ORIGINAL ARTICLE

Biogeography, vicariance and conservation of snakes of the neglected and endangered Caatinga region, north-eastern Brazil

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ABSTRACT

Aim Our aims were to test the predictions of the vicariance model, searching for natural, non-random biogeographical units using data on snake distributions, and to assess the conservation of biogeographical patterns and underlying processes in the poorly studied Caatinga region.

Location Caatinga region, north-eastern Brazil.

Methods We revised and georeferenced 7352 snake occurrence records at point localities, by direct examination of voucher specimens in zoological collections and revision of literature data. We tested two predictions of the vicariance model via biotic element analysis using two datasets (all taxa and endemics) mapped onto a 1° × 1° square grid across the Caatinga. Finally, we examined the overlap between recovered biogeographical units and spatial patterns of habitat loss and protected area coverage.

Results We recorded 112 snake species from the Caatinga, of which 22 (20%) are endemics. The predictions of the vicariance model were corroborated by the detection of groups of species with significantly clustered ranges (biotic elements). The analysis with the full dataset detected eight biotic elements, and three endemic biotic elements were found when only using endemics. The three endemic biotic elements correspond to core areas of biotic elements detected with the larger dataset. The average habitat loss for species forming biotic elements was 46%, and was similar among biotic elements. Protected area coverage is different for species from different biotic elements, and most species' ranges are very poorly represented in protected areas.

Main conclusions The Caatinga harbours a peculiar snake fauna with significantly clustered species ranges concordant with the predictions of the vicariance model. Our results, representing the first formal test of vicariance patterns in the Caatinga, detected poor overlap between biotic elements and protected areas, indicating that biogeographical patterns and processes are largely unprotected in this imperilled and neglected Neotropical region.

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INTRODUCTION

A critical step for biogeography is to define and delineate basic distribution patterns, which provide the basis for hypotheses on the evolution of biodiversity (Carvalho, 2010).

Moreover, knowledge of patterns of regionalization promotes the understanding and conservation of diversification processes (Cracraft, 1994; Carvalho *et al.*, 2011). Natural biogeographical units are the most valuable source of information on which spatial portions of biodiversity should be conserved

(Crisci, 2000; Whittaker *et al.*, 2005). Among the criteria for the detection of areas of high biodiversity value, patterns of endemism are of central relevance and correspond to a core issue in biogeographical science (Pullin, 2002).

The clustering of distribution areas is one of the most prominent biogeographical patterns, and one general testable mechanism that might cause this pattern is vicariance (Hausdorf & Hennig, 2006). The vicariance model (Croizat *et al.*, 1974; Rosen, 1978; Nelson & Platnick, 1981) postulates that diversification is the result of fragmentation of ancestral biotas caused by emerging barriers. Although the concept of vicariant speciation is clear and well defined, the detection and delimitation of areas of endemism is often problematic (Harold & Mooi, 1994; Szumik *et al.*, 2012). The dispersal of species across barriers over time often results in sympatry of species that originated in different areas of endemism (Anderson, 1994). Additionally, the size and the different configurations of ancestral ranges before the vicariance event can also confuse the patterns of species segregation between areas of endemism (Cracraft, 1994). Under these conditions of imperfect allopatry, biogeographical units are usually complex and distribution data alone are often unable to define areas of endemism (Hausdorf, 2002). Biotic element analysis therefore emerged as an alternative method for detecting biogeographical units (Hausdorf & Hennig, 2003, 2006).

One of the corollaries of vicariance is that the ranges of taxa that have originated in the same area will be more similar to one another than to the ranges of taxa that have originated in other areas. Thus, the vicariance model predicts a significant clustering of species' ranges, and these clustered ranges define a biotic element, a group of taxa whose ranges are more similar to one another than to those of other such groups (Hausdorf, 2002; Hausdorf & Hennig, 2003, 2006). Biotic element analysis tests patterns of vicariance without requiring strict allopatry, and is based on the assumption that, under a vicariant scenario, groups of significantly clustered and non-random species ranges should be detectable (Hausdorf, 2002). As in other methods that aim to delimit fundamental biogeographical units (e.g. Morrone, 1994; Morrone & Marques, 2001), the baseline data for biotic element analysis are raw species occurrences along an arbitrary square grid, and not previously defined biogeographical subdivisions (Hausdorf & Hennig, 2006).

Biogeographical studies in open Neotropical landscapes (e.g. Prado & Gibbs, 1993; de Queiroz, 2006; Nogueira *et al.*, 2011; Camardelli & Napoli, 2012) are far less abundant than in forested areas (e.g. Müller, 1973; Prance, 1982; Silva & Sites, 1995; Amorim & Pires, 1996; Haffer, 1997; Costa *et al.*, 2000; Carnaval, 2002; da Silva *et al.*, 2004). Although similarities have been detected among South American open areas, including the Caatinga, Cerrado and Chaco (see Prado, 2000; Velloso *et al.*, 2002), the Caatinga is recognized as a unique floristic province and has been treated as a biogeographical unit in most previous studies (Prado & Gibbs, 1993; Pennington *et al.*, 2000; Prado, 2000; de Queiroz, 2006; Cardoso & de Queiroz, 2010).

There have been few biogeographical analyses based on raw distribution data in the Caatinga but previous work has shown that the flora (de Queiroz, 2006) and fauna (de Carvalho *et al.*, 2013) of the Caatinga have complex histories, and seem to be formed by elements of different origins (Gregorin *et al.*, 2008; Guedes, 2012). Studies on distribution patterns in Neotropical open areas are required as a fundamental step towards understanding the history and evolution of Neotropical biotas. Distribution data on snakes or amphibians have been considered insufficient to define biogeographical patterns in the Caatinga (Rodrigues, 2003). Data on lizards indicate that endemism is associated with sandy soils, highlighting priority areas for conservation in the Caatinga (see Rodrigues, 1986, 1991a,b,c, 2003, 2004).

The aims of our study were: (1) to define natural biogeographical units in the Caatinga region by identifying non-random clusters of codistributed snake species (biotic elements); (2) to provide the first test of the predictions of the vicariance model in the Caatinga; and (3) to assess the conservation of biogeographical patterns and processes by contrasting regionalized species distributions with habitat loss and protected area cover.

