10°S
-15°S
-20°S
-25°S
N
400
200
0
400 Km
1
2
3
3/15
4
4/6
5
5/10
6
7
8
9
10
11
12
13
14
15
16
17
18

Figure 1 – Biogeographical units detected with group-specific and combined datasets (below) with biotic element (BE) analysis and endemicity analysis (NDM). Grey colour indicates the Cerrado limits. Biogeographical units classification according to the main geomorphological places: 1 – Parecis Plateau. 2 – Guimarães Plateau. 3 - Caiapônia Plateau. 4 – Veadeiros Plateau. 5 - Pantanal/Bodoquena regions. 6 - Central Brazilian Plateau. 7 – Jalapão region. 8 – Canastra region. 9 – Tocantins-Araguaia Basin. 10 - Central Paraná Basin Plateau. 11 - Serra Geral plateau. 12 – Espinhaço mountain range. 13 - *Serranía Huanchaca*. 14 - *Serra da Borda* region. 15 – Roncador plateau. 16 – Upper Parnaíba region. 17 – *Chapada das Mesas*. 18 – without core area. See Figure 2 for more details of geomorphogical places.

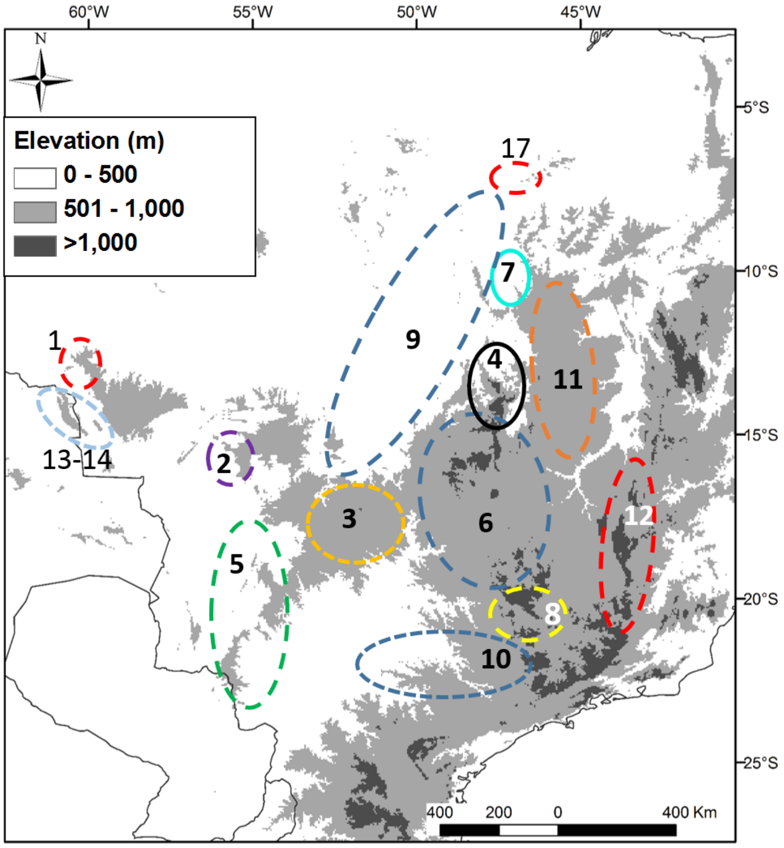

Figure 2 – Main geomorphological surfaces where herpetofaunal biogeographic units are located: 1 – Parecis Plateau (mainly on isolated sandy savannas surrounded by Amazonian forest). 2 – Guimarães Plateau ("*Chapada"* region). 3 – Caiapônia Plateau region (includes also part of Alcantilados, Rio Verde and north of Paraná Basin plateaus). 4 – Veadeiros Plateau (including associated headwaters). 5 – Pantanal region and Bodoquena Plateau (and associated small reminiscent plateaus). 6 – Central Brazilian Plateau. 7 – Jalapão region (including some regions of the Tocantins depression and reminiscent tabletops of Serra Geral Plateau). 8 – Canastra Plateau region (including neighbouring plateaus of South Minas Gerais including Poços de Caldas, Alto Rio Grande). 9 – Tocantins–Araguaia Basin (and associated depression). 10 – Central Paraná Basin Plateau (and the associated depression over the Paraná River Basin = "*paulistania"*). 11 – Serra Geral plateau (= "*Chapadão Ocidental do Rio São Francisco*"). 12 – Espinhaço mountain range (only southern portions over the Cerrado/Atlantic Forest ecotone). 13 – *Serranía Huanchaca*. 14 – *Serra da Borda* (the smaller plateau on the right). 17 – *Chapada das Mesas* region (and neighbouring reminiscent plateaus).

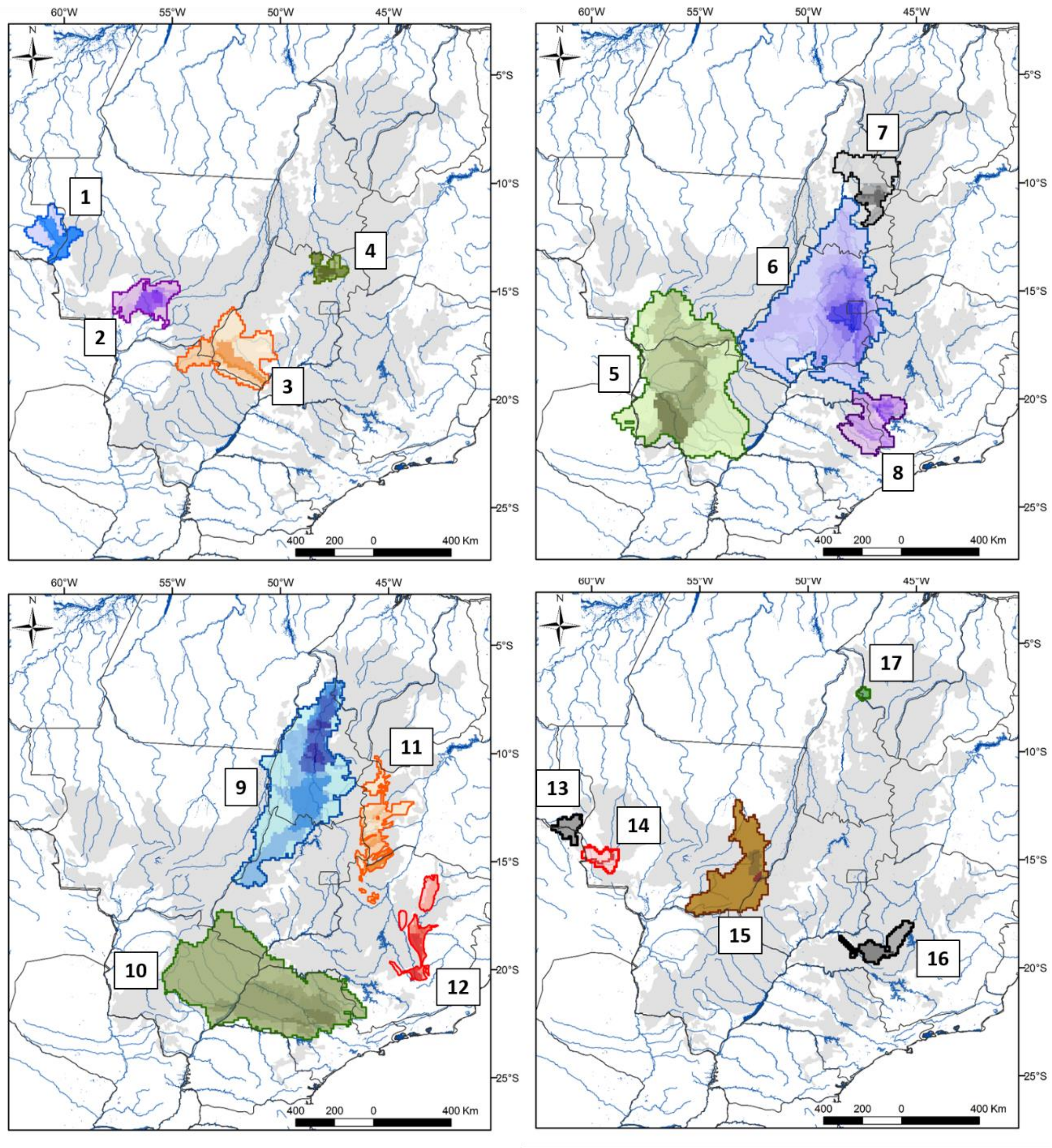

Figure 3 – Numbers 1 to 12: Biotic elements (BE) defined with the combined dataset that are consistent with the areas of endemism of NDM. Numbers 13 to 17 are other biogeographic units variations found in the study. Thick lines indicate the BE limits as the areas with the occurrence of at least two species that compose each BE (or more than 25% of the species in areas 9–12, for more accurate delimitation). Gradient colours of each BE indicates richness. Grey colour indicate the Cerrado limits. BE classification according to the main geomorphological units: 1 – Parecis Plateau. 2 – Guimarães Plateau. 3 – Caiapônia Plateau. 4 – Veadeiros Plateau. 5 – Pantanal/Bodoquena region. 6 – Central Brazilian Plateau. 7 – Jalapão. 8 – Canastra Plateau. 9 – Tocantins–Araguaia basin. 10 – Central Paraná basin Plateau. 11 – Serra Geral Plateau. 12 – Espinhaço mountain range. 13 – Serranía Huanchaca. 14 – Serra da Borda region. 15 – Roncador Plateau. 16 – Upper Parnaíba region. 17 – Chapada das Mesas.

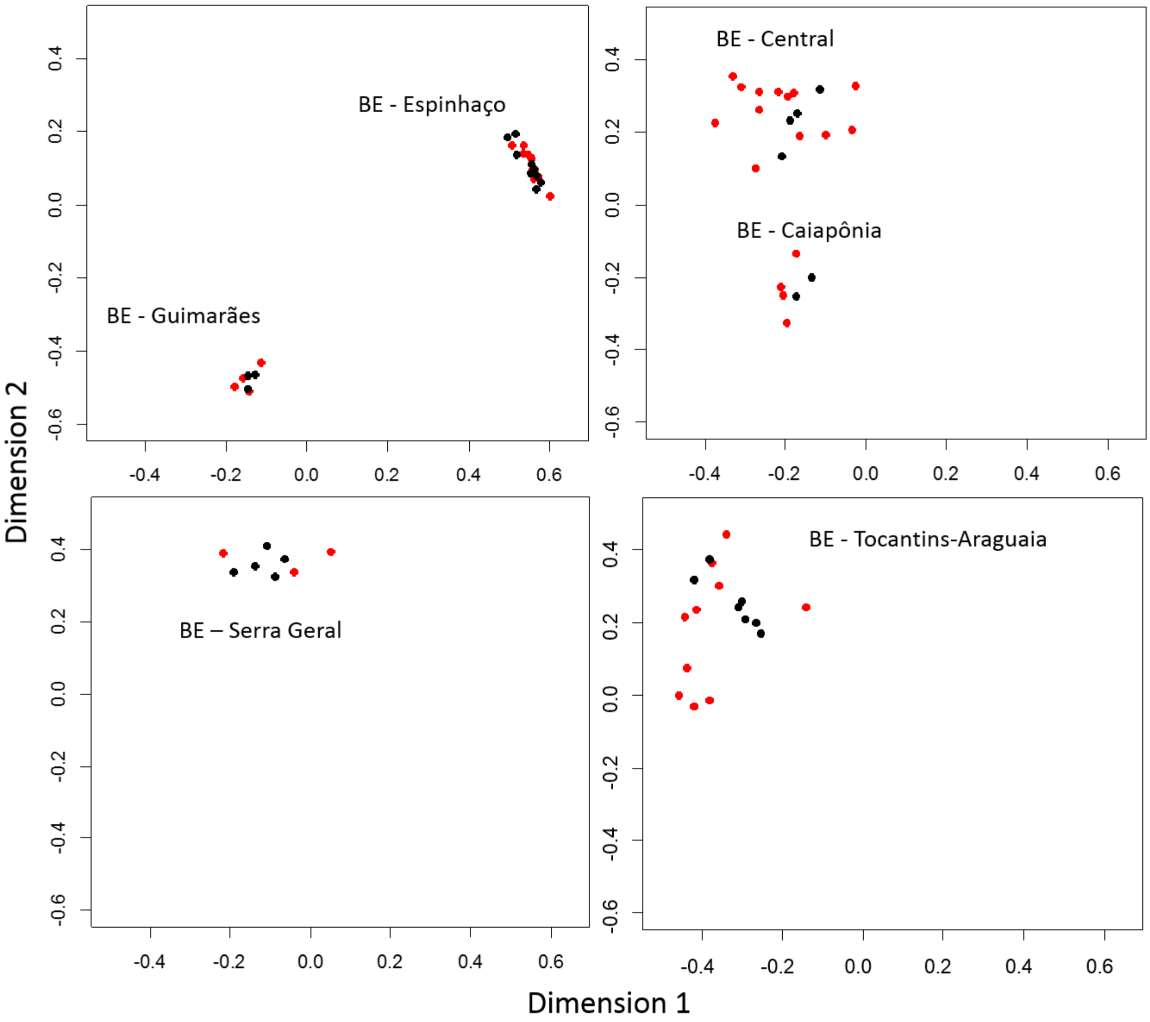

Figure 4 – *Prabclus* results of species clusters in the first two dimensions of a non-metric multidimensional scaling ordination of ranges of squamates (red dots) and anurans (black dots) over biotic elements (BEs) of the Cerrado herpetofauna – Combined dataset.

