



# The role of strict nature reserves in protecting genetic diversity in a semiarid vegetation in Brazil

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## Abstract

Genetic diversity is an important component of biodiversity, providing the means for species to evolve and adapt in changing environments. Although regions that retain high genetic diversity provide ideal targets for conservation due to their evolutionary potential, they have been poorly mapped in the Neotropics. Here, we mapped genetic diversity, expressed in this study by nucleotide diversity, for five lizards, four amphibians, and one spider widely distributed in the Brazilian Caatinga, a semiarid vegetation. We identified areas that contain higher genetic diversity, which may be used to establish conservation priorities for the region, and evaluated their representativeness within strict nature reserves. Our results show that only 1.5% of the areas holding higher genetic diversity are within strict nature reserves. However, we show that very high genetic diversity regions are over-represented inside strict nature reserves and encompass areas such as “Brejo Paraibano”, Catimbau National Park, and part of the Borborema plateau. Thus, the maintenance of biota’s evolutionary potential relies upon the inclusion of areas with higher genetic diversity in future conservation planning.

**Keywords** Genetic diversity · Mitochondrial DNA · Priority areas · Wildlife conservation

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## Introduction

Over the last few centuries human activity has deeply influenced the environment by promoting pervasive habitat loss, the spread of disease, climate change, biological invasions, and overexploitation of natural resources (Pimm and Raven 2000; Lips et al. 2006; Worm et al. 2006; Sinervo et al. 2010; Bellard et al. 2012; Both and Grant 2012; Pontes-da-Silva et al. 2018). Consequently, Earth has been facing a global biodiversity crisis, where many species will likely be extinct in the near future (Pimm and Raven 2000; Barnosky et al. 2011; Ceballos et al. 2015). The loss of biodiversity can alter ecosystem functions and compromise important services such as food and wood production, fresh water availability, access to plants with pharmaceutical properties, and climate regulation (Cardinale et al. 2012). Thus, one of the greatest challenges of the twenty-first century is to ensure the persistence and viability of biodiversity over time (Rands et al. 2010). However, limited resources available for conservation and the high economic and social costs of setting land aside to create protected areas make conservation prioritization crucial to ensure the most cost-effective conservation choices (Moilanen and Arponen 2011). In this context, primary information about how biodiversity is spatially organized at its multiple levels (e.g., taxonomic, phylogenetic, genetic, and functional) is vital for the selection and creation of priority areas that will effectively protect biodiversity in the long-term (Pino-Del-Carpio et al. 2014).

The availability of genetic information has altered the way in which species' evolutionary histories are determined and has improved understanding of the origins of biodiversity (Avice 2000; Seehausen et al. 2014). In addition, this information has been used as a proxy to evaluate the extent of anthropogenic impacts on the future of species and populations (Hoffmann and Sgrò 2011; Miraldo et al. 2016; Razgour et al. 2017). Thus, the spatial organization of genetic diversity may aid effective decision-making in conservation planning (Margules and Pressey 2000). Areas with high genetic diversity are not expected to be randomly distributed in geographic space (Carnaval et al. 2014; Rosauer et al. 2016). Spatial patterns of genetic diversity may result from population persistence in refugia during past climatic fluctuations (Carnaval et al. 2009), contact of divergent populations at hybrid zones (Nettel et al. 2008), and adaptive variation due to environmental gradients (Vandergast et al. 2013). In addition, higher genetic diversity may also be related to larger population sizes and higher migration rates (Frankham 1996; Frankham et al. 2002). Conversely, the loss of genetic diversity is associated with increased inbreeding and frequency of deleterious alleles, loss of adaptive potential, and a greater sensitivity to stochastic events, which can lead to higher extinction probabilities (Frankham et al. 2002). Because of a recent burst of phylogeographic studies (Beheregaray 2008), genetic data is now available for several mega diverse regions, including the Brazilian Caatinga, one of the least studied areas in the Neotropical region (Turchetto-Zolet et al. 2013).

