

1 **Climate change should drive mammal defaunation in tropical dry forests**

2

3 Mario R. Moura<sup>1,2\*</sup>, Gibran A. Oliveira<sup>3</sup>; Adriano P. Paglia<sup>4</sup>, Mathias M. Pires<sup>1</sup>,

4 Bráulio A. Santos<sup>2,5</sup>

5

6 <sup>1</sup> Departamento de Biologia Animal, Instituto de Biologia, Universidade Estadual de

7 Campinas, Campinas, SP 13082-862, Brazil

8 <sup>2</sup> Departamento de Ciências Biológicas, Universidade Federal da Paraíba, Areia, PB 58397-

9 000, Brazil

10 <sup>3</sup> Programa de Pós-Graduação em Ciências Biológicas, Universidade Federal da Paraíba, João

11 Pessoa, PB 58051-900, Brazil

12 <sup>4</sup> Departamento de Biologia Geral, Universidade Federal de Minas Gerais, Belo Horizonte,

13 MG 31270-910, Brazil

14 <sup>5</sup> Departamento de Sistemática e Ecologia, Universidade Federal da Paraíba, João Pessoa, PB

15 58051-900, Brazil

16 \* Corresponding author: Mario R. Moura, [mariormoura@gmail.com](mailto:mariormoura@gmail.com)

17

18 **ABSTRACT**

19 Human-induced climate change has intensified negative impacts on socioeconomic factors,

20 the environment, and biodiversity, including changes in rainfall patterns and an increase in

21 global average temperatures. Drylands are particularly at risk, with projections suggesting

22 they will become hotter, drier, and less suitable for a significant portion of their species,

23 potentially leading to mammal defaunation. We use ecological niche modelling and

24 community ecology biodiversity metrics to examine potential geographical range shifts of

25 non-volant mammal species in the largest Neotropical dryland, the Caatinga, and evaluate

26 impacts of climate change on mammal assemblages. According to projections, 85% of the  
27 mammal species will lose suitable habitats, with one quarter of species projected to  
28 completely lose suitable habitats by 2060. This will result in a decrease in species richness for  
29 more than 90% of assemblages and an increase in compositional similarity to nearby  
30 assemblages (i.e., reduction in spatial beta diversity) for 70% of the assemblages. Small-sized  
31 mammals will be the most impacted and lose most of their suitable habitats, especially in  
32 highlands. The scenario is even worse in the eastern half of Caatinga where habitat  
33 destruction already prevails, compounding the threats faced by species there. While species-  
34 specific responses can vary with respect to dispersal, behaviour, and energy requirements, our  
35 findings indicate that climate change can drive mammal assemblages to biotic  
36 homogenisation and species loss, with drastic changes in assemblage trophic structure. For  
37 successful long-term socioenvironmental policy and conservation planning, it is critical that  
38 findings from biodiversity forecasts are considered.

39

40 **Keywords:** Beta-diversity, Biotic homogenisation, Body size, Drylands, Ecological Niche  
41 Models; Mammals

## 42 INTRODUCTION

43 Defaunation typically refers to the depletion of fauna caused by overexploitation, habitat  
44 destruction, and invasive species (Dirzo et al., 2014; Redford, 1992). At large spatial scales,  
45 defaunation may generate complex spatial patterns rather than a simple reduction in species  
46 richness, which depend on species-specific responses to defaunation drivers and landscape  
47 configuration (Bogoni et al., 2020) Climate change adds another layer of complexity to the  
48 spatial consequences of defaunation, since, besides posing an additional threat to wildlife, it is  
49 expected to reshape species distribution patterns. In response to a changing the climate,  
50 species can be displaced to regions with more favourable conditions, experiencing either  
51 geographic range contraction or expansion (Lenoir & Svenning, 2015). Species with higher  
52 tolerance to environmental change (e.g., disturbance-adapted, habitat generalists, wide-  
53 ranging, and synanthropic species) are less likely to be affected and may even expand their  
54 occurrence to novel habitats. In contrast, more sensitive species (e.g., habitat specialists,  
55 narrow-ranging species) may lose suitable areas and eventually becoming locally extinct  
56 (Filgueiras et al., 2021). These differences in species responses have the potential to change  
57 richness and composition of local assemblages, ultimately affecting biodiversity patterns.

58         The widespread loss of specialist species reduces local species richness (alpha  
59 diversity) and may increase the similarity in species composition across space, decreasing  
60 beta diversity, a phenomenon termed biotic homogenisation (Mckinney & Lockwood, 1999).  
61 Most often, biotic homogenization also result from increases in local richness due to the  
62 colonization of species assemblages by generalists (Filgueiras et al., 2021; Socolar et al.,  
63 2016). However, species redistribution may also increase the spatial heterogeneity in  
64 assemblage composition, either due to the gain of disturbance-adapted species or to the loss of  
65 widespread species (Socolar et al., 2016). Although studies on the effects of climate change  
66 over biodiversity patterns often emphasize the biotic homogenization due to species loss

67 (Clavel et al., 2011; Hidasi-Neto et al., 2019; Moura et al., 2023), the prevalence each of  
68 those process is likely context dependent, and spatial patterns will vary according to species  
69 composition, the level of spatial heterogeneity in environmental conditions and the severity of  
70 climate changes.

71 The potential effects of biotic homogenization have been studied mostly in tropical  
72 rainforests (Sales et al., 2020), leaving other types of systems highly subject to climate change  
73 understudied. Because future climate projections also include changes in the volume,  
74 frequency, and geography of rainfalls (IPCC, 2021), climate change is particularly worrying  
75 for regions already facing scarcity of water. For instance, drylands are expected to become  
76 hotter, drier, and less suitable for a significant portion of their species (Aguirre-Gutiérrez et  
77 al., 2020). If these projections are confirmed, it is likely that drylands will gradually become  
78 impoverished, homogenised, and driven towards desertification (Moura et al., 2023; Torres et  
79 al., 2017). One of Earth's most vulnerable drylands, the Caatinga, is also the largest tropical  
80 dry forest in South America (Banda-R et al., 2016; Hoekstra et al., 2004; Silva et al., 2017). In  
81 addition to being affected by chronic disturbances (Antongiovanni et al., 2020), this semiarid  
82 region underwent a high degree of defaunation associated with habitat loss and poaching in  
83 the past five centuries (Alves et al., 2012; Barboza et al., 2016; Bogoni et al., 2020), showing  
84 a high proportion of locally threatened species, including endemic ones (Leal et al., 2005)  
85 Besides being an ideal study system to the consequences of climate change on biodiversity  
86 distribution patterns, investigating the response of tropical dry forest mammals to climate  
87 change can help elucidate impacts of environmental change on dryland biodiversity.

88 In the Caatinga drylands, about half of the mammal species are non-volant  
89 (Carmignotto & Astúa, 2018). Although many of these species are shared with neighbouring  
90 biomes (Carmignotto et al., 2012), the composition of Caatinga mammals reflects a complex  
91 biogeographic history that has involved periodical expansions and retractions of tropical dry

92 forests across different mountain ranges along the Pleistocene (Silva et al., 2017). On the one  
93 hand, Caatinga species have historically experienced high climatic variation (Costa et al.,  
94 2018), which may have selected organisms able to keep pace with climate change (Riddell et  
95 al., 2021; Schloss et al., 2012). If so, future climate change would have limited influence on  
96 species richness and composition of mammal assemblages. However, if Caatinga species are  
97 already near their physiological limits (Araújo et al., 2013) or have relied on highland humid  
98 enclaves as refuges over evolutionary time (Werneck et al., 2011), further increases in arid  
99 conditions could trigger a range shift in these species with consequences for assemblage  
100 structure.

101         Herein, we used ecological niche modelling and community ecology biodiversity  
102 metrics to examine potential geographical range shifts of non-volant mammal species in the  
103 Caatinga and evaluate impacts of climate change on mammal assemblages. We combined data  
104 on species distribution and body mass to investigate projected changes in geographical  
105 patterns of mammal richness and spatial dissimilarity across different future climate  
106 scenarios. Specifically, we sought to determine whether the balance between potential range  
107 contraction or expansion may increase or decrease species richness (alpha diversity) and how  
108 those changes in distribution may impact homogenisation or heterogenisation of faunal  
109 composition (beta diversity) across space. Because ecological losses are often non-random,  
110 with large-sized and longer-lived non-volant mammals disappearing first (Carmona et al.,  
111 2021; Cooke et al., 2019), we also examined how changes in average body mass per  
112 assemblage (if any) was linked to species loss and biotic homogenisation. Because the  
113 elevational gradient around highlands appears to sustain more favourable conditions for non-  
114 volant mammals (Becker et al., 2007), we expected relatively lower changes in species  
115 richness and composition of mammal assemblages at higher elevations, with overall decline  
116 in richness and biotic homogenization associated with a reduction in average body mass.

117

## 118 **METHODS**

### 119 **Species Data**

120 We compiled occurrence data of Caatinga non-volant mammals searching for different term  
121 combinations: “mamíferos”, “caatinga”, “nordeste”, “dataset”, “northeast”, “dryland”, and  
122 “mammals” in Google Scholar, identifying 185 mammal species known to occur in the  
123 Caatinga. We then used 19 published studies to extracted occurrence records collected  
124 between 1957 and 2021 (Asfora et al., 2011; Brennand et al., 2013; Culot et al., 2019; Feijó &  
125 Langguth, 2013; Freitas, 1957; Gardner, 2008; Geise et al., 2010; Gurgel-Filho et al., 2015;  
126 Lima et al., 2017; Malcher et al., 2017; Mares et al., 1981; Mendonça et al., 2018; Nagy & Reis  
127 et al., 2020; Nascimento & Feijó, 2017; Oliveira et al., 2003; Patton et al., 2015; Pires &  
128 Wied, 1965; Santos et al., 2019; Souza et al., 2019). We also incorporated data from the  
129 mastozoological collection of Universidade Federal da Paraíba (the largest mammal collection  
130 of Northeastern Brazil) and other collections included in the Global Biodiversity Information  
131 Facility (GBIF, 2023). We included species occurrence records if information was available  
132 on coordinates, collection year, and species taxonomy in agreement with specialized literature  
133 (Carmignotto & Astúa, 2018; Feijó et al., 2016; Feijó & Langguth, 2013; Gardner, 2008;  
134 Gurgel-Filho et al., 2015; Nascimento & Feijó, 2017; Oliveira & Langguth, 2004; Patton et  
135 al., 2015; Quintela et al., 2020). After excluding the bat species, our database summed 39,459  
136 occurrence records for 93 species of non-volant mammals.

137 We used the *CoordinateCleaner* R package (Zizka et al., 2019) to remove duplicates  
138 and geoprocessing errors (records distant less than 1 km from municipality, state, or country  
139 centroids, or located over water), leading to 18,758 records. To reduce the potential effect of  
140 sampling bias and spatial autocorrelation in the occurrence dataset, we randomly filtered one  
141 occurrence record for each species within a radius of ~10 km (Kramer-Schadt et al., 2013). At

142 this point, all species in the database had at least 5 occurrence records. Our final dataset  
143 included 11,900 unique occurrence records of 93 species distributed across the Neotropical  
144 realm (Fig. S1). Information on mammal body mass was extracted from the *EltonTraits*  
145 (Wilman et al., 2014), *Phylacine* (Faurby et al., 2018) and *Combine* databases (Soria et al.,  
146 2021) and complemented through specialised literature (see Data Availability for complete  
147 sources on body mass data).

148

### 149 **Current and future projections**

150 We used 19 bioclimatic variables from the *WorldClim* v2.1 (Fick & Hijmans, 2017) in the  
151 spatial resolution of 5 arc-min (~100 km<sup>2</sup> pixel) to represent the current climate. The global  
152 bioclimatic layers were cropped to the extent of Neotropical realm (i.e., our model's  
153 background). To avoid problems with multicollinearity and reduce the dimensionality of  
154 predictor layers, we conducted a principal component analysis on the bioclimatic layers and  
155 retained the predictor axes that cumulatively explained 95% of data variation (De Marco &  
156 Nóbrega, 2018). We projected the linear relationships between raw predictors and principal  
157 components onto new layers representing future climate scenarios using the PCA loading  
158 coefficients derived from climatic data.

159 The future climate projections can vary according to different Shared Socioeconomic  
160 Pathways (SSPs) that consider distinct paths to greenhouse gas emissions and the human  
161 demographic growth (IPCC, 2021). We employed climate projections for the optimistic (SSP  
162 245) and pessimistic (SSP 585) scenarios for the period of 2041-2060 (hereafter 2060) and for  
163 the period 2081-2100 (hereafter 2100), both derived from the 6th IPCC Assessment Report  
164 (IPCC, 2021). The SSPs were created in agreement with different Generalised Circulation  
165 Models (GCMs) that simulate climatic alterations considering various atmospheric processes  
166 (IPCC, 2021). To minimise uncertainties about the choice of a particular GCM (Diniz-Filho et

167 al., 2009; Thuiller et al., 2019), we selected the five distinct GCMs, namely: BCC-CSM2-MR,  
168 CNRM-CM6-1, IPSL-CM6A-LR, MIROC6, and MRI-ESM2-0.

