

# Conserving the Brazilian semiarid (Caatinga) biome under climate change

Guilherme de Oliveira · Miguel Bastos Araújo ·  
Thiago Fernando Rangel · Diogo Alagador ·  
José Alexandre Felizola Diniz-Filho

Received: 23 February 2012 / Accepted: 23 July 2012 / Published online: 5 August 2012  
© Springer Science+Business Media B.V. 2012

**Abstract** The Caatinga is a semiarid biome of the northeast of Brazil with only 1 % of its territory currently conserved. The biome's biodiversity is highly threatened due to exposure to land conversion for agricultural and cattle ranch. Climate forecasts predict increases in aridity, which could pose additional threats to the biome's biodiversity. Here, we ask if the remnants of natural vegetation in Caatinga biome, where endemic terrestrial vertebrate species occur, are likely to retain more climatic suitability under climate change scenarios than other less pristine areas of the biome. In order to assess changes in climate suitability across individual species ranges, ensemble forecasting was used based on seven bioclimatic envelope models, three atmosphere–ocean general circulation models, and two greenhouse emission gas scenarios for 2020, 2050, and 2080. We found that most species will gain climatic suitability in the natural vegetation remnants of the Caatinga. Such gains are even greater than the expected to occur within random sets of areas with size similar to the natural

**Electronic supplementary material** The online version of this article (doi:[10.1007/s10531-012-0346-7](https://doi.org/10.1007/s10531-012-0346-7)) contains supplementary material, which is available to authorized users.

G. de Oliveira (✉) · T. F. Rangel · J. A. F. Diniz-Filho  
Laboratório de Ecologia Teórica e Síntese, Departamento de Ecologia, Instituto de Ciências Biológicas  
I, Universidade Federal de Goiás, Caixa Postal 131, Goiânia, GO CEP 74001-970, Brazil  
e-mail: guilhermeoliveirabio@yahoo.com.br

G. de Oliveira  
Programa de Pós-Graduação Ecologia e Evolução, Universidade Federal de Goiás,  
Caixa Postal 131, Goiânia, GO CEP 74001-970, Brazil

M. B. Araújo  
Integrative Biology and Global Change Group, Department of Biodiversity and  
Evolutionary Biology, National Museum of Natural History, CSIC, 28006 Madrid, Spain

M. B. Araújo · D. Alagador  
Rui Nabeiro Biodiversity Chair, CIBIO, University of Évora,  
Largo dos Colegiais, 7000 Évora, Portugal

M. B. Araújo  
Department of Biology, Center for Macroecology, Evolution and Climate,  
University of Copenhagen, 2100 Copenhagen, Denmark

vegetation remnants. Our results suggest that natural vegetation remnants will likely play a role of climate refuges for endemic vertebrate species, so efforts should be concentrated in these regions.

**Keywords** Ensemble of forecasts · Species climatic suitability · Natural vegetation remnants · Endemic vertebrates

## Introduction

The Caatinga is a biome composed predominantly by xerophytic, woody, thorny, and deciduous physiognomies (Da Costa et al. 2007; Sampaio 1995), with a hot and dry climate (Veloso et al. 1991), occupying more than 750,000 km<sup>2</sup> in the northeast of Brazil. This is a semiarid region with drought periods lasting longer than 11 months per year (Ab'Saber 1977). The Caatinga's unique climatic conditions, hot and dry, provide adaptive singularities on its biodiversity, driving species to evolve specific physiologies and reproductive behaviors (e.g., Rodrigues 1996, 2003; Vieira et al. 2009). Thus, Caatinga contains a great number of singular hot-and-dry-adapted species. Nonetheless this biome has been described as a region with a low number of endemic (e.g., Andrade-Lima 1982; Prance 1987; Vanzolini et al. 1980). Consequently, its biodiversity has been widely ignored by conservation policies, with only 1 % of its territory included within protected areas (Leal et al. 2005).

The perception that the Caatinga has low biodiversity might be partly due to the region being poorly sampled. Indeed, some studies concluded that the biome has higher species richness and a greater number of endemic species than previously thought (see Leal et al. 2003, 2005). All in all, there are good reasons to start investigating the main threats to biodiversity in the region and develop conservation priorities, particularly because the area is already being exposed to high level of conversion of natural land by agriculture, mainly slash and burn (Mamede and Araújo 2008), and cattle ranches (Pereira et al. 2003). Currently, almost half of the Caatinga is already converted (Castelletti et al. 2004).

