

1 **Pervasive impacts of climate change on the woodiness and ecological generalism of dry**
2 **forest plant assemblages**

3
4 **SRT:** Climate change-driven biotic changes in tropical dry forests

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16
17 **Abstract:** Climate emergency is a significant threat to biodiversity in the 21st century, but
18 species will not be equally affected. In summing up different species' responses at the local
19 scale, we can assess changes in the species quantity and composition of biotic assemblages.
20 Here we investigated climate change driven variation in species richness and spatial beta-
21 diversity using modelled distributions of 2,841 plant species in Caatinga, the largest dry
22 forest region of South America. More than 99% of plant assemblages were projected to
23 lose species by 2060, with biotic homogenisation — the decrease in spatial beta-diversity —

24 **forecasted in 40% of the Caatinga. Replacement of narrow-range woody species by wide-**
25 **range non-woody ones should impact at least 85% of Caatinga plant assemblages. The**
26 **future increase in aridity will change patterns of woodiness and ecological generalism of**
27 **tropical dry forest plant assemblages, and ultimately erode ecosystem services linked to**
28 **biomass productivity and carbon storage.**

29

30 Climate change has been altered the environmental conditions experienced by many
31 species on Earth ¹. If species tolerances do not encompass the novel climatic conditions, they
32 may be forced to change their phenology or geographic range to track suitable climates ^{2,3}.
33 Spatial changes in the geographic range of species can alter the composition of species
34 assemblages ⁴. While certain species can colonise new sites in the future, most may not disperse
35 quickly enough to avoid local extinctions, with the extinction risk being greatest for species with
36 low vagility and narrow distribution ⁵. High local extinctions of narrow-range species and the
37 potential colonisation of new sites by wide-range species can lead to the biotic homogenisation
38 of species assemblages ⁶, and the eventual loss of ecosystem functions provided by such species
39 ⁷. Because the climate emergency is a higher threat for tropical species ^{2,5}, long-term
40 conservation planning will benefit from understanding how different tropical ecosystems are
41 subject to biotic changes ^{8,9}.

42 Climate change has induced the biotic homogenisation of plant assemblages in several
43 ecosystems around the world ¹⁰, including drylands ^{8,11,12}. It has been suggested that dryland
44 plants already experience a high water deficit and are close to their climatic tolerances ⁹. One of
45 the world's largest and floristically richest tropical dry forest is found in northeastern Brazil —
46 the Caatinga — with 912,529 km² ^{13,14}. Future climate projections indicate increases in aridity,

47 with subsequent desertification of some areas within the Caatinga¹⁵. Previous research has
48 shown that climate change should drive range contraction of endemic Caatinga plant species,
49 especially those with more specialised life history attributes¹⁶. Indeed, the colonisation and
50 extinction rates of species assemblages may be affected by species geography and life-history
51 attributes¹⁷. Narrow-range species tend to be more sensitive to climate change, whereas wide-
52 range species often exhibit broader climatic niches and thus high ecological generalism¹⁸.
53 Among flowering plants, the growth form is known to reflect species ecophysiology¹⁹, with
54 woody plant species likely exhibiting limited adaptability to climate change due to their longer
55 generation time and slower rates of climatic niche evolution relative to non-woody plants²⁰.

56 We applied ecological niche models (ENMs) under an ensemble modelling framework to
57 estimate the current and future geographic distribution patterns of 2,841 Caatinga plant species,
58 and then assessed potential biotic changes in local plant assemblage richness ($\Delta S = S_{\text{future}} -$
59 S_{current}) and spatial beta-diversity ($\Delta\beta_{\text{SOR}} = \beta_{\text{SOR, future}} - \beta_{\text{SOR, current}}$) in response to climate change
60 (see Methods). Our investigation considered the latest projections on future climate scenarios²¹
61 for 2060 and 2100, under the business-as-usual (SSP245) and non-mitigation (SSP585)
62 scenarios. Ensemble models showed good predictive performance, with an average Sørensen
63 similarity index of 0.934 (SD = 0.043, range = 0.703–1.00; Fig. S2). Because our results were
64 qualitatively similar for 2060 and 2100, we focused on 2060 projections for brevity (see
65 Extended Data for results concerning the year 2100).

66

67 **RESULTS**

68 Climate change will drastically alter plant biodiversity in one of the world's largest
69 seasonal tropical dry forests, the Caatinga. Our projections show that almost 90% of Caatinga

70 plant species will lose suitable areas by 2060, particularly narrow-range species (Fig 1). The
71 current distribution of Caatinga plant species will decrease on average by 37.4% and 43.9% in
72 the SSP245 and SSP585 scenarios, respectively. No Caatinga plant species is projected to lose its
73 entire suitable area within the Neotropics, but in the Caatinga, from 62 (SSP245) to 89 (SSP585)
74 species could be regionally extinct —100% of range loss— by 2060, and between 141 (SSP245)
75 and 349 (SSP585) species could be regionally extinct by 2100.