Supplementary Information

Table 1 – Species classified in areas of endemism (AOE) by endemicity analysis (NDM) or in biotic elements (BE) analysis with anuran (An), squamate (Sq) and combined datasets. Species not classified in any biogeographic unit are denoted by noise (N). W = widespread biogeographic units. A roman number indicates repeated biogeographic units. * indicates species included in this study. Main geomorphological places: 1 – Parecis plateau. 2 – Guimarães plateau. 3 – Caiapônia plateau. 4 – Veadeiros plateau. 5 – Pantanal and Bodoquena. 6 – Central Brazilian Plateau. 7 – Jalapão. 8 – Canastra plateau. 9 – Tocantins–Araguaia basin. 10 – Central Paraná basin plateau. 11 – Serra Geral plateau. 12 – Espinhaço mountain range. 13 – Serranía Huanchaca. 14 – Serra da Borda. 15 – Roncador plateau. 16 – Upper Parnaíba region. 17 – 'Chapada' das Mesas. 18 – Without core area.

Species	Order	BE Combined	NDM Combined	BE Squamata	BE Anura
Ameiva parecis	*Sq*	BE 1	AOE 1	BE 1	NA
Apostolepis striata	*Sq*	BE 1	AOE 1	BE 1	NA
Bachia didactyla	*Sq*	BE 1	N	BE 1	NA
Allobates brunneus	*An*	BE 2	N	NA	BE 2
Ameerega braccata	*An*	BE 2	AOE 2	NA	BE 2
Dendropsophus tritaeniatus	*An*	BE 2	N	NA	BE 2
Phyllomedusa centralis	*An*	BE 2	AOE 2	NA	BE 2
Pristimantis crepitans	*An*	BE 2	N	NA	BE 2
Pristimantis dundeei	*An*	BE 2	AOE 2	NA	BE 2
*Proceratophrys huntingtoni**	*An*	BE 2	AOE 2	NA	BE 2
Amphisbaena absaberi	*Sq*	BE 2	N	N	NA
Amphisbaena brevis	*Sq*	BE 2	N	BE 2	NA
Amphisbaena cuiabana	*Sq*	BE 2	N	BE 2	NA
Amphisbaena neglecta	*Sq*	BE 2	AOE 2	BE 2	NA
Apostolepis lineata	*Sq*	BE 2	N	BE 2	NA
Dendropsophus araguaya	*An*	BE 3	AOE 3	NA	BE 3
Pristimantis ventrigranulosus	*An*	BE 3	AOE 3 II	NA	BE 3
*Proceratophrys dibernardoi**	*An*	BE 3	AOE 3 II	NA	BE 3
Scinax pusillus	*An*	BE 3	AOE 3	NA	BE 3
*Ameiva jacuba**	*Sq*	BE 3	N	N	NA
Leposternon cerradensis	*Sq*	BE 3	AOE 3	N	NA
Chiasmocleis centralis	*An*	BE 4	N	NA	N
Hypsiboas ericae	*An*	BE 4	AOE 4	NA	BE 6 - 4
Leptodactylus tapiti	*An*	BE 4	AOE 4	NA	BE 6 - 4
*Proceratophrys bagnoi**	*An*	BE 4	AOE 4 II	NA	BE 6 - 4
*Proceratophrys rotundipalpebra**	*An*	BE 4	AOE 4	NA	BE 6 - 4
Trilepida fuliginosa	*Sq*	BE 4	N	W III	NA
Elachistocleis matogrosso	*An*	BE 5	N	NA	BE 5
Amphisbaena bedai	*Sq*	BE 5	AOE 5	BE 5	NA
Amphisbaena leeseri	*Sq*	BE 5	N	BE 5	NA
Apostolepis intermedia	*Sq*	BE 5	AOE 5	BE 5	NA

Species	Order	BE Combined	NDM Combined	BE Squamata	BE Anura
Micrurus tricolor	*Sq*	BE 5	N	BE 5	NA
Phalotris matogrossensis	*Sq*	BE 5	N	BE 5	NA
Xenodon matogrossensis	*Sq*	BE 5	N	BE 5	NA
Allobates goianus	*An*	BE 6	AOE 6	NA	BE 6 - 4
Bokermannohyla pseudopseudis	*An*	BE 6	N	NA	BE 6 - 4
*Bokermannohyla sapiranga**	*An*	BE 6	AOE 6	NA	BE 6
Hypsiboas buriti	*An*	BE 6	AOE 6	NA	BE 6
Hypsiboas goianus	*An*	BE 6	AOE 6	NA	BE 6
Hypsiboas phaeopleura	*An*	BE 6	AOE 4 II	NA	BE 6 - 4
Odontophrynus salvatori	*An*	BE 6	N	NA	BE 6 - 4
Phyllomedusa oreades	*An*	BE 6	AOE 4 II	NA	BE 6 - 4
Proceratophrys goyana	*An*	BE 6	N	NA	BE 6 - 4
Proceratophrys vielliardi	*An*	BE 6	AOE 6	NA	BE 6
Scinax centralis	*An*	BE 6	N	NA	BE 6
Scinax skaios	*An*	BE 6	AOE 6	NA	BE 6 - 4
Scinax tigrinus	*An*	BE 6	AOE 6	NA	BE 6
Amphisbaena anaemariae	*Sq*	BE 6	N	BE 6	NA
Amphisbaena mensae	*Sq*	BE 6	AOE 6	BE 6	NA
Apostolepis albicollaris	*Sq*	BE 6	N	BE 6	NA
Apostolepis sp. 1	*Sq*	BE 6	AOE 6	BE 6	NA
Enyalius aff. *bilineatus*	*Sq*	BE 6	AOE 6	BE 6	NA
Ameivula jalapensis	*Sq*	BE 7	AOE 7	BE 7	NA
Ameivula mumbuca	*Sq*	BE 7	AOE 7	BE 7	NA
Amphisbaena acrobeles	*Sq*	BE 7	AOE 7	BE 7	NA
Apostolepis longicaudata	*Sq*	BE 7	AOE 7	BE 7	NA
Apostolepis polylepis	*Sq*	BE 7	N	BE 7	NA
Bachia oxyrhina	*Sq*	BE 7	N	BE 7	NA
Kentropyx sp.	*Sq*	BE 7	AOE 7	BE 7	NA
*Siagonodon acutirostris**	*Sq*	BE 7	AOE 7	BE 7	NA
Bokermannohyla ibitiguara	*An*	BE 8	AOE 8	NA	BE 8 I
Dendropsophus rhea	*An*	BE 8	AOE 10 II	NA	BE 8 I
Hypsiboas stenocephalus	*An*	BE 8	AOE 8	NA	BE 8 I
Odontophrynus monachus	*An*	BE 8	AOE 8	NA	BE 8 I
Phyllomedusa ayeaye	*An*	BE 8	AOE 8	NA	BE 8 I
Scinax canastrensis	*An*	BE 8	AOE 8	NA	BE 8 I
Scinax maracaya	*An*	BE 8	N	NA	BE 8 I
*Scinax pombali**	*An*	BE 8	AOE 8	NA	BE 8 I
Liotyphlops schubarti	*Sq*	BE 8	AOE 10	BE 10 II	NA
*Adenomera saci**	*An*	BE 9	N	NA	BE 9
Adenomera sp. 2	*An*	BE 9	N	NA	BE 9
Allobates aff. *brunneus*	*An*	BE 9	N	NA	BE 9
Barycholos ternetzi	*An*	BE 9	N	NA	BE 9
Dendropsophus anataliasiasi	*An*	BE 9	N	NA	BE 9
Dendropsophus cruzi	*An*	BE 9	N	NA	BE 9

Species	Order	BE Combined	NDM Combined	BE Squamata	BE Anura
*Proceratophrys branti**	*An*	BE 9	N	NA	BE 9
Pseudis tocantins	*An*	BE 9	N	NA	BE 9
Rhinella ocellata	*An*	BE 9	N	NA	BE 9
Scinax constrictus	*An*	BE 9	N	NA	BE 9
Amphisbaena kraoh	*Sq*	BE 9	AOE 7	BE 7	NA
Amphisbaena saxosa	*Sq*	BE 9	AOE 9	BE 7	NA
Apostolepis nelsonjorgei	*Sq*	BE 9	N	W III	NA
Bachia micromela	*Sq*	BE 9	AOE 9	BE 7	NA
Bachia psamophila	*Sq*	BE 9	AOE 9	BE 7	NA
Gymnodactylus amarali	*Sq*	BE 9	N	W III	NA
Hydrodynastes melanogigas	*Sq*	BE 9	N	BE 9	NA
Phalotris labiomaculatus	*Sq*	BE 9	N	BE 9	NA
Proceratophrys moratoi	*An*	BE 10	AOE 10 II	NA	N
Ameiva aff. *parecis*	*Sq*	BE 10	AOE 10 II	BE 10 II	NA
Amphisbaena sanctaeritae	*Sq*	BE 10	AOE 10	BE 10 II	NA
Bothrops itapetiningae	*Sq*	BE 10	N	W	NA
Erythrolamprus frenatus	*Sq*	BE 10	N	BE 10	NA
Mussurana quimi	*Sq*	BE 10	N	W	NA
Phalotris lativittatus	*Sq*	BE 10	N	BE 10 II	NA
Phalotris multipunctatus	*Sq*	BE 10	N	BE 10	NA
Philodryas livida	*Sq*	BE 10	N	BE 10	NA
Rhachidelus brazili	*Sq*	BE 10	N	W	NA
Trilepida koppesi	*Sq*	BE 10	N	BE 10	NA
Xenodon nattereri	*Sq*	BE 10	N	W	NA
Oreobates remotus	*An*	BE 11	AOE 11	NA	BE 11
Rhinella inopina	*An*	BE 11	AOE 11	NA	BE 11
Trachycephalus mambaiensis	*An*	BE 11	N	NA	BE 11
Amphisbaena carli	*Sq*	BE 11	N	BE 11	NA
*Bachia geralista**	*Sq*	BE 11	AOE 11	BE 11	NA
*Leposternon maximus**	*Sq*	BE 11	AOE 11	BE 11	NA
Psilophthalmus sp.	*Sq*	BE 11	N	BE 11	NA
Stenocercus quinarius	*Sq*	BE 11	N	BE 11	NA
Bokermannohyla alvarengai	*An*	BE 12	AOE 12 III	NA	BE 12
Bokermannohyla nanuzae	*An*	BE 12	AOE 12 IV	NA	BE 12
Bokermannohyla sagarana	*An*	BE 12	AOE 12 IV	NA	BE 12
Bokermannohyla saxicola	*An*	BE 12	AOE 12 IV	NA	BE 12
Crossodactylus bokermanni	*An*	BE 12	AOE 12 III	NA	BE 12
Crossodactylus trachystomus	*An*	BE 12	AOE 12 IV	NA	BE 12
Hylodes otavioi	*An*	BE 12	AOE 12 II	NA	BE 12
Hypsiboas cipoensis	*An*	BE 12	AOE 12 IV	NA	BE 12
Leptodactylus camaquara	*An*	BE 12	AOE 12 IV	NA	BE 12
Leptodactylus cunicularius	*An*	BE 12	N	NA	BE 12
Phasmahyla jandaia	*An*	BE 12	AOE 12 II	NA	BE 12
Phyllomedusa megacephala	*An*	BE 12	AOE 12 III	NA	BE 12

Species	Order	BE Combined	NDM Combined	BE Squamata	BE Anura
Physalaemus deimaticus	*An*	BE 12	N	NA	BE 12
Physalaemus evangelistai	*An*	BE 12	AOE 12 IV	NA	BE 12
Proceratophrys cururu	*An*	BE 12	AOE 12 IV	NA	BE 12
Scinax cabralensis	*An*	BE 12	AOE 12 IV	NA	BE 12
Scinax curicica	*An*	BE 12	AOE 12 III	NA	BE 12
Scinax machadoi	*An*	BE 12	AOE 12 II	NA	BE 12
Scinax pinima	*An*	BE 12	AOE 12 II	NA	BE 12
Thoropa megatympanum	*An*	BE 12	AOE 12 III	NA	BE 12
*Atractus spinalis**	*Sq*	BE 12	AOE 12 II	BE 12	NA
Bothrops aff. *neuwiedi*	*Sq*	BE 12	N	BE 12	NA
Eurolophosaurus nanuzae	*Sq*	BE 12	AOE 12 III	BE 12	NA
Gymnodactylus guttulatus	*Sq*	BE 12	N	BE 12	NA
Heterodactylus lundii	*Sq*	BE 12	N	BE 12	NA
Placosoma cipoense	*Sq*	BE 12	AOE 12 II	BE 12	NA
Rhachisaurus brachylepis	*Sq*	BE 12	AOE 12 I	BE 12	NA
Tantilla boipiranga	*Sq*	BE 12	N	BE 12	NA
*Trilepida jani**	*Sq*	BE 12	AOE 12 II	BE 12	NA
*Tropidophis preciosus**	*Sq*	BE 12	AOE 12 II	BE 12	NA
Tropidurus montanus	*Sq*	BE 12	N	BE 12	NA
Proceratophrys strussmannae	*An*	BE 14	N	NA	N
Amphisbaena steindachneri	*Sq*	BE 14	N	N	NA
Bothrops aff. *mattogrossensis*	*Sq*	BE 14	N	N	NA
Ameerega berohoka	*An*	BE 15	AOE 3	NA	BE 3
Osteocephallus aff. *taurinus*	*An*	BE 15	N	NA	N
Amphisbaena silvestrii	*Sq*	BE 15	N	BE 18	NA
Amphisbaena talisiae	*Sq*	BE 15	N	N	NA
*Bokermannohyla napolii**	*An*	BE 16	N	NA	BE 16
Bokermannohyla ravida	*An*	BE 16	N	NA	BE 16
Bokermannohyla sazimai	*An*	BE 16	AOE 8	NA	BE 16
Ischnocnema penaxavantinho	*An*	BE 16	N	NA	BE 16
Phyllomedusa araguari	*An*	BE 16	N	NA	BE 16
Adenomera sp. 1	*An*	BE 17	AOE 17	NA	N
Elachistocleis bumbameuboi	*An*	BE 17	AOE 17	NA	N
Apostolepis sp. 2	*Sq*	BE 17	AOE 17	BE 9	NA
Adenomera martinezi	*An*	N	N	NA	N
Ameerega flavopicta	*An*	N	N	NA	BE 6
Ameerega picta	*An*	N	AOE 5	NA	BE 5
Dendropsophus cerradensis	*An*	N	N	NA	N
Coleodactylus brachystoma	*Sq*	N	N	W II	NA
*Hylodes sazimai**	*An*	N	N	NA	N
Hypsiboas botumirim	*An*	N	N	NA	N
Hypsiboas jaguariaivensis	*An*	N	N	NA	N
Leptodactylus sertanejo	*An*	N	N	NA	N
Lysapsus caraya	*An*	N	N	NA	N