169

### 170 **Ecological niche models**

171 Recent investigations have showed that 17 occurrence records would be necessary to build  
172 traditional ecological niche models (ENMs) for species in the Caatinga (Sampaio &  
173 Cavalcante, 2023; van Proosdij et al., 2016). Because almost 20% of mammal species herein  
174 considered did not reach this occurrence threshold, we separated our dataset into species with  
175 either  $<20$  presences (considered as ‘rare’) or  $\geq 20$  presences (considered as ‘common’). We  
176 then applied the traditional ENM approach to model habitat suitability of common species  
177 and used the Ensemble of Small Models (ESM) approach (Breiner et al., 2015) to model the  
178 rare species. Before modelling, we established the calibration (accessible) area of each species  
179 as a buffer around its occurrence records, with a width size equal to the maximum nearest  
180 neighbour distance among pairs of occurrences (Barve et al., 2012). Within each species  
181 calibration area, we computed pseudo-absences using the ratio of 0.5 presence-absence for  
182 common species and 0.1 for rare species to avoid very unbalanced models while maximising  
183 sampling units (Barbet-Massin et al., 2012; Liu et al., 2019). To increment discriminatory and  
184 explanatory capacities of models, we allocated pseudoabsences following the environmentally  
185 constrained method, based on the lowest suitable region predicted by a climate envelope  
186 (Engler et al., 2004; Lobo & Tognelli, 2011).

187 Considering that the algorithm choice can affect the habitat suitability estimation  
188 (Diniz-Filho et al., 2009; Rangel & Loyola, 2012), we computed an ensemble of projections  
189 using four algorithms. For the species modelled using the traditional ENM approach, we used  
190 the following algorithms: Generalised Linear Models (using linear and quadratic terms),  
191 Generalised Additive Models (using smooth terms with three dimensions), Maximum Entropy



192 (using 10,000 background points and default features based on *MaxNet* package; Phillips et  
193 al., 2017), and Random Forests (with the *mtry* parameter automatically tuned by growing  
194 1000 trees through *tuneRF* function in *randomForest* package; Breiman, 2001; Liaw &  
195 Wiener, 2002). For the species modelled using the ESM approach, we used the Generalised  
196 Linear Models, Generalised Additive Models (using smooth terms with two dimensions), and  
197 Gradient Boosting Models (using learning rate of 0.1 and 100 trees), and Neural Networks  
198 (with 2 hidden layers, and decay parameters of 0; Breiner et al., 2018). For each method and  
199 rare species, we obtained the ESM by averaging the habitat suitability of bivariate models  
200 weighted by their respective model Somers' D [ $D = 2 \times (AUC - 0.5)$ ] (Breiner et al., 2015).  
201 The ESMs computed for the four abovementioned methods were then used to build an  
202 ensemble of projections for each rare species.

203         When projecting ENMs to new regions or time periods, it is possible to project habitat  
204 suitability for conditions outside the range represented by the training data (Elith et al., 2010).  
205 To account for the impact of model extrapolation on each species projection, we computed  
206 the Mobility-Oriented Parity (MOP) metric (Owens et al., 2013) within the calibration area of  
207 each species. We calculated the MOP metric by measuring the Euclidean distance between  
208 environmental conditions of the projected pixel and the nearest 10% training data  
209 observations (Montti et al., 2021). The MOP metric was further normalized to 1 and  
210 subtracted from 1 to reflect environmental similarity (Owens et al., 2013). We filtered habitat  
211 suitability estimates for projected pixels showing very high (MOP values  $\geq 0.9$ ), high (MOP  $\geq$   
212 0.8), and moderate (MOP  $\geq 0.7$ ) environmental similarity with the training data. To minimise  
213 issues with unlimited dispersal, we restricted all projections to the respective calibration area  
214 defined for each species.

215         We calibrated the models using 5-folds cross-validation, with 80% of randomly  
216 selected observations (presences and pseudo-absences) used for training, and the remaining

217 20% used for testing at each iteration (Roberts et al., 2017). Model performance was  
218 evaluated through computation of Sorensen similarity index (ranging from 0 to 1) between  
219 observations and binary predictions (Leroy et al., 2018)□. The habitat suitability threshold  
220 selected to make predictions binary was chosen to maximise the Sorensen index. We also  
221 computed complementary metrics of model performance, True Skill Statistic (TSS, ranging  
222 from -1 to 1) and Area Under Curve (AUC, ranging from 0 to 1) (Liu et al., 2011), to  
223 facilitate comparisons across literature. For the current climate, and for each combination of  
224 GCM, SSP, and year, we computed the ensemble model as the average weighted habitat  
225 suitability across algorithms, with the Sorensen index used as weight (Andrade et al., 2020).  
226 The ensemble model was then made binary using average weighted binarization threshold,  
227 with weights given by the Sorensen's index of the respective algorithm (Andrade et al., 2020;  
228 Thuiller et al., 2019). We used the standard deviation of habitat suitability across the GCMs as  
229 a measure of future model uncertainty.

230       Lastly, we applied spatial constraints *a posteriori* to minimise overprediction issues  
231 associated with species binary maps derived from ENMs. We used the occurrence-based  
232 threshold method (OBR) to exclude unreachable patches of current suitable habitats for each  
233 species (Mendes et al., 2020). This approach assumes that suitable patches are reachable if  
234 they either overlap with species presence records (occupied patch) or are within an edge-edge  
235 distance threshold of an occupied suitable patch (Mendes et al., 2020). We defined the  
236 distance threshold as the maximum nearest neighbour distance among pairs of occurrences of  
237 each species. All computations were performed in R 4.2.0 (R Core Team, 2022) using the  
238 *ENMTools* package (Andrade et al., 2020) to build the traditional ENMs and the *flexsdm*  
239 package (Velazco et al., 2022) to compute the ESMs.

240

241 **Assemblage-level biodiversity metrics**

242 We divided the Caatinga using an equal-area projection grid cell of  $10 \times 10$  km. We overlaid  
243 our grid cells (i.e., species assemblages) with binary maps to build presence-absence matrices  
244 for the current time and each future scenario (2060 SSP245, 2100 SSP245, 2060 SSP585, and  
245 2100 SSP585). To represent the aggregate model uncertainty in future scenarios, we used the  
246 average standard deviation of habitat suitability for species in each grid cell (species  
247 assemblage). More specifically, we initially averaged the variances (i.e., the squared  
248 deviations) for species habitat suitability in each cell, and then square rooted the outcome to  
249 get the average standard deviation (AvgSD) for each future year–SSP scenario combination  
250 (2060 SSP245, 2060 SSP585, 2100 SSP245, and 2100 SSP585).

251 Species richness corresponded to the number of species ( $S$ ) present in each grid cell.  
252 The spatial beta-diversity was represented by the multisite Simpson dissimilarity index –  $\beta_{SIM}$   
253 (Baselga, 2010), which is recommended for macroecological investigations given its  
254 independence of richness differences (Kreft & Jetz, 2010). We computed  $\beta_{SIM}$  between each  
255 focal cell and its immediate neighbouring cells. However, the number neighbouring cells is a  
256 proxy to area and can therefore affect the  $\beta_{SIM}$  via species-area relationship (Baselga, 2013).  
257 To circumvent this issue, we randomly selected four neighbouring cells around each focal cell  
258 to compute  $\beta_{SIM}$ . We repeated this procedure 100 times and extracted the average  $\beta_{SIM}$  across  
259 iterations to obtain the per cell  $\beta_{SIM}$ . Computations were performed in R using the *betapart*  
260 package (Baselga & Orme, 2012).

261 For each grid cell, we also computed the geometric mean of  $\log_{10}$  body mass across its  
262 member species ( $Avg_{mass}$ ) as a proxy for the structure of mammal assemblages (Bogoni et al.,  
263 2020). We calculated the richness difference between future and current period ( $\Delta S = S_{future} -$   
264  $S_{current}$ ) and change in spatial beta-diversity ( $\Delta\beta_{SIM} = \beta_{SIM,future} - \beta_{SIM,current}$ ) to identify species  
265 assemblages subject to biotic homogenization ( $\Delta\beta_{SIM} < 0$ ) or heterogenization ( $\Delta\beta_{SIM} > 0$ ).  
266 Similarly, we computed the ratio of average body mass of future to current projections

267 (MassRatio =  $\text{Avg}_{\text{mass.future}} / \text{Avg}_{\text{mass.current}}$ ) to quantify relative changes in mammal  
268 assemblages. MassRatio < 1 indicated future assemblage with lower average body mass than  
269 today, while MassRatio > 1 indicated the opposite.

270 To assess the influence of potential topographical refuges in shaping assemblage-level  
271 biodiversity metrics in Caatinga, we also categorised grid cells between lowlands (i.e., areas  
272 <500 m elevation) and highlands (i.e., areas >500 m elevation). The threshold of 500 meters  
273 allowed the detection of the five major Caatinga mountain ranges (e.g., Chapada Diamantina,  
274 Planalto da Borborema, Chapada do Araripe, Serra da Ibiapaba, and the highest parts of the  
275 Serra da Capivara and Serra das Confusões, see Fig. S2). We used Kruskal-Wallis tests to  
276 assess whether the medians of (i) Current species richness, (ii)  $\Delta S$ , (iii)  $\text{Avg}_{\text{mass.current}}$ , and (iv)  
277 MassRatio differed between assemblages subject to biotic homogenisation ( $\Delta\beta_{\text{SIM}} < 0$ ) or  
278 heterogenisation ( $\Delta\beta_{\text{SIM}} > 0$ ) or located in lowlands versus highlands. Linear relationships  
279 between projected changes in species richness ( $\Delta S$ ), changes in spatial beta-diversity ( $\Delta\beta_{\text{SIM}}$ ),  
280 relative changes in average body mass (MassRatio), and aggregated model uncertainty  
281 (AvgSD) were verified through a modified t-test (Dutilleul, 1993) to spatially correct the  
282 degrees of freedom of correlation coefficients. Computations were performed in R using the  
283 package *SpatialPack* (Osorio et al., 2014).

284

## 285 **RESULTS**

286 Across all non-volant mammal species in the Caatinga, the ensemble models showed  
287 moderate to high predictive performance using either the traditional Ecological Niche  
288 Modelling approach (median Sørensen similarity index = 0.68, range = 0.52–0.98; median  
289 TSS = 0.52, range = 0.12–0.97; median AUC 0.78, range=0.52–0.99) or the Ensemble of  
290 Small Models approach (median Sørensen similarity index = 0.60, range = 0.24–0.89; median  
291 TSS = 0.6, range = 0.19–0.98; median AUC 0.85, range=0.43–0.99; Fig. S3). Although

292 quantitative differences emerged between the SSP scenarios (SSP245 and SSP585) and year  
293 (2060 and 2100), results were qualitatively similar. Therefore, we focused here on projections  
294 for 2060 and SSP245, and based on highly similar environmental conditions (MOP values  $\geq$   
295 0.9), but see the Supporting Information for results on complementary projections.

296 About 87% of non-volant mammal species were projected to lose suitable areas by  
297 2060, with substantial reductions of suitable areas (i.e., >50% of geographic range loss)  
298 occurring mainly inside the Caatinga (Fig. S4). For at least 12 modelled species (12.8%),  
299 suitable habitats within the Caatinga were projected to be completely absent by 2060 under  
300 the SSP245 scenario (Fig. 1), with this number reaching 28 species (30%) under the  
301 pessimistic scenario (SSP585) by 2100 (Figs S5-S6). Our ensemble models projected that  
302 four species would currently show suitable habitats only outside the Caatinga, suggesting  
303 potential source-sink dynamics for these species (Fig. 1). However, it is worth noting that four  
304 out of the five species without projected suitable habitats (*Dasyprocta azarae*, *Gracilinanus*  
305 *microtarsus*, *Mirmecophaga tridactyla*, and *Priodontes maximus*, ) lacked occurrence records  
306 in the Caatinga, despite being listed in regional checklists (Carmignotto & Astúa, 2018).