76 At the assemblage-level, more than 99% of plant assemblages in the Caatinga will lose
77 species by 2060 (Fig. 2b and c). Biotic homogenisation ($\Delta\beta_{\text{SOR}} < 0$) is expected in about 40% of
78 Caatinga plant assemblages, particularly in species-poor regions currently dominated by non-
79 woody and wide-range species (Fig. 2e and f). Relative to regions subject to biotic
80 heterogenisation, the future homogenised plant assemblages currently harbour lower species
81 richness ($\chi^2 = 3834.9$, $df = 7$, $p < 0.001$, Fig. 3a), lower proportion of woody species ($\chi^2 =$
82 1008.6 , $df = 7$, $p < 0.001$, Fig. 3b), and higher proportion of wide-range species ($\chi^2 = 1953.1$, df
83 $= 7$, $p < 0.001$, Fig. 3c). Although we projected a pervasive decrease in woodiness and an
84 increase in the ecological generalism of plant assemblages, the magnitude of such changes
85 differs between future homogenised or heterogenised regions. Plant assemblages facing
86 homogenisation risk by 2060 showed lower species loss ($\chi^2 = 4478.8$, $df = 7$, $p < 0.001$, Fig. 3d),
87 higher decrease in relative contribution of woody species ($\chi^2 = 1419.3$, $df = 7$, $p < 0.001$, Fig.
88 3e), and lower increase in relative contribution of wide-range species ($\chi^2 = 1662.6$, $df = 7$, $p <$
89 0.001 , Fig. 3f) than assemblages subject to heterogenisation.

90 We observed a predominance of assemblages with a higher proportion of non-woody and
91 wide-range species in the northern and middle-west regions of the Caatinga, whereas
92 assemblages with relatively more woody and narrow-range species occurred in the southern and

93 northeastern Caatinga (Fig. 4). Under the business-as-usual scenario, 98.4% of plant assemblages
94 will experience a reduction in the proportion of woody species ($WoodyRatio < 1$), slightly less
95 than in the non-mitigation scenario (98.9% of assemblages). The relative contribution of wide-
96 range species will increase ($WideRatio > 1$) in most assemblages in both SSP scenarios (86.1%
97 in the SSP245 and 85.3% in the SSP585, Fig. 4b and c). In all SSP scenarios investigated, the
98 increase in spatial beta-diversity of plant assemblages was directly related to species loss (Fig. 5a
99 and b), with changes in relative contribution of wide-range species linked to the decrease in
100 proportion of woody species (Fig. 5c and d).

101

102 **DISCUSSION**

103 The exacerbated decrease in plant richness can erode ecosystem services in Caatinga by
104 2060. In drylands worldwide, the role of plant richness in productivity stability is as important as
105 that of climate and edaphic conditions²². Under high aridity, species-rich assemblages are more
106 critical for ecosystem stability, whereas functionally distinct species minimise variation in the
107 temporal delivery of ecosystem services at low aridity²². Climate change is expected to increase
108 aridity in Caatinga, particularly in the central-southern region¹⁵, where our projections indicate a
109 higher species loss of plant assemblages. To worsen the situation, 98.4–98.9% of Caatinga plant
110 assemblages will lose relatively more woody than non-woody species, which should enhance the
111 impacts on biomass productivity and carbon storage in drylands^{23,24}.

112 Aridity may favour the establishment of wide-range plant species²⁵. Since most wide-
113 range plant species in Caatinga have non-woody growth-forms²⁶, the projected increase in
114 aridity in this region will lead to structural changes in vegetation complexity. With higher aridity,
115 dryland ecosystems face a vegetation decline phase due to the reduction of leaf area and canopy

116 cover²⁷. Aridification can also promote compositional change²⁸ and reduce the beta-diversity of
117 dryland plant assemblages²⁹. As environmental filtering can better explain the beta-diversity of
118 herbs and shrubs than that of trees^{30,31}, woody species' distributions are likely at a lower
119 equilibrium with climate than those of non-woody species, implying that woody species may not
120 keep pace with climate change. Projected changes in the species richness and beta-diversity of
121 Caatinga plant assemblages can therefore underestimate the impacts of climate change on plant
122 assemblages with higher levels of woodiness.

123 The impacts of climate change are often expected to be less severe in mountainous
124 regions³². Although elevational gradients can allow species to track more suitable climates over
125 time, the spatial configuration of mountainous areas can limit elevational range shifts³³,
126 particularly for woody species³⁴. In the Caatinga, the four most relevant highlands — where
127 many narrow-range woody species concentrates — are disconnected from each other and located
128 in transitional zones in the south (*Chapada Diamantina*), east (*Planalto da Borborema*) and
129 central-northwest (*Chapada do Araripe* and *Serra da Ibiapaba*), which impose additional
130 dispersal constraints on woody species there. Threats to woody species and their ecosystem
131 functions could be considerably greater than those we project. Vertebrates and invertebrates
132 interacting with woody plants — herbivores, seed dispersers, and pollinators — will have to
133 couple with the sudden changes in availability and composition of plant resources^{35,36},
134 ultimately scaling up the potential for disruption of biotic interactions³⁷.