MATERIALS AND METHODS

Study area

The Caatinga is considered a unique natural biogeographical region (Müller, 1973; Ab'Sáber, 1974, 2003; Kinzey, 1982; Cracraft, 1985; Mares *et al.*, 1985; Prado & Gibbs, 1993; Pennington *et al.*, 2000; Prado, 2000, 2003; Cardoso & de Queiroz, 2010). Its distribution extends throughout north-eastern Brazil (Prado, 2003; IBGE, 2004) from 2°54′ S to 17°21′ S (Ab'Sáber, 1974; Andrade-Lima, 1981), and covers about 1,000,000 km^2. The Caatinga is an open, mostly semi-arid landscape, typical of interplateau depressions (Ab'Sáber, 1974), with high mean annual temperatures, scarce and irregular rainfall, low relative humidity and high solar radiation, and is drained by largely intermittent and seasonal rivers (Ab'Sáber, 1974; Velloso *et al.*, 2002; Prado, 2003). The Caatinga is not physically homogeneous, showing considerable variation in vegetation structure (Andrade-Lima, 1975; see colour pictures in Guedes, 2012), and has been divided into eight subregions based on soil, climate, plant composition, geomorphology and geology (Velloso *et al.*, 2002).

The limits of the Caatinga considered in this study (see Appendix S1 in Supporting Information) encompass the limits considered in both IBGE (2004) and Velloso *et al.* (2002). Although earlier biogeographical studies excluded mountain areas from the Caatinga or included these areas as enclaves of Atlantic forest (Carnaval, 2002; Carnaval & Moritz, 2008), we agree with Velloso *et al.* (2002) and Camardelli & Napoli (2012) that these highlands are part of the Caatinga region. We excluded the Amazonian Caatinga because it is not historically related to the Caatinga of north-eastern Brazil (Anderson, 1981). Insular areas were also not considered.

Data sources

We obtained data from the revision of 7102 voucher specimens in 17 zoological collections, and 250 records from the literature, resulting in 7352 analysed records (Appendix S1). All records are based on voucher specimens, carefully examined by one or more authors, and identified based on current taxonomy. Literature sources were also selected according to criteria of geographical and taxonomic reliability, and the presence of voucher lists. Records in electronic databases, including unchecked, error-prone raw museum data, were not used (see discussion in Nogueira *et al.*, 2011; Zaher *et al.*, 2011; Guedes, 2012). Snake taxonomy follows Zaher *et al.* (2009) and Grazziotin *et al.* (2012).

We included in our analysis every species with at least one vouchered record within the Caatinga region. Geographical coordinates were obtained in electronic gazetteers, scientific literature, direct visual inspection in ARCVIEW 10.1 (ESRI, 1999) and GOOGLE EARTH, and by contacting collectors for precise coordinates. In the absence of accurate information on geographical coordinates, we used municipality centroids.

Analyses

Endemic species were those with locality records fully or largely coincident with the approximate limits of the Caatinga, as in Nogueira *et al.* (2011).

The predictions of the vicariance model were tested by means of biotic element analysis (Hausdorf, 2002; Hausdorf & Hennig, 2003, 2006), based on a presence/absence matrix resulting from species records mapped onto 1° latitude × 1° longitude cell grids, superimposed onto the Caatinga map. Biotic element analysis was implemented in the PRABCLUS package (Hausdorf & Hennig, 2003) in the R statistical software (R Core Team, 2012). We performed biotic element analysis using two datasets: all species recorded in the Caatinga, and endemic species only.

Two predictions of the vicariance model were tested herein: that the division of ancestral biotas by vicariance should produce significantly co-distributed groups of taxa (biotic elements), and that closely related species resulting from vicariance should form different biotic elements (see Hausdorf & Hennig, 2004).

Test for clustering of distribution areas

We tested for the presence of significantly clustered, regionalized species ranges, as an indicator of vicariance events. This test is based on the distances between the range limits of the examined taxa, and requires a distance measure between species' ranges, a test statistic, and a null model for the generation of sets of ranges. We used the Kulczynski distance metric because it does not overestimate distances between sympatric taxa of differing range sizes (Hausdorf & Hennig, 2003). We used the T test statistic, which is based on the assumption that, given a significant clustering of ranges,

distances between ranges of the same cluster will be smaller than those between ranges of distinct clusters (Hausdorf & Hennig, 2003). The distribution of the test statistic under the null model is approximated by Monte Carlo simulation. Artificial ranges are produced under the constraint that their cell number distribution approximates the actual distribution of the number of cells per range, the richness distribution of cells approximates the observed distribution, and the tendency to form discontinuous areas is governed by a parameter that is estimated from the data (Hausdorf & Hennig, 2003, 2006). Thus, this analysis compares the real distributions with a null model, testing if the degree of clustering of species ranges can be explained by varying the number of taxa per cell and the spatial autocorrelation of the empirical data alone (Hausdorf & Hennig, 2003).

Determination of biotic elements

We used model-based Gaussian clustering (MBGC) as implemented in the software MCLUST (Hausdorf & Hennig, 2003). This method infers the number of meaningful clusters and ranges that cannot be adequately assigned to any biotic element (noise component). MBGC operates on a data set in which the cases are defined by variables on a metric scale. Therefore, we performed non-metric multidimensional scaling (NMDS) on the matrix of Kulczynski distances, specifying a four-dimension solution. MCLUST needs an initial estimate of noise for which we used the software NNCLEAN (Byers & Raftery, 1998). As suggested by Hausdorf & Hennig (2003, 2006), we set the NNCLEAN constant k = number of species/40 (i.e. three for the larger dataset, and one for the endemic dataset).