Species	Order	BE Combined	NDM Combined	BE Squamata	BE Anura
Oreobates heterodactylus	*An*	N	N	NA	N
*Proceratophrys carranca**	*An*	N	AOE 12 IV	NA	N
Rhinella scitula	*An*	N	N	NA	BE 5
Rhinella veredas	*An*	N	N	NA	N
Scinax lutzorum	*An*	N	AOE 17	NA	N
Amphisbaena crisae	*Sq*	N	N	BE 18	NA
*Amphisbaena maranhensis**	*Sq*	N	N	N	NA
Amphisbaena miringoera	*Sq*	N	N	N	NA
Apostolepis serrana	*Sq*	N	N	BE 18	NA
Apostolepis vittata	*Sq*	N	N	N	NA
Atractus albuquerquei	*Sq*	N	N	N	NA
Bachia cacerensis	*Sq*	N	N	N	NA
Bothrops lutzi	*Sq*	N	N	N	NA
Bothrops marmoratus	*Sq*	N	N	BE 10 II	NA
Bothrops mattogrossensis	*Sq*	N	N	W II	NA
Bothrops neuwiedi	*Sq*	N	N	BE 6	NA
Bothrops pauloensis	*Sq*	N	N	BE 6	NA
Erythrolamprus maryellenae	*Sq*	N	N	N	NA
Hoplocercus spinosus	*Sq*	N	N	W II	NA
Kentropyx vanzoi	*Sq*	N	N	N	NA
Manciola guaporicola	*Sq*	N	N	N	NA
Micrurus brasiliensis	*Sq*	N	N	N	NA
Phalotris concolor	*Sq*	N	N	N	NA
Stenocercus sinesaccus	*Sq*	N	N	N	NA
Trilepida brasiliensis	*Sq*	N	N	BE 11	NA
Tropidurus callathelys	*Sq*	N	AOE 1	N	NA
Tropidurus chromatops	*Sq*	N	AOE 1	N	NA
Tropidurus insulanus	*Sq*	N	N	N	NA
Chiasmocleis albopunctata	*An*	W	N	NA	W
Dendropsophus elianeae	*An*	W	N	NA	W
Dendropsophus jimi	*An*	W	N	NA	W
Eupemphix nattereri	*An*	W	N	NA	W
Hypsiboas lundii	*An*	W	N	NA	W
Odontophrynus cultripes	*An*	W	N	NA	W
Apostolepis goiasensis	*Sq*	W	N	W	NA
Bothrops moojeni	*Sq*	W	N	W	NA
Cercosaura albostrigata	*Sq*	W	N	W	NA
Drymoluber brazili	*Sq*	W	N	W	NA
Epicrates crassus	*Sq*	W	N	W	NA
Kentropyx paulensis	*Sq*	W	N	W	NA
Micrabelpharus atticolus	*Sq*	W	N	W	NA
Norops meridionalis	*Sq*	W	N	W	NA
Phalotris nasutus	*Sq*	W	N	W	NA
Simophis rhinostoma	*Sq*	W	N	W	NA

Species	Order	BE Combined	NDM Combined	BE Squamata	BE Anura
Tropidurus itambere	*Sq*	W	N	W	NA
Xenopholis undulatus	*Sq*	W	N	W	NA
Apostolepis ammodites	*Sq*	W II	N	W III	NA
Apostolepis flavotorquata	*Sq*	W II	N	W III	NA
Lygophis paucidens	*Sq*	W II	N	W III	NA
Tupinambis quadrilineatus	*Sq*	W II	N	W III	NA
Rhinella cerradensis	*An*	W III	N	NA	N
Bachia bresslaui	*Sq*	W III	N	N	NA
Salvator duseni	*Sq*	W III	N	N	NA

CAPÍTULO 2

Biogeografia histórica de Anura e Squamata do Cerrado

Article type: Original Article

Historical biogeography of anurans and squamates of the Cerrado hotspot

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Running Header: Historical biogeography of the Cerrado herpetofauna

ABSTRACT

Aim. To investigate the historical relationships among biogeographical units detected for endemic anurans and squamates of the Brazilian Cerrado, depicting congruent events between areas and between these two major evolutionary groups.

Location. Cerrado savannas, central portion of South America.

Methods. Based on biotic elements detected for Cerrado endemic anurans and squamates, we created general-area cladograms (GAC) using PACT and Three-area statements analyses.

Results. The final GAC derived from PACT yielded 34 terminals, of which half represented coincident patterns. From these patterns, more 70% were composed of at least one anuran and one squamate species, suggesting a common spatial-temporal regionalization pattern for both groups. Three-area statements results shown a similar sequence of events, depicting a main division of the Cerrado in West and Central/Southeast areas, with older events occurring at places like Parecis, Espinhaço and Serra Geral.

Main conclusions. We found a predominance of vicariance events. The major evolutionary events of the Cerrado herpetofauna occurred throughout Miocene until Pleistocene, probably related with major events of uplift and subsequent dissections of plateaus that influenced ancestral ranges of both anurans and squamates. Some biotic elements were involved in more than one event, and some of them presented a reticulated history, indicating greater complexity of historical events in some areas in relation to others.

Keywords. Herpetofauna, PACT, cladistic biogeography, evolution, Neotropics, vicariance, biotic elements, Three-area statements

INTRODUCTION

Identifying the mechanisms and process that generate endemism patterns is a major step in understanding the evolution of biotas (Nelson & Platnick, 1981; Cracraft, 1988; Anderson, 1994**).** Moreover, such knowledge is central for conservation efforts aiming to protect biogeographical processes at continental scales (Pressey *et al*., 1993; Faith, 1994; Klein *et al*., 2009). From the delimitation of different biogeographic units (i. e. biotic elements, areas of endemism), it is possible to verify if such endemism pattern corresponds to general process, like vicariance (Hausdorf, 2002). One way is to verify if closely related species are distributed over different biotic elements (Hausdorf & Hennig, 2004). However, common distributional patterns could also be generated by many unrelated events between distinct groups - generating only coincident ranges, but not real areas of endemism - (Craw, 1983; Donoghue & Moore, 2003). Therefore, only with the aid of phylogenetic information it is possible to infer if regionalization patterns were generated by a general historical processes, providing clues on the history of areal relationships and on the formation of biotas (Platnick & Nelson, 1978; Morrone, 1994; Humphries & Parenti, 1999).

As phylogenetic relationships of only one taxon are not enough to resolve the histories of speciation of any given group or area, the analysis of many simpatric taxa can reveal general events, and discriminate these from clade-specific ones (Lieberman, 2003; Folinsbee & Brooks, 2007). If area cladograms of different groups show similar topological structure, then similar events should be invoked to explain regionalization patterns (Rosen, 1975; Folinsbee & Evans, 2012). Several methods have been proposed to uncover historical biogeographic patterns, and there has been a debate regarding which methods are more appropriate (Veller *et al*., 2003; Parenti & Ebach, 2009). Some methods employed a kind of data modification to include only the information about sister-group relationships to infer area-relationships, to depict the main vicariant events (Nelson & Platnick, 1981; Humphries & Parenti, 1999), while others use all data, including widespread species and paralogy, without modification (Wiley, 1988). The second approach provides opportunities to interpret not only vicariance-driven biotic diversification, but also taxon-pulse and dispersal-driven biotic diversification (Wojcicki & Brooks, 2004; Halas *et al*., 2005; Eckstut *et al*., 2011).

Nevertheless, without temporal information, even the same general topology between different area cladograms is not enough. General patterns may also be generated by pseudo-congruence, a coincident area relationships pattern generated by different events at different times (Cunningham & Collins, 1994). Such pseudo-congruent patterns can often mislead historical interpretations, and can only be detected if temporal information is included in the analysis (Upchurch & Hunn, 2002; Donoghue & Moore, 2003).

Many regionalization hypotheses were proposed at different scales within the Neotropical region, based on different groups, from harvestmen to snakes (Silva, 1997; Pinto-da-Rocha *et al*., 2005; Nogueira *et al*., 2011; Guedes *et al*., 2014; Morrone, 2014). The Cerrado region is the largest block of Neotropical savannas. Located in the centre of South America, and it harbours a rich and highly endemic herpetofauna, composed by more than 480 species of anurans and squamates (Nogueira *et al*., 2011; Valdujo *et al*., 2012a; Azevedo *et al., in prep*.). A great proportion of its herpetofauna is derived from Gondwanan lineages plus some immigrants from North America that arrived at different times over the Tertiary (Colli, 2005). It has been hypothesized that events from the Tertiary until Pleistocene, including Andean tectonism, elevation of plateaus, and marine introgressions, have strongly shaped the distributions of the Cerrado biota

(Silva, 1997; Colli *et al*., 2002). The coincident spatial clustering of species ranges of very different groups such as anurans and squamates across some biotic elements, mainly localized over different plateau areas in Cerrado, is an evidence of such general influence (Azevedo *et al*., *in prep*). However, this strongly non-random, regionalized pattern is based only on raw distribution data and geographical coincidence across ranges, with no information on temporal and historical hierarchy among these taxa and their corresponding areas.

Herein we used historical biogeographical analyses and temporal information derived from molecular dating to identify congruent and unique biogeographical events between anurans and squamates of the Cerrado, uncovering and describing patterns of historical areal relationships. The aims of our study are to: (1) to investigate historical relationships between the biogeographical units of the Cerrado herpetofauna; (2) to distinguish between congruent and unique events between both herpetofaunal groups; (3) to verify if the coincidence of distributions between anurans and squamates in the Cerrado are related to the same historical process and; (4) to interpret these results in the light of available information on the geological history of central Brazil and the Neotropics.

METHODS

Cerrado regionalization hypothesis

The Cerrado region is subdivided in at least 12 main biotic elements, delimited by the distribution of endemic anuran and squamate species (Azevedo *et al.*, *in prep*). Four of these biotic elements are composed mainly by one group (only squamates, BEs 1 and 7; mainly anurans, BEs – 4 and 8), and the remaining nine contain representatives of both groups (Figure 1). We included *Serranía Huanchaca* + *Serra da Borda* region in our regionalization hypotheses (areas between the BEs – 1 and 2), because we have lineages with important phylogenetic information in that region. We considered these areas as the same biogeographic unit as indicated in Azevedo et al., (*in prep.*).

Data sources

Phylogenetic hypotheses – We used phylogenies that contained at least three terminal taxa distributed over biotic elements of the Cerrado herpetofauna. For squamates we used phylogenies of pitvipers of the *Bothrops neuwiedi* group (Machado *et al*., 2014), the teiid lizards genus *Kentropyx* (Werneck *et al*., 2009), and *Ameiva* (Giugliano 2009; Giugliano *et al*., 2013), plus phylogeographical hypotheses for *Phyllopezus pollicaris* (Gamble *et al*., 2012) and *Micrablepharus atticolus* (Santos *et al*., 2014). For anurans we used the phylogenies of *Phyllomedusa megacephala* group (Faivovich *et al*., 2010), the genus *Pseudopaludicola* (Veiga-Menoncello et al., 2014), the *Rhinella marina* species group (Vallinoto *et al*., 2010) and the phylogeography of *Hypsiboas albopunctatus* (Prado *et al*., 2012).

Molecular dating – Of the selected phylogenies, those of *Phyllomedusa megacephala* group and *Pseudopaludicola* were not dated in the original studies. Therefore, we dated these phylogenies using *BEAST version 1.8.0 (Drummond *et al*., 2006; Drummond & Rambaut, 2007). We obtained the mtDNA sequences produced by the mentioned systematic works from GenBank (accession number in Table 1, **SI**). We aligned the sequences using Clustal X (Thompson *et al*., 1997). As no fossils of these groups are known, we used an indirect calibration method based on substitution rates to provide at least a relative idea about the divergence times of these groups. We used uncorrelated relaxed clocks to allow for rate heterogeneity among lineages and a simple birth process prior - Yule (Aldous, 2001). We used the estimated value of “0.0069 substitutions/my” divergence rate for amphibians mitochondrial DNA (Macey *et al*., 1998), with 1% standard deviation, and the normal prior on the global substitution rate. Results were checked for convergent distributions using Tracer, version 1.8.0 (Rambaut & Drummond, 2003).

Biogeographical analysis

Before the analyses, each phylogenetic tree was converted into a taxon–area cladogram (TAC), by replacing names of each terminal with their respective areas - biotic elements. In the case of phylogeographies, we considered as terminals, the well-delimited populations. As biotic elements are characteristically diffuse (Hausdorf & Hennig, 2003), we did not include species that occurred only marginally in a particular BE. Species were assigned to BEs only if occurring in their core areas (darker areas in the Figure 1, see similar delineation in Nogueira *et al*., 2011). Whenever possible, we used only the geographical information contained in the original phylogenetic studies, to avoid bias by inadequately including populations not analysed.