135 We have shown how climate change can jeopardise Caatinga plant biodiversity, but much
136 of this region is also affected by chronic disturbances³⁸ that can operate synergistically with
137 climate change, and intensify the impacts of biodiversity loss on ecosystem functions³⁹.
138 Caatinga already lost half its original cover, and more than 90% of the remaining fragments have

139 less than 500 ha.³⁸ For some non-woody, self-pollinated, and wind-dispersed species, this
140 scenario may not prevent range expansion, but our projections show an extensive reduction in
141 suitable areas for most woody and non-woody species. Interestingly, the western half of the
142 Caatinga, where biotic changes are most pronounced, also concentrates the most conserved dry
143 forest remnants³⁸. This coincident spatial configuration imposes both a challenge and an
144 opportunity to expand the protected area network to assure the connectivity and long-term
145 persistence of Caatinga plant assemblages. Caatinga still figures with around 1% of the original
146 extension covered by strictly protected areas⁴⁰, far beyond the more recent thresholds
147 established under the post-2020 Global Biodiversity Frame of conserving 30% of Earth's land by
148 2030⁴¹. As a member of the Convention on Biological Diversity and the sole holder of the
149 Caatinga, Brazil will have a crucial role in conserving the most extensive tropical dry forest in
150 South America.

151

152 **METHODS**

153 **Species data**

154 We compiled occurrence records of Caatinga flowering plants from the scientific literature and
155 herbarium records, available at the Global Biodiversity Information Facility⁴² and speciesLink
156 (splink.cria.org.br). We restricted the spatial coverage of the species occurrence dataset to the
157 Neotropical region and recorded a total of 4,890,681 occurrences for 8,629 species. Records that
158 were duplicated, with georeferencing errors or uncertain identification were excluded. To reduce
159 the potential effect of sampling bias and spatial autocorrelation in the occurrence dataset, we
160 randomly filtered one occurrence record for each species within a radius of ~10 km⁴³ leading to
161 1,024,363 occurrences of 7,936 species. Preliminary inspections indicated that many species

162 occurred marginally in the Caatinga. Because our focus was on typical Caatinga plants, we kept
163 only those species with at least 10% of their occurrences within the Caatinga, resulting in
164 345,848 occurrences of 4,534 species. We excluded species with fewer than 15 occurrence
165 records⁴⁴ and kept for subsequent modelling procedures 335,091 records of 2,841 species
166 belonging to 776 genera and 141 botanical families (Fig. S1).

167 We gathered data on the growth-form of Caatinga flowering species using the Botanical
168 Information and Ecology Network⁴⁵, the Plant Trait Database⁴⁶, and the Brazilian Flora 2020⁴⁷,
169 complemented by pertinent literature^{26,48,49}. For each species, we assigned one out of seven
170 growth form types: tree, shrub, palm tree, woody vine, herb, herbaceous vine, or succulent. For
171 species with multiple growth-form categories we assigned the growth form agreed upon by most
172 sources⁵⁰. We then grouped the species into two categories: (i) woody (trees, shrubs, palms, and
173 woody vines) and (ii) non-woody species (herbs, herbaceous vines, and succulents). Growth-
174 form was assigned to 2,476 angiosperm species (1,341 woody and 1,135 non-woody species,
175 Table S1), covering 87.2% of species in our database.

176

177 **Current and future climate projections**

178 We used the 19 bioclimatic variables from the WorldClim database, version 2.1⁵¹ to represent
179 the current climate. Bioclimatic layers were downloaded at 5 arc-min (~10 km) and cropped to
180 the extent of the Neotropical realm (our background). To avoid problems with multicollinearity
181 and reduce the dimensionality of predictor layers, we performed a principal component analysis
182 (PCA) and retained the first six axes representing the principal components as climate predictors.
183 PCA axes explained 96.8% of the variation in the original data. We used PCA loading

184 coefficients to project the linear relationship between raw predictors and principal components
185 onto new layers representing future climate scenarios.

186 We considered future climate projections for the periods 2041–2060 (hereafter 2060) and
187 2081–2100 (hereafter 2100) following the 6th Assessment Report of the Intergovernmental Panel
188 on Climate Change ²¹. We used two Shared Socioeconomic Pathways (SSP) for each period:
189 SSP245 and SSP585 as a business-as-usual and non-mitigation scenario, respectively. Because
190 the selection of different generalised circulation models (GCM) is recognised as a source of
191 uncertainty in projecting the future habitat suitability of species ⁵², we used five GCMs for each
192 combination of the period and SSP, namely: BCC-CSM2-MR, CNRM-CM6-1, IPSL-CM6A-LR,
193 MIROC6, and MRI-ESM2-0.