Conservation of biotic elements

We analysed the conservation of biogeographical patterns and processes by comparing the rates of habitat loss of species within and among biotic elements, and by quantifying the total coverage of protected areas intersecting the distributions of species that formed different biotic elements. First, we estimated the distribution areas for each species via minimum convex polygon (see IUCN, 2013), or with 10 km radius buffers around unique or disjunct locality records. Habitat loss for each species was calculated based on the overlay of range polygons and official data on deforestation in Brazil up to 2008 (MMA, 2008; Appendix S1). The rates of habitat loss for species within each biotic element were compared using Kolmogorov–Smirnov tests (see Crawley, 2007). The expected habitat loss for a given species (Appendix S2) was calculated as the product of its distribution area and the average percentage of habitat loss of all species within its biotic element. We used the logit transformation calculated in the R package CAR (R Core Team, 2012) for observed and expected habitat loss values, because they correspond to proportions of the distribution area of species (see Warton & Hui, 2011). Habitat loss among biotic

elements was compared using the Kruskal–Wallis test (Hollander & Wolfe, 1973). To calculate the coverage of protected areas for each species in biotic elements (Appendix S2), we overlapped range polygons and strictly protected areas (categories I–III; Dudley, 2008) of the current Brazilian protected area system (WWF, 2013). The logit-transformed (see Warton & Hui, 2011) proportion of species protection among biotic elements was compared using a Kruskal–Wallis test (Hollander & Wolfe, 1973) and multiple comparison tests (see Siegel & Castellan, 1988), implemented in the R package PGIRMESS (R Core Team, 2012). For all statistical analyses, we used a significance level of $\alpha = 0.05$. All spatial analyses were performed using software XTOOLS PRO, an extension of ARCVIEW 10.1 (ESRI, 1999).

RESULTS

Species richness and endemism

We recorded 112 snake species in the Caatinga, belonging to nine families, and including 22 endemic species (Appendix S2), which represent 20% of the regional richness. Half of the endemic species show very restricted distributions less than 20,000 km^2 (according to IUCN, 2013), with the other half showing a wide distribution in the Caatinga (see Guedes, 2012).

Test for clustering of distribution data

Biotic element analysis of the full dataset (112 species), including both endemics and non-endemics, corroborated the major predictions of the vicariance model: ranges were significantly clustered, forming localized biotas across the Caatinga. The observed T statistic was 0.44, significantly smaller ($P = 0.0001$) than values expected by chance for 1000 artificial populations, which varied from 0.44 to 0.58, with a mean of 0.50. To test whether these results were a direct effect of species interchange with adjacent regions, we repeated the analyses with the endemic dataset (22 species). In this second analysis, the T statistic was 0.39, again significantly smaller ($P = 0.003$) than values expected by chance, which varied between 0.38 and 0.65, with a mean of 0.46.

Determination of biotic elements

As both tests indicated that the Caatinga snake fauna is divided into species groups with significantly regionalized ranges, the next step was to determine the biotic elements. To this end, we used species clusters in the first two dimensions of the NDMS. The analysis with the full dataset detected 72 species in the noise component (Fig. 1a), while 40 species (36%) contributed to the detection of eight biotic elements (Fig. 2, Appendix S2): biotic element 1 (BE1) was formed by 11 species, with a core area in the Chapada Diamantina plateau complex; biotic element 2 (BE2) grouped seven species, mainly in the São Francisco dunes;
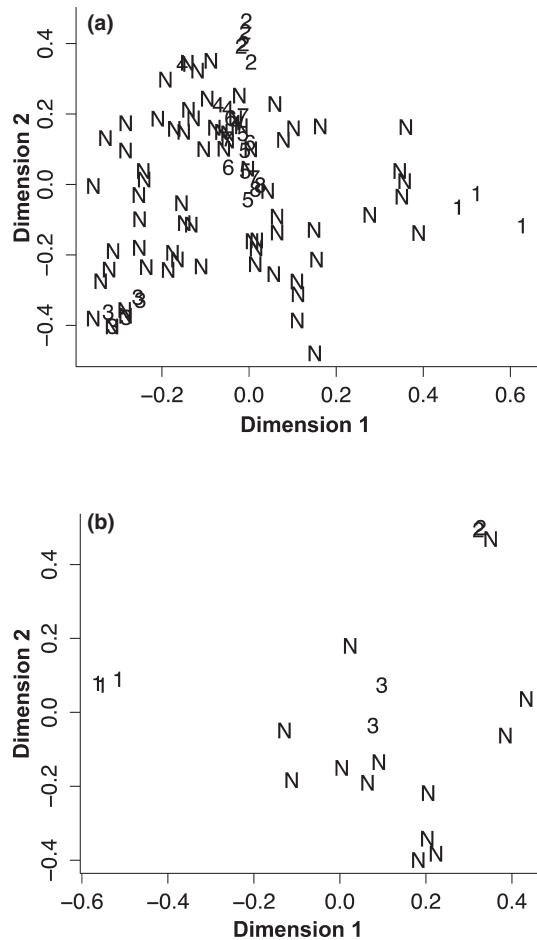

Figure 1 Species clusters in the first two dimensions of a non-metric multidimensional scaling analysis, obtained according to the ranges of (a) 112 Caatinga snake species (endemics and non-endemics), and (b) 22 endemic snake species, mapped on a 1° × 1° cell grid, analysed in MCLUST. Characters indicate model-based clustering with noise (N).

biotic element 3 (BE3) was formed by six species, mostly ranging along the Ibiapaba–Araripe plateau complex; biotic element 4 (BE4) grouped four species with a core area in the Jequitinhonha River valley; biotic elements 5 (BE5), 6 (BE6) and 8 (BE8) were formed by four, three, and two species, respectively, all widespread in the Caatinga lowland semi-arid region; and biotic element 7 (BE7) was formed by three species in peripheral areas of the Caatinga.

Eight genera contained at least two species included in biotic elements (Appendix S2): *Bothrops*, *Micrurus*, *Typhlops* and *Xenodon* (two species each), *Apostolepis* and *Rodriguesophis* (three species each), and *Oxyrhopus* and *Erythrolamprus* (four species each). The second prediction of the vicariance model (see Hausdorf & Hennig, 2004) was corroborated, as congeneric species were scattered among different biotic elements ($\chi^2 = 46.57$; $P = 0.31$).

