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Original research article

Should I stay or should I go? Climate change effects on the future of Neotropical savannah bats





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HIGHLIGHTS

- Climate change will impact 36 Cerrado's bat species if displacement is not considered.
- Important areas for bat species occurrence in 2050 are located more than 281 km away from current ones.
- Future competition for space between agriculture and biodiversity may enhance the impacts of climate change.
- Corridors to facilitate bat's movement must be implemented to mitigate such expected impacts.

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ABSTRACT

Most extant species are survivors of the last climate change event 20,000 years ago. While past events took place over thousands of years, current climate change is occurring much faster, over a few decades. We modelled the potential distribution area of bat species in the Brazilian Cerrado, a Neotropical savannah, and assessed the potential impacts of climate change up to 2050 in two scenarios. First we evaluated what the impact on the distributions of bat species would be if they were unable to move to areas where climate conditions might be similar to current ones. The novelty of our paper is that, based on least-cost-path analyses, we identified potential corridors that could be managed now to mitigate potential impacts of climate change. Our results indicate that on average, in the future bat species would find similar climate conditions 281 km southeast from current regions. If bat species were not able to move to new suitable areas and were unable to adapt, then 36 species (31.6%) could lose > 80% of their current distribution area, and five species will lose more than 98% of their distribution area in the Brazilian Cerrado. In contrast, if bat species are able to reach such areas, then the number of highly impacted species will be reduced to nine, with none of them likely to disappear from the Cerrado. We present measures that could be implemented immediately to mitigate future climate change impacts.

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1. Introduction

Climate change is a frequent event in the Earth's history and at least four major events have occurred in the last 420,000 years (Petit et al., 1999). The speed of current climate change is likely to pose a serious threat to a large number of

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species (Bradshaw and Holzapfel, 2006). Despite the uncertainties of climate-change models, it is necessary to implement measures now to prevent the negative effects of this process (Ekins and Speck, 2013). Currently, there are 40 (0.7%) mammal species, 814 (7.8%), birds 76 (1.2%) amphibians, 69 (1.6%) reptiles and 175 (4.4%) fish assessed by IUCN that might be experiencing habitat shifts and modification due to climate change (IUCN, 2015).

The impacts of a number of climate change scenarios on the geographic distribution of fauna and flora have been assessed by using ecological niche modelling over a wide range of taxa and locations (Chapman et al., 2014). The vulnerability of each species will depend on a combination of degree of exposure, sensitivity and adaptive capacity. Although accurate predictions on impacts are needed, they are difficult to formulate (Dawson et al., 2011). Three fundamental aspects of animal and plant shifts are among the most discussed. The first is about the methods to generate accurate models of future distribution (Araújo et al., 2005; Diniz-Filho et al., 2009). The second aspect concerns the adaptive capacity of organisms to move to newly suitable areas (Bradshaw and Holzapfel, 2006; Rebelo et al., 2010). Third, the localisation of the suitable niches in the future has received considerable attention (Schloss et al., 2012).

The Brazilian Cerrado is an area of considerable conservation importance that is at risk from climate change. The region consists of savannah-like vegetation that was shaped by past climatic oscillations of the Tertiary and Quaternary. The biodiversity of the Cerrado may have increased because of earlier interchanges with neighbouring forested biomes (da Silva and Bates, 2002). Because of a heterogeneous geology and geomorphology, and high diversity in soil types and climate (Eiten, 1972; Furley and Ratter, 1988), the Cerrado is a mosaic continuum of different phytophysiognomies ranging from grasslands to closed canopy forests (Eiten, 1972).