General Area Cladogram using the PACT algorithm – Phylogenetic Analysis for Comparing Trees (PACT) has recently emerged as a biogeographical method that provides an general-area cladogram for vicariance-driven biotic diversification, taxon-pulse and dispersal-driven biotic diversification, enabling the distinction between general and unique events (Wojcicki & Brooks, 2004; Eckstut *et al*., 2011). We combined each taxon–area cladogram by hand to form a general-area cladograma (GAC) using the PACT algorithm (Wojcicki & Brooks, 2004, 2005). PACT works comparing two TACs at time, and adding (superimposing) one over the other (Table 2, **SI**, for an example). First, all taxon–area cladograms are converted to Venn diagrams

(Table 1). The first selected TAC to compare is the template, where common elements [Y] (terminals and nodes) with a second taxon-area cladogram are combined: “Y + Y = Y”, and novel elements (N) are added at the point they first appear: “Y + N = YN”. Three additional rules complete the algorithm: (1) If two terminals are connected at different nodes, they will not be combined: “Y(Y− = Y(Y−”, (2) Common elements (Y) between two cladograms are combined even in the presence of novel elements (Y + YN = YN); and (3) “YN + YN – YNN”, when Y is the same for each, but N is different. As PACT follows Assumption 0, we did not removed or modified information of each input phylogeny (Wiley, 1988).

Reducing pseudo-congruent patterns - To avoid connecting ‘Ys’ of different ages (pseudo-congruence), we used the temporal information from dated phylogenies to construct the GAC, making the final area cladogram temporally consistent (Lim, 2008). Before using PACT, we classified elements of each TAC-Venn-diagram according to the dated phylogenies (Figure 1, **SI**). So, if a template-TAC shows a split between the most ancestral clade at the Pleistocene, as: ($A_{\mathrm{Pleistocene}}$(BC)) and another TAC shows the split at the Miocene, (A_{Miocene}(BC)), we did not join these two ‘As’ as we would according to the the first rule. Instead, we considered these as two different events, resulting in (A_{Miocene}($A_{\mathrm{Pleistocene}}$(BC))). We did not use absolute ages of each phylogeny. Instead, we classified each node age in a categorical interval: late (0-0.781my) or early (0.781-2.58my) Pleistocene; late (2.58-3.6my) or early (3.6-5.3my) Pliocene; and late (5.3-11.6my) or mid Miocene (11.6-16my) as suggested by Eckstut (2013). We joined only patterns of these categorical dates that are temporally nested (i.e. if the template Venn-diagram: ($A_{early\text{-}Pleistocene}$(BC)) will be joined with the input Venn-diagram: ($A_{late\text{-}Pliocene}$(BC)) the result is: ($A_{e\text{-}Pleistocene/l\text{-}Pliocene}$(BC)). This approach leads to an indirect inclusion of a great proportion of confidence intervals from molecular dating in our analysis, avoiding bias of using only mean ages of nodes (Graur & Martin, 2004; Hedges & Kumar, 2004).

We described the possible alternative GAC constructions because, with the great number of areas used here (thirteen), the potential for ambiguous placement of specific taxa would seem to be high. The ambiguity could be also caused by the topology of the input cladograms (Folinsbee & Brooks, 2007).

Interpreting the PACT - GAC – To depict all events of each lineage in the general-area cladogram, we gave a standard numerical code to each of the branches and nodes for each taxon–area cladogram and mapped them over the GAC (Figure 1, **SI**). We considered as congruent events those composed by two or more lineages in the final GAC derived from PACT. We depicted which of these congruent events are composed by both groups (i. e. with at least one anuran and one squamate species), and which patterns are characteristic of each lineage (with at least two anuran species, or with at least two squamate species). Finally, we used these congruent patterns to infer historical processes over time at the Cerrado region.

We used the Lieberman protocol to distinguish vicariance from biotic expansion in general nodes (Lieberman & Eldredge, 1996; Lieberman, 2003): Using the Fitch (1971) parsimony algorithm in Mesquite (Maddison & Maddison, 2001), we optimized the ancestral areas for nodes. To favoured general events over unique clade-specific events, for cases of Multiple Areas in Single Terminals [MASTs], we represented each MASTs as a polytomy, with each terminal derived from respective TAC transformed in a single terminal. This causes the algorithm to favour repeated events over a single event. Then, from the optimization of ancestral areas, transitions between ancestral nodes and descendent nodes (or terminals) that involved decreased range sizes (decreasing of number of biotic elements from ancestral to descendent nodes) were considered as possible cases of vicariance. Transitions that involved geographical expansion (increase in numbers of biotic elements) were considered as possible cases of biotic expansion events (geo-dispersal).

Three-area analysis – In order to visualize the main areal-relationships for the Cerrado herpetofauna, reducing the influence of widespread taxa and paralogy in the GAC construction, we conducted Three-area statements Analysis (Nelson & Ladiges, 1991). Using LisBeth program, version 1.3 (Bagils *et al*., 2012), we conduced Paralogy-free Subtree analysis (Nelson & Ladiges, 1996) to handle redundant areas in the TACs, and Transparent Method to handle Multiple Areas in Single Terminals [MASTs] (Ebach *et al*., 2005). We then used LisBeth to construct the intersection tree, which summarizes the information shared by optimal trees (most parsimonious trees found by 3-area analysis). To evaluate results, we used the retention index (Farris, 1983; Archie, 1989), equivalent to the percentage of 3-areas included in the intersection tree (the final GAC), and the completeness index (Bagils *et al*., 2012), that is the proportion of 3-areas present in all optimal trees also present in the intersection tree. Low values of completeness index indicate that few characters support the cladogram. Unlike PACT or BPA (analysis based on Assumption 0), that include information of relationships based in shared areas (i. e. if a species inhabits areas A and B, this information is used to infer a close relationship between these areas), 3-area analysis uses only phylogenetic relationships among taxa to solve the relationships among areas they inhabit (using Assumption 2). To understand the influence of too young or too old events, we also performed three-area analysis with temporally partitioned taxon cladograms (Upchurch & Hunn, 2002), first deleting only events at Pleistocene (collapsing nodes connected at that date) in the input TACs, and then deleting only events at Miocene in the input TACs.

RESULTS

General-Area Cladogram from PACT

The resulting node ages of BEAST for each phylogeny dated by our study are shown in the supplementary information (Table 3), together with all cladograms and respective TACs derived from the original phylogenetic works (Table 3 and Figure 1, **SI**).

The GAC resulting from PACT shows 34 operational taxonomic units -“OTUs” or terminals - (Figure 2). We represented multiple areas in single terminals as polytomies (steps of GAC construction in Figure 2, **SI**). Many cases of widespread taxa over the input taxon area-cladograms (TACs) produced ambiguous placements of specific taxa in the GAC. At least in two situations, species with widespread ranges (*Rhinella schneideri* and *Bothrops mattogrossensis*) resulted in terminals in the TACs that could not be adequately allocated with other terminals and were represented by the OTUs named “widespread” in the GAC (OTUs 15 and 16). *Kentropyx paulensis*, another species with a widespread range (over six biotic elements) generates a TAC that could be allocated at terminal positions in the GAC (OTUs 29-34), but only a systematic study at the population level could solve the relationships among these terminals.

Interpreting the GAC

Coincident topologies of taxon-area cladograms in the final GAC include 17 OTUs (thick lines, Figure 2), indicating that half (17 of 34) of all patterns found with the actual information for the Cerrado herpetofauna are coincident. Such pattern indicates the fit of the cladograms, but a priori, not congruent events (see the nodal congruence below). From these coincident fits, 13 OTUs (76%) are composed by at least one anuran and one squamate species. Three of these coincident fits are composed only by squamates (18%), including Parecis, Jalapão and Paraná basin Plateau BEs (OTUs 1, 11 and 34), and one is composed only by anurans (6%) at the Guimarães BE (OTU 28). In these situations, the lack of anuran or squamate species should be related to the data deficiency for each group in different areas and times: no anuran phylogeny includes species from the Parecis BE, and only one anuran phylogeny includes taxa in the Serra Geral BE – (*Rhinella marina* group). The remaining OTUs represents 12 unique events for squamates (35% of total) and 5 unique (15%) events for anurans.

Some areas were related to each other by sister-group relationships of different clades (nodes linked by black vertical lines, Fig. 2), while others are connected by widespread lineages that occur in more than one biotic element (linked by red lines, Figure 2). This result in 17 areal-relationships in the former case, but this number might be slightly higher. For example, the first 3 OTUs are connected only by shared widespread species. This could represent up to 3 independent splits of these areas in relation to remaining Cerrado, with secondary post-especiational dispersal, or alternatively, failure to response the vicariance event, and so on. Of these 17 areal-relationships, at least nine are based on congruent events between more than one taxa. Nevertheless, as already mentioned, this number might be higher up to 13 congruent events between areas (if counting the red nodes).

Main biogeographical events for the Cerrado herpetofauna

In general, there was a predominance of presumed vicariance events over presumed biotic expansion events (Table 2). Along the Miocene, at least three western areas of the Cerrado - Parecis, Guimarães, and Pantanal/Bodoquena BEs - were involved in congruent events (Figures 2 and 3). Using the Lieberman protocol at general nodes, these events were considered presumed vicariance events (GAC with the reconstruction of ancestral ranges, Figure 3 **SI**). The dates of events in the first two OTUs derived from each dated TAC vary across a wide time frame at Miocene, with more ancient events beginning more than 15 million years ago, and ending about 6 Mya (grey bars, Figure 2). Between 5 to 11 Mya, Espinhaço BE (OTU 9), and then, Serra Geral/Jalapão BEs (OTUs 10 and 11), were involved in presumed vicariance events at the east portion of the Cerrado (Table 2, Figures 2 and 3). Next, a biotic expansion event occurred at Miocene/Pliocene transition from areas like Guimarães, Serra Geral and Espinhaço BEs to adjacent areas like Tocantins/Araguaia basin and Central Paraná Plateau (Table 2, Figure 3).

Vicariance events in the southeast Cerrado (Paraná basin and Canastra region BEs) predominated along the Pliocene (Table 2, Figure 3). At the late Pliocene and through Pleistocene, presumed vicariance events occurred in the west (Huanchaca/Borda and Guimarães BE), in the southeast, at Espinhaço**,** and in central areas like Caiapônia and Central Plateau BEs. At the Pleistocene, many unique, lineage-specific events occurred, especially between Espinhaço, Paraná Plateau and Canastra BEs (nodes **k**, **p** and **s**). Finally, a biotic expansion event occurred over the more connected areas over the central Brazil, like Caiapônia, Central Plateau, Veadeiros, Serra Geral and Paraná basin Plateau (Table 2, Figure 3).

Pseudo-congruence was highlighted by the presence of repeated areas over the GAC, which represent different events separated by time. Cases of pseudo-congruence involves Guimarães, Espinhaço, Serra Geral and Paraná basin BEs. These areas appear to be involved in recent events over the Pleistocene, as well as in older events in the Pliocene and Miocene. On the other hand, Huanchaca/Borda, Caiapônia, Pantanal/Bodoquena and Jalapão BEs appear only once, even taking into account the unique events over the GAC. Additionally, Canastra and Parecis BEs appears only once as congruent events.

GAC of Three-item analysis

The intersection tree (Figure 4 – A) derived from three optimal trees gives a retention index (RI) = 71.6% (representing 159 of 223 optimal TACs found by Paralogy–free Subtree and Transparent method analyses). The completeness index (CI) was 51.1%, indicating incongruences among optimal trees and the intersection tree, probably related to reticulated history of some biotic elements.

A general picture of historical areal relationships could be drawn as follows: The basal division of the Parecis BE (node **a**) is followed by Serra Geral and Jalapão BEs (node b, Figure 4 – A). This reinforce that basal relation of Parecis and Guimarães depicted by PACT, may have been caused only by secondary dispersal. Next, a main difference between the PACT and Thee–area analysis appears: a main division of the Cerrado areas (at node **d**) between west/central (node **e**) and southwest/central (node **j**) biotic elements (Figure 4–A).

The relationships among areas nested inside nodes **e** and **j** are more affected by the reticulation, by the lack of dates and by the need of more distributional and phylogenetic information: the relationships within node **i** are due to a unique event between two species of the *Bothrops neuwiedi* group. The relationship between

Veadeiros BE basal to Pantanal BE (node **f**), is derived from a unique and very ancient sister group relationship found in the *Phyllopezus pollicaris* phylogeography.

The general–area cladogram derived from TACs without events at Pleistocene (Figure 4 – B; RI = 70.8%; CI = 48.3%) and the GAC without events at Miocene (Figure 4 – C; RI = 74.4%; CI = 73.6%) resulted in quite different relationships between the areas. In the GAC of Miocene/Pliocene events (Figure 4 – B), biotic elements of a more or less continuum areas at central/south Cerrado, including Veadeiros, Central Plateau, Caiapônia and Paraná basin BEs, are nested together (node **e**), in crown position in relation to western areas like Guimarães, Parecis and Pantanal/Bodoquena BEs.

In the Pliocene/Pleistocene cladogram (Figure 4 – C), Paraná basin, Espinhaço and Central Plateau are shown basal in relation to western areas like Guimarães and Tocantins/Araguaia basin, similar to the General events cladogram (Figure 4–A), but slightly different from the cladogram of older events (Figure 4–B). The main reticulated pattern occurs between Veadeiros and Caiapônia, closed related with central/south biotic elements in the Miocene/Pliocene GAC, and then related to western areas in Pliocene/Pleistocene GAC. The Jalapão BE also showed a reticulated pattern in relation to the Serra Geral (Figure 1 – A) and Central/South biotic elements. The area cladogram of Miocene/Pliocene (Figure 1 – B) is more comparable with PACT general–area cladogram (Figure 2), with a similar sequence of events beginning in western areas, passing by Serra Geral and Espinhaço, and ending in less resolved central/southern areas relationships.

