



Biogeographic tools help to assess the effectiveness of protected areas for the conservation of anurans in the Mantiqueira mountain range, Southeastern Brazil

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ABSTRACT

Herein, we present the first comprehensive study of anurans biogeography and conservation in an important mountain chain of the Atlantic Forest bioregion (AF), the Mantiqueira Mountain Range (MMR). We use biotic element analyses to test biogeographical units previously established through a preliminary Parsimony Analysis of Endemicity based on the distribution of anuran species found on the MMR. Furthermore, we assess the actual status of species richness, endemism, weighted endemism, and discuss conservation strategies based on habitat loss, and protected areas (PA) representativeness for the Areas of Endemism and biotic elements (BEs) recovered. We found nine biogeographical units in MMR. **Biodiversity metrics identified small patches of high biodiversity throughout MMR, including five that match with the BEs.** All BEs recovered present a massive rate of habitat loss and four of them are poorly safeguarded in established protected areas. Our analysis enables linking the BEs of anurans to different areas topographically delimited along the MMR, probably due to the historical process related to climate shifts of the AF. We hypothesize that vicariant speciation should have been a strong driver of diversification in Anura. However, the current MMR protected area system is not safeguarding most of the areas of biogeographical relevance detected in our analyses. The results found here could be used to provide guidance to establish or review current protected areas delimitations, which demonstrate the inefficiency of the current PA system in safeguarding biodiversity. The *ad hoc* manner to establish protected areas is failing to preserve anuran biodiversity and therefore the evolutionary history of MMR. Although our results are focused solely on anurans, the biogeographical units found represent the biogeographic history of MMR and should be used as an objective and effective criteria to improve the conservation strategies and planning of protective areas.

1. Introduction

The search for species distribution patterns and their evolutionary origins is the main goal of biogeographic studies (Lomolino, Brown, & Sax, 2009; Morrone, 2009). At global and continental scales, general patterns of species distributions, species richness, endemism richness and rarity have been determined for some groups in recent studies on species diversity (Antonelli et al., 2018; Guedes et al., 2018; Holt et al., 2013; Jenkins, Alves, Uezu, & Vale, 2015; Moura, Villalobos, Costa, &

Garcia, 2016; Olson et al., 2001; Vilhena & Antonelli, 2015). On the other hand, biogeographical studies conducted in smaller geographic scales (e.g. mountain ranges, islands, watersheds or biomes) are not frequent and patterns of distribution at these scales are still poorly understood (Hoorn, Perrigo, & Antonelli, 2018).

The endemism of a taxon refers to its distribution being restricted to a recognized area (de Candolle, 1820; Morrone, 2014). Areas of endemism (AoE) gather recognized biogeographic homologies (Morrone & Crisci, 1995) and therefore are expected to represent isolated

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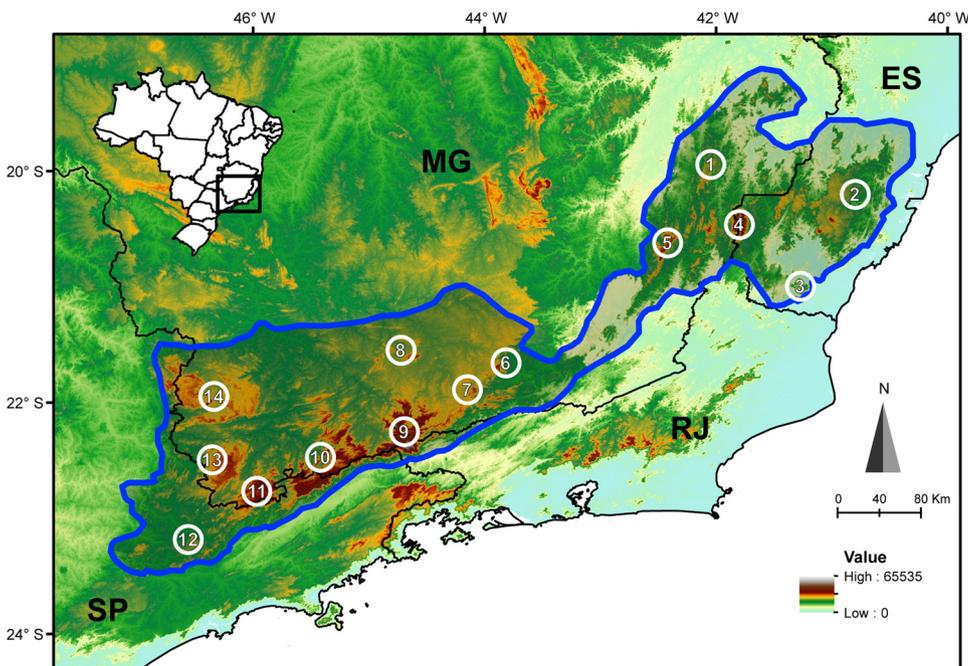


Fig. 1. Map showing the boundaries and main regions of the Mantiqueira mountain range: (1) Serras do Baixo Rio Doce, (2) Boa Vista Range, (3) Serra das Torres, (4) Caparaó Massif, (5) Brigadeiro Range, (6) Ibitipoca Range, (7) Rio Preto Range, (8) São José Range, (9) Itatiaia Plateau, (10) Campos do Jordão Plateau, (11) Monte Verde Plateau, (12) Japi Range, (13) Lindóia Plateau, and (14) Poços de Caldas Plateau. MMR = Mantiqueira mountain range; MG = Minas Gerais State; ES = Espírito Santo State; RJ = Rio de Janeiro State; SP = São Paulo State. The boundaries of the Brazilian states can be seen in the upper left corner. MMR limits are highlighted in blue borderline (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

biogeographical units. Geomorphological and climatic changes through time have shaped the distribution of the biota and can not be disregarded in the identification of biogeographical units (Crisci, 2001; Michaux, 2008). These units might be the result of vicariance events. The relationships between areas in which their endemic species originated from the same vicariance events reflect their history of speciation (Van Veller, Kornet, & Zandee, 2002). Thus, AoE identification can be used to establish, primarily, a hypothesis about the origin of endemism and potential priority areas for conservation. In a first step, analyses such as the Parsimony Analysis of Endemicity (PAE) become an alternative to explore this subject, providing hypotheses that should be tested in further analyses (DaSilva, Pinto-da-Rocha, & Souza, 2015).