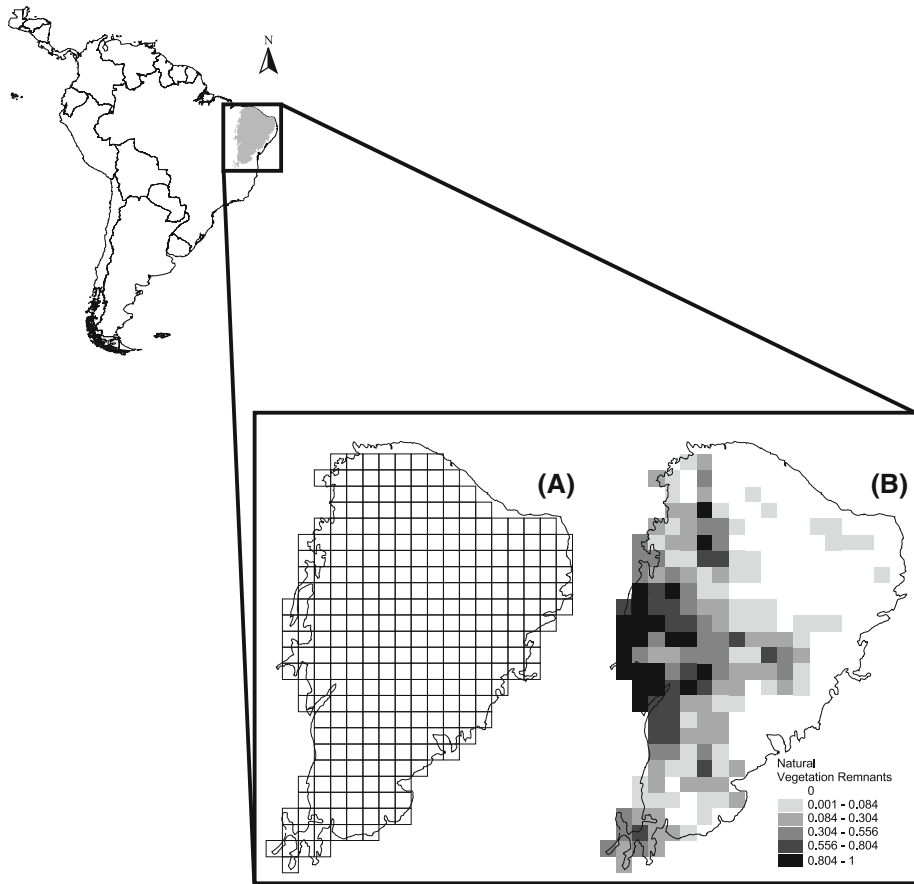
Existing human pressures are likely to threaten species' persistence in the biome, and the situation could be worse if climate changes in a way that further disturbs the Caatinga's biodiversity. The slight variation in temperature and precipitation of Caatinga (Silva 2004) has an important role in the spatial patterns of its species richness (de Oliveira and Diniz-Filho 2010). Predicted climate change scenarios (i.e., drier and warmer), might turn the Caatinga into a desert (Salazar et al. 2007), with worrying consequences for biodiversity.

The aim of this paper is three-fold. Firstly, we examine if natural vegetation remnants will retain climatic suitability for Caatinga's terrestrial vertebrate endemic species under climate change scenarios. Secondly, we examine if losses of climate suitability in natural vegetation remnants are greater or smaller than across the other areas of the biome. Thirdly, we investigate the relationship between species' climatic suitability gains against species' climatic suitability losses across natural vegetation remnants in the Caatinga, so to identify areas that are more suitable for conservation efforts in the future.

## Materials and methods

### Species and climate data

The Caatinga region was divided into 296 grid cells of  $0.5 \times 0.5^\circ$  of spatial resolution (Fig. 1a), and overlaid with maps of extent of occurrence of 32 terrestrial vertebrate



**Fig. 1** Geographical region of Caatinga showing **a** 296 grid cells with 0.5° latitudinal and longitudinal spatial resolution and **b** proportion of natural vegetation remnants

species that are endemic to this region (Leal et al. 2003). Data were retrieved from NatureServe ([www.natureserve.org](http://www.natureserve.org)), the Eisenberg and Redford (1999) field guide, and reviews from scientific literature and museum collections (Appendix A—Supplementary Material), and were then used to derive maps of species' presences and absences in our grid. Originally, there are 46 Caatinga's known vertebrate endemics (Leal et al. 2003; de Oliveira and Diniz-Filho 2011), but because of the requirements of the modeling methods we excluded species occurring in less than five cells, as well as species occurring in all cells (see Appendix A—Supplementary Material).

Climatic data for species modelling were compiled from WorldClim online database ([www.worldclim.org](http://www.worldclim.org); Hijmans et al. 2005) for both baseline and future conditions. Future scenarios for 2020 (averaged from 2010 to 2039 interval), 2050 (averaged from 2040 to 2069 interval), and 2080 (averaged from 2070 to 2099 interval) were based on three atmosphere–ocean general circulation models (AOGCMs), including the Canadian Centre for Climate Modelling Analysis (CCCMA), the Australia's Commonwealth Scientific and Industrial Research Organization (CSIRO), and the Hadley Centre for Climate Predictions and Research's General Circulation Model (HADCM3). Two families of greenhouse

emission gas (GEG) scenarios (A2 and B2) were used. For each period we averaged values of mean of maximum temperature, the sum of annual precipitation and the standard deviation of annual precipitation within each cell.

The A2 scenario reflects a world where global population will increase, and economic development is regionally oriented (IPCC 2000). While B2, on the other hand, emphasizes local solutions on economic, social, and environmental sustainability, the population growth will increase at a rate lower than A2 scenario, and is also oriented toward local protection and social equity (IPCC 2000). Thus, one can state that A2 GEG scenario is more pessimistic than B2.

### Bioclimatic envelope modelling

Ensemble forecasting methodologies for defining the species' potential distributions (Araújo and New 2007; see also Peterson et al. 2011) were implemented following the methodology described in Diniz-Filho et al. (2009a, 2010). For each species, we randomly divided occurrence data into 75 % for calibration and 25 % for validation, and this process was repeated 50 times. Seven different bioclimatic envelope models (BEMs) were used, including BIOCLIM (Busby 1991), Euclidian and Mahalanobis Distances (Farber and Kadmon 2003), Generalized Linear Models (GLM) (McCullagh and Nelder 1989), machine learning approaches such as Genetic Algorithm for Rule Set Production (GARP) (Stockwell and Noble 1992), Random Forest (Breiman 2001), and Maximum Entropy (MAXENT) (Phillips et al. 2006).

These models were run with BioEnsembles software (Diniz-Filho et al. 2009a), which is an integrated computational platform that implements some methods as BIOCLIM and distance-based BEMs, and also includes source code translated from different sources (e.g. GARP from OpenModeler, <http://openmodeller.sourceforge.net/>), integration with external software (e.g. MAXENT uses the original software), or methods implemented in R (e.g. GBM, FDA, ANN) (see Thuiller et al. 2010) when presence-absence data are available. We use all seven possible combinations of climatic variables described above ( $2^n - 1$ , where “ $n$ ” is the number of variables). Thus, for each species and BEM run, we have a final number of 350 models, referring to the multiplication of 50 cross validated sets by seven possible combinations of climatic variables. We presented the results as a proportion of the presences predicted by each of the seven BEMs for baseline and for each combination of AOGCMs and GEG scenario for the years 2020, 2050 and 2080 in all 350 models, converted as frequency values. Herein we use these frequencies as a proxy of climatic suitability of each species in each of the 296 grid cells.