194

195 **Ecological niche models**

196 For each species, we computed pseudoabsences using the same number of observed presences to
197 maintain the presence-absence ratio of 1:1 ⁵³. Pseudoabsences were allocated following the
198 environmentally constrained method, based on the lowest suitable region predicted by a climate
199 envelope ⁵⁴. The choice of the statistical method or algorithm can affect the resulting predictions
200 from an ecological niche model (ENM) depending on the initial modelling conditions ⁵⁵. We
201 computed an ensemble of projections for each species to minimise uncertainty around the ENM
202 method ⁵⁶. The ensemble included projections with six methods: Climate envelope (BIOCLIM),
203 Gower Environmental Distance (DOMAIN), Generalised Linear Models, Generalised Additive
204 Models, Maximum Entropy, and Random Forests. We used the species accessible area to mask
205 its respective projections to avoid predicting habitat suitability for regions unreachable by a
206 species within the time frame of projected climate change. The accessible area for each species

207 was defined by a buffer with a width size equal to the maximum nearest neighbour distance
208 among pairs of occurrences⁵⁷. Models were calibrated for the baseline period using 4-fold cross-
209 validation, 75% of randomly selected samples used for model training and the remaining 25%
210 used for testing in each iteration.

211 To evaluate model performance, we measured the similarity between predictions and
212 observations using the Sørensen similarity index, which is independent of species prevalence⁵⁸.
213 It is necessary to binarise the species habitat suitability according to some threshold value to
214 compute the Sørensen index. We used the species suitability value that maximised the Sørensen
215 index for each algorithm at the baseline period. The ensemble model for each species was
216 computed as the average weighted suitability, with weights given by the Sørensen index
217 calculated for each algorithm. We used the average binarisation threshold weighted by the
218 Sørensen index to binarise the ensemble habitat suitability into presence-absence maps for each
219 species in current time and future scenarios.

220 We applied an occurrence-based restriction to keep only the patches of suitable habitat
221 considered reachable by a species⁵⁹ to minimise overprediction issues associated with presence-
222 absence maps derived from ENMs. Patches of suitable habitats are assumed to be reachable by
223 the species if they overlap with a presence record or are within an edge-edge distance threshold
224 of an occupied suitable patch⁵⁹. This distance threshold was defined as the maximum nearest
225 neighbour distance among pairs of occurrences of the respective species. Computations were
226 performed in R 4.1.0⁶⁰ using the package *ENMTML*⁶¹.

227

228 **Spatial patterns of beta-diversity, woodiness, and ecological generalism**

229 We mapped the Caatinga using an equal-area projection grid cell of 10×10 km of spatial
230 resolution to assess changes in beta-diversity spatial pattern. Using the binary maps for the
231 ensemble projection, we built species presence-absence matrices for projections based on the
232 current time and for each combination of the future period (2060 and 2100) and the SSP scenario
233 (SSP245 and SSP585). We only considered species presence in a grid cell if they occupied at
234 least 50% of the cell area. The spatial beta-diversity for each grid cell was measured by the
235 Sørensen-based multiple-site dissimilarity index, β_{SOR} ⁶², computed for the cell set formed by the
236 focal cell and its immediately adjacent neighbour cells. Because the size of the cell set can affect
237 the β_{SOR} value⁶³, we applied a subsampling procedure to randomly select four neighbour cells
238 around each focal cell 100 times to compute the average β_{SOR} across iterations. We used the β_{SOR}
239 difference between each future and current scenario ($\Delta\beta_{\text{SOR}} = \beta_{\text{SOR.future}} - \beta_{\text{SOR.current}}$) to identify
240 plant assemblages (cells) subject to biotic homogenisation ($\Delta\beta_{\text{SOR}} < 0$) or heterogenisation
241 ($\Delta\beta_{\text{SOR}} > 0$). We also calculated the difference between future and current species richness ($\Delta S =$
242 $S_{\text{future}} - S_{\text{current}}$). Computations were performed in R using the *betapart* package⁶⁴.

243 We used the species growth form to compute the proportion of woody species in each
244 plant assemblage (WoodyProp) to assess potential changes in the assemblage-level patterns of
245 woodiness and ecological generalism. To measure the assemblage-level ecological generalism,
246 we initially classified as narrow-range plant species whose range size distribution was below the
247 first quartile (~100 mil km²) of current projected distribution within Caatinga, or otherwise wide-
248 range. Then, we extracted the proportion of wide-range species in each plant assemblage
249 (WideProp). We calculated WoodyProp and WideProp for the current and future scenarios and
250 used the ratio of future to current time to represent the relative change in woodiness
251 (WoodyRatio = $\text{WoodyProp}_{\text{future}} / \text{WoodyProp}_{\text{current}}$) and ecological generalism (WideRatio =