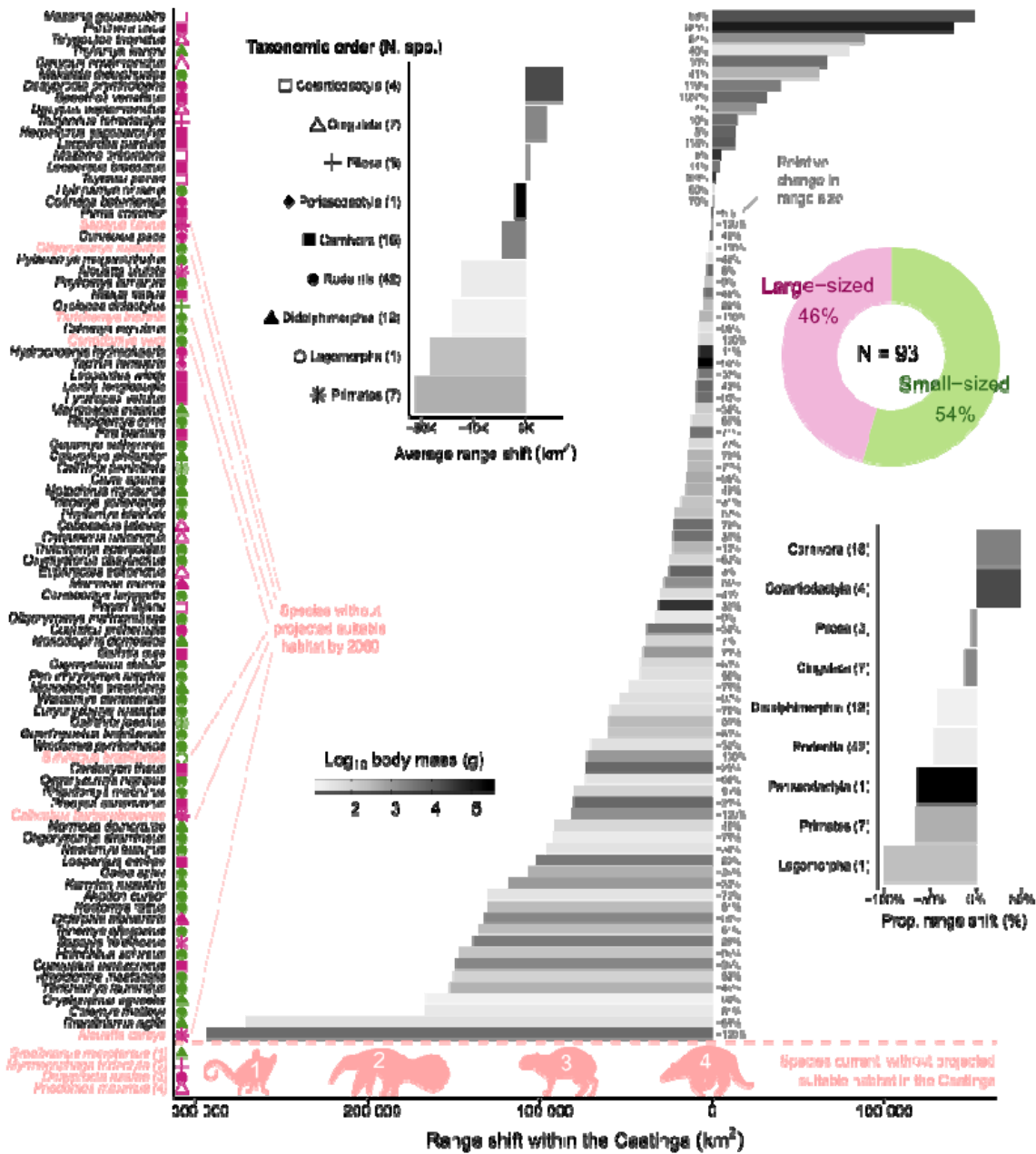
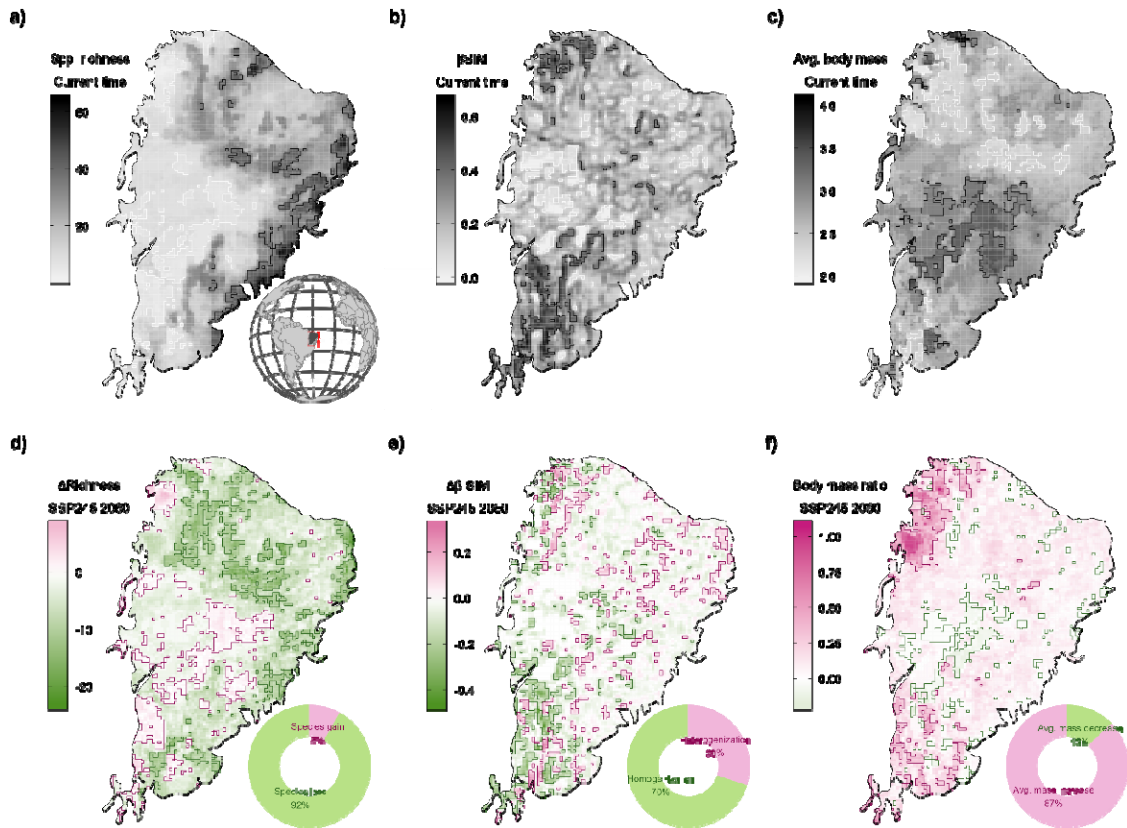


Figure 1. Projected range shift for non-volant mammals in the Caatinga. The four species below the red dashed line showed no current suitable habitats within the Caatinga, although they are projected to occur elsewhere in the Neotropical realm. Species labelled in red elsewhere indicate taxa without projected suitable habitats for 2060 according to the scenario SSP245. Symbol colour on the left panel indicate if species body mass is  $\leq 1$  kg (green, small-sized) or not (pink, large-sized). Symbol shape follow the taxonomic order indicated in the top-left inset plot. See Figs S4-S6 for results on complementary projections.

315 Species loss was projected for 91.6% of species assemblages, with an average richness  
316 difference of -4.7 species (range  $\Delta S = -23-8$ ) across all assemblages, whereas 69.9% of  
317 assemblages showed projected biotic homogenisation (Fig. 2). Median current species  
318 richness is higher in regions projected to become more heterogeneous ( $\chi^2 = 1167.7$ , d. f. = 7,  $p$   
319  $< 0.001$ , Fig. 3a). Similarly, future assemblages projected to be more heterogeneous in the  
320 future showed the most pronounced species loss (Fig. S11, Table S1), particularly those in  
321 northern Caatinga (Fig. 2), with model uncertainty increasing with richness difference (Fig.  
322 S20). Notably, model projections showed low uncertainty across regions subject either to  
323 biotic homogenisation or heterogenization (Fig. S21). Assemblages located in lowlands or  
324 highlands showed similar changes in species richness and spatial-beta diversity (Figs S12 and  
325 S17-18).

326 Average body mass in current assemblages was generally higher in lowlands than in  
327 highlands ( $\chi^2 = 435.6$ , d. f. = 7,  $p < 0.001$ , Fig. 3c). Surprisingly, 87.7% of assemblages were  
328 projected to experience an increase in average body mass of their member species,  
329 particularly in the southern and northwestern portions of Caatinga (Fig. 2). The relative  
330 change in average body mass was not associated with changes in either species richness (Figs  
331 4c and S14d) or biotic change (Figs 4e and S15d), but tended to slightly increase with  
332 elevation (Fig. S12i-l). Across most the SSP scenarios, time periods, and levels of  
333 extrapolation constraints, our findings indicated no relationship between changes in average  
334 body mass and aggregated model uncertainty (Fig. S22).



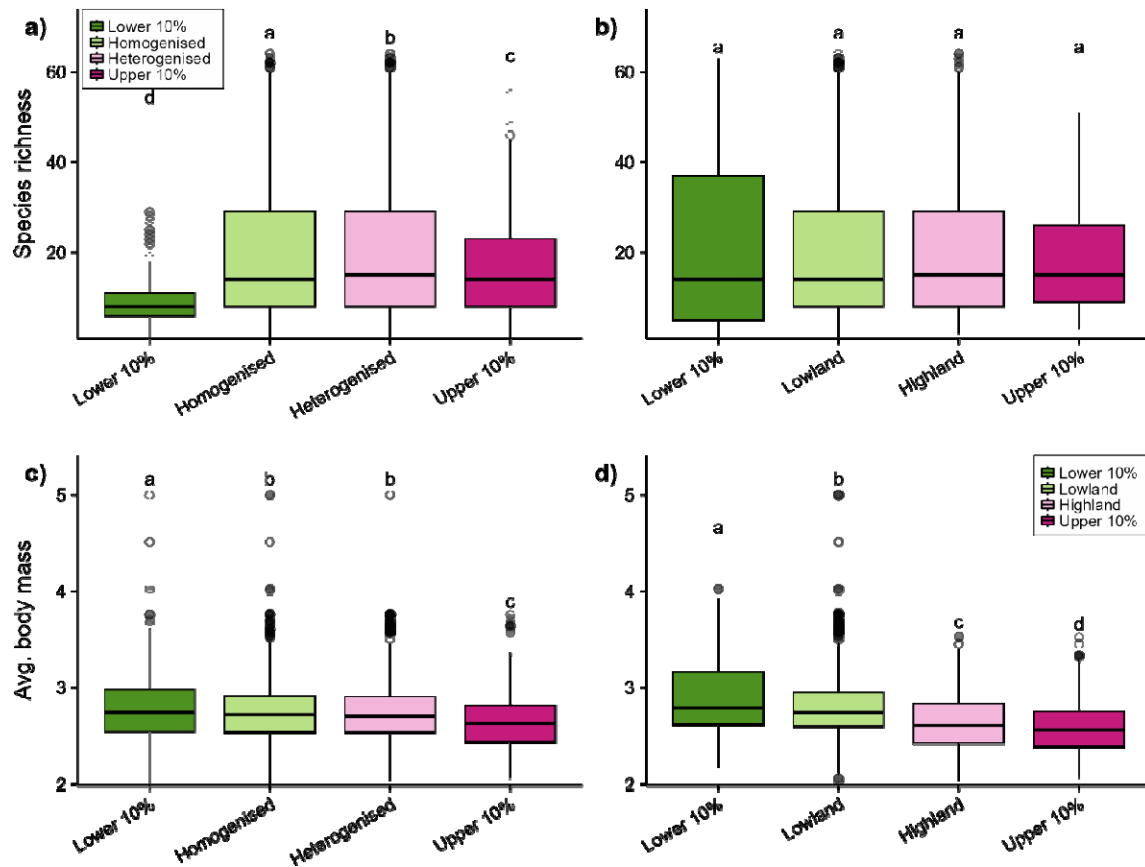


335

336 **Figure 2. Geographical patterns of species richness, spatial beta-diversity, and average body mass for**  
337 **mammals in the Caatinga.** (a) Current species richness, (b) Spatial beta-diversity ( $\beta_{SIM}$ ), (c) Average  $\log_{10}$  body  
338 mass (g), (d) Projected richness difference ( $\Delta S$ ), (e) Projected change in spatial beta-diversity ( $\Delta\beta_{SIM}$ ), (f)  
339 Projected relative change in average body mass. All geographical patterns were derived from species projections  
340 holding at least 90% of environmental similarity with training data. The contour lines denote the assemblages  
341 (cells) in the upper and lower 10% of the mapped pattern. Plots are shown for the scenario SSP245 at the year  
342 2060. See Figs S7-S10 for results on complementary projections and mapped uncertainty.

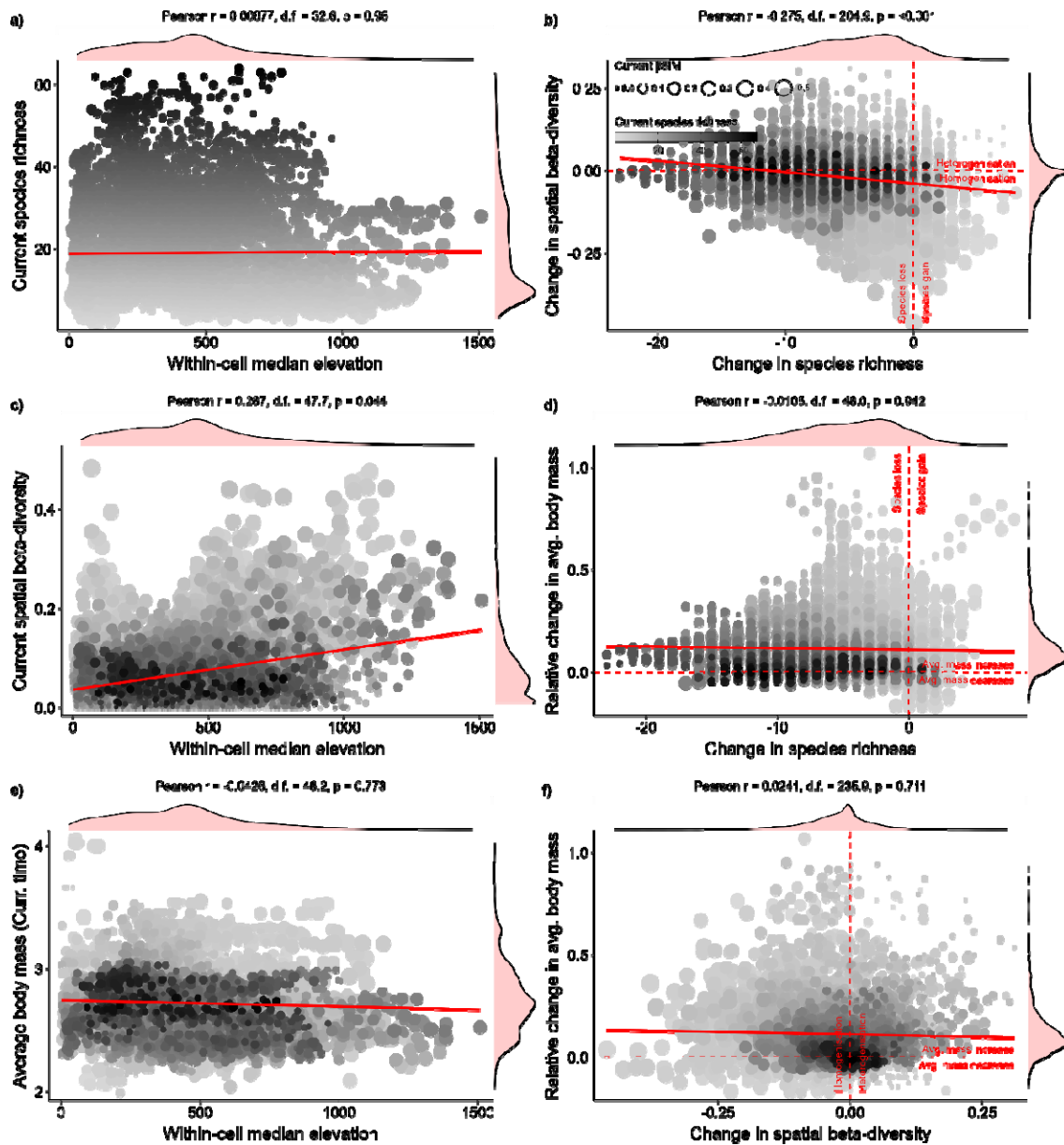
343





344

345 **Figure 3. Species richness and average body mass across mammal assemblages at different elevations and**  
346 **levels of biotic change.** (a-b) Species richness and (c-d) average body mass. Each box denotes the median  
347 (horizontal line), the 25th and 75th percentiles, the 95% confidence intervals (vertical line), and outliers (black  
348 dots). Boxplots in darker greenish or pinkish colours denote were computed using the upper and lower 10%  
349 assemblages (cells) in terms of biotic change (a, c) and elevation (b, d). Small capital letters denote the results of  
350 the Kruskal–Wallis tests for the difference in medians across assemblages subject to different levels of biotic  
351 homogenisation or located in lowlands or highlands (boxplots holding the same letter show statistically similar  
352 median values under  $p = 0.05$ , using Bonferroni correction). Plots are shown for the scenario SSP245 at the year  
353 2060. See Figs S11-S12 and Tables S1-S2 for complementary projections.