Recent research has shown that climate change is likely to drastically alter the potential distribution of Cerrado plant species, with many species potentially experiencing a reduction of 50%–90% in their geographical range (Siqueira and Peterson, 2003). These changes in distribution are particularly important when plant species with economic and cultural importance are involved. Endemic species such as *Lychnophora ericoides* (Brazilian arnica) and *Caryocar brasiliense* (souari nut) are used in medicine and as food, and may lose >90% of their geographic distribution across the Cerrado (Simon et al., 2013). Such species may no longer be economically viable for many rural communities in the future (Nabout et al., 2011). Besides the range reduction, plant species will be restricted to suitable places located in the most degraded area of Brazil (southern and eastern regions of Cerrado) (Collevatti et al., 2011; Simon et al., 2013). For Cerrado birds, the same suitable areas in the future have been predicted (Marini et al., 2009). However, climate change may affect savannah-dependent bird species less harshly than forest and grassland-dependent species (Marini et al., 2009).

Agricultural expansion is the primary cause of the reduction of the Cerrado (Klink and Machado, 2005) and current estimates indicate an annual rate of loss of 0.7%, i.e. 700,000 ha/year (Brasil, 2011). Due to the short time frame (last 40 years) and high rate of continuous deforestation, the Cerrado is nowadays considered to be the most threatened savannah in the world and one of the most threatened biomes in Brazil (da Silva and Bates, 2002). Even though the Cerrado is a hotspot for biodiversity (Myers et al., 2000), top-down decision-making does not reflect its urgent conservation needs. This is reflected by the small amount of protected areas (<3% of the original area) in the Cerrado (Klink and Machado, 2005).

Although few bat surveys have been conducted in the Cerrado (Bernard et al., 2011), bats play important social and economic roles in the local people's lives. Bats pollinate and disperse seeds of locally used plants (including the aforementioned *C. brasiliensis*). Bats also eat large numbers of insect pests in the Cerrado (Aguiar and Antonini, 2008; Bobrowiec and Oliveira, 2012). Understanding how climate change may affect the future distribution of bats in the Cerrado is therefore important from conservation and sustainability perspectives.

Few climate change models have incorporated present land use in their evaluation of potential barriers for biodiversity niche shifts (Faleiro et al., 2013). Whether species will be able to establish populations in areas that match the current set of environmental conditions will depend largely on the current fragmentation status of suitable habitat (Lawler et al., 2013). Thus, here we used the ecological niche model approach to map current distribution patterns of bat species distributed in the Brazilian Cerrado. We compared such scenarios with maps reflecting future environmental conditions. To highlight our primary objective, the effect of climate change on bats was verified and actions that might mitigate potential impacts identified and proposed. Our basic assumption is that climate change will decrease current environmental suitability for bats in the Cerrado by modifying the temperature, precipitation regime and occurrence of extreme climate events. These abiotic parameters are those previewed to be changed in the near future (IPCC, 2003; van Vuuren et al., 2011). Under such scenario, the bats of the Cerrado would have only two options: (a) move to new suitable areas or (b) try to adapt to new climate conditions in the Cerrado region.

In this paper, our predictions are that if bats are not able to disperse to new suitable areas, then their habitats will shrink causing significant impacts on species persistence. On the other hand, bats that are able to disperse to new suitable areas may have problems reaching such areas depending on current landscape connectivity and habitat health.

To evaluate those predictions, we defined two scenarios to assess the bats' response to climate. The first scenario is based on the assumption that species will not be able to disperse, that is to say they will not reach the future suitable areas outside of their current range. The second scenario considers that species will use the future suitable areas, but to that they will have to face a very fragmented and human-dominated landscape. We identify routes that would facilitate the movement of bats into areas that may become more suitable for them in the future, and highlight these routes as priorities for conservation.



Fig. 1. Location of the Brazilian Cerrado (green area), the grid created for spatial analysis (cells of 0.5×0.5 decimal degrees) and bat species occurrences used for ecological niche modelling. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2. Data and methods

2.1. Study area

The Cerrado is the largest continuous savannah in South America. It is comparable in size to Western Europe, and covers 23% of the land surface of Brazil (da Silva and Bates, 2002). Nevertheless, only 20% of its original vegetation has remained undisturbed (Myers et al., 2000). Brazil has a large agribusiness economy, and has the 7th largest economy globally (World Bank, 2014). The Cerrado plays a significant role in the country's economy contributing 23.6% to the 2012 Brazilian GDP (Brasil, 2014).