252 WideProp_{future} / WideProp_{current}) of plant assemblages. WoodyRatio and WideRatio above 1
253 indicate a future increase in the assemblage-level proportions of woody and wide-range species,
254 respectively. We used Kruskal-Wallis tests to assess whether the medians of (i) Current species
255 richness, (ii) ΔS , (iii) WoodyProp_{current}, (iv) WoodyRatio, (v) WideProp_{current}, and (vi) WideRatio
256 differ between assemblages subject to biotic homogenisation ($\Delta\beta_{\text{SOR}} < 0$) or heterogenisation
257 ($\Delta\beta_{\text{SOR}} > 0$). Linear relationships between changes in species richness (ΔS) and spatial beta-
258 diversity ($\Delta\beta_{\text{SOR}}$), and changes in the relative contribution of woody (WoodyRatio) and wide-
259 range (WideRatio) species were verified through a modified t-test⁶⁵ to spatially correct the
260 degrees of freedom of correlation coefficients. Computations were performed in R using the
261 packages *SpatialPack*⁶⁶.

262

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419

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426

427 **AUTHOR CONTRIBUTIONS**

428 MRM, FAON, and BAS conceived the study; FAON compiled the data, MRM and FAON
429 analysed the data. MRM developed the figures and led the writing. All authors contributed
430 critically to the drafts and gave final approval for publication.

431

432 **COMPETING INTEREST STATEMENT**

433 Authors declare no competing interests.

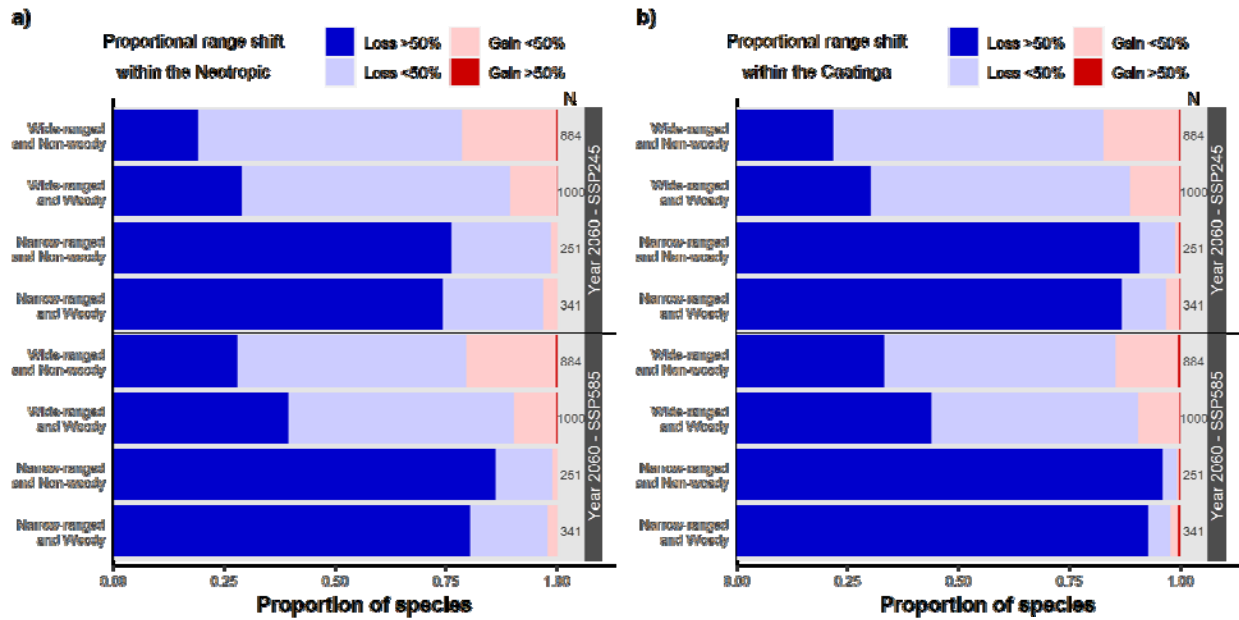
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435 **ADDITIONAL INFORMATION**

436 Supplementary Information is available for this paper, including Supplementary Tables (S1–S2)

437 and Supplementary Figures (S1–S7).