DISCUSSION

We found that vicariant process were the main driver of speciation for the Cerrado herpetofauna throughout the Neogene and Quaternary. The presence of groups of squamates and anurans species with coincident distributions over the Cerrado region is the first indication that some general process, like vicariance and/or some kind of congruent dispersal (or the formation of biological refuges), shaped the Cerrado biota in some regions, regardless of the biological characteristics of each group (Azevedo *et al.*, *in prep*). Biotic elements of the Cerrado herpetofauna are mainly composed by poor dispersers like many fossorial squamates (Nogueira *et al.*, 2011), a factor that may have helped in the identification of such vicariant pattern, less prone to be obscured by extensive post-speciational dispersal (Hausdorf & Hennig, 2006). The detection of at least three biotic expansion events and the presence of reticulated relationships between areas may also suggest a taxon-pulse like pattern of diversification (Erwin, 1981; Halas *et al.*, 2005).

The majority of speciation events within the Cerrado in our study occurred less than 12 Mya, in conformity with the findings for vascular plants (Simon *et al.*, 2009), suggesting a recent major diversification of the Cerrado lineages, in coincidence with the expansion of other savannas in the world (Edwards *et al.*, 2010). The high levels of species endemism and the rarity of endemic genera in the Cerrado region (see Nogueira *et al.*, 2011; Valdujo *et al.*, 2012) is another indication of the possible recent assembly of the Cerrado herpetofauna. That diversification events are also parallel with the timing of Amazonian amphibian diversification (Santos *et al.*, 2009). However, some deep events related to the Cerrado herpetofauna occurred in places like Parecis, Espinhaço, Guimarães and Serra Geral, from mid Miocene until early Pliocene, instead of the

Pleistocene. Furthermore, the single endemic lizard genus of Cerrado, the monotypic *Hoplocercus,* may have an ancient origin, even before the Miocene (Torres-Carvajal & de Queiroz, 2009). Then, the lack of endemic genera should be related to the incipient systematic knowledge. As more dated phylogenies of species-rich genera like *Amphisbaena*, *Apostolepis*, *Tropidurus* and *Proceratophrys* become available, more ancient diversification events could be discovered.

Most congruent events of the Cerrado Herpetofauna may coincide with major events of the geomorphological evolution of the South America. During the middle Cenozoic, areas harbouring many of the recovered biotic elements were uplifted and separated by major peripheral depressions (Ab'Saber, 1983). These areas are formed by a heterogeneous set of formations, including rocks of different sedimentary origins in Parecis, Bodoquena, Serra Geral and Jalapão (Filho & Karmann, 2007; Villela & Nogueira, 2011; Ross, 2013). There are also formations originated from very ancient continental Precambrian crystalline igneous and high-grade metamorphic rocks over the Central Plateau, Veadeiros and especially at the Espinhaço range (Pinto, 1986; Saadi, 2013). In part due to these different compositions, some of these areas were uplifted and others subsided at different rates (Silva, 1997). The development of the peripheral depressions also increased the isolation of the mentioned areas at different rates, in part, due to these different compositions (Ab'Saber, 1998) and, should be the main factor for the isolation of the associated fauna over different times along Miocene, Pliocene and Pleistocene.

These peripheral depressions have isolated ancestral populations not only by physical barriers, but also by the instability of the Cerrado vegetation in these places, constantly colonized by forested or arid formations along historical climatic changes (Ab'Saber, 1983). Compared to these depressions, the plateaus showed more stable habitat composition, and probably retained savanna-gallery forest mosaics along large periods of time (Silva, 1997; Brown Jr. & Gifford, 2002). The Cerrado vegetation also expanded over these lower areas in some periods, and the presumable biotic expansion events depicted in our GAC should be related to these savanna-vegetation expansions, providing connectivity among different areas, especially between disjunct plateaus. The biotic expansion showed by our GAC in the Pleistocene may be correlated with the emergence of the actual climatic conditions that caused the Cerrado expansion towards its current extension, while other vegetation types retracted (Werneck, 2011). These expansions and retractions of the Cerrado from refuge areas probably occurred many times, even before the Pleistocene, like in other South American domains (Haffer & Prance, 2002).

In addition to these expansions and retractions of the Cerrado, some areas remained more or less geologically instable, and these factors may have reflected in the reticulated history of some areas like the Espinhaço, with more tectonic activity (at Miocene/Pliocene and Pleistocene) and geomorphological complexity than more stable areas at the Central Plateau (Saadi, 2013). The isolation of ancestral populations leading to speciation throughout different times, created a pseudo-congruent pattern in the results of Three-area analysis that was depicted in the PACT results. These reticulations and pseudo-congruencies highlighted the dynamic character of biogeographical units, and impose technical difficulties to reconstructing their history (Nihei, 2008). Moreover, such pseudo-congruence also indicate that evolutionary processes may occur more frequently in certain places, (i. e. Espinhaço or Guimarães BEs), which may have implications for the conservation of evolutionary process (Balmford *et al*., 1998; Moritz, 2002).

However, there are many source of errors in the estimation of node ages in phylogenies (Graur & Martin, 2004; Hedges & Kumar, 2004) that could be responsible for the supposed pseudo-congruences found in some areas (Upchurch, 2008), although the majority of the area-duplications depicted by our results derived from the topology of the input TACs. Moreover, other biotic elements involved in only one congruent event may show a pseudo-congruent pattern that was impossible to detect in our dataset. Using only criteria of two or more species to consider a congruent event, any new information derived from additional phylogenies could transform one of the 14 unique events shown here in a new congruent event.

On the other hand, these events depicted by PACT could not correspond to a real pseudo-congruences. The formation of a geographical barrier could be a gradual event, increasing the isolation of two areas over a wide range of time. This implies that in principle, depending of some characteristics of the organisms involved (i. e. more or less dispersal ability), a geographical barrier could isolate a population of one species before and, as the barrier develops (i. e. the increasing width of the river valleys between two plateau areas) another species becomes isolated. Different habitat preferences can also cause temporal disparity (i. e. sandy substrate habitats could fragment more quickly than rocky substrate during geological uplift, and their respective habitat-specialist taxon should exhibit a pseudo-congruent pattern; Riddle & Hafner, 2006). Even if the barrier appears suddenly, different species could speciate at different times because of intrinsic characteristics, such as higher evolutionary rates, or more limited dispersal ability.

Therefore, the results of the Three-area analysis provide a broad picture of the general patterns regardless of temporal information. The division of the Cerrado region in central/southwest and eastern areas, more or less divided by the Tocantins-Araguaia basin and associated depression (Figure 5), was better depicted with the Three-area results, and is parallel with the division found in phytogeography patterns of vascular plants (Novaes *et al*., 2013). The basal position of Parecis, Serra Geral and Jalapão biotic elements was concordant between the two analyses, even considering that the two former areas have a poor representation of lineages in our phylogenies. These regions have a sedimentary origin (Radambrasil, 1981; Nascimento, 1991) and after the general Tertiary cycles of uplift, their arenitic tabletops may have eroded before the more continuum areas of the central and southwest, formed by a more resistant clay rich deposits, which, form, nowadays, larger blocks of continuous plateaus.

The reticulated patterns found in our analysis may be reinforced if we include species that occur in the adjacent phytogeographic domains. Especially for anurans, the proximity to adjacent domains is important for the composition of the communities, even for the endemics (Valdujo *et al*., 2012b). As an example, in the phylogeny of the *Phyllomedusa megacephala* group, the species *P. rohdei* occurs in forested areas along the Atlantic Forest, and its the sister species *P. megacephala*, occurs at the Espinhaço. In that case, the TAC would indicate the close relation between Espinhaço and Atlantic Forests, basal to other Cerrado areas, like Canastra, while other phylogenies indicate that the Espinhaço range is more related to other Cerrado areas like Canastra or Paraná basin BEs (*Bothrops neuwiedii* group).

Azevedo *et al* (*in prep*, chapter 1) hypothesized that the coincident ranges of the squamates and anuran species over the Cerrado region could be due to the same events. In accordance with that idea, most congruent events depicted here were composed by at least one anuran and one squamate species. Nevertheless, patterns restricted to anurans or to squamates, such as the prevalence of squamates in the Parecis and Jalapão BEs, have a parallel in the general events found here, only affecting members of squamates in that biotic elements. Moreover, some events seem to have affected more some lineages than others, even in the regions with coincident distribution of anurans and squamates, like in the Guimarães BE at Pliocene/Pleistocene boundary (OTU 29), that affected only anurans. In fact, if considering only congruent events of each group individually, the pattern found here would be different, with the sequence of congruent events of (Espinhaço(Paraná(Guimarães(Veadeiros+Central, Caiapônia) for anurans and (Parecis(Pantanal/Bodoquena(Serra Geral, Jalapão(Central, Caiapônia + Paraná) for squamates and additional information might show if this is the real pattern, or only due to the actual knowledge.

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TABLES

Table 1 – Venn diagrams of each phylogeny used in our analysis. Red letters represents the distribution of a single clade over more than one biotic element. A – Parecis, B – Guimarães, C – central Paraná Plateau, D –Jalapão, E - Central Brazilian Plateau, F –Espinhaço, G – Pantanal/Bodoquena, H –Tocantins-Araguaia Basin, I – Serra Geral, J –Caiapônia Plateau, K – Veadeiros Plateau, L –Canastra Plateau, M – Huanchaca/Borda Plateau region.

Lineages	Venn diagrams
Ameiva parecis group	(A(J,C))
Bothrops neuwiedi group	(ID(CL(F(EJK)))((JEK)(HKEJGB)))
Hypsiboas albopunctatus	(B((CF)((EJK)(CF))))
Kentropyx pauloensis group	(BA(G(D(EICBJK))))
Micrablepharus atticolus	(B(JC((A)(HE))))
Phyllomedusa megacephala group	(F(L(B(EK))))
Phyllopezus pollicaris	(F(KH(G))((KI)(IDH)))
Pseudopaludicola saltica group	(G(F(BE(F,C))))
Pseudopaludicola ternetzi group	((B,M)(CE))
Rhinella marina group (central-north clade)	(I(A-M(IJE)))

Table 2 – Events between ancestral and descendent congruent nodes or terminals in the GAC using reconstructed ancestral ranges over nodes (Lieberman protocol), to distinguish vicariance from congruent dispersal (biotic expansion).

Nodes/Terminals	Presumable event	Place (Biotic elements)
a - OTU 1-2	Vicariance	Parecis, Guimarães* isolation
c - OTU 4	Vicariance	Pantanal isolation
c - f	Vicariance	Veadeiros isolation**
f - OTU 9	Vicariance	Espinhaço*** isolation
g - h	Vicariance	Serra Geral and Jalapão isolation
g - i	Biotic expansion	To Tocantins/Araguaia, Paraná Plateau.
i - OTU 13	Vicariance	Paraná Plateau*** isolation
i - o	Ambiguous	Range shift to Canastra, Central, Huanc./Bor.
o - OTU 19	Vicariance	Canastra isolation
o - OTU 20	Vicariance	Paraná Plateau isolation
q - OTU 22	Vicariance	Huanchaca/Borda isolation
q - r	Ambiguous	Range shift to Espinhaço and Caiapônia
r - OTU 27	Vicariance	Espinhaço isolation
t - OTU 28	Vicariance	Guimarães isolation
t - u	Vicariance	Caiapônia/Central isolation
u - OTUs 29-34	Biotic expansion	From Central/Caiapônia to adjacent areas

* The following general nodes remained including Guimarães BE, which may indicate that vicariance split involves only the Parecis biotic element at that point, with posterior dispersal of some species to Guimarães BE.

** At that point, Veadeiros BE was involved only in unique events over the terminals.

*** Remained included in the next nodes due lineage-specific subsequent events.

FIGURES

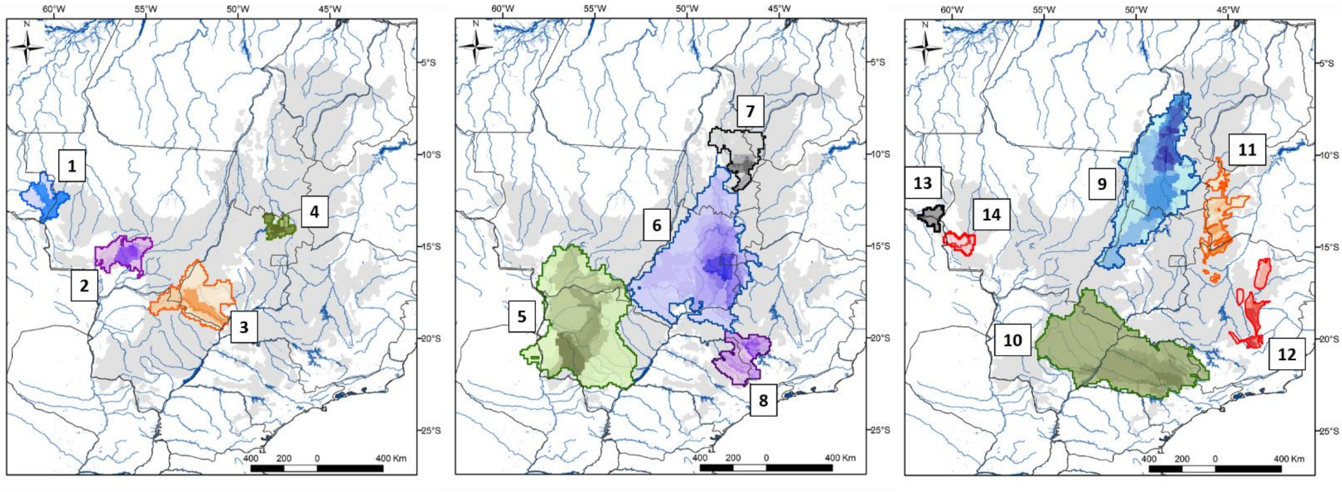


Figure 1 – Biotic elements (BE) defined by distribution of herpetofaunal species (Azevedo *et al*, *in prep*). The thick lines indicate the BE limits as the areas with the occurrence of two or more species. The gradient colours of each BE indicate the richness, with the darker tones indicating the approximate core area of each biotic element. The grey colour indicate the Cerrado limits. Biotic elements classification according to the main geomorphological places: places: 1 – Parecis Plateau. 2 – Guimarães Plateau. 3 – Caiapônia Plateau. 4 – Veadeiros Plateau. 5 – Pantanal and Bodoquena regions. 6 – Central Brazilian Plateau. 7 – Jalapão region. 8 – Canastra region. 9 – Tocantins–Araguaia basin. 10 – Central Paraná basin Plateau. 11 – Serra Geral Plateau. 12 – Espinhaço mountain range. 13 – *Serranía de Huanchaca*. 14 – *Serra da Borda*.