In this paper we considered the official boundaries of the Brazilian Cerrado (Brasil, 2004), which covers an area of 2.03 million km² (Fig. 1), but we have excluded Cerrado extensions through Bolivia and Paraguay, and the enclaves in the neighbouring Brazilian biomes such as the Amazonia, Caatinga (seasonal dry forest) and Atlantic Forest.

The Cerrado is considered to be the most biodiverse savannah in the world (Mittermeier et al., 1999). Currently, there are more than 12,600 plant species recorded in the region (Mendonça et al., 2008) and up to 450 vascular plants can be found in a single hectare (Eiten, 1994). The fauna includes 251 mammal species (Paglia et al., 2012), 850 birds (approximately half of Brazilian birds) (Silva, 1995), 237 reptiles and amphibians (Costa et al., 2007), and >1500 fish.

2.2. Species occurrence and niche modelling

To model the potential distribution of bats that occur and may occur in the Cerrado we initially used a database composed of 262 bat species recorded in 20,143 localities in South America, including all 178 bat species registered in Brazil (Nogueira et al., 2014). A total of 7350 (36.4%) records represent the geographical distribution of Brazilian bats obtained by the first author after continuous review of specialised literature and voucher specimens in museums. The other 13,538 records (62.6%) are from the Global Biodiversity Information Facility–GBIF (http://www.gbif.org) for bats present in other South American countries except Brazil (see Supplementary Material, Table 2, Appendix A).

For the purpose of this study, the occurrence of each bat species in one locality was counted only once to avoiding spatial overlap of records. Only species with at least five localities of occurrence were considered in the analysis. Therefore, our database comprised 14,936 records of 221 species.

We used Maxent v3.2.1.software (Phillips et al., 2004) to model bat species environmental suitability in the present and in 2050. Maxent was chosen to run all models, not just because it is the most widely used program for ecological niche models, but also as it is very robust. Maxent has been systematically compared to other algorithms and its predictive performance has been consistently similar to other methods (Elith et al., 2006).

We used a climate dataset of \sim 5 × 5 km of spatial resolution (2.5 min of latitude/longitude) available at WorldClim page (Hijmans et al., 2004) and a set of 20 variables (19 bioclimatic variables plus a digital elevation model). For future climate conditions, we downloaded the corresponding set of bioclimatic variables for all 16 global circulation models available for the Representative Concentration Pathways 4.5 (RCP 4.5). The RCP 4.5 is the result of a model for possible future climate (in 2050 in our case) in which the mean annual temperature would increase from 0.9 to 2.0°C (IPCC, 2003; van Vuuren et al., 2011). We used 16 climatic models and each model had 19 variables, thus we used the *raster* package in R (Hijmans et al., 2014) to average each bioclimatic variable and to export them in a compatible format for use with Maxent.

In order to avoid co-linearity among bioclimatic variables, we proceeded as in other similar studies (Costa et al., 2010). First, we built a matrix of each bioclimatic variable value according to each bat species occurrence, using the *raster* package in R. Then, we calculated the Pearson correlation index among the 19 pairs of variables and eliminated one of the two variables where the correlation index was equal to or greater than 0.7. After our selection, we used a set of variables: altitude, annual mean temperature (Bio1), mean diurnal temperature range (Bio2), isothermality (Bio3), temperature seasonality (Bio4), maximum temperature of the warmest month (Bio5), annual precipitation (Bio12), precipitation of the driest month (Bio14) and precipitation seasonality (Bio15).

Initially we used the geographical area of South America to create the models for all bat species with ten or more records. As explained below, the models were subsequently cropped to the boundaries of the Cerrado. We created 10 replicates for each species modelled and used the bootstrap option for validation. The bootstrap rule is recommended for modelling species with few occurrences (Phillips and Dudík, 2008) because all available points can be used (with replacements) to train and to test the models. We used 20% of each species occurrence to test the models as a general procedure, and kept the average model for each species. Following the procedures given by Peterson et al. (2008) and Peterson (2012) we used the Partial ROC (Receiver Operating Characteristic) to test whenever a model was significant or not. The method basically generates a ROC-AUC (Area Under the Curve) ratio, where the AUC at the given 1-ommission threshold is compared with the AUC of a random model (i.e., a model with AUC at 50%). The procedure was replicated 1000 times for each species, being that the number of test points was randomly changed at each run. We considered a model as valid when 95% of the runs presented values above 1 (Barve, 2008).