The analysis with the endemic dataset detected 13 species in the noise component (Fig. 1b), while nine (40%) species contributed to the detection of three biotic elements (Fig. 3,
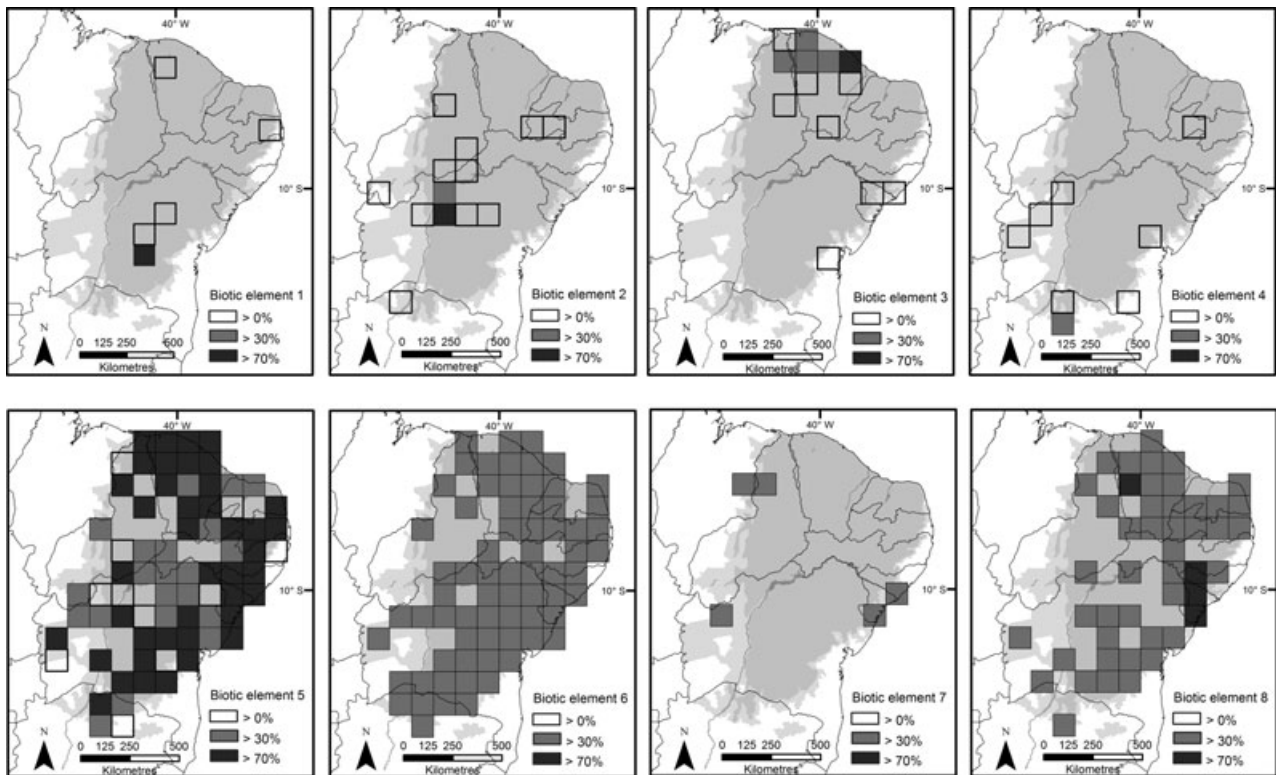
Figure 2 Distribution of biotic elements (BE 1–8) recovered according to the range of 112 Caatinga snakes (endemics and non-endemics). Shadings indicate the areas where > 70%, > 30% and > 0% of the species of an element are present.

Appendix S2): endemic element 1 (EE1) includes four species and was congruent with the core area of BE2, in the São Francisco dunes; endemic element 2 (EE2) includes three species, and was largely congruent with the core of BE3, in the Ibiapaba–Araripe plateau complex; and endemic element 3 (EE3) grouped two species, widespread throughout the Caatinga region and previously included in BE5.

Conservation of biogeographical patterns

Average habitat loss for the 40 species that defined biotic elements was 46%, with no significant differences between observed and expected habitat loss for species within each biotic element (Appendix S3). Moreover, habitat loss was not significantly different for species from different biotic elements (Figs 4a & 5; Kruskal–Wallis test: $K = 13.48$, d.f. = 7, $P = 0.06$).

Among the 40 species defining the eight biotic elements, sixteen are not protected by conservation units. Fourteen species have only a small portion of their ranges protected (0.3% to 21.6%) and only 10 species are fully protected, with 100% of their ranges within reserves (Appendix S2). The area covered by conservation units within the range of each species was significantly different among biotic elements (Figs 4b & 5; Kruskal–Wallis test: $K = 29.80$, d.f. = 7, $P < 0.001$), with species in BE1 significantly more protected than those in BE2, BE4 and BE7 (Figs 4b & 5).

DISCUSSION

Species richness, endemism and regionalization

The Caatinga has been previously considered poorly known regarding diversity of vertebrates, including birds and mammals (e.g. Gregorin *et al.*, 2008; Pereira & Geise, 2009). Even for these better-studied groups, endemism levels are considered low (Willig, 1983; Mares *et al.*, 1985), probably due to the paucity of basic knowledge, and the lack of detailed and comprehensive syntheses. Early interpretations of the Caatinga herpetofauna considered it to be a subset of the Cerrado and the Atlantic forest coastal faunas (Vanzolini, 1974, 1976; Vanzolini *et al.*, 1980), but our results show a rich and peculiar snake fauna, including 22 endemic species, or 20% of the total richness.