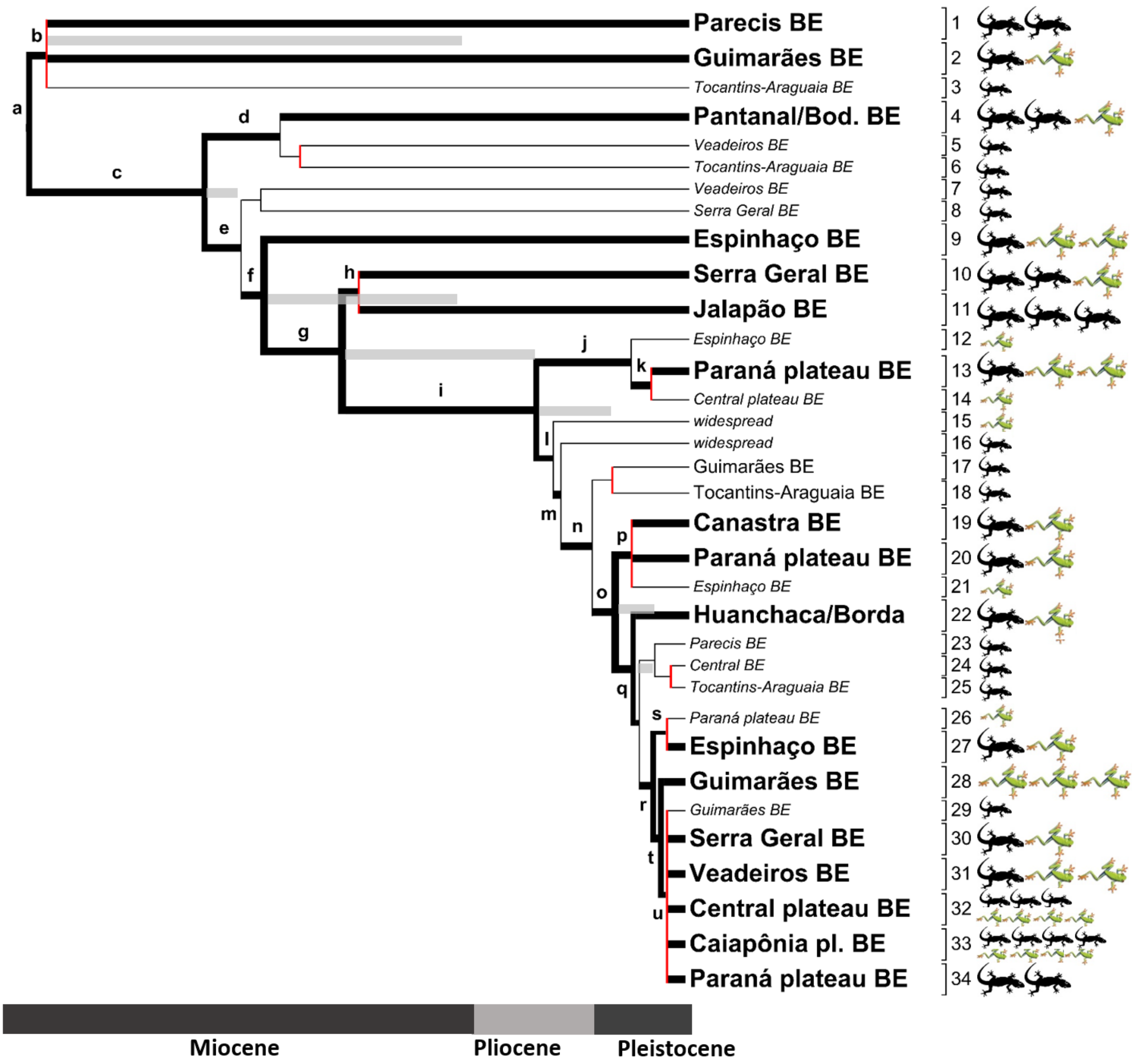


Figure 2 – General-Area Cladogram (GAC) derived from PACT analysis. The biotic elements (BE) in bold indicate coincident fits between more than one lineage from the original taxon-areas cladograms (TACs). Thick black lines also indicate coincidence between two or more TACs. Thin lines represent unique, clade-specific events of each TAC. Red vertical lines indicate areal relationships derived from the information of species distributed over more than one BE. In those cases, the split between these areas, if real, could not be dated in the GAC. Green symbols on the right, represent the number of anuran lineages in each terminal, while black symbols represent squamates. The split of each branch was positioned at the oldest event date in the original TACs, while grey bars represent the time range until the youngest event (see a protocol to calibrate GACs in Folinsbee & Evans, 2012). Major nodes were coded from "a" to "u".

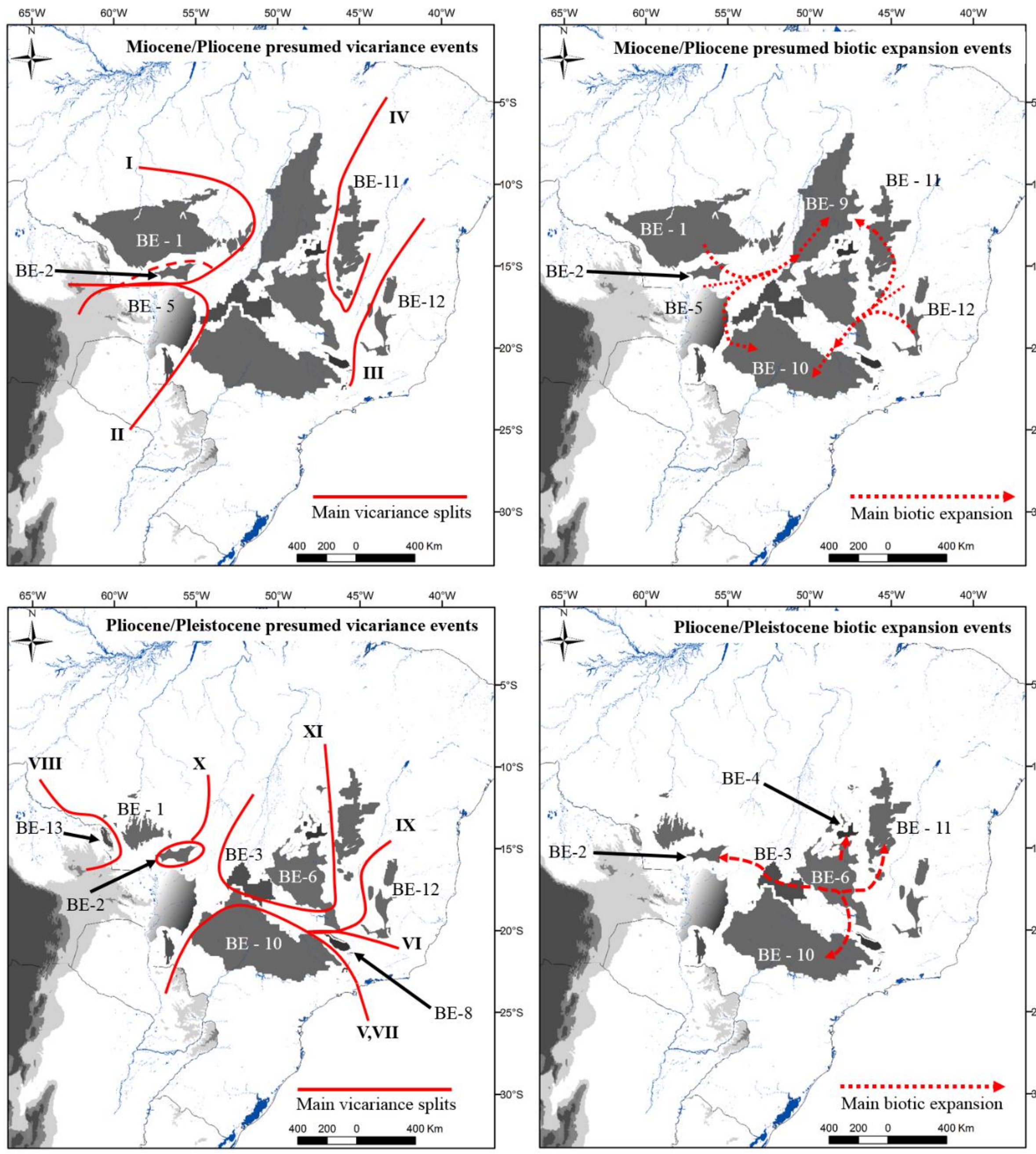


Figure 3 – Map with main vicariance splits and dispersal routs of the Cerrado Herpetofauna. I – Parecis (Guimarães?) isolation; II – Pantanal/Bodoquena isolation; III – Espinhaço isolation; IV – Serra Geral/Jalapão isolation; V – Central Paraná Plateau isolation; VI – Canastra isolation; VII – Central Paraná Plateau isolation; VIII – *Huanchaca/Borda* isolation; IX – Espinhaço isolation; X – Guimarães isolation. XI – Caiapônia/Central plateaus isolation. See Fig. 1 for the biotic element names.

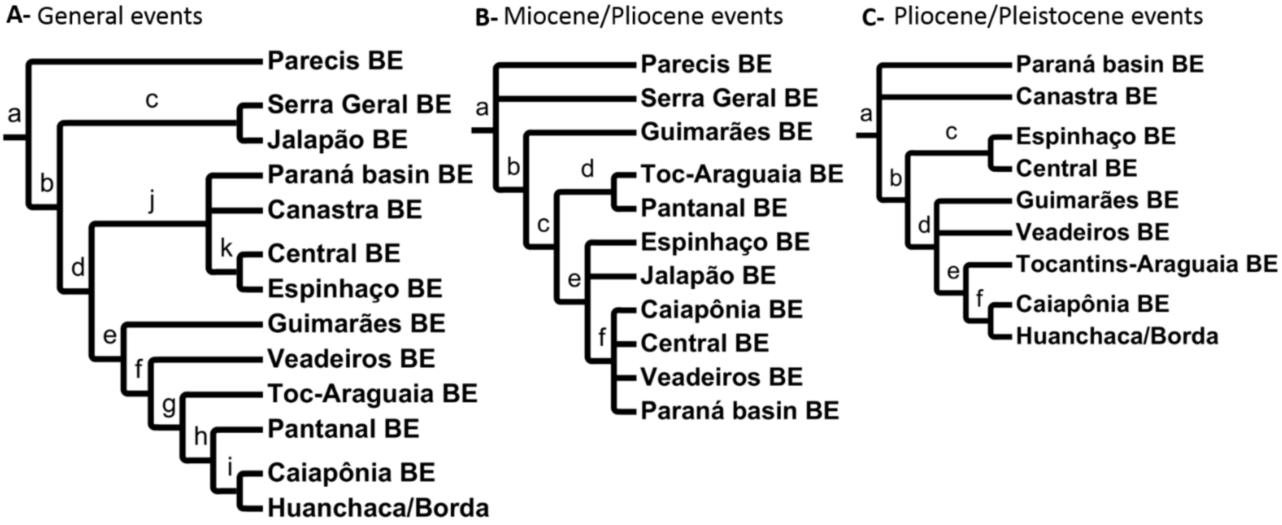


Figure 4 - Intersection trees derived from Three-area analysis showing the areal relationships among the Cerrado biotic elements (Figure 1). **A**- General-area cladogram (GAC) derived from complete taxon-area cladograms (TACs). **B** – GAC derived from TACs without events over the Pleistocene. **C** – GAC derived from TACs without events over the Miocene. The nodes are labelled from **a** to **k**.

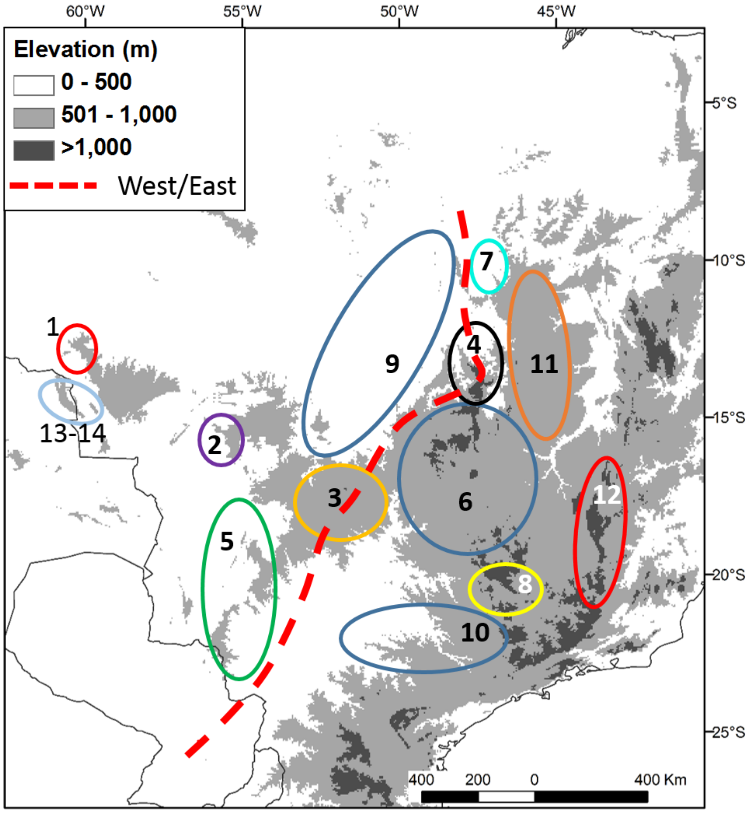


Figure 5 – Main current geomorphological surfaces where biotic elements of Cerrado are located (adapted from Azevedo *et al*., *in prep*). Dashed line represent the major division depicted by three–area analysis in Western and Eastern Cerrado. Biotic elements: 1 – Parecis Plateau. 2 – Guimarães Plateau. 3 – Caiapônia Plateau. 4 – Veadeiros Plateau. 5 – Pantanal and Bodoquena regions. 6 – Central Plateau. 7 – Jalapão. 8 – Canastra Plateau. 9 – Tocantins–Araguaia basin. 10 – Central Paraná basin Plateau. 11 – Serra Geral Plateau. 12 – Espinhaço mountain range. 13 – Serranía Huanchaca. 14 – Serra da Borda.