Finally, we matched species' climatic suitability with regions that have remnants of Caatinga's natural vegetation (*sensu* Araújo 2004; Alagador et al. 2011). We multiplied model frequencies for the baseline and for each combination of AOGCMs and GEG scenarios for the years 2020, 2050, and 2080 by the summed proportion of “wildlands” and “forested” anthropogenic biomes (Ellis and Ramankutty 2008; see Fig. 1b) within each grid cells. These anthropogenic biomes are global surrogates of lands where there is no human occupation by urbanization, agriculture or pasture, in Caatinga region, “wildlands” refers to regions where sparse tree covers are, and “forested” are related to forests that have minimum traces of human occupation practices. Thus they were used as a generalization of where species are expected to find suitable environments and where conservation conflicts can be minimized (*sensu* Balmford et al. 2001; Araújo and Rahbek 2007; and reviewed by Luck 2007).

## Verifying the gains and losses of climate suitability for species

We used a null model to evaluate the extent to which regions that have natural vegetation remnants will retain more (or less) species' climatic suitability relatively to randomly selected regions in the Caatinga area (Alagador et al. 2011; Araújo et al. 2011). First, we subtracted the proportions of species' climatic suitability inside regions of natural vegetation remnants forecasted for the combinations of AOGCMs and GEG scenarios in the years 2020, 2050, and 2080 by the baseline proportions, to evaluate the empirical number of winner (positive differences) and loser (negative differences) species inside these areas.

Next, we rearranged, with 1,000 random permutations, the empirical total coverage of natural vegetation remnants, totaling the amount of 58.44 cells, across the 296 grid cells. All 296 cells in our grid had the same chance to be filled by natural cover on proportions that varies according to the real grid cells' proportions. By multiplying the baseline and forecasted species climatic suitability across the entire biome by each of these randomized proportions of natural vegetation remnants, and subtracting them, we obtained a frequency distribution of the number of climate change winner and loser species across Caatinga. So, the projected number of winners and losers inside the natural vegetation remnants were compared with the values from the randomized ones to establish significance levels. These randomization analyses were performed with the R statistical package (R Development Core Team 2009), using code published by Araújo et al. (2011).

## Proactive conservation planning

Regions of natural vegetation remnants with greater gains of climatic suitability for some species may also have others species losing climatic suitability. Such conflicting patterns would lead to optimization problems in conservation planning because priorities would have either to focus on a number of species, leaving others aside, or focus on all species thus increasing conservation costs.

To evaluate the degree to which conservation conflicts may arise when planning for climate change (Garcia and Araújo 2009), we split the expected climatic suitability trends into two spatial layers. One containing only the sum (across species) of positive suitability shifts into the future (gains). The other containing the sum (across species) of negative suitability shifts (losses). Notice that regions that have a great amount of natural vegetation remnants could have highest values of gains or losses of climatic suitability only because of size effects. To correct for this bias, we divided the values of gains and losses by the proportion of natural vegetation remnants. Then we made a regression analysis (ordinary least squares—OLS) between the sum of all species climatic suitability gains across natural vegetation remnants and the sum of all species climatic suitability losses in the same remnant vegetated areas.

Grid data display strong spatial structure (autocorrelation), which can inflate the Type I error of the significance tests due to non-independence of the cells (Diniz-Filho et al. 2003; Legendre 1993). We measured this spatial structure using Moran's *I* coefficients calculated from the model residuals, which ranges between  $-1$  (completely negative spatial autocorrelation) to  $1$  (completely positive spatial autocorrelation). For the present analyses, these Moran's *I* coefficients were calculated for 10 geographic distance classes in the Caatinga grid system, forming a spatial correlogram. Once autocorrelation is observed, it is necessary to apply methods of spatial regression to avoid misinterpretation of partial coefficients (see Bini et al. 2009; Dormann et al. 2007; Hawkins et al. 2011).

To correct the interpretation of the direction of the standard coefficients of the species suitability losses in the natural remnant vegetation areas (see below), we used eigenvector spatial filters (see Griffith 2003). These filters were obtained using Spatial Eigenvector Mapping (SEVM) (Borcard and Legendre 2002; Diniz-Filho and Bini 2005; Griffith and Peres-Neto 2006), and are given by the eigenvectors extracted from a pairwise geographic distance matrix, truncated at a distance of 175.25 km (note that analyses were restricted to cells with natural vegetation remnants). Eigenvectors extracted from this matrix represent the spatial structure at multiple scales, the first of which refers to broad and the last of which to fine scales (Diniz-Filho and Bini 2005). We selected all filters that, together, minimized the spatial autocorrelation in the residuals model, using the gains of climatic suitability inside cells that have natural vegetation remnants as response variable and the losses as predictors, at a Moran's  $I$  as low as 0.05 for the first distance class (see Griffith and Peres-Neto 2006). Then these selected spatial filters were used as explanatory variables in the OLS together with the losses of species climatic suitability within natural vegetation remnants areas. The spatial analysis was performed using SAM (Spatial Analysis in Macroecology) software v.4.0 (Rangel et al. 2006, 2010).

The interpretation of the relationship between the amount of species gains and losses of climate suitability is straightforward: if the standard coefficient of the losses within natural vegetation remnants is positive, this suggests that regions where some species will have more gains will be the same where other species will have more losses, and vice versa. To guide secure conservation efforts for all species together we expected a negative standard coefficient of the losses of climatic suitability within natural vegetation remnants.