2.3. Spatial analysis with the models

We created binary maps (1 = potential presence, 0 = absence) for present and future scenarios for all species using the 10th percentile training logistic threshold to reclassify the models. Then, we cropped the maps to fit the Cerrado boundaries and tabulated each pair of species to produce a 'gain-lose' map. Basically, these maps contained three classes: areas present today that will not be present in the future (environmental suitability loss); areas that are present today and will be present in the future (environmental suitability refuges); and areas that are not present today but will be present in the future (environmental suitability percent). We used the number of pixels per class as a proxy of the size of each bat species' potential distribution.

To calculate the coordinates of the centre of gravity (centre of distribution or centre of mass) for each pair of maps per species, in current and future potential distribution, we used the *SDMTools* package (VanDerWal et al., 2014). To calculate the direction (azimuth) and the distance between the two centres of gravity for each species we used the *gDistance* package (van Etten, 2014). We tested if the species displacement directions (the azimuth value) would be different from the expected, by chance or not, by applying a test of circular homogeneity (Watson's test), available in the *circular* package (Lund, 2013). We also used the coordinates of the centres of distribution of each species to calculate a potential dispersion route from current to future distributions. In order to do that, we used the least-cost path method and modelled a hypothetical path between two points accordingly to a surface cost map (the origin is the point of current distribution and the destination is the point of future distribution). We used an inverted map of current environmental suitability as a surface cost, meaning that higher values of environmental suitability would favour the displacement between two points, whilst lower values would constrain displacement.

To add more reality to our surface cost map, we used the native vegetation remnants map for the Cerrado (Brasil, 2009b) and eliminated all deforested areas up to the year of 2010. In this case, we applied a high value to the deforested areas, arbitrarily set as 1000 to force the model to avoid deforested areas and look for suitable areas. We used the package *gDistance* to create the least-cost path between the origin and destination points. Using the *raster* package, we converted all paths to a raster format and overlaid them to generate a map with the concentration (spatial agreement) of paths. We used the Zero-inflated count data regression available in the *pscl* package (Jackman, 2015) to test the relationship of corridor concentration and the fragmentation status of different regions of the Cerrado, as described below.



Fig. 2. Distribution of frequency of the potential loss of areas of environmental suitability under the climate change scenario (2050) for Cerrado bat species. A represents a situation without displacement, whilst B represents a scenario with species displacement. Numbers above the bars represent the number of bat species in each class.

2.4. Fragmentation status of the Cerrado

Initially, we divided the biome into 676 regular cells of 0.5×0.5 decimal degrees (Fig. 1) and calculated landscape metrics for each one. We converted the native vegetation shape file of the Cerrado (Brasil, 2009a) to a raster file with 120 m of spatial resolution and used the package *SDMTools* to extract several landscape metrics for each cell. From the 38 available landscape metrics provided by the function ClassStat (package *SDMTools*), we selected seven landscape metrics plus the mean nearest-neighbour distance to characterise fragmentation status (Supplementary Table 1, Appendix A). We estimated the mean distance between all fragments in a cell by calculating the distance from centroid to centroid for each pair of fragments. These procedures were done for each of the 676 cells and only fragments larger than 40 ha were considered.

The status of fragmentation for each cell was defined by performing a principal component analysis with the package *FactoMiner* (Husson et al., 2014). We kept the first two components and classified all cells accordingly to the cell position in two dimensional space: 1 for the first quadrant (positive values on the first component and negative values on the second component), 2 for the second quadrant (negative values in both components), 3 (negative values on the first and positive on the second component), and 4 (positive values on both components). We assumed that each quadrant would represent a distinct fragmentation status.