A biogeographic model based on vicariance events assumes that an ancestral population split into other new population (speciation) after the formation of a barrier that limited or obviated the gene flow among ancestral populations (Hausdorf & Hennig, 2003). Nevertheless, vicariance events cannot be observed, at least in most cases, because they result from geological time and the past barrier might no longer exist (Hausdorf, 2002). Then, to identify areas which resulted from a vicariant event, two assumptions must be made: (i) the division of an ancestral biota produces groups of taxa significantly regionalized, thus creating natural biogeographical units; and, (ii) closely related species must be found within distinct biotic elements (Hausdorf & Hennig, 2003; Hausdorf, 2002). Therefore, range congruence in the distribution between at least two species bounded by a hypothetical barrier might be explained by an event of vicariance and referred as a biotic element (BEs). Biotic elements can be determined by the use of distribution data and are suitable for use as biogeographical units (Hausdorf, 2002).

The Atlantic Forest (AF) is known for hosting high levels of endemic species and threats, which has rendered it the status of a biodiversity hotspot (Mittermeier, Turner, Larsen, Brooks, & Gascon, 2011). The high rates of habitat loss and fragmentation in recent decades have led to the AF being reduced to only 11.4–16 % of its original coverage, diminished into disconnected and small fragments (Pompeu et al., 2018; Ribeiro, Metzger, Martensen, & Ponzoni, 2009). Furthermore, the ongoing scenario of protected areas (PA) in the AF is worrisome, since only 2.4 % of AF is under full protection, and the habitat loss is increasing steadily (Jenkins et al., 2015; Oliveira et al., 2017).

The evolutionary history of the origin and biota diversification are strongly indicated for consideration in the spatial definition of

conservation priorities (Moritz, 2002). However, most PA in the AF do not meet this biogeographical criteria, in part due to difficulty in identifying spatial surrogates to evolutionary processes and in part due to the political decisions in conservation prioritization (Carvalho, Brito, Crespo, & Possingham, 2011; Lemes, Melo, & Loyola, 2014; Rodrigues et al., 2004). By identifying biogeographical units as a result of vicariance events, the sequence of historical events that modeled the biogeographic distribution of species could be safeguarded into these areas (Cracraft, 1985). Further, it is worth mentioning that the analysis of the distribution patterns and evolution based on only one higher taxon may work for other groups, since vicariance usually operates along several taxa in a given area (Hausdorf, 2002).

The Mantiqueira Mountain Range (MMR), completely embedded in the AF, represents a complex of irregular mountain chains (Becker, Rodriguez, & Zamudio, 2013) and has been considered an anuran hotspot by Silva, Peixoto, Leite, Feio, & Garcia, 2018 and others (Jenkins et al., 2015; Moura et al., 2016; Vasconcelos, Silva, Santos, Prado, & Provete, 2019). MMR also harbors high rates of endemic anurans (Cruz & Feio, 2007; Silva, Peixoto, Leite, Feio, & Garcia, 2018) and species with restricted distribution ranges (Villalobos, Dobrovolski, Provete, & Gouveia, 2013). Some biogeographic studies have included MMR (DaSilva et al., 2015; Neves et al., 2018), but to date none of them focused on a detailed biogeographical analysis nor provided specific information to guide its creation and maintenance. Herein, we conducted the first comprehensive biogeographic study on MMR anurans, linking the achieved results with conservation purposes. Our goals are the following: (i) identifying biogeographic regions for conservation, using anuran distribution data and biogeographical analyses as backbone; (ii) analyzing the efficiency of the current system of protected areas for conservation of the MMR anuran biota; and (iii) drawing new insights regarding conservation in the MMR.

2. Material and methods

2.1. Study area

The Mantiqueira Mountain Range (Fig. 1) extends to c.a. of 800 km, covering part of the states of São Paulo, Rio de Janeiro, Minas Gerais and Espírito Santo in Southeastern Brazil (Cruz & Feio, 2007; Gatto et al., 1983; Silva, Peixoto, Leite, Feio, & Garcia, 2018). The highlands

are formed by hills with different altimetric ranges, which have different regional names (e.g. Campos do Jordão plateau, Poços de Caldas plateau, Brigadeiro range, Caparaó massif). In addition, the Pomba River, a tributary of the Paraíba do Sul River, divides the MMR into two regions: northern Mantiqueira; and, southern Mantiqueira (Silva, Peixoto, Leite, Feio, & Garcia, 2018). The altitude ranges from lowlands related with Doce and Pomba rivers c.a. 100 m a. s. l., to peaks such as Pico da Bandeira 2892 m a.s.l. and Pico das Agulhas Negras 2791 m a.s.l.. The MMR geology comprises a pre-Silurian gneiss and granite and a disjunct strata of different rock types (Benites, Schaefer, Simas, & Santos, 2007; Gatto et al., 1983). The typical climate is the humid subtropical, with dry winter and temperate summer (Cwb) (Alvares, Stappe, Sentelhas, & Gonçalves, 2013). Semideciduous forests are present in inner regions of the MMR, besides an ombrophilous forest in wetter areas, relicts of mixed humid forests at mid-to-high elevations, and the highland grasslands (called “campos de altitude”) at high altitudes (Silva, Peixoto, Leite, Feio, & Garcia, 2018; Vasconcelos, Santos, Rossa-Feres, & Haddad, 2011).