Restricted to northeastern Brazil, the Caatinga is the largest area of Seasonally Dry Tropical Forests in South America, covering  $\sim 850,000$  km<sup>2</sup> or 11% of the Brazilian territory (Prado and Gibbs 1993; Pennington et al. 2000). This area is bordered on the west and south by the Cerrado savannas and on the east by the Atlantic Forest. The Caatinga climate is highly unpredictable with at least 5–6 months of severe drought, and a rainy season where precipitation can be less than 600 mm/year (Reis 1976; Gentry 1995; Mooney et al. 1995; Prado 2003). Its vegetation is a mosaic of xerophytic and deciduous vegetation, semiarid thorn scrubs, and forest formations (Leal et al. 2005; Werneck 2011).

The Caatinga is highly threatened by intensive human occupation, the transposition of its major river (São Francisco River), pastures, grazing, logging, agriculture, and desertification (Leal et al. 2005; Marinho et al. 2016; Silva and Barbosa 2017). Additionally, less than 1% of its area is covered by strict nature reserves (Category Ia, sensu IUCN protected area category system; Leal et al. 2005), all severely underfunded (Oliveira and Bernard 2017). Several governmental initiatives were conducted over the last 15 years for conservation in the Caatinga, including definition of priority areas for conservation, creation of new strict nature reserves, combating desertification, and mitigating the effects of drought. Recently, economic, social, and environmental layers were used to generate cost–benefit surfaces and indicate priority areas for conservation (MMA 2016). However, data on genetic, phylogenetic, and functional diversity for most taxa is not available, despite the importance of such data for long-term species and community maintenance.

Here, we gathered mitochondrial DNA data for ten species of widely distributed animals in the Caatinga to map their genetic diversity across the region. Specifically, our goals were: (1) identify areas that concentrate higher genetic diversity for multiple taxa; and (2) evaluate their representativeness within strict nature reserves.

## Materials and methods

### Targeted species and molecular data

We generated mtDNA sequences for two lizards (*Lygodactylus klugei* and *Tropidurus hispidus*) and three amphibians (*Corythomantis greeningi*, *Leptodactylus chaquensis*, and *Rhinella jimi*). All these tissue samples were either collected by the authors or obtained from herpetological collection donations. Additionally, we repurposed mtDNA sequences from GenBank for three lizards (*Ameivula ocellifera*, *Phyllopezus pollicaris*, and *T. semi-taeniatus*), one amphibian (*Pleurodema diplolister*), and one spider (*Sicarius cariri*). In total, we used five lizards, four amphibians, and one spider. We included species with different ecological requirements and dispersal abilities. For example, while *L. klugei* is a small arboreal lizard with low dispersal ability, *L. chaquensis* is a large terrestrial frog with high dispersal ability. Although some species are not restricted to the Caatinga, their distribution ranges cover most of this region. In addition, none of the species are currently listed in the Brazilian list of threatened species (ICMBio 2018). To be included in this study, species had to satisfy two criteria: (1) have at least two samples per locality, and (2) be well sampled throughout their distribution in the Caatinga (i.e., samples distributed across more than 50% of the distribution of species). Further information on taxa, sequence source, and length, and genetic markers used in this study are presented in Table 1.

### Mapping genetic diversity

To identify how genetic diversity is currently distributed within the Caatinga, we built a spatial surface of genetic diversity for each focal taxon using conventional kriging implemented in the R package “geoR” (Ribeiro and Diggle 2001). Conventional kriging is an interpolation method that allows the prediction of values for non-sampled regions from observed values of sampled regions using fixed covariance parameters in a global neighborhood approach (Ribeiro and Diggle 2001). We calculated nucleotide diversity ( $\pi$ ) at each locality for each taxon using the R package “pegas” (Paradis 2010). Then, we