3. Results

At least 118 bat species occur in the Brazilian Cerrado (Supplementary Table S2, Appendix A), corresponding to 66.3% of all bat species recorded in Brazil (Nogueira et al., 2014), hence comprising 10.5% of all bat species in the world (Simmons, 2006) and 47.0% of the mammals known from the Cerrado. According to our models, another 24 species could potentially occur in the biome (Supplementary Table S2, Appendix A). A total of 14 species was not modelled due to the lack of occurrences (less than 10 records). Among the modelled species, 13 of them did not present a significant model, considering the Partial ROC test. Therefore, the following results are for 116-modelled species, being 95 (81.1% of all Cerrado's species) with the confirmed occurrence in the Cerrado and another 20 that are expected to occur in the biome.

Our results revealed that if species of bats were not able to reach suitable areas in the future (i.e. with no dispersal following the environmental suitability loss scenario), 36 bat species (31.6%) are predicted to lose more than 80% of their suitable habitat (Fig. 2(a)). Five species (*Hsunycteris thomasi, Thyroptera discifera, Sturnira magna, Sturnira tildae* and *Vampyrodes caraccioli*) are predicted to lose more than 98% of their suitable areas and could present unviable populations in the Cerrado (Supplementary Table S2, Appendix A).

The environmental suitability loss scenario with no dispersal also suggests that 25 species (21.9%) could lose <20% of their current area of distribution (Fig. 2(a)). However, if the species were able to reach suitable areas in the future, then 77



Fig. 3. The directions and magnitude of the potential displacements between current (year 2000) and future environmental areas (year 2050) for 110 bat species found in the Brazilian Cerrado. The circular graphic in the detail shows the frequency of species according to the expected directions of displacement.

species (67.5%) are predicted to lose <20% of their suitable habitat (Fig. 2(b)) and only three species (2.6%) would lose more than 80% of their distribution. No bat species is predicted to have no remaining habitat in the Cerrado if dispersal can occur.

The displacement analysis suggests that the future suitable areas will be located, on average, 281.0 km (N = 110, S.D. = 254.0, max = 1567.5 km) distant, mainly in southeastern directions (Fig. 3). Such directions differ significantly from a direction expected by chance (Watson's test = 1.1964, p < 0.01). The paths among points created with the least-cost analysis showed that most corridors are concentrated on the mid-south of the Cerrado, one of its most fragmented regions (Fig. 4) as shown by the landscape metrics analysis.

The principal component analysis (PCA) categorised the Cerrado into four different regions according to fragmentation status (Fig. 5). The first two components of the PCA accounted for 69.8% of the original variance (Fig. 5; Table 1). The comparison of cells located in quadrants 1 and 4, with cells located in quadrants 2 and 3, shows that the former cells were characterised as having fewer but larger patches of remaining natural vegetation, therefore a greater mean patch size (Table 2). This situation can also be seen in Fig. 5, where the first component groups cells 2 or 3, according to metrics such as edge density and number of patches. The potential displacement corridors between current and future suitable areas tend to be concentrated in more fragmented cells (quadrants 2 and 3) (Fig. 6) than in the less fragmented ones (quadrants 1 and 4) (z = 5.321, p < 0.01).

4. Discussion

We predicted impacts of climate change on the future distribution of bats of the Brazilian Cerrado according to two different scenarios: one scenario that does not consider species dispersal and a second scenario that assumes future suitable areas will be reached by bat species. In both scenarios the local bat fauna would suffer impacts, from relatively low severity to the potential local extinction for some species. These scenarios are useful to define strategies that could dampen the negative effects of climate change, which is expressed here in terms of loss of environmental suitability. Our analyses were performed within the current Cerrado boundary, although we are aware that current boundaries might change in the future in response to climatic change (Siqueira and Peterson, 2003).