SUPPLEMENTARY INFORMATION

TABLES

Table 1 – Mitochondrial DNA sequences from GenBank used to date phylogenies.

Taxon	Voucher	GenBank	Sequences	Locality
Pseudopaludicola saltica	ZUEC 14239	KJ147002.1	12S and 16S, tRNA-Val	Mato Grosso: Chapada dos Guimarães
Pseudopaludicola saltica	ZUEC 14240	KJ147003.1	12S and 16S, tRNA-Val	Mato Grosso: Chapada dos Guimarães
Pseudopaludicola saltica	ZUEC 14291	KJ146994.1	12S and 16S, tRNA-Val	Minas Gerais: Uberlândia
Pseudopaludicola saltica	ZUEC 14292	KJ146995.1	12S and 16S, tRNA-Val	Minas Gerais: Uberlândia
Pseudopaludicola saltica	ZUEC 19553	KJ147053.1	12S and 16S, tRNA-Val	Minas Gerais: Serra da Moeda
Pseudopaludicola saltica	ZUEC 19556	KJ147051.1	12S and 16S, tRNA-Val	Minas Gerais: Serra da Moeda
Pseudopaludicola murundu	CFBH-T1467	KJ147008.1	12S and 16S, tRNA-Val	São Paulo: Rio Claro
Pseudopaludicola murundu	ZUEC 14286	KJ147032.1	12S and 16S, tRNA-Val	São Paulo: Rio Claro
Pseudopaludicola mineira	ZUEC 14317	KJ147027.1	12S and 16S, tRNA-Val	Minas Gerais: Serra do Cipó
Pseudopaludicola mineira	ZUEC 14318	KJ147026.1	12S and 16S, tRNA-Val	Minas Gerais: Serra do Cipó
Pseudopaludicola ameghini	UFMT 8543	KJ146976.1	12S and 16S, tRNA-Val	Mato Grosso: Chapada dos Guimarães
Pseudopaludicola ameghini	ZUEC 14138	KJ146977.1	12S and 16S, tRNA-Val	Mato Grosso: Chapada dos Guimarães
Pseudopaludicola ameghini	ZUEC 14140	KJ146975.1	12S and 16S, tRNA-Val	Mato Grosso: Chapada dos Guimarães
Pseudopaludicola ameghini	ZUEC 13923	KJ147047.1	12S and 16S, tRNA-Val	Mato Gross: Vila Bela Sta. Trindade
Pseudopaludicola ameghini	ZUEC 13924	KJ147045.1	12S and 16S, tRNA-Val	Mato Gross: Vila Bela Sta. Trindade
Pseudopaludicola ameghini	ZUEC 13925	KJ147046.1	12S and 16S, tRNA-Val	Mato Gross: Vila Bela Sta. Trindade

Taxon	Voucher	GenBank	Sequences	Locality
Pseudopaludicola ameghini	ZUEC 14146	KJ147048.1	12S and 16S, tRNA-Val	Mato Gross: Vila Bela Sta. Trindade
Pseudopaludicola ternetzi	DZSJRP 6445	KJ147012.1	12S and 16S, tRNA-Val	São Paulo: Icém
Pseudopaludicola ternetzi	DZSJRP 6446	KJ147011.1	12S and 16S, tRNA-Val	São Paulo: Icém
Pseudopaludicola ternetzi	DZSJRP 6456	KJ147010.1	12S and 16S, tRNA-Val	São Paulo: Icém
Pseudoudicola sp.	ZUEC 13928	KJ146992.1	12S and 16S, tRNA-Val	M.Grosso: Poconé
Pseudopaludicola sp.	ZUEC 13930	KJ147040.1	12S and 16S, tRNA-Val	M.Grosso: Poconé
Pseudopaludicola ternetzi	DZSJRP 8723	KJ147029.1	12S and 16S, tRNA-Val	São Paulo: Icém
Pseudopaludicola ternetzi	UFMT 15753	KJ147054.1	12S and 16S, tRNA-Val	Goiás: Uruaçu
Pseudopaludicola ternetzi	UFMT 15754	KJ147055.1	12S and 16S, tRNA-Val	Goiás: Uruaçu
Pseudopaludicola ternetzi	UFMT 18061	KJ147056.1	12S and 16S, tRNA-Val	Goiás: Uruaçu
Pseudopaludicola ternetzi	ZUEC 14169	KJ146986.1	12S and 16S, tRNA-Val	Minas Gerais: Uberlândia
Pseudopaludicola ternetzi	ZUEC 14171	KJ146987.1	12S and 16S, tRNA-Val	Minas Gerais: Uberlândia
Pseudopaludicola ternetzi	ZUEC 14172	KJ147042.1	12S and 16S, tRNA-Val	Minas Gerais: Uberlândia
Pseudopaludicola ternetzi	SMRP 266.6	KJ147043.1	12S and 16S, tRNA-Val	Minas Gerais: Uberlândia
Phyllomedusa megacephala	CFBH 10225	GQ366269.1	12S and 16S RNA; tRNA-Val ; cytb	Minas Gerais: Serra do Cipó
Phyllomedusa megacephala	MCNAM 6339	GQ365955.1	12S and 16S RNA; tRNA-Val ; cytb	Minas Gerais: Serra do Cipó
Phyllomedusa ayeaye	CFBH 15672	GQ365932.1	12S and 16S RNA; tRNA-Val ; cytb	São Paulo: PE das Furnas
Phyllomedusa ayeaye	CHUNB 51421	GQ366244.1	12S and 16S RNA; tRNA-Val ; cytb	São Paulo:PN Serra da Canastra
Phyllomedusa centralis	CHUNB 12571	GQ366261.1	12S and 16S RNA; tRNA-Val ; cytb	Mato Grosso: Chapada dos Guimarães

Taxon	Voucher	GenBank	Sequences	Locality
Phyllomedusa centralis	UFMT 6221	GQ365947.1	12S and 16S RNA; tRNA-Val ; cytb	Mato Grosso: Chapada dos Guimarães
Phyllomedusa oreades	CHUNB 56871	GQ365963.1	12S and 16S RNA; tRNA-Val ; cytb	Goiás: PE Serra de Caldas
Phyllomedusa oreades	CHUNB 56869	GQ366274.1	12S and 16S RNA; tRNA-Val ; cytb	Goiás: PE Serra de Caldas
Phyllomedusa azurea	MLP DB 2795	GQ366250	12S and 16S RNA; tRNA-Val ; cytb	Argentina: Chacabuco, Charata

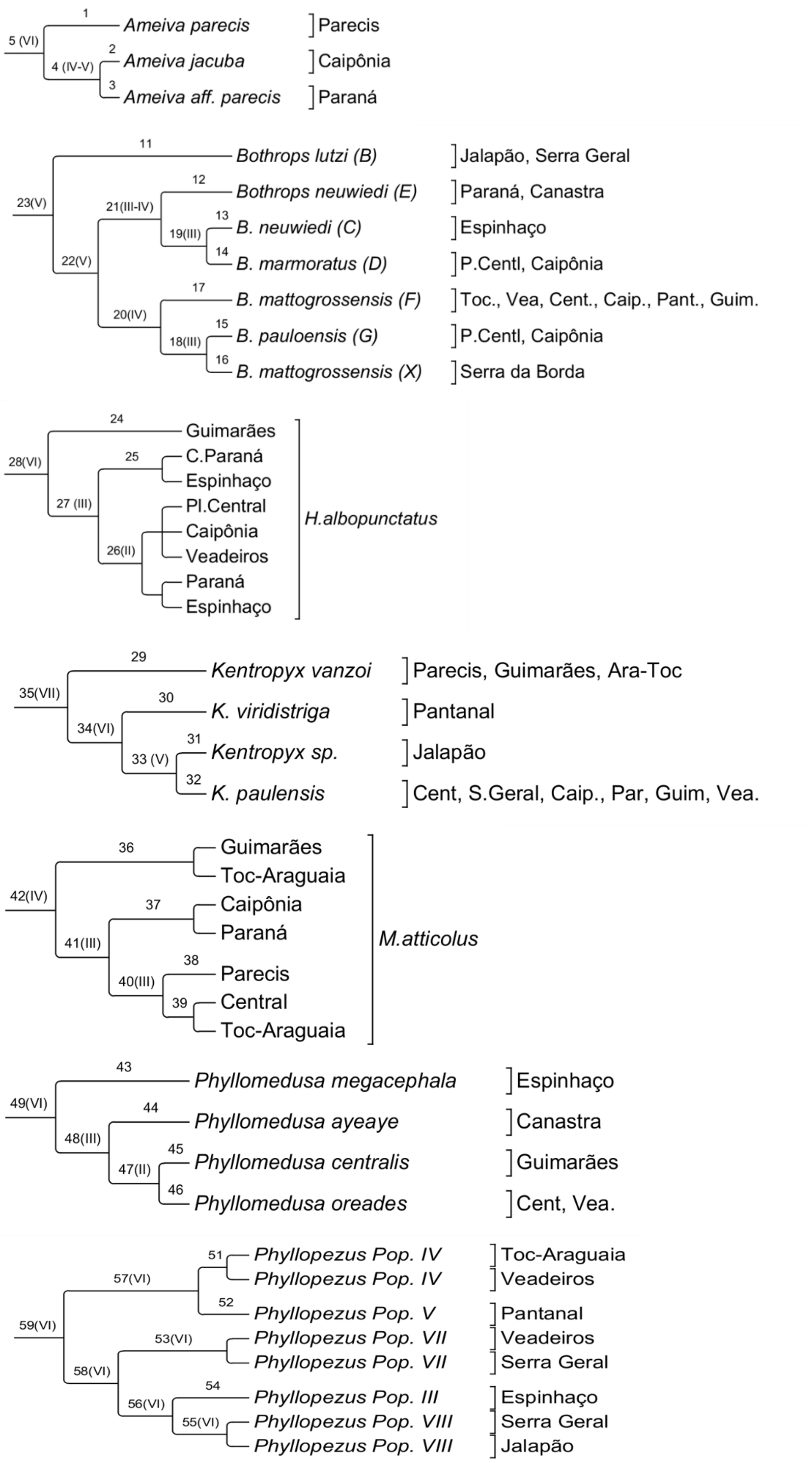
Table 2 - Example of how PACT works. Note that the true positioning of E in relation to H needs more data or temporal information.

Template diagram	Input diagram
(A(B(H(CD))))	**(A(B(E(CD))))**
First, we compare the elements of each cladogram, denoting Y for the common elements and N for the different. Then we use the PACT rules to combine both diagrams.	
A – Y; **B** – Y; **H** – N; **C** – Y, **CD** - Y	**A** – Y; **B** – Y; **E** – N; **C** – Y; **D** – Y. **CD** – Y
Using the rule 'Y + Y = Y', we can combine the A, B, C, D and CD of the two diagrams. Using the rule 'Y + N = YN', we can combine E + CD, and then, H + E(CD) resulting in:	
(A(B(H(E(CD)))))	

Table 3 – Node ages and Epoch classification of each input phylogeny.

Group	Node	date (mi years)	Epoch	Souce
Ameiva parecis	5	±8,5 (±2,0)	late Miocene	Giugliano et al., in press
Ameiva parecis	4	±1,9 (±1,0)	early Pleistocene	Giugliano et al., in press
Bothops neuwiedi	23	4,64 (±1,0)	early Pliocene	Machado et al., 2013
Bothops neuwiedi	22	4,26 (±1,0)	early Pliocene	Machado et al., 2013
Bothops neuwiedi	21	2,35 (±1,0)	late Pliocene	Machado et al., 2013
Bothops neuwiedi	20	3,25 (±1,0)	late Pliocene	Machado et al., 2013
Bothops neuwiedi	19	1,56 (±1,0)	early Pleistocene	Machado et al., 2013
Bothops neuwiedi	18	1,63 (±1,0)	early Pleistocene	Machado et al., 2013
Hypsiboas albopunctatus	28	5,88 (±1,6)	late Miocene	Prado et al., 2012
Hypsiboas albopunctatus	27	0,84 (±0,2)	early Pleistocene	Prado et al., 2012
Hypsiboas albopunctatus	26	0,69 (±0,2)	mid Pleistocene	Prado et al., 2012
Kentropyx	35	±17,0 (±6,0)	early Miocene	Werneck et al., 2009
Kentropyx	34	±12,5 (± 5,0)	mid Miocene	Werneck et al., 2009
Kentropyx	33	±4,0 (±3,5)	early Pliocene	Werneck et al., 2009
Micrablepharus atticolus	42	2,9 (±0,6)	late Pliocene	Santos et al., 2013
Micrablepharus atticolus	41	1,8 (±0,5)	early Pleistocene	Santos et al., 2013
Micrablepharus atticolus	40	1,4 (±0,3)	early Pleistocene	Santos et al., 2013
Phyllomedusa	49	5,98 (±4,2)	late Miocene	This study
Phyllomedusa	48	1,29 (±1,0)	early Pleistocene	This study
Phyllomedusa	47	0,4 (±0,3)	mid Pleistocene	This study
Phyllopezus policaris	59	±11,6 (±4,5)	late Miocene	Werneck et al., 2009
Phyllopezus policaris	58	±11,5 (±4,5)	late Miocene	Werneck et al., 2009
Phyllopezus policaris	56	±11,4 (±4,5)	late Miocene	Werneck et al., 2009
Phyllopezus policaris	57	±10,5 (±4,5)	late Miocene	Werneck et al., 2009
Pseudopaludicola. gr.saltica	68	12,7 (±11,0)	late/mid Miocene	This study
Pseudopaludicola. gr.saltica	67	7,65 (±7,0)	late Miocene	This study
Pseudopaludicola. gr.saltica	66	4,0 (±3,7)	early Pliocene	This study
Pseudopaludicola. gr.saltica	62	1,55 (±2,0)	early Pleistocene	This study
Pseudopaludicola. gr.saltica	65	1,24 (±1,6)	early Pleistocene	This study
Pseudopaludicola. gr.ternetzi	73	2,28 (±1,7)	early Pleistocene	This study
Pseudopaludicola. gr.ternetzi	72	0,89 (±0,6)	mid Pleistocene	This study
Rhinella gr. marina	78	±9,0 (±3,7)	late Miocene	Maciel et al., 2010
Rhinella gr. marina	77	±3,5 (±0,5)	late/early Pliocene	Maciel et al., 2010