354

355 **Figure 4. Change in species richness, spatial beta-diversity, average body mass of mammal assemblages in**  
 356 **Caatinga.** Plots (a, c, e) illustrate the relationship between assemblage-level biodiversity metrics at the current  
 357 time and elevation, whereas plots (b, d, f) indicate how changes in biodiversity metrics are inter-related. All  
 358 geographical patterns were derived from species projections holding at least 90% of environmental similarity  
 359 with training data. Pearson correlations at the top of each panel were based on spatially corrected degrees of  
 360 freedom. Plots are shown for the scenario SSP245 at the year 2060. See Figs S13-S22 for results on  
 361 complementary projections.

362 **DISCUSSION**

363 Drylands in northern South America are expected to face temperature rise of up to 2.7°C by  
364 2060, with changes in the number of consecutive dry days increasing by as much as 21 days  
365 (IPCC, 2021). Our study reveals the potential for such changes to drastically erode the  
366 diversity of non-volant mammals in the Caatinga. Our projections indicate that most species  
367 will lose suitable environmental conditions within the Caatinga, while a few will expand their  
368 distribution, which will result in lower species richness and increased compositional similarity  
369 to nearby assemblages. Our results show that the biotic homogenisation and species loss are  
370 projected in opposite directions, with species gain occurring mostly in regions that are  
371 currently species-poor. Although the current beta-diversity is higher in highlands than  
372 lowlands, projected changes in biotic composition are only weakly or not at all associated  
373 with elevation. Most assemblages are expected to lose small-sized mammals, while large-  
374 sized species are projected to colonise neighbouring assemblages. Overall, we reveal how  
375 climate change strengthen the defaunation of non-volant mammals and produce complex  
376 spatial patterns in the largest tropical dry forest of South America.

377 Despite mammal adaptations to survive in drylands (e.g., insectivorous diet, night  
378 activity, and subterranean shelters), climate change can restrict their physiology and fitness by  
379 increasing dehydration, overheating, starvation, and reducing reproduction (Fuller et al.,  
380 2021). The projected loss of suitable habitat for almost 90% of all non-volant mammals of  
381 Caatinga suggests that these species will have to cope with extreme climate conditions for  
382 their dispersion across the biome. Among the main climatic “losers”– species with greatest  
383 suitable habitat loss – are primates and the Brazilian cottontail rabbit, but several species from  
384 the orders Didelphimorphia and Rodentia also emerge, such as the agile gracile opossum  
385 (*Gracilinanus agilis*), the long-tailed climbing mouse (*Rhipidomys mastacalis*), and the white-  
386 spined Atlantic spiny-rat (*Trinomys albispinus*). These animals are typically small-sized and

387 occupy lower trophic levels, usually producing a greater number of offspring when compared  
388 with large-sized mammals (Carmignotto & Astúa, 2018; Feijó & Langguth, 2013; Santini et  
389 al., 2013). The few “winner” species include the brown brocket (*Mazama gouazoubira*), the  
390 black-rumped agouti (*Dasyprocta prymnolopha*), which have a wide-ranging distribution and  
391 a large body size (Carmignotto & Astúa, 2018; Hetem et al., 2014; Santini et al., 2013), and  
392 different species of armadillos, which generally have wide tolerance to warm-dry climates  
393 (Soibelzon, 2019). These examples illustrate how animals with low vagility can be  
394 disproportionately impacted by climate change, which is supported by our findings on the  
395 decrease in the relative contribution of small-sized species across mammal assemblages.

396         The drastic species loss projected for the assemblages of non-volant mammals can be  
397 attributed to changes in dispersal, behaviour, and resource availability due to increasing  
398 aridity (Marengo et al., 2017; Torres et al., 2017). Firstly, increased aridity can shorten the  
399 optimal period for foraging and breeding (Hetem et al., 2014), and ultimately impact the  
400 ecological fitness and maintenance of mammal populations (Fuller et al., 2021). Secondly,  
401 geographical barriers may further restrict dispersal and hinder access to suitable habitats  
402 (Fuller et al., 2021). Thirdly, hotter and dryer conditions can reduce aboveground biomass  
403 (Rito et al., 2017; Souza et al., 2019) and alter floristic composition (Rito et al., 2017; Vieira  
404 et al., 2022), thereby impacting competition for food resources not only to herbivores, but also  
405 to omnivores and carnivores (Marinho et al., 2020; Oliveira & Diniz-Filho, 2010) □ □ . Since  
406 mammals can exhibit size-dependent variation in vagility, behaviour, and energy needs  
407 (Ramesh et al., 2015; Santini et al., 2013; Shipley et al., 1994), prolonged periods of heat and  
408 droughts can trigger heterogeneous species responses and enhance negative biotic  
409 interactions, ultimately leading to the depletion of faunal assemblages.

410         The predominance of highly-vagile large-sized species across lowland assemblages  
411 and the faster turnover of small-sized species in highlands help to explain the increase in

412 mammal beta-diversity along elevational gradients in the Caatinga (Lopez et al., 2016; Melo  
413 et al., 2009). While small-sized mammals certainly occur across Caatinga lowlands, the future  
414 homogenisation is expected to be primarily driven by the loss of suitable habitats for typically  
415 small-sized mammals – adults weighting  $\leq 1$  kg, *sensu* Chiarello (2000) – which constitute  
416 54% of species in the region (Fig. 1). The current predominance of small-sized mammals  
417 across highlands can be related to species persistence through elevational range shift across  
418 time (Chen et al., 2011), which is especially important in the Caatinga due to its climate  
419 instability when compared with other regions in South America (Costa et al., 2018).  
420 Therefore, the impoverished and compositionally similar mammal assemblages in the  
421 lowlands may have resulted from the historic accumulation of local extinctions in the  
422 Caatinga, particularly of small-sized species with low vagility (Schloss et al., 2012).

423 Ecological niches of large-sized species may have been underestimated due to past  
424 hunting and overexploitation (Sales et al., 2022), which could further increase in the relative  
425 contribution of large-sized species in shaping mammal assemblage. However, our data entries  
426 may have missed species entirely if past defaunation resulted in the extinction of large-sized  
427 species in the Caatinga. Ungulates like the tapir, peccaries, and different deer species that had  
428 wider ranges before European colonization are considered locally extinct across most regions  
429 within the biome limits (Barboza et al., 2016). The largest extant mammal in most sites, and  
430 the ones projected to increase in range are armadillos, which can be very resilient and often  
431 thrive in human-modified landscapes (Bovo et al., 2018; Magalhães et al., 2023), with most  
432 small mammals including rodents and marsupials projected to undergo range contractions  
433 while the potential range of some of the larger-bodied extant species are projected to increase,  
434 the average body mass increases as well. In that sense the pattern we found of increasing  
435 mean average body mass is the consequence of the expansion of opportunistic species as well  
436 as a legacy of past defaunation. It is worth noting that while the geographical pattern of

437 average body mass indicates a general increase in the relative contribution of large-sized  
438 species, intraspecific responses may cause mammal body size to decrease in response to a  
439 warming climate (Gardner et al., 2011; Villar & Naya, 2018).

440 While methodical choices and theoretical limitations like climate uncertainty, dispersal  
441 limitations, niche conservatism and model transferability (Barve et al., 2012; Diniz-Filho et  
442 al., 2009; Guisan & Thuiller, 2005; Owens et al., 2013; Thuiller et al., 2019) may have  
443 affected our projections, we minimized these issues by offering an ensemble of projections  
444 across various modelling algorithms (Araújo & New, 2007). We also implemented an  
445 ensemble of future projections across different generalized circulation models and future  
446 scenarios of climate change (Diniz-Filho et al., 2009; Thuiller et al., 2019). We also applied  
447 species-specific spatial restrictions to remove unreachable patches of projected suitable  
448 habitats and minimise overprediction issues related to unlimited dispersal by constraining  
449 projections to species-specific calibration areas (Mendes et al., 2020). In addition,  
450 assumptions of niche conservatism are likely applicable to mammals in the Caatinga, as the  
451 upper limits of mammal thermal tolerance are highly conserved in tropical species (Araújo et  
452 al., 2013; Khaliq et al., 2015). To minimise model transferability issues, we constrained  
453 habitat suitability estimates to environmental conditions similar to those in the training data  
454 (Owens et al., 2013). Although the models used in this study varied quantitatively, the  
455 projected changes consistently pointed in the same direction, conveying a unified message.

456 Our findings indicate a higher species loss for mammal assemblages in the eastern half  
457 of Caatinga, which is also affected by chronic disturbances (Antongiovanni et al., 2020). The  
458 highly fragmented and diminished vegetation cover of eastern Caatinga (Castanho et al.,  
459 2020) impose additional challenges for non-volant mammals to track suitable habitats (Alves  
460 et al., 2020), further contributing to depauperate the trophic structure of species assemblages  
461 (Mendoza & Araújo, 2019). Although mammal assemblages subject to high species loss

462 exhibit more future uncertainty, a more optimistic outlook is unlikely as these regions also  
463 overlap with heavily settled human-modified landscapes in the Caatinga (Antongiovanni et  
464 al., 2018, 2020) and regions projected to vegetation complexity and diversity (Moura et al.,  
465 2023). Therefore, the severe defaunation of Caatinga mammal assemblages is a probable  
466 outcome, with small-sized species loss driven by climate change – at least partially – and the  
467 depauperating of large-sized mammal further exacerbated by overexploitation and habitat  
468 destruction (Alves et al., 2023; Bogoni et al., 2020). In the long-term, this drastic  
469 simplification of mammal assemblages can disrupt biotic interactions and impact ecosystem  
470 services in tropical dry forests, by reducing the potential for vegetation regeneration and  
471 carbon storage (Bello et al., 2015; Fricke et al., 2022; Gardner et al., 2019). The success of  
472 long-term socioenvironmental policy and biodiversity conservation planning necessitates that  
473 findings derived from biodiversity forecasts are considered.

474

## 475 REFERENCES

- 476 Aguirre-Gutiérrez, J., Malhi, Y., Lewis, S. L., Fauset, S., Adu-Bredu, S., Affum-Baffoe, K.,  
477 Baker, T. R., Gvozdevaite, A., Hubau, W., Moore, S., Peprah, T., Ziemińska, K.,  
478 Phillips, O. L., & Oliveras, I. (2020). Long-term droughts may drive drier tropical forests  
479 towards increased functional, taxonomic and phylogenetic homogeneity. *Nature*  
480 *Communications*, 11(1), 1–10. <https://doi.org/10.1038/s41467-020-16973-4>
- 481 Alves, R. R. N., Gonçalves, M. Br., & Vieira, W. L. S. (2012). Caça, uso e conservação de  
482 vertebrados no semiárido Brasileiro. *Tropical Conservation Science*, 5(3), 394–416.  
483 <https://doi.org/10.1177/194008291200500312>
- 484 Alves, T. S., Alvarado, F., Arroyo-Rodríguez, V., & Santos, B. A. (2020). Landscape-scale  
485 patterns and drivers of novel mammal communities in a human-modified protected area.  
486 *Landscape Ecology*, 35(7), 1619–1633. <https://doi.org/10.1007/s10980-020-01040-6>