**Table 1** Information about taxa, genetic marker, sequence length, and source of the data used in this study

| Order    | Family           | Species                         | Gene       | Sequence length (bp) | Source of sequence      |
|----------|------------------|---------------------------------|------------|----------------------|-------------------------|
| Araneae  | Sicariidae       | <i>Sicarius cariri</i>          | COI        | 715                  | Magalhaes et al. (2014) |
| Anura    | Leptodactylidae  | <i>Pleurodema diplolister</i>   | COI        | 601                  | Thomé et al. (2016)     |
| Anura    | Leptodactylidae  | <i>Leptodactylus chaquensis</i> | COI        | 546                  | This study              |
| Anura    | Bufoinae         | <i>Rhinella jimi</i>            | 16s        | 508                  | This study              |
| Anura    | Hylidae          | <i>Corythomantis greeningi</i>  | 16s        | 471                  | This study              |
| Squamata | Teiidae          | <i>Ameivula ocellifera</i>      | 12s        | 370                  | Oliveira et al. (2015)  |
| Squamata | Gekkonidae       | <i>Lygodactylus klugei</i>      | ND4        | 680                  | This study              |
| Squamata | Phyllodactylidae | <i>Phyllopezus pollicaris</i>   | Cytb       | 943                  | Werneck et al. (2012)   |
| Squamata | Tropiduridae     | <i>Tropidurus hispidus</i>      | COI        | 584                  | This study              |
| Squamata | Tropiduridae     | <i>Tropidurus semitaeniatus</i> | 16s + Cytb | 931                  | Werneck et al. (2015)   |

standardized these metrics (ranging from 0 to 1) to bring nucleotide diversity metrics to the same scale among taxa, so each of them could contribute equally to the analysis. The standardization procedure is a conservative approach given the challenges associated with the use of different genetic markers with distinct rates of evolution. Localities less than 15 km apart were merged, and nucleotide diversity averaged. Subsequently, we interpolated nucleotide diversity estimates among localities (kriging) for each species and summed the resulting maps for all species together to obtain the final spatial surface of genetic diversity. Although some sampled localities are outside the Caatinga, they are close to the border of this region, and we used these localities as buffers to prevent low genetic diversity estimates at the borders of the biome due to inadequate sampling.

Our dataset contained unequal sampling within localities. To ensure that sampling did not bias our results, we performed a linear regression for each species between the number of sequences per locality and nucleotide diversity. The number of sequences per locality did not affect nucleotide diversity, except for *C. greeningi*. This relationship however was not significant when extreme values were removed, indicating that low sampling was most likely related to the positive relationship found (only 8 localities were sampled). Thus, we kept *C. greeningi* in our final analyses. Information on nucleotide diversity for each sampled locality, species-specific interpolated maps, errors associated with kriging, and individual linear regressions are presented in supplementary material.

## Conservation assessment

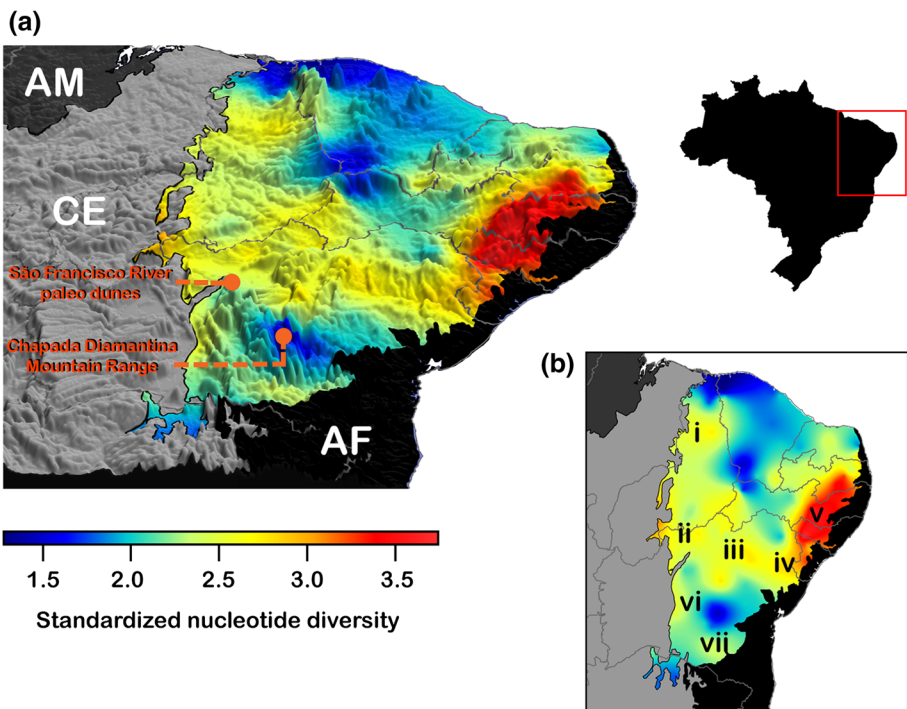
To assess how much the current network of Caatinga strict nature reserves overlaps with higher genetic diversity areas and suggest conservation targets, we mapped regions with above-median genetic diversity. Subsequently, we divided those areas into three categories: (I) moderate diversity: areas with genetic diversity between 50th and 75th percentile; (II) high diversity: areas with genetic diversity between 75th and 90th percentile; and (III) very high diversity: areas with genetic diversity above the 90th percentile. Next, we added the 2008 shapefile of vegetation cover for the Caatinga and kept only higher genetic diversity, nonimpacted areas on the map. We used strict nature reserves defined by the Brazilian Ministry of the Environment to evaluate how genetic diversity is safeguarded by protected