Our results provide the first formal tests of the prominent role of vicariant patterns in shaping Caatinga snake distributions, and corroborate previous studies indicating that the Caatinga region is not homogeneous (Velloso *et al.*, 2002; de Queiroz, 2006; Cardoso & de Queiroz, 2010; Camardelli & Napoli, 2012). The high richness and endemism of snakes detected in our study led to the recovery of regionalized biotas in diverse habitats throughout the Caatinga, including open highland areas such as the Chapada Diamantina plateau complex (BE1) and the sandstone tablelands of the Ibiapaba–Araripe plateau complex (BE3, EE2).
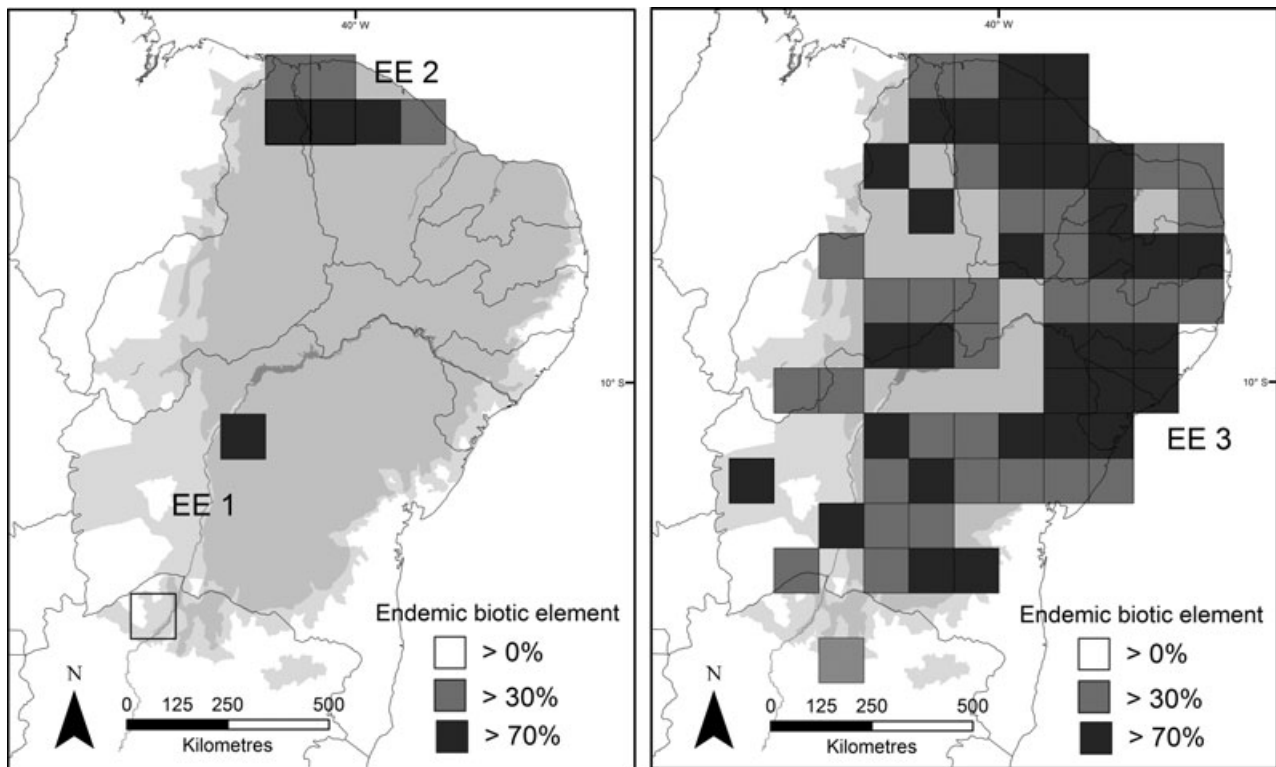
Figure 3 Distribution of endemic biotic elements (EE 1–3) recovered according to the range of 22 endemic Caatinga snakes. Shadings indicate areas where > 70%, > 30% and > 0% of the species of an element are present.

Lowland biotic elements (BE5, BE6, BE8 and EE3) were also recovered, being formed by species found sympatrically throughout most of the Caatinga interplateau depressions, and corresponding to a large biogeographical unit encompassing most of the Caatinga region. These biotas may be interpreted as the most typical of the Caatinga, and are found throughout the entire region, in its most characteristic semi-arid depressions. This indicates that lowland semi-arid Caatinga areas represent a natural biogeographical unit typical of north-eastern Brazil, and not a simple artefact of faunal interchange with adjacent regions, as previously stated (Vanzolini, 1974, 1976; Vanzolini *et al.*, 1980). The distribution patterns of the species that compose these lowland biotic elements is similar to that of other terrestrial vertebrates (Müller, 1973; Kinzey, 1982; Cracraft, 1985; Mares *et al.*, 1985; Costa *et al.*, 2000; Goldani *et al.*, 2006) that define the Caatinga as a unique natural biogeographical unit associated with low-lying aridlands dominated by xeromorphic open vegetation. This distribution pattern lends no support to the division of the Caatinga lowlands into northern Sertaneja depression and southern Sertaneja depression, as suggested by Velloso *et al.* (2002). Other lowland areas harbouring localized biotas include the sandy soils of the São Francisco dunes (BE2), the Jequitinhonha River valley (BE4), and peripheral areas of the Caatinga related to the Atlantic forest and the Cerrado.

The core areas of most biotic elements were generally coincident with biogeographical units proposed in previous studies of plants (Velloso *et al.*, 2002; de Queiroz, 2006; Cardoso & de Queiroz, 2010) and vertebrates (Müller, 1973; Kinzey, 1982; Cracraft, 1985; Mares *et al.*, 1985; Costa *et al.*, 2000; Goldani *et al.*, 2006; Camardelli & Napoli, 2012) (Table 1). A recent biogeographical study of amphibians, using parsimony analysis of endemicity, recovered eight areas of endemism in the Caatinga (Camardelli & Napoli, 2012). Most of those comprised mountain ranges, interpreted as areas of speciation and biotic refuges, which remained stable throughout the Quaternary climatic shifts (Carnaval, 2002; Carnaval & Moritz, 2008). Areas with sandy soils were detected as areas of high levels of endemism in studies on lizards (Rodrigues, 1986, 1991a,b,c, 2003, 2004), and are interpreted as a result of palaeo-Quaternary sand depositional areas along the São Francisco river channel, the most important perennial river in the Caatinga.