- 487 Alves, T. S., Alvarado, F., Arroyo-Rodríguez, V., & Santos, B. A. (2023). Foxes and goats:  
488 the outcome of free-ranging livestock farming in Brazilian dry forests. *Biodiversity and*  
489 *Conservation*, 32(2), 715–734. <https://doi.org/10.1007/s10531-022-02520-8>
- 490 Andrade, A. F. A., Velazco, S. J. E., & De-Marco, P. (2020). ENMTML: An R package for a  
491 straightforward construction of complex ecological niche models. *Environmental*  
492 *Modelling & Software*, 125(October 2019), 104615.  
493 <https://doi.org/10.1016/j.envsoft.2019.104615>
- 494 Antongiovanni, M., Venticinque, E. M., & Fonseca, C. R. (2018). Fragmentation patterns of  
495 the Caatinga drylands. *Landscape Ecology*, 33(8), 1353–1367.  
496 <https://doi.org/10.1007/s10980-018-0672-6>
- 497 Antongiovanni, M., Venticinque, E. M., Matsumoto, M., & Fonseca, C. R. (2020). Chronic  
498 anthropogenic disturbance on Caatinga dry forest fragments. *Journal of Applied Ecology*,  
499 57(10), 2064–2074. <https://doi.org/10.1111/1365-2664.13686>
- 500 Araújo, M. B., Ferri-Yáñez, F., Bozinovic, F., Marquet, P. A., Valladares, F., & Chown, S. L.  
501 (2013). Heat freezes niche evolution. *Ecology Letters*, 16(9), 1206–1219.  
502 <https://doi.org/10.1111/ele.12155>
- 503 Araújo, M. B., & New, M. (2007). Ensemble forecasting of species distributions. *Trends in*  
504 *Ecology & Evolution*, 22(1), 42–47. <https://doi.org/10.1016/j.tree.2006.09.010>
- 505 Asfora, P. H., Palma, A. R. T., Astúa, D., & Geise, L. (2011). Distribution of *Oecomys*  
506 *catherinae* Thomas, 1909 (Rodentia: Cricetidae) in northeastern Brazil with karyotypical  
507 and morphometrical notes. *Biota Neotropica*, 11(2), 415–424.  
508 <https://doi.org/10.1590/S1676-06032011000200039>
- 509 Banda-R, K., Delgado-Salinas, A., Dexter, K. G., Linares-Palomino, R., Oliveira-Filho, A.,  
510 Prado, D., Pullan, M., Quintana, C., Riina, R., Rodriguez M, G. M., Weintritt, J.,  
511 Acevedo-Rodriguez, P., Adarve, J., Alvarez, E., Aranguren B, A., Arteaga, J. C.,



- 512 Aymard, G., Castano, A., Ceballos-Mago, N., ... Pennington, R. T. (2016). Plant  
513 diversity patterns in neotropical dry forests and their conservation implications. *Science*,  
514 353(6306), 1383–1387. <https://doi.org/10.1126/science.aaf5080>
- 515 Barbet-Massin, M., Jiguet, F., Albert, C. H., & Thuiller, W. (2012). Selecting pseudo-  
516 absences for species distribution models: How, where and how many? *Methods in*  
517 *Ecology and Evolution*, 3(2), 327–338. [https://doi.org/10.1111/j.2041-](https://doi.org/10.1111/j.2041-210X.2011.00172.x)  
518 210X.2011.00172.x
- 519 Barboza, R. R. D., Lopes, S. F., Souto, W. M. S., Fernandes-Ferreira, H., & Alves, R. R. N.  
520 (2016). The role of game mammals as bushmeat in the Caatinga, northeast Brazil.  
521 *Ecology and Society*, 21(2), art2. <https://doi.org/10.5751/ES-08358-210202>
- 522 Barve, N., Barve, V., Jiménez-valverde, A., Lira-noriega, A., Maher, S. P., Peterson, A. T.,  
523 Soberón, J., & Villalobos, F. (2012). The crucial role of the accessible area in ecological  
524 niche modeling and species distribution modeling. *Ecological Modelling*, 222(11), 1810–  
525 1819. <https://doi.org/10.1016/j.ecolmodel.2011.02.011>
- 526 Baselga, A. (2010). Partitioning the turnover and nestedness components of beta diversity.  
527 *Global Ecology and Biogeography*, 19(1), 134–143.
- 528 Baselga, A. (2013). Multiple site dissimilarity quantifies compositional heterogeneity among  
529 several sites, while average pairwise dissimilarity may be misleading. *Ecography*, 36(2),  
530 124–128. <https://doi.org/10.1111/j.1600-0587.2012.00124.x>
- 531 Baselga, A., & Orme, C. D. L. (2012). betapart: an R package for the study of beta diversity.  
532 *Methods in Ecology and Evolution*, 3(5), 808–812.
- 533 Becker, A., Körner, C., Brun, J.-J., Guisan, A., & Tappeiner, U. (2007). Ecological and Land  
534 Use Studies along Elevational Gradients. *Mountain Research and Development*, 27(1),  
535 58–65. <http://www.jstor.org/stable/4540681>
- 536 Bello, C., Galetti, M., Pizo, M. A., Magnago, L. F. S., Rocha, M. F., Lima, R. A. F., Peres, C.

- 537 A., Ovaskainen, O., & Jordano, P. (2015). Defaunation affects carbon storage in tropical  
538 forests. *Science Advances*, *1*(11). <https://doi.org/10.1126/sciadv.1501105>
- 539 Bogoni, J. A., Peres, C. A., & Ferraz, K. M. P. M. B. (2020). Extent, intensity and drivers of  
540 mammal defaunation: a continental-scale analysis across the Neotropics. *Scientific*  
541 *Reports*, *10*(1), 14750. <https://doi.org/10.1038/s41598-020-72010-w>
- 542 Bovo, A. A. de A., Magioli, M., Percequillo, A. R., Kruszynski, C., Alberici, V., Mello, M. A.  
543 R., Correa, L. S., Gebin, J. C. Z., Ribeiro, Y. G. G., Costa, F. B., Ramos, V. N., Benatti,  
544 H. R., Lopes, B., Martins, M. Z. A., Diniz-Reis, T. R., Camargo, P. B. de, Labruna, M.  
545 B., & Ferraz, K. M. P. M. de B. (2018). Human-modified landscape acts as refuge for  
546 mammals in Atlantic Forest. *Biota Neotropica*, *18*(2). [https://doi.org/10.1590/1676-](https://doi.org/10.1590/1676-0611-bn-2017-0395)  
547 [0611-bn-2017-0395](https://doi.org/10.1590/1676-0611-bn-2017-0395)
- 548 Breiman, L. (2001). Random Forests. *Machine Learning*, *45*(1), 5–32.  
549 <https://doi.org/10.1023/A:1010933404324>
- 550 Breiner, F. T., Guisan, A., Bergamini, A., & Nobis, M. P. (2015). Overcoming limitations of  
551 modelling rare species by using ensembles of small models. *Methods in Ecology and*  
552 *Evolution*, *6*(10), 1210–1218. <https://doi.org/10.1111/2041-210X.12403>
- 553 Breiner, F. T., Nobis, M. P., Bergamini, A., & Guisan, A. (2018). Optimizing ensembles of  
554 small models for predicting the distribution of species with few occurrences. *Methods in*  
555 *Ecology and Evolution*, *9*(4), 802–808. <https://doi.org/10.1111/2041-210X.12957>
- 556 Brennand, P. G. G., Langguth, A., & Percequillo, A. R. (2013). The genus *Hylaeamys*  
557 Weksler, Percequillo, and Voss 2006 (Rodentia: Cricetidae: Sigmodontinae) in the  
558 Brazilian Atlantic Forest: geographic variation and species definition. *Journal of*  
559 *Mammalogy*, *94*(6), 1346–1363. <https://doi.org/10.1644/12-MAMM-A-312.1>
- 560 Carmignotto, A. P., & Astúa, D. (2018). Mammals of the Caatinga: Diversity, ecology,  
561 biogeography, and conservation. In *Caatinga: The Largest Tropical Dry Forest Region*

- 562            *in South America*. [https://doi.org/10.1007/978-3-319-68339-3\\_8](https://doi.org/10.1007/978-3-319-68339-3_8)
- 563 Carmignotto, A. P., Vivo, M. de, & Langguth, A. (2012). Mammals of the Cerrado and  
564            Caatinga. In *Bones, Clones, and Biomes* (pp. 307–350). University of Chicago Press.  
565            <https://doi.org/10.7208/chicago/9780226649214.003.0014>
- 566 Carmona, C. P., Tamme, R., Pärtel, M., de Bello, F., Brosse, S., Capdevila, P., González-M.,  
567            R., González-Suárez, M., Salguero-Gómez, R., Vásquez-Valderrama, M., & Toussaint,  
568            A. (2021). Erosion of global functional diversity across the tree of life. *Science*  
569            *Advances*, 7(13). <https://doi.org/10.1126/sciadv.abf2675>
- 570 Castanho, A. D. A., Coe, M., Andrade, E. M., Walker, W., Baccini, A., Campos, D. A., &  
571            Farina, M. (2020). A close look at above ground biomass of a large and heterogeneous  
572            seasonally dry tropical forest-caatinga in north east of Brazil. *Anais Da Academia*  
573            *Brasileira de Ciencias*, 92(1), 1–18. <https://doi.org/10.1590/0001-3765202020190282>
- 574 Chen, I.-C., Hill, J. K., Ohlemüller, R., Roy, D. B., & Thomas, C. D. (2011). Rapid Range  
575            Shifts of Species Associated with High Levels of Climate Warming. *Science*, 333(6045),  
576            1024–1026. <https://doi.org/10.1126/science.1206432>
- 577 Chiarello, A. G. (2000). Density and Population Size of Mammals in Remnants of Brazilian  
578            Atlantic Forest. *Conservation Biology*, 14(6), 1649–1657.
- 579 Clavel, J., Julliard, R., & Devictor, V. (2011). Worldwide decline of specialist species:  
580            Toward a global functional homogenization? *Frontiers in Ecology and the Environment*,  
581            9(4), 222–228. <https://doi.org/10.1890/080216>
- 582 Cooke, R. S. C., Eigenbrod, F., & Bates, A. E. (2019). Projected losses of global mammal and  
583            bird ecological strategies. *Nature Communications*, 10(1), 2279.  
584            <https://doi.org/10.1038/s41467-019-10284-z>
- 585 Costa, G. C., Hampe, A., Ledru, M. P., Martinez, P. A., Mazzochini, G. G., Shepard, D. B.,  
586            Werneck, F. P., Moritz, C., & Carnaval, A. C. (2018). Biome stability in South America

- 587 over the last 30 kyr: Inferences from long-term vegetation dynamics and habitat  
588 modelling. *Global Ecology and Biogeography*, 27(3), 285–297.  
589 <https://doi.org/10.1111/geb.12694>
- 590 Culot, L., Pereira, L. A., Agostini, I., Almeida, M. A. B., Alves, R. S. C., Aximoff, I., Bager,  
591 A., Baldovino, M. C., Bella, T. R., Bicca-Marques, J. C., Braga, C., Brocardo, C. R.,  
592 Campelo, A. K. N., Canale, G. R., Cardoso, J. C., Carrano, E., Casanova, D. C., Cassano,  
593 C. R., Castro, E., ... Galetti, M. (2019). Atlantic Primates: a dataset of communities and  
594 occurrences of primates in the Atlantic Forests of South America. *Ecology*, 100(1).  
595 <https://doi.org/10.1002/ecy.2525>
- 596 De Marco, P., & Nóbrega, C. C. (2018). Evaluating collinearity effects on species distribution  
597 models: An approach based on virtual species simulation. *PLOS ONE*, 13(9), e0202403.  
598 <https://doi.org/10.1371/journal.pone.0202403>
- 599 Diniz-Filho, J. A. F., Bini, L. M., Rangel, T. F., Loyola, R. D., Hof, C., Nogués-Bravo, D., &  
600 Araújo, M. B. (2009). Partitioning and mapping uncertainties in ensembles of forecasts  
601 of species turnover under climate change. *Ecography*, 32(6), 897–906.  
602 <https://doi.org/10.1111/j.1600-0587.2009.06196.x>
- 603 Dirzo, R., Young, H. S., Galetti, M., Ceballos, G., Isaac, N. J. B., & Collen, B. (2014).  
604 Defaunation in the Anthropocene. *Science*, 345(6195), 401–406.  
605 <https://doi.org/10.1126/science.1251817>
- 606 Dutilleul, P. (1993). Modifying the t Test for Assessing the Correlation Between Two Spatial  
607 Processes. *Biometrics*, 49(1), 305–314.
- 608 Elith, J., Kearney, M., & Phillips, S. (2010). The art of modelling range-shifting species.  
609 *Methods in Ecology and Evolution*, 1(4), 330–342. [https://doi.org/10.1111/j.2041-](https://doi.org/10.1111/j.2041-210X.2010.00036.x)  
610 [210X.2010.00036.x](https://doi.org/10.1111/j.2041-210X.2010.00036.x)
- 611 Engler, R., Guisan, A., & Rechsteiner, L. (2004). An improved approach for predicting the

- 612 distribution of rare and endangered species from occurrence and pseudo-absence data.  
613 *Journal of Applied Ecology*, 41(2), 263–274. <https://doi.org/10.1111/j.0021->  
614 8901.2004.00881.x
- 615 Faurby, S., Davis, M., Pedersen, R. Ø., Schowanek, S. D., Antonelli, A., & Svenning, J.  
616 (2018). PHYLACINE 1.2: The Phylogenetic Atlas of Mammal Macroecology. *Ecology*,  
617 99(11), 2626–2626. <https://doi.org/10.1002/ecy.2443>
- 618 Feijó, A., & Langguth, A. (2013). Mamíferos de médio e grande porte do Nordeste do Brasil:  
619 distribuição e taxonomia, com descrição de novas espécies. *Revista Nordestina de*  
620 *Biologia*, 3–225.
- 621 Feijó, A., Nunes, H., & Langguth, A. (2016). Mamíferos da Reserva Biológica Guaribas,  
622 Paraíba, Brasil. *Revista Nordestina de Biologia*, 24(1), 57–74.
- 623 Fick, S. E., & Hijmans, R. J. (2017). WorldClim 2: new 1 km spatial resolution climate  
624 surfaces for global land areas. *International Journal of Climatology*, 37(12), 4302–4315.  
625 <https://doi.org/10.1002/joc.5086>
- 626 Filgueiras, B. K. C., Peres, C. A., Melo, F. P. L., Leal, I. R., & Tabarelli, M. (2021). Winner–  
627 Loser Species Replacements in Human-Modified Landscapes. *Trends in Ecology &*  
628 *Evolution*, 36(6), 545–555. <https://doi.org/10.1016/j.tree.2021.02.006>
- 629 Freitas, C. A. de. (1957). Notícia sobre a peste no Nordeste. *Revista Brasileira de*  
630 *Malariologia e Doenças Tropicais*, 9(1), 123–133.
- 631 Fricke, E. C., Ordonez, A., Rogers, H. S., & Svenning, J.-C. (2022). The effects of  
632 defaunation on plants' capacity to track climate change. *Science*, 375(6577), 210–214.  
633 <https://doi.org/10.1126/science.abk3510>
- 634 Fuller, A., Mitchell, D., Maloney, S. K., Hetem, R. S., Fonsêca, V. F. C., Meyer, L. C. R., van  
635 de Ven, T. M. F. N., & Snelling, E. P. (2021). How dryland mammals will respond to  
636 climate change: the effects of body size, heat load and a lack of food and water. *Journal*