areas. Finally, we tested whether strict nature reserves protect the higher genetic diversity areas more than expected by chance. For this analysis, we randomized the locations of the strict nature reserves in the Caatinga 500 times while keeping both the size and shape of the nature reserves and our final genetic diversity surface constant. Then, we calculated the area of the three categories described above within the randomized protected areas. In addition, we also calculated this metric considering all above-median areas placed inside protected areas (i.e. categories I, II, and III together).

## Results

Genetic diversity for the ten taxa is heterogeneously distributed across the Caatinga (Fig. 1). The average of genetic diversity across the surface, after summing the standardized maps, was  $2.32 \pm 0.41$  (range 1.2–3.74) standardized nucleotide diversity. We found the highest genetic diversity in the northeastern Caatinga, and lowest genetic diversity in the northwestern and southern Caatinga, the remaining areas having average genetic diversity values (Fig. 1).

Our resulting map shows above-median genetically diverse areas divided in the three proposed categories (I, II, and III), along with non-impacted areas and current strict nature



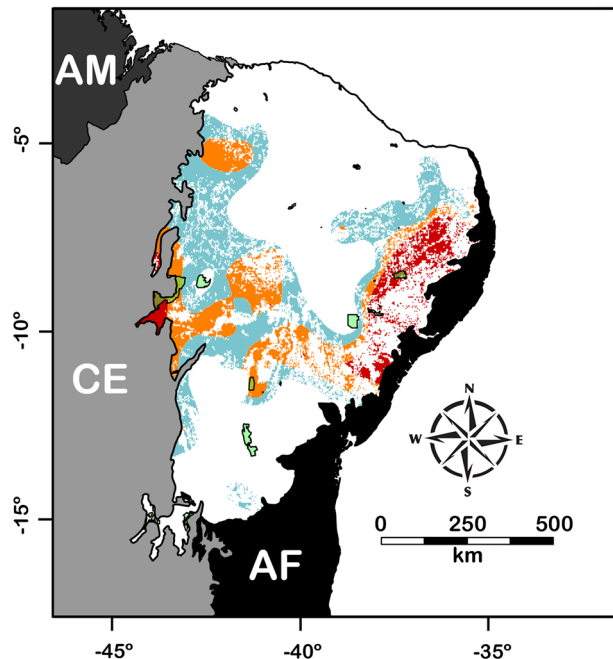
**Fig. 1** Multi-taxa genetic diversity surface across the Caatinga, as estimated by interpolation of standardized nucleotide diversity: **a** 3D map of genetic diversity coupled with terrain complexity and **b** 2D map of genetic diversity. Genetic diversity ranges from blue (lowest genetic diversity) to red (highest genetic diversity). (i) northwestern (ii) midwestern (iii) central, (iv) mideastern, (v) northeastern, (vi) southwestern, (vii) southeastern. AM Amazon, CE Cerrado, AF Atlantic Forest, gray lines = limits of the Brazilian states