2.2. Data source

We gathered species distribution data by compiling anuran distribution records from the following Brazilian natural history collections: Coleção de Anfíbios do Museu de Ciências Naturais, Pontifícia Universidade Católica de Minas Gerais (MCNAM); Coleção Célio F. B. Haddad; Universidade Estadual Paulista “Júlio de Mesquita Filho” (CFBH); Coleção de Anfíbios, Universidade Federal de Juiz de Fora (CAUFJF); Coleção de Anfíbios, Centro de Coleções Taxonômicas, Universidade Federal de Minas Gerais (UFMG); Laboratório de Zoologia dos Vertebrados, Universidade Federal de Ouro Preto (LZV); Museu de Biologia Prof. Mello Leitão, Instituto Nacional da Mata Atlântica (MBML); Museu Nacional, Universidade Federal do Rio de Janeiro (MNRJ); Museu de Zoologia, Universidade de São Paulo (MZUSP); Museu de Zoologia João Moojen, Universidade Federal de Viçosa (MZUFV); and Museu de Zoologia Prof. “Adão José Cardoso”, Universidade Estadual de Campinas (ZUEC). We also increased our database by including distribution data from literature (Almeida, Gasparini, & Peloso, 2011; Mângia, Santana, Cruz, & Feio, 2014; Moura, Motta, Fernandes, & Feio, 2012; Peixoto et al., 2013; Pimenta, Cruz, & Caramaschi, 2014). We provide a list of all species of amphibians from the MMR in Appendix A.1. We followed the systematics and nomenclature of Duellman, Marion, and Hedges (2016) and Frost (2018).

Georeference coordinates of each species were computed using Google Earth after carefully surveying the collection vouchers and/or bibliography and, whenever possible, contacting the collectors for confirmation. We used the centroids of the municipalities and protected areas, when precise locality data were not available. We conducted analyses based on two datasets, one containing all anuran species recorded in the MMR (Complete Dataset, CD) and the other presenting a subset having only highly associated species to the MMR (Endemic Dataset, ED). We considered as highly associated species those in which the records were coincident with the limits of the MMR, i.e. those species with at least 80 % of its distribution matching the MMR limits (Guedes, Sawaya, & Nogueira, 2014; Nogueira, Ribeiro, Costa, & Colli, 2011). The datasets were built from 0.5×0.5 degrees grid cells superimposed onto the MMR limits. The matrices with binary characters (presence and absence) were prepared using SpeciesGeoCodeR (Töpel et al., 2016). The CD was distributed along 54 grid cells, while ED was found in 28 grid cells.

2.3. Analyses

We performed five analyses: (i) PAE (Rosen & Smith, 1988; Rosen, 1988) was performed in order to rise a hypothesis of Areas of Endemism (AoE) using CD; (ii) we tested the first prediction of the vicariance model and identified BEs in the MMR based on anuran distribution data

(i.e., same binary matrix used in PAE, including both CD and ED) - then, we tested if the second prediction of the vicariance model of speciation could explain the BEs we had found; (iii) we analysed the distribution pattern of species richness of anurans for both CD and ED; (iv) we identified the weight of highly associated species throughout the MMR; and, (v) finally, for each biotic element found, we calculated the amount of habitat loss and protection. Spatial analyses were performed using software XTools Pro, an extension of ArcMap 10.1 (ESRI, 1999). For the sake of standardization, all the analyses, were conducted in SAD 69 datum, and the spatial analyses, in South American Alberts Equal Area Conic projection. For all statistical analyses, we adopted the significance level of $\alpha = 0.05$.

2.3.1. Parsimony analysis of endemism (PAE)

We used the $0.5^\circ \times 0.5^\circ$ grid cells superimposed in MMR limits (Appendix A) to run PAE in order to identify higher level of endemism from species distribution data. Fifty four grids showed congruence of at least two species in each grid, a methodological criteria required to establish operational biogeographic units for the analysis (see DaSilva et al., 2015; Morrone, 1994; Platnick, 1991) (details below).

PAE consists of a parsimony search on a matrix whose localities (areas) are considered terminal taxa. The presence/absence of species in these areas is coded as binary characters (Morrone, 1994; Rosen & Smith, 1988; Rosen, 1988). The method follows the assumption zero, i.e., considering vicariance as a first-order explanation (Van Veller et al., 2002; Zandee & Roos, 1987) and assuming shared occurrences of species among areas as evidence of common history (Rosen, 1988; Rosen and Smith, 1988). Despite all criticism of the application and limits of PAE (Nihei, 2006), it is still useful to identify potential areas of endemism, especially from grid cells (Morrone, 2014). The results of PAE are expressed as area cladograms where the monophyletic groups found represent areas of endemism.