## Results

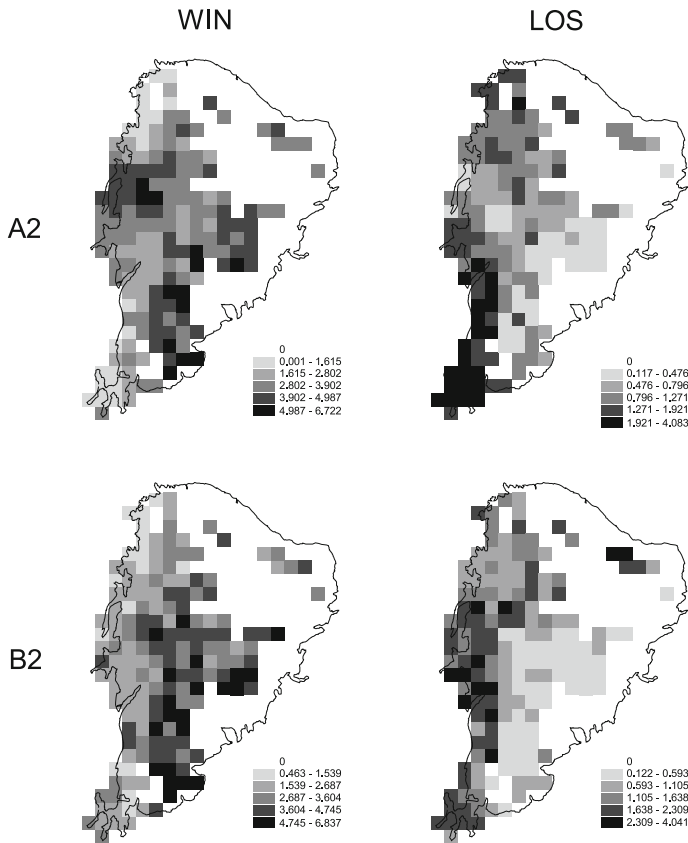
Most endemic species are projected to gain climatic suitability in natural vegetation remnants of the Caatinga, and this is true across all combinations of AOGCMs and GEG for the years 2020, 2050, and 2080 (Table 1). In general, all mammals and lizards with small observed range sizes that inhabit sand dunes will gain climatic suitability inside natural vegetation remnants. On the other hand, birds and lizards with large observed range sizes in forests and sand dunes will lose climatic suitability inside these areas (see Appendix B—Supplementary Material).

Moreover, vegetation remnants will retain more climate suitability for species than random regions across the biome, while losses of climate suitability in vegetated remnants is no different than the random regions (Table 1). However, only CCCMA-AOGCM presented acceptable significance levels (i.e.,  $P$  lower than 0.05 critical value) for most of the winner-species across the model combinations. All the results of HADCM3-AOGCM, and more than a half of the results of CSIRO-AOGCM presented values for winner-species that can occur by chance only.

The highest gains in climate suitability for species were recorded in the eastern natural vegetation remnants, while losses of climate suitability were mainly recorded in the western regions of Caatinga (Fig. 2, and for all combinations of AOGCMs and GEG scenarios for the years 2020, 2050, and 2080 see Appendix C—Supplementary Material). All combinations of AOGCMs and GEG scenarios for the years 2020, 2050, and 2080 have a significant spatial structure (Moran's  $I$  in the first distance class ranging from 0 to 200 km,  $P < 0.01$ ), so SEVM was applied to correct for bias in Type I error of regression coefficients. Thus, after correcting these biases, all standard coefficients of climatic suitability losses presented a negative relationship in all scenarios (Table 2), indicating that species, together, will have opposite patterns of gains and losses of climatic suitability in natural vegetation remnants.

**Table 1** Numbers of terrestrial vertebrate endemic species projected to gain (winners) and to lose (losers) climatic suitability inside regions that have natural vegetation remnants in Caatinga region for different combination of time periods, atmosphere–ocean general circulation models (AOGCMs) and greenhouse emission gas (GEG) scenarios, with their respective *P* values when compared with a random proportion of natural vegetation remnants across the entire area of Caatinga (*P*)

		2020				2050				2080			
		Winners	<i>P</i>	Losers	<i>P</i>	Winners	<i>P</i>	Losers	<i>P</i>	Winners	<i>P</i>	Losers	<i>P</i>
CCCCMA													
A2	19		0.139	13	0.666	18	0	14	0.998	23	0.076	9	0.732
B2	17		0	15	0.941	19	0.008	13	0.937	16	0	16	0.999
CSIRO													
A2	19		0.002	13	0.981	21	0.148	11	0.611	20	0.168	12	0.505
B2	22		0.045	10	0.798	17	0	15	0.999	20	0.075	12	0.658
HADCM3													
A2	25		0.21	7	0.503	27	0.509	5	0.187	23	0.282	9	0.575
B2	24		0.272	8	0.481	25	0.382	7	0.363	23	0.098	9	0.803



**Fig. 2** Spatial patterns of the sums of gains (WIN) and losses (LOS) of species' climatic suitability within areas that have natural vegetation remnants for the year 2080, using the CCCMA atmosphere–ocean general circulation model (AOGCM) for the families A2 and B2 of greenhouse emission gas (GEG) scenarios. Results for all combinations of AOGCMs and GEG scenarios for the years 2020, 2050 and 2080 are presented in Appendix C—Supplementary Material

## Discussion

### Species' gains and losses

Caatinga's biodiversity has been affected by rudimentary agricultural and cattle ranches practices during more than 500 years, since colonization periods in the XVI century (Coimbra-Filho and Câmara 1996; Leal et al. 2005). Thus, the current species that occur in the biome are what remains after this extinction filter effect (Cardillo et al. 2005, 2006) of natural land conversion. Here, we assumed that only purely ecological and phylogenetically structured species' traits that respond to environmental variation (i.e., niche conservatism) will affect future range shifts on Caatinga's terrestrial vertebrates (Diniz-Filho and Bini 2008). Thus Caatinga's species that could not shift their ranges to places climatically suitable after their habitat degradation (i.e. driven only by strong phylogenetic components) were already extinct.