- 637           of *Experimental Biology*, 224(Suppl\_1). <https://doi.org/10.1242/jeb.238113>
- 638 Gardner, A. L. (2008). *Mammals of South America, volume 1: Marsupials, xenarthrans,*  
639           *shrews, and bats* (Vol. 1). University of Chicago Press.
- 640 Gardner, C. J., Bicknell, J. E., Baldwin-Cantello, W., Struebig, M. J., & Davies, Z. G. (2019).  
641           Quantifying the impacts of defaunation on natural forest regeneration in a global meta-  
642           analysis. *Nature Communications*, 10(1), 4590. [https://doi.org/10.1038/s41467-019-](https://doi.org/10.1038/s41467-019-12539-1)  
643           12539-1
- 644 Gardner, J. L., Peters, A., Kearney, M. R., Joseph, L., & Heinsohn, R. (2011). Declining body  
645           size: a third universal response to warming? *Trends in Ecology & Evolution*, 26(6), 285–  
646           291. <https://doi.org/10.1016/j.tree.2011.03.005>
- 647 GBIF. (2023). *Global Biodiversity Information Facility – Free and Open Access to*  
648           *Biodiversity Data* (p. Selected mammal species occurrences).  
649           <https://doi.org/10.15468/dl.zncm2h>
- 650 Geise, L., Paresque, R., Sebastião, H., Shirai, L. T., Astúa, D., & Marroig, G. (2010). Non-  
651           volant mammals, Parque Nacional do Catimbau, Vale do Catimbau, Buíque, state of  
652           Pernambuco, Brazil, with karyologic data. *Check List*, 6(1), 180.  
653           <https://doi.org/10.15560/6.1.180>
- 654 Guisan, A., & Thuiller, W. (2005). Predicting species distribution: Offering more than simple  
655           habitat models. *Ecology Letters*, 8(9), 993–1009. [https://doi.org/10.1111/j.1461-](https://doi.org/10.1111/j.1461-0248.2005.00792.x)  
656           0248.2005.00792.x
- 657 Gurgel-Filho, N. M., Feijó, A., & Langguth, A. (2015). Pequenos mamíferos do Ceará  
658           (marsupiais, morcegos e roedores sigmodontíneos) com discussão taxonômica de  
659           algumas espécies. *Revista Nordestina de Biologia*, 23(2), 3–150.
- 660 Hetem, R. S., Fuller, A., Maloney, S. K., & Mitchell, D. (2014). Responses of large mammals  
661           to climate change. *Temperature*, 1(2), 115–127. <https://doi.org/10.4161/temp.29651>

- 662 Hidasi-Neto, J., Joner, D. C., Resende, F., Monteiro, L. de M., Faleiro, F. V., Loyola, R. D.,  
663 & Cianciaruso, M. V. (2019). Climate change will drive mammal species loss and biotic  
664 homogenization in the Cerrado Biodiversity Hotspot. *Perspectives in Ecology and*  
665 *Conservation*, 17(2), 57–63. <https://doi.org/10.1016/j.pecon.2019.02.001>
- 666 Hoekstra, J. M., Boucher, T. M., Ricketts, T. H., & Roberts, C. (2004). Confronting a biome  
667 crisis: global disparities of habitat loss and protection. *Ecology Letters*, 8(1), 23–29.  
668 <https://doi.org/10.1111/j.1461-0248.2004.00686.x>
- 669 IPCC. (2021). *Climate Change 2021: The Physical Science Basis. Contribution of Working*  
670 *Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate*  
671 *Change* (V. Masson-Delmotte, P. Zhai, A. Pirani, S. L. Connors, C. Péan, S. Berger, N.  
672 Caud, Y. Chen, L. Goldfarb, M. I. Gomis, M. Huang, K. Leitzell, E. Lonnoy, J. B. R.  
673 Matthews, T. K. Maycock, T. Waterfield, O. Yelekçi, R. Yu, & B. Zho (eds.)).  
674 Cambridge University Press.
- 675 Khaliq, I., Fritz, S. A., Prinzing, R., Pfenninger, M., Böhning-Gaese, K., & Hof, C. (2015).  
676 Global variation in thermal physiology of birds and mammals: evidence for phylogenetic  
677 niche conservatism only in the tropics. *Journal of Biogeography*, 42(11), 2187–2196.  
678 <https://doi.org/10.1111/jbi.12573>
- 679 Kramer-Schadt, S., Niedballa, J., Pilgrim, J. D., Schröder, B., Lindenborn, J., Reinfelder, V.,  
680 Stillfried, M., Heckmann, I., Scharf, A. K., Augeri, D. M., Cheyne, S. M., Hearn, A. J.,  
681 Ross, J., Macdonald, D. W., Mathai, J., Eaton, J., Marshall, A. J., Semiadi, G., Rustom,  
682 R., ... Wilting, A. (2013). The importance of correcting for sampling bias in MaxEnt  
683 species distribution models. *Diversity and Distributions*, 19(11), 1366–1379.  
684 <https://doi.org/10.1111/ddi.12096>
- 685 Kreft, H., & Jetz, W. (2010). A framework for delineating biogeographical regions based on  
686 species distributions. *Journal of Biogeography*, 37(11), 2029–2053.

- 687 <https://doi.org/10.1111/j.1365-2699.2010.02375.x>
- 688 Leal, I. R., Da-Silva, J. M. C., Tabarelli, M., & Lacher, T. E. (2005). Changing the Course of  
689 Biodiversity Conservation in the Caatinga of Northeastern Brazil. *Conservation Biology*,  
690 *19*(3), 701–706. <https://doi.org/10.1111/j.1523-1739.2005.00703.x>
- 691 Lenoir, J., & Svenning, J. C. (2015). Climate-related range shifts - a global multidimensional  
692 synthesis and new research directions. *Ecography*, *38*(1), 15–28.  
693 <https://doi.org/10.1111/ecog.00967>
- 694 Leroy, B., Delsol, R., Hugueny, B., Meynard, C. N., Barhoumi, C., Barbet-Massin, M., &  
695 Bellard, C. (2018). Without quality presence-absence data, discrimination metrics such  
696 as TSS can be misleading measures of model performance. *Journal of Biogeography*,  
697 *45*(9), 1994–2002. <https://doi.org/10.1111/jbi.13402>
- 698 Liaw, A., & Wiener, M. (2002). Classification and Regression by randomForest. *R News*,  
699 *2*(3), 18–22. <https://cran.r-project.org/doc/Rnews/>
- 700 Lima, F., Beca, G., Muylaert, R. L., Jenkins, C. N., Perilli, M. L. L., Paschoal, A. M. O.,  
701 Massara, R. L., Paglia, A. P., Chiarello, A. G., Graipel, M. E., Cherem, J. J., Regolin, A.  
702 L., Oliveira Santos, L. G. R., Brocardo, C. R., Paviolo, A., Di Bitetti, M. S., Scoss, L.  
703 M., Rocha, F. L., Fusco-Costa, R., ... Galetti, M. (2017). ATLANTIC-CAMTRAPS: a  
704 dataset of medium and large terrestrial mammal communities in the Atlantic Forest of  
705 South America. *Ecology*, *98*(11), 2979–2979. <https://doi.org/10.1002/ecy.1998>
- 706 Liu, C., Newell, G., & White, M. (2019). The effect of sample size on the accuracy of species  
707 distribution models: considering both presences and pseudo-absences or background  
708 sites. *Ecography*, *42*(3), 535–548. <https://doi.org/10.1111/ecog.03188>
- 709 Liu, C., White, M., & Newell, G. (2011). Measuring and comparing the accuracy of species  
710 distribution models with presence-absence data. *Ecography*, *34*(2), 232–243.  
711 <https://doi.org/10.1111/j.1600-0587.2010.06354.x>



- 712 Lobo, J. M., & Tognelli, M. F. (2011). Exploring the effects of quantity and location of  
713 pseudo-absences and sampling biases on the performance of distribution models with  
714 limited point occurrence data. *Journal for Nature Conservation*, 19(1), 1–7.  
715 <https://doi.org/10.1016/j.jnc.2010.03.002>
- 716 Lopez, L. C. S., Figueiredo, M. S. L., Fracasso, M. P. A., Mesquita, D. O., Anjos, U. U., &  
717 Grelle, C. E. V. (2016). The role of local versus biogeographical processes in influencing  
718 diversity and body size variation in mammal assemblages. *Ecology and Evolution*, 6(5),  
719 1447–1456. <https://doi.org/10.1002/ece3.1978>
- 720 Magalhães, R. A., Massara, R. L., de Oliveira, F. S., & Rodrigues, F. H. G. (2023). The  
721 Brazilian three-banded armadillo is widely distributed in a human-modified landscape in  
722 northeastern Brazil. *Mammal Research*, 68(1), 53–62. [https://doi.org/10.1007/s13364-](https://doi.org/10.1007/s13364-022-00651-5)  
723 [022-00651-5](https://doi.org/10.1007/s13364-022-00651-5)
- 724 Malcher, S. M., Pieczarka, J. C., Geise, L., Rossi, R. V., Pereira, A. L., O'Brien, P. C. M.,  
725 Asfora, P. H., Fonsêca da Silva, V., Sampaio, M. I., Ferguson-Smith, M. A., &  
726 Nagamachi, C. Y. (2017). *Oecomys catherinae* (Sigmodontinae, Cricetidae): Evidence  
727 for chromosomal speciation? *PLOS ONE*, 12(7), e0181434.  
728 <https://doi.org/10.1371/journal.pone.0181434>
- 729 Marengo, J. A., Torres, R. R., & Alves, L. M. (2017). Drought in Northeast Brazil—past,  
730 present, and future. *Theoretical and Applied Climatology*, 129(3–4), 1189–1200.  
731 <https://doi.org/10.1007/s00704-016-1840-8>
- 732 Mares, M. A., Willig, M. R., Streilein, K. E., & Lacher, T. E. (1981). *The mammals of*  
733 *northeastern Brazil: a preliminary assessment*. Carnegie Museum of Natural History.
- 734 Marinho, P. H., Fonseca, C. R., Sarmiento, P., Fonseca, C., & Venticinque, E. M. (2020).  
735 Temporal niche overlap among mesocarnivores in a Caatinga dry forest. *European*  
736 *Journal of Wildlife Research*, 66(2), 34. <https://doi.org/10.1007/s10344-020-1371-6>

- 737 Mckinney, M. L., & Lockwood, J. L. (1999). Biotic homogenization: a few winners  
738 replacing many losers in the next mass extinction. *Trends in Ecology & Evolution*,  
739 5347(11), 450–453.
- 740 Melo, A. S., Rangel, T. F. L. V. B., & Diniz-Filho, J. A. F. (2009). Environmental drivers of  
741 beta-diversity patterns in New-World birds and mammals. *Ecography*, 32(2), 226–236.
- 742 Mendes, P., Velazco, S. J. E., de Andrade, A. F. A., & De Marco, P. (2020). Dealing with  
743 overprediction in species distribution models: How adding distance constraints can  
744 improve model accuracy. *Ecological Modelling*, 431(August 2019), 109180.  
745 <https://doi.org/10.1016/j.ecolmodel.2020.109180>
- 746 Mendonça, A., Percequillo, A. R., Camargo, N. F., Ribeiro, J. F., Palma, A. R. T., Oliveira, L.  
747 C., Câmara, E. M. V. C., & Vieira, E. M. (2018). Cerrado Small Mammals: abundance  
748 and distribution of marsupials, lagomorphs, and rodents in a Neotropical savanna.  
749 *Ecology*, 99(8), 1900–1900. <https://doi.org/10.1002/ecy.2367>
- 750 Mendoza, M., & Araújo, M. B. (2019). Climate shapes mammal community trophic structures  
751 and humans simplify them. *Nature Communications*, 10(1), 5197.  
752 <https://doi.org/10.1038/s41467-019-12995-9>
- 753 Montti, L., Velazco, S. J. E., Travis, J. M. J., & Grau, H. R. (2021). Predicting current and  
754 future global distribution of invasive *Ligustrum lucidum* W.T. Aiton: Assessing  
755 emerging risks to biodiversity hotspots. *Diversity and Distributions*, 27(8), 1568–1583.  
756 <https://doi.org/10.1111/ddi.13303>
- 757 Moura, M. R., do Nascimento, F. A. O., Paolucci, L. N., Silva, D. P., & Santos, B. A. (2023).  
758 Pervasive impacts of climate change on the woodiness and ecological generalism of dry  
759 forest plant assemblages. *Journal of Ecology*, 111(8), 1762–1776.  
760 <https://doi.org/10.1111/1365-2745.14139>
- 761 Nagy-Reis, M., Oshima, J. E. de F., Kanda, C. Z., Palmeira, F. B. L., Melo, F. R., Morato, R.