We produced a matrix containing 54 grid cells and 226 anuran records from MMR. We edited the CD matrix using Mesquite version 3.10 (Maddison & Maddison, 2018) and then analyzed it in TNT version 1.5 (Goloboff & Catalano, 2016; Goloboff, Farris, & Nixon, 2008) using a hypothetical ancestor area as outgroup to root the most parsimonious trees found (matrix available in Appendix B.2). Given the number of terminals, we performed a search for most parsimonious trees (area cladograms) via traditional heuristic algorithms. We obtained the starting trees via Wagner searches with random start seed of terminals, followed by Tree Bisection and Reconnection branch swap. We ran 500 replicas, saving 200 trees of each replica and up to 24,000 trees during the tree search replicas. Other search strategies were employed including the use of new technology algorithms (Goloboff, 1999; Nixon, 1999) and changing search parameters (see supplementary material of Romano, Gallo, Ramos, & Antonioli, 2014 for details). We calculated Bremer support (Bremer, 1994) for the clades found in most parsimonious strict consensus tree using “bremer” script. Consistency (CI) and Retention (RI) indexes were computed using “stats” script.

2.3.2. Biotic element analysis (BE)

The first vicariance model was tested for MMR anurans using biotic element analysis (Hausdorf & Hennig, 2003; Hausdorf, 2002). Thus, the BE will comprise groups of taxa in which the distributions are significantly more similar to one another than to those taxa from a different group. In order to test the prediction of the vicariance model, three specifications must be made: (i) setting a distance measure between the distribution limits of the examined taxa, (ii) assigning the null model to generate distribution range groups; and, (iii) performing a statistical test to verify the validity of the model (Hausdorf & Hennig, 2003). We chose *geco* coefficient because it considers the geographical relationships among the occupied units, the grid cells (Hausdorf & Hennig, 2006). For the required *geco* tuning constant, we use $f = 0.2$. This value is indicated when the grid resolution is coarse in relation to the species presence (Hausdorf & Hennig, 2006). Thus, we follow the

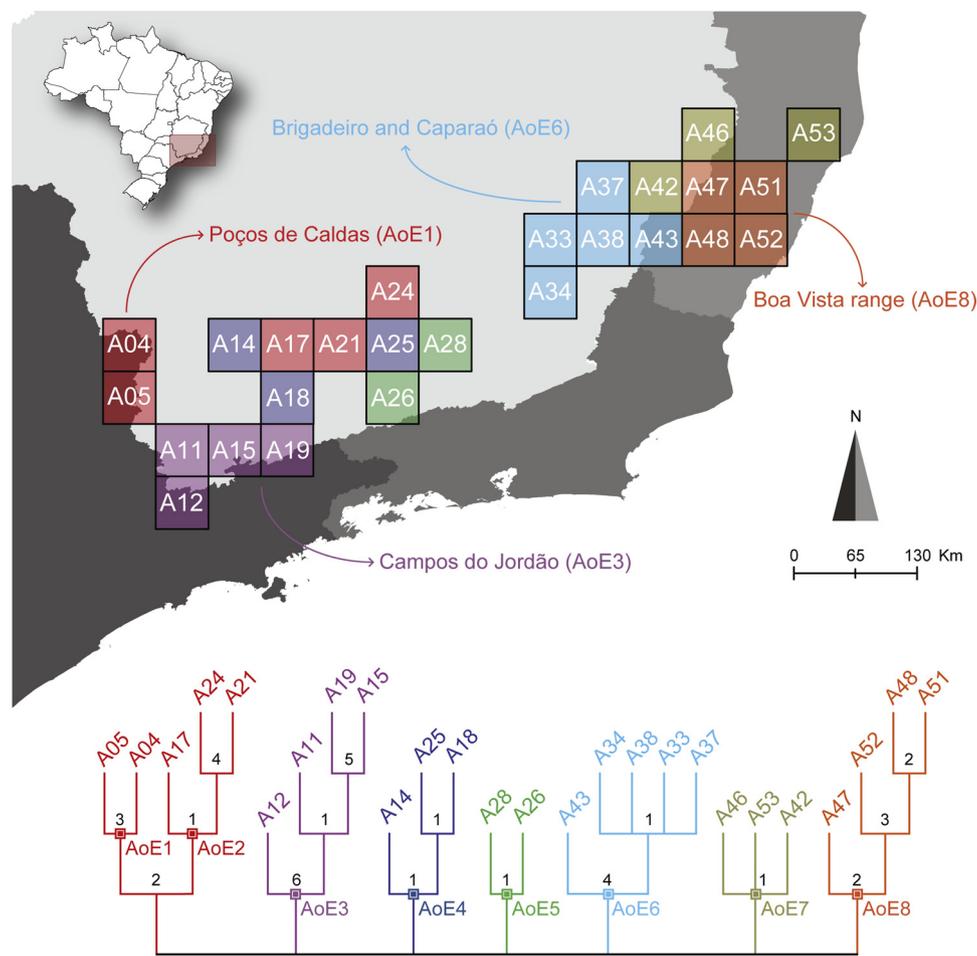


Fig. 2. Results of Parsimony Analysis of Endemicity (PAE). Map showing 26 out of the 54 quadrants used as terminals in PAE (above) and strict consensus area cladogram resulted from the search for most parsimonious trees (below). The most relevant Areas of Endemism (AoE) interpreted as priority for conservation and discussed in the text are highlighted in the map. The eight AoE found are shown in area cladogram. The numbers above the nodes (in black) are Bremer supports for each clade. See text for further details and Appendix A for the complete topology including all quadrants used as terminals to perform the PAE.

authors that tested a range of values and indicated the choice of higher ($f = 0.2$) best fitted to our case. The input file was based on the construction of binary matrices resulting from species records (CD and ED). The biotic element analysis was implemented in *Prabclus* package (Hausdorf & Hennig, 2003), available in R (R Core Team, 2019).