FIGURES


5 (VI)
1
Ameiva parecis
Parecis
4 (IV-V)
2
Ameiva jacuba
Caipônia
3
Ameiva aff. parecis
Paraná
23(V)
11
Bothrops lutzi (B)
Jalapão, Serra Geral
22(V)
21(III-IV)
12
Bothrops neuwiedi (E)
Paraná, Canastra
19(III)
13
B. neuwiedi (C)
Espinhaço
14
B. marmoratus (D)
P.Centl, Caipônia
20(IV)
17
B. mattogrossensis (F)
Toc., Vea, Cent., Caip., Pant., Guim.
18(III)
15
B. pauloensis (G)
P.Centl, Caipônia
16
B. mattogrossensis (X)
Serra da Borda
28(VI)
24
Guimarães
27 (III)
25
C.Paraná
Espinhaço
26(II)
Pl.Central
Caipônia
Veadeiros
Paraná
Espinhaço
H.albopunctatus
35(VII)
29
Kentropyx vanzoi
Parecis, Guimarães, Ara-Toc
34(VI)
30
K. viridistriga
Pantanal
33 (V)
31
Kentropyx sp.
Jalapão
32
K. paulensis
Cent, S.Geral, Caip., Par, Guim, Vea.
42(IV)
36
Guimarães
Toc-Araguaia
41(III)
37
Caipônia
Paraná
40(III)
38
Parecis
39
Central
Toc-Araguaia
M.atticolus
49(VI)
43
Phyllomedusa megacephala
Espinhaço
48(III)
44
Phyllomedusa ayeaye
Canastra
47(II)
45
Phyllomedusa centralis
Guimarães
46
Phyllomedusa oreades
Cent, Vea.
59(VI)
57(VI)
51
Phyllopezus Pop. IV
Toc-Araguaia
Phyllopezus Pop. IV
Veadeiros
52
Phyllopezus Pop. V
Pantanal
58(VI)
53(VI)
Phyllopezus Pop. VII
Veadeiros
Phyllopezus Pop. VII
Serra Geral
56(VI)
54
Phyllopezus Pop. III
Espinhaço
55(VI)
Phyllopezus Pop. VIII
Serra Geral
Phyllopezus Pop. VIII
Jalapão

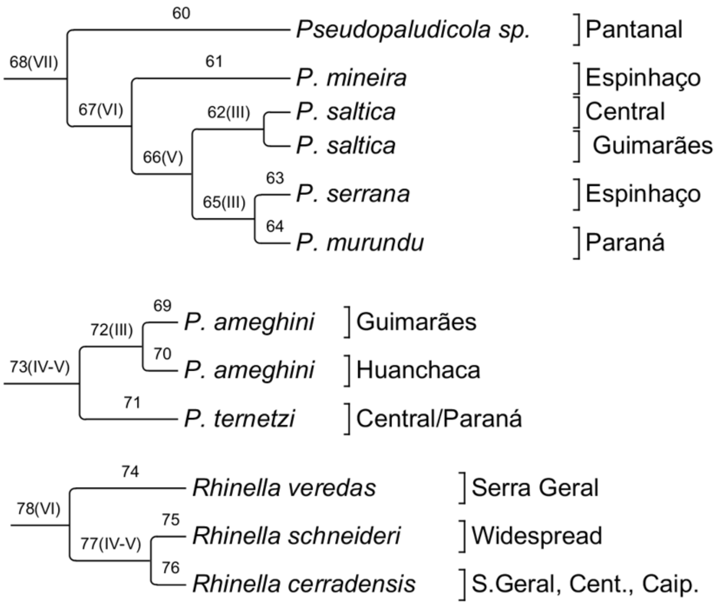


Figure 1 – Phylogenies and taxon-area-cladograms (TACs), with the respective code numbers for terminals and nodes. Roman numerals represents each Epoch: I – Late Pleistocene; II – Mid Pleistocene; III – Early Pleistocene; IV – Late Pliocene; V – Early Pliocene; VI – Late Miocene; VII Mid Miocene. For *Bothrops neuwiedi* group and *Pseudopaludicola*, we used only the localities of specimens used in the respective systematic studies.

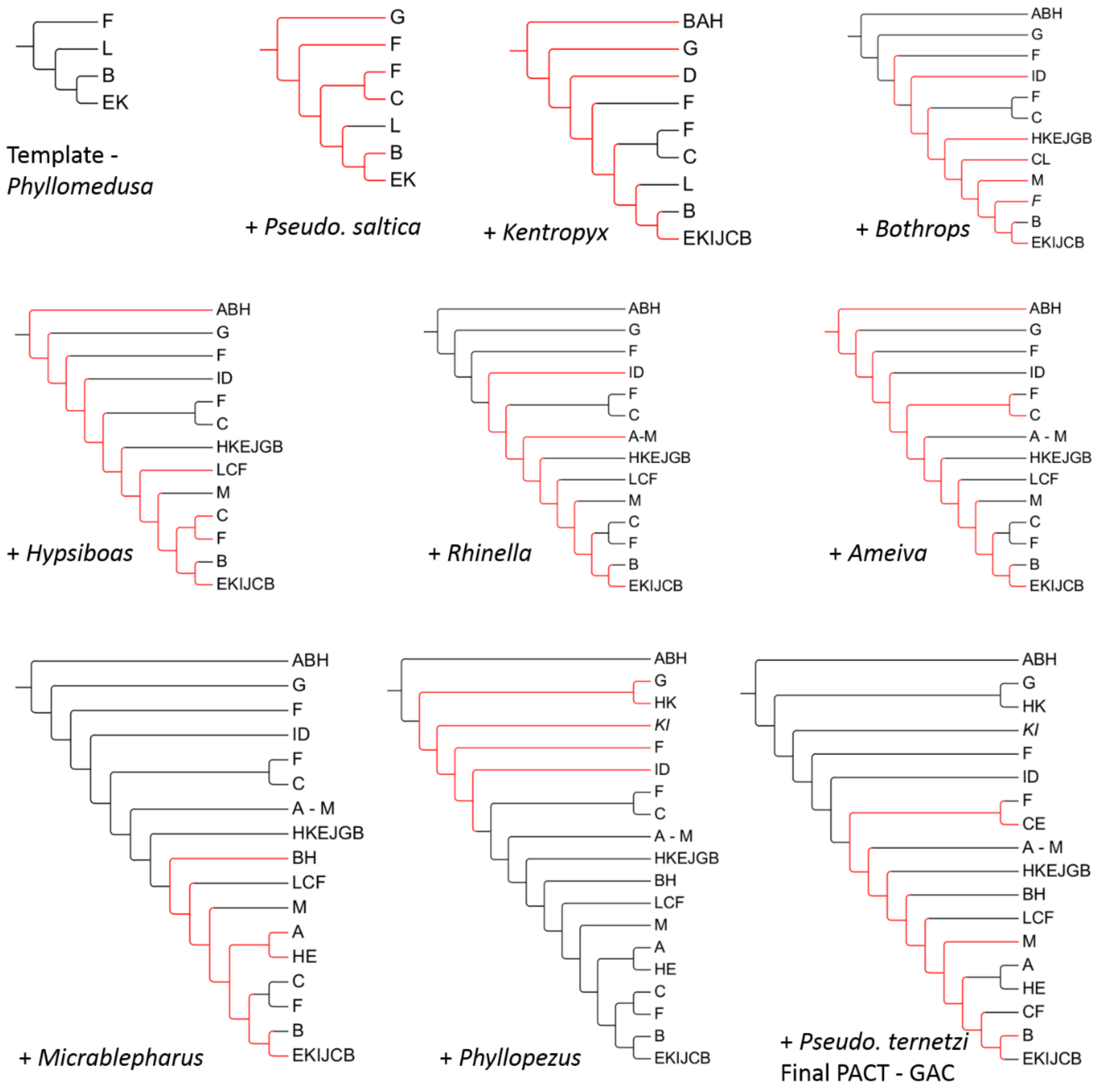


Figure 2 – Step-by-step generation of GAC using PACT algorithm. Biotic elements: A –Parecis Plateau, B – Guimarães Plateau, C – Paraná Plateau, D – Jalapão, E – Central Plateau, F – Espinhaço, G – Pantanal/Bodoquena, H – BE Tocantins–Araguaia basin, I –Serra Geral Plateau, J – Caiapônia Plateau, K – Veadeiros Plateau, L – Canastra, M – Huanchaca/Borda Plateau region.

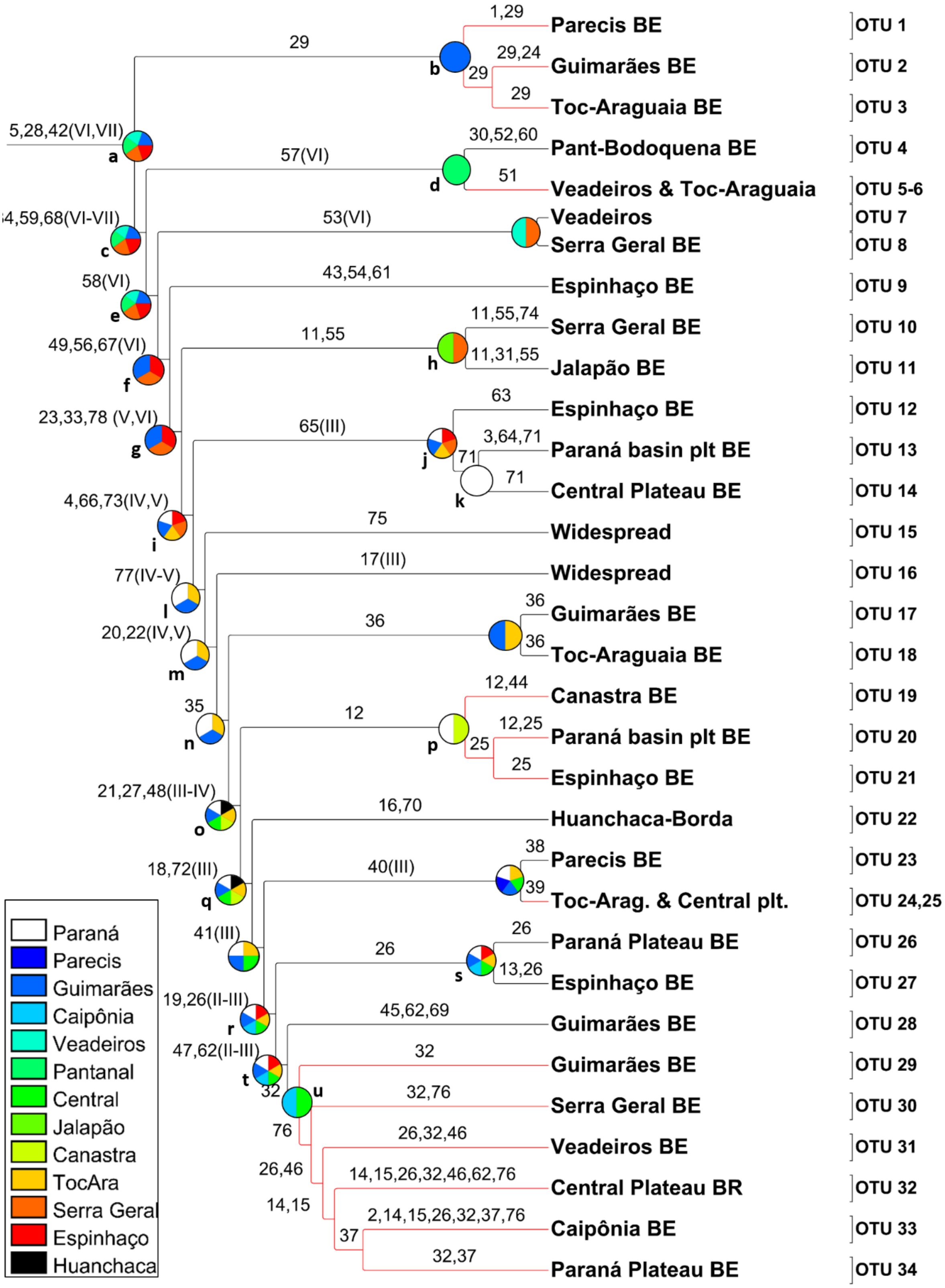


Figure 3 – Expanded General-area cladogram derived from PACT to show the number coding derived from each TAC and the inferred ancestral areas over the nodes inferred by Fitch parsimony algorithm. Major nodes from **a** to **u.** Roman numerals represents each Epoch: I – Late Pleistocene; II – Mid Pleistocene; III – Early Pleistocene; IV – Late Pliocene; V – Early Pliocene; VI – Late Miocene; VII Mid Miocene. Red line represented polytomy expanded to depict the number coding of each lineage.