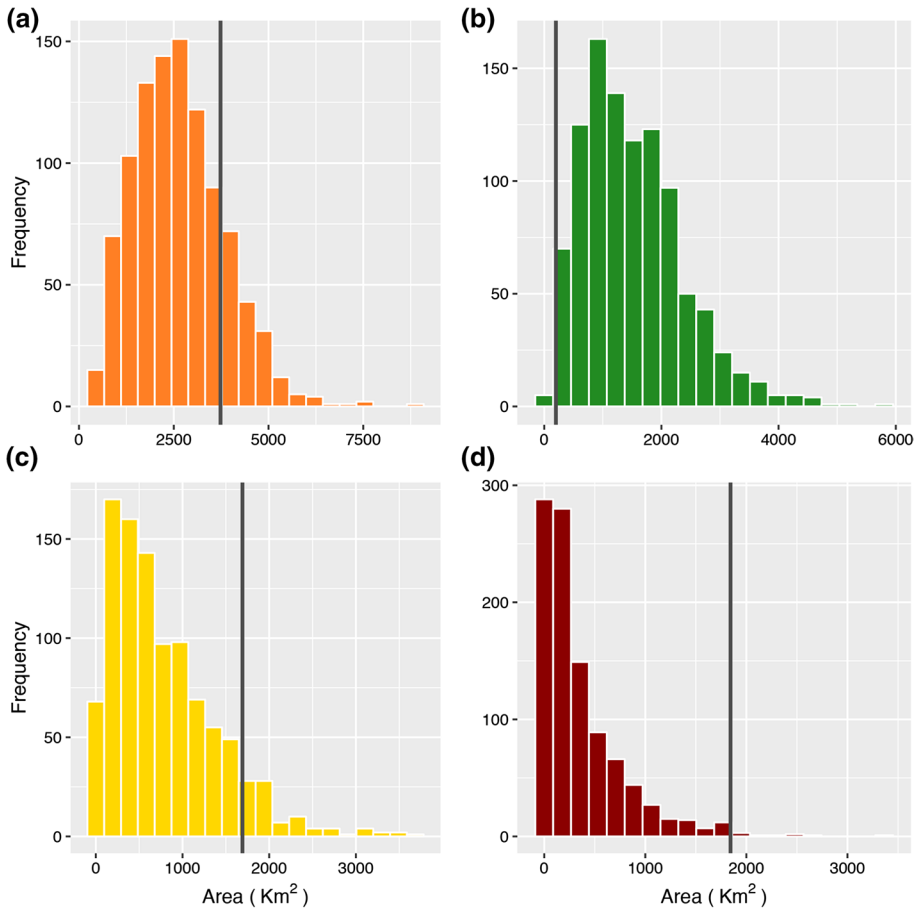
reserves in the Caatinga (Fig. 2). We calculated that only 57% (236,881 km<sup>2</sup>) of higher genetic diversity regions are non-impacted and could be set for immediate conservation purposes (Fig. 2). Additionally, our results show that 136,011 km<sup>2</sup> (16.5% of the Caatinga) has moderate diversity, 68,608 km<sup>2</sup> (8.3%) has high diversity, and only 32,261 km<sup>2</sup> (3.9%) contains very high diversity (Fig. 2). However, only 3733 km<sup>2</sup> of such areas, which represent 1.5% of the areas holding higher genetic diversity, are under strict protection (0.45% of the Caatinga, Fig. 2). Within strict nature reserves, 199 km<sup>2</sup> (0.02% of the Caatinga) corresponds to moderate genetic diversity areas, 1691 km<sup>2</sup> (0.20% of the Caatinga) to high genetic diversity, and 1843 km<sup>2</sup> (0.22%) to very high genetic diversity. We found that above-median and high genetic diversity areas inside strict nature reserves are not different than expected by chance (Fig. 3a, b,  $p=0.304$  and  $0.156$ , respectively). Additionally, moderate genetic diversity areas are underrepresented inside strict nature reserves (Fig. 3c,  $p=0.002$ ). Conversely, very high genetic diversity areas are more protected than would be expected by chance alone (Fig. 3d,  $p=0.012$ ).

## Discussion

This study provides the first spatially explicit estimate of species genetic diversity across multiple taxa in the Caatinga. Our findings show that for the species analyzed in this study, the northeastern Caatinga concentrates the highest level of genetic diversity, representing potential sources of evolutionary novelty. Our results indicate that while very high genetic diversity areas are overrepresented within strict nature reserves, moderate genetic diversity areas are underrepresented. Additionally, strict nature reserves safeguard the same amount of overall and high genetic diversity areas as would be expected by chance.