Following the first model of vicariance, we found anurans from MMR that belonged to different groups of species with significantly regionalized ranges. Then, we proceeded with the analyses in which the BE were estimated using the model-based Gaussian clustering (MBGC) as implemented in the R package *MClust* (Fraley & Raftery, 1998). We plotted clusters of species in nonmetric multidimensional scaling (NMDS 1 and 2) (Legendre & Legendre, 2012) on the *geco* matrix, using Kruskal algorithm. As suggested by literature (Hausdorf & Hennig, 2003), we used the constant k equal to the number of species/40, rounded up to the next integer (six for the complete dataset and two for the endemic dataset). The clusters were then identified as BE to the CD and endemic biotic element (EE) to the ED. Thus, we performed the Chi-square test on both datasets to investigate the distribution of congeneric species among biotic elements.

2.3.3. Species richness and georeferenced weighted endemism analyses

We analyzed the species richness of the MMR anuran species region using SpeciesGeoCodeR, for both datasets CD and ED. The MMR anuran richness pattern was explored by combining 0.1×0.1 grids with pointy-locality occurrence data from multiple species, which allows determining which species occur in each polygon and, then, computing

a summary about species distribution and diversity (Töpel et al., 2016).

We mapped the weighted endemism, i.e. species richness weighted by restriction in extent of occurrence, by applying the georeferenced implementation of weighted endemism proposed by Guerin, Ruokolainen, and Lowe (2015) to individual records from the CD. First, we calculated the endemism weighted and created maps to represent the MMR endemism, using the distance spanning species occurrences as weights. Then, we tested the significance deviance under a null expectation model, using $nreps = 1000$ to determine the expected null distribution of endemism for each observed value of species richness.

2.3.4. Habitat loss and protection of biotic elements

We tested if the biotic elements are protected by comparing the rates of habitat loss of the species that form each biotic element. First, we estimated the distributional areas for each species by plotting the minimum convex polygon (MCP) of all endemic and non-endemic species with three or more records (Guedes et al., 2014; IUCN, 2013). The distribution areas of species with a single record, or two disjoint localities, were considered by 10 km radius buffers around the point (same protocol used by Guedes et al., 2014; IUCN, 2013; Silva, Peixoto, Leite, Feio, & Garcia, 2018).

We calculated the potential habitat loss for each species based on the overlap of species minimum convex polygons and official data on deforestation in Brazil up to 2008 (MMA, 2008), which is the current information available. Also, the coverages of PA for each species in BE were calculated by overlapping the minimum convex polygons and the

strictly protected areas, equivalent to IUCN categories I–III (Dudley, 2008), of the Brazilian protected areas currently in operation (WWF, 2013). To verify the occurrence of statistical differences among the species forming each biotic element, we compared the rates of habitat loss for the species within each BE, using the Kolmogorov–Smirnov test (Crawley, 2007). The expected habitat loss for a given species was calculated as the product of its distribution area and the average percentage of habitat loss of all species within its biotic element (Guedes et al., 2014).

We used the logit transformation calculated in the R package *car* (R Core Team, 2019) for observed and expected habitat loss values, since they correspond to proportions of the distribution area of species (Warton & Hui, 2011). The logit-transformed proportion of species protection and habitat loss among BE was compared using a Kruskal–Wallis test (Hollander & Wolfe, 1973) and multiple comparison tests (Siegel & Castellan, 1988) were implemented in the R package *pgirmess* (R Core Team, 2019).

3. Results

We obtained 16,069 records (4319 were individual records/unique localities for 226 species, Appendix A), from 15 families, in the MMR. Eighty-three species out of the total (36 %), from nine families were considered highly associated to the MMR.

3.1. Parsimony analysis of endemism

We obtained 124 most parsimonious trees with 771 steps, CI = 0.293 and RI = 0.559 (Appendix A). Twenty-six quadrants clustered in eight AoE (Fig. 2). These AoE represent some continuous quadrants in regions such as Poços de Caldas plateau (AoE1) and Campos do Jordão plateau (AoE3), and some areas that represent more than one unit, such as Brigadeiro range/Caparaó massif (AoE6). In addition, some areas were represented by quadrants spatially disjointed, such as AoE5 and AoE8. Some recognized AoE presents high Bremer support and therefore are likely to represent isolated biogeographic units of importance for conservation: Poços de Caldas plateau (AoE1, Bremer = 3, eight highly associated species); Campos do Jordão plateau (AoE3, Bremer = 6, four highly associated species); Brigadeiro range/Caparaó massif (AoE6, Bremer = 4, three highly associated species); and, Boa Vista range (AoE8, Bremer = 2, one highly associated species). Moreover, 18 species are unique to the AoE1, AoE3, AoE6 and AoE8 (7.96 %) and 23 occur along the eight AoE found in PAE analysis (10.17 %).

3.2. Biotic elements

Our results for both CD and ED datasets, met the first prediction of the vicariance model showing the occurrence of distinguishable localized biotas across the MMR. For CD, the T statistic was 0.266 and smaller (p -value < 0.001) than expected by chance (for 1,000 artificial populations, T ranged between 0.272 and 0.338, mean = 0.310). For ED, the T statistic was 0.306 and smaller (p -value < 0.001) than expected by chance (for 1,000 artificial populations, T varied between 0.309 and 0.387, mean = 0.345).

In the analysis using the CD, 173 species (76 %) contributed to the detection of two biotic elements (Fig. 3A), whereas 53 species (24 %) were included in the noise component (Appendix A). The biotic element one (BE 1) is formed by 105 species distributed throughout the area of the MMR BE 2 is formed by 18 species distributed in the southern portion of the MMR, with disjoint distribution in Poços de Caldas plateau (occupying two grid cells), Itatiaia plateau (one grid cell) and Ibitipoca range (one grid cell) (Fig. 3B).