438 **FIGURE LEGENDS**



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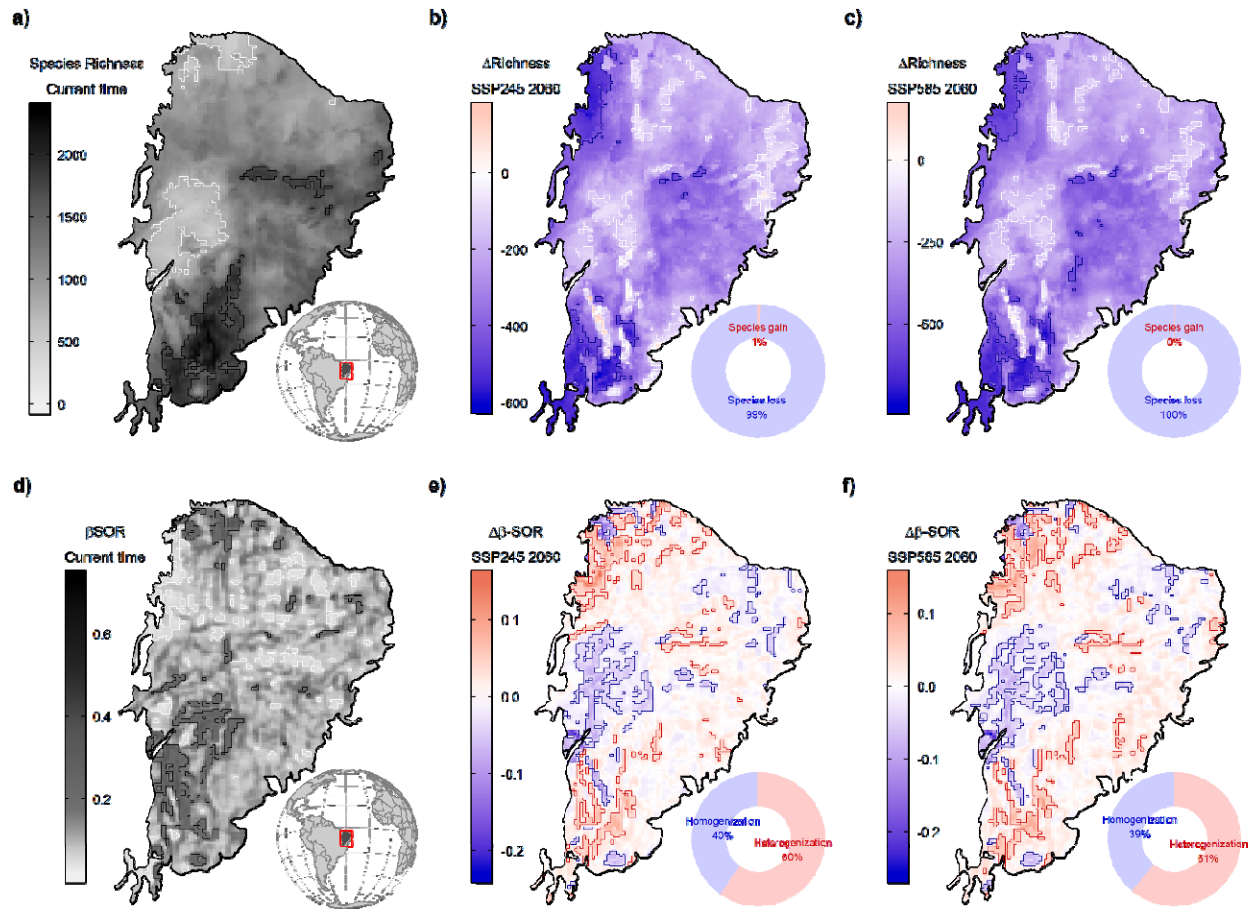
440 **Fig 1. Projected range shift for species holding different levels of woodiness and ecological**

441 **generalism.** Range shifts were computed separately within the (a) Neotropics and (b) Caatinga.

442 The results are shown for 2060 under the business-as-usual (SSP245) and non-mitigation

443 (SSP585) scenarios. See Fig. S3 for results concerning 2100.