**Fig. 2** Priority areas for conservation derived from higher genetic diversity regions and nonimpacted areas. Blue areas within Caatinga present moderate diversity, orange areas have high diversity, and red areas exhibit very high diversity. Green polygons represent current strict nature reserves





**Fig. 3** Null distribution of genetic diversity inside strict nature reserves through 500 randomizations for: **a** above-median genetic diversity, **b** moderate genetic diversity, **c** high genetic diversity, and **d** very high genetic diversity

### Pattern of genetic diversity

Many regions with high genetic diversity coincide with regions previously reported to have high species richness and endemism in the Caatinga. A similar pattern was found in tree species from temperate forests in South America, where high species richness was associated with areas of high genetic diversity (Souto et al. 2015). In our study, a continuous block in the northeast Caatinga, near the contact zone with the Atlantic Forest, recovered the highest values of genetic diversity, which encompasses areas such as “Brejo Parai-bano”, Catimbau National Park, and part of the Borborema plateau. This area was recently highlighted as a region of great biodiversity potential (Garda et al. 2017). Areas with average genetic diversity were congruent with endemism areas recovered for squamates at the center of the Caatinga (Guedes et al. 2014; Oliveira and Diniz-Filho 2010; Mesquita et al. 2017), amphibians at the east edge of the ecoregion (Camardelli and Napoli 2012; Oliveira and Diniz-Filho 2010; Garda et al. 2017), and mammals in parts of the east edge of the

Caatinga moving towards its center (Oliveira and Diniz-Filho 2010). In addition, located in the midwestern Caatinga, the São Francisco River paleo dunes (Fig. 1) was recovered as an area of average genetic diversity. This region is recognized as a prominent diversification center for squamates that covers only 7000 km<sup>2</sup> (~0.8% of the Caatinga extension), but about 17% of lizard species from the Caatinga are endemic to this region (Rodrigues 1996; Mesquita et al. 2017). Furthermore, plant species were also reported as endemic to this formation (Rocha et al. 2004). The mideastern Caatinga has also been reported as holding high levels of species richness for amphibians and reptiles (Garda et al. 2013; Pedrosa et al. 2014). Despite the recent recognition that the Caatinga has high levels of richness and endemism, most of this region is still largely unsampled or insufficiently sampled (Tabarelli & Vicente 2004; Cavalcanti et al. 2014). We encourage future research at all higher genetic diversity areas to determine if they are also congruent with centers of species richness and endemism.

The processes that have driven the evolution of the Caatinga biota have been complex during its evolutionary history. The increased aridity during the Pleistocene led to a conspicuous demographic expansion across many species (Gehara et al. 2017; also see Thomé et al. 2016). In addition, studies have also shown the importance of ancient diversification (Werneck et al. 2012; Magalhaes et al. 2014; Lanna et al. 2018), niche differentiation (Fonseca et al. 2018), climate (Oliveira and Diniz-Filho 2010; Oliveira et al. 2017), bottlenecks (Magalhaes et al. 2014), founder effects (Oliveira et al. 2015), and rivers (Werneck et al. 2015) in determining the current patterns of genetic structure. Nonetheless, spatial patterns of diversity are not homogeneous among different groups and our genetic diversity map showed differences with respect to that from bird species richness, for example. Any diversity map potentially mirrors differences in underlying ecological, evolutionary, and historical processes. For example, Oliveira and Diniz-Filho (2010) showed that environmental instability was the best predictor of amphibian and reptile richness, whereas dry conditions acted as constraints. Meanwhile, species richness for birds and mammals is linked to environmental energy and is restricted by hot environmental conditions. Thus, species-specific ecological and physiological preferences and tolerances can lead to differential spatial patterns of distribution.

Surprisingly, a large extension of the Chapada Diamantina was recovered showing low genetic diversity (Fig. 1). This region is well-recognized for harboring high levels of endemism and richness and holds a unique biota (Juncá et al. 2005). The Chapada Diamantina is located at the northern end of the Espinhaço Range, a large block of disjunct mountains stretching from southeastern Brazil to south of the Caatinga that share a complex geomorphological and evolutionary history (Rapini et al. 2008; Bitencourt and Rapini 2013). The Chapada Diamantina may hold a dissimilar evolutionary history in comparison to the rest of the Caatinga. As our study evaluated genetic trends of widely distributed Caatinga species, they might not serve as a proxy for Chapada Diamantina evolutionary history. Despite the low genetic diversity found for areas of the Chapada Diamantina, this region exhibited the most divergent populations in some cases (e.g., *Ameivula ocellifera* in Oliveira et al. 2017). Other possible explanations could be related to recent colonization of the Chapada Diamantina by widespread Caatinga species. A recent study showed that there is strong support for synchronous effective population size expansion since the Late Pleistocene in the Caatinga (Gehara et al. 2017). Five species included in the Gehara et al. (2017) study were also included in our analysis (*Ameivula ocellifera*, *Lygodactylus klugei*, *Phyllopezus pollicaris*, *Pleurodema diplolister*, and *Rhinella jimi*). Thus, we hypothesize that most of the species analyzed in this study have only recently expanded their range to the