We excluded from the analyses 12 endemic species that have less than five cells of range size, due to the limitation of our analyses. However, some of these species are



**Table 2** Standard coefficients relating the map of the total gains in climatic suitability for the analyzed species with the map containing the total losses of climatic suitability for different combination of time periods, atmosphere–ocean general circulation models (AOGCMs) and greenhouse emission gas (GEG) scenarios, with their respective  $P$  values ( $P$ ), the explanatory power of the model ( $R^2$ ),  $P$  value of the model, and the number of filters used to minimize the Moran's  $I$  coefficient in the residuals values as low as 0.05 level

	2020					2050					2080				
	Standard coefficient	$P$	$R^2$	Model's $P$	Filters	Standard coefficient	$P$	$R^2$	Model's $P$	Filters	Standard coefficient	$P$	$R^2$	Model's $P$	Filters
CCCMA															
A2	−0.568	0	0.56	0	2	−0.427	0	0.255	0	1	−0.369	0	0.625	0	5
B2	−0.541	0	0.472	0	2	−0.333	0	0.344	0	3	−0.419	0	0.43	0	3
CSIRO															
A2	−0.251	0	0.08	0	1	−0.275	0	0.368	0	3	−0.461	0	0.523	0	6
B2	−0.153	0.04	0.167	0	3	−0.339	0	0.598	0	3	−0.279	0	0.546	0	5
HADCM3															
A2	−0.553	0	0.37	0	2	−0.649	0	0.559	0	3	−0.49	0	0.765	0	7
B2	−0.502	0	0.44	0	4	−0.621	0	0.512	0	4	−0.571	0	0.711	0	6

considered under threat of extinction, for example the Lear's Macaw (*Anodorhynchus leari*) and the Araripe Manakin (*Antilophia bokermanni*), that are bird species classified as endangered and critically endangered, respectively (IUCN 2011). Currently the Araripe Manakin range contains no natural vegetation remnants and the Lear's Macaw has only 31 % of its range covered by pristine vegetation, due to agriculture pressures, mainly by slash and burn activities (IUCN 2011). Projections of climatic change induced suitability gains or losses for these species is challenging, because data are at very coarse resolution (for discussion see Diniz-Filho et al. 2009b; Engler et al. 2011).

Also it should be noted that we forecasted species' distributions within the Caatinga and disregarded dynamics occurring elsewhere. The distribution of the entire biome can change (Salazar et al. 2007) and species occurring in transition regions between Caatinga and Amazonian Forest, Cerrado, and Atlantic Forest might, in the future, find climatic suitability inside Caatinga region. For example, gallery forests in the southern part of the Caatinga are used by primates allowing them to penetrate into the biome (Marinho-Filho and Veríssimo 1997). This phenomenon provides evidence that species of the Atlantic Forest fauna can penetrate into the Caatinga. If such a scenario was verified, it would be possible that new predators, parasites, and competitors could invade the Caatinga thus threatening local endemics (e.g., Kleinbauer et al. 2010; Thomas 2010).

Another possibility is that, with climate change, new suitable areas might emerge prompting endemics to move in order to track climate suitability (e.g., Marini et al. 2009). Whatever the scenario, biodiversity conservation in such a changing environment will certainly offer additional challenges to the existing ones. In some cases, vegetated areas characteristic of the Caatinga biome might be modified, thus threatening local endemic species and in other cases new opportunities for conservation will emerge outside traditional Caatinga's pristine areas.

### Proactive conservation planning

Regions predicted to have the greatest gains of species' climatic suitability do not coincide with the regions predicted to witness the greatest climatic suitability losses for others species. This pattern of impacts of climate change suggests that effective conservation can be achieved at a relatively low cost. However, underlying the spatial structure of climate impacts are human occupation pressures and land degradation. In particular, the regions with natural vegetation remnants, where species are likely to have more gains of climatic suitability, are located in the central Caatinga (see Fig. 2; Appendix C—Supplementary Material). This area is known to be susceptible to desertification (Salazar et al. 2007), because of the coupled effects of increasing temperatures, reduction of precipitation, and land degradation (Darhoh 1998; Geist and Lambin 2004; Sivakumar 2007).

Moreover, under future climate scenarios, potential displacements of Caatinga's biome can affect the spatial pattern of human occupation practices. This is because most of the agricultural practices and cattle ranches in this region use rudimentary techniques that are strongly dependent on climatic characteristics (e.g., Mamede and Araújo 2008). Furthermore, changes in land use in the Caatinga can influence the regional climate and thus alter the structure of surrounding biomes (e.g., Malhado et al. 2010) making a redistribution of agriculture and cattle ranches scenarios more probable. Thus, if the neighboring regions of natural vegetation remnants gaining climatic suitability for species will become climatically appropriate for practices of agriculture, cattle ranches, and urbanization, conservation strategies will compete with socioeconomics interests (sensu Balmford et al. 2001; and discussion on Diniz-Filho et al. 2009b). On the other hand, if these regions become hostile

enough to avoid land degradation by human occupation practices, they have the potential to become important regions for conservation.