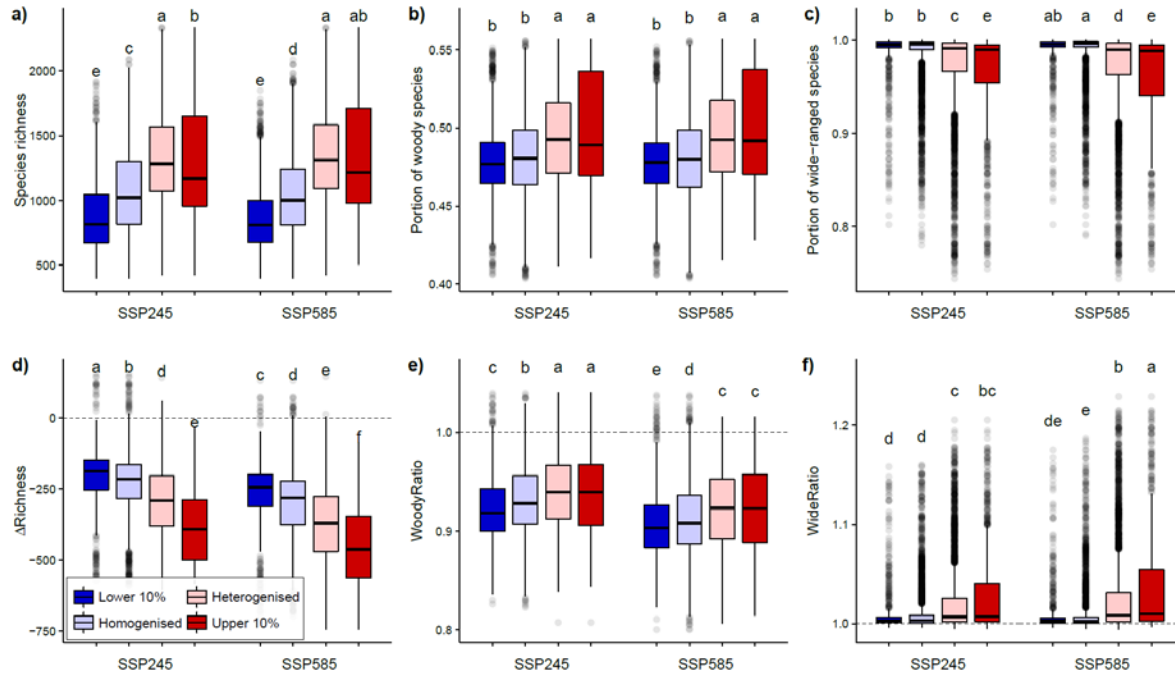
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446 **Fig 2. Geographical patterns of plant species richness and spatial beta-diversity in the**
447 **Caatinga.** (a) Projected species richness at the current time. Expected change in species richness
448 (ΔS) across plant assemblages under the (b) business-as-usual (SSP245) and (c) non-mitigation
449 (SSP585) scenarios in 2060. (d) Spatial beta-diversity (β_{SOR}) for the current time. Expected
450 change in spatial beta-diversity ($\Delta\beta_{SOR}$) across plant assemblages under (e) SSP245 and (f)
451 SSP585 scenarios for 2060. The contour lines denote the assemblages (cells) in the upper and
452 lower 10% of the mapped pattern. See Fig. S4 for results concerning 2100.

453



454

455 **Fig 3. Assemblage-level metrics across regions subject to different levels of projected biotic**

456 **change by 2060.** Each box denotes the median (horizontal line) and the 25th and 75th

457 percentiles. Vertical lines represent the 95% confidence intervals, and black dots are outliers.

458 Small capital letters denote the results of the Kruskal–Wallis tests for the difference in medians

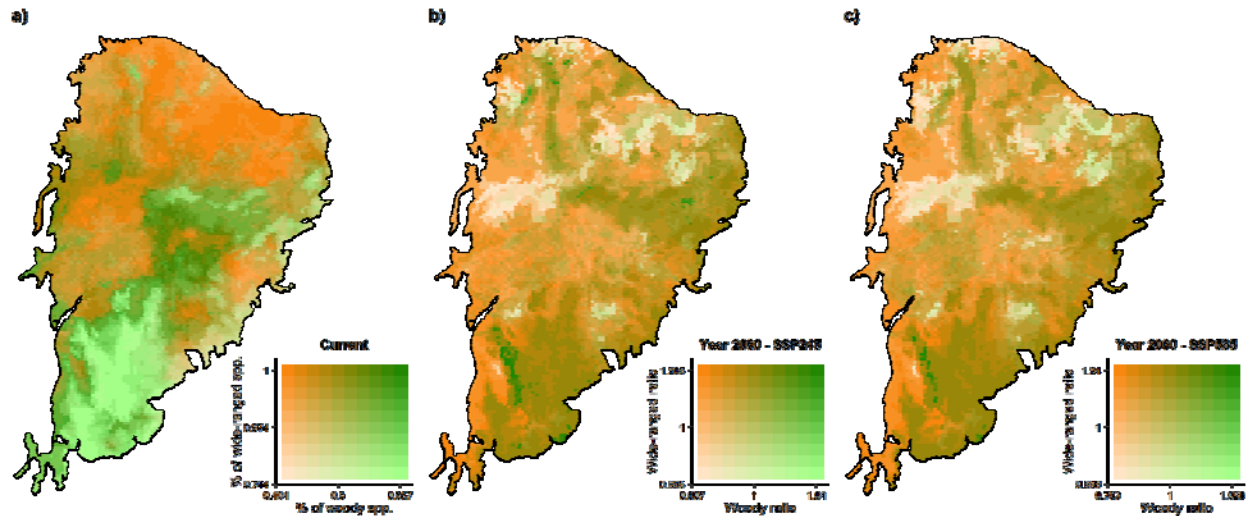
459 across assemblages subject to different levels of biotic homogenisation ($p = 0.05$, using

460 Bonferroni correction). Woody and wide ratios above 1 indicate an increase in the assemblage-

461 level proportion of woody and wide-range species in the future. See Fig. S5 for results

462 concerning 2100.