Chapada Diamantina as well as other low diversity areas. Alternatively, they also could have persisted in these areas with very low effective population size, which also could account for the patterns of low genetic diversity.

## Conservation

Even though very high genetic diversity areas are overrepresented inside protected areas, the network of protected areas in the Caatinga is still not sufficient to protect current spatial patterns of genetic diversity. Currently, only 1.5% of the higher genetic diversity areas are protected by strict nature reserves. This pattern is also shared with other Seasonally Dry Tropical Forests in the Neotropical region (Banda-R et al. 2016). Several threats (e.g., human occupation, grazing, and logging) are causing a desertification process in parts of the Caatinga, with at least one-third of this region already under imminent desertification risk (Leal et al. 2005; Marinho et al. 2016; Silva and Barbosa 2017). Despite this scenario, we identified large areas of the Caatinga that still have great potential for conservation due to their higher genetic diversity across multiple species (see Fig. 2). Additionally, our findings may assist the identification of potential ecological corridors. We found a large patch of higher genetic diversity areas in the northeastern Caatinga (see Fig. 2). In a recent study, Antongiovanni et al. (2018) found that although only half of the Caatinga is covered by original vegetation, the remaining fragments include relatively well connected large-sized patches. However, authors warned that these fragments are still highly susceptible to human disturbance. Thus, maintenance and connection of these areas will be central to protect the Caatinga biodiversity in the long-term.

Conservation actions (e.g., prioritization mapping, exploratory research, creation of protected areas, ecological corridors, and biodiversity monitoring) are urgently needed to avoid loss of genetic diversity. Declining genetic diversity can increase inbreeding rates and decrease fitness within populations, dramatically increasing the risk of population collapses and eventually species extinctions (Reed and Frankham 2003; Frankham 2005; Jordan et al. 2016). Genetic diversity is known to provide the necessary information for populations to evolve and adapt in changing environments (Frankham et al. 2002), thus is essential to guarantee viability and persistence of biodiversity over time.

Although we found that very high genetic diversity areas are represented more than expected by chance in strict nature reserves, their absolute area still safeguards only a small portion of the evolutionary history of the Caatinga. Consequently, the vast majority of these areas are unprotected, which stresses the urgency for conservation actions that minimize the loss of biodiversity given current threats. Therefore, reconciling our findings with taxonomic, phylogenetic, and functional diversity as well as economic and social information will be crucial for effective decision-making in conservation planning. Additionally, because our dataset depicts only a small fraction of the Caatinga species richness, it is necessary that future studies investigate the generality of our findings and include more species and taxonomic groups, as well as wider genetic coverage within each species. In particular, we expect, for example, concordant patterns of genetic diversity in groups that show similar patterns of species richness. We also stress that one key direction will be to incorporate species with discordant patterns of diversity (e.g., our findings and bird species richness) to provide a broader perspective.

## Concluding remarks

Based on the spatially explicit multi-taxon approach, we show that genetic diversity is heterogeneously distributed throughout the Caatinga landscape. Some of the higher genetically diverse areas match species rich areas, while other localities with high levels of endemism and species richness have low genetic diversity for the species analyzed. Additionally, we show potential target areas for conservation due to their higher genetic diversity. Finally, we highlight that the growing amount of genetic information available in GenBank for a multitude of species has enabled researchers to address several new biological questions via data repurposing. The integration of this information into conservation planning can be used to more effectively protect biodiversity in the long-term. Thus, we emphasize that our approach has the potential to inform conservation priorities around the world in a refined way that it is not possible using only distributional species maps.

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