More detailed information about regionalization was obtained based on the analysis with the endemic dataset, which detected seven endemic elements (EE; Fig. 3C–F) based on the range of 29 species of anurans (35 % of the total), whereas 65 % of them (54 species) are

associated to the noise component (Appendix A). Endemic element one (EE1) is formed by seven species and was located in Itatiaia and Campos do Jordão plateaus (Fig. 3C). EE2 is formed by six species in the Boa Vista range. EE3 and EE4 are formed by three endemic species each and corresponded to the Itatiaia plateau and the Caparaó massif, respectively (Fig. 3D). EE5 and EE6 are formed by three species distributed in Boa Vista range and Campos do Jordão /Itatiaia plateaus (Fig. 3E). Finally, EE7 is formed by three species and was placed in Poços de Caldas plateau (two grid cells) and in the low region in central MMR (two disjoint grid cells) (Fig. 3F).

The second prediction of the vicariance model found congeneric species distributed in distinct biotic elements for both BE and EE (BE: Chi-square = 62.612, p -value = 0.08239; EE: Chi-square = 104.78, p -value = 0.5215).

3.3. Species richness, endemism richness and weighted endemism

Anuran species richness is not uniformly distributed throughout the MMR (Fig. 4A), but is higher in regions of high altitudes. The Boa Vista range showed higher richness, specifically in Santa Teresa region in the north of Boa Vista region. High richness were also observed in Brigadeiro range/Caparaó massif, Itatiaia plateau, Poços de Caldas plateau and the lower region in the depression between the southern and northern MMR. In agreement with these results, endemism richness was high in Santa Teresa region and Itatiaia plateau (Fig. 4B). Furthermore, five regions were well weighted in the richness parameter: Santa Teresa region, Caparaó massif/Brigadeiro range, Itatiaia plateau, Campos do Jordão plateau, and Poços de Caldas plateau (Fig. 4C).

3.4. Habitat loss and protection of biotic elements

Habitat loss for nine BEs shows an average of 72.5 % and ranged from 32.5 % in EE3 to 92.5 % in BE1 (Fig. 5A and Appendix B). No significant differences were detected between the observed and expected habitat loss for species within each biotic element (Appendix A). Moreover, habitat loss was significantly different among different biotic elements and endemic biotic elements (Kruskal–Wallis test: chi-squared = 55.75, p -value < 0.001).

All EEs show an average protection of 28 % (Fig. 5B and Appendix B). Poços de Caldas plateau presents only a narrow PA, and BE1 also presented low rates of protection. Moreover, other six BEs showed rates below 50 %, and only one of them (EE4) presented rates above 75 % of protection. The sizes of protected area within the range of each species were significantly different among endemic biotic elements (Kruskal–Wallis test: chi-squared = 52.42, p -value < 0.0001).

4. Discussion

We retrieved nine BEs based on the distribution pattern of anurans in the MMR. Some of these BEs are compatible with the AoE found: EE1, EE3 and EE5 with AoE3; EE2 with AoE7; EE4 with AoE6; and, EE6 with AoE8. Besides, the distribution of biodiversity metrics, with endemism, richness and weighted richness in areas topographically isolated, revealed a strong correlation among these patterns, corroborating the singularity of these areas into AF (Brooks et al., 2006). The habitat loss calculated for the biogeographic units found revealed high probability that several species will be threatened soon since the current protected area system is ineffective. For example, they do not encompass the biogeographic units revealed by the anuran species studied here, which demonstrates that most BEs are currently unprotected.

Previous studies, using other taxa as models to determinate patterns of distribution in AF, concluded that species distribution is not homogeneous (Amorim & Pires, 1996; DaSilva et al., 2015; Silva, Peixoto, Leite, Feio, & Garcia, 2018; Silva, Sousa, & Castelletti, 2004). We found similar results among anuran distribution, with clusters of species at regions with high elevations, such as Caparaó plateau, Brigadeiro

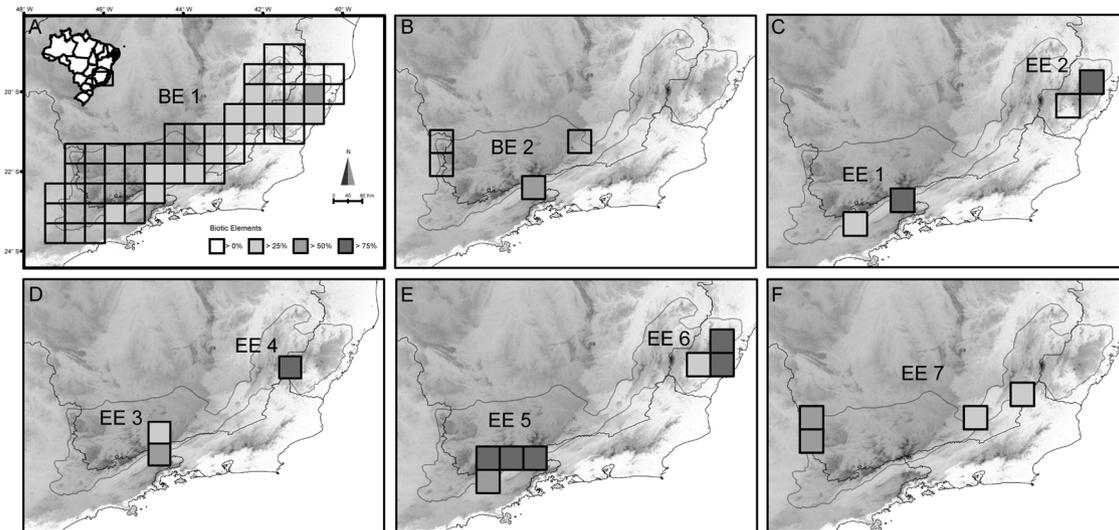


Fig. 3. Distribution of biotic elements (A and B) and endemic elements (C–F) recovered according to the range of 226 and 83 Mantiqueira anuran species (complete and endemic dataset, respectively).