### Uncertainties from AOGCMs and GEG scenarios

Forecasting species' distributions under climate change can generate different results depending on the models used, resulting in uncertainty sources coming from environmental and species data sets and the techniques used for this purpose (Araújo and New 2007). Some previous studies have shown that the main sources of uncertainty in modeling are related to BEMs and AOGCMs (e.g., Buisson et al. 2010; Diniz-Filho et al. 2009a; Garcia et al. 2012). Thus we opted to present the results for all BEMs as a probabilistic density function, and separately for combinations of AOGCMs and GEG scenarios. When we compared the spatial patterns of species climatic suitability gains and losses within Caatinga natural vegetation remnants in the A2 and B2 GEG scenarios across AOGCMs (see Appendix C—Supplementary Material), they did not present marked differences, suggesting that Caatinga's endemics will respond similarly under different concentrations of CO<sub>2</sub> on the atmosphere resulting from different human socioeconomic behaviors. Otherwise, comparing the AOGCMs, HADCM3 presented discrepant results from CCCMA and CSIRO, where species will gain climatic suitability at northwest region of natural vegetation remnants, and will lose it at centre-south regions (see Appendix C—Supplementary Material). Nonetheless, HADCM3 presented the same contrasting patterns of gains and losses of species climatic suitability of the others AOGCMs, and the interpretation of conservation efforts remains similar as for CCCMA and CSIRO.

### Concluding remarks

Despite the low conservation priority that is usually given to the Caatinga, the biome contains a greater number of species and endemic species that is often admitted. Climate change is projected to cause some areas to present higher climatic suitability for species than others, but areas with important natural remnants of vegetation tend to be among the areas winning climatic suitability. These are good news as it suggests that current important areas for biodiversity in the biome are also likely to play a role as climate refugia towards the end of the century. Obviously, fine grained studies would be required in order to provide detailed analysis about the location of these refugia. Else, coarse data can be used to statistically downscale projections, but there are associated uncertainties with this process that need being understood (Araújo et al. 2005). In our study we adopted a coarse filter approach (Whittaker et al. 2005) to identify the biogeographic regions that will likely play a major role for the conservation of endemic species in the region. The identification of such coarse areas can be taken as a first step of systematic conservation planning (Margules and Pressey 2000), aiming at discriminating regions of conservation importance that would be further subjected to more detailed planning (e.g. Araújo et al. 2002; Williams et al. 2005).

Proactive conservation action in the Caatinga is timely since natural vegetation remnants are likely to suffer modifications with climate change and these changes might coexist with alterations in the spatial patterns of socioeconomic pressure and land conversion into agriculture and cattle ranches. One example is the Integration Project of the São Francisco basin (Ministério da Integração Nacional) which is designed to facilitate irrigation for croplands and livestock in the region.

**Acknowledgments** The authors are grateful to two anonymous reviewers, and to the cooperation project of Fundação para Ciência e a Tecnologia and Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (FCT-CAPES, Portugal–Brasil). GO is supported by Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) doctoral fellowship (Proc. No. 552961/2008-6), and work by TFR and JAFDF on climate change and BEMs have been continuously supported by CNPq productivity grants and by the “Rede Nacional de Mudanças Climáticas” of INPE. GO was sponsored by CAPES-Balcão (Proc. No. 5201-09-8) while visiting the Universidade de Évora, Rui Nabeiro Biodiversity Chair, Portugal. DA was supported by a postdoctoral studentship (SFRH/BPD/51512/2011) awarded by FCT. Research by MBA, JAFDF, and TLFVBR is supported by the FCT Range Shift project.

## References

- Ab'Saber NA (1977) Espaços ocupados pela expansão dos climas secos na América do Sul, por ocasião dos períodos glaciais quaternários (SériePaleoclimas,3). Instituto de Geografia/USP, São Paulo
- Alagador D, Martins MJ, Orestes-Cerdeira J, Cabeza M, Araújo MB (2011) A probability-based approach to match species with reserves when data are in different resolutions. *Biol Conserv* 144:811–820
- Andrade-Lima D (1982) Present-day forest refuges in northeastern Brazil. In: Prance GT (ed) *Biological diversification in the tropics*. Columbia University Press, New York, pp 245–254
- Araújo MB (2004) Matching species with reserves—uncertainties from using data at different resolutions. *Biol Conserv* 118:533–538
- Araújo MB, New M (2007) Ensemble forecasting of species distributions. *Trends Ecol Evol* 22:42–47
- Araújo MB, Rahbek C (2007) Conserving biodiversity in a world of conflicts. *J Biogeogr* 34:199–200
- Araújo MB, Williams PH, Turner A (2002) A sequential approach to minimise threats within selected conservation areas. *Biodivers Conserv* 11:1011–1024
- Araújo MB, Thuiller W, Williams PH, Reginster I (2005) Downscaling European species atlas distributions to a finer resolution: implications for conservation planning. *Glob Ecol Biogeogr* 14:17–30
- Araújo MB, Alagador D, Cabeza M, Lafourcade B, Nogués-Bravo D, Thuiller W (2011) Climate change threatens European conservation areas. *Ecol Lett* 14:484–492
- Balmford A, Moore JL, Brooks T, Burgess N, Hansen LA, Williams P, Rahbek C (2001) Conservation conflicts across Africa. *Science* 291:2616–2619
- Bini LM, Diniz-Filho JAF, Rangel TFLVB, Akre TSB, Albaladejo RG, Albuquerque RS, Aparicio A, Araújo MB, Baselga A, Beck J, Belloq MB, Böhning-Gaese K, Borges PAV, Castro-Parga I, Chey VK, Chown SL, De Marco P, Dobkin DS, Ferrer-Castán D, Field R, Filloy J, Fleishman E, Gómez JF, Hortal J, Iverson JB, Kerr JT, Kissling WD, Kitching IJ, León-Cortéz JL, Lobo JM, Montoya D, Morales-Castilla I, Moreno JC, Oberdorff T, Olalla-Tárraga MÁ, Pausas JG, Qian H, Rahbek C, Rodríguez MÁ, Rueda M, Ruggiero A, Sackmann P, Sanders NJ, Terribile LC, Vetaas OR, Hawkins BA (2009) Coefficient shifts in geographical ecology: an empirical evaluation of spatial and non-spatial regression. *Ecography* 32:193–204
- Borcard D, Legendre P (2002) All-scale spatial analysis of ecological data by means of principal coordinates of neighbour matrices. *Ecol Model* 153:51–68
- Breiman L (2001) Random forest. *Mach Learn* 45:5–32
- Buisson L, Thuiller W, Casajus N, Lek S, Grenouillet G (2010) Uncertainty in ensemble forecasting of species distributions. *Glob Change Biol* 16:1145–1157
- Busby JR (1991) BIOCLIM: a bioclimate analysis and prediction system. In: Margules CR, Austin MP (eds) *Nature conservation: cost effective biological surveys and data analysis*. CSIRO, Melbourne, pp 64–68
- Cardillo M, Mace GM, Jones KE, Bielby J, Bininda-Emonds ORP, Sechrest W, Orme CDL, Purvis A (2005) Multiple causes of high extinction risk in large mammal species. *Science* 309:1239–1241
- Cardillo M, Mace GM, Gittleman JL, Purvis A (2006) Latent extinction risk and the future battlegrounds of mammal conservation. *Proc Natl Acad Sci USA* 103:4157–4161
- Castelletti CHM, Silva JMC, Tabarelli M, Santos AMM (2004) Quanto ainda resta da Caatinga? Uma estimativa preliminar. In: Silva JMC, Tabarelli M, Lins L (eds) *Biodiversidade da Caatinga: áreas e ações prioritárias para a conservação*. Ministério do Meio Ambiente, Brasília, pp 92–100
- Coimbra-Filho AF, Câmara IG (1996) Os limites originais do bioma Mata Atlântica na região Nordeste do Brasil. Fundação Brasileira para Conservação da Natureza, Rio de Janeiro
- Da Costa RC, de Araújo FS, Lima-Verde LW (2007) Flora and life-form spectrum of deciduous thorn woodland (caatinga) in northeastern, Brazil. *J Arid Environ* 68:237–247