However, although Quaternary climatic shifts and relative stability along highland areas may have been important in determining regionalization patterns (see Haffer, 1997; Carnaval & Moritz, 2008), major tectonic events in the Palaeogene and Neogene, with their dramatic effects on relief, hydrography and geomorphology, may also be identified as key drivers of vicariant patterns in the Caatinga region and in the Neotropics (Cole, 1986; da Silva, 1997). Not surprisingly, the biotic elements we recovered are mostly segregated between highland (Chapada Diamantina and Ibiapaba–Araripe plateaus) and lowland areas (São Francisco dunes, Jequitinhonha river valley, Caatinga semi-arid lowlands), indicating that
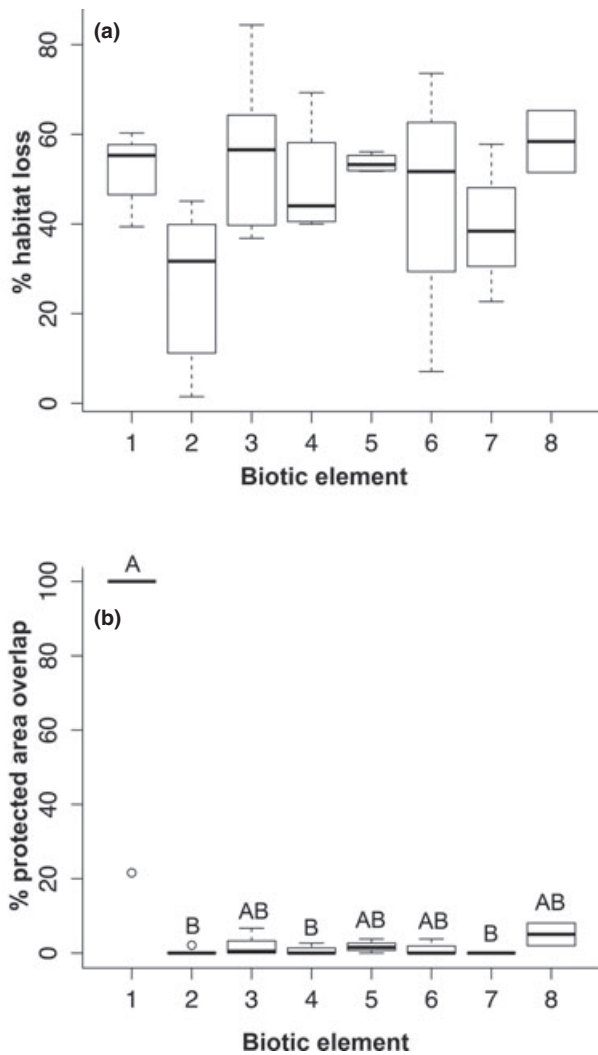
Figure 4 (a) Percentage of habitat loss of species per biotic elements 1–8. Horizontal bars = median; box = first and third quartiles; whiskers = minimum and maximum values. (b) Percentage of protected areas overlap with species in each biotic element 1–8. Horizontal bars = median; box = first and third quartiles; whiskers = minimum and maximum values. Common letters indicate non-significant differences.

topography may have played an essential role in vicariant processes, as already proposed for biotic elements in the adjacent Cerrado region (see Nogueira et al., 2011).

Conservation of biogeographical patterns

Although the Caatinga is the largest semi-arid Neotropical region and the only exclusively Brazilian natural ecoregion, little attention has been given to the conservation of its varied and complex biotas, and their contribution to Brazilian and Neotropical biodiversity has been largely underestimated (da Silva et al., 2004). Estimates of habitat loss in the Caatinga vary between 30.4% and 51.7% (Castelletti et al., 2004; Leal et al., 2005). Of the Brazilian natural regions, the Caatinga shows the smallest extent of legally protected areas, which

currently protect only 6.4% of the region. Considering only areas of strict protection (IUCN categories I–III), this percentage drops to less than 1% of the Caatinga (Leal et al., 2005).

Current priority areas for the conservation of the Caatinga herpetofauna were determined by the combination of high richness, endemism and the presence of threatened/rare species (see Rodrigues, 2003, 2004). A total of 19 areas were listed as priorities for the creation of eight protection areas (Rodrigues, 2004). Due to a lack of information, only snakes that were restricted to the sandy dunes of the São Francisco River were considered (Rodrigues, 2004), but most of the core ranges of biotic elements recovered in our study coincide with priority areas determined by Rodrigues (2004), and also with previous areas of endemism or natural regions described for the Caatinga (Mares et al., 1985; Velloso et al., 2002; de Queiroz, 2006; Camardelli & Napoli, 2012).

Although the core ranges of most biotic elements coincide with priority areas, few species within the biotic elements are adequately covered by protected areas (see Fig. 5). Thus, the existing reserve network clearly fails to represent the biodiversity and biogeographical patterns and processes of the Caatinga. The lowland Caatinga harbours the most wide-ranging biotic elements (BE5, BE6, BE8 and EE3) and hosts at least six endemic snake species (Guedes, 2012), and yet is protected by only 13 conservation units. Thus, we agree with Camardelli & Napoli (2012) and recommend the creation of integral protection conservation units in lowland Caatinga areas. Other priorities include the São Francisco dunes area (BE2, EE1) and the Ibiapaba–Araripe plateau complex (BE3, EE2), both of which are virtually unprotected by the current reserve system (see Fig. 5). Although other biotic elements are also poorly protected, the three areas mentioned above are of higher relevance, as they are determined by endemic species, whose conservation depends on targeted actions within the Caatinga. The single protected biotic element is the Chapada Diamantina plateau complex (BE1) which, however, harbours no endemic species of snakes, at least given current taxonomic knowledge.