463



464

465 **Fig 4.** Patterns of woodiness and ecological generalism of plant assemblages in the Caatinga. (a)

466 Proportion of woody and wide-ranged species in plant assemblages. Relative change in the

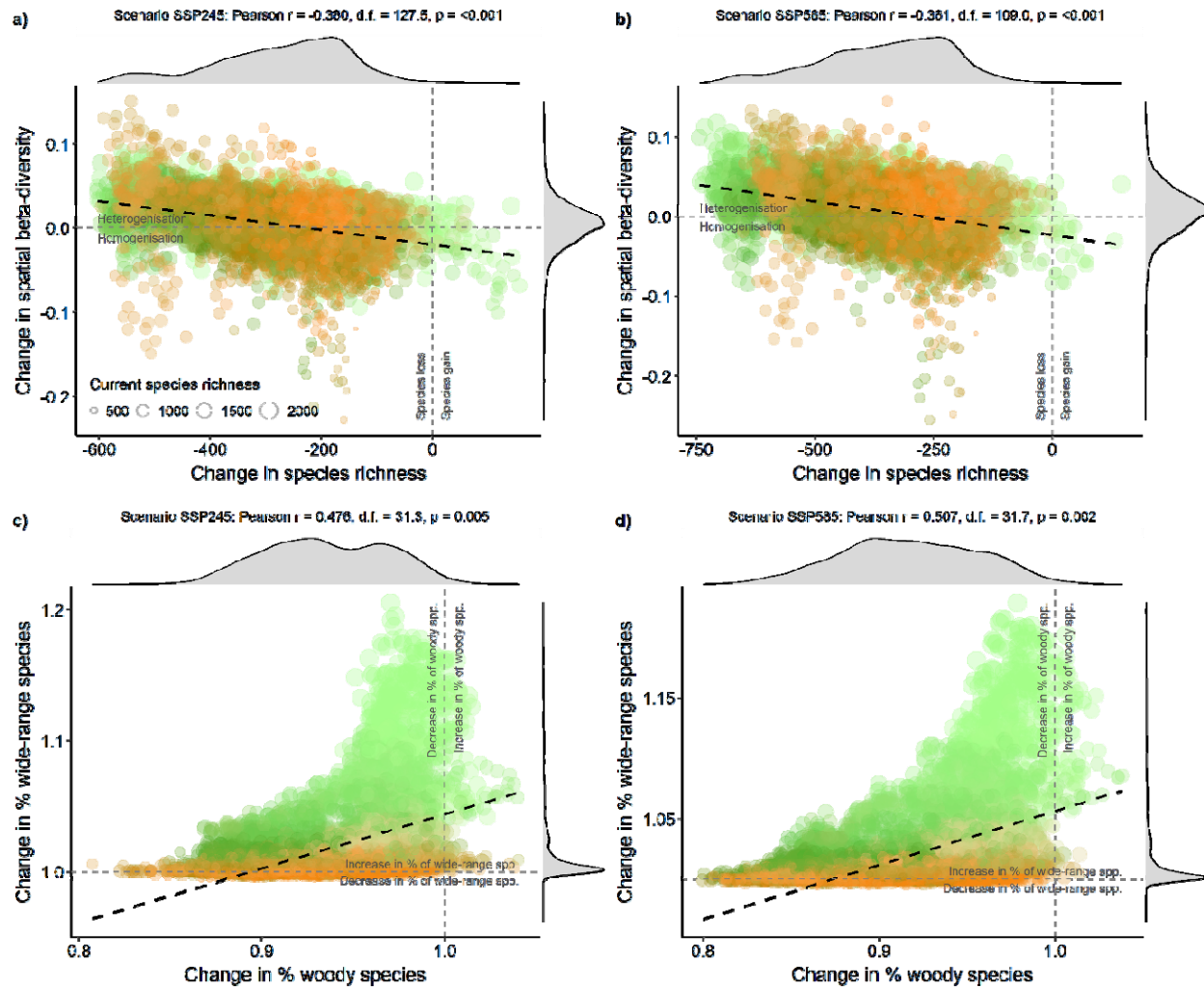
467 proportion of woody and wide-range species between 2060 and the current time under the (b)

468 business-as-usual, SSP245 and (c) non-mitigation, SSP585 scenarios. Woody and Wide-range

469 ratios above 1 indicate an increase in the assemblage-level proportion of woody and wide-range

470 species in the future. See Fig. S6 for results concerning 2100.

471



472

473 **Fig 5. Projected change in species richness, spatial beta-diversity, woodiness, and ecological**

474 **generalism in Caatinga plant assemblages by 2060.** Relationship between differences in

475 species richness (ΔS) and spatial beta-diversity ($\Delta\beta_{SOR}$) in the scenarios (a) Business-as-usual,

476 SSP245, and (b) Non-mitigation SSP585. Relationship between change in relative contribution

477 of woody (WoodRatio) and wide-range (WideRatio) species. Symbol colours follow species

478 assemblage representation in Fig. 4a. Pearson correlations on the top of each panel were based

479 on spatially corrected degrees of freedom. See Fig. S7 for results concerning 2100.