- 762 G., Bonjorne, L., Magioli, M., Leuchtenberger, C., Rohe, F., Lemos, F. G., Martello, F.,  
763 Alves □ Eigenheer, M., Silva, R. A., Silveira dos Santos, J., Priante, C. F., Bernardo, R.,  
764 Rogeri, P., Assis, J. C., ... Ribeiro, M. C. (2020). Neotropical Carnivores: a data set on  
765 carnivore distribution in the Neotropics. *Ecology*, *101*(11).  
766 <https://doi.org/10.1002/ecy.3128>
- 767 Nascimento, F. O., & Feijó, A. (2017). Taxonomic revision of the tigrina *Leopardus tigrinus*  
768 (Schreber, 1775) species group (Carnivora, Felidae). *Papéis Avulsos de Zoologia (São*  
769 *Paulo)*, *57*(19), 231. <https://doi.org/10.11606/0031-1049.2017.57.19>
- 770 Oliveira, F. F. de, & Langguth, A. (2004). Pequenos mamíferos (Didelphimorphia e Rodentia)  
771 de Paraíba e Pernambuco, Brasil. *Revista Nordestina de Biologia*, 19–86.
- 772 Oliveira, G., & Diniz-Filho, J. A. F. (2010). Spatial patterns of terrestrial vertebrates richness  
773 in Brazilian semiarid, Northeastern Brazil: Selecting hypotheses and revealing  
774 constraints. *Journal of Arid Environments*, *74*(11), 1418–1426.
- 775 Oliveira, J. A., Gonçalves, P. R., & Bonvicino, C. R. (2003). Mamíferos da Caatinga. In I. R.  
776 Leal, M. Tabarelli, & J. M. C. Da-Silva (Eds.), *Ecologia e Conservação da Caatinga*  
777 (pp. 275–335). Universidade Federal de Pernambuco.
- 778 Osorio, F., Vallejos, R., Cuevas, F., & Mancilla, D. (2014). *SpatialPack: Package for*  
779 *analysis of spatial data* (p. <http://spatialpack.mat.utfsm.cl>).  
780 <http://spatialpack.mat.utfsm.cl>
- 781 Owens, H. L., Campbell, L. P., Dornak, L. L., Saupe, E. E., Barve, N., Soberón, J., Ingenloff,  
782 K., Lira-Noriega, A., Hensz, C. M., Myers, C. E., & Peterson, A. T. (2013). Constraints  
783 on interpretation of ecological niche models by limited environmental ranges on  
784 calibration areas. *Ecological Modelling*, *263*, 10–18.  
785 <https://doi.org/10.1016/j.ecolmodel.2013.04.011>
- 786 Patton, J. L., Pardiñas, U. F. J., & D'Elía, G. (2015). *Mammals of South America, volume 2:*

- 787 *Rodents*. University of Chicago Press.
- 788 Phillips, S. J., Anderson, R. P., Dudík, M., Schapire, R. E., & Blair, M. E. (2017). Opening  
789 the black box: an open-source release of Maxent. *Ecography*, *40*(7), 887–893.  
790 <https://doi.org/10.1111/ecog.03049>
- 791 Pires, F. D. A., & Wied, M. (1965). *The type specimens of Brazilian mammals collected by*  
792 *Prince Maximilian zu Wied. American Museum Novitates*. *2209*, 1–21.
- 793 Quintela, F. M., Da Rosa, C. A., & Feijó, A. (2020). Updated and annotated checklist of  
794 recent mammals from Brazil. *Anais Da Academia Brasileira de Ciências*, *92*(suppl 2).  
795 <https://doi.org/10.1590/0001-3765202020191004>
- 796 R Core Team. (2022). *R: A Language and Environment for Statistical Computing* (p. v.  
797 4.2.0). The R Foundation for Statistical Computing Platform.
- 798 Ramesh, T., Kalle, R., Sankar, K., & Qureshi, Q. (2015). Role of body size in activity budgets  
799 of mammals in the Western Ghats of India. *Journal of Tropical Ecology*, *31*(4), 315–  
800 323. <https://doi.org/10.1017/S0266467415000188>
- 801 Rangel, T. F., & Loyola, R. D. (2012). Labeling Ecological Niche Models. *Natureza &*  
802 *Conservação*, *10*(2), 119–126. <https://doi.org/10.4322/natcon.2012.030>
- 803 Redford, K. H. (1992). The Empty Forest. *BioScience*, *42*(6), 412–422.  
804 <https://doi.org/10.2307/1311860>
- 805 Riddell, E. A., Iknayan, K. J., Hargrove, L., Tremor, S., Patton, J. L., Ramirez, R., Wolf, B.  
806 O., & Beissinger, S. R. (2021). Exposure to climate change drives stability or collapse of  
807 desert mammal and bird communities. *Science*, *371*(6529), 633–636.  
808 <https://doi.org/10.1126/science.abd4605>
- 809 Rito, K. F., Tabarelli, M., & Leal, I. R. (2017). Euphorbiaceae responses to chronic  
810 anthropogenic disturbances in Caatinga vegetation: from species proliferation to biotic  
811 homogenization. *Plant Ecology*, *218*(6), 749–759. <https://doi.org/10.1007/s11258-017->

- 812 0726-x
- 813 Roberts, D. R., Bahn, V., Ciuti, S., Boyce, M. S., Elith, J., Guillerá-Arroita, G., Hauenstein,  
814 S., Lahoz-Monfort, J. J., Schröder, B., Thuiller, W., Warton, D. I., Wintle, B. A., Hartig,  
815 F., & Dormann, C. F. (2017). Cross-validation strategies for data with temporal, spatial,  
816 hierarchical, or phylogenetic structure. *Ecography*, *40*(8), 913–929.  
817 <https://doi.org/10.1111/ecog.02881>
- 818 Sales, L. P., Galetti, M., Carnaval, A., Monsarrat, S., Svenning, J., & Pires, M. M. (2022).  
819 The effect of past defaunation on ranges, niches, and future biodiversity forecasts.  
820 *Global Change Biology*, *28*(11), 3683–3693. <https://doi.org/10.1111/gcb.16145>
- 821 Sales, L. P., Galetti, M., & Pires, M. M. (2020). Climate and land use change will lead to a  
822 faunal “savannization” on tropical rainforests. *Global Change Biology*, *26*(12), 7036–  
823 7044. <https://doi.org/10.1111/gcb.15374>
- 824 Sampaio, A. C. P., & Cavalcante, A. M. B. (2023). Accurate species distribution models:  
825 minimum required number of specimen records in the Caatinga biome. *Anais Da*  
826 *Academia Brasileira de Ciências*, *95*(2), e20201421. <https://doi.org/10.1590/0001-3765202320201421>
- 828 Santini, L., Marco, M. Di, Visconti, P., Baisero, D., Boitani, L., & Rondinini, C. (2013).  
829 Ecological correlates of dispersal distance in terrestrial mammals. *Hystrix*, *24*(2), 181–  
830 186. <https://doi.org/10.4404/hystrix-24.2-8746>
- 831 Santos, P. M., Bocchiglieri, A., Chiarello, A. G., Paglia, A. P., Moreira, A., Souza, A. C.,  
832 Abba, A. M., Paviolo, A., Gatica, A., Medeiro, A. Z., Costa, A. N., Gallina, A. G.,  
833 Yanosky, A. A., Jesus, A., Bertassoni, A., Rocha, A., Bovo, A. A. A., Bager, A., Mol, A.  
834 C., ... Galetti, M. (2019). Neotropical Xenarthrans: a data set of occurrence of  
835 xenarthran species in the Neotropics. *Ecology*, *100*(7). <https://doi.org/10.1002/ecy.2663>
- 836 Schloss, C. A., Nuñez, T. A., & Lawler, J. J. (2012). Dispersal will limit ability of mammals

- 837 to track climate change in the Western Hemisphere. *Proceedings of the National*  
838 *Academy of Sciences of the United States of America*, 109(22), 8606–8611.  
839 <https://doi.org/10.1073/pnas.1116791109>
- 840 Shipley, L. A., Gross, J. E., Spalinger, D. E., Hobbs, N. T., & Wunder, B. A. (1994). The  
841 scaling of intake rate in mammalian herbivores. *The American Naturalist*, 143(6), 1055–  
842 1082.
- 843 Silva, J M C, Barbosa, L. C. F., Leal, I. R., & Tabarelli, M. (2017). The Caatinga:  
844 Understanding the challenges. In J M Cardoso da Silva, I. R. Leal, & M. Tabarelli (Eds.),  
845 *Caatinga: The Largest Tropical Dry Forest Region in South America* (pp. 3–19).  
846 Springer.
- 847 Silva, José M C, Leal, I. R., & Tabarelli, M. (2017). Caatinga. In José Maria Cardoso da  
848 Silva, I. R. Leal, & M. Tabarelli (Eds.), *Caatinga: The Largest Tropical Dry Forest*  
849 *Region in South America*. Springer International Publishing. [https://doi.org/10.1007/978-](https://doi.org/10.1007/978-3-319-68339-3)  
850 [3-319-68339-3](https://doi.org/10.1007/978-3-319-68339-3)
- 851 Socolar, J. B., Gilroy, J. J., Kunin, W. E., & Edwards, D. P. (2016). How Should Beta-  
852 Diversity Inform Biodiversity Conservation? *Trends in Ecology & Evolution*, 31(1), 67–  
853 80. <https://doi.org/10.1016/j.tree.2015.11.005>
- 854 Soibelzon, E. (2019). Using Paleoclimate and the Fossil Record to Explain Past and Present  
855 Distributions of Armadillos (Xenarthra, Dasypodidae). *Journal of Mammalian*  
856 *Evolution*, 26(1), 61–70. <https://doi.org/10.1007/s10914-017-9395-8>
- 857 Soria, C. D., Pacifici, M., Di Marco, M., Stephen, S. M., & Rondinini, C. (2021). COMBINE:  
858 a coalesced mammal database of intrinsic and extrinsic traits. *Ecology*, 102(6), e03344.  
859 <https://doi.org/10.1002/ECY.3344/SUPPINFO>
- 860 Souza, D. G., Sfair, J. C., de Paula, A. S., Barros, M. F., Rito, K. F., & Tabarelli, M. (2019).  
861 Multiple drivers of aboveground biomass in a human-modified landscape of the Caatinga

- 862 dry forest. *Forest Ecology and Management*, 435, 57–65.  
863 <https://doi.org/10.1016/j.foreco.2018.12.042>
- 864 Souza, Y., Gonçalves, F., Lautenschlager, L., Akkawi, P., Mendes, C., Carvalho, M. M.,  
865 Bovendorp, R. S., Fernandes □ Ferreira, H., Rosa, C., Graipel, M. E., Peroni, N., Cherem,  
866 J. J., Bogoni, J. A., Brocardo, C. R., Miranda, J., Zago da Silva, L., Melo, G., Cáceres,  
867 N., Sponchiado, J., ... Galetti, M. (2019). Atlantic Mammals: a data set of assemblages  
868 of medium □ and large □ sized mammals of the Atlantic Forest of South America.  
869 *Ecology*, 100(10). <https://doi.org/10.1002/ecy.2785>
- 870 Thuiller, W., Guéguen, M., Renaud, J., Karger, D. N., & Zimmermann, N. E. (2019).  
871 Uncertainty in ensembles of global biodiversity scenarios. *Nature Communications*,  
872 10(1), 1–9. <https://doi.org/10.1038/s41467-019-09519-w>
- 873 Torres, R. R., Lapola, D. M., & Gamarra, N. L. R. (2017). Future Climate Change in the  
874 Caatinga. In *Caatinga* (pp. 383–410). Springer International Publishing.  
875 [https://doi.org/10.1007/978-3-319-68339-3\\_15](https://doi.org/10.1007/978-3-319-68339-3_15)
- 876 van Proosdij, A. S. J., Sosef, M. S. M., Wieringa, J. J., & Raes, N. (2016). Minimum required  
877 number of specimen records to develop accurate species distribution models. *Ecography*,  
878 39(6), 542–552. <https://doi.org/10.1111/ecog.01509>
- 879 Velazco, S. J. E., Rose, M. B., Andrade, A. F. A., Minoli, I., & Franklin, J. (2022). flexsdm:  
880 An R package for supporting a comprehensive and flexible species distribution  
881 modelling workflow. *Methods in Ecology and Evolution*, 13(8), 1661–1669.  
882 <https://doi.org/10.1111/2041-210X.13874>
- 883 Vieira, L. A. F., Tabarelli, M., Souza, G., Queiroz, R. T., & Santos, B. A. (2022). Divergent  
884 herb communities in drier and chronically disturbed areas of the Brazilian Caatinga.  
885 *Perspectives in Ecology and Conservation*, Early view.  
886 <https://doi.org/10.1016/j.pecon.2021.12.002>

- 887 Villar, C. H., & Naya, D. E. (2018). Climate change and temporal trends in body size: the  
888 case of rodents. *Oikos*, *127*(8), 1186–1194. <https://doi.org/10.1111/oik.04884>
- 889 Werneck, F. P., Costa, G. C., Colli, G. R., Prado, D. E., & Sites Jr, J. W. (2011). Revisiting  
890 the historical distribution of Seasonally Dry Tropical Forests: new insights based on  
891 palaeodistribution modelling and palynological evidence. *Global Ecology and*  
892 *Biogeography*, *20*(2), 272–288. <https://doi.org/10.1111/j.1466-8238.2010.00596.x>
- 893 Wilman, H., Belmaker, J., Simpson, J., de la Rosa, C., Rivadeneira, M. M., & Jetz, W. (2014).  
894 EltonTraits 1.0: Species-level foraging attributes of the world’s birds and mammals.  
895 *Ecology*, *95*(7), 2027–2027. <https://doi.org/10.1890/13-1917.1>
- 896 Zizka, A., Silvestro, D., Andermann, T., Azevedo, J., Duarte Ritter, C., Edler, D., Farooq, H.,  
897 Herdean, A., Ariza, M., Scharn, R., Svantesson, S., Wengström, N., Zizka, V., &  
898 Antonelli, A. (2019). CoordinateCleaner: Standardized cleaning of occurrence records  
899 from biological collection databases. *Methods in Ecology and Evolution*, *10*(5), 744–751.  
900 <https://doi.org/10.1111/2041-210X.13152>