Our results show that snakes are valuable models in biogeographical studies, if detailed syntheses and data-collection efforts are provided. The lack of detailed range data, or the so-called 'Wallacean shortfall' (Whittaker et al., 2005), has been used as an argument against the use of species distributions in conservation strategies (see discussion in Brooks et al., 2004). Our results, based on raw distribution records alone, clearly detected localized biotas. We highlight the utility of raw distribution data and related regionalization patterns as key primary information sources for representative and scientifically sound conservation strategies, even in relatively poorly sampled tropical regions. The lack of biogeographical resolution should no longer be identified as one of the reasons behind the low levels of protection of the Caatinga. The necessary step is now to implement conservation action in accordance with the biogeographical patterns detected herein, which we interpret as the results of historical and vicariant processes.
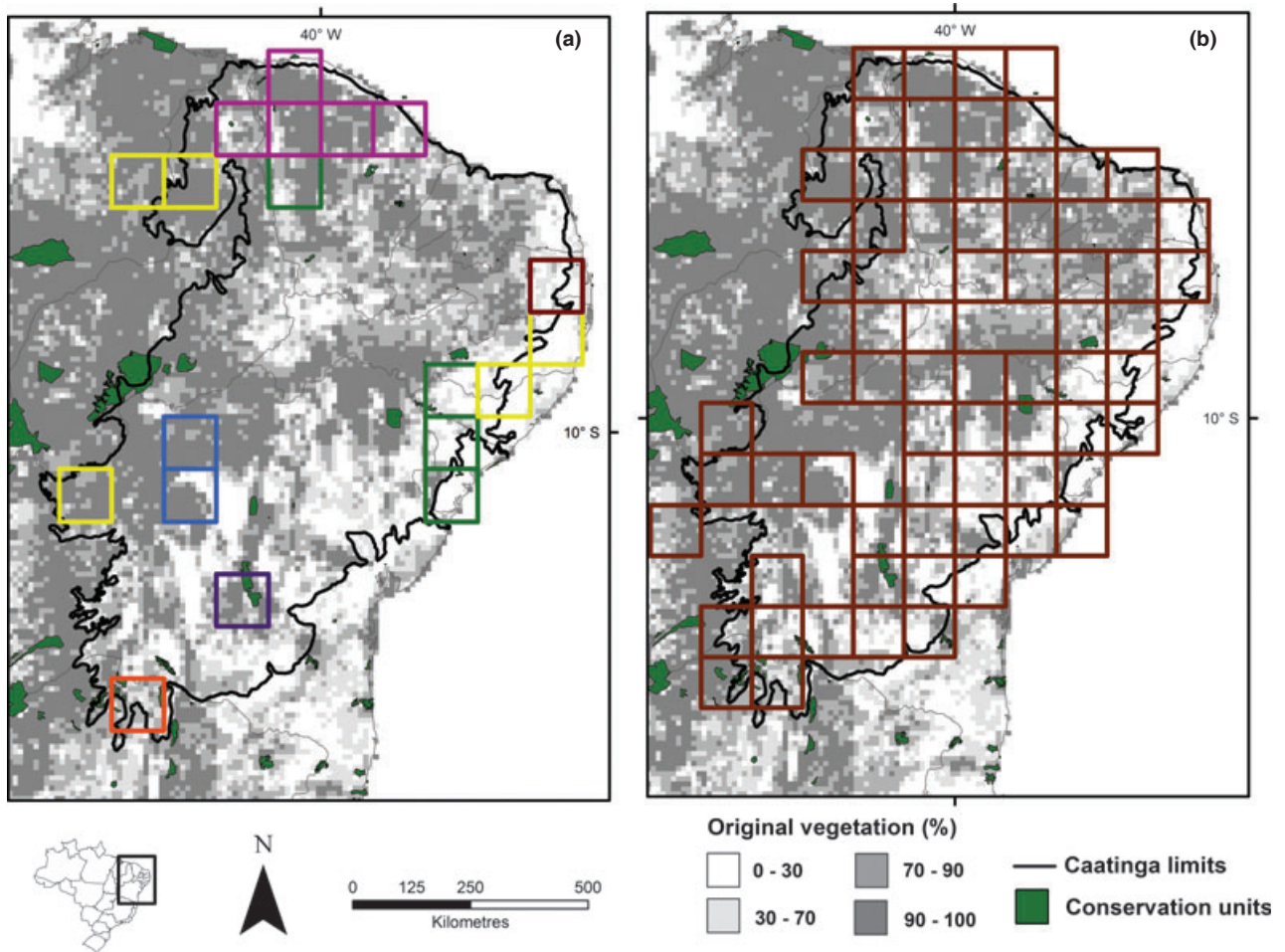
Figure 5 Core areas of biotic elements (BE), protected areas (in green), and percentage of original vegetation in the Caatinga region up to 2008. (a) BE1: Chapada Diamantina plateau complex (in purple); BE2: São Francisco dunes (blue); BE3: Ibiapaba–Araripe plateau complex (magenta); BE4: Jequitinhonha river valley (orange); BE7: peripheral Caatinga (yellow); (b) BE5, 6, and 8: Caatinga region (widespread, brown).

Biogeographical patterns are central to representative conservation strategies (Saiz *et al.*, 2013) with recent studies highlighting the validity of biotic elements as surrogates for the evolutionary processes in conservation planning (Carvalho *et al.*, 2011). Narrow ranges define a key aspect of rarity, making localized endemics intrinsically susceptible to threats (Whittaker *et al.*, 2005; see examples in Nogueira *et al.*, 2010). Localized narrow endemics tend, moreover, to be poorly represented in conservation planning strategies based on habitat classes or other coarse-scale biodiversity surrogates (Araújo *et al.*, 2001). Given the widespread paucity of detailed phylogenetic or phylogeographical data (Carvalho *et al.*, 2011) – coupled with the urgent need for setting spatial priorities in highly threatened regions – the incorporation of biotic elements into conservation strategies should be seen as key for safeguarding the evolutionary significance of biodiversity (Carvalho *et al.*, 2011; Nogueira *et al.*, 2011).

Our results clearly indicate that, apart from wide-ranging conservation strategies aimed at the Caatinga as a whole, more focused, localized actions are also necessary to safeguard narrow-ranging biotic elements, such as those in the Ibiapaba–Araripe plateau complex or the São Francisco dunes (Rodrigues, 1986). Conservation strategies should focus on currently unprotected biogeographical units as major conservation priorities. The fact that habitat loss is still relatively homogeneous across biogeographical units in the Caatinga indicates that spatial opportunities still exist for representing and conserving biogeographical patterns and processes in this highly threatened Neotropical region.