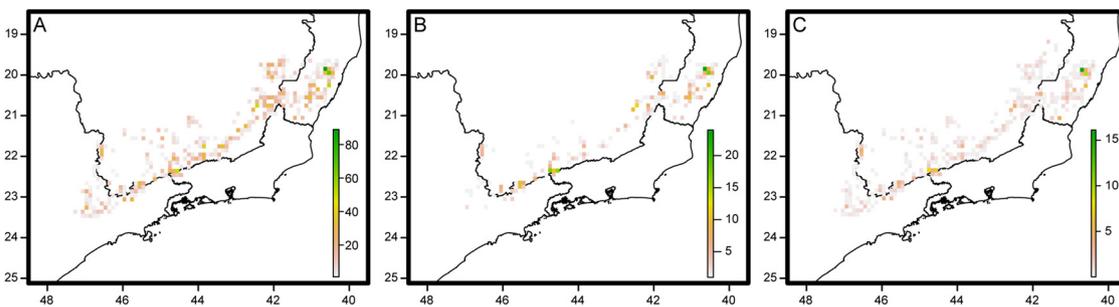


Fig. 4. Graphic representation of the results of biodiversity metrics from anuran in the Mantiqueira range. The grids for these analyses are $0.1 \times 0.1^\circ$ resolution. (A) distribution of species richness of all anurans from the MMR; (B) distribution of endemism richness of the endemic species anurans from the MMR; (C) weighted endemism of anuran species (endemism for sampling effort in each grid).

range, Boa Vista range, Campos do Jordão plateau and Itatiaia plateau.

Despite all criticism of the application and limitation of PAE (Nihei, 2006), we have confirmed its usefulness to identify potential AoE, from grid cells (accordingly with Morrone, 2014) and in restricted regions. The AoE found via PAE were consistent with BEs, which demonstrates their efficiency as a preliminary approach to establish biogeographic units that guide further analyses (DaSilva et al., 2015).

Stable areas in highly changeable environments could have allowed the rise of different phylogenetic lineages through time, leading to singular areas in history and composition, as corroborated by molecular studies based on anuran species (Brown et al., 2018; Menezes et al., 2016; Tonini, Costa, & Carnaval, 2013). Alternatively, the topography of mountain ranges in Southeastern Brazil is expected to favor genetic

diversification of anurans, breaking the AF up into small patches that promote speciation by geographic isolation through time (Haddad & Prado, 2005; Vasconcelos, Prado, Silva, & Haddad, 2014). Both – historical climate dynamics and topographical complexity – create barriers that shaped ancestral areas, and, therefore, could indicate patterns of anuran distributions determinate by vicariant speciation in the MMR.

Moreover, the patterns found for anurans in this study could be similar with other groups of species, such as those with small range of distribution and even with poor dispersal capabilities (Lester, Ruttenberg, Gaines, & Kinlan, 2007). Thus, we hypothesize that vicariant speciation should be a strong driver of diversification in Anura. To our knowledge, there is no clear pattern of anuran distribution identified in areas within AF with similar relief, such as Serra do Mar and

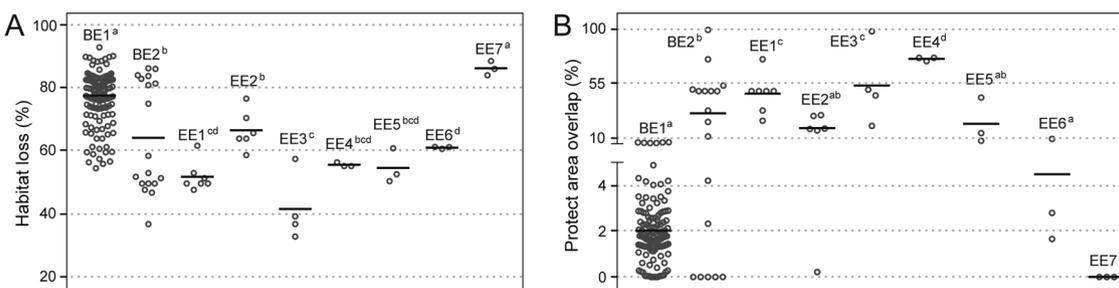


Fig. 5. (A) Percentage of habitat loss of species per biotic elements (BE1 and BE2) and endemic biotic elements (EE1–EE7). Horizontal bars = median. (B) Percentage of protected area overlap with species in each biotic elements (BE1 and BE2) and endemic biotic elements (EE1–EE7). Horizontal bars = median. Common letters indicate significant differences.

Espinhaço mountain range. However, we supposed that coherent distribution patterns can be identified in those areas.

Our analysis enables us to link the BE of anurans to different areas delimited topographically along the MMR, probably due to the historical process related to the AF climate shifts. During the Pleistocene, the climate fluctuation shaped refuges (i.e., nearly unchanged areas) along AF (Rull, 2009). All BEs found comprise areas with sheltered topography. These BEs therefore could be interpreted as areas of vicariant speciation (biotic refuges), which remained stable throughout the Quaternary climatic shifts (Carnaval & Moritz, 2008; Carnaval et al., 2014; Rull, 2009).