- Darhoh MBK (1998) The nature, causes and consequences of desertification in the drylands of Africa. *Land Degrad Dev* 9:1–20
- de Oliveira G, Diniz-Filho JAF (2010) Spatial patterns of terrestrial vertebrates richness in Brazilian semiarid, Northeastern Brazil: selecting hypotheses and revealing constraints. *J Arid Environ* 74:1418–1426
- de Oliveira G, Diniz-Filho JAF (2011) Evaluating environmental and geometrical constraints on endemic vertebrates of the semiarid Caatinga. *Basic Appl Ecol* 12:664–673
- Diniz-Filho JAF, Bini LM (2005) Modelling geographical patterns in species richness using eigenvector-based spatial filters. *Global Ecol Biogeogr* 14:177–185
- Diniz-Filho JAF, Bini LM (2008) Macroecology, global change and the shadow of forgotten ancestors. *Global Ecol Biogeogr* 17:11–17
- Diniz-Filho JAF, Bini LM, Hawkins BA (2003) Spatial autocorrelation and red herrings in geographical ecology. *Global Ecol Biogeogr* 12:53–64
- Diniz-Filho JAF, Bini LM, Rangel TFLVB, Loyola RD, Hof C, Nogués-Bravo D, Araújo MB (2009a) Partitioning and mapping uncertainties in ensemble of forecasts of species turnover under climate change. *Ecography* 32:897–906
- Diniz-Filho JAF, De Oliveira G, Bini LM, Loyola RD, Nabout JC, Rangel TFLVB (2009b) Conservation biogeography and climate change in the Brazilian Cerrado. *Nat Conserv* 7:100–112
- Diniz-Filho JAF, de Marco P, Hawkins BA (2010) Defying the course of ignorance: perspectives in insect macroecology and conservation biology. *Insect Conserv Divers* 3:172–179
- Dormann CF, McPherson J, Araújo MB, Bivand R, Bolliger J, Carl G, Davies RG, Hirzel A, Jetz W, Kissling WD, Kühn I, Ohlemüller R, Peres-Neto P, Reineking B, Schröder B, Schurr FM, Wilson R (2007) Methods to account for spatial autocorrelation in the analysis of distributional species data: a review. *Ecography* 30:609–628
- Eisenberg JF, Redford KH (1999) *Mammals of neotropics*. The University of Chicago Press, Chicago/London
- Ellis EC, Ramankutty N (2008) Putting people in the map: anthropogenic biomes of the world. *Front Ecol Environ* 6:439–447
- Engler R, Randin CF, Thuiller W, Dullinger S, Zimmermann NE, Araújo MB, Pearman PB, Lay G, Piedallu C, Albert CH, Choler P, Coldea G, de Lamo X, Dirnböck T, Gégout J, Gómez-García D, Grytnes J, Heegaard E, Høistad F, Nogués-Bravo D, Normand S, Puşcaş M, Sebastià M, Stanisci A, Theurillat J, Trivedi MR, Vittoz P, Guisan A (2011) 21st century climate change threatens mountain flora unequally across Europe. *Glob Change Biol* 17:2330–2341
- Farber O, Kadmon R (2003) Assessment of alternative approaches for bioclimatic modelling with special emphasis on the Mahalanobis distance. *Ecol Model* 160:115–130
- García RA, Burgess ND, Cabeza M, Rahbek C, Araújo MB (2012) Exploring consensus in 21st century projections of climatically suitable areas for African vertebrates. *Glob Change Biol* 18:1253–1269
- Geist HJ, Lambin EF (2004) Dynamic causal pattern of desertification. *Bioscience* 54:817–830
- Griffith DA (2003) *Spatial autocorrelation and spatial filtering—gaining understanding through theory and scientific visualization*. Springer, Berlin
- Griffith DA, Peres-Neto PR (2006) Spatial modeling in ecology: the flexibility of eigenfunction spatial analysis. *Ecology* 87:2603–2613
- Hawkins BA, Rodríguez MÁ, Weller SG (2011) Global angiosperm family richness revisited: linking ecology and evolution to climate. *J Biogeogr* 38:1253–1266
- Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005) Very high resolution interpolated climate surfaces for global land areas. *J Climatol* 25:1965–1978
- IPCC (Intergovernmental Panel on Climate Change) (2000) A special report of IPCC working group III
- IUCN (2011) IUCN red list of threatened species. Version 2010.1. [www.iucnredlist.org](http://www.iucnredlist.org). Accessed 15 June 2011
- Kleinbauer I, Dullinger S, Peterseil J, Essl F (2010) Climate change might drive the invasive tree *Robinia pseudacacia* into nature reserves and endangered habitats. *Biol Conserv* 143:382–390
- Leal IR, Tabarelli M, Silva JMC (2003) *Ecologia e conservação da Caatinga*. Editora Universitária, Recife
- Leal IR, Silva JMC, Tabarelli M, Lacher TE Jr (2005) Changing the course of biodiversity conservation in the Caatinga of Northeastern Brazil. *Conserv Biol* 19:701–706
- Legendre P (1993) Spatial autocorrelation—trouble or new paradigm. *Ecology* 74:1659–1673
- Luck GW (2007) A review of relationships between human population density and biodiversity. *Biol Rev* 82:607–645
- Malhado ACM, Pires GF, Costa MH (2010) Cerrado conservation is essential to protect the Amazon rainforest. *Ambio* 39:580–584
- Mamede MA, Araújo FS (2008) Effects of slash and burn practices on a soil seed bank of Caatinga vegetation in Northeast Brazil. *J Arid Environ* 72:458–470