Future prospects

The detection of basic biogeographical units provided herein is only the necessary first step towards interpreting diversification processes (see Morrone, 1994, 2009). Vicariance events may not be the single explanatory factor for the regionalized patterns we recovered (see Hausdorf & Hennig, 2003); thus, recent integrative studies (see Wiens *et al.*, 2011; Condamine *et al.*, 2012, 2013a,b; Pirie *et al.*, 2012; Töpel *et al.*, 2012;

Table 1 Biotic elements and endemic species detected in the present study, according to Caatinga areas of endemism recovered in previous studies.

Caatinga areas	Biotic elements (present study)	Endemic species	References
Peripheral areas	BE3, BE7 and BE8	Snakes: *Dendrophidion atlantica* and *Atractus* aff. *maculatus*	Müller (1973), Prance (1982), Amorim & Pires (1996), da Silva *et al.* (2004), Barbo (2012)
Aratanha, Maranguape and Baturité ranges	BE3 and EE2	Amphibians: *Adelophryne maranguapensis*. Snakes: *Apostolepis* aff. *pymi*, *Oxyrhopus* sp. and *Atractus ronnie*	de Queiroz (2006), Cardoso & de Queiroz (2010), Camardelli & Napoli (2012)
Borborema plateau	BE1	Plants: *Ameroglossum* spp., *Mimosa borboremae*. Snakes: *Tantilla marcovani* and *Lioheterophis iheringi*	Velloso *et al.* (2002)
Caatinga region	BE5, BE6, BE8 and EE3	Snakes: *Bothrops erythromelas*, *Erythrolamprus viridis*, *Apostolepis cearensis*, *Epictia borapeliotes* and *Micrurus* sp.	Müller (1973), Kinzey (1982), Mares *et al.* (1985), Cracraft (1985), Costa *et al.* (2000), Porzecanski & Cracraft (2005), Goldani *et al.* (2006)
Campo Maior complex	BE7	No endemic species	Velloso *et al.* (2002), de Queiroz (2006), Cardoso & de Queiroz (2010)
Chapada Diamantina plateau complex	BE 1 and BE 2	Plants: *Raylea* spp., *Mysanthus* spp., *Holoregmia* spp., *Mimosa irrigua*, *Chamaecrista eitenorum*, *Portulaca werdermannii*, *Melocactus glaucences* and *Arrojoadoa bahiensis*. Amphibians: *Bokermannohyla juiju*, *B. itapoty*, *Rupirana cardosoi* and *Strabomantis aramunha*	Velloso *et al.* (2002), de Queiroz (2006), Cardoso & de Queiroz (2010), Camardelli & Napoli (2012)
Ibiapaba–Araripe plateau complex	BE1, BE3, BE8 and EE2	Plants: *Hyptidendron ametystoide*. Birds: *Antilophia bokermanni*. Mammals: *Chiroderma vizzotoi*. Snakes: *Apostolepis* aff. *pymi*, *Oxyrhopus* sp. and *Atractus ronnie*.	Velloso *et al.* (2002), de Queiroz (2006), Cardoso & de Queiroz (2010)
Jequitinhonha River valley	BE4	Amphibians: *Aplastodiscus cavicola*, *A. weygoldti* and *Xenohyla eugenioi*	Camardelli & Napoli (2012)
Jibóia range	BE3 and BE4	Amphibians: *Allobates ofersioides* and *Gastrotheca flamma*	Camardelli & Napoli (2012)
São Francisco dunes	BE2 and EE1	Plants: *Pterocarpus monophyllus*, *Dioclea marginata*, and *Eugenia* sp. Arthropods: *Remummucia mauryi*. Mammals: *Proechimys yonenagae*. Amphisbaenians: *Amphisbaena hastata*, *A. ignatiana*, *A. frontalis* and *A. arda*. Lizards: *Calyptommatus leiolepis*, *C. nicterus*, *C. sinebrachiatus*, *Eurolophosaurus amathites*, *E. divaricatus*, *Tropidurus psammonastes* and *T. pinima*. Snakes: *Apostolepis gaboi*, *A. arenaria*, *Rodriguesophis chui*, *R. scriptorcibatus*, *Typhlops amoipira* and *T. yonenagae*.	Velloso *et al.* (2002), de Queiroz (2006), Cardoso & de Queiroz (2010)

Dawson *et al.*, 2013) have encouraged the combination of multiple layers of data from ecology, distribution, fossils and genetics, as well as palaeogeographical and palaeoclimatical data, to understand the diversification/speciation history of areas based on different groups of animals and plants.

Crucial questions about the history of Caatinga biotas remain unanswered. Were biotic elements the result of a single or general explanatory event? Have Caatinga biotas been formed by a common historical process, or have regional codistribution patterns been generated by more complex pseudocongruent histories (*sensu* Donoghue & Moore, 2003)? The apparent segregation of biotic elements among different topographical and geomorphological divisions of the Caatinga points to major tectonic events already identified as major

drivers of Neotropical biodiversity as plausible explanatory factors of diversification (Cole, 1986; Nogueira *et al.*, 2011). However, temporal congruence among the biotic elements we detected and ancient geomorphological events has not yet been formally tested in the Caatinga.

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SUPPORTING INFORMATION

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

Appendix S1 Maps of the Caatinga region, showing locality records of snakes and habitat loss.

Appendix S2 List of snakes from the Caatinga, data on range size, habitat loss and protected area coverage in biotic elements.

Appendix S3 Kolmogorov–Smirnov tests of rates of expected and observed habitat loss within each biotic element.

BIOSKETCHES

Thaís Barreto Guedes is interested in diversity, taxonomy, biogeography, and conservation of squamate reptiles. She aims to decipher the main evolutionary and ecological processes that have shaped current biodiversity of South American open landscapes.

Ricardo J. Sawaya is a professor of biogeography, zoology and ecology. His research interests include geographic distribution on both local and regional scales, ecophylogenetics, conservation and evolutionary history of organisms.

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Author contributions: T.B.G. and C.N. conceived the ideas; T.B.G. collected and analysed the biogeographical data, assisted by C. N.; T.B.G. wrote the first draft; R.J.S. led conservation analyses assisted by C.N. and T. B. G.; all authors contributed equally with interpretation and discussion of the results, writing the final version of the manuscript together.

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