Some recent papers that have evaluated the potential impacts of climate change on animals (Pacifici et al., 2015) have mainly assessed predicted changes in distribution rather than evaluating the potential of species to adapt to climate change. In our case bats may have limited adaptive potential given their slow reproductive rates relative to the speed of climate



Fig. 4. Fragmentation status of the Brazilian Cerrado represented in cells of 0.5×0.5 decimal degrees. Areas in light and dark green are less fragmented than pink and dark pink areas. Each class (1–4) represents a quadrant in a PCA analysis based on seven landscape metrics for existing native fragments in 2009. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)



Fig. 5. Definition of the fragmentation status of the Cerrado vegetation (quadrants 1–4) based on the two first components of PCA analysis. Each quadrant is characterised by the corresponding landscape metrics. Acronyms: total remaining area (rem), largest patch index (lpi), mean nearest neighbour (dist), number of fragments (nump), edge density (edge), mean shape index (msi) and mean patch size (mps).

change. In general, it is expected that species should move from their current areas of occurrence to the new climatesuitable areas or to have their populations reduced in size due to the loss of environmental suitability (Ehrlen and Morris, 2015; Thomas et al., 2004). Since it is expected that endothermic organisms (such as bats) have a tendency to maintain their

Table 1

Eigen values and factor loadings for the principal component analysis performed with landscape metrics in the Brazilian Cerrado.

	Cmp 1	Cmp 2	Cmp 3
Variance (%)	56.22	16.07	13.45
Cumulative variance	56.22	72.29	85.74
Edge	-0.937	0.197	0.134
Nump	-0.870	0.148	0.149
Dist	0.279	-0.246	0.920
Msi	0.503	0.703	0.017
Mps	0.525	0.662	0.209
Lpi	0.914	-0.246	-0.104
Area	0.927	-0.101	-0.027

Table 2

Values of landscape metrics used on the fragmentation analysis of the Brazilian Cerrado. Each parameter represents a summary for cells (an area of 0.5 × 0.5 degrees) belonging to each quadrant (1–4) resultant from a PCA analysis.

Metric	Parameter	Q1 N = 260	Q2 N-124	Q3 N = 185	$\begin{array}{l} \mathrm{Q4} \\ \mathrm{N} = 102 \end{array}$
Area—total area extant in a cell (in hectares)	Mean	203765.7	86476.7	65223.6	218514.8
	Min	57599.9	3104.4	10674.3	55099.8
	Max	301800.5	161527.4	153238.2	304595.7
	SD	46603.8	40098.8	31444.2	68883.2
Lpi—largest patch index	Mean	0.912	0.424	0.257	0.894
	Min	0.413	0.031	0.018	0.357
	Max	1.000	0.893	0.859	1.000
	SD	0.114	0.226	0.192	0.171
Dist—mean nearest-neighbour distance (in km)	Mean	26.80	27.70	20.00	24.60
	Min	12.10	17.70	0.00	0.00
	Max	33.29	32.59	31.73	32.60
	SD	3.17	2.44	7.90	6.10
Nump—number of fragments in a cell	Mean	75.5	315.0	361.8	26.5
	Min	3	52	60	1
	Max	346	1116	1096	137
	SD	61.9	174.2	210.8	34.1
Edge—edge density in a cell	Mean	0.0012	0.0039	0.0050	0.0000
	Min	0.0001	0.0016	0.0015	0.0000
	Max	0.0030	0.0093	0.0102	0.0029
	SD	0.0006	0.0007	0.0019	0.0006
Mps—mean patch (fragment) size (in hectares)	Mean	7530.1	352.1	283.3	60313.1
	Min	515.7	29.5	27.1	942.1
	Max	100600.1	1117.4	1313.3	302695.7
	SD	11801.9	238.1	264.7	89065.9
Msi—mean shape index	Mean	1.5396	1.5098	1.4847	1.7748
	Min	1.2124	1.3016	1.2572	1.1840
	Max	2.2185	1.9723	2.1100	3.5889
	SD	0.1488	0.1043	0.1192	0.4296

niche adaptation (Araújo et al., 2013), it is plausible to assume that mitigation actions for climate change should focus on environmental management including the creation or maintenance of natural vegetation corridors.