901

## 902 **ACKNOWLEDGEMENTS**

903 We are grateful to Pedro C. Estrela, Anderson Feijó, Thais Kubik, Daniel P. Silva and Cibele  
904 R. Bonvicino for comments on previous versions of this manuscript. To the Mammal  
905 Collection from Universidade Federal da Paraíba for providing occurrences data. To  
906 Fundação de Amparo à Pesquisa do Estado de São Paulo for grants to MRM (FAPESP  
907 #2021/11840-6 and #2022/12231-6) and MMP (FAPESP #2019/25478-7). To Conselho  
908 Nacional de Desenvolvimento Científico e Tecnológico for grants (CNPq #312178/2019-0  
909 and #307260/2022-4) and to Universidade Federal da Paraíba (PVA-13357-2020) for grants  
910 to BAS. To Re:wild and Dimensions Sciences Bridges for grants to GAO. To Fundação de  
911 Amparo à Pesquisa do Estado de Minas Gerais for grants to APP. To Coordenação de



912 Aperfeiçoamento de Pessoal de Nível Superior for a scholarship to GAO and fellowship to  
913 APP.

914

#### 915 **COMPETING INTERESTS**

916 The authors have no relevant financial or non-financial interests to disclose.

917

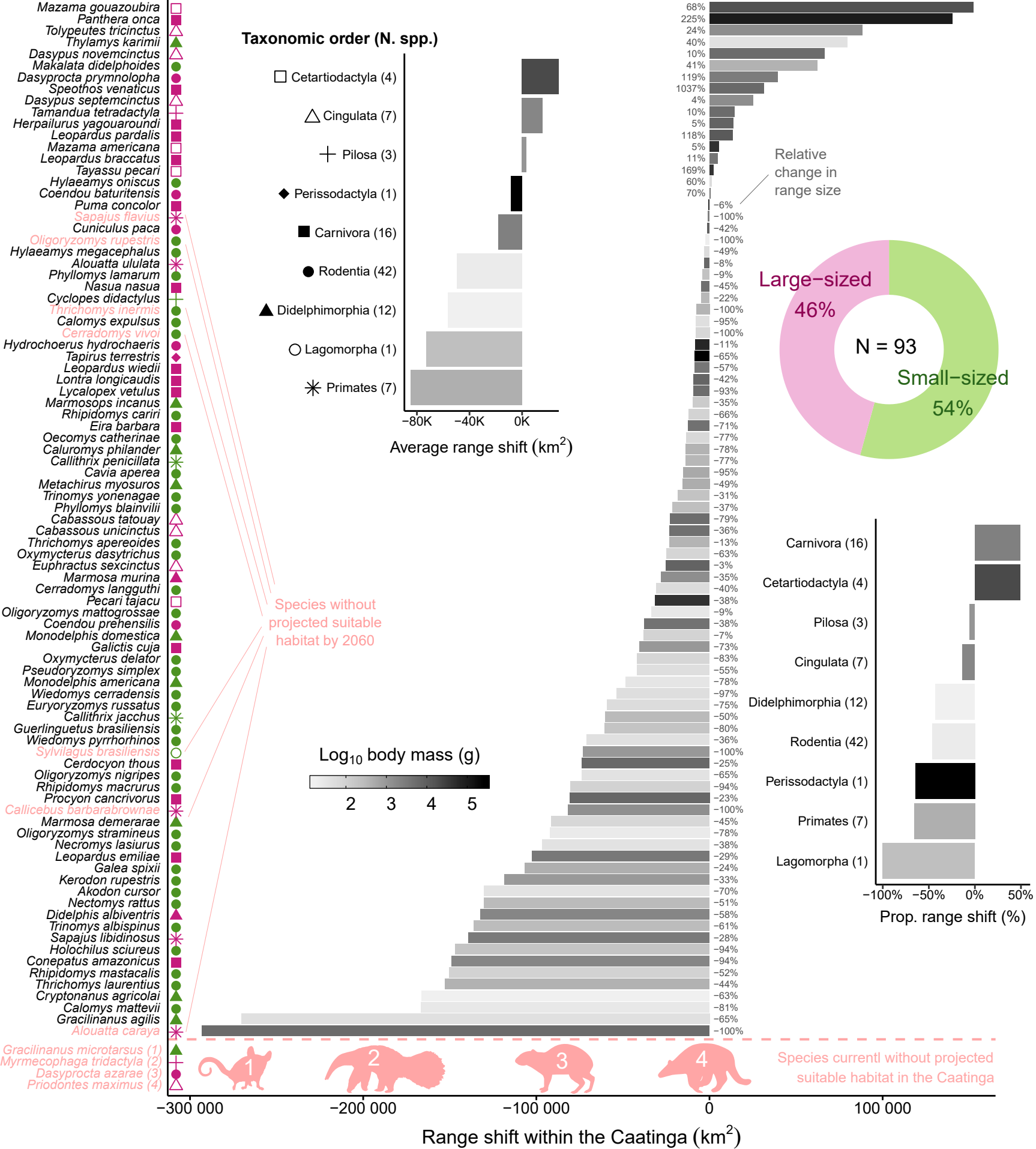
#### 918 **AUTHOR CONTRIBUTIONS**

919 MRM, GAO, and BAS conceived the study; GAO and APP compiled the data; MRM  
920 analysed the data. MRM developed the figures and led the writing. All authors contributed  
921 critically to the drafts and gave final approval for publication.

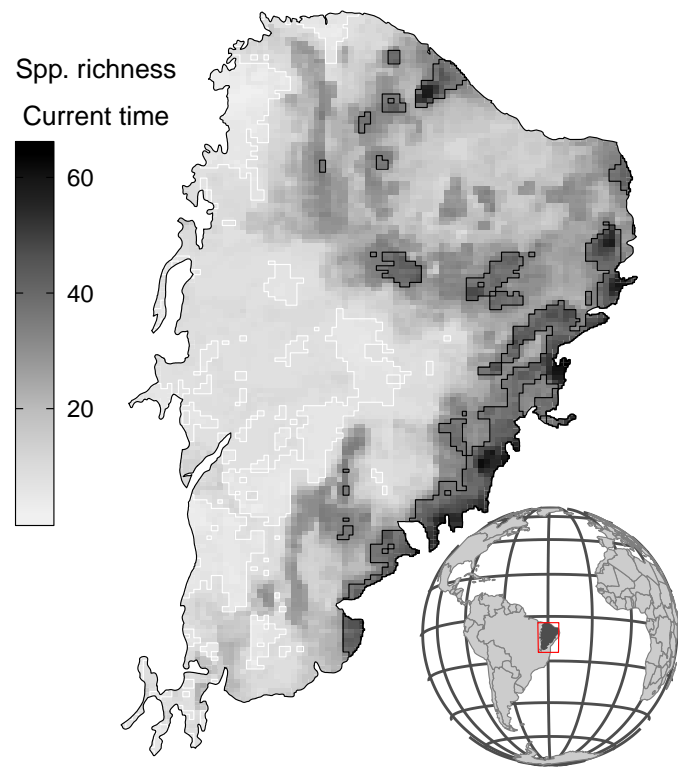
922

#### 923 **SUPPLEMENTARY MATERIAL**

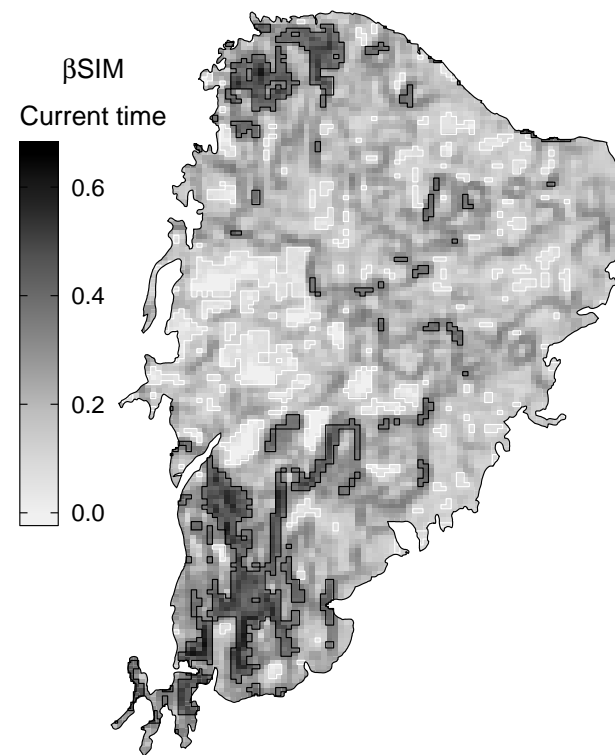
924 Supplementary Material is available for this manuscript, including Supplementary Tables  
925 (S1–S2) and Supplementary Figures (S1–S22).



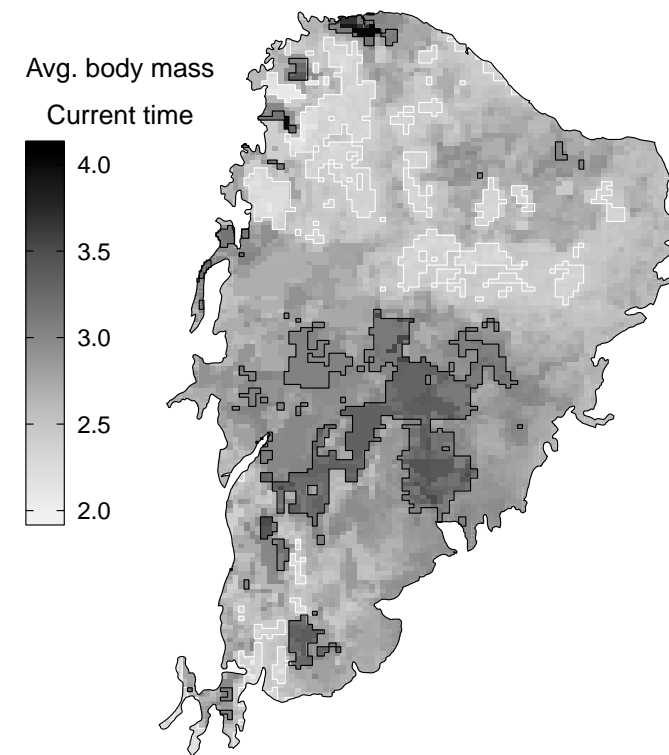
a)



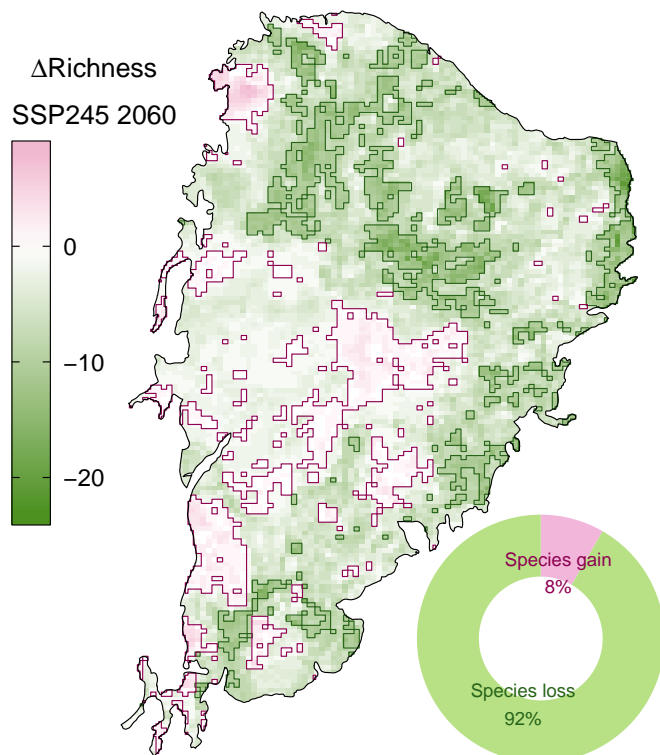
b)



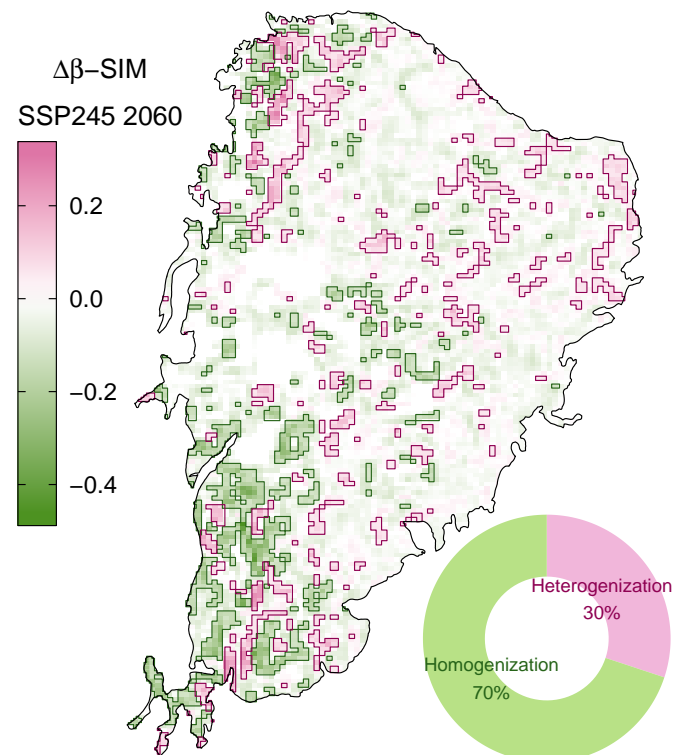
c)



d)



e)



f)