- Margules CR, Pressey RL (2000) Systematic conservation planning. *Nature* 405:243–253
- Marinho-Filho J, Veríssimo EW (1997) The rediscovery of *Callicebus personatus barbarabrownae* in Northeastern Brazil with a new Western limit for its distribution. *Primates* 38:429–433
- Marini MÁ, Barbet-Massin M, Lopes LE, Jiguet F (2009) Major current and future gaps of Brazilian reserves to protect Neotropical savanna birds. *Biol Conserv* 142:3039–3050
- McCullagh P, Nelder JA (1989) Generalized linear models. Chapman and Hall, Boca Raton
- Pereira IM, Andrade LA, Sampaio EVSB, Barbosa MRV (2003) Use-history effects on structure and flora of Caatinga. *Biotropica* 35:154–165
- Peterson AT, Soberon J, Pearson RG, Anderson RP, Martinez-Meyer ER, Nakamura M, Araújo MB (2011) Ecological niches and geographical distributions, monographs in population biology, vol 49. Princeton University Press, Princeton
- Phillips SJ, Anderson RP, Schapire RE (2006) Maximum entropy modelling of species geographic distributions. *Ecol Model* 190:231–259
- Prance GT (1987) Vegetation. In: Whitmore TC, Prance GT (eds) *Biogeography and quaternary history in tropical America*. Oxford Science Publications, Oxford
- R Development Core Team (2009) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. Available from <http://www.r-project.org>
- Rangel TFLVB, Diniz-Filho JAF, Bini LM (2006) Towards an integrated computational tool for spatial analysis in macroecology and biogeography. *Global Ecol Biogeogr* 15:321–327
- Rangel TFLVB, Diniz-Filho JAF, Bini LM (2010) SAM: a comprehensive application for spatial analysis in macroecology. *Ecography* 33:46–50
- Rodrigues MT (1996) Lizards, snakes, and amphisbaenians from the quaternary sand dunes of the middle Rio São Francisco, Bahia, Brazil. *J Herpetol* 30:513–526
- Rodrigues MT (2003) Herpetofauna da Caatinga. In: Leal IR, Tabarelli M, Silva JMC (eds) *Ecologia e conservação da Caatinga*. Editora Universitária, Recife, pp 181–236
- Salazar LF, Nobre CA, Oyama MD (2007) Climate change consequences on the biome distribution in tropical South America. *Geophys Res Lett* 34:1–16
- Sampaio EVSB (1995) Overview of the Brazilian Caatinga. In: Bullock SH, Mooney HA, Medina E (eds) *Seasonally tropical dry forests*. Cambridge University Press, Cambridge, pp 35–63
- Silva VPR (2004) On climate variability in Northeast Brazil. *J Arid Environ* 58:575–596
- Sivakumar MKV (2007) Interactions between climate and desertification. *Agric Forest Meteorol* 142:143–155
- Stockwell DRB, Noble IR (1992) Inductions of sets of rules from animal distribution data: a robust and informative method of data analysis. *Math Comput Simul* 33:385–390
- Thomas CD (2010) Climate, climate change and range boundaries. *Divers Distrib* 16:488–495
- Thuiller W, Lafourcade B, Engler R, Araújo MB (2010) BIOMOD 2009—a platform for ensemble forecasting of species distributions. *Ecography* 32:369–373
- Vanzolini PE, Ramos-Costa AMM, Vitt LJ (1980) Répteis das Caatingas. Academia Brasileira de Ciências, Rio de Janeiro
- Veloso HP, Rangel-Filho ALR, Lima JCA (1991) Classificação da vegetação brasileira, adaptada a um sistema universal. IBGE-Departamento de Recursos Naturais e Estudos Ambientais, Rio de Janeiro
- Vieira WLS, Santana GD, Arzabe C (2009) Diversity of reproductive modes in anuran communities in the Caatinga drylands of northeastern Brazil. *Biodivers Conserv* 18:55–66
- Whittaker RJ, Araújo MB, Jepson P, Ladle RJ, Watson JEM, Willis KJ (2005) Conservation biogeography: assessment and prospect. *Divers Distrib* 11:3–23
- Williams PH, Hannah L, Andelman S, Midgley GF, Araújo MB, Hughes G, Manne L, Martinez-Meyer E, Pearson R (2005) Planning for climate change: identifying minimum-dispersal corridors for the Cape Proteaceae. *Conserv Biol* 19:1063–1074