Boa Vista range, Itatiaia plateau, Caparaó massif, and Poços de Caldas plateau were those small patches singulars, which present high levels of species richness, endemism richness and weighted endemism. Therefore, the biodiversity observed in these areas can be consistently interpreted as a result of the vicariance process. In addition, some BEs (EE 1, EE 2, EE 5, EE 6, and EE 7) superimposed Brazilian government the priority areas for biodiversity conservation (MMA, 2016). They also match areas classified as high priority for the conservation of vertebrates (Oliveira et al., 2019), and areas recognized as biologically important for anuran conservation in South America (Vasconcelos et al., 2019), revealing the importance of these areas for the maintenance of biodiversity. These results reinforce the importance of the BEs found in MMR for the conservation of anurans.

The current MMR protected area system is not safeguarding most of the areas of biogeographical relevance detected in our analyses. As aforementioned, the BEs indicate biogeographic processes, representing concentrations of range-restricted species in target areas. As expected, once the MMR is fully within the AF domain, one of the most endangered hotspots in the world (Mittermeier et al., 2011), the rate of habitat loss in the BEs is high. Nevertheless, the forest cover in the MMR was higher than the observed average for the AF (72.5 % versus 84–89 %; Ribeiro et al., 2009). However, the higher forest coverage seen in MMR is probably a bias due to the high elevation and rugged topography of the MMR, which hinders anthropic influence (Ribeiro et al., 2009). The estimates of habitat loss in BE1 were inferior to the average found in the AF. However, only 17.5 % of the original forest coverage remnants of the MMR fall into an existent PA (Pompeu et al., 2018). If only the BEs coverage areas are considered, only 28 % of it is superimposed into the established PA. Thus, it seems urgent to create new PAs and increase the monitoring of the existing PA in order to properly protect their biodiversity.

The results found here could be used to provide guidance to establish or review current PA delimitations. For instance, in the northern portion of the MMR the BEs presented low rates of protection. The Boa Vista range (AoE 8, EE 2, EE 8) comprise areas with large remnants of forest (Morellato & Haddad, 2000). Then, efforts to protect these areas would be valuable as they would preserve portions with original remnants of AF. Besides, the protected area located in Poços de Caldas plateau (AoE1 and EE7) needs to be revised. Only a small portion of EE7 is effectively protected. Moreover, this plateau is greatly impacted by bauxite mining and eucalyptus planting. For that reason Barros et al. (2012) considered that the biodiversity of this biogeographic unit is at risk. However, this region is heavily populated, with only small AF fragments preserved, which precludes the creation of a large PA in Poços de Caldas plateau (Barata, Castro, & Martins-Loução, 2017). Thus, our results reinforce the need for the creation of other small PAs, similar to the privative ones (Reserva Particular do Patrimônio Natural, RPPN). Connectivity among those fragments is recommended for the maintenance of this singular area (Barata et al., 2017).

Other biogeographic units were recovered in the southern region of the MMR, in Campos do Jordão plateau (AoE3 and EE5), while the Itatiaia plateau (BE2, EE1, EE3, and EE5) lacks effective protection. Although suggested (Instituto Oikos de Agroecologia, 2009), the implementation of a PA in this region had not been carried out until now (Pompeu et al., 2018). This PA covering more than 87.000 ha would

constitute an important corridor in this region (Becker et al., 2013). A large and representative PA in an area threatened by high rate of habitat loss is extremely important.

Only one protected area completely overlapped a biogeographic unit found in the Caparaó massif (EE4). This area possesses three endemic anuran species and can be biogeographically connected to Brigadeiro range, according to the results found on PAE (AoE6) and should be considered as a priority for conservation. On the other hand, as aforementioned, most biogeographic units found are not satisfactorily included in the current protected areas, which demonstrates the inefficiency of the current PA system in safeguarding biodiversity, considering our results using anuran species distribution pattern as a biogeographic model. Surely, the *ad hoc* manner to establish protected areas (Pressey, 1994; Rodrigues et al., 2004) is failing to preserve anuran biodiversity and therefore the evolutionary history of MMR. The biogeographical analyses conducted here and their application to solve biodiversity conservation problems are the main goals of conservation biogeography (Whittaker et al., 2005). Therefore, our study is a first step to guarantee the conservation of species found in MMR.

5. Conclusions

The combined use of biogeographical methods (PAE and BE) and biodiversity metrics (richness, habitat loss, PA overlap) proved to be effective to find singular priority areas for anuran conservation in the MMR. The result of both, biogeographic methods and biodiversity metrics, recovered high levels of species richness and endemism associated to the evolutionary history of anuran diversification (speciation) driven by vicariance. These highly diverse biogeographic units represent important areas, but remain unprotected. Four of these areas in the MMR – Poços de Caldas plateau, Campos do Jordão plateau, Itatiaia plateau, and Boa Vista range – have become a priority for an effective conservation biogeography strategy. However, today, such areas are poorly safeguarded by established areas of preservation (national parks, environmental reserves, RPPNs, etc.). Therefore, a revision of current MMR protected areas is an urgent need. Further prospects on MMR amphibian conservation and biodiversity study should focus on the areas we identified as major conservation priorities. We predict that further biogeographic studies, including other groups of animals or plants, will refine our finding and/or identify new areas of biogeographical relevance in MMR. We expect that the increasing use of approaches similar to that applied here may increase the knowledge about conservation biogeography, so as to guide the creation of effective new policies for biodiversity conservation.

Declaration of Competing Interest

The authors declare that they have no conflict of interest.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.jnc.2020.125799>.

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