Mitigation actions to attenuate negative impacts of climate change have been proposed in a range of studies conducted worldwide. However, most of them are related to carbon sequestration (Canadell and Raupach, 2008), food production and security (Godber and Wall, 2014; Ogle et al., 2014) or changes on the energetic matrix (Anand et al., 2015; Lähtinen et al., 2014). Specifically for biodiversity conservation under climate change scenarios, a recent compilation of papers (N = 113) that had proposed mitigation actions (N = 524) indicated that increasing connectivity (designing biodiversity corridors, removing barriers, or reforestation, for example) was the most frequent suggestion among a set of 16 categories (Heller and Zavaleta, 2009). It is not a surprise that increasing connectivity has been the most frequent suggestion, because one of the basic strategies for species conservation is the reduction of the isolation of populations in human-dominated landscapes (Beier and Noss, 1998; Briers, 2002; Gilbert-Norton et al., 2010; Root-Bernstein and Ladle, 2010). Furthermore, under climate change scenarios species could become locally extinct if they are not able to shift and track regions with suitable environmental conditions (Thomas et al., 2004). As indicated in this paper, almost a quarter of Cerrado's species will lose a significant part of their habitat and five of them could be locally extinct under the conditions modelled. Currently, these five species are of least concern according to IUCN criteria, but the most recent assessment considers only the size of species distribution and a supposed stability on their populations (IUCN). However, up to now, no modelling has been



Fig. 6. Location of corridors of dispersal between current and future environmental suitable areas for Cerrado bats. The classes (1–7) refer to the spatial agreement of different corridors.

applied to verify changes on habitat coverage, environmental suitability, population trends or effects of climate change to define conservation status for bats.

The identification of potential dispersal routes could be critical (Lawler et al., 2013) and the inclusion of information about habitat suitability could improve the efficacy of habitat corridors and species persistence in fragmented landscapes, as demonstrated by other studies (Gregory et al., 2014).

The displacement analysis conducted here, combined with the fragmentation analysis, suggest that conservation efforts should be concentrated in two regions if we are willing to mitigate the impacts of climate change on bats of the Cerrado.

First, increasing connectivity among fragments should be promoted in the centre of the Cerrado. This is where most of the bat species could potentially utilise effective dispersal corridors from current to future suitable habitats. Many factors can affect fragment connectivity, including the degree of accessibility of natural vegetation patches by animals or plant propagules. Although bats species have a relatively high dispersal ability compared with other mammals, the adoption of a stepping-stone scheme as a strategy to increase the landscape connectivity could benefit them. Even small bats can fly distances of up to 3.8 km between roosting and feeding sites (Aguiar et al., 2014). Thus they can fly short distances over deforested areas, and the stepping stone scheme can facilitate dispersal and diminish the chance of local extinction. Species with low wing loadings and low aspect ratios may travel the shortest distances (Jones et al., 1995), and these may benefit most from enhanced connectivity over short distances.

Moreover, the current fragmentation status combined with low native vegetation cover in the southern Cerrado suggests that some environmental management is necessary. Although the expected impacts of climate change on bats can involve a variety of aspects, including roost availability, foraging behaviour, reproduction timing, range limits (biogeography), incidence of extreme weather events, and diseases risk (Sherwin et al., 2013), the availability of high quality native habitat is probably essential for their persistence in any landscape, as demonstrated by some theoretical studies (Sondgerath and Schroder, 2002).

Future suitable areas are predicted to be largely present in the southeastern and southern Cerrado, although these regions possess a large number of small fragments. Thus, landscape management in these regions should aim to restore degraded areas and enlarge fragments of native vegetation. As demonstrated by other studies, this is a valid conservation measure that can be used as an alternative to the establishment of ecological corridors (Falcy and Estades, 2007). Fragmentation can cause deleterious effects on biodiversity and the loss of ecosystem services, especially in small (Haddad et al., 2015) and isolated

fragments (Villard et al., 2014). The combination of changes in land use and climate is important for defining priority regions for conservation, as demonstrated for non-volant mammals in the Brazilian Cerrado (Faleiro et al., 2013).

The five species that could be threatened in the future are currently considered as of least concern (IUCN). All are widespread, relatively common and thought to occur in large subpopulations. Although, all of them are indicated as potentially occurring in the Cerrado, the literature information associates them with streams and moist areas (Gardner, 2007) except *Thyroptera discifera* that has a verified record in the biome (Bezerra et al., 2005). *Sturnira magna* and *S. tildae*, as well as *Vampyrodes caraccioli* are primarily frugivorous. *Vampyrodes caraccioli* is larger than *Sturnira magna* and *S. tildae*. *H. thomasi* and *Thyroptera* are respectively nectarivorous and insectivorous, and both smaller than the frugivorous species. Other bat species recorded in the Cerrado have similar characteristics in terms of size and diet. We did not find any relationship between these factors and the amount of area that will be reduced in the future. Thus, one possible explanation to the risks potentially experienced by these five species is the location or their geographical distribution, which will be heavily impacted by climate change as indicated by our models.

4.1. Constraints and difficulties facing the implementation of mitigation actions in the Brazilian Cerrado

The Brazilian Cerrado is a natural region currently threatened by huge human pressure, measured in terms of the deforestation rate: in 2008 the deforestation rate was 14, 200 km² out of 2 million km² (Brasil, 2011), more than twice the deforestation rate observed for the Amazon in the same period (data available at http://www.obt.inpe.br/prodes/rates/r2008.htm). Thus, even if the simple maintenance of remaining natural vegetation in the Cerrado biome is a big challenge, the enlargement by management or restoration of degraded areas is a huge but important challenge for mitigating future climate change impacts.

A significant anthropogenic threat to the Cerrado is the expansion of the agricultural frontier. The region is an important area for the Brazilian agribusiness, which competes, and is likely to continue to compete, with biodiversity for space. Suitable areas for bat species in the future will be located in the southern parts of the biome, especially in the Goiás, Minas Gerais and São Paulo states. Previous studies assessing the effect of climate change on the biodiversity of Cerrado, for instance, on plants (Siqueira and Peterson, 2003) and birds (Marini et al., 2009) have shown the same displacement pattern found in our study. Such similarity may be due in part to the use of the same environmental database for modelling (the global climate models from Intergovernmental Panel on Climate Change—IPCC). The Brazilian Agricultural Research Corporation (EMBRAPA) also used the IPCC models to develop future scenarios for Brazilian agriculture (Assad and Pinto, 2008). Monocultures such as soybean or coffee could have a reduction of 41.3% and 33.0% respectively on their current suitable areas for plantation in Brazil. The models created for these monocultures indicate a displacement of suitable climate conditions to the southern regions in Brazil overlapping with where suitable conditions for many bats, plants and birds are predicted to occur.

Although human-dominated landscape and deforested areas impose major constraints for bat species displacement, the potential competition for space between agriculture and native species can in fact enhance the impacts of climate change. Therefore, urgent measures should be adopted immediately to ensure that (1) fragments of natural habitats will not disappear due to deforestation and (2) areas designated as agricultural plantations in the future should also include the necessary natural areas to ensure the continued existence of bat species. Without this environmental safeguarding, a repetition of past Cerrado dire conservation failures may be experienced.

5. Conclusions

Climate change is likely to have an impact on bats associated with the Brazilian Cerrado by reducing their current range sizes. This reduction could be compensated if the species are able to expand their distribution to similar areas that will exist in the southern portions of the biome. However, current rates of deforestation in the biome and the potential displacement of monocultures such as soybean, coffee or sugarcane to the same suitable regions for the bats, could enhance the impacts of climate change. Therefore, we recommend the adoption of urgent conservation actions to ensure the persistence of bat species in the long term.

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Appendix A. Supplementary material

Supplementary material related to this article can be found online at http://dx.doi.org/10.1016/j.gecco.2015.